EFFECTS OF SHELTERWOOD AND PATCH CUT HARVESTS ON A POST WHITE-NOSE SYNDROME BAT COMMUNITY IN THE CUMBERLAND PLATEAU IN EASTERN KENTUCKY

THESIS

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in Forest and Natural Resource Sciences in the
College of Agriculture, Food, and Environment
at the University of Kentucky

By

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Lexington, Kentucky

2020

Abstract of Thesis

EFFECTS OF SHELTERWOOD AND PATCH CUT HARVESTS ON A POST WHITE-NOSE SYNDROME BAT COMMUNITY IN THE CUMBERLAND PLATEAU IN EASTERN KENTUCKY

The impact of shelterwood and patch cuts harvests on bat communities was tested at three sites in Eastern Kentucky. Shelterwood harvests had 50% of the basal area and understory removed to create a uniform spacing of residual trees. Patch cuts had 1-hectare circular openings created to remove 50% of the basal area creating an aggregated spacing of residual trees. Acoustic detectors were deployed to assess activity levels pre-harvest. Sites were then sampled from 1 – 2 years post-harvest to determine differences. Pre-harvest data revealed little acoustic activity for the *Myotis* spp. at two sites. The remaining site had high activity of *Myotis* pre-harvest. All sites saw a large increase in bat activity post-harvest. Activity of low-frequency and mid-frequency bats increased in response to the harvests. Big brown and red bats were commonly captured within forest harvests. Tri-colored bats also captured, suggesting forest harvests could improve habitat. *Myotis* activity did not increase post-harvest at the site with a known population. Netting efforts revealed a remnant population of northern long-eared bats (*Myotis septentrionalis*). These bats were radio-tagged and tracked to day-roosts. All day roosts were in upslope habitats within 100 m of forest roads created for maintenance and logging operations.

Keywords: Eastern Kentucky, shelterwood, patch cut, timber harvest, northern long-eared bat

Phillip Lee Arant

Signature

August 20, 2020

Date

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Acknowledgements

My project was a collaborative effort between Forestland Group, LLC, Kentucky Department of Fish and Wildlife Resources, Kentucky Division of Forestry, U.S. Fish and Wildlife Service, and the University of Kentucky, Department of Forestry and Natural Resources and would not have been possible without the support, time, and effort supplied by each one of them. I am grateful for the funding from Forestland Group, LLC, and the U.S. Fish and Wildlife Service.

I would like to thank Chris Osborne, the staff at Robinson Forest, and Robinson Center for Appalachian Resource Sustainability (RCARS). Chris, David, and Erwin thank you for clearing the roads to my study site and making the road usable. I appreciate the countless hours you spent making my project possible. RCARS, I am grateful for you providing me with housing throughout my project and for accommodating the ridiculous hours of a bat biologist.

Debbie and Leslie, thank you for everything you do around the Forestry and Natural Resources Department. I cannot imagine my project functioning without your assistance.

Dr. Lacki thank you for being my mentor and providing me with this opportunity. This project and work would not have been possible without your planning and guidance. Dr. Stringer thank you for making an abstract idea a reality.

Chase, thank you for your assistance in the field and with ‘R’ coding. You saved me countless hours of time and made the processing of hundreds of spreadsheets and hundreds of thousands of cells of data possible. I appreciate your hours of field work

helping me collect various data. Thanks for being a great coworker and friend. Andrea thank you for taking the time to assist me.

My technicians: Randi Lesagonicz, Charles Fairies, Ryan Trenkamp, Brittany Watson, Austyn Harriman, David Hejna, Jessica Dewey, Jarrod Vanover, Jeb Ayers, Zach Hackworth, and Maya Yomboro. I appreciate your hours of hard works and your persistence in the face of daunting challenges and countless obstacles. I am also grateful for your patience as I learned what it meant to lead people. David and Austyn thanks for the moral support you provided well beyond your job, over the years you have become my friends. I appreciate you being a part of my life.

Marissa and Ali, I am grateful for your support, assistance trouble shooting, patience, and friendship. I cannot thank you enough for the countless number of times you answered my phone calls to discuss various problems. I could not have produced the quality of work presented within this thesis without your assistance. Perhaps more importantly, I am eternally grateful for your emotional support throughout this process. Thank you for being my friends.

To my friends, Chad, Kassidy, Jesse, Ben, Wes, and Grayson thank you for emotional support. I greatly appreciate you guys listening to my rants and helping me work through my problems. I love you guys and appreciate you always being there.

Mom thanks for being there for me and supporting my dreams. I appreciate you being a constant source of support.

Table of Contents

List of Tables

List of Figures

Introduction

Bats in eastern Kentucky are all insectivorous. Species present in the region include big brown bat (EPFU, *Eptesicus fuscus*), evening bat (NYHU, *Nycticeius humeralis*), eastern red bat (LABO, *Lasiurus borealis*), hoary bat (LACI, *L. cinereus*), silver-haired bat (LANO, *Lasionycteris noctivagans*), tri-colored bat (PESU, *Perimyotis subflavus*), northern long-eared bat (MYSE, *Myotis septentrionalis*), Indiana bat (MYSO, *M. sodalis*), little brown bat (MYLU, *M. lucifugus*), eastern small-footed bat (MYLE, *M. leibii*), Rafinesque big-eared bat (CORA, *Corynorhinus rafinesquii*), and Virginia big-eared bat (COTO, *C. townsendii virginianus*). Bats utilize echolocation in a variety of ways and thus have several different types of calls. Search phase calls are used to navigate on the landscape and members of the same species typically exhibit the same pattern when they navigate. Characteristics such as duration, F_{max}, F_{min}, $F_{mean,}$ and shape of echolocation calls help in determining species identification (Britzke *et al,* 2011). These calls vary across regions and several dialects can occur throughout a species range. However, each species can produce a wide range of calls beyond its typical pattern, confounding call identification among sympatric, non-related bats.

Bats use other types of calls to communicate between individuals. Social calls communicate information such as roost locations and prey sources. Pfalzer and Kusch (2003) found four types of calls. One type of call functions in communicating information between infants and mothers. These calls assisted in tandem flights and might function to communicate feeding site and roost locations. A second type of call is used to attract mates. A third is used by hindered or distressed bats. A final call is used in aggressive interactions. This type of call can be used to inhibit feeding activity of other individuals.

Insectivorous bats reduce the time between calls when approaching prey. This pattern occurs for all species and is called a feeding buzz. Bats capture prey by primarily two approaches. Insects can be captured during flight in the mouth, chiropatagium (wing membrane) or uropatagium (tail membrane). This method is commonly referred to as 'aerial hawking.' Insects can also be captured from vegetative and ground surfaces, a behavior known as gleaning. Although many insectivorous bat species show a preference for one method over the other, most are capable of feeding by both approaches.

Insectivorous bats are often divided into feeding guilds, based on their low, medium, and high call frequencies, especially the F_{max} (i.e., maximum frequency produced) of their calls. Low-frequency bats (open-space foragers) include hoary bat, big brown bat, and silver-haired bat. Low frequency calls travel farther than high frequency calls, permitting these bats to forage effectively within open air space away from forest clutter. Rafinesque's big-eared bat and Virginia big-eared bat also have low frequency calls; however, these species are gleaners that specialize on the capture of insect prey (primarily moths) from the surface of rocks and vegetation. Consequently, the use of low intensity calls by these bats are inaudible to many moth species and are also difficult to detect using acoustic devices. Medium-frequency bats (edge-space foragers) include eastern red bat, evening bat, and tri-colored bat. These species have intermediate call strength and intensity allowing these bats to feed in a variety of habitats, including forest edges. The Myotis species, Indiana bat, little brown bat, northern long-eared bat, and eastern small-footed bat, are high-frequency bats (closed-space foragers) which can successfully feed in micro-habitats with more vegetative clutter. These species are commonly associated with forested habitats. Of these species, the northern long-eared bat and eastern small-footed bat also use gleaning behavior to capture insect prey. As with Corynorhinus species, these bats emit calls of low intensity and use passive listening for insect generated sounds to aid in the capture of prey (Faure *et al.*, 1993).

Flying and maintaining normothermic body temperatures is energetically expensive. The high surface area to volume ratio of bats further increases their energetic demands. Insectivorous bats compensate for their high energy requirements by choosing roosts to passively rewarm, using the microclimate they roost in to influence their return to a normothermic condition. As an additional step bats can use torpor. Torpor allows bats to lower their body temperature to limit energy consumption. Females use and modulate these behaviors to allocate greater energy stores to fetal development and juvenile growth rates (Chruszcz and Barclay, 2002).

During the diurnal period of each day most forest-dwelling insectivorous bats occupy roosts to access predictable temperature regimes, to protect themselves from predators, and for protection from inclement weather. Foliage-roosting species, such as the eastern red bat, hoary bat, and tri-colored bat, typically roost within the canopy of trees, often associated with clusters of dead leaves or needles. Female hoary bats and eastern red bats have between 2 to 4 pups each year and roost solitarily. Tri-colored bats also have 2 pups per year, but are more communal in their roosting behavior, with several reproductive females gathering together to form small maternity colonies. Male silver-haired bats summer in Kentucky and also use trees and stumps for roosting. A majority of these bats, however, do not reside in Kentucky during the winter months and briefly migrate through the state during early-summer and autumn (Perry *et al.,* 2010).

Corynorhinus species roost in caves, bridges, attics, and trees. Females form maternity colonies and males form bachelor colonies that are separate from maternity sites. These bats only have a single pup per year and are more often associated with forests near cliff habitats in eastern Kentucky. Because they are moth specialists, evidence of their feeding habits can easily be discerned as these bats often carry their prey back to roosts to eat where they discard the elytra and other inedible parts to the floor of the roost.

Big brown bats form maternity colonies in trees and a variety of structures including bat boxes and attics. They have one to two pups per year. Females of the species can form large maternity colonies exceeding several hundred individuals. Males often form bachelor colonies but can also be found with females in maternity roosts. The pups take about a month to reach volancy. Evening bats roost in a variety of structures including trees, buildings, and bat boxes, but are most often found in the cavities of trees. They produce twins or triplets.

The Myotis species in eastern Kentucky all give birth to a single pup. Eastern small-footed bats are strongly associated with talus slopes, cliffs and other rock features. Females form small maternity colonies within these structures. Indiana bats roost beneath bark in dead or living trees, but occasionally are found in bat boxes. Extensive research has shown these bats prefer areas of high solar exposure. Maternity colonies can contain up to several hundred individuals, while males roost singly or in small bachelor colonies. Little brown bats roost in anthropogenic structures such as attics and barns. Occasionally they are located in trees under bark or in cavities, and have been found roosting in association with other Myotis species. These bats form small to large maternity colonies of up to several hundred individuals. Northern long-eared bats roost under the bark of dead trees, in bat boxes, and within small tree cavities. These bats form smaller maternity colonies, usually from 25 to 50 females. Landscape-scale studies show these bats are often associated with large tracks of interior forest where minimal edge habitat exists.

Insect prey is less available during winter months. Bats in eastern Kentucky either migrate to areas with weather that is typically above freezing or make shorter movements and hibernate in nearby caves and mines. Hoary bat, silver-haired bat, and some eastern red bats migrate extensive distances during fall to warmer areas. Silver-haired bats hibernate within tree stumps, cliffs, or buildings. Eastern red bats hibernate within the foliage of leaves or on the forest floor within leaf litter. Hoary bats remain active throughout much of the winter after arriving to warmer climates including the southern United States where food supplies remain available during winter months. Little is known about evening bats during winter, other than they do not hibernate in caves, and it is likely that they migrate south only to roost in trees during winter as well.

Indiana bat, little brown bat, northern long-eared bat, eastern small-footed bat, tri-colored bat, big brown bat, Virginia big-eared bat, and Rafinesque big-eared bat typically migrate short distances to caves, mines and rock outcrops to hibernate from November to March. Although migrations can be over 220 km (Roby *et al.*, 2019). Rafinesque's big-eared bats arouse during hibernation and are known to frequently switch roost locations throughout winter. Myotis species, big brown bat, and tri-colored bat put on larger amounts of fat reserves prior to hibernation and periodically arouse to drink, void their waste, and recharge their immune system function; although feeding can occur during warm periods.

White-nose syndrome was first discovered in Howe's Caverns in upstate New York in 2006. With a likely origin from Europe, the disease has been spread by both bats and people. People transmit the disease by carrying fungal spores on clothing and gear between caves. Bats carry the spores in their pelage as they move among different cave systems during fall swarming, hibernation, and spring staging. These transmission methods have facilitated the spread of the fungus across North America within the last 14 years. It is likely the disease will eventually spread throughout the continent. Previously common bat species, including little brown bat and northern long-eared bat, have been decimated by the fungus with mortality numbers in the millions.

Psuedogymnoascus destructans is the fungus responsible for white-nose syndrome. The fungus is a saprotroph that opportunistically infects bats (Raudabaugh and Miller, 2013). The disease is named for the white hyphae of the fungus that often occur on the muzzle of bats. The fungus causes flaking of the skin along the forearms of the wings and necrosis of wing tissue in later stages. The fungus optimally grows from 12.5 to 15.8 °C with an upper limit of growth at 20 °C (Verant *et al.,* 2012). Various physiological impacts from the fungus results in more frequent arousal of bats causing them to burn necessary fat reserves, become dehydrated, and exhibit excessive immune response often resulting in death. The fungus can persist and reproduce in caves without bats, and has likely become a permanent resident in North American caves.

Little brown bat, northern long-eared bat, tri-colored bat, and Indiana bat are species severely impacted by the fungus (Thogmartin *et al.,* 2013; Vonhof *et al.,* 2015, 2016; US Department of Interior, 2015; USFWS, 2019). These species often hibernate in micro-sites that possess optimal growth conditions for the fungus, cluster during hibernation facilitating spread of the fungus, and/or have insufficient fat reserves to sustain multiple arousals from the fungus. Death rates have varied throughout ranges and populations, but have been as high as 98% in some hibernacula in eastern U.S. Evidence post-arrival of white nose syndrome suggests the disease has reshaped the bat communities of eastern North America.

Individual bats that have survived the initial impact of the fungus are adopting alternative hibernation strategies including hibernating in alternate roosts (i.e., basements, hollow trees, culverts, railroad tunnels, and bridges), reducing cluster size which minimizes spread of the fungus within hibernacula, and moving to warmer or cooler microclimates within cave systems. Some populations are evolving resistance to the pathogen (Frank *et al.,* 2019), with larger body mass associated with many survivors. Recently, local populations of bat species in infected areas are beginning to increase or stabilize (Reichard *et al*., 2014, Dobony and Johnson, 2018). Regardless, these populations remain vulnerable, are poorly documented, and possess low reproductive rates that will take decades to recover.

Amelon (2007) found that little brown bats were positively associated with bottomland forest, water sources, and negatively associated with heavily trafficked roads and non-forested lands. Starbuck *et al.,* (2015) found northern long-eared bats were associated with pole-stage, closed canopy forests with understory clutter and water. Amelon (2007) found northern long-eared bats were positively associated with dense, cluttered forests, water, and larger mature forests. They were negatively associated with non-forested habitat and young forests. Yates and Muzika (2006) found northern long-eared bats were detected in areas with limited forest edge. Starbuck *et al.,* (2015) found tri-colored bats were found on forest dominated landscapes in areas which were recently burned. Amelon (2007) found tri-colored bats were positively associated with forested habitat with limited clutter and water. They were negatively associated with non-forested habitats and young, cluttered forests. Yates and Muzika (2006) found tri-colored bats were found in areas with scattered large trees, high canopy closure, and substantial understory vegetation at 2-3 m. Womack *et al.,* (2013) found that Indiana bats forage in areas of high canopy cover. These bats preferentially chose to forage in forested areas instead of agricultural areas. Yates and Muzika (2006) determined Indiana bat presence was associated with larger woodlands mixed with open habitats.

Following white-nose syndrome, other trends were also observed. Pauli *et al.* (2015) saw a trade-off between foraging and roosting habitat. Medium to high-intensity removals of single-tree selection harvests maximized both foraging and roosting habitat for northern long-eared bats and Indiana bats by creating openings. Removing all forest harvests would negatively impact bats by minimizing openings within forests. Jachowski *et al.* (2014) concluded competition influenced temporal and spatial activity of bats. The loss of little brown bats and northern long-eared bats appeared to result in a shift in activity of big brown bats.

Brooks *et al.* (2017) found insect prey and bats did not response to different sizes of openings, either small 0.2 - 6 ha, medium 2.1 - 5.6 ha, or large 6.2 - 18.5 ha. Big brown bat, eastern red bat, and tri-colored bat were frequently found within openings.

Myotis made up only 2% of the calls, where previously the little brown bat had comprised 25% of recorded calls.

Northern long-eared bats, in particular, tend to avoid foraging in open spaces. Owen *et al.* (2003) found that northern long-eared bats preferred foraging within diameter limited harvests and road corridors; however, they also made use of the extensively available intact forest. Henderson and Broders (2008) found that northern long-eared bats predominately foraged in riparian areas within dense forests. Their foraging and commuting in agricultural areas were focused on linear features such as tree rows.

This study compares two silvicultural techniques commonly used in regeneration of forests, shelterwood harvests and patch cuts, to assess if commercially viable harvests could benefit bats. Shelterwood harvests are a silvicultural technique used in regeneration. Trees are harvested and the mid-story and clutter are removed. A certain basal area of trees is retained, 50% of the commercial timber volume in this study, in order to shade the forest floor or provide seeds. The cuts are uniform in nature and provide an open environment for bats to feed (Lacki *et al.* 2007). No site preparations occurred.

Patch cuts are another silvicultural technique used in regeneration. In this study, 50% of the commercial timber volume within the treatment area were harvested in small circular groups a hectare in size. All trees within these groups are removed. These gaps mimic natural disturbance and allow shade intolerant species to grow by increasing light exposure. Unlike the uniform shelterwood harvests the disturbance in patch cuts is aggregated in small pockets and surrounded by intact forest. These pockets provide large amounts of edge habitat for bats to feed (Lacki *et al.* 2007). No site preparations occurred.

Although other studies on silviculture practices such as patch cuts and shelterwood harvests have been performed, my study provides replication across multiple study sites across two physiographic regions. For my study, patch cuts and shelterwood harvests were implemented in three field sites. I hypothesized these harvests would cause different responses between feeding guilds of bats. Low frequency echolocators, including big brown bat, hoary bat, and silver-haired bat should be attracted to cuts. The open space presented in both forest harvests should provide enhanced foraging space because it has lower amounts of clutter. Medium frequency echolocators, such as evening bat and eastern red bat, should be attracted to the edges of cuts. Patch cut harvests should be more attractive than shelterwood or unharvested forest to these species. Myotis species should have a negative response to the harvests because the clutter is being removed from the environment. However, in post-WNS communities this could be difficult to test due to the low number of Myotis species present within the region.

These hypotheses were evaluated with a combination of several techniques: acoustic monitoring, light trapping, and mist netting. Acoustic monitoring provided two metrics of data to evaluate activity, calls and pulses. Detectors were placed at ridgetop, mid-slope, and riparian positions to discern any differences in activity levels. Light trapping provided data on the prey base and was performed to offer a possible explanation to account for any difference in bat activity levels demonstrated between the different harvest conditions. Previous experiments have demonstrated prey may aggregate at the edges of harvests which can be attractive to predators (Dodd *et al.* 2012).

Mist netting was performed to confirm acoustic monitoring results and verify species presence. In the event target Myotis species, *Myotis septentrionalis* or *Myotis sodalis*, were captured tracking devices would be attached to collect data on roost locations. Locating roosts would allow population levels to be evaluated and roosts protected. Ideally, roosts would be located within the harvest location and protected during the harvests to evaluate whether bats would roost within the forest harvests.

Study Areas

Three study areas (Figure 1): Robinson Forest (*Big Laurel Ridge and Medicine Hollow tract*), private TIMO property (*Beech tract*), and Kentucky Ridge State Forest (*Kentucky Ridge tract*), were established within the Cumberland Plateau and Cumberland Mountains physiographic regions to study response of insectivorous bats to patch cut harvests and shelterwood harvests. The eastern Kentucky region has elevations ranging from 200 - 500 m (McGrain, 1983). The terrain is rugged and largely covered with mixed mesophytic forests (Braun, 1950). Eastern Kentucky has sandstone cliffs and a variety of caves formed from both the sandstone and limestone that occur throughout the region (McGrain, 1983; Simpson and Florea, 2009).

Robinson Forest (Laurel Ridge tract)

Robinson Forest is located near Clayhole, Kentucky. The forest is situated between the cities of Jackson and Hazard in the southeastern corner of the state. The main block of Robinson Forest is approximately 4,047 ha and, in total, the entire Forest is nearly 6,070 ha. This forested landscape lies within Breathitt, Knott, and Perry counties. Robinson Forest was purchased by E.O. Robinson and Fredrick W. Mowbray in 1908. The forest was then clear cut to extract the timber; harvesting of timber on the forest ended by 1922. The land was donated in 1923 to the University of Kentucky agricultural department to conduct research into improved logging practices, and to help educate the public of eastern Kentucky (Krupa and Lacki, 2002).

The forest has been subjected to many types of disturbance throughout the years including clear cutting, fires, mining, and invasion by exotic plant species (Krupa and Lacki, 2002). Many settlers built homes illegally on the forest, with most evicted in the 1920's and 1930's. Evictions angered many of the settlers and arson, as a form of response, has continued over the last 90 years, resulting in >80% of the forest having been burned at some point in time (Krupa and Lacki, 2002). During the 1970's, and again in the 1990's, mining companies have strip mined sections of the outer blocks of the forest to procure coal (Krupa and Lacki, 2002). Even today the forest is experiencing disturbance. Robinson Forest serves as a working forest used to execute a variety of forestry experiments such as SMZ studies, wildlife clearings, and small harvests aimed at determining best management practices for forestry (Krupa and Lacki, 2002). The forest has a maintained road system which allows researchers to access study areas. A small camp exists near the western end of the main block, with several log cabin buildings that function as housing and dining facilities for research staff and other guests of the University of Kentucky.

Despite the impacts of invasive plants, logging, fires and mining, the forest has developed into a second growth mature forest with diverse plant and animal communities. Forests are mixed mesophytic (Braun, 1950), typical of much of the Cumberland Plateau. At the time of the study, bottomlands were mesic and comprised of maple (*Acer*)-beech (*Fagus*)-poplar (*Liriodendron*) stands, with hemlock (*Tsuga*)-*Rhododendron* communities interspersed. Mid-slopes supported oak-beech-maple forest, and forest habitats on ridge tops, due to the xeric sandy soils, were comprised of oak (*Quercus)*-pines (*Pinus*) or oak-hickory (*Carya*) stands. The different community types and variations in stand age and composition on the forest, the latter as a result of the extensive disturbance history, provided a complex mosaic of habitats for use by forest-dwelling bats.

TIMO Property (Beech tract)

The Beech tract is named for its prominent stands of American beech (*Fagus grandifolia*). The 121-ha study site is located 16 km east of Jackson, Kentucky, in Breathitt County. The property is owned by Forestland Group, LLC. Historically, much of the property was forested. The unharvested ridge tops were dominated by oak -hickory stands, with riparian and mid-slope positions comprised of beech -oak -maple stands. The study site possessed historic skid trails, but these were overgrown with trees and were unlikely to function as flyways for bats. The landscape surrounding the study site was open with sparse tree cover and open fields on all sides. A small farm still operated on the property and had small openings in the previously forested landscape maintained for several decades.

Kentucky Ridge State Forest (Kentucky Ridge tract)

The tract within Kentucky Ridge State Forest is a mixed mesophytic forest situated in the Cumberland Mountains at the edge of the Cumberland Plateau in eastern Kentucky. Located in Bell County, the forest is approximately 22.5 km southwest of Pineville. The forest is managed by the Kentucky Division of Forestry. Kentucky Ridge State Forest is

6,172 ha in size. The forest is managed for sustainable timber production, wildlife habitat, and recreational opportunities (forestry.ky.gov). The study site is 121 ha in size and adjacent to route 190. The landscape surrounding the study site is primarily forested, with small patches of open space containing park facilities and private homes.

The study site had previously been harvested and now supports second growth forest. Several old skid trails still exist throughout the forest. These trails were overgrown by small trees and shrubs and, in some segments, were capable of functioning as flight corridors for bats. The study site is bordered by an active ATV trail which is frequently used by locals.

The study site had several distinct stand types. Bottomland forests were dominated by mesic communities comprised of maple -beech -poplar, with hemlock-*Rhododendron* stands interspersed. Ridge tops supported xeric communities comprised of oak-hickory with an understory of mountain laurel (*Kalmia latifolia*). A nearly pure stand of eastern hemlock (*Tsuga canadensis*) and rosebay rhododendron (*Rhododendron maximum*) covered one of the ridge tops. Mid-slope communities were dominated by bottomland species, with xeric oaks and hickories interspersed.

Figure 1. Map of field sites in Kentucky. Laurel Ridge rests within Robinson Forest near Buckhorn, KY, the Beech site is outside of Jackson, KY, and Kentucky Ridge is outside of Pineville, KY.

Experimental Design

Each study site was approximately 120 ha in size. Within each study site, three ca. 40-ha treatments included unharvested forest, patch cut harvests, and shelterwood harvests. For each 40-ha patch cut harvest, approximately 23, 1-ha patch cuts, were delineated for timber removal. Shelterwood harvests removed 50% of the basal area and cleared the understory of woody vegetation throughout the treatment area.

The pre-treatment transects for acoustic sampling were established by dividing the study area into three approximately equal units; each one to become one of three post-treatments following timber harvesting, including shelterwood harvest, patch cut harvest, and unharvested forest. Based upon the maximum length of each unit, a number was randomly generated to select for the closest point to two predominant slope directions, i.e., north/south or east/west. The closest ridge top to each random point became the starting point of each transect. The riparian point was placed adjacent to the closest stream to the selected ridge top, with mid-slope points placed at an elevation halfway between the riparian and ridge top points. Exact placement of the units was determined from ground surveys. When possible, units were preferably located in the vicinity of closed canopy roads, streams, and canopy gaps.

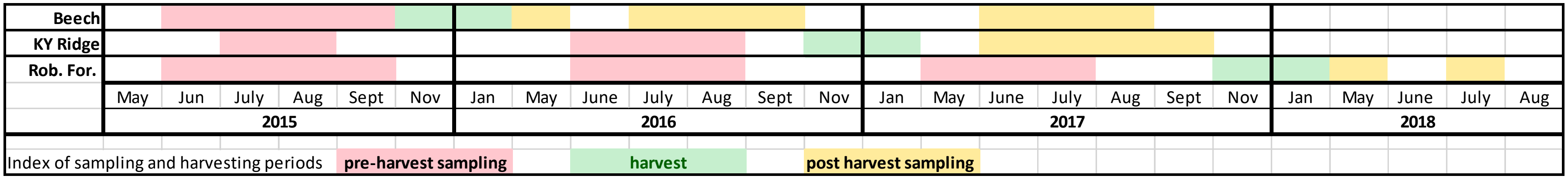
Pre-treatment acoustic sampling took place in summer 2015 at all three study sites. Activity was monitored using Song Meter 3 units and SMU-1 microphones (Wildlife Acoustics, Maynard, MA). The SM3 units were housed within pelican cases, with microphones placed within PVC pipe and tied to a tree at 1.5-m aboveground (Figure 2). Each location where an acoustic unit was deployed was geolocated with a Garmin GPSMAP 64. These units are accurate within 5 to 15 meters, depending on conditions. In 2015 and 2016, the microphone was housed within PVC pipe for protection from the elements and to prevent damage from wildlife; however, the additional shielding created secondary harmonics, limiting the quality and resolution of call characteristics. Because this study has long-term objectives, a decision was made to remove the shielding for 2017 and 2018.

The samples from all study sites were intended to be analyzed together. An ANOVA was performed on the pre-harvest data. Differences were detected in the activity level of silver-haired bats and Myotis (Table 1). Due to the differences found in activity levels pre-harvest, data from the three sites were analyzed independently.

The original plan was for all study sites to be harvested in the winter of 2015, however, that did not occur (Figure 3). Harvesting of the Beech tract was completed over the winter of 2015 and early spring 2016. Transect points BE1, BE2, and BE3 at the Beech study site were not re-sampled in 2016 and 2017 because they were not located in the shelterwood harvest due to a miscommunication of the harvest location. These locations were replaced with BES1, BES2, and BES3 (Figures 4, 5). Because local markets for timber shifted the original harvest site in the Laurel Ridge tract was no longer a viable option (Figure 6). Two transects from the original study site were lost and two new transects were placed within the new harvest area (Figure 7). This was followed by harvesting of the Kentucky Ridge tract during the winter of 2016 and early spring 2017 (Figure 1). The Laurel Ridge tract at Robinson Forest was harvested over the winter of 2017 and early spring 2018 (Figure 1).

It was decided to modify transect layouts with patch cut harvest treatments. Instead of the original locations, sample points were moved to the closest patch cut from the original transect point to more directly assess bat response to patch cuts. Because the riparian areas of patch cut harvest units were not harvested, the riparian sampling point was moved to a patch cut at the mid-slope position, again, to increase the number of patch openings sampled. This resulted in a ridge top and two mid-slope sampling points along each transect in patch cut harvest treatments following timber removal. This occurred for all patch cut harvests sampled during 2016 to 2017. At Laurel Ridge, I sampled the riparian area of the patch cuts. Patch cut sampling at Robinson Forest followed the pre-harvest transects. Points at the ridge top and mid-slope positions were moved to the closest patch cut available. The riparian point remained in the same position as the pre-harvest surveys. With all sampling of patch cuts, SM3 units were located at the immediate edge of the cut and pointed towards the center of the patch cut opening.

Figure 2. Acoustic set-up. The microphone is tied onto the tree and rests in PCV pipe, while the unit is chained to the tree.



	2015						2016							2017							2018				
	May	Jun	July	Aug	Sept	Nov	Jan	May	June	July	Aug	Sept	Nov	Jan	May	June	July	Aug	Sept	Nov	Jan	May	June	July	Aug
Beech		🟥	🟥	🟥	🟥	🟩	🟩	🟨		🟨	🟨	🟨				🟨	🟨	🟨							
KY Ridge			🟥	🟥					🟥	🟥	🟥		🟩	🟩		🟨	🟨	🟨	🟨						
Rob. For.		🟥	🟥	🟥	🟥				🟥	🟥	🟥				🟥	🟥	🟥			🟩	🟩	🟨		🟨	

Index of sampling and harvesting periods 🟥 **pre-harvest sampling** 🟩 **harvest** 🟨 **post harvest sampling**

Figure 3. Timeline of forest harvests and acoustic sampling for all study sites.

Table 1. Site differences in estimated species activity based upon Kaleidoscope species assignments in three sites, Laurel Ridge in Robinson Forest, Clayhole, KY, Beech Tract, Oakdale, KY, and Kentucky Ridge State Forest, Chenoa, KY, in Eastern Kentucky.

Parameter	**Beech**	**Kentucky Ridge**	**Laurel Ridge**	**df**		**F-value**	**P-value**
	Mean ± SE	Mean ± SE	Mean ± SE	x	y		
COTO	0.107 ± 0.0347	0.0606 ± 0.0296	0.0517 ± 0.024	2	310	1.01	0.365
EPFU	3.15 ± 0.835	2.21 ± 0.721	1.06 ± 0.393	2	310	2.58	0.0771
LABO	2.47 ± 0.679	1.43 ± 0.387	1.42 ± 0.308	2	310	1.3	0.273
LACI	2.24 ± 0.806	0.545 ± 0.124	1.28 ± 0.299	2	310	1.74	0.177
LANO	3.49 ^{a} ± 0.779	1 ^{b} ± 0.318	0.803 ^{b} ± 0.228	2	310	6.52	0.00169
MYLE	0.0611 ± 0.0210	0.0758 ± 0.0328	0.0345 ± 0.017	2	310	0.794	0.453
MYLU	1.53 ± 0.431	0.258 ± 0.0817	1.06 ± 0.242	2	310	2.76	0.0645
MYSE	2.48 ^{ab} ± 0.757	0.0455 ^{b} ± 0.0258	4.41 ^{a} ± 0.819	2	310	6.7	0.00142
MYSO	0.0534 ^{b} ± 0.0463	0.0909 ^{ab} ± 0.0417	0.302 ^{a} ± 0.0841	2	310	4.61	0.0107
NYHU	0.0763 ± 0.0369	0.0152 ± 0.0152	0.0431 ± 0.0226	2	310	0.881	0.416
PESU	2.02 ± 0.619	1.17 ± 0.418	0.759 ± 0.262	2	310	1.9	0.151

^{a,b} Within rows, means without common letters are groups with statistical difference.

Methods and Materials

Acoustic Sampling

Bat activity was assessed during the summers of 2015 to 2018. In 2015, all three tracts were sampled twice from 17 June to 16 September. During 2016, each site was sampled three times from 23 May to 11 September. In 2017, two of the three sites, Beech and Kentucky Ridge, were sampled three times between 7 June and 7 September, with Laurel Ridge sampled twice from 23 May and 20 July. Only Laurel Ridge was sampled in 2018; two times from 22 May to 13 July.

Activity was monitored using Song Meter 3 units and SMU-1 microphones (Wildlife Acoustics, Maynard, MA). The SM3 units were housed within pelican cases, with microphones placed within PVC pipe and tied to a tree at 1.5-m aboveground (Figure 2). Each location an acoustic unit was deployed was geolocated with a Garmin GPSMAP 64. These units are accurate within 5 to 15 m, depending on conditions. During each sampling session, acoustic sampling occurred for a minimum of three consecutive nights to account for random variation in nightly activity patterns. Data were collected from sunset to sunrise each night of sampling. The sunrise and sunset times were determined by a program in the SM3 units.

The pre-treatment transects contained a ridge top, mid-slope, and riparian sampling point (Figure 4, 6, 7, 8). Unharvested treatments and shelterwood harvests largely maintained the same transect layout post-harvesting as during pre-treatment sampling. Ideally, the acoustic units were deployed at the same point pre- and post-harvest. However, points were moved in some instances, typically within a few meters, due to a previous tree used to mount a unit being lost in the harvest. Patch cuts did not have a riparian area sampled, as described in the experimental design section (Figures 5, 9). Units were directed towards the center of the patch cut.

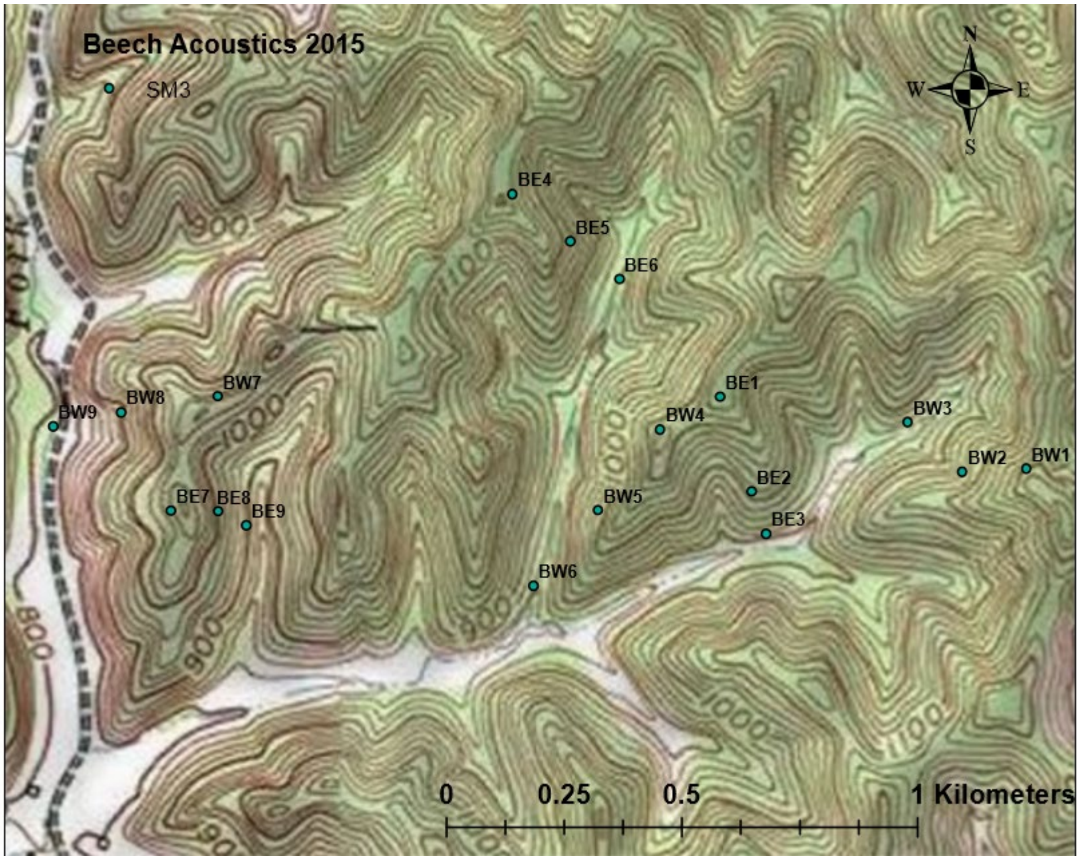


Figure 4. Pre-harvest (2015) acoustic transects at the Beech tract.

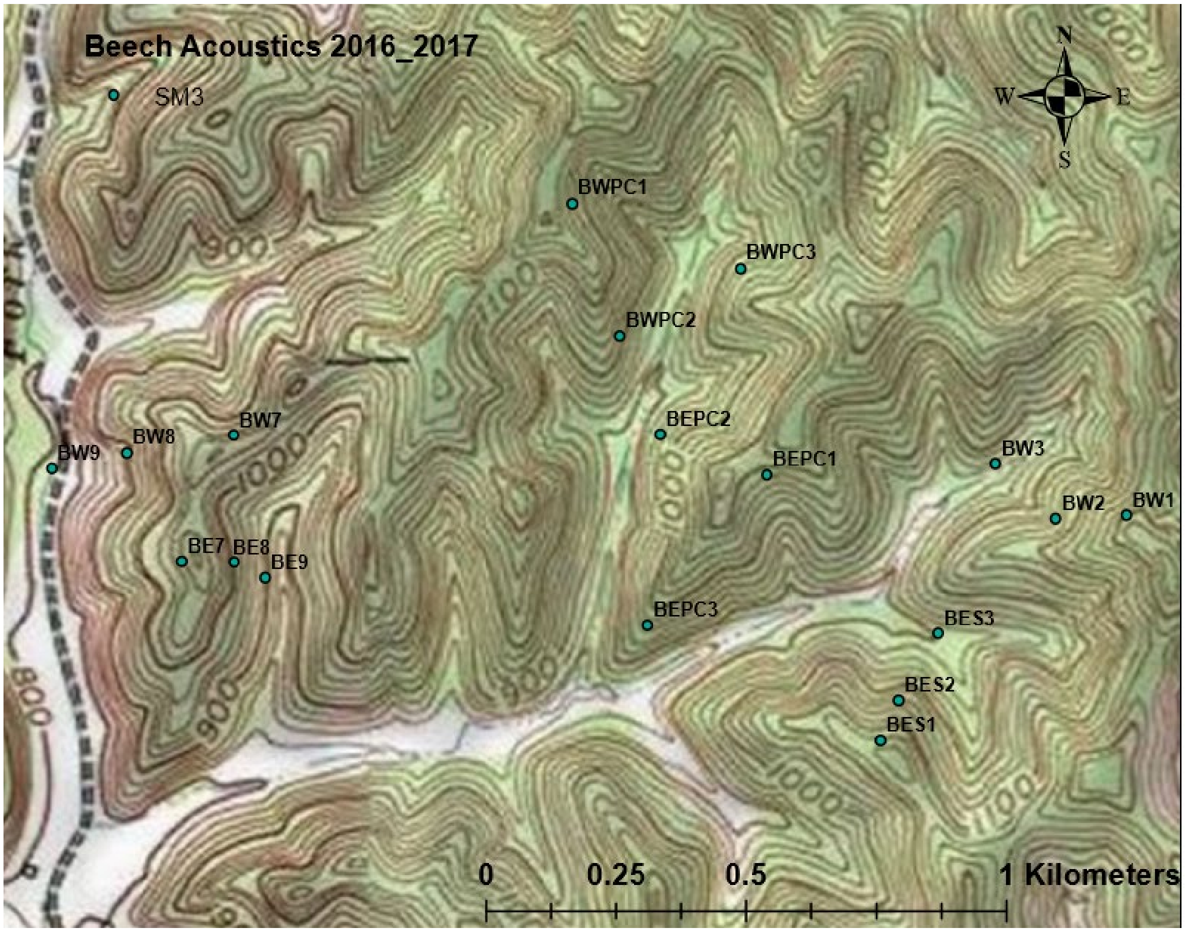


Figure 5. Post-harvest (2016-17) acoustic transects at the Beech tract.

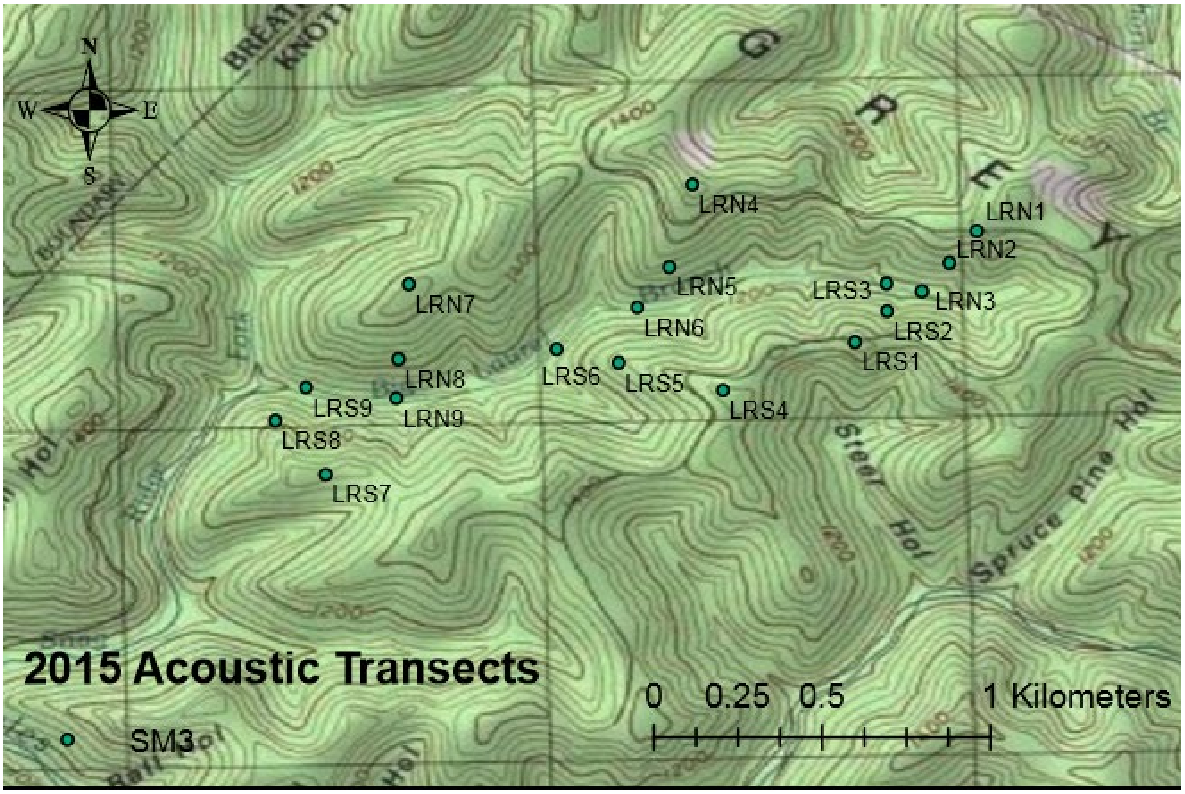


Figure 6. Pre-harvest (2015) acoustic transects at the Laurel Ridge tract, Robinson Forest.

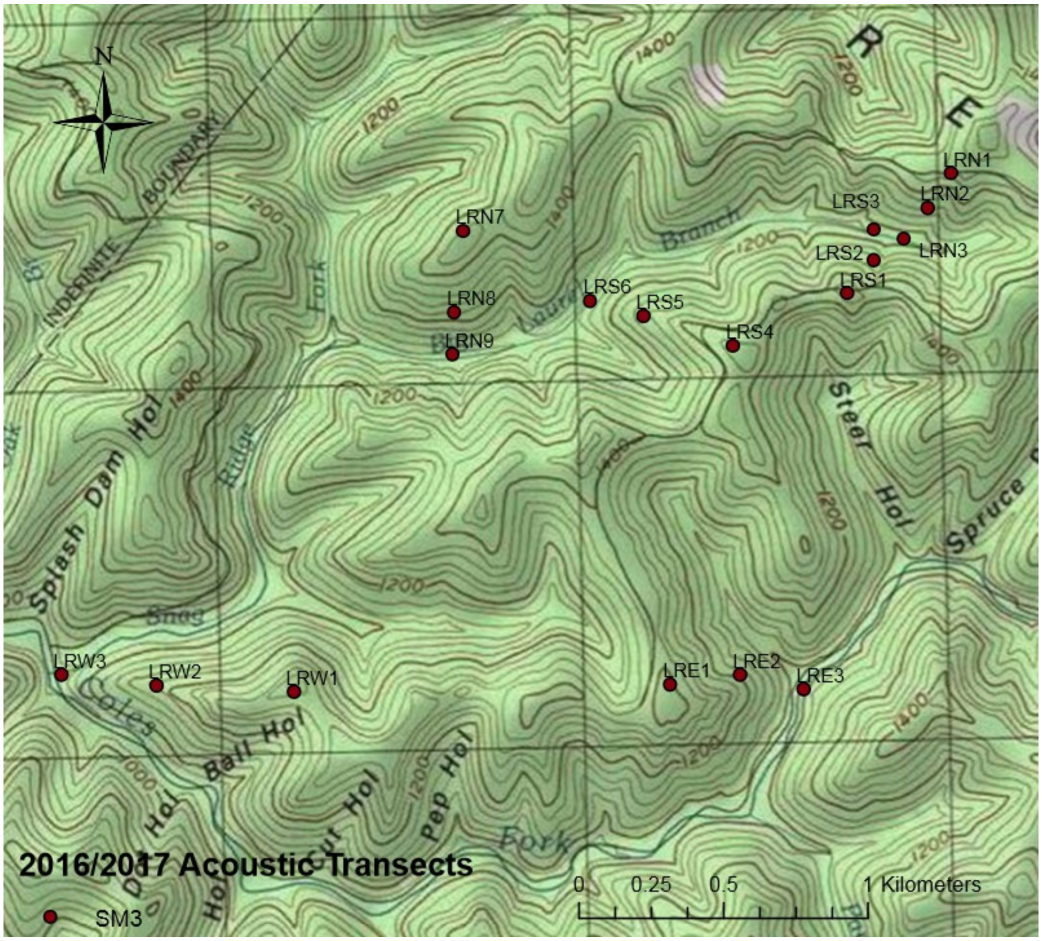


Figure 7. Pre-harvest (2016-17) acoustic transects at the Laurel Ridge tract, Robinson Forest.

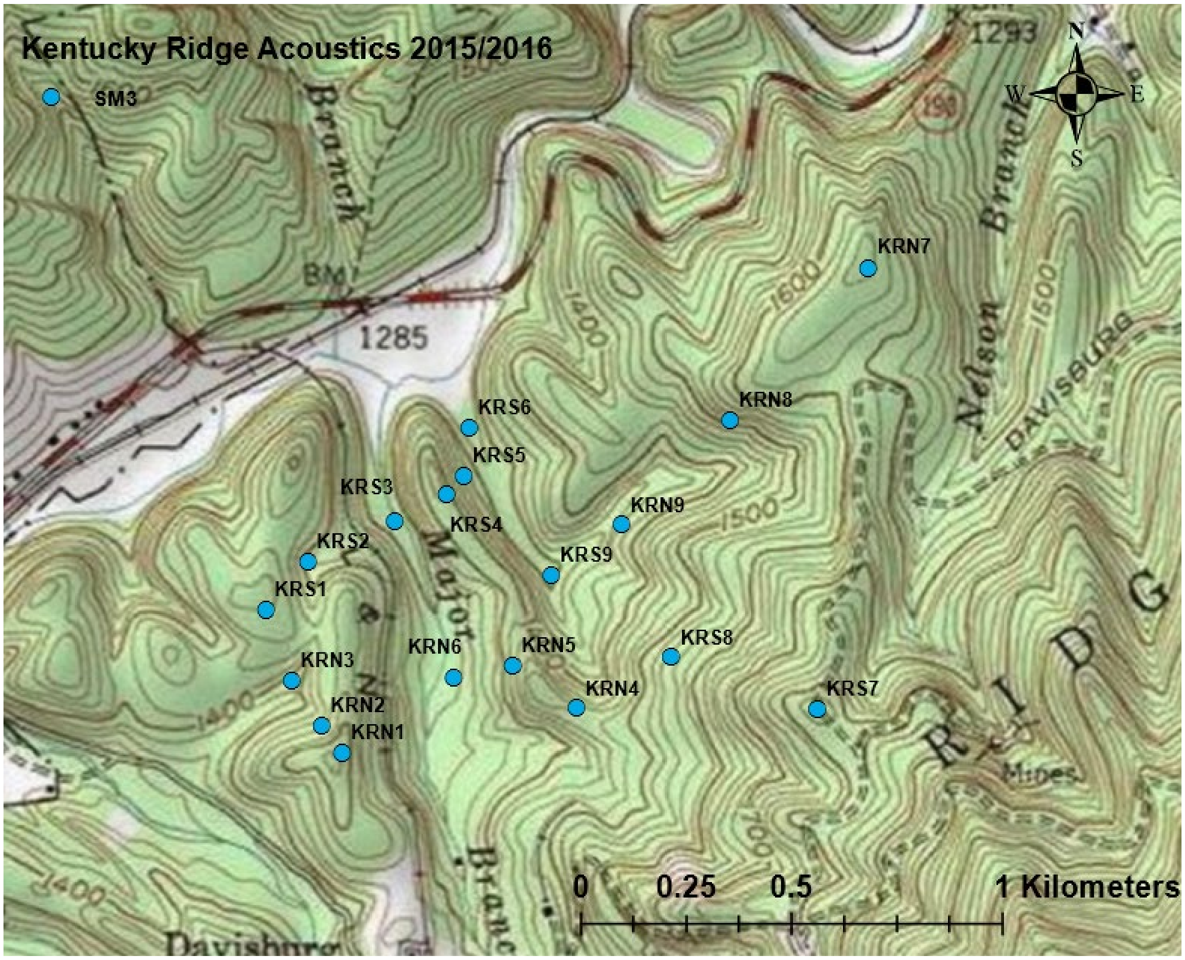


Figure 8. Pre-harvest (2015-16) acoustic transects at the Kentucky Ridge tract.

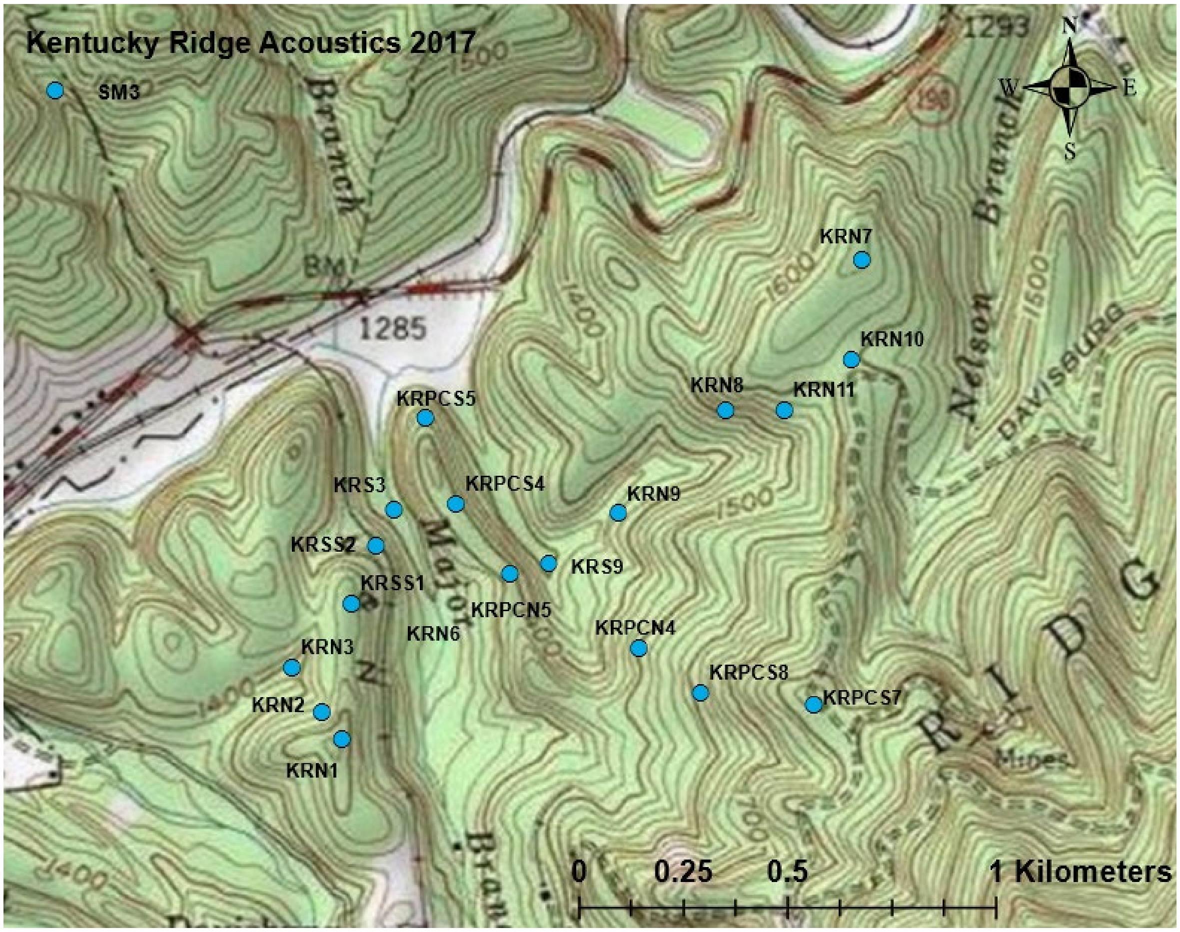


Figure 9. Post-harvest (2017) acoustic transects at the Kentucky Ridge tract.

Analysis of Acoustic Data

Acoustic data were analyzed using Kaleidoscope v. 3.1.8 (Wildlife Acoustics, Maynard, MA). Data were analyzed in two separate forms, number of pulses and number of calls per species. Both species level identifications and number of pulses were determined by Kaleidoscope set to the Kentucky filter to identify species. A few calls assigned to species known to not occur in eastern Kentucky, gray bat (*Myotis grisescens*) and southeastern bat (*M. austroriparius*), were deemed misclassified and not analyzed. Data were compiled, organized, and analyzed using ‘R’ statistical software 3.5.0 -Joy in

Playing (R Core Team 2013). The packages nlme, agricolae, plyr, magrittr, ggplot2, qcc, multcomp, and dplyr were accessed during data analysis. Data were sorted with a filter function to remove any call with ≤ 4 pulses, a quality less than 10, and a margin greater than 0.3. Count and aggregate were used to summarize the data for statistical tests. Coding is provided (Appendix I).

A quasi-poisson model of pulses was ran to compare activity differences between slope positions within a treatment. A quasi-poisson model was performed for year, as a proxy for pre- and post-harvest data, on the call data to assess how species responded to harvests.

Arthropod Sampling and Analysis

Light trap sampling occurred in pre- and post-harvest sites from late July 2015 thru early September 2017. Each location where a light trap was deployed was geolocated with a Garmin GPSMAP 64. These units are accurate within 5 to 15 m, depending on conditions. Universal backlight traps (Bioquip Products Inc., Rancho Dominguez, CA) were used to sample positively phototactic arthropods active at sampling sites. Arthropods were euthanized by Nuvan Prostrips; active ingredient - DDVP or 2,2-Dichlorovinyl dimethyl phosphate (Amvac, Los Angeles, CA). In 2015, I deployed light traps by hanging them from a tree 50 m from any active acoustic unit at ridge top, mid-slope, and riparian slope positions (Figures 10, 11, 12, 13, 14). During 2016 and 2017, I deployed traps only at mid-slope points due to time and labor constraints (Figures 15, 16). Traps were operated from sunset to sunrise on nights without rain. Specimens were put in plastic containers and placed in a freezer for long-term storage. Captured insects were keyed to taxonomic Order and enumerated.

In total, 109 samples (76 unharvested, 17 shelterwood, and 16 patch cut) were collected from the three field sites (Beech n = 33, Kentucky Ridge n = 43, and Laurel Ridge n = 33) over the course of three summers. Pre-harvest data were collected from all field sites in 2015. During that period, 23 light trap samples from unharvested forests were collected. One transect of light traps was established at the Beech property and resulted in 5 successful samples (2 ridge top, 2 mid-slope, and 1 riparian). One transect of light traps was established at Laurel Ridge resulting in 6 successful samples (2 ridge top, 2 mid-slope, and 2 riparian). Two transects were placed at Kentucky Ridge State Forest and resulted in 12 successful samples (4 ridge top, 4 mid-slope, and 4 riparian).

In late-2015 and early-2016 the Beech tract was harvested. All samples collected from each site during 2016 were at mid-slope positions. Sampling was intended to have an unharvested sample coupled with two harvest treatment samples at the Beech property; however, consistent trap failures resulted in harvest samples not always being paired with an unharvested sample. During 2016, 15 samples (4 unharvested, 4 shelterwood, and 7 patch cut) were collected from the Beech property. Kentucky Ridge had 13 samples collected and Laurel Ridge had 16 samples successfully collected. In total, 44 successful samples were collected in 2016.

In late-2016 and early-2017 the Kentucky Ridge site was harvested. All samples collected from each site in 2017 were at mid-slope positions. Samples were intended to have an unharvested sample coupled with two harvest treatment samples at the two harvested properties (Beech and Kentucky Ridge); however, trap failures resulted in harvest samples not always being paired with unharvested samples. The Beech site had 13 successful samples (4 unharvested, 5 shelterwood, and 4 patch cut). Kentucky Ridge had 18 successful samples (5 unharvested, 5 shelterwood, and 8 patch cut). Laurel Ridge had 11 successful unharvested samples. In total, 42 samples were collected during 2017.

Although light traps are designed to primarily capture Lepidopterans (moths) other orders of insects were commonly found in traps. Analysis was performed on the insect orders which appeared in greater than 60% of my sampling effort. Data for arthropod captures were analyzed using ‘R’ statistical software 3.5.0 -Joy in Playing (**R** Core Development Team, 2013). The packages nlme, agricolae, plyr, magrittr, ggplot2, qcc, multcomp, and dplyr were accessed during data analysis. I used multi-way analysis of variance (ANOVAs) to detect differences in total abundance, order count, and number of individuals for the five dominant orders collected separately, i.e., Lepidoptera, Coleoptera, Diptera, Hemiptera, and Hymenoptera. I examined differences by slope position, tract, year, and treatment. I used slope position and treatment as fixed effects, with tract as the random effect.

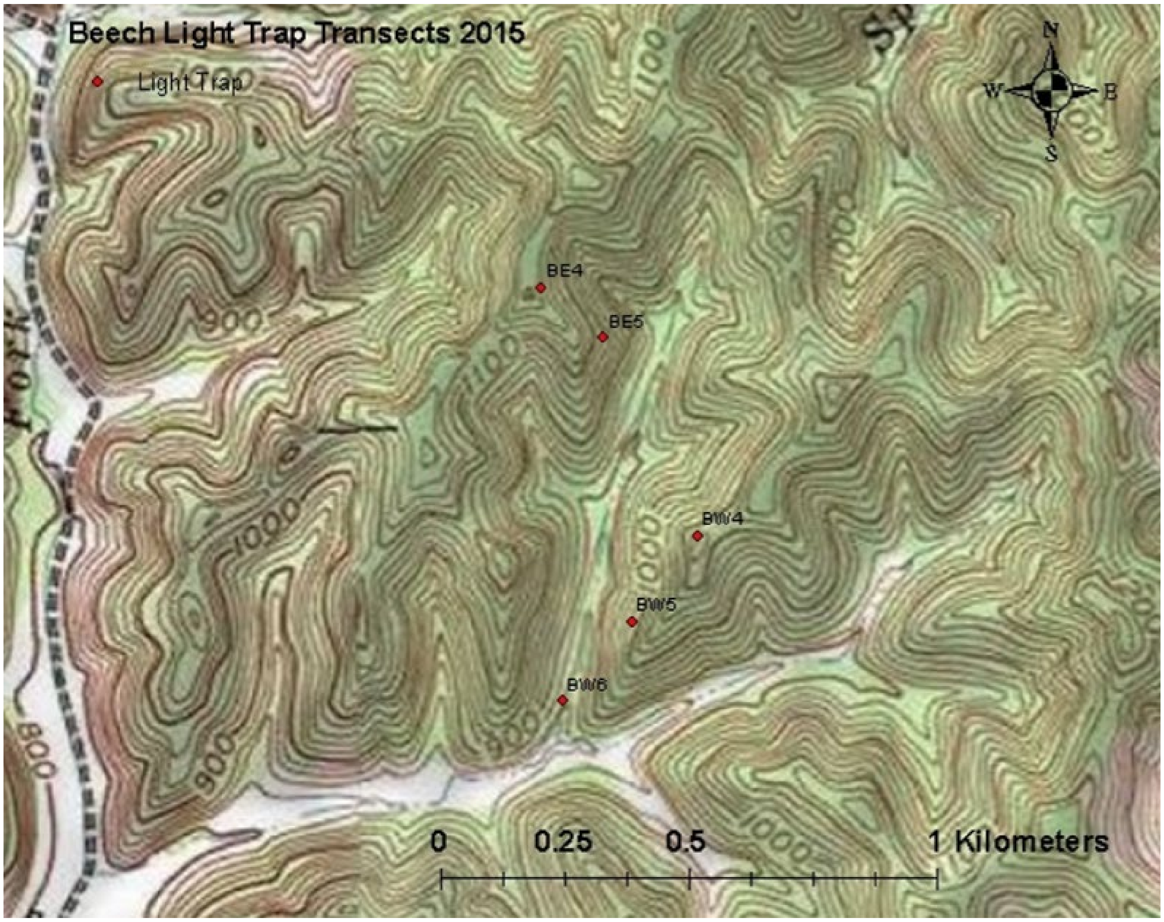


Figure 10. Pre-harvest (2015) light trap transects at the Beech tract.

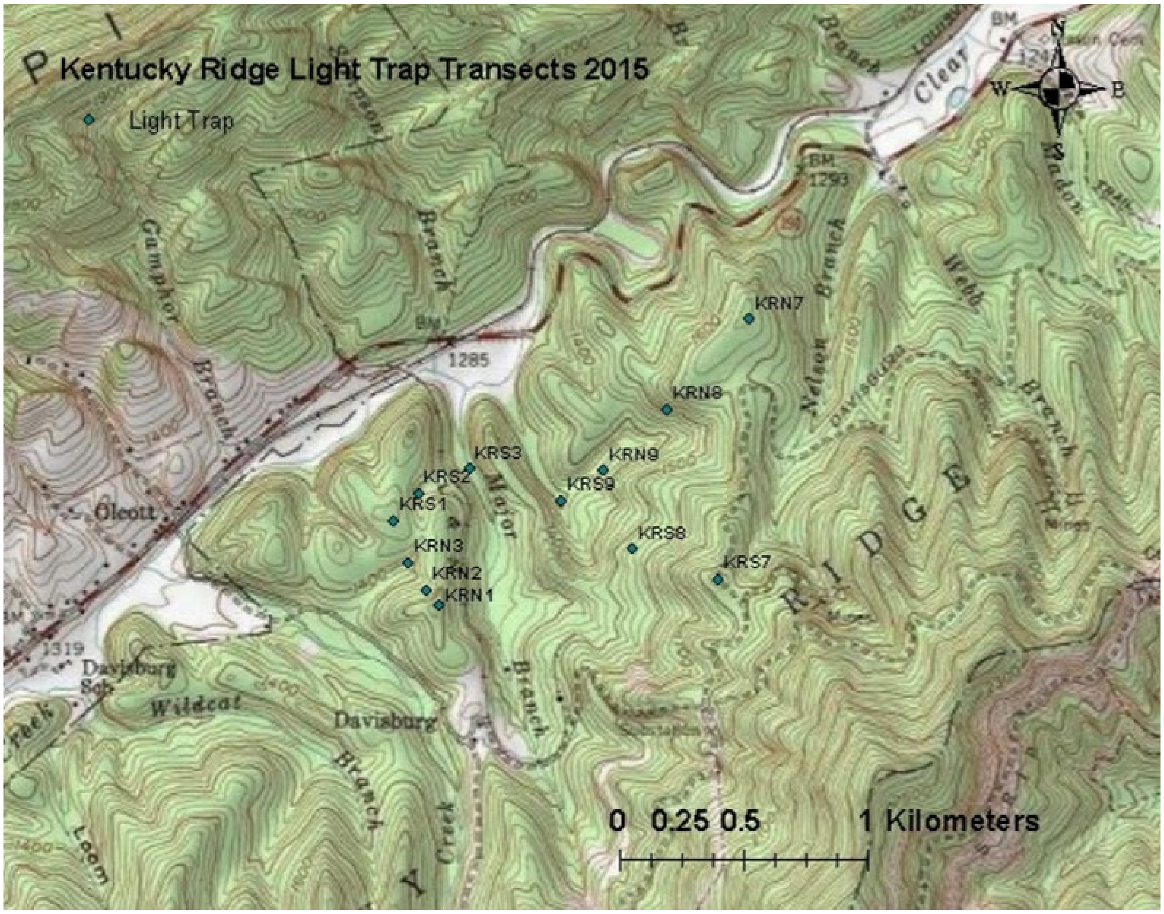


Figure 11. Pre-harvest (2015) light trap transects at the Kentucky Ridge tract.

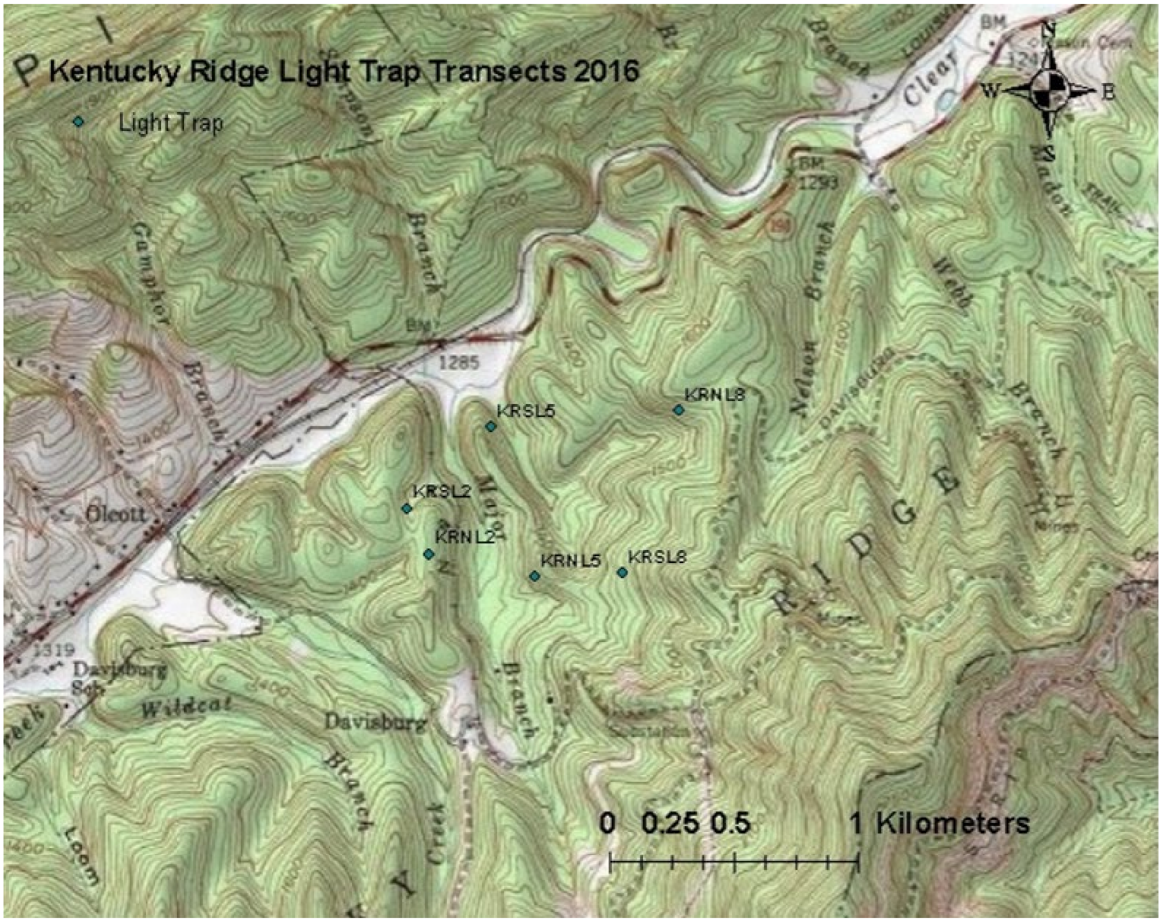


Figure 12. Pre-harvest (2016) light trap transects at the Kentucky Ridge tract.

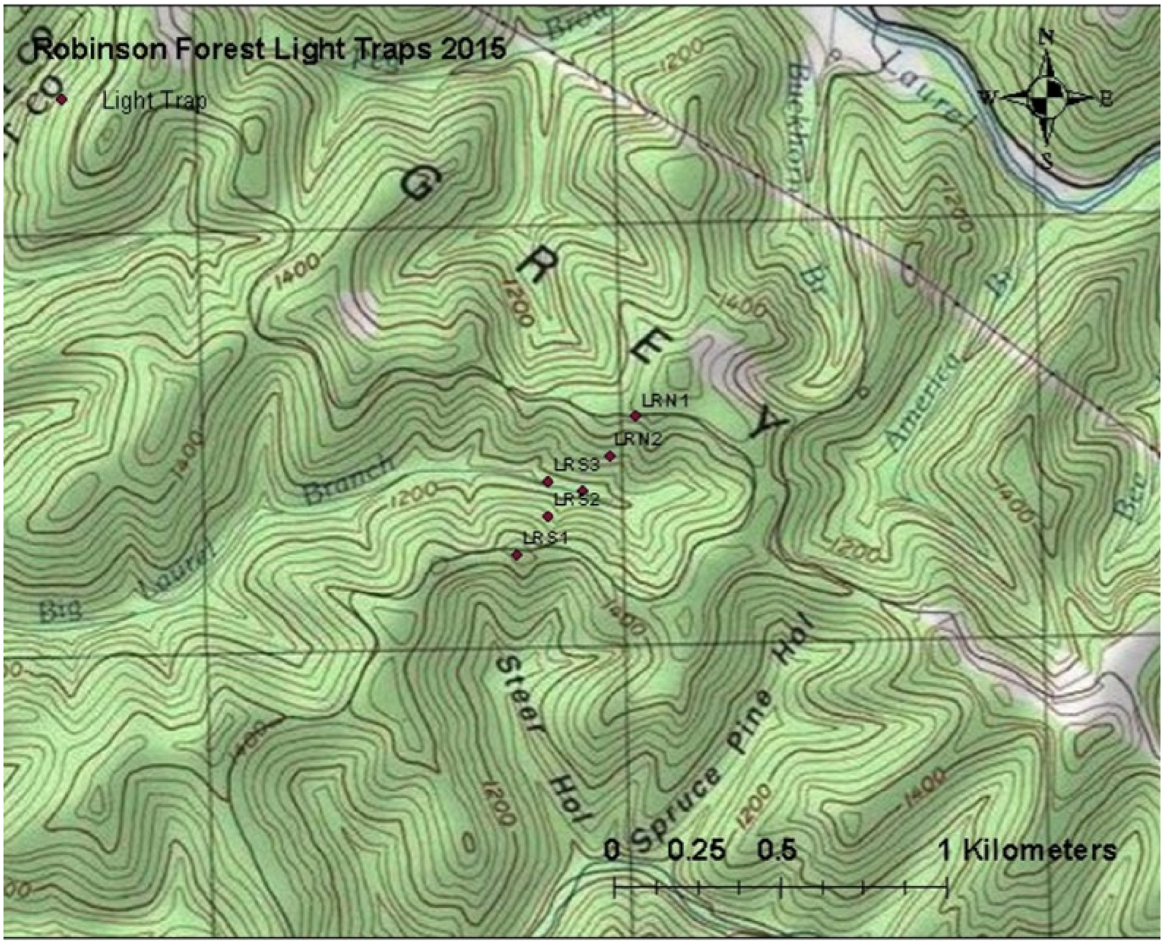


Figure 13. Pre-harvest (2015) light trap transects at the Laurel Ridge tract, Robinson Forest.

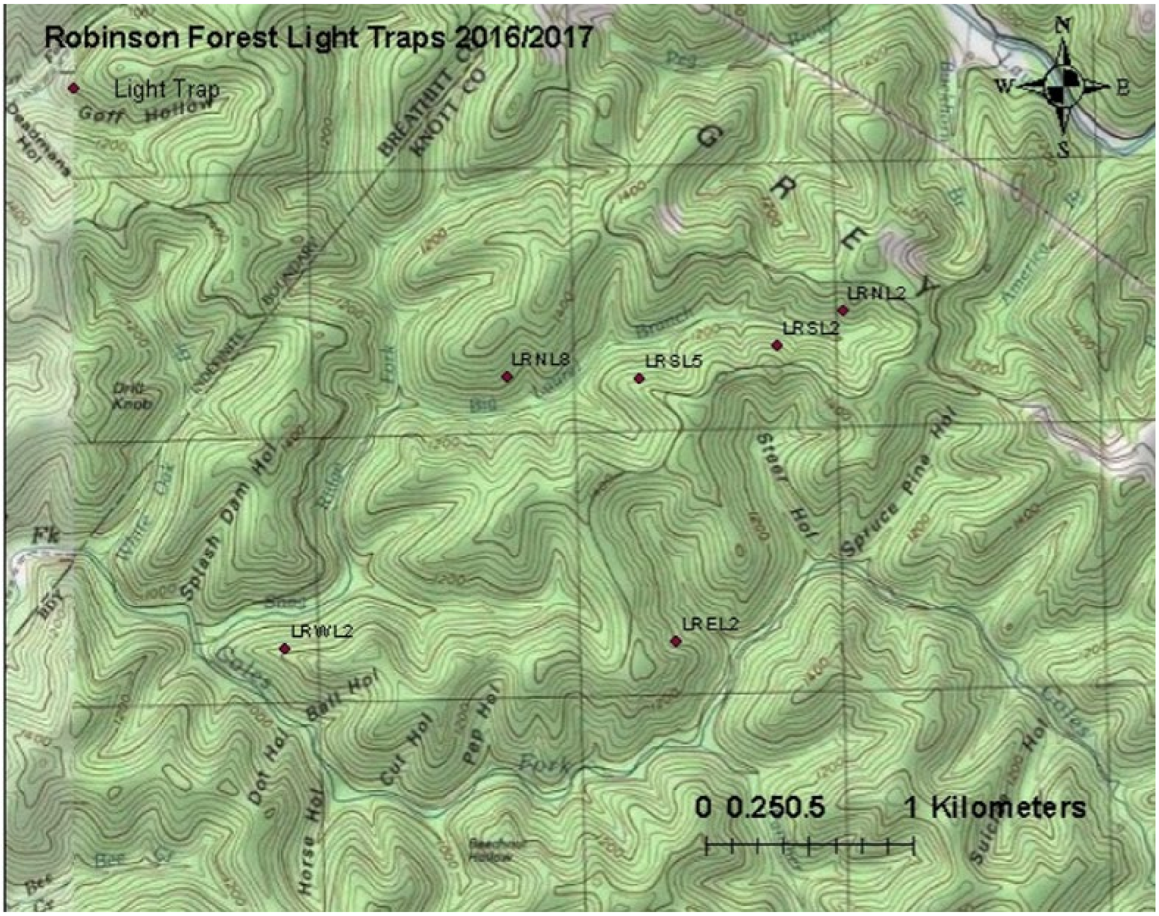


Figure 14. Pre-harvest (2016-17) light trap transects at the Laurel Ridge tract, Robinson Forest.

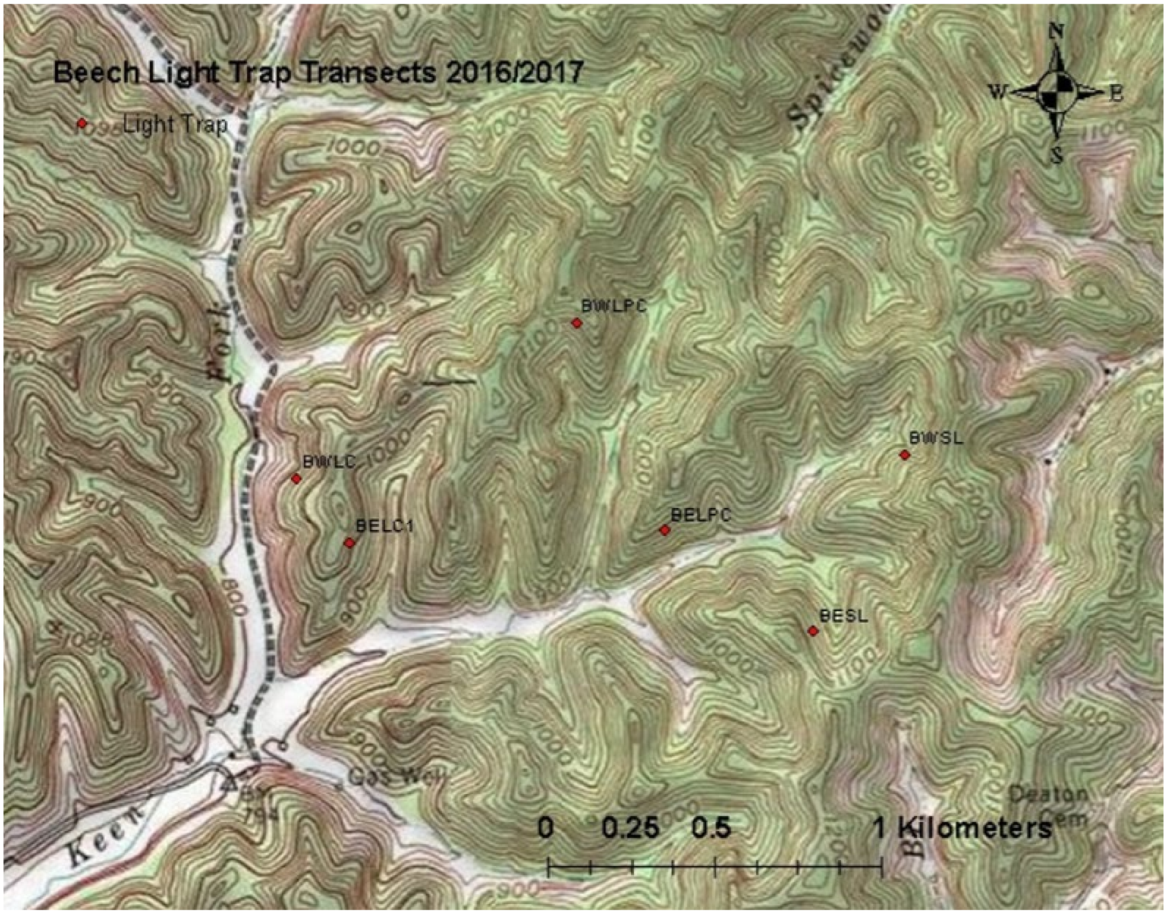


Figure 15. Post-harvest (2016-17) light trap transects at the Beech tract.

Figure 16. Post-harvest (2017) light trap transects at the Kentucky Ridge tract.

Mist Net Sampling

Bats were captured at Robinson Forest from 19 May to 20 August 2016, 9 May to 1 August 2017, and 23 May to 13 July 2018. Netting sites were determined, in part, based upon results of acoustic data, with netting taking place in the vicinity of sampling points with high amounts of acoustic activity of Myotis bats. Robinson Forest was netted in four locations: camp, Little Buckhorn, Big Laurel Ridge, and Medicine Hollow from 2016 through 2018. Roughly 103 net nights occurred, with each net night being a pole set left up for several hours. Big Laurel Ridge and Medicine Hollow were within the study site, Laurel Ridge tract. Netting was rotated between these sites to capture and radio-tag northern long-eared bats from 2016 through 2017. Netting during 2018 was focused on determining species presence and presence of northern long-eared bats at the Laurel Ridge tract post-harvest. Camp was netted to train technicians to extract bats, determine species and sex of bats present in buildings, and determine if pups were being successfully reared in the residential buildings.

Closed canopy roads and streams were typical locations where nets were set to capture bats. Net were predominately placed across single-lane dirt roads using 2.6 X 2.6-m mist nets. However, net width ranged from 2.6 to 18 m in length and varied from single to triple-high sets depending on the location surveyed. Nets were raised using Avinet poles (Dryden, NY) as single highs, and as double and triple highs with the forest filter pole system (Bat Conservation and Management, Inc., Carlisle, PA). Post-harvest skidder trail roads, patch cuts, intact areas near shelterwood harvests, and the edge of logging roads were also sampled with nets using the forest filter system.

Additional mist netting occurred at the Beech tract from May to September 2015 to 2017 at two habitat types, along streams within the unharvested section and in the skidder trails between patch cuts. Eleven net nights occurred, 9 in 2016 and 2 in 2017. The patch cuts at the Beech tract were surveyed with the forest filter system. Netting at the Beech tract was aimed at confirming determining species presence on the site.

I collected data on all bats captured, including: mass (g), right forearm length (mm), reproductive condition, Reichard wing score (Reichard and Kunz 2009), sex, age (Brunet-Rossinni and Wilkinson 2009), height in net, and presence of parasites. Age was determined by shining a light through the joints of the finger bones. Adult bones are ossified, and light does not pass through. Juvenile bones are not fully ossified, and light passes between the bones in the finger joints. Pregnancy was determined by a swollen stomach. Palpation for fetuses did not occur. Lactation was determined when a patch of hair around the mammary glands was absent. Reproductive status of males was determined by examining the scrotal region for descended epididymes. During 2016, all captured bats were banded with 2.4- or 2.9-mm aluminum bands supplied by the Kentucky Department of Fish and Wildlife Resources (KDFWR). Bands were attached with banding pliers. Males were banded on the right forearm and females on the left forearm. In 2017 and 2018, only federally protected species were banded.

Radio-Telemetry

I attached radio-transmitters to captured Myotis bats to radio-track them to roost trees. Northern long-eared bats and Indiana bats were either banded or fitted with a transmitter. No individual received both to ensure <5% of the bat’s body mass was added (Aldridge and Brigham 1988). LB-2XT transmitters (Holohil Systems, Ltd., Ontario, Canada) were glued between the shoulder blades of bats with surgical cement (Perma-Type Company, Inc., Plainville, CT). I tracked radio-tagged bats to roost trees daily using 3 or 5-element yagi antennae (Wildlife Materials, Inc., Murphysboro, IL) combined with either Icom IC-R20 radio receivers (Icom America, Inc, Kirkland, WA), R-1000 receivers (Communication Specialists, Inc., Orange, CA), or TRX-2000 receivers (Wildlife Materials, Inc., Murphysboro, IL). Bats were searched for each day until the transmitter was found dead or the bat could not be located for 3 consecutive days. In order to locate a signal, the yagi was placed out the window as we drove down the roads on Robinson Forest. The extensive road network allowed us to cover a large portion of the forest and was present in both riparian and ridgetop areas. If a signal was not located from the road network, we hiked from ridgetop to ridgetop to attempt to locate a signal. The signal was only periodically checked for beyond the 3-day limit if the bat was not located.

Description of Day Roosts

Trees located by radio-telemetry and confirmed by exit counts were designated as roost trees. Tree roosts that I located were identified to species and decay class recorded. Each located roost was geolocated with a Garmin GPSMAP 64. These units are accurate within 5 to 15 m, depending on conditions. The tree also received a permanent tree tag. I also sampled trees at randomly chosen plots. Random plots were assigned either 0 or 180 degrees to ensure they were located on either ridge top or mid-slope positions; the only landscape positions where northern long-eared bats were found roosting. These plots were determined using a random compass orientation between 0 or180 degrees, and a random distance >50 m from a known roost tree. Trees in a 10-m radius around each random sampling point were measured. I collected data on species and decay class for all stems with a dbh greater than 2.54 cm.

As bats were tracked to multiple roost trees, an exit count was performed the first night after a new roost was discovered. Counts started 20 min before sunset and ended 10 min after the last bat emerged from the roost. Personnel positioned themselves in an orientation that ensured the bats were silhouetted against the sky.

Results

Acoustic Sampling

Acoustic sampling occurred in pre-harvest sites from late July 2015 thru early September 2017. During 2015, 310 nights of acoustic sampling data were collected from the Beech, Kentucky Ridge, and Laurel Ridge tracts. Data were used to determine the pre-harvest assemblage of bats present. Significant differences were found between sites for the number of silver-haired bat and northern long-eared bat calls. More silver-haired bat calls were detected at the Beech tract than Kentucky Ridge or Laurel Ridge tracts. More northern long-eared bat calls were detected at Laurel Ridge than at the Kentucky Ridge or Beech tracts (Table 1). The observed difference in bat assemblages across sites pre-harvest resulted in analyses being made for each site separately.

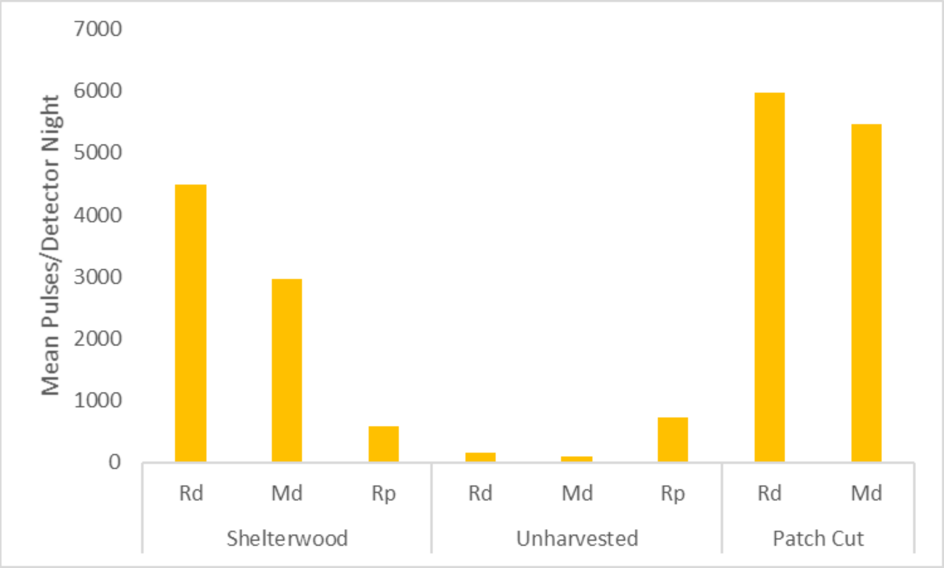
In total, 649 acoustic nights (1 detector per night = acoustic night) of data were collected at the Beech tract. Post-harvest, 2016 and 2017, 154 acoustic nights of data were collected from unharvested forest, 173 from the shelterwood, and 163 from the patch cut. At the Kentucky Ridge tract, 492 acoustic nights of data were collected. Post-harvest 2017, 59 acoustic nights were collected from the unharvested forest, 77 from the shelterwood harvests, and 63 from the patch cut harvests.

Figure 17 is a qualitative comparison of the harvest types. Data from Laurel Ridge is provided, but will not be extensively discussed because it occurred after my thesis work had concluded. Both the shelterwood and patch cut harvests had higher activity than the unharvested treatment at the Beech and Kentucky Ridge sites. The ridgetop and mid-slope positions in patch cuts had similar activity levels at both Beech and Kentucky Ridge sites. The ridgetop position in the shelterwood had higher activity than the mid-slope position at both the Beech and Kentucky Ridge sites, and both positions had higher activity than the respective unharvested sections. Laurel Ridge had high activity in the ridgetop of the impacted control, likely because the ridgetop roads were harvested. The high activity in the riparian area of the shelterwood in Laurel Ridge was likely due to the stream being perennial and wider than the intermittent streams near the control and patch cut treatments.

A quasi-poisson model comparing years showed significant increase in activity post-harvest at the Kentucky Ridge (649 acoustic nights) and Beech properties (492 acoustic nights). A quasi-poisson model comparing slope positions post-harvest, showed differences between shelterwood slope positions. At the Beech property the ridge top and mid-slope positions had more bat activity than the riparian positions. The shelterwood harvest ridge top at the Kentucky Ridge tract had more bat activity than the mid-slope or riparian positions. No difference was found between the ridgetop and mid-slope positions within patch cuts (Table 2).

A quasi-poisson model comparing species activity pre-and post-harvest was performed for the Beech (601 acoustic nights) and Kentucky Ridge sites (435 acoustic nights). At the Beech tract activity increased for big brown bat, red bat, silver-haired bat, evening bat, and tri-colored bat. Activity of little brown bat increased the second-year post-harvest, but not the first year. No consistent trend occurred with hoary bat. Activity of northern long-eared bat decreased; activity of Indiana bat was too infrequent to determine any patterns (Table 3). At the Kentucky Ridge tract activity increased for Rafinesque big-eared bat, big brown bat, red bat, silver-haired bat, hoary bat, little brown bat, and tri-colored bat. No consistent trend was observed for evening bat. Activity of northern long-eared bat and Indiana bat was too low to determine any patterns (Table 4). The harvest at Laurel Ridge occurred after the completion of my thesis work and will not be detailed in this document; however, Figure 18 serves as a visual reference of results including the post-harvest data from the Laurel Ridge tract.

a.


Mean Pulses/Detector Night
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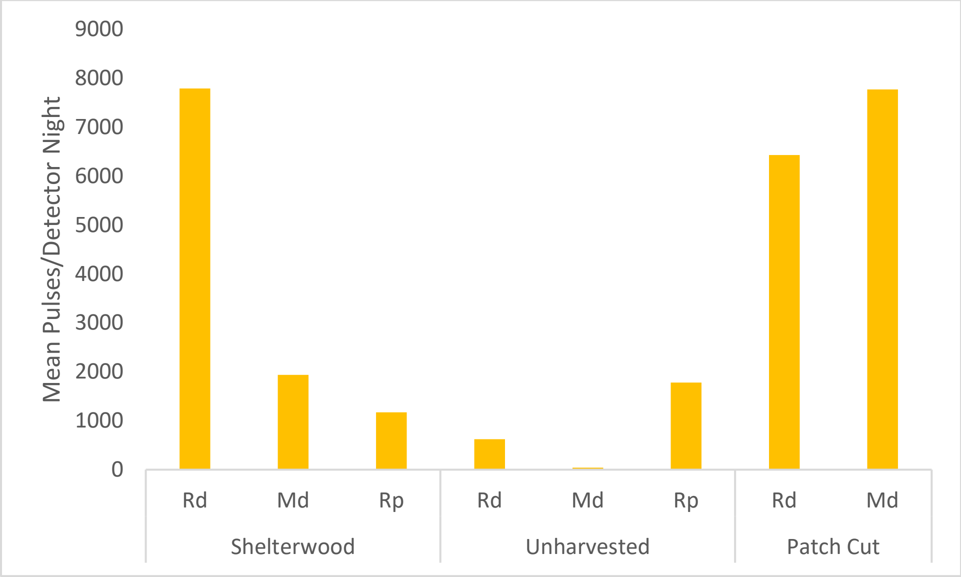
6000
5000
4000
3000
2000
1000
0
Rd
Md
Rp
Rd
Md
Rp
Rd
Md
Shelterwood
Unharvested
Patch Cut

b.


Mean Pulses/Detector Night
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8000
7000
6000
5000
4000
3000
2000
1000
0
Rd
Md
Rp
Rd
Md
Rp
Rd
Md
Shelterwood
Unharvested
Patch Cut

c.

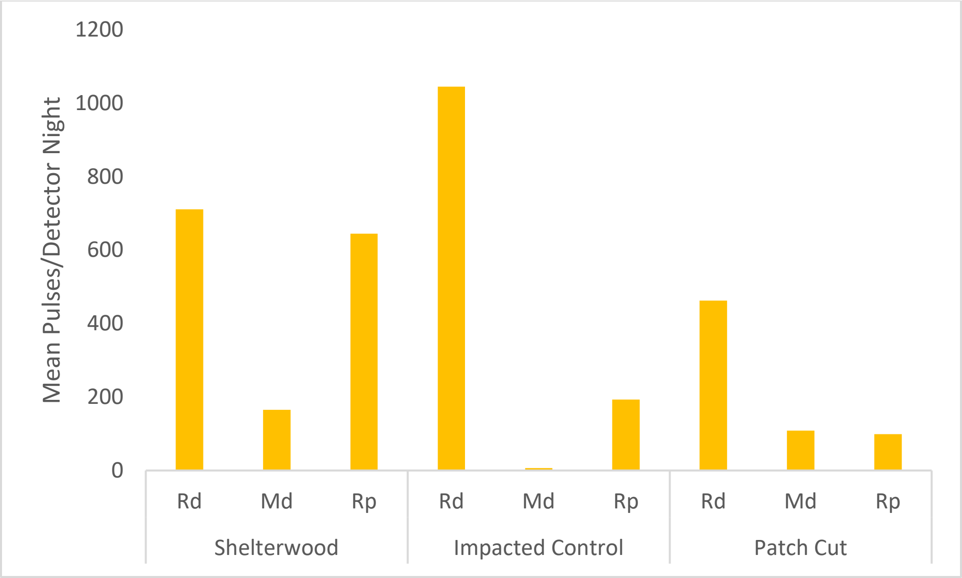
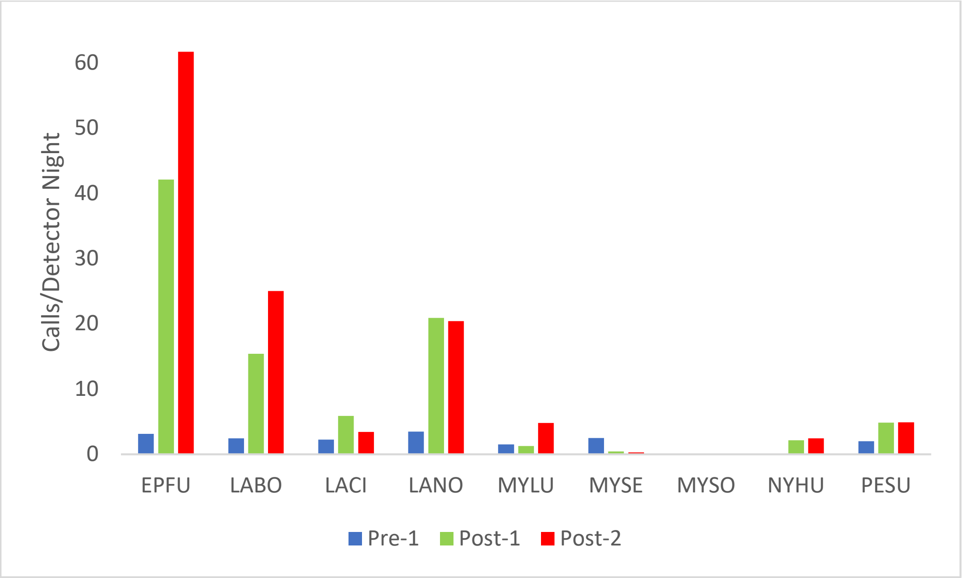
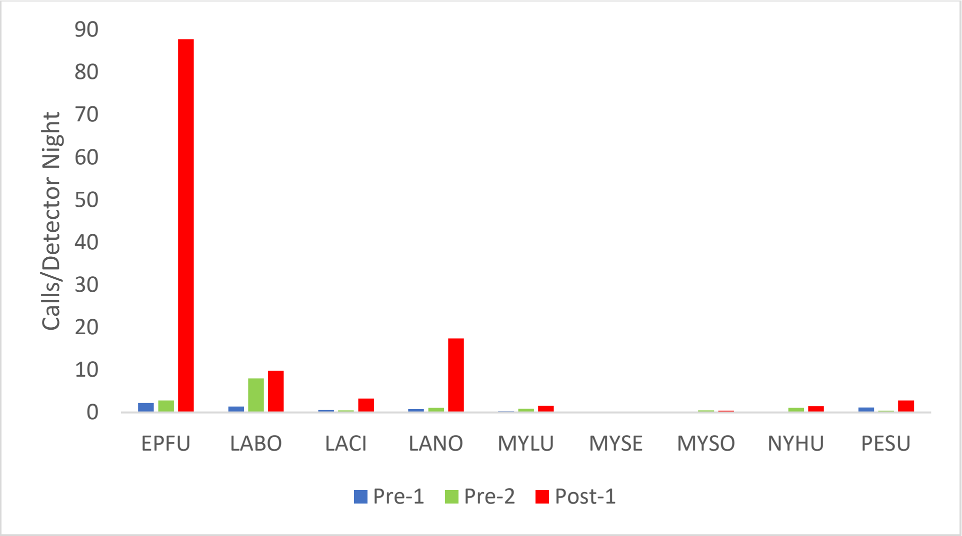


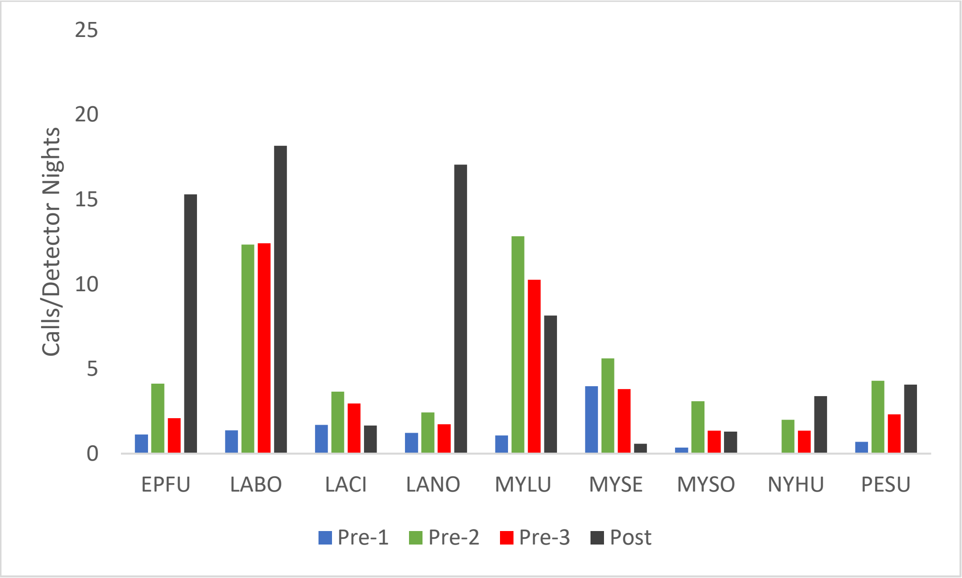
Figure 17. Comparison of activity of bats in different treatments and slope positions; ridgetop (rd), mid-slope (md), and riparian (rp). Beech (a), Kentucky Ridge (b), and Laurel Ridge (c) tracts in eastern Kentucky.

a.





b.



c.

Figure 18. Activity of bat species pre-and post-harvest at; Beech (a), Kentucky Ridge (b), and Laurel Ridge (c) tracts in eastern Kentucky. (Blue (2015), Green (2016), Red (2017), and Black (2018). The pre-x designation denotes the site had not yet been harvested and the number of seasons the site has been sampled pre-harvest. The post-x designation denotes the site has been harvested and the number of seasons the site has been sampled post-harvest.

Table 2. Comparison of mean pulses per detector night at the slope position in each treatment at Beech tract, Oakdale, KY and Kentucky Ridge State Forest, Chenoa, KY.

Parameter	**Ridgetop**	**Mid-slope**	**Riparian**	**df**		**F-value**	**P-value**
	Mean ± SE	Mean ± SE	Mean ± SE	x	y		
Control Beech	149 ^{a} ± 36	84.3 ^{a} ± 23.6	723 ^{b} ± 166	2	154	13.1	<0.001
Shelterwood Beech	4490 ^{a} ± 556	2960 ^{a} ± 362	573 ^{b} ± 122	2	173	28.4	<0.001
Patch Cut Beech	5980 ± 1040	5470 ± 791	N/A	1	163	0.144	0.705
Control Kentucky Ridge	626 ^{b} ± 219	38.9 ^{a} ± 9.64	1780 ^{ab} ± 556	2	59	4.63	0.0135
Shelterwood Kentucky Ridge	7990 ^{a} ± 1320	1940 ^{b} ± 250	1170 ^{b} ± 341	2	77	20.2	<0.001
Patch Cut Kentucky Ridge	6430 ± 1510	7770 ± 1510	N/A	1	63	0.437	0.511

^{a,b} Within rows, means without common letters are groups with statistical difference.

Table 3. Pre- and post-harvest species activity (calls per detector night) based upon Kaleidoscope species assignments at Beech tract, Oakdale, KY.

Parameter	**2015 - Pre**	**2016 – Post 1st**	**2017 – Post 2nd**	**df**		**F-value**	**P-value**
	Mean ± SE	Mean ± SE	Mean ± SE	x	y		
COTO	0.106 ^{a} ± 0.0347	0.317 ^{b} ± 0.0595	0.163 ^{a} ± 0.0315	2	601	4.97	0.00725
EPFU	3.15 ^{a} ± 0.835	42.1 ^{b} ± 4.92	61.7 ^{c} ± 7.46	2	601	19.8	<0.001
LABO	2.47 ^{a} ± 0.679	15.4 ^{b} ± 1.51	25 ^{c} ± 2.95	2	601	21.6	<0.001
LACI	2.24 ^{a} ± 0.806	5.87 ^{ab} ± 0.68	3.44 ^{b} ± 1.04	2	601	4.2	0.0154
LANO	3.49 ^{a} ± 0.779	20.9 ^{b} ± 1.84	20.4 ^{b} ± 2.83	2	601	14.5	<0.001
MYLE	0.0611 ± 0.0210	0.0284 ± 0.0106	0.022 ± 0.0976	2	601	2.12	0.121
MYLU	1.53 ^{a} ± 0.431	1.26 ^{a} ± 1.53	4.8 ^{b} ± 0.881	2	601	11.5	<0.001
MYSE	2.48 ^{a} ± 0.757	0.419 ^{b} ± 0.0881	0.304 ^{b} ± 0.0661	2	601	13.3	<0.001
MYSO	0.0534 ± 0.0463	0.0732 ± 0.0210	0.119 ± 0.0292	2	601	1.19	0.304
NYHU	0.0763 ^{a} ± 0.0369	2.13 ^{b} ± 0.222	2.44 ^{b} ± 0.285	2	601	21.5	<0.001
PESU	2.02 ^{a} ± 0.619	4.83 ^{b} ± 0.647	4.9 ^{b} ± 0.721	2	601	4.28	0.0143

^{a,b,c} Within rows, means without common letters are groups with statistical difference.

Table 4. Pre- and post-harvest species activity (calls per detector night) based upon Kaleidoscope species assignments at Kentucky Ridge State Forest, Chenoa, KY.

Parameter	**2015 - Pre**	**2016 - Pre**	**2017 – Post 1st**	**df**		**F-value**	**P-value**
	Mean ± SE	Mean ± SE	Mean ± SE	x	y		
COTO	0.0606 ^{a} ± 0.0296	0.114 ^{a} ± 0.0531	1.63 ^{b} ± 0.389	2	435	9.38	<0.001
EPFU	2.21 ^{a} ± 0.721	2.8 ^{a} ± 0.901	87.8 ^{b} ± 9.29	2	435	51	<0.001
LABO	1.42 ^{a} ± 0.387	7.98 ^{ab} ± 2.22	9.79 ^{b} ± 1.38	2	435	3.38	0.0351
LACI	0.545 ^{a} ± 0.124	0.52 ^{a} ± 0.0853	3.26 ^{b} ± 0.506	2	435	17.4	<0.001
LANO	0.803 ^{a} ± 0.228	1.11 ^{a} ± 0.247	17.4 ^{b} ± 1.42	2	435	79.4	<0.001
MYLE	0.0758 ^{ab} ± 0.0328	0.194 ^{a} ± 0.0571	0.0558 ^{b} ± 0.0193	2	435	3.47	0.0319
MYLU	0.258 ± 0.0817	0.863 ± 0.151	1.53 ± 0.417	2	435	2.71	0.0679
MYSE	0.0455 ± 0.0258	0.0514 ± 0.0203	0.0609 ± 0.0235	2	435	0.0897	0.914
MYSO	0.0909 ± 0.0417	0.508 ± 0.139	0.381 ± 0.124	2	435	1.53	0.218
NYHU	0.0152 ± 0.0152	1.09 ± 0.426	1.46 ± 0.245	2	435	2.86	0.0582
PESU	1.17 ^{a} ± 0.418	0.417 ^{a} ± 0.0791	2.85 ^{b} ± 0.447	2	435	14.2	<0.001

^{a,b,c} Within rows, means without common letters are groups with statistical difference.

Arthropod Sampling

Data for arthropods by slope position (ridge top, mid-slope, and riparian) generated in 2015 were compared using ANOVAs. Seven separate tests were ran for each metrics of insect presence: total abundance of insects, number of arthropod orders, lepidopteran abundance (moths), coleopteran abundance (beetles), hymenopteran abundance (wasps, bees and ants), dipteran abundance (flies and mosquitoes), and hemipteran abundance (true bugs) (Table 5). Ridge top communities contained a higher mean abundance of insects and lepidopterans than riparian communities (Table 5). Mid-slope communities were not different than ridge top or riparian communities (Table 5). There was no difference between the ridge top and mid-slope samples (Table 5). There was no difference among ridge top, mid-slope, and riparian communities in number of arthropod orders, coleopteran abundance, hymenopteran abundance, dipteran abundance, or hemipteran abundance (Table 1).

Data for all years of sampling (2015, 2016, and 2017) were compared using ANOVAs. Seven separate tests were ran for each metrics of insect presence: total abundance of insects, number of arthropod orders, lepidopteran abundance, coleopteran abundance, hymenopteran abundance, dipteran abundance, and hemipteran abundance (Table 6). The number of arthropod orders collected was significantly different between 2015 and 2017 (Table 2), with the mean number of orders in 2015 being higher than in 2017. The outcome was potentially influenced by sampling effort. Most of the additional orders collected were incidental and sporadic observations, and would have likely been detected in a more intensive survey in 2017. There was no difference in the number of orders collected between 2016 and 2015, or 2016 and 2017. No difference was found between 2015, 2016, and 2017 in the total abundance of insects, lepidopteran abundance, coleopteran abundance, hymenopteran abundance, dipteran abundance, or hemipteran abundance (Table 6). Variation among sites (Beech, Kentucky Ridge, Laurel Ridge) was compared using seven different metrics of insect presence with no difference observed for any metric evaluated (Table 7).

The harvest treatment type (unharvested, shelterwood, and patch cut) was evaluated using seven separate ANOVA tests on the total abundance of insects, number of arthropod orders, lepidopteran abundance, coleopteran abundance, hymenopteran abundance, dipteran abundance, and hemipteran abundance (Table 8). The mean number of lepidopterans collected was lower at shelterwood and patch cut stands than unharvested stands (Table 8). There was no difference between shelterwood and patch cut stands (Table 8). No difference was found among treatment type in total abundance of insects, number of arthropod orders, coleopteran abundance, hymenopteran abundance, dipteran abundance, or hemipteran abundance (Table 8).

Table 5. Effects of slope position on insect diversity and abundance (# per trap night) at three sites: Laurel Ridge, Clayhole, KY; Beech tract, Oakdale, KY; and Kentucky Ridge State Forest, Chenoa, KY.

Parameter	Ridgetop	Mid-slope	Riparian	df	F	p-value
	Mean SE	Mean SE	Mean SE	x, y		
Total Abundance	701^{ab}, 152	386^{ab}, 76.3	259^{b}, 40	2, 20	4.68	0.0215
Number of Orders	6.25, 0.366	6, 0.535	6.42, 0.896	2, 20	0.122	0.886
Lepidoptera	546^{a}, 106	315^{ab}, 69.9	196^{b}, 37.7	2, 20	4.98	0.0176
Coleoptera	130, 16.8	47.8, 86.4	36.4, 8.38	2, 20	0.932	0.410
Hymenoptera	10.1, 2.11	9.5, 2.62	8.57, 2.26	2, 20	0.107	0.899
Diptera	4.5, 1.32	3.63, 0.730	2.71, 1.57	2, 20	0.515	0.605
Hemiptera	6, 2.79	7.25, 4.19	4.71, 1.46	2, 20	0.159	0.854

^{a,b} Within rows, means without common letters are groups with statistical difference.

Table 6. Effects of year on control samples of insect diversity and abundance (# per trap night) at three sites: Laurel Ridge, Clayhole, KY; Beech Tract, Oakdale, KY; and Kentucky Ridge State Forest, Chenoa, KY.

Parameter	2015	2016	2017	df	F	p-value
	Mean SE	Mean SE	Mean SE	x, y		
Total Abundance	386, 76.3	386, 42.5	516, 97.5	2, 58	1.13	0.330
Number of Orders	6^{a}, 0.535	6.58^{ab}, 0.222	4.8^{b}, 0.414	2, 58	8.56	0.0005
Lepidoptera	315, 69.9	294, 33.4	456, 84.8	2, 58	2.32	0.107
Coleoptera	47.8, 16.8	68.6, 12.4	38.3, 9.39	2, 58	1.66	0.199
Hymenoptera	9.5, 2.62	7.52, 1.01	13.2, 4.61	2, 58	1.2	0.308
Diptera	3.63, 0.730	5.61, 0.982	4.7, 2.55	2, 58	0.238	0.789
Hemiptera	7.25, 4.19	3.61, 1.4	2.85, 1.05	2, 58	0.954	0.391

^{a,b} Within rows, means without common letters are groups with statistical difference.

Table 7. Site differences in light trap sampling for insect diversity and abundance (# per trap night) at three sites: Laurel Ridge, Clayhole, KY: Beech tract, Oakdale, KY; and Kentucky Ridge State Forest, Chenoa, KY.

Parameter	Beech	Kentucky Ridge	Laurel Ridge	df	F	p-value
	Mean SE	Mean SE	Mean SE	x, y		
Total Abundance	443, 97.8	409, 42.9	470, 69.2	2, 73	0.266	0.767
Number of Orders	5.77, 0.323	6.53, 0.283	5.61, 0.331	2, 73	2.6	0.0813
Lepidoptera	317, 53.8	333, 35.3	393, 62	2, 73	0.523	0.595
Coleoptera	111, 53.1	51.1, 9.92	52.5, 10.9	2, 73	2.12	0.128
Hymenoptera	5.92, 0.902	7.8, 1.04	12.6, 2.88	2, 73	2.14	0.125
Diptera	2.39, 0.549	5.5, 1.04	5.06, 1.60	2, 73	0.916	0.405
Hemiptera	3.15, 1.04	4.8, 1.41	3.94, 1.45	2, 73	0.239	0.788

[a,b] Within rows, means without common letters are groups with statistical difference.

Table 8. Effects of harvest treatment on insect diversity and abundance (# per trap night) at two sites, Beech Tract, Oakdale, KY, and Kentucky Ridge State Forest, Chenoa, KY.

Parameter	Control	Patch Cut	Shelterwood	df	F	p-value
	Mean SE	Mean SE	Mean SE	x, y		
Total Abundance	392, 58.5	303, 70.6	237, 49.2	2, 43	1.58	0.218
Number of Orders	5.39, 0.311	5.31, 0.395	5.24, 0.474	2, 43	0.0314	0.969
Lepidoptera	342[a], 56	171[b], 34.8	137[b], 28.9	2, 43	7.29	0.0019
Coleoptera	36.9, 8.8	119, 49	88.5, 33.1	2, 43	1.19	0.315
Hymenoptera	5.46, 0.867	4.94, 1.09	4.88, 1.46	2, 43	0.0626	0.939
Diptera	2.92, 0.645	3.75, 1.23	2.29, 0.731	2, 43	0.655	0.525
Hemiptera	2.15, 1.06	0.875, 0.301	1.18, 0.346	2, 43	1.17	0.32

[a,b] Within rows, means without common letters are groups with statistical difference.

Mist Net Sampling

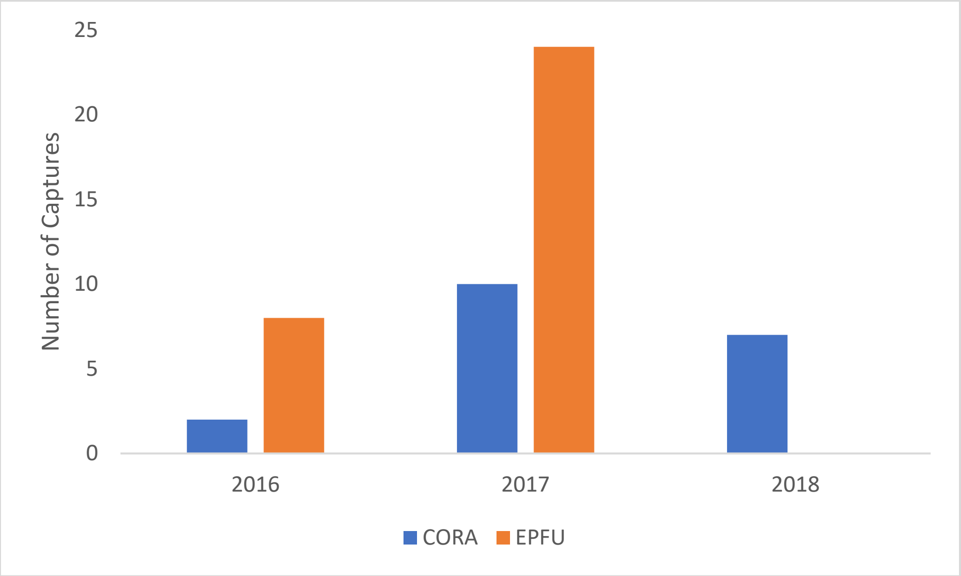
The camp at Robinson Forest has several maternity colonies of bats. A maternity colony of big brown bats numbering around 100 individuals roosted within the attics in two separate cabins. The office had a small bachelor colony of big brown bats, along with a small bachelor colony of Rafinesque big-eared bats, and a small maternity colony of Rafinesque big-eared bats. These groups live within different spaces within the structure and often emerge from different entrances. Both maternity colonies successfully rear young on a yearly basis.

Mist netting efforts at Robinson Forest resulted in the capture of 36 northern long-eared and one Indiana bat from 2016 through 2017 (Figure 19). Most northern long-eared bats were captured in 2.6 m nets over closed canopy ridge top roads. Sixteen northern long-eared bats (10 females, 4 males, and 2 juveniles) and one lactating female Indiana bat were radio-tagged and tracked. Ten northern long-eared bats (8 females, 2 males) were successfully tracked to day-roosts. The Indiana bat was not located despite use of a Cessna 172 plane being flown over the site in a 19.3-km radius. Other species captured, included adult male, female, and juvenile eastern red bats and big brown bats. I also captured two male silver-haired bats and one Rafinesque big-eared bat.

Two additional northern long-eared bats were captured during 2018 after the forest was harvested. One juvenile northern long-eared bat was captured adjacent to the shelterwood harvest on a ridge top road. Adult male, female, and juvenile eastern red bats and big brown bats were captured within the harvest treatments. A post-lactating female and a juvenile tri-colored bat were also captured in the riparian area adjacent to the shelterwood harvest.

Netting efforts at the Beech site resulted in the capture of eastern red bats, big brown bats, and tri-colored bats. Adult male, female, and juvenile eastern red bats, big brown bats, and tri-colored bats were captured within the openings of the patch cut harvest area.

a.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CORA
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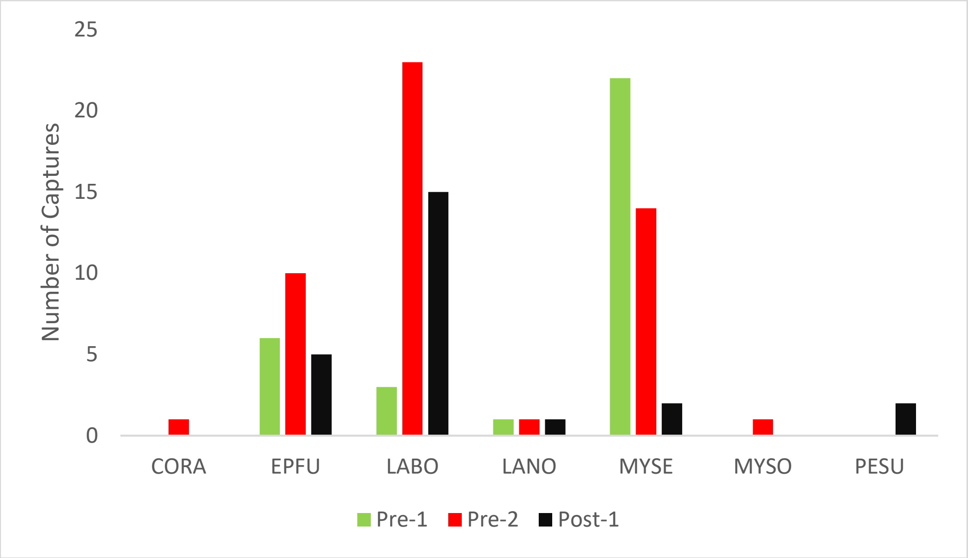
b.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Post-1

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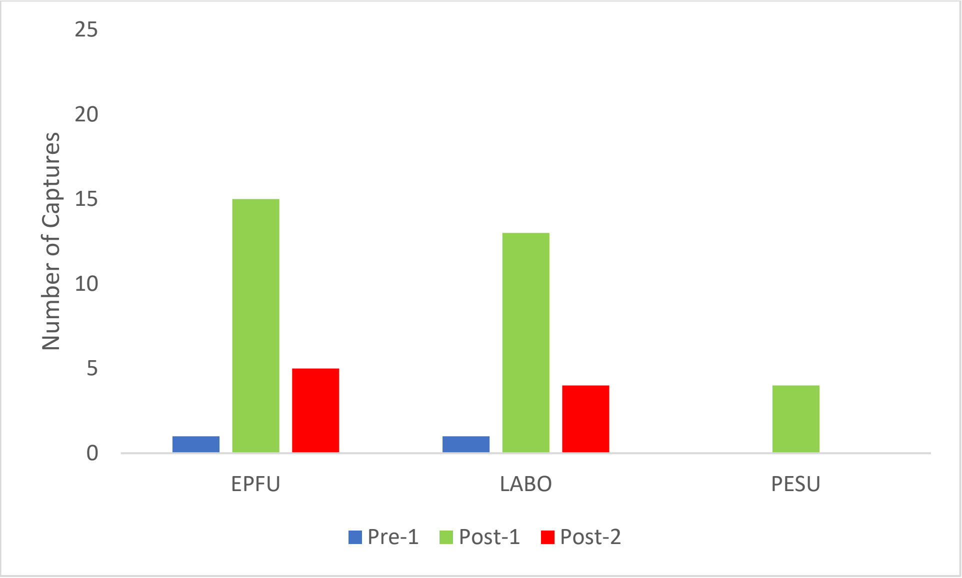

Figure 19. Results of bats captured during mist netting efforts. (a) Bats captured during mist netting efforts at Robinson Forest's camp. (b) Bats captured during surveys on Robinson Forest. (c) Bats captured during surveys on the Beech tract. (Blue (2015), Green (2016), Red (2017), and Black (2018).

Radio Tracking and Roost Trees

Sixteen individual northern long-eared bats had a radio-tag attached: males (4), females (10), and juveniles (2). Females (8) and males (2) were tracked to 20 different day roosts. Bats roosted in a five tree species: red maple (*Acer rubrum*), scarlet oak (*Quercus coccinea*), pitch pine (*Pinus rigida*), black oak (*Q. velutina*), tulip poplar (*Liriodendron tulipifera*), and an unidentified snag (Table 9). Based upon random tree plots red maple was the most prominent tree species for roosting in the forest and occurred in various conditions from dead with peeling bark, declining trees with cavities, and live trees with small cavities (Table 10).

All roosts were within 100 m of a ridge top road (Figure 20), suggesting these bats preferentially chose roosts in the vicinity of forested flight corridors. Exit counts varied across the season. In early May, before pregnancy was detected individuals often roosted solitarily in small cavities large enough for only a single individual, within shaded areas of the forest with minimum solar exposure. At late-stage pregnancy and early lactation, adult females switched roosting preferences. Individuals clustered together in cavities or under bark in trees with reduced amounts of canopy cover. Trees occupied during this time had larger diameters and were predominately sub-canopy stems. Maximum group sizes of bats and consistent fission- fusion behavior was observed. As pups became closer to volancy, the size of the maternity colonies decreased although the type of roost did not change. Once pups became volant females chose roosts with reduced canopy cover and fewer surrounding trees. Roost switching was minimal, with females staying at the same site for several days in a row. Roost counts post-volancy were often of two individuals. In one case, a bat which was not radio-tagged was often a weak flyer and observed gliding out of the roost. Several times it was observed falling to the ground and the radio-tagged female would search the area to retrieve it. The trend lasted for a week or so. Females captured beyond this time roosted in a variety of roosts and seemed to be less selective. Males also displayed less selective behavior in roost choice. In late summer, bats roosted in a variety of structures including knotholes, peeling park, and small cavities. Individuals continued to roost near flyways. There were insufficient data to form an idea on their choice of canopy cover.

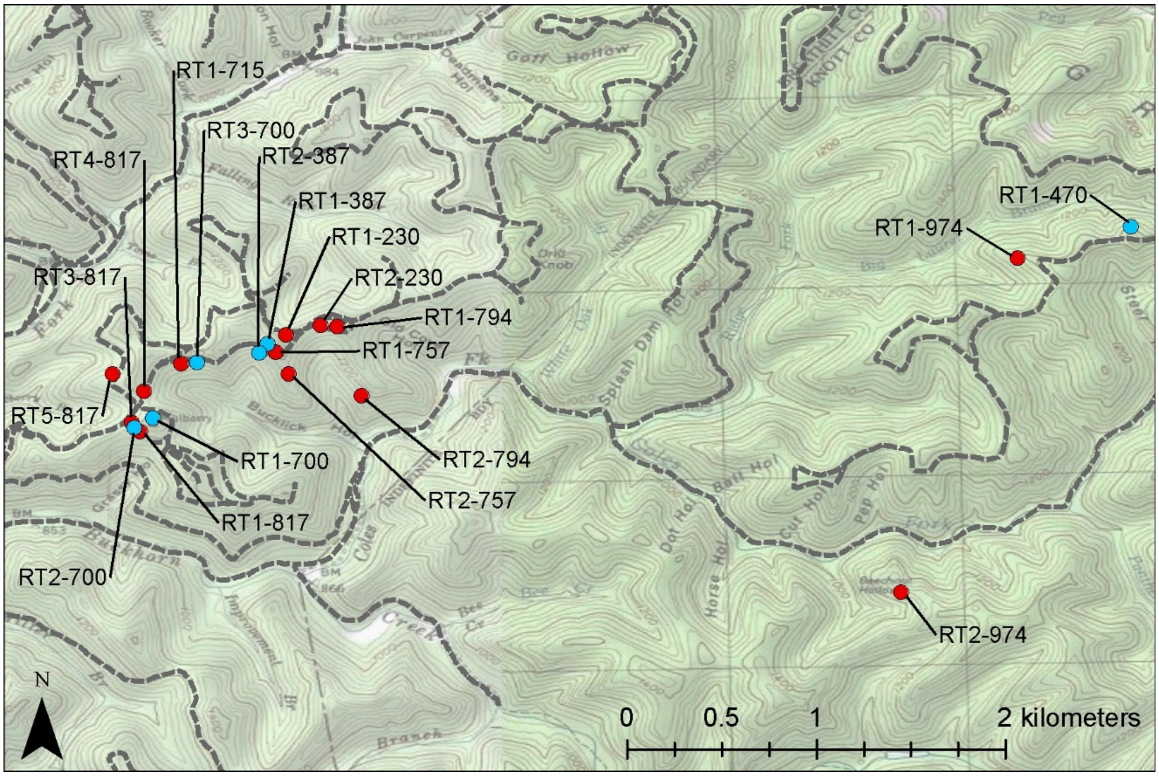

Figure 20. Roost trees located at Robinson Forest during tracking efforts from 2016-2017. Red dots are maternity roosts used by pregnant or lactating females. Blue dots are roost trees used by bats. The grey dotted line is the maintained closed canopy forest road. RT2-794 and RT2-974 both have non-maintained roosts within close proximity to the roosts which are not shown on the map because they are not mapped or maintained.

Table 9. Roost trees and emergence counts of located northern long-eared bats, Robinson Forest, KY.

Roost Tree	Sex	Reproductive Status	Species	Dbh (inch)	Roost Character	Snag Class	Emergence Count	Date
RT1-817	Female	Pregnant	Scarlet Oak	10.6	Under Bark	5	13	5/25/16
RT3-817	Female	Pregnant	Scarlet Oak	22.1	Dead Limb	1	4	5/27/16
RT4-817	Female	Pregnant	Red Maple	4.1	Cavity	1	1	5/28/16
RT5-817	Female	Pregnant	Red Maple	6.1	Cavity	4	24	5/29/16
RT1-974	Female	Lactating	Scarlet Oak	4.5	Under Bark	4	3	7/17/16
RT2-974	Female	Lactating	Scarlet Oak	10.1	Cavity	2	2	7/19/16
							2	7/20/16
							2	7/21/16
							2	7/23/16
RT1-470	Female	Post-lactating	Red Maple	2.1	Cavity	1	1	8/5/16
RT1-700	Female	Pregnant	Snag	11.6	Cavity	5	1	5/11/17
RT2-700	Female	Pregnant	Red Maple	4.5	Cavity	2	0	5/13/17
RT3-700	Female	Pregnant	Red Maple	2.6	Cavity	1	1	5/15/17
RT1-230	Female	Lactating	Tulip Poplar	21.1	Under Bark	4	3	6/7/17
RT2-230	Female	Lactating	Scarlet Oak	17.1	Under Bark	4	2	6/8/17
RT1-715	Female	Lactating	Black Oak	10.2	Under Bark	4	8	6/7/17
							13	6/8/17
							15	6/9/17
							21	6/10/17
RT1-757	Female	Lactating	Scarlet Oak	6.1	Under Bark	4	-	6/17/17
RT2-757	Female	Lactating	Scarlet Oak	26.5	Under Bark	4	7	6/18/17
							3	6/20/17
RT1-387	Male	Non-reproductive	Red Maple	4.2	Dead Limb	1	0	6/18/17
RT2-387	Male	Non-reproductive	Scarlet Oak	9.9	Under Bark	4	1	6/19/17
RT1-794	Female	Lactating	Red Maple	1.6	Cavity	4	1 (carrying pup)	6/25/17
RT2-794	Female	Lactating	Pitch Pine	7.8	Under Bark	4	2	6/28/17
							2	6/29/17

Table 10. Potential roost trees (snags and cavities) present within tree plots at Robinson Forest in Eastern Kentucky.

Species	**Number**	**Roosts Used by MYSE**
Red Maple	57	7
Scarlet Oak	30	7
Sourwood	21	0
Chestnut Oak	16	0
Black Oak	8	1
Downy Serviceberry	6	0
Black Gum	5	0
White Oak	4	0
Sugar Maple	4	0
Tulip Poplar	4	1
Cucumber Magnolia	3	0
Red Oak	3	0
Pitch Pine	2	1

Discussion

The difference in activity patterns among species pre-harvest was likely due to the differences in forest structure across landscapes at the three sites. The Beech tract was a 40-ha forest adjacent to seed tree harvests which left a lower, undetermined basal area. The Beech tract provided excellent habitat for open space foragers before it was harvested which explains why it had statistically higher numbers of silver-haired bat calls than the other sites. To access the tract, bats were required to fly through the surrounding harvest. The risk of predation could have acted as deterrent for smaller bat species to forage within the harvest (Swystun *et al.,* 2001). Kentucky Ridge was a mosaic with a variety of features from farmlands, active roads, and tracts of intact forest. The well trafficked road could have acted as a barrier to some species (Bennett *et al.,* 2013). Robinson Forest is largely an intact interior forest with various harvests interspersed throughout. These areas are connected by a series of dirt roads along the ridgetops and streams. Robinson Forest's extensive road system within an interior forest likely provided suitable habitat for several species, especially the northern long-eared bat.

Pre-harvest data showed higher activity at ridge top and riparian areas than mid-slope areas. The difference in activity was due to streams and ridge top roads functioning as flyways (Menzel *et al.,* 2002; Caldwell *et al.,* 2019). The structural complexity and degree of clutter varied among sampling locations in pre-harvest sampling. Eastern Kentucky is a mixed mesophytic forest with a large variety of tree species and habitats. Most ridge top points were placed along roads or trails; however, some points were not and were instead in interior forest locations. A ridge top sampling location at Kentucky Ridge was a hemlock-rhododendron forest while another in Laurel Ridge was a closed canopy road. Mid-slope sites had varying degree of clutter ranging from thickets of rhododendron to mostly open forest. Riparian corridors varied widely in size. Streams ranged from first to third order. Stream width affects canopy closure which determines aerial flight space throughout the flight corridor. Size of flight corridors have been shown to influence bat species presence and levels of activity (O'Keefe *et al.,* 2013). This variation among sampling locations at the same slope position resulted in some areas not producing pre-harvest calls which limited the power of the statistical models.

Both Beech and Kentucky Ridge tracts had an increase in bat activity post-harvest. Shelterwood harvests and patch cuts had higher activity than the unharvested control stand and the pre-harvest data. Increases in bat activity after forests have been thinned or logged occurred in other studies (Titchenell *et al.,* 2011; O'Keefe *et al.,* 2013; Silvis *et al.,* 2016). Activity increased by over an order of magnitude at both sites, and within both treatments. Most of this activity can be attributed to big brown bats for the Beech and Kentucky Ridge tracts. Large numbers of calls from silver haired bats occurred within the forest harvests and it is possible these bats increased in activity within forest harvests. These bats are open-space foragers which take advantage of the newly created space for foraging. Eastern red bats also increased in activity at both sites post-harvest and were the second biggest contributor to the increase in activity. It appears eastern red bats behaved as generalists that were active in both harvests and interior forests. Evening bats increased in activity at the Beech tract post-harvest. However, there was no significant increase in activity at the Kentucky Ridge tract. Hoary bats had a mixed response to harvests; however, sampling units were placed at 1.5 m in height and likely missed some calls of these bats. Microphones placed higher or in open space may have detected more activity. Brigham *et al.,* (1997) found that hoary bats foraged well above the canopy. I had predicted hoary bats should have increased in activity because they are open-space foragers with high aspect ratios and high wing loadings (Lacki *et al.,* 2007). Also, Owen *et al.* 2004 found an increase in hoary bat activity post-harvest.

Unharvested sections in both the Beech and Kentucky Ridge tracts saw the highest activity levels in the riparian areas post-harvest. Other harvest projects have seen high levels of activity within riparian areas near harvests (O'Keefe *et al.,* 2013; Caldwell *et al.,* 2019). Riparian zones likely continue to act as flyways, especially for clutter-adapted species traversing through the harvests. The ridgetop at Kentucky Ridge saw a large increase in activity post-harvest. The activity was likely bats commuting along the ridgetop road to the forest harvests. The shelterwood harvests in both sites had the highest activity on the ridgetop and the lowest activity in the riparian area. The mid-slope in the Beech tract shelterwood had statistically similar activity to the ridgetop, while the mid-slope in the Kentucky Ridge tract was statistically similar to the riparian area in bat activity. The variation in responses was likely due to structural differences between sites. Loggers complied with FSC® standards for Best Management Practices (BMPs) and Streamside Management Zones (SMZs) across all study sites (FSC-US 2010). Complying with these standards left Kentucky Ridge with larger patches of vegetation in the shelterwood harvest than the Beech tract due to slope condition and the size of the streams within the harvest. The structural similarity between all patch cuts likely explains the uniform response seen across sites and slope positions.

Barclay (1999) eloquently explained that echolocation is a tool for bats to navigate across the landscape and capture prey, and is not intended to necessarily convey species specific information. Call output from all acoustic software packages, including Kaleidoscope, is based on probabilities, and calls of similar species can be misclassified, especially poor-quality calls (Murray *et al.,* 2001; Russo *et al.,* 2017). Thus, some level of misidentifications is assumed to have occurred within the dataset and the possibility of misclassification influences my interpretation of data patterns and test outcomes with the acoustic analyses presented.

Silver-haired bats are migratory, with subadult males being summer residents in Kentucky (Perry *et al.,* 2010). However, KDFWR has recently seen increased numbers of male silver-haired bats captured in Kentucky (T. Wethington, KDFWR, unpublished data). I captured two different silver-haired bats during my netting efforts, and both captures were males with large numbers of mites. A higher number of big brown bats were captured within forest harvests. On two different occasions over ten different individuals were captured in a single night. Kaleidoscope and other acoustic software programs often misclassify big-brown bat calls as silver-haired bats (Humboldt State University, 2011). The low number of captured individuals and potential for misclassification of calls suggests patterns seen for silver-haired bat activity could be influenced by the large number of big brown bats present within the harvests.

My netting efforts did not result in the capture of an evening bat, and while my netting efforts were not extensive, the data suggests they are not a prevalent species within my study site. Netting resulted in the capture of a large number of red bats which have a similar call to evening bats (Humboldt State University, 2011). Red bat calls could have impacted trends detected for evening bats. However, it is also possible this species has moved into the area, and future work should include netting data to validate species presence. Evening bat is currently expanding its range, including in Kentucky, and is becoming a common species in forested areas once dominated by *Myotis* (Thalken et al., 2018a).

Little brown bats are present in the region but were not captured historically during surveys at Robinson Forest nor were they detected during my netting efforts (Krupa and Lacki, 2002). However, these bats are historically present in these counties (T. Wethington, KDFWR, unpublished data). These bats tend to prefer riparian areas and could be present along the large streams just outside of the forest, or along the larger streams within the forest. My netting efforts focused on ridgetops and it is possible I did not net extensively enough to capture the sparse individuals present. Little brown bat calls overlap in characteristics with Indiana bat calls, and share similarities with calls of northern long-eared bats (Humboldt State University, 2011). Little brown bats have suffered tremendous declines in Appalachia and the Midwest and are now rare throughout the region (Dzal *et al.,* 2011; Thogmartin *et al.,* 2012). Indiana bats have also suffered declines across the Appalachia recovery unit, but historically were not a common species (USFWS, 2019). Netting efforts revealed Indiana bats were present on the site; however, their captures were infrequent compared to northern long-eared bat. Northern long-eared bat was the second most captured species on Robinson Forest. The species continues to decline but remnant populations remain in a few counties in Kentucky, West Virginia, and eastern Ohio (Reynolds *et al.*, 2016, Cruz *et al.*, 2018). Trends seen for Indiana and little brown bats could be influenced by misclassification of northern long-eared bat calls.

Rafinesque big-eared bats are hard to detect with acoustic surveys and will not be discussed (Hurst and Lacki, 1999). Detections were limited even within Robinson Forest where two known maternity colonies are present.

Tri-colored bats increased their levels of activity in forest harvests. I only captured tri-colored bats in harvested areas during my study. Granted I seldom mist netted streams or water sources. Studies showed tri-colored bats in Western Kentucky roosted within 2.5 km of their original capture location (Schaefer, 2017). Tri-colored bats have relatively small movements, travelling 300 - 5000 m from a capture location (Veilleux *et al.,* 2001; Leput, 2004; Quinn and Broders, 2007); roost between 25 to 186 m from edge habitat (Veilleux, 2001; Veilleux *et al.,* 2003; Leput, 2004, Veilleux *et al.,* 2004; O'Keefe, 2009); and, roost between 34 - 212 m from water sources (Veilleux, 2001; Veilleux *et al.,* 2003; Leput, 2004; Poissant *et al.,* 2010). Their small home ranges and movements, along with the capture of several life stages, suggests they are actively choosing to forage and possible roost within harvested areas.

Myotis activity did not increase within forest harvests. Other studies have found closed-spaced foragers avoid foraging in harvests (Owen *et al.,* 2003; Patriquin and Barclay, 2003; Henderson and Broders, 2008; Titchenell *et al.,* 2011; Cadwell *et al.,* 2019). Several factors likely contribute to *Myotis* not foraging extensively within the harvest treatments. Lepidopterans, a favorite prey of these bats, decreased in number in response to cuts, suggesting reduced prey availability (Table 3, 4). Myotis bats may experience an increase in competition from big brown bats and eastern red bats, which increase their feeding activity in areas post-harvest for the available prey (Table 3, 4) Silvicultural practices, patch cuts and shelterwood harvests, both remove sub-canopy clutter. Sub-canopy clutter has been correlated to Myotis activity in other studies (Dodd *et al.,* 2012). White-nose syndrome has severely affected Myotis populations, especially those of northern long-eared bat, little brown bat, and Indiana bat (Dzal *e et al.*, 2011; Thogmartin *et al.,* 2012; Thomas and Toomey, 2017; Thalken *et al.,* 2018b). In a post-WNS world, interior forests in eastern North America are likely not at carrying capacity for closed-space foraging bat species. Given that prey are equally or more abundant than within unharvested areas (Table 8), and competition is now likely reduced within interior forest ecosystems, surviving Myotis bats may choose to occupy forested habitat to avoid competition and have increased access to prey. Variation in response to forest harvesting by tri-colored bats and Myotis bats has been documented across several studies (Yates and Muzika, 2006; Amelon, 2007; Womack *et al.,* 2013; Starbuck *et al.,* 2015). These differences may be attributed to the different level of competition present at each study area.

My study filled a research gap and provides replication across multiple areas with species-level resolution based upon acoustic and netting data (Menzel *et al.,* 2002; Adams *et al.,* 2009; Jung *et al.,* 2012; O'Keefe *et al.,* 2013; Silvis *et al.,* 2016). Captures of northern long-eared bats at Robinson Forest, post-white-nose syndrome, provide evidence for a relict population of these bats. The lack of activity of these bats in harvests, however, suggests they do not actively forage within cuts.

My study could be improved upon with additional replication and long-term data at each study area. Landscape features such as stream size and surrounding features such as forest harvests should be included within replicates. It is likely that larger riparian zones might help maintain activity of interior species if they are adjacent to interior forest. Detectors left out across an entire season might help discern how activity changes throughout the night, reproductive period, and seasons.

Forest harvesting temporarily impacts foraging habitat of northern long-eared bats; however, once the site regenerates the heavily compacted skid trails and harvest roads do not re-grow trees. These trails stay open and become surrounded by closed canopy forest. These areas become long-term flyways within the forest which are heavily trafficked by many bat species, especially *Myotis* (Menzel *et al.,* 2002; Caldwell *et al.,* 2019). All captures of northern long-eared bats occurred on these roads. Eastern red bats, big brown bats, and a Rafinesque big-eared bat were also captured along roads. The northern long-eared bats also preferred to roost on ridge tops near these flyways. Other studies have shown northern long-eared bats prefer ridge top roosting positions (Thalken *et al.,* 2018b; Thalken and Lacki, 2018; Cruz *et al.,* 2018).

The capture of juvenile northern long-eared bats within 50 m of the shelterwood harvest at the Laurel Ridge tract suggests the species uses the area for reproduction, at least to some extent. Forest harvests may take some potential roost trees, both primary and secondary, but northern long-eared bats will continue using a harvested site (Silvis *et al.,* 2015).

It is unknown if northern long-eared bats use torpor in the same manner as Indiana bat and little brown bat. Summer colony sizes of northern long-eared bats are smaller on average than those of Indiana bat and little brown bat and can occur in interior forest locations which do not have as high a solar exposure. Average sizes of northern long-eared bat colonies were historically larger than seen in my study (Sasse and Pekins, 1996 [n = 36]; Foster and Kurta, 1999 [n = 60]; Menzel *et al*., 2002 [n = 65]; Lacki *et al.*, 2009 [n = 56]). However, these are far smaller than that of little brown bat or Indiana bat colonies which commonly range into the hundreds. Further, Lacki and Schwierjohann (2001) found sizes in Eastern Kentucky to average 25.3 ± 10.2 bats during the pregnancy period, which is similar to the colony sizes recorded in my study. These differences suggest the species may use torpor more frequently or enter deeper torpor than little brown bat or Indiana bat to conserve energy and, thus, do not need to be as gregarious or select warmer roosts. Their behavior patterns likely explain their historically large numbers in interior forests. However, unlike Indiana bat and little brown bat this may require a species to seek out a variety of roosting microclimates to meet their shifting energetic needs throughout the summer season. An interesting example of this can be seen by the switching of a colony of northern long-eared bats from tree roosts to a barn during pregnancy and lactation (Henderson and Broders, 2008).

Northern long-eared bats choose to roost in different microclimates and in different numbers throughout the season. Their behavior can be grouped into five distinct phrases. First, use of small shaded cavity roosts during early pregnancy that permit females to engage in torpor bouts to conserve energy, which also slows the development of offspring and allows pregnant females to replenish lost fat reserves from winter hibernation. Second, during late-stage pregnancy and early lactation females switch roosts, with individuals clustering together in cavities or under bark in trees with low canopy cover. Trees used are predominately sub-canopy stems with peeling bark or cavities. During this time, females cluster to conserve heat and likely limit torpor use, with the clustering behavior likely facilitating faster growth of young. Third, the same types of trees are selected for in mid to late-lactation. However, the colony counts are smaller as females reduce colony size, possibly to minimize parasite loads and predation risks. As the young are now larger, it is likely that less body heat is required to maintain growth of non-volant young. Fourth, once pups become volant, females choose roosts with low canopy cover and few surrounding trees. Roost switching is minimal with a female staying at the same site for several days in a row. Females choose roosts in areas of reduced clutter perhaps to minimize flight collisions. The splintering of the colonies also reduces predation risk to vulnerable young who are learning to fly and are easy targets. Fifth, females captured after young become fully volant roost in a variety of structures and are less selective. During this time bats roost in a variety of micro-sites including knotholes, peeling park, and small cavities, and frequently switch roosting sites likely to select micro-climates suitable for minimizing energy expenditure and utilizing torpor to restore lost fat reserves for hibernation. Adult males displayed the fifth stage behavior throughout the season.

A variety of roosting patterns of northern long-eared bats has been seen in other studies. Lacki and Schwierjohann (2001) saw variation in colony size across reproductive conditions. The largest numbers were during pregnancy and decreased throughout lactation. Thalken (2018) and Garroway and Broders (2008) found differences in roosts between reproductive classes of northern long-eared bats. Other studies have shown big brown bat, western long-eared bat (*Myotis evotis*), and little brown bat change roosts to facilitate use of a different torpor strategy (Dzal and Brigham, 2013; Chruszcz and Barclay, 2002; Lausen and Barclay, 2003).

Data suggest that bat species actively decide whether or not to engage in torpor use based upon their energetic needs and that of their young. The smaller roost counts toward the end of the maternity season for many tree-roosting species suggest that bats balance risks based on energetic needs, access to available food sources, and predation risk.

Prior to white-nose syndrome, tri-colored bat and northern long-eared bat were common species in forested landscapes of eastern North America. Their populations have dramatically declined throughout their distributions (Francl *et al.,* 2012). Despite severe declines, however, some regional populations appear to be stabilizing (Dobony and Johnson, 2018; Frank *et al.,* 2019). Northern long-eared bat populations have persisted across multiple seasons of possible exposure to white-nose syndrome (Cruz *et al.,* 2018). As more impacted populations of northern long-eared bat become extirpated, remaining populations will become increasingly important to the survival of the species. The population within Central-Appalachia could become critical for the survival of the species, as some of these bats may adopt unknown hibernation locations and strategies that allow them to survive the harsh winter without succumbing to WNS. Based on my data, silvicultural management of forests can be done in a way which is consistent with providing habitat for surviving northern long-eared bats.

Research is beginning to suggest that surviving individuals are relying on alternative hibernation strategies such as hibernating in basements, tree cavities, culverts, and other locations which do not allow for the growth of the fungus. The population found in the coastal plains of North and South Carolina is one example of alternative hibernation strategies. Northern long-eared bats which live there are active year-round and continue to use tree roosts throughout winter and, thus, are not susceptible to WNS (Jordan, 2020). Individuals are also behaviorally adapting to the fungus. Individuals are storing more body fat to survive the arousals caused by the fungus (Lacki *et al*., 2015). Winter habitat that facilitates successful hibernation is a limiting factor in the recovery of many species, including the northern long-eared bat and tri-colored bat. Forest harvests also provide valuable habitat to bats within Appalachia. Big brown bat, eastern red bat, hoary bat, and tri-colored bat use these areas for foraging. Northern long-eared bats and possible tri-colored bats appear to roost within or near these harvests. Thus, patch cuts and shelterwood harvests may be valuable tools to promote successful reproduction in bat species that use harvested areas during summer months.

Management Recommendations

Shelterwood harvests and patch cuts improve habitat quality for red, big brown, and tri-colored bats. Immediately after harvests, *Myotis* did not increase activity in patch cuts or shelterwood harvests in my study. However, I believe harvests can provide essential habitat. The skid trails and harvest roads that allow harvested trees to be extracted often become heavily compacted and limit future tree growth in the corridor. Once the surrounding trees re-grow, these closed canopy spaces become semi-permanent flyways within the forest which are heavily trafficked by many bat species, including *Myotis* (O'Keefe *et al.,* 2013; Silvis *et al.,* 2016; Ketzler *et al.,* 2018). My study supports these observations. Myotis calls on Laurel Ridge occurred frequently on detectors placed along the roads. All of the northern long-eared bats I captured were on these ridgetop roads. The roost trees I located were within 100 m of the road. Other studies have also found northern long-eared bats to prefer roosting on ridgetops. Cruz *et. al* (2018) found that northern long-eared bats commonly roost within rocket boxes placed within forest harvests for utility lines within Appalachia. These populations return annually and successfully rear young. Unless harvests become a pervasive landscape issue, I believe they do not negatively affect the presence of northern long-eared bats.

When planning harvests, unharvested sections should be retained near or adjacent to shelterwood harvests or patch cuts. These areas provide foraging space to Myotis species and limit foraging competition with big brown bat, hoary bat, and eastern red bat. I recommend placing permanent small, unpaved dirt roads along ridgetops for long-term roosting potential for northern long-eared bats. These roads function as flight corridors and the dead trees adjacent to the road provide roosting habitat. These roads should be designed to have increased canopy closure as the site develops post-harvest. Maximizing connections between roads on different ridges to create a flyway matrix would be ideal. This matrix should allow for bats to travel and feed throughout the forest landscape. Any snag or tree with a cavity next to ridge top roads should be surveyed for bat use before it is cleared as these trees are likely to be potential roosting habitat. Natural roosts should also be sustained through active management such as retaining snags during harvests, especially those on forest edges and along roads. If need be, these natural roosts can be supplemented with rocket boxes placed within different microclimates on the landscape.

Forest harvests create openings in the forest providing foraging habitat for open-space foragers such as big brown bat and generalists such as the eastern red bat. Although eastern red bat, big brown bat, and hoary bat are currently common species in forested landscapes, management may be necessary for these species in the future. Prior to white-nose syndrome, little brown bats, tri-colored bats, and northern long-eared bats were common species in many areas (U.S. Department of the Interior, 2015). These formerly common species are clearly in need of conservation now and in the future. Hoary bat and eastern red bat are currently being killed in large numbers at wind turbines during migration (Kunz *et al.,* 2007). These impacts are likely to result in population level changes to these species as well.

Permits

All animal handling procedures used were approved by the University of Kentucky under IACUC Assurance No.: A3336-01. Data collection was supported through permits from the Kentucky Department of Fish and Wildlife Resources (SC1511245; SC1611176; SC171115; SC1811148) and the U.S. Fish and Wildlife Service (TE38522A-1).

Appendix I

Insect Analysis

```
#ANOVA
Detect <-lm(Count ~ Treatment,data = KR)
anova(Detect)
summary(Detect)
```

Quasi-Poisson Analysis

```
#Sorting Call Data
Pulses <- read.csv("C:/Users/PHILLIP/Desktop/Zeros Added Master.csv")

#Filter out poor quality call data for accurarcy
Filtered <- Pulses %>% filter(PULSES >= 4)
Filtered <- Filtered %>% filter(Qual <= 10)
Filtered <- Filtered %>% filter(MARGIN >= 0.3)

#Summarize data
Count <- count(Pulses, c("AUTO.ID","SITE","DATE.12","YEAR","Treatment", "Position","LOCATION"))
agg.sum <- aggregate(formula= freq ~ DATE.12 + Position + SITE + AUTO.ID + LOCATION + YEAR + Treatment, data= Count, FUN=sum)
write.csv(agg.sum, file = 'C:/Users/PHILLIP/Desktop/Filter Count.csv')

#View data and run Poisson
p <- ggplot(aes(x = Treatment, y = freq), data = Pulses)
p + geom_boxplot() + facet_wrap(~ Treatment)
Pulse <-glm(freq ~ Treatment,data = Pulses, family = 'poisson')

# Check for overdispersion
# First is probably best as it can take variables into account
deviance(Pulse)/df.residual(Pulse)
# Another way, seems similar and gives more info
qcc.overdispersion.test(Pulses$Abundance, type = 'poisson')

# Quasipoisson adjusts standard errors based on the amount of overdispersion
# Estimates will stay the same but SEs will be larger
```

```
Pulses2 <-glm(freq ~ Treatment,data = Pulses, family = 'quasipoisson')
summary(Pulses2)

# Pull out means and SEs
str(Pulses2)
newdata <- data.frame(Treatment = unique(Pulses$Treatment))
pred <- predict(Pulses2, se.fit = TRUE, newdata = newdata, dispersion = 20.68806, type = 'response')
# Can get same result (SE models) using a Poisson as long as you correct for overdispersion
# Can find the overdispersion value in the summary of the quasipoisson model
cbind(newdata, pred)

# Check residuals
plot(Pulses2)
plot(resid(Pulses2) ~ Pulses2$fitted.values)

# Compare groups using generalized linear hypothesis test
Pulses2_glht <- glht(Pulses2, linfct = mcp(Treatment = 'Tukey'))

# Use the Bonferroni adjustment to adjust p-values and account for multiple comparisons
summary(Pulses2_glht, test = adjusted('bonferroni'))
cld(Pulses2_glht)

# Run an Ftest
summary(Pulses2_glht, test = Ftest())
```

Quasi-Poisson (Treatment)

```
Treatment <- read.csv("C:/Users/PHILLIP/Desktop/Pulses Summed.csv")

#Transform Year to a Factor
Treatment$Year <- factor(Treatment$YEAR)

B <- Treatment %>% filter(SITE == 'Beech')
B <- B %>% filter(YEAR != '2015')

p <- ggplot(aes(x = Treatment, y = PULSES), data = B)
```

```
p + geom_boxplot()
Pglm <-glm(PULSES ~ Treatment,data = B, family = 'poisson')

#ANOVA for comparison to data output
Detect <-lm(PULSES ~ Treatment,data = B)
anova(Detect)
summary(Detect)

# Check for overdispersion
# First is probably best as it can take variables into account
deviance(Pglm)/df.residual(Pglm)
# Another way, seems similar and gives more info
qcc.overdispersion.test(B$PULSES, type = 'poisson')

# Quasipoisson adjusts standard errors based on the amount of overdispersion
# Estimates will stay the same but SEs will be larger
Qglm <-glm(PULSES ~ Treatment,data = B, family = 'quasipoisson')
summary(Qglm)

# Pull out means and SEs
str(Pglm)
newdata <- data.frame(Treatment = unique(B$Treatment))
pred <- predict(Pglm, se.fit = TRUE, newdata = newdata, dispersion = 4570.679, type = 'response')
# Can get same result (SE models) using a Poisson as long as you correct for overdispersion
# Can find the overdispersion value in the summary of the quasipoisson model
cbind(newdata, pred)

out <- LSD.test(Detect,"Treatment", p.adj = "bonferroni")
out
out$means$std/(sqrt(out$means$r))

# Compare groups using generalized linear hypothesis test
Qglm_glht <- glht(Qglm, linfct = mcp(Treatment = 'Tukey'))

# Use the Bonferroni adjustment to adjust p-values and account for multiple comparisons
```

```
summary(Qglm_glht, test = adjusted('bonferroni'))
cld(Qglm_glht)

# Run an Ftest
summary(Qglm_glht, test = Ftest())
```

Quasi-Poisson (Pre- and Post-Harvest)

```
Year <- read.csv("C:/Users/PHILLIP/Desktop/Count Data with 0 for Species Added.csv")

#Transform Year to a Factor
Year$YEAR <- factor(Year$YEAR)

B <- Year %>% filter(SITE == 'Beech')
COTO <- B %>% filter(AUTO.ID == 'COTO')

p <- ggplot(aes(x = YEAR, y = freq), data = COTO)
p + geom_boxplot()
Pglm <-glm(freq ~ YEAR,data = COTO, family = 'poisson')

#ANOVA for comparison to data output
Detect <-lm(freq ~ YEAR,data = COTO)
anova(Detect)
summary(Detect)

# Check for overdispersion
# First is probably best as it can take variables into account
deviance(Pglm)/df.residual(Pglm)
# Another way, seems similar and gives more info
qcc.overdispersion.test(COTO$freq, type = 'poisson')

# Quasipoisson adjusts standard errors based on the amount of overdispersion
# Estimates will stay the same but SEs will be larger
Qglm <-glm(freq ~ YEAR,data = COTO, family = 'quasipoisson')
summary(Qglm)
```

```
# Pull out means and SEs
#Doesn't work accurately
str(Pglm)
newdata <- data.frame(YEAR = unique(COTO$YEAR))
pred <- predict(Pglm, se.fit = TRUE, newdata = newdata, type = 'response')
# Can get same result (SE models) using a Poisson as long as you correct for overdispersion
# Can find the overdispersion value in the summary of the quasipoisson model
cbind(newdata, pred)

out <- LSD.test(Detect,"YEAR", p.adj = "bonferroni")
out
out$means$std/(sqrt(out$means$r))

# Compare groups using generalized linear hypothesis test
Pglm_glht <- glht(Pglm, linfct = mcp(YEAR = 'Tukey'))

# Use the Bonferroni adjustment to adjust p-values and account for multiple comparisons
summary(Pglm_glht, test = adjusted('bonferroni'))
cld(Pglm_glht)

# Run an Ftest
summary(Pglm_glht, test = Ftest())
```

Quasi-Poisson (Slope Position)

```
Treatment <- read.csv("C:/Users/PHILLIP/Desktop/Pulses Summed.csv")

#Transform Year to a Factor
Treatment$Year <- factor(Treatment$YEAR)

B <- Treatment %>% filter(SITE == 'Beech')
B <- B %>% filter(YEAR != '2015')
Position <- B %>% filter(Treatment == "Control" )
Position <- B %>% filter(Treatment == "Patch Cut" )
Position <- B %>% filter(Treatment == "Shelterwood" )
```

```
p <- ggplot(aes(x = Position, y = PULSES), data = Position)
p + geom_boxplot()
Pglm <-glm(PULSES ~ Position,data = Position, family = 'poisson')

#ANOVA for comparison to data output
Detect <-lm(PULSES ~ Position,data = Position)
anova(Detect)
summary(Detect)

# Check for overdispersion
# First is probably best as it can take variables into account
deviance(Pglm)/df.residual(Pglm)

# Quasipoisson adjusts standard errors based on the amount of overdispersion
# Estimates will stay the same but SEs will be larger
Qglm <-glm(PULSES ~ Position,data = Position, family = 'quasipoisson')
summary(Qglm)

#SE and Groupings for ANOVA
out <- LSD.test(Detect,"Position", p.adj = "bonferroni")
out
out$means$std/(sqrt(out$means$r))

# Compare groups using generalized linear hypothesis test
Qglm_glht <- glht(Qglm, linfct = mcp(Position = 'Tukey'))

# Use the Bonferroni adjustment to adjust p-values and account for multiple comparisons
summary(Qglm_glht, test = adjusted('bonferroni'))
cld(Qglm_glht)

# Run an Ftest
summary(Qglm_glht, test = Ftest())
```

Code Designed by Wendy Leuenberger

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Effects of Shelterwood Harvests and Patch Cuts on Habitat Use of Myotis species in the central Appalachians. Arant, P.L. 2016. Kentucky Bat Working Group. Falls of the Rough, KY

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Permits and Certificates

Endangered/Threatened Species Federal Recovery Permit (TE75551C-0)
Qualified Bat Surveyor – Pennsylvania
Wetland Delineation and Regional Supplement Training – Swamp School in Pennsylvania

RESEARCH ARTICLE

The hidden value of trees: Quantifying the ecosystem services of tree lineages and their major threats across the contiguous US

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Citation: Cavender-Bares JM, Nelson E, Meireles JE, Lasky JR, Miteva DA, Nowak DJ, et al. (2022) The hidden value of trees: Quantifying the ecosystem services of tree lineages and their major threats across the contiguous US. PLOS Sustain Transform 1(4): e0000010. https://doi.org/10.1371/journal.pstr.0000010

Editor: Isabel Marques, University of Lisbon: Universidade de Lisboa, PORTUGAL

Received: September 30, 2021

Accepted: February 11, 2022

Published: April 5, 2022

Data Availability Statement: All data and related metadata underlying reported findings have been deposited in the Data Repository of the University of Minnesota, a public data repository: https://conservancy.umn.edu/handle/11299/220692.

Funding: This work was supported by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the National Science Foundation DBI-1052875. The funders had no role in study design, data collection and analysis,

Abstract

Trees provide critical contributions to human well-being. They sequester and store greenhouse gasses, filter air pollutants, provide wood, food, and other products, among other benefits. These benefits are threatened by climate change, fires, pests and pathogens. To quantify the current value of the flow of ecosystem services from U.S. trees, and the threats they face, we combine macroevolutionary and economic valuation approaches using spatially explicit data about tree species and lineages. We find that the value of five key ecosystem services with adequate data generated by US trees is \$114 billion per annum (low: \$85 B; high: \$137 B; 2010 USD). The non-market value of trees from carbon storage and air pollution removal far exceed their commercial value from wood products and food crops. Two lineages—pines and oaks—account for 42% of the value of these services. The majority of species face threats from climate change, many face increasing fire risk, and known pests and pathogens threaten 40% of total woody biomass. The most valuable US tree species and lineages are among those most threatened by known pests and pathogens, with species most valuable for carbon storage most at risk from increasing fire threat. High turnover of tree species across the continent results in a diverse set of species distributed across the tree of life contributing to ecosystem services in the U.S. The high diversity of taxa across U.

decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

S. forests may be important in buffering ecosystem service losses if and when the most valuable lineages are compromised.

Author summary

Humans benefit from trees in many ways, including the role they play in regulating climate, filtering air pollution and providing food, fiber and fuel. Trees also face increasing risks of damage and mortality from global change forces, threatening the benefits forests and plantations provide. Trees in the contiguous US generate over $114 billion per year from five key ecosystem services. The "hidden" value of trees—the non-market value from carbon storage and air pollution filtration—far exceeds their commercial value. Most tree species face threats from climate change, many face increasing risk of exposure to major forest fires, and 40% of total woody biomass is threatened by pests and pathogens. The most valuable US tree species and groups—including the pines and the oaks, which also contain the highest numbers of species—are under threat from pests and pathogens. The services generated by trees come from many different lineages across the tree of life as a consequence of the high turnover in the species and lineages across regions. The study highlights the importance of sustaining ecosystem services from the diversity of trees that grow across the US.

Introduction

Trees contribute to human well-being by sequestering and storing greenhouse gasses, filtering air pollutants, providing aesthetic and recreational benefits, provisioning wood, food, and other marketable products, and creating habitat for numerous other species [1–3]. The abundance and composition of US trees is changing due to a complex set of accelerating global change drivers, including increasing invasive pests and pathogens [4,5], greater frequency of major fires [6], and changing climatic regimes [7]. These threats have the potential to undermine the benefits trees provide and the societal value they could provide to future generations. In this study we seek to determine the ecosystem services value of US trees and of individual phylogenetic lineages across the tree of life, identify the services that contribute most to their value and quantify the extent to which these services are threatened by global change. We ask how the non-market value of trees compares to their commercial value, and whether the tree species and lineages that currently provide the greatest benefits are facing substantial global change threats. In doing so, we provide a baseline accounting—as comprehensively as feasible given current data—of the value of US tree ecosystem services, the major threats they face, and their distribution in geographical and macroevolutionary space.

We synthesize existing data sources to estimate the annual net monetary value of five key ecosystem services provided by over 400 tree species across the contiguous US. Our analysis includes two regulating services—climate and air quality regulation—and three provisioning services—managed production of wood products, food crops and Christmas trees. Spatially explicit information by species was available for these five services. We did not include other important ecosystem services generated by trees, such as aesthetics or recreation, because spatially explicit information by species was not available.

Analyses of regulating and provisioning ecosystem services supported by biodiversity typically use ecosystems or landscapes [8] rather than individual species [9] or lineages as the unit of study, even though conservation efforts frequently target species, particularly rare or endangered species [10] and consider their phylogenetic context [11,12]. To our knowledge, no assessment currently exists of the service value of individual tree species and tree lineages. Filling this gap can increase our basic knowledge of the tree species and lineages on which we depend and contribute to precision management of forests—efforts that focus on the health and growth of individual species or lineages, considering their symbionts, pests and pathogens, environmental preferences and physiological tolerances. In this study, we assess for the first time, to our knowledge, the production of ecosystem services of individual tree species in the contiguous U.S. based on their characteristics and tree inventories that allow them to be mapped accurately across space. The contiguous U.S. refers to the lower 48 states not including Alaska and Hawaii.

No single tree species has the physiological tolerance to occur in all forests across a continent. Over time, different species have evolved that collectively tolerate a wide range of climatic and environmental gradients [13]. The tree of life comprises all of the phylogenetic lineages—groups of species with shared ancestry—that have evolved on Earth. These span larger climatic and environmental gradients than individual member species [14,15]. Due to their shared ancestry, species in a lineage share characteristics unique to that group in terms of genetic potential, form, and traits that influence ecosystem function and contribute to ecosystem services and can also influence susceptibility to certain threats [16–19]. Some ecosystem services, such as edible fruit production, will be concentrated in certain lineages with particular characteristics. Such narrowly distributed services may be at risk if those lineages become threatened. Other ecosystem services, such as carbon storage, will be distributed broadly across the tree of life, given that all trees store carbon. However, if dominant tree species or lineages that provide a large fraction of these services are threatened, then the provisioning of these services is also at risk, at least for a period of time before other species grow to take their place.

As a consequence of the evolved variation among species in physiological tolerances and niches, the turnover—or beta diversity [13,20,21]—of tree species and phylogenetic lineages across major environmental gradients may be important to generating the full value of tree ecosystem services. While we do not explicitly consider the value of tree biodiversity in terms of net biodiversity effects—enhanced productivity [22,23], multifunctionality, resilience [24] and ecosystem services [25] of diverse tree stands compared to expectations from monocultures—we consider how the breadth of tree species and tree lineages across the tree of life that inhabit the range of environments across the contiguous US contribute to current ecosystem services. To do so, we map the value of trees and calculate the economic contributions to these services of every US tree species and lineage.

To gain insight into where trees are most threatened regionally and by what type of threat, we map where trees are most threatened by pests and pathogens [4], climate change [7] and increases in the frequency of major fires [6]. We further calculate the extent to which each tree species is threatened to understand how these threats are differentially distributed among taxa. Vulnerability to these threats varies among species both because of differences in physiology and spatial proximity to threats [26–28]. Environmental change, pests, and disease are anticipated to cause decline in some species and lineages that currently provide high levels of services in certain regions of the U.S. [29–31]. We identify the locations across the U.S. and across the tree of life where service value is likely to be most affected. This analysis identifies potential problems that can be targeted by precision forestry management practices [10]. Our approach goes beyond previous work by allowing us to identify where tree conservation and threat mitigation will be most valuable and which specific lineages within a landscape deserve particular attention.

Results

Between 2010 and 2012, trees in US forests, orchards, and plantations provided nearly $114 billion (B) per year (low: $85 B, high: $137 B; 2010 USD) in net value via two regulating services (climate and air quality regulation) and three provisioning services (wood products, tree crops and Christmas tree production) (Fig 1A). Climate regulation benefits via carbon storage in tree biomass represented 51% of this net annual value, while preventing human health damages due to air pollution filtering by trees, i.e., air quality regulation, represented 37% of the annual net value. The remaining 12% of the net annual value came from provisioning services. Estimates of provisioning services are more precise than the estimates of annual regulating service values. The differences in precision are driven mainly by the differences in the available information about the per unit values—or prices—of these ecosystem services. The provisioning services analyzed here generate commercial products that have a market price. In contrast,

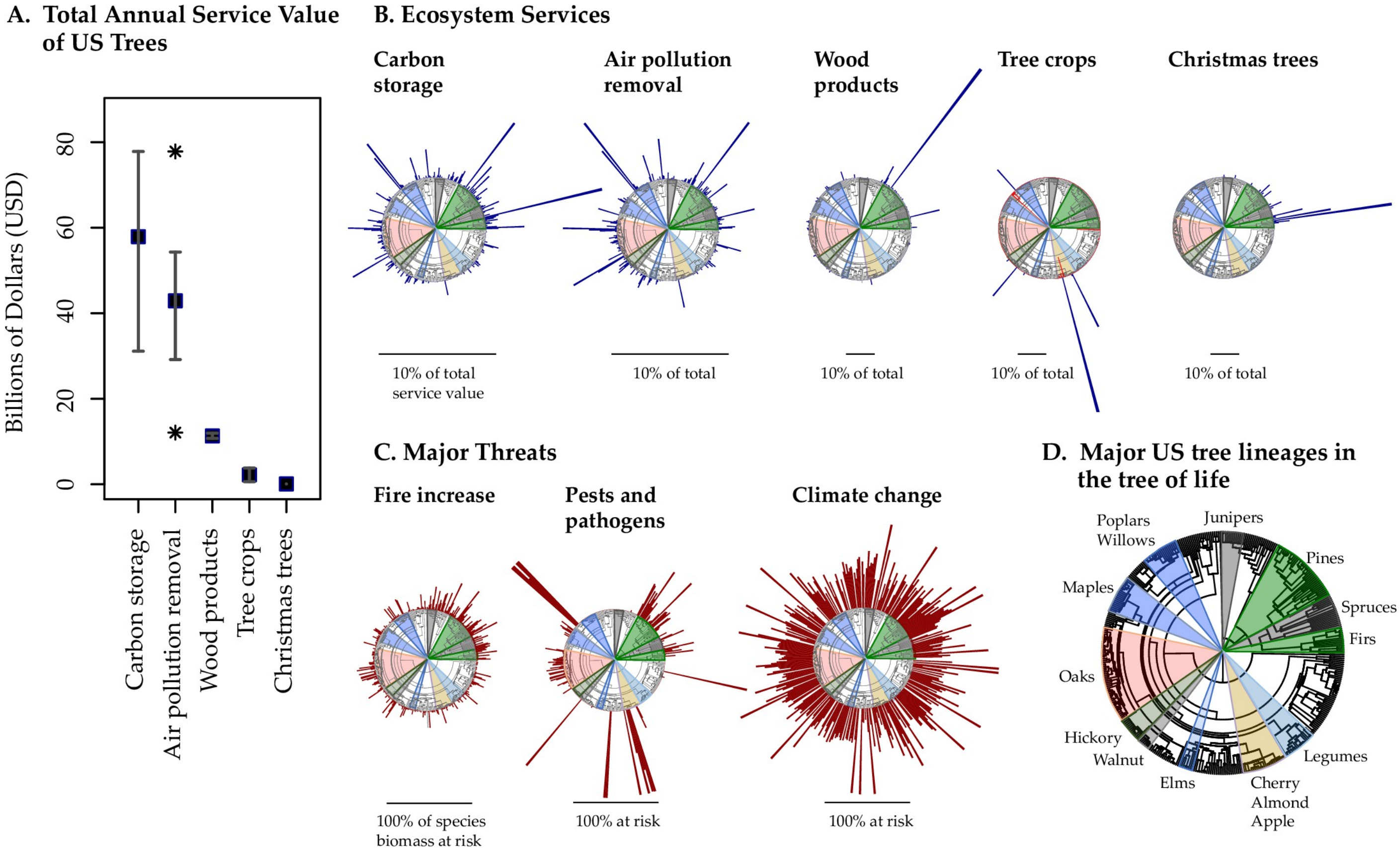

Fig 1. (A) Total net annual ecosystem service values provided by contiguous US trees between 2010 and 2012. The squares give mean estimated value and the error bars show the range in expected values. (B) Ecosystem service annual value (blue bars) and (C) potential threats (brown bars) for tree species across the tree of life. Ecosystem service value bars emanating from each tree of life measure the percentage of total service value generated by each species. Threats bars emanating from each tree of life measure represent the proportion of each species' current total biomass at risk from the indicated threat. Climate change refers to tree biomass threatened from changes in multiple temperature and precipitation variables. (D) Phylogeny of the US trees, with color wedges indicating the location of particular clades (also shown in (B) and (C) trees of life). Note that ecosystem service values for some tree crop species in B are negative and shown in red pointing inward. See the Methods and Data section for details on error bound calculations in A. The error bound around air quality regulation reflects uncertainty in the air pollution dose–human health damage response function. Asterisks for air quality regulation represent the additional uncertainty created when the uncertainty in the value of a statistical life (VSL) is included in the calculation of human health damages avoided by tree-based filtering of air pollution. Contributions of tree species to carbon annual value (B) (and total ecosystem service value) are significantly more dispersed across different branches of the tree of life than expected at random—with mean phylogenetic distances, MPD = 489 (P = 0.012) and MPD = 475 (P = 0.037)—while contributions of tree species to crop value are significantly more clustered within certain branches of the tree of life than expected at random (MPD = 189, P = 0.001). The threat from increases in frequency of severe fires is significantly overdispersed across the phylogeny (C), (MPD = 505, P = 0.001), while pests and pathogen threats are more likely to threaten a close relative that is also threatened than expected at random (MNTD = 52, P = 0.001). See S2 Table for details.

https://doi.org/10.1371/journal.pstr.0000010.g001

the per unit values of climate and air quality regulating services, given by the social cost of carbon (SCC) and the value of a statistical life (VSL), respectively, are estimated with a range of models with different sets of assumptions and simplifications, all using imperfect data, leading to large error bounds [32–35].

Most valuable tree lineages in US forests, plantations, and orchards

Benefits provided by trees in the US are distributed across the tree of life (Fig 1B), yet two major lineages—the pines (*Pinus*) and the oaks (*Quercus*)—respectively generated $25.4 B and $22.3 B in net benefit annually between 2010 and 2012 and are by far the most valuable genera in the contiguous US (Table 1). Both lineages have a high number of species that occupy diverse ecological niches and collectively contribute to their high abundance and biomass across the continent [15]. Pines dominated annual net revenues from wood products at $7.4 B, due in part to the high volume of wood produced and partly due to their higher than average price. Pines generate more than five times the timber net revenue of any other genus (Table 1). Oaks had the highest annual climate ($10.7 B) and air quality regulation values ($11.0 B). All US tree species provide some carbon storage and air quality regulation service value. A species' air quality regulation value depends on its abundance and total leaf area as well as the proximity to human populations affected by pollution [28,36]. Consequently the importance of oaks for regulating service value can be attributed to the high number of species and large populations sizes of many of those species across the US landscape; and in the case of air quality regulation, their abundance near large human population centers.

Within the family Rosaceae, the genus *Prunus*, which includes almonds, peaches, and cherries, contributed nearly $2.0 B to US agricultural net revenue annually between 2010 and 2012 (*Prunus* species made up 35.1% of all tree crop acreage between 2010–2012), while the apple genus (*Malus*) contributed more than $0.94 B. Although apple's market value per unit of yield was not very high between 2010 and 2012, it was the third most planted tree crop genus, only behind *Prunus* and *Citrus*. The *Citrus* genus (family Rutaceae), is also an important crop genus in the US (the second most widely planted genus between 2010 and 2012). However, the annual net returns from citrus products were negative between 2010 and 2012 due to abnormally low citrus market prices [37] and the prevalence of citrus greening bacterial disease in Florida and to a lesser extent, Arizona and California [38].

For the set of ecosystem services examined here, the most valuable tree species in the US as of 2010–2012 were loblolly pine (*Pinus taeda*), generating $12.9 B (low: $11.0 B; high: $14.3 B;

Table 1. The most valuable contiguous US tree genera ranked according to aggregate net annual value (2010 USD) generated across five ecosystem services between 2010 and 2012: annual climate regulation value via carbon storage, annual air quality regulation via health damages avoided due to air pollution removal (PM$_{2.5}$ and O$_3$), and annual net revenue from wood products, tree crops, and Christmas tree production.

Rank	Common Name	Scientific Name	Aggregate	Climate Regulation	Air Quality Regulation	Wood Products	Tree Crops	Christmas Trees
1	Pine	*Pinus*	$25,389,289,489	$10,597,549,418	$7,402,536,592	$7,380,913,415		$8,290,065
2	Oak	*Quercus*	$22,327,731,163	$10,702,056,084	$11,048,359,855	$577,315,224		
3	Maple	*Acer*	$11,074,529,157	$5,243,370,527	$5,534,340,848	$296,817,782		
4	Douglas-fir	*Pseudotsuga*	$8,555,113,301	$5,908,159,459	$1,455,004,741	$1,183,176,063		$8,773,039
5	Hemlock	*Tsuga*	$4,467,535,785	$3,008,325,009	$1,225,172,716	$234,038,059		
6	Cherry/Almond	*Prunus*	$4,125,822,231	$780,954,517	$1,074,096,913	$217,688,989	$2,053,081,812	
7	Spruce	*Abies*	$3,839,147,244	$2,885,232,261	$818,850,801	$75,832,332		$59,231,849
8	Hickories	*Carya*	$3,598,686,663	$1,738,261,008	$1,752,900,146	$60,175,136	$47,350,374	
9	Tulip tree	*Liriodendron*	$3,009,207,291	$1,373,715,800	$1,499,753,000	$135,738,491		
10	Ash	*Fraxinus*	$2,908,276,099	$1,384,668,426	$1,454,588,583	$69,019,090		

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2010 USD) in net value annually and Douglas-fir (*Pseudotsuga menziesii*). Almond trees generated $2.5 B annually between 2010 and 2012, the highest annual net return across all crop trees in the US (low: $1.9 B; high $3.1 B) (S1A Table). The high almond tree value was due to their abundance (471,259 ha; 20,397 more ha per annum than the next most abundant fruit tree, oranges) *and* high market price (between 2010 and 2012, the nominal price of a pound of almonds was $1.99; of all the tree crops, only pistachios had a higher per pound market price during this period).

Variation among species in ecosystem service value

Tree species with high carbon storage value, the most valuable service, are more evenly dispersed across the tree of life than expected at random (NRI = -2.04, P = 0.02, S2 Table). Air quality regulation value is distributed at random across the tree of life (NRI = -0.54, ns). At a finer scale looking only at close relatives, nearest evolutionary neighbors tend to have similar air quality regulation values (NTI = 1.61, P = 0.02, S2 Table), even though these clusters of similar and closely related species are spread across all lineages.

Unlike the regulating services, tree crops are significantly clustered in the tree of life (NRI = 4.35, P = 0.001, S2 Table) and include relatively few lineages, such as trees in the Rose family (almonds, apples, pears, and cherries) (Fig 1B, Table 1). Many lineages provide wood products, but the amounts vary widely among species within those lineages, and the most valuable species are not significantly clustered within any lineage. The overall value of ecosystem services for the benefits evaluated are dispersed more evenly across the tree of life than expected at random (NRI = -1.69, P = 0.037), consistent with trends found at global scale [39]. Species that generate individual services—like tree crops, wood products, or Christmas trees—tend to be found in different places in the tree of life, and the overdispersion of the most valuable service (carbon) shows that many different lineages contain abundant species that contribute to carbon storage.

Spatial variation in ecosystem services of trees across the contiguous U.S.

The spatial distribution of ecosystem services produced by US trees between 2010 and 2012 largely reflects forest, plantation, and orchard distribution (Fig 2). Climate and air quality regulation service values are a direct consequence of where forests grow; they cover most of the contiguous US, excluding grassland and desert biomes (Figs 2A and 2B). However, health damages avoided by tree-based air pollution removal values tend to be greatest near large urban areas that are surrounded by forests. Between 2010 and 2012 people living in eastern urban areas, particularly the New York, Boston, Pittsburgh, and Atlanta areas, as well as Seattle and California's Bay Area benefited greatly from air pollution removal by forests between 2010 and 2012 (Fig 2B, S1H and S1I Text, S7 and S8 Tables, S3 Fig). Trees can also filter and absorb pollutants released by forest fires [28,40]. However, our air quality regulation service valuation is only based on the industrial and transportation-related emissions that trees filter and absorb.

The most valuable tree crops are grown on the coasts, in the Southwest, and in warm and arid climates, often where forests do not grow (Fig 2C). Tree crops produce the highest net returns in California but also generate high net values in several Southwest, Southern, and Eastern states. In contrast, timber production is concentrated in a subset of the regions that also produce high climate regulation and air pollution removal values, including the Southeast and the Pacific Northwest, as well as in the Northeast and Upper Midwest (Fig 2D).

Both services and threats are spatially heterogeneous, with different kinds of services and threats concentrated in different parts of the contiguous U.S. (Figs 2 and 3). Climate change threatens species in all parts of the continent (Fig 3A), while pest and pathogen threats are

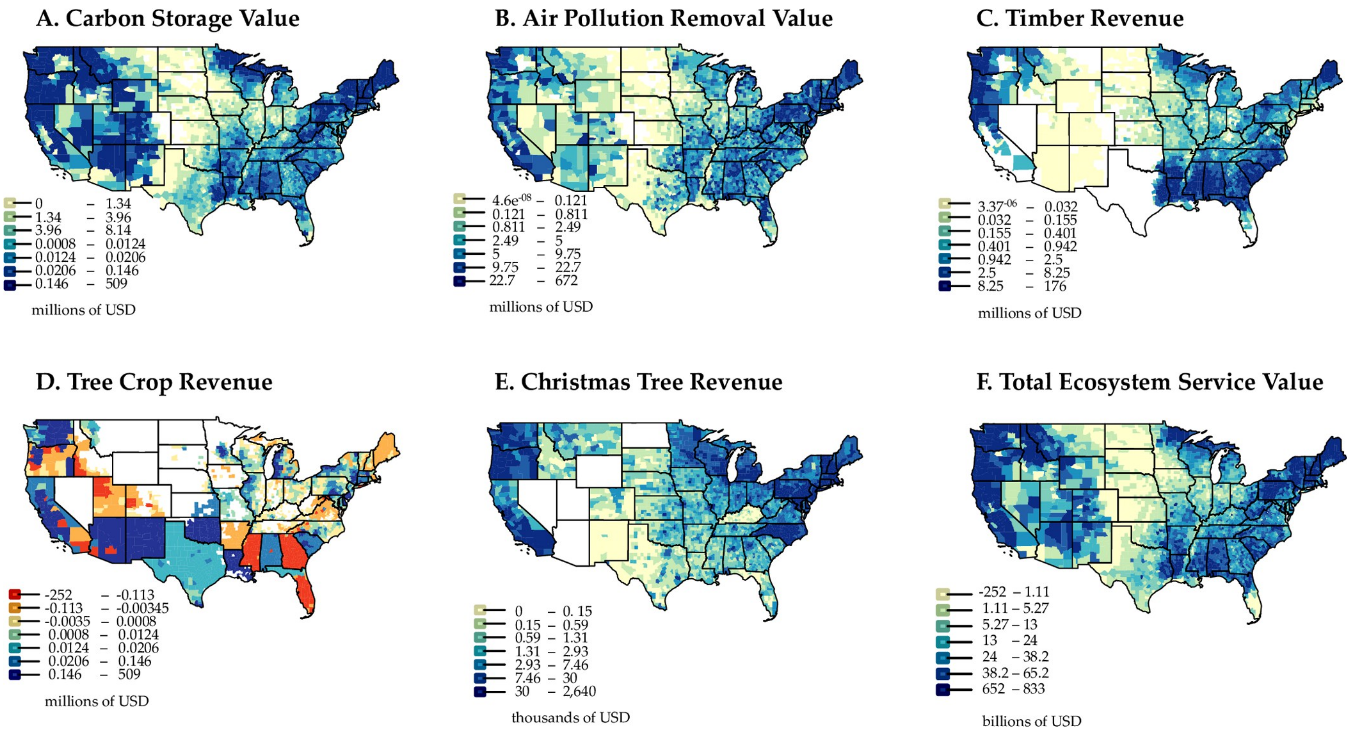

Fig 2. Annual net ecosystem service value generated between 2010 and 2012 (in 2010 USD) (A) climate regulation via carbon storage, (B) air quality regulation via human health damages avoided by tree-based filtering of air pollution (C), wood product net revenue (D) tree crop net revenue, (E) Christmas tree net revenue, (F) and the total value across all five services in contiguous US counties across the U.S. Darker shades of blue indicate higher annual net values. Shades of orange and red represent negative net annual values. Missing data are indicated in white. A-D are reported in millions of USD, E in thousands of USD and F in billions of USD. Annual Tree crops, wood product, and Christmas values account for costs of production while annual provisioning service values (climate and air quality regulation) have no cost of production (these values are incidental). See Methods and Data for details of how values are allocated to counties.

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strongest in counties of the Southwest and Southeast (Fig 3B). Major wildfires are expected to increase especially in California and the Intermountain West (Fig 3C), coincident with where carbon annual storage value is highest (Fig 2A).

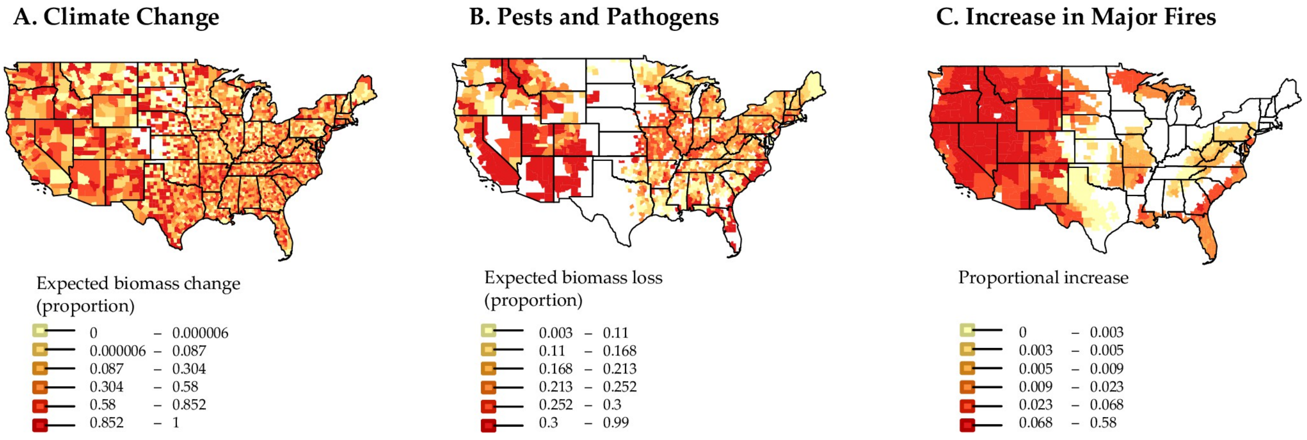

Fig 3. Magnitude of county-level threats across the contiguous US. Darker colors indicate greater threat to the biomass currently located in the county. Missing data are indicated in white. (A) Proportion of current total tree biomass in each county that is expected to be exposed to climatic regimes (determined from multiple precipitation and temperature variables) outside the current range that they can tolerate as of 2050. (B) Proportion of current tree basal area in each county that is expected to be lost to pest and pathogen outbreaks as of 2050. (C) Proportional increase in fire exposure (number of expected major fires per week compared to the 20th century maximum) per county as of 2050. See Methods and Data section for details of how values are allocated to counties.

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Low similarity in the tree species that provide ecosystem service value in different regions

We generally found low similarity in the tree species (Fig 4 and S1 Fig) that provide ecosystem services in different regions. Thus, different tree species tend to account for the same ecosystem service in different ecodivisions. Ecodivisions represent regional ecological units (Fig 4C) of environmental similarity. Tree crops, which are frequently planted in geographically disparate but climatically similar regions, were an exception. Species similarity values (possible range: 0–1) averaged across pairs of ecodivisions, were much higher for tree crops (0.54, SD 0.23) than for carbon storage (0.09, SD 0.13), air quality regulation (0.07, SD 0.13) or wood products (0.04, SD 0.1). Lineage (or phylogenetic) similarities of tree services (S1 Fig) among ecodivisions were always higher than species similarities, indicating that different species in the same lineage (e.g., oaks) provide services in different regions. Lineage similarities among regions were again higher for tree crops (0.68, SD 0.16) than for carbon storage (0.56, SD 0.14), air quality regulation (0.55, SD 0.14) or wood products (0.53, SD 0.19). However, Christmas trees, calculated for states only, showed very high lineage similarities among states (0.8, SD 0.24), despite very low species similarities (0.18, SD 0.19), as all of the different tree species that provide this service are from the same major branch in the tree of life.

Pines provided the greatest wood product net revenue in a number of regions, although in some regions Douglas-fir or oak trees provided more of this service. Overall, we found low similarity (high spatial turnover) in the species that provide the ecosystem services we evaluated (Fig 4, S1 Fig) because different species—and to a lesser extent, different lineages—grow

	A. Species similarity			B. Phylogenetic similarity		
	Median	Mean	SD	Median	Mean	SD
Carbon Storage Annual Value	0.02	0.09	0.13	0.54	0.56	0.14
Air Pollution Removal Value	0.01	0.07	0.13	0.54	0.55	0.14
Wood Products Annual Net Revenue	0.00	0.04	0.10	0.50	0.53	0.19
Tree Crop Annual Net Revenue	0.50	0.54	0.23	0.68	0.68	0.17

C. Ecodivisions in US Forests

Fig 4. Similarities among species (A) and phylogenetic lineages (B) in the trees that contribute to ecosystems in different ecodivisions (C) of contiguous US forests. Shown are the mean, median and standard deviation of pairwise similarities across ecodivisions using 1-Bray-Curtis dissimilarities (species similarities) and phylosor (Bryant et al. 2008) similarities (phylogenetic similarities), with values ranging between 0 and 1. Higher values indicate many of the same species or lineages contribute to the ecosystem service in different ecodivisions (1 = all of the same species or lineages contribute), while lower values indicate different species or lineages contribute to an ecosystem service in different ecodivisions (0 = none of the same species or lineages contribute). Ecodivisions are defined by the USDA Forest Service (C). See S1 Fig for details.

https://doi.org/10.1371/journal.pstr.0000010.g004

in different regions. Consequently, the current total ecosystem service value of trees in the US results from many different species that occur naturally or are planted across different climates and environments.

Species and lineages most threatened by regional and global change

The important ecosystem services that trees provide are under threat from global change. Climate change, measured as the percentage of the species' biomass expected to be exposed to levels of annual temperature, precipitation, and aridity in 2050 that is outside of the range they can tolerate, fire frequency and intensity, measured by average projected change in fire frequency in the counties that contain the species, and the growing number of invasive pests and pathogens are all projected to impact the health, mix, and spatial distribution of U.S. tree populations. Most tree species in the U.S. are threatened by climate change. Due to increasing aridity, alone, 45% of species are anticipated to have at least 10% of their current biomass encounter climates outside their current climatic envelope. Eighty-eight percent of tree species are projected to have at least 10% of their biomass exposed to climates outside the current climate envelope, impacting nearly 40% of total tree biomass in the contiguous U.S. Known pests and pathogens are threatening 16% of tree species, potentially impacting up to 40% of total tree biomass. Increased fire frequency is expected to impact 40% of species, meaning that these species are expected to encounter at least one additional major fire somewhere across their range (Table 2).

We evaluated the dispersion of these threats across the phylogeny. Threats to tree species were dispersed widely among lineages (S2 Table), except for known pests and pathogens, which clustered within certain lineages (NTI = 2.66, P = 0.001, S2 Table), including the oak and pine genera as well as in most of the crop species (Fig 1C). Consequently, tree species that are known to be at risk of damage from pests and pathogens—measured as the fraction of the species' current biomass (tree crop species) or basal area (non-tree crop species) threatened by pests and pathogens—are also significantly more likely to have close relatives also at risk. Tree vulnerability to enemy attacks is tightly linked to phylogenetic identity, given long-term evolutionary processes that drive enemy-host compatibility [17,41,42]. Therefore, phylogenetic lineage is a strong predictor of risk. However, we acknowledge that the pattern may reflect biases in human knowledge as the pests and pathogens that affect the most abundant and most valuable species are the most studied [43]. Risks to less abundant or less valuable tree species, including novel pathogens that could spread to other species, may not be well understood.

In contrast to pests and pathogens, which have high phylogenetic specificity, the vulnerability of tree species and lineages to changes in climate depends most on where species are

Table 2. Summary of the percent of tree biomass and tree species threatened from climate change linked to increasing aridity, multivariate climate change including changes in temperature, precipitation and aridity, known pests and pathogens, and increased fire exposure.

Threat	% of total tree biomass threatened	Threat threshold description	% of tree species threatened
Climate change–aridity	11.3%	Species with more than 10% of their biomass under threat from climate change–aridity	46%
Multivariate climate change	39%	Species with more than 10% of their biomass under threat by multidimensional climate change (temperature, precipitation, aridity)	88%
Pests and pathogens	40%	Species with more than 10% of their biomass under threat by pests and pathogens	16%
Increasing fire frequency	NA*	Species expected to be exposed to one additional major fire on average across their range	40%

*It was not possible to estimate percent of tree biomass threatened with increased fire frequency.

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distributed in relation to predicted climate changes. Tree species forecast to have high exposure to climate threats are widely dispersed–no different from random dispersion–across the tree of life (NRI = -0.30, S2 Table), given that changes in climate are expected across the country. Similarly, the threat due to increases in fire frequency is overdispersed—more evenly spread than random dispersion—across the tree of life (NRI = -4.59, P<0.001, S2 Table), indicating that the spatial distribution of species in regions where fire is increasing matters most in predicting the threat, not their phylogenetic lineage.

Associations between services and threats by species

Known pests and pathogens are predicted to disproportionally affect species that generate high annual net climate regulation, air quality regulation, and wood product values (Fig 5A). Some of this positive association is undoubtedly driven by an abundance effect. Species with higher abundance generate more economic value, all else equal. More abundant species may also attract a higher prevalence of insects and pathogens and enable faster spread, exacerbated by the fact that some of the most abundant species are closely related and hence more susceptible to the same threats [41,44]. Pests and pathogens of more abundant species may also be better documented. The only other statistically significant positive associations between species-level economic value and species-level threats are 1) wood product value and degree of risk due to climate change and 2) carbon storage value and the risk of increasing frequency of major fires. These associations are less easily explained by species abundances and are likely linked to a spatial confluence of high value species and these particular threats.

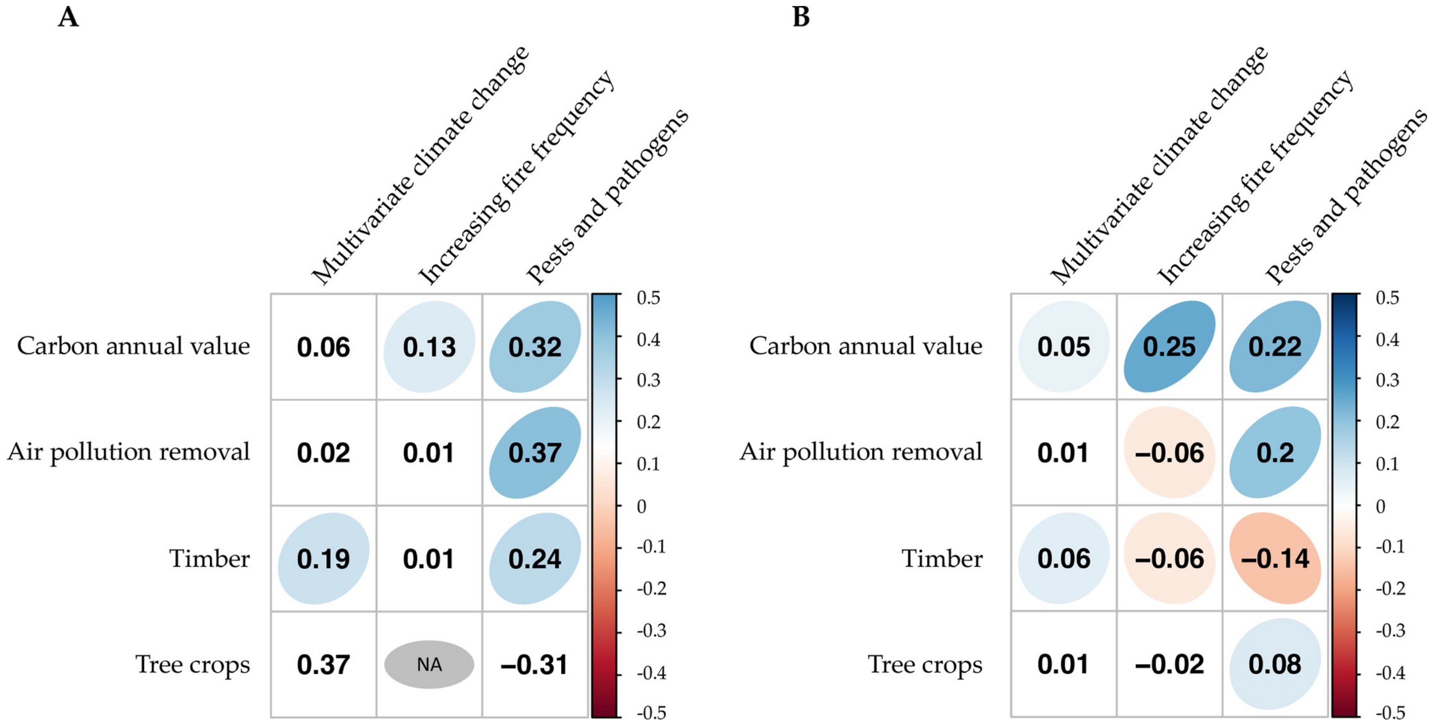

Fig 5. Associations between annual net ecosystem service values of tree species in the US and their predicted threats and drivers of change based on Spearman's rank-order correlations. A) Species-level correlation coefficients (rho) between annual net ecosystem service value and predicted threats. B) Spatial correlations between annual net ecosystem service value and predicted threats by US counties. Colors (blue) indicate significant positive associations, indicating more valuable tree species are under more threat. Darker colors indicate stronger correlations. Service values refer to those generated between 2010 and 2012. Modeled expectations for changes in frequencies of major fire are not available in some regions precluding accurate estimation of their potential threat to some tree crop species in A; correlation is not shown.

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Spatial association of services and threats

Spatial associations between tree services and threats largely parallel species associations (compare Fig 5B to 5A). The counties with highest carbon annual value from trees coincide with those most impacted by increases in fire frequency, pests and pathogens, and climate change. Likewise, air pollution removal values are highest in counties most threatened by pests and pathogens. Pest and pathogen threats—strongest in counties of the Southwest and Southeast—are negatively associated with timber value, but positively associated with tree crop values.

The only major disagreement between species- and spatial-level tree service and threat correlations is found in the wood product–pest and pathogen nexus. While the most valuable wood product (timber) species are disproportionately affected by pests and pathogens, many of the counties that produce more timber value are less affected by pest and pathogen threats than counties that produce less timber. Given that species vary in abundance and counties vary in diversity, we do not necessarily expect species and spatial correlations to correspond. We further note that the associations are determined by non-parametric spearman-rank correlations which depend on the rank order rather than the magnitude of values. The discrepancy could also be linked to spatial variability in the spread of pests and pathogens and where timber is produced. Some of the major pests and pathogens that impact important timber species in the western and central US have not yet invaded or do not currently impact areas with high wood product production in the northeastern and southeastern US. For example, mountain pine beetle (*Dendroctonus ponderosae*), a species of pine bark beetle that carries pathogenic fungi, yeast and bacteria, has caused considerable damage in British Columbia and the western U.S. to pines that are valuable timber species [45,46]. However, it is currently not present in the northeastern or southeastern U.S., both regions that have high timber production [47]. Similarly, the oak wilt fungus (*Bretziella fagacearum*), which is killing widely distributed and valuable oak species in the central U.S., has not yet invaded the eastern U.S. [29,48], including regions where timber production is high.

Discussion

This study shows that the "hidden" value of trees—the non-market value from carbon storage and air pollution filtration—far exceeds their commercial value. The most valuable U.S. tree species and groups—including the pines and the oaks, which also contain the highest numbers of species—account for 42% of the value of these services and are under greater threat from pests and pathogens than other lineages. Overall, nearly 90% of species face substantial threats from climate change, many face increasing fire risk, and 40% of total woody biomass is threatened by pests and pathogens (Table 2). For the ecosystem services quantified in the current study—climate and air quality regulation, and three commercial provisioning services (wood products, tree crops and Christmas tree production)—trees in the contiguous U.S. contributed over $114 B annually (2010 USD) in value. The broad distribution of services across the tree of life is a consequence of the high turnover in composition (beta diversity) across the continent, highlighting the importance of sustaining a diverse group of trees for human health and well-being across the U.S.

Regulating ecosystem services in different regions of the country are provisioned by different tree species, such that each region gets their climate and air quality regulation services from a different set of species. No single species is responsible for a large portion of the calculated annual service value, and individual tree species differ markedly in their ecosystem service value. Consistency of these services across regions depends on the maintenance of tree diversity across the country as the species that provide the highest values arise from species across the tree of life (Fig 1B). In contrast to individual species, two genera, the pines and oaks, contribute disproportionately to the five ecosystem services we assess, generating nearly $47.7 billion each year (Table 1). These two highly valuable lineages are also the most diverse, with a large number of individual species occupying diverse niches that span the continent.

These important genera are at risk from lineage-specific pests and pathogens that have specialized for specific branches of the tree of life. Other global change threats, including climate change and fire, impact lineages all across the tree of life. Wildfires are a dangerous threat, particularly in the western regions, as they (at least temporarily) destroy tree service supply while at the same time creating local and regional air pollution [49] that will be less effectively mitigated by trees. As forest ecosystems are impacted by global change, the mix of tree species that provide critical ecosystem services will be altered. The consequences of these changes are unknown and could lead to losses in ecosystem benefits and human well-being but could also plausibly lead to an increase in some services. Anticipating the consequences of these changes remains a critical challenge.

Our estimate of the annual value of ecosystem services provided by trees depends on the stock of trees at the time of evaluation (2010–2012), and as such represents a static snapshot of the value of trees. A full dynamic analysis of the value of trees would attempt to estimate the present value of the flow of ecosystem services through time incorporating the potential future trajectories for distribution of trees and the potential future trajectories for prices for services. Such an analysis should incorporate potential future threats from pests and pathogens, fire, climate change, and other risks. How forest composition would change in response to such threats requires analysis of what species might be well-adapted to future conditions, and what species might expand should a pest or pathogen reduce the abundance of a currently common tree species. Further, we treat climate change, pests, and fires as independent threats, due to the complexity of the modeling of their relationships and the availability of data. Addressing these issues is an important but challenging goal for future research.

The current analysis likely understates the value provided by U.S. trees for several reasons. First, most urban ecosystems are not considered in this analysis. The USFS Forest Inventory Analysis (FIA) databases used in this analysis only include natural forests and tree stands managed for productive use, of which few are in urban areas [50,51]. No nationwide spatial database of urban trees exists. Inclusion of urban trees in the analysis would significantly increase the value of health damages avoided due to tree-based air pollution removal, given that air quality improvement benefits are greatest in the most population dense areas [28]. Urban trees would also increase our estimate of climate regulation value. For example, Nowak et al. [50] estimate 643 M Mg of carbon are stored in urban areas, which translates to $2.31 B (2010 USD) annually using our climate regulation valuation approach (see the Methods and Data section). Second, due to data limitations, we omitted many regulating ecosystem services that trees provide, such as erosion control, flood regulation [52], storm surge regulation [53], urban heat island regulation [54], energy savings due to shade [55], and species habitat provision. Nowak et al. [56] estimate that trees and forests in urban areas in the continental U.S. annually reduce electricity use by 38.8 M MWh and heating use by 246 M MMBtus, translating to $7.8 B in energy savings annually. We also leave out the contribution of trees to recreation, ornamental, spiritual, and aesthetic values [57–61]. Including these services in our analysis would greatly increase the value provided by U.S. trees.

A complete accounting of the value provided by U.S. trees would also require estimates of the damages trees cause and the cost of their maintenance. While we do account for some of the costs of providing and maintaining wood product, tree crop, and Christmas tree products, there may be additional hidden costs we do not capture, such as the full cost of water used for almond tree production in California. Tree-related damages include pollen and sap-related irritations, injuries to people and property caused by falling trees and limbs, and their role in generating fires [62–65]. Further, while trees remove some of the air pollution humans would otherwise inhale, trees can exacerbate the damage caused by air pollution. For example, in certain urban street grids, trees block airflow, trapping pollution that would otherwise dissipate [66]. Additionally, trees are a source of the volatile organic compounds (VOCs) isoprene and monoterpenes, which contribute to tropospheric ozone and secondary particle formation [67]. However, trees simultaneously decrease VOCs potentially leading to a slight net reduction [68]. We were unable to include all service and disservice values, a task no study to date has systematically tackled.

The estimated annual values of the climate and air quality regulation have large uncertainty due largely to uncertainty in the social cost of carbon and the value of a statistical life (i.e., the value that people assign to small reductions in the risk of premature death due to improvements in environmental quality). Further imprecision is introduced to the air quality regulation value because of uncertainty in the air pollution dose–mortality response function, although the uncertainty in VSL alone explains approximately 90% of the range in air pollution removal value (S7 Table). The estimated annual values of the provisioning services are more precise because they are calculated from the market price for the per unit value of tree crops, wood products, and Christmas trees, as well as reliable production volume data.

The hidden value of regulating services is the most important source of value generated by trees. Regulating services are currently provisioned from a diverse collection of evolutionary lineages across the continent. The same services are provided by different species in each region—suggesting that regulating services lost due to local or regional extinction of particular species could (eventually) be provided by other species. However, replacement or evolutionary adaptation by tree populations will take time [69–71] during which regulating services may be reduced. In areas where substitute provider species do not emerge or lag times are extensive—which is likely given the long generation times and slow evolutionary rates of many trees—policy intervention will be necessary to preserve the climate and air quality regulation services. Regulating services are not sold on markets and are often not appreciated by the public; therefore, market forces cannot be expected to fill gaps in future regulating services without additional policy instruments [72]. Mechanisms—such as carbon payments, if designed properly—may help enhance regulating services [73].

In contrast to regulating services, provisioning services are generated primarily from a small number of crop trees that cluster within a small portion of the tree of life (NRI = 4.35, P = 0.001, S2 Table). Threats to these relatively few tree species and lineages with high provisioning service value are likely to be managed by landowners given the financial rewards to threat mitigation can be captured in existing markets. For example, there are commercial incentives to invest in protection against pests and pathogens that target commercially valuable species like grafting one species onto rootstock of a closely related species that is more resistant to pathogens or abiotic stress [74]. Further, changing environmental conditions may create incentives for these species to be grown in new locations [75,76].

Left unchecked, threats posed by lineage-specific pests and pathogens that target forest trees are of particular concern because major losses of dominant species and lineages that currently have high ecosystem service value would undermine forest capacity to provision these benefits. Currently, the most valuable and diverse tree species and lineages, the pines and the oaks, are under increasing threats from pests and pathogens, such as pine beetle [77,78] and oak wilt [29]. These threats appear to be increasing partially as a consequence of climate change [30, 48], and multiple threats can interact, exacerbating outcomes [79]. The results presented here highlight the importance of targeted management efforts to slow the spread of these diseases and agents of forest decline. Despite successes in developing resistant strains of crop trees and containing pathogen threats, the number of disease and insect threats that currently put trees at risk is alarming [29, 80, 81], threatening over 40% of U.S. forest biomass [82]. Chestnut blight and Dutch elm disease are two powerful examples of how once-dominant tree species that provided many services were decimated by disease [4].

The high diversity of taxa across U.S. forests may be important in buffering ecosystem functions service losses if and when the most valuable lineages are compromised. If major losses of tree taxa are incurred as a consequence of rising threats, other species will need to fill those voids to maintain ecosystem services. Sustaining the value that trees currently contribute to human well-being depends on sustaining the many tree species and lineages that collectively occupy the diversity of ecological niches across the continent. To do so requires intentional management of forests and trees in the face of myriad and simultaneous global change threats. Our study provides information and an approach that can contribute to precision forestry practices and ecosystem management—an approach that is applicable to other regions globally.

Materials and methods

Ecosystem services

We measured the net value of five tree-related ecosystem services by accounting for the value of benefits provided, minus the direct costs incurred to produce these services when applicable. Climate regulation and air pollution removal have no direct costs. The sources of direct costs for wood products production are in S3 Table and [83]; for tree crops and Christmas tree production, the sources are in S4 Table. These five services all had publicly available data, national coverage, and well-vetted valuation methods. These five services included two regulating services (climate regulation and air pollution removal) and three provisioning services (wood products, tree crops, and Christmas trees). We did not analyze services such as recreation, wildlife habitat, coastal protection, and aesthetic benefits derived from trees because these services either lacked a nationwide database or a suitable methodology linking benefits to specific tree species.

Annual value of climate regulation via carbon storage. Forest carbon stocks (live aboveground and belowground carbon) of trees by species by county were estimated using data and methods from the U.S. Forest Service (USFS) Forest Inventory and Analysis (FIA) [84]. Total standing live aboveground carbon stocks was estimated following the method of Woodall et al. [85]. The live belowground carbon stocks were modeled as a function of the aboveground live tree carbon stocks following [84] (see S1 Text D).

The FIA data does not include carbon stored in fruit and nut orchards or Christmas tree farms. We calculated estimates for live aboveground carbon for fruit and nut orchards and Christmas tree farms by species by county. Christmas tree farms have short harvest rotations; fruit and nut orchards have longer rotations. We set carbon storage values for these production systems equal to the mean carbon stored in an orchard or farm's biomass halfway through its rotation (see S5 Table, S1E Text). We use county level data on orchard acreage to get carbon stored by fruit and nut trees by county [86]. Only state level acreage is reported for Christmas tree farms. We allocated Christmas tree farm acreage to counties based on county-level population (U.S. Census Bureau 2016; see S1F Text, S6 Table). Overall results for carbon storage are insensitive to county allocation for Christmas tree farms because the latter make up 0.0004% of total calculated carbon storage.

To measure the monetary value of carbon storage for a single year we computed an annualized value for the social cost of carbon (ASCC) (S1G Text). The ASCC is derived from the social cost of carbon (SCC), which is an estimate of the present value of damages from releasing one ton of carbon into the atmosphere. SCC represents the value of carbon storage in perpetuity. We converted SCC to an annualized value (ASCC) that represents the value of carbon storage for a single year. We used a range of SCC values to calculate a range of ASCC values. SCC estimates include \$38.57 Mg^{-1} of C in 2010 \$ assuming a 5% discount rate, \$119.58 Mg^{-1} of C in 2010 \$ assuming a 3% discount rate, and \$192.87 Mg^{-1} of C in 2010 \$ assuming a 2.5% discount rate [87]. These values translate to ASCCs of \$1.93 Mg^{-1} of C in 2010 \$ for a 5% discount rate, \$3.59 Mg^{-1} of C in 2010 \$ for a 3% discount rate, and \$4.82 Mg^{-1} of C in 2010 \$ for a 2.5% discount rate.

Annual value of air quality regulation via avoided health damages due to tree-based air pollution removal. Removing air pollutants from the atmosphere provides benefits to human health, crop and timber yields, visibility, materials, and recreational opportunities [88,89]. Here, we calculated the value of the reduction in human mortality from removal of fine particulate matter ($PM_{2.5}$) and ozone (O_3) from the atmosphere by trees. Reductions in human mortality are the largest of the benefits generated by improving air quality [90].

The benefits from pollution reductions by trees were determined using estimates of the amount of pollution removed by tree species by county by pollutant [28,50], the 2011 National Emissions Inventory [91], and the AP3 integrated assessment model [92–94]. Nowak et al. [28,50] provide estimates of each pollutant removed by species by county by year. We then converted measures of annual pollutant removed by a species in a county to annual average improvements in ambient air quality, measured in $\mu g/m^3$/year, by dividing the μg/year removed in a county by the volume of air space in the county (land area *x* vertical height in meters, see S1H Text).

The AP3 model links emissions of common air pollutants by county in the U.S. to the ambient concentrations $PM_{2.5}$ and O_3 in each county. Using the National Emissions Inventory, AP3, and U.S. EPA's value of statistical life (VSL) estimate of \$7,570,229 (2015 USD), we computed county-level exposures, mortality risk, and monetary damages associated with the baseline level of 2011 emissions [94]. We calculated the average annual damage caused by a pollutant in a county in 2011 (in \$ 2010) by dividing the monetary damage predicted by AP3 for that pollutant in 2011 in the county by the ambient concentration of the pollutant in the county in 2011.

We found the expected annual value of $PM_{2.5}$ removal by a tree species in a county by multiplying the average damage caused by $PM_{2.5}$ in the county (measured in $\$/\mu g/m^3$) by the amount of the $PM_{2.5}$ removed by the species in the county over the course of a year (also measured in $\mu g/m^3$). We repeat this process to estimate the annual value generated by a species in a county that removes O_3 from the atmosphere. In Fig 1A shows the expected value of air pollution removal across all species, counties, and the two pollutants.

We used a Monte Carlo analysis to characterize the statistical uncertainty associated with our estimates. Specifically, we constructed two normal distributions, with means and variances that corresponded to the estimated distributions associated with U.S.-EPA's VSL [95] and the concentration-response parameters for $PM_{2.5}$ [96] and for O_3 [97]. We made 1,000 draws from these distributions, calculating benefits of pollution removal by species by county for each draw–thus constructing species and county specific empirical distributions of our benefit estimates. We calculate two sets of 5th and 95th percentile national-level estimates across both pollutants. One set of estimates only uses the uncertainty in the concentration-response function (the mean VSL is always used when constructing this 5th and 95th percentile). The other set of estimates uses uncertainty in both concentration-response function and VSL (S1 H and S1I Texts, S7 and S8 Tables, S3 Fig).

Annual value of wood product production. 2012 roundwood production data (including fuelwood, pulp, and sawlogs) were used at the county level [98]. Some of the roundwood production data in the dataset are attributed to individual species. The remaining production data are reported at the species group level in the dataset. We attributed species group output in a county to individual species output in that county according to each species' proportion of net volume in the county's total sawlog production from the 2007 to 2012 USFS FIA surveys. We calculated the annual monetary value of a species' roundwood production in a county by multiplying its annual roundwood production in cubic feet by the annualized net value of a cubic foot of harvested roundwood. The annualized harvested roundwood net values assume that all stands are managed as even-age rotation forests. The rotation period or harvest age for each species in a state is given by the FIA. Additional assumptions used when calculating annualized harvested roundwood values include using biomass growth functions parameterized with FIA data [99–101], observed 1998–2014 mean stumpage prices continuing indefinitely (in 2010 USD; S4 Table), and stand establishment costs in 2010 USD [83]. We calculated the expected annualized net value of wood roundwood production across all species and counties. We generated 5th and 95th percentile values of roundwood production at the species and county level using 5th and 95th percentile biomass growth functions for each species in each county. In all cases, we used a 5 percent per annum discount rate (S3 Table, S1 Text A).

Annual value of tree crop production. We calculated annualized net revenues for 21 fruit and nut tree species (S4 Table). We used information on the typical rotation length and the typical number of years between establishment and the production of marketable fruits or nuts to calculate the proportion of years the species produces fruits or nuts. Using state-level data on fruit and nut farm-gate prices for the years 2010 to 2012, state-level data on yields per acre for the years 2010 to 2012 (adjusted by the proportion of years the species produces fruits or nuts), and county-level tree crop acreage data for the years 2010 to 2012 [86], we calculated annual revenue in the years 2010, 2011, and 2012 at the species and county level. Then we used enterprise budget sheets to calculate several estimates of annualized per acre production cost for each species in each county. The expected annualized net revenue for a species in a county across the 2010 to 2012 period is equal to the 2010 to 2012 average annual revenue from that species in that county minus the mean county-level annualized production cost estimate for that species (see S1B Text) and is calculated for all species across all counties. Low and high estimates of annualized net revenue at the species and county level were also generated by using species and county-specific low and high estimates of annualized production cost (S4 Table and S1B Text).

Annual value of Christmas tree production. The number of Christmas trees sold and average price paid (2010 USD) in 2009 by species in each state were determined from USDA data (data were not available for the years 2010 to 2012; see S1C Text) [102]. We then used the sales and price data to estimate annual Christmas tree revenue by species and state. We used enterprise budget sheets to produce several estimates of annualized production cost for each species in each state. Finally, we allocated state and species-level annualized net return (in 2010 USD) from Christmas trees production to the county level using 2010 county-level population [103].

We calculated the expected annualized net value of Christmas tree production across all species and counties. In the mean value estimate we used the mean annualized production cost for each species in each state. Because annualized production costs are uncertain we also generated a low and high annualized net value of Christmas tree production for each species in each state with a low and high estimate of annualized production cost for each species in each state (S1C Text).

Species and lineage similarity in service provisioning across regions and states and dispersion of services across the tree of life

To understand the extent to which individual services are provisioned by similar or different lineages in different geographic regions, we computed matrices of similarity for tree species across USFS ecodivisions—which represent ecologically and climatically similar regions

(Fig 4A and S2 Fig). For species we calculated similarity as 1-D, where D was a matrix of Bray-Curtis dissimilarities to determine the relative proportion of similar species in any two samples. We also examined tree species in the context of their phylogenetic history. Each lineage—or branch—in the tree of life evolved from a common ancestor accumulating novel genes and characteristics over time reflecting the evolutionary diversification process. Consequently, species are organized hierarchically nested within lineages of larger and larger size. For lineages, we calculated matrices of phylogenetic similarity using the PhyloSor [20] method, which calculates the proportion of shared branch length on the tree of life between two samples. For each service, we weighted each species by its service value in each ecodivision. Christmas tree services were only calculated for states, because data were only available at the state level, not the county level, resulting in insufficiently resolved spatial information to aggregate them at the ecodivision level.

The dispersion of ecosystem services across the tree of life was analyzed by calculating the standardized effect sizes of the mean phylogenetic distance (SES MPD), reported as the Net Relatedness Index (NRI) (-1 x observed z value of MPD) and mean nearest taxon distance (SES MNTD), reported as the Nearest Taxon Index (NTI) (-1 x observed z value of MNTD) [104] with the 'phylogeny pool' null model—to draw species with equal probability from the tree of life—using the picante package in R [105]. The approach allows inference of whether services are more clustered or evenly spread across the phylogeny and whether close relatives share more or less similar service values than expected by chance (S2 Table and S1J Text). The phylogeny (S1 Data) was based on [14] and pruned to include the species in the study. Species not in [14] were assigned to the appropriate genus based on APG III and IV.

Threats to US trees

Climate change. We assessed the threat posed by climate change by 2050 as the proportion of the biomass of each species that is projected to be exposed to climatic conditions that are outside of their current range geographic distribution. Rasters for North America's current and projected climate were obtained from the AdaptWest Project [106]. County level threat for each climate variable was calculated as the sum of the biomass of species under threat divided by the total biomass in that county (S1L Text).

We chose to separately quantify climatic envelopes using mean annual temperature, total annual precipitation and aridity. Temperature and precipitation have been shown to directly impact the growth, spatial distribution, and management of trees [107–109]. Annual mean temperature and total precipitation are highly correlated with interannual measures (e.g. winter precipitation, winter-summer temperature differential, etc.) of these variables so that as a tree species moves out of its annual climatic envelope so too would the species experience movement away from the associated interannual envelope.

To capture the interaction of temperature and precipitation we assess an index of aridity obtained from the AdaptWest Project calculated as the maximum temperature of the warmest month divided by the mean summer precipitation. Drought stress has been shown to negatively impact the provision of forest services throughout the contiguous US [110]. Warmer temperatures can amplify the stress incurred by drought conditions leading to reduced tree growth and higher tree mortality particularly in the Western US [7,31].

For species that extend their ranges into Mexico where climatic conditions may be more arid, Global Biodiversity Information Facility (GBIF) data for all of North America was used to compute their climatic envelope instead of using the FIA data, ensuring that tolerances to aridity were not underestimated. To reduce the effect of outliers, we used the 1% and 99% quantiles of each climatic variable to define the envelope.

Pests and pathogens. To quantify the threat from pests and pathogens for forest species, we compiled the proportion of basal area of each species projected to be lost in each county due to disease outbreaks, as estimated by the US Forest Service [81]. Data referenced by common names were converted to scientific names. We estimated the threat for each species by taking the average projected proportional basal area loss in each county weighted by the proportion of the total biomass of the species in each county. Threats at the county level were calculated as the average predicted basal area loss of all species in the county weighted by the proportion of the biomass of each species in the county (S1K Text).

To quantify the threat from pests and pathogens for tree crop species, we used data from the USDA's Animal and Plant Health Inspection Service [111]. This website identifies each pest and pathogen that affects each fruit and nut tree species in each state. The fraction of each fruit and nut tree species biomass threatened by each pest and pathogen across the contiguous US is given by the amount of the species biomass in states threatened by the pest or pathogen divided by the total species biomass. We also calculated the fraction of fruit and nut tree species biomass threatened by one or more pest and pathogens across the contiguous US in similar fashion.

Forest fires. Forest fire threat was quantified as the projected change in the number of large fires per week per county from the historical late 20th century climate forcing to the mid-21st century forcing scenario as described [112]. We used the spatial raster from [112] to compute the fire threat for each county by taking the mean of the pixels that fell within the county. We then estimated the fire threat for each species as the average projected change in fire frequency in the counties the species occurs in, weighed by the species biomass in that county. Our species-level fire threat estimate is also in units of fires per week and negative values denote a decrease in the threat of major fires whereas positive values indicate an increase in the threat of major fires (see S1M Text).

Associations between ecosystem services and threats

To test for associations between the ecosystem services value of individual tree species and the degree of threat each faces, we calculated Spearman rank-order correlations between services and threats aggregated by species. Similarly, to test for spatial associations between the ecosystem service value of forests or plantations within each county and the degree of threat facing trees in that county, we calculated Spearman rank-order correlations between threats and services aggregated at the county level.

Supporting information

S1 Fig. A-D) Species similarities (1-Bray-Curtis pairwise dissimilarities) between ecodivisions in the tree species provisioning annual climate regulation value, (B) annual air quality regulation value, (C) annual wood product net revenue, and (D) annual tree crop net revenue. E-H) Lineage or "phylogenetic" similarities for the same ecosystem services using Phylosor [20] in the picante package in R [105], which gives the pairwise fraction of shared branch-lengths on the tree of life between two ecodivisions. For species and lineage similarities, green = high similiarity in composition (0.66–1), yellow = intermediate similarity in composition (0.33–0.66); orange = low similarity in composition (0–0.33).
(PDF)

S2 Fig. USDA Forest Service map showing the ecosystem divisions (ecodivisions) for the contiguous U.S.
(PDF)

S3 Fig. Annual county-level air quality regulation value per square mile (2010 USD) between 2010 and 2012 and location of continental US urban areas (light blue).
(PDF)

S1 Table. A) The most valuable continental US tree species ranked according to 2010 to 2012 annual ecosystem service value production (USD 2010), showing the highest value species for all services combined and individually for annual climate regulation value via carbon storage, annual air quality regulation via health damages avoided due to air pollution removal ($PM_{2.5}$ and O_3), and annual net revenue from wood products, tree crops, and Christmas tree production. B) The top twenty tree species forecasted to encounter threats from known pests and pathogens, multivariate climate change and increased fire exposure. The extent of threat to each species is given as the % biomass threatened—by pests and pathogens or by climate change forecasted by 2050 for mean annual temperature, total annual precipitation and aridity —or as the % increase in the number of weeks each species is exposed to fire by 2050.
(PDF)

S2 Table. Dispersion of ecosystem services across the tree of life. High mean phylogenetic distance (SES MPD; column "MPD obs Z") and high mean nearest taxon distance (MNTD; column "MNTD obs Z") (weighted by dollar value) indicate that services are dispersed widely across the tree of life (SES MPD) and that close relatives tend to have different ecosystem service values (SES MNTD), respectively. Negative values indicate that the services tend to be clustered within lineages (SES MPD) and that close relatives tend to provision services similarly (SES MNTD). Observed MPD and MNTD values (mpd.obs and mntd.obs) are shown relative to the mean (MPD rand mean and MNTD rand mea) and standard deviation (MPD rand SD and MNTD rand SD) of simulated values, based on 999 randomizations (runs) of species across the phylogeny. Standardized effect sizes—SES MPD and SES MNTD—are shown as z scores (MPD obs Z and MNTD obs Z); P values (MPD obs P and MNTD obs P) indicate whether services or threats are significantly clustered or overdispersed compared to random expectation. Significantly clustered ecosystem services are bolded. Significantly overdispersed services are italicized.
(PDF)

S3 Table. Sources of stumpage prices used to calculate the annual net value of wood production in the continental US.
(PDF)

S4 Table. Low and high estimated annualized A) orchard (tree crop) production costs (USD 2011 per acre) by state and B) Christmas tree production costs per tree species and state (USD 2010). Data sources are listed below each table.
(PDF)

S5 Table. Annual Mg of C sequestered by the biomass of an active orchard acre by tree crop species. Data sources are shown.
(PDF)

S6 Table. Amount of carbon stored in a 5-year old stand of trees in species groups that are often used as Christmas Trees.
(PDF)

S7 Table. Estimated mean and 5th and 95th percentile annual value of avoided health damages across the continental US due to tree-based removal of $PM_{2.5}$ and O_3 between 2010

and 2012 (Billions of 2010 USD).
(PDF)

S8 Table. Ordinary least squares estimate of a county's annual air quality regulation value per square mile regresses on the county's standardized distance to nearest large urban area (s) and the county's standardized carbon storage as of 2010–2012 per square mile (as a proxy for tree biomass abundance). Column (I) gives results of a model with standardized distance to the nearest *large* urban area, column (II) gives results with standardized average distance to nearest *five large* urban areas, column (III) gives results with standardized distance to the nearest urban area (regardless of size), and column (IV) gives results with standardized average distance to nearest *five* urban areas (regardless of size).
(PDF)

S1 Text. Further details of the methods and calculations are given in text sections A-N: A. Annual net value of wood product production. B. Annual net value of tree crop (fruits and nuts) production value. C. Annual net value of Christmas tree production. D. Annual value of climate regulation via carbon storage in US forests. E. Annual value of climate regulation via carbon storage in orchards. F. Annual value of climate regulation via carbon storage on Christmas tree farms. G. Annualized Social Cost of Carbon. H. Annual value of air quality regulation via avoided health damages from tree-based removal of air pollutants. I. Explaining annual air quality regulation values across the US. J. Phylogenetic dispersion of ecosystem services. K. Threats from tree pests and pathogens. L. Threats from climate change. M. Threats from change in frequency of major fires. N. References
(PDF)

S1 Data. Phylogeny in newick format.
(TXT)

Acknowledgments

Mary Shelley (SESYNC), Ian Muñoz (SESYNC), Belinda Befort (University of Minnesota), Chris Woodall (USFS), John Lyle Anderson (Bowdoin College), and Dylan Dilla (Bowdoin College) contributed to data retrieval, data compilation, scripting, data analysis and/or data synthesis.

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Characteristics of Black Bear Dens in the Southern Appalachian Region
Author(s): William G. Wathen, Kenneth G. Johnson, Michael R. Pelton
Source: *Bears: Their Biology and Management*, Vol. 6, A Selection of Papers from the Sixth International Conference on Bear Research and Management, Grand Canyon, Arizona, USA, February 1983 (1986), pp. 119-127
Published by: International Association of Bear Research and Management
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CHARACTERISTICS OF BLACK BEAR DENS IN THE SOUTHERN APPALACHIAN REGION

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Abstract: Dens of radio-instrumented black bears (*Ursus americanus*) were examined in the southern Appalachian Mountains from 1973 to 1982. Most dens were in tree cavities high above ground. Entrance height differed among tree species with high entrances in yellow poplars (*Liriodendron tulipifera*) and low entrances in chestnut oak (*Quercus prinus*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*). Den tree species differed with elevation, macrotopography, and microtopography. Both tree dens and ground dens were characterized by high microtopographic position. Chestnut oaks and northern red oaks (*Q. rubra*) comprised 10 of 15 tree dens in the exterior of the study area. Extensive use of these 2 species indicates the importance of incorporating site provisions into timber management plans in the Southern Appalachian Region.

Int. Conf. Bear Res. and Manage. 6:119–127

Black bears exhibit considerable versatility in den selection in various parts of their range. In regions with harsh winters most dens are excavations beneath standing trees, stumps, and fallen logs, or excavations directly into the hillside (Erickson 1964, Beecham 1980, Tietje and Ruff 1980). Jonkel and Cowan (1971) found most bears in Montana denned at the base of hollow trees and Beecham (1980) found some black bears in Idaho denned at the base of live trees. Dens in rock crevices are important to black bears in the southwestern United States (LeCount 1980, Graber 1981, Novick et al. 1981), and Lindzey and Meslow (1976) reported bears used stumps of fallen trees in Washington.

In the southeastern United States, black bears extensively use tree cavities high above ground. Use of tree dens has been reported in the mountainous regions of the southeast (Pelton et al. 1980, Johnson et al. 1981, Lentz and Marchinton 1983), and the river bottoms of Arkansas (Smith 1985) and Louisiana (Taylor 1971). Hamilton and Marchinton (1980) recorded a single instance of a black bear using a tree den in the North Carolina coastal plain, although they usually denned on the ground in a thick "Carolina bay" vegetation type. Other occasional instances of bears denning in trees have been reported in Michigan (Switzenberg 1955), Washington (Lindzey and Meslow 1976), and Pennsylvania (G. Alt, pers. commun.).

The denning period of black bears in the Southern Appalachian Region may extend from late November to early May (Johnson and Pelton 1980, Eiler 1981, Wathen 1983) and the birth of cubs occurs during this time. Because of the time and energy spent denning, during which bears do not eat, drink, urinate, or defecate (Folk et al. 1972), adequate dens may be important to survival and reproductive success. Tree dens may be superior to ground dens in the Southern Appalachian Region because they are relatively dry and secluded (Eiler 1981, Johnson and Pelton 1981). Johnson et al. (1978) reported that tree dens afforded bears a 15.0% energy savings compared to ground dens.

Little is known about the dynamics of cavity formation or the longevity of tree dens. However, preliminary tree age data collected by increment boring indicate that den trees are very old (275–300 years; Johnson and Pelton 1980). Current U.S. Dep. Agric., For. Serv. (USFS) timber rotations of 80–100 years for hardwoods have raised concerns that den tree resources may be reduced and adversely impact southern Appalachian black bear populations.

Our objectives are to report on den tree species and types of ground dens used by black bears in the Southern Appalachian Region and to describe characteristics of dens and their relevance to den selection. The physical and site characteristics of chestnut oak and northern red oak dens are presented and discussed relative to timber management practices in this region because they are used extensively as tree dens.

We gratefully acknowledge all those who assisted in field data collection. R. Wathen assisted tremendously in manuscript preparation. Financial support was provided by McIntire-Stennis Proj. No. 27, Agric. Exp. Sta. and Dep. of For., Wildl., and Fish, Univ. of Tenn., Knoxville, and the Tenn. Wildl. Resour. Agency.

STUDY AREA

The study area included the Great Smoky Mountains National Park (GSMNP) and adjacent Cherokee National Forest (CNF). The study concentrated in the northwestern quadrant of the GSMNP and the

Tellico Ranger District of the CNF, consisting of 994 km^2 and located between 35° 20′ 35° 47′ N latitude and 83° 05′ and 84° 20′ W longitude (Fig. 1).

The Great Smoky and Unicoi mountains occur in the Unaka Range of the Blue Ridge Province of the southern division of the Appalachian Highlands (Fenneman 1938). The area is mountainous with steep slopes. Much of the CNF is accessible by logging roads whereas most of the GSMNP is accessible only by foot trail.

Elevations range from 230 to 2,024 m and climate varies with elevation. Average annual precipitation ranges from 140 to 220 cm at lower and higher elevations, respectively. Average annual temperature ranges from 14 C at elevations below 450 m to 8 C at elevations above 1,900 m (Stephens 1969).

Rock formations are classified in the Ocoee Series of the late Precambrian (King et al. 1968). Soils are predominantly of the Ramsey association, and characterized by low fertility, low water holding capacity, and susceptibility to erosion (Anonymous 1945, 1953). Most of the area is unsuitable for agriculture.

The vegetation of GSMNP is diverse and classified as topographic climax or secondary (Whittaker 1956). Six major forest types are recognized within the GSMNP: cove hardwood, hemlock, northern hardwood, closed oak, open oak-pine, and spruce-fir (Shanks 1954). Intensive logging was prevalent in the GSMNP from the 1900s until park establishment in 1934 (Lambert 1961). Approximately 39% of GSMNP is virgin, and many cull trees remain (Johnson and Pelton 1981).

As part of the CNF, Tellico Ranger District is managed for multiple use and sustained yield of timber, outdoor recreation, watershed, and wildlife resources. Timber is managed on an even-aged rotation. A 67 km^2 bear sanctuary, where no bear hunting is allowed, has been established in a portion of the Tellico Ranger District. Annual bear hunts are held in December in other portions of the CNF. Bears in the GSMNP are unexploited except for illegal hunting.

Four main sections are recognized in the study area: 1) Sugarland/Elkmont area (Sugarland Mountain), 2) Bote Mountain/Defeat Ridge/Tremont area (Bote Mountain), 3) Parsons Branch Road/Bunker Hill area (PNR), and 4) Tellico Ranger District of the Cherokee National Forest (CNF) (Fig. 1). The PBR and CNF sections were similar in habitat and elevation and designated as the "exterior" of the study area. Sugarland Mountain and Bote Mountain were designated as the "interior" of the study area.

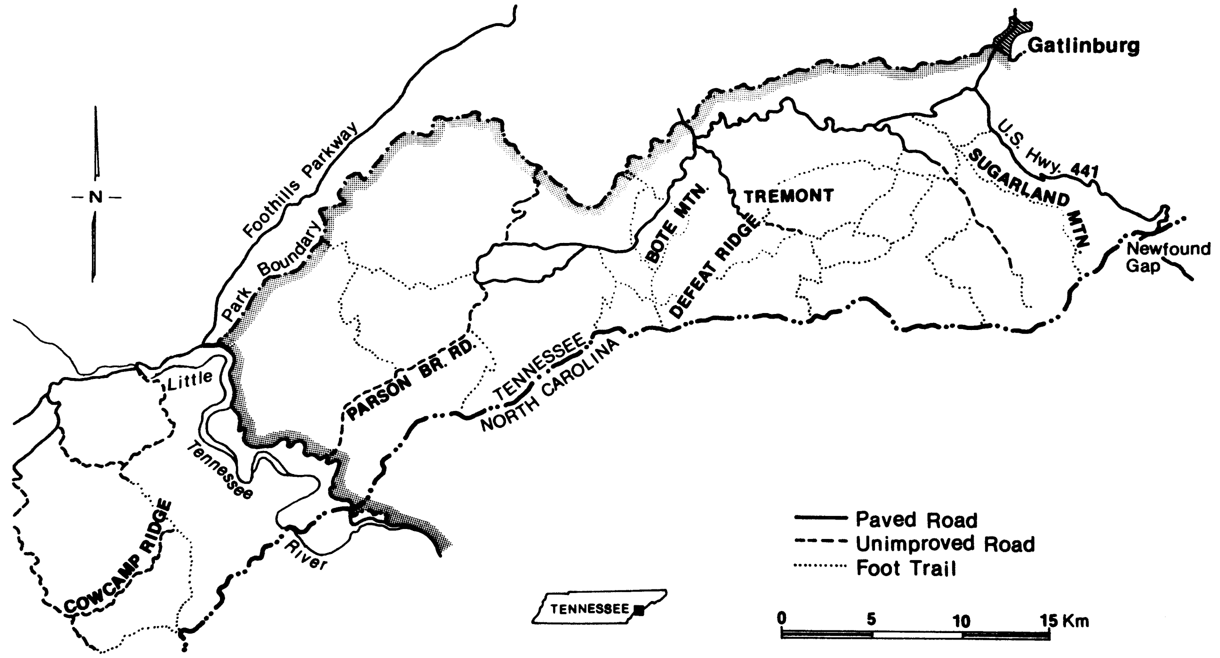

Fig. 1. The Southern Appalachian Region black bear den site study area.

METHODS AND MATERIALS

Black bears were captured with Aldrich spring-activated foot snares or barrel traps, immobilized with M-99 (etorphine hydrochloride) or phencyclidine hydrochloride. Radiotransmitters (Wildlife Materials, Inc., Carbondale, Ill. and Telonics, Inc., Mesa, Ariz.) were attached to selected individuals (N = 66) for further monitoring. A 1st premolar was extracted to determine age by the cementum annuli technique (Willey 1974).

Dens of radio-instrumented bears were located and physical and site characteristics were measured during the winter or after den emergence. Topography was measured in 2 ways: microtopographic (micro) position was measured as the percentage of elevational distance of the den from the nearest ridgetop to the bottom of the nearest concavity; macrotopographic (macro) position was measured as the percentage distance of the den from the large ridge most affecting the local topography to the nearest downslope stream (ridgetop = 0%, mid-slope = 50%, cove bottom = 100%) (Golden 1974:51). Other site parameters recorded included elevation, slope steepness and aspect, forest type, and understory density. Den physical characteristics measured included entrance size, entrance aspect, diameter at breast height (DBH) of tree dens, and height of entrance above ground (tree dens). Cavity dimensions of some tree dens were not obtained because the den was occupied or the den presented physical constraints. Cavity dimensions of black bear dens in the GSMNP were previously reported by Johnson and Pelton (1981).

Statistical analysis of parametric data was performed using t-test and analysis of variance (ANOVA). Variables analyzed with ANOVA were compared with the least-squares means (SAS 1982). Analysis of categorical data was performed with the G-test (Sokal and Rohlf 1969:561). The 0.05 probability level was accepted as significant, but all probabilities are presented to clarify data interpretation (Tacha et al. 1982).

RESULTS AND DISCUSSION

Ninety-five dens of 14 male and 52 female black bears were examined from 1973 to 1982. A majority (55.8%) of the dens were located in tree cavities high above the ground ($\bar{x}$ = 11.9 m). Den tree species included chestnut oak (N = 13), northern red oak (N = 10), eastern hemlock (*Tsuga canadensis*) (N = 6), yellow poplar (N = 5), yellow birch (N = 5), black gum (*Nyssa sylvatica*) (N = 4), red maple (N = 4), black cherry (*Prunus serotina*) (N = 1), scarlet oak (*Q. coccinea*) (N = 1), yellow buckeye (*Aesculus octandra*) (N = 1), and an American chestnut snag (*Castanea dentata*) (N = 1). Ground dens included cavities under roots of wind-tilted trees (N = 12), rock crevices (N = 10), tree stumps (N = 9), overblown logs (N = 4), ground nests (N = 4), and at the base of live trees (N = 3).

Physical Characteristics of Dens

The DBH of tree dens averaged 100.7 cm (Table 1). The DBH of tree stump dens ($\bar{x}$ = 112.4 cm) and den cavities at the base of live trees ($\bar{x}$ = 102.7 cm; Table 2) indicated that large trees were important in the formation of ground dens as well as tree dens (Johnson and Pelton 1981).

Entrances of ground dens ($\bar{x}$ = 0.316 m^2; Table 2) and tree dens ($\bar{x}$ = 0.392 m^2; Table 1) were similar. However, several (N = 8) ground dens (primarily ground nests and overblown logs) were without discrete measurable entrances and were not included in the analysis of entrance data. Therefore, the calculated mean entrance size of ground dens (0.316 m^2) is underestimated. Cavities at the base of live trees, root system cavities, and rock crevices generally had small entrances into protected cavities. Cavities under overblown logs and those associated with tree stumps typically were less protective, and ground nests offered little or no protection from climatic elements.

Eighteen of 35 tree dens had entrances at the top of the main truck and 17 had lateral openings. No species exhibited a disproportionate number of side or top entrances. Entrances at the top ot the main truck ($\bar{x}$ = 0.623 m^2) were larger (P < 0.01) than side entrances ($\bar{x}$ = 0.293 m^2). Lentz and Marchinton (1983) calculated that 11% of the heat retention of a tree den could be accounted for by the position of the entrance. Side entrances provided greater heat retention than top entrances (Thorkelson and Maxwell 1974, Lentz and Marchinton 1983), possibly a result of the size of the entrances, but also related to the view factor (Thorkelson and Maxwell 1974, Johnson et al. 1978).

Lentz and Marchinton (1983) indicated that depth of cavity below the entrance provided most (59%) of the heat retention capabilities of tree dens. Although this parameter was measured for only a portion of our tree dens (N = 17, $\bar{x}$ = 2.2 m; Johnson and Pelton 1981), the relative depths for the remaining sample were visually estimated. Eight tree dens had cavities extending to the base of the tree; most ($N = 7$) of these were chestnut oaks. The average depth was 8.7 m, about 4 times the 2.2 m average depth reported by Johnson and Pelton (1981). Based on cavity depth, chestnut oak dens probably offer some heat retention advantages over other den trees. However, some of these advantages may be negated by generally larger entrances (Table 1) and ground moisture associated with ground level dens (Johnson and Pelton 1981).

The entrances to tree dens averaged 11.9 m (range 5.1–27.5) above ground, with significant differences ($P < 0.0001$) among species (Table 1). High entrances occurred in yellow poplar ($\bar{x} = 21.3$ m) and yellow buckeye ($\bar{x} = 19.8$ m), and low entrances occurred in chestnut oak ($\bar{x} = 9.4$ m), red maple ($\bar{x} = 9.2$ m), and yellow birch ($\bar{x} = 8.7$ m). Entrances above the ground offer black bears seclusion and tree dens may be especially important to females (Eiler 1981, Johnson and Pelton 1981). Bears in dens with higher entrances were less likely than others to be disturbed by researchers. In this study, females denned higher ($\bar{x} = 12.4$ m) in trees than males ($\bar{x} = 9.5$ m, $P < 0.04$). Several investigators have indicated that female black bears are more selective of den sites (Erickson 1964, Johnson and Pelton 1981, Lentz et al. 1981), and the higher entrances to their dens may reflect selection for more seclusion.

More den entrances had western than eastern aspects (G = 5.024, $P < 0.03$). Ground dens (G = 2.206, $0.10 < P < 0.50$) did not reflect this relationship as well as tree dens (G = 2.750, $0.05 < P < 0.10$). The predominance of westerly openings to tree cavities may reflect the effect of the prevailing westerly winds on cavity formation. Most (92%) tree den cavities apparently resulted from wind breakage of large limbs and ensuing natural decay.

Table 1. Mean physical and site characteristics of black bear tree dens in the Southern Appalachian Region.

Tree den species	N	DBH (cm)	Entrance height above ground (m)	Entrance size (m^2) (H[cm] by W[cm])	Elevation (m)	Slope (degrees)	Microtopographic position (%)	Macrotopographic position (%)
Chestnut oak	13	91.5	9.4	0.566 (159.8 by 33.5)	771.4	30.2	23.9	23.9
Northern red oak	10	99.4	13.3	0.372 (91.0 by 38.6)	982.1	30.9	29.2	44.0
Eastern hemlock	6	121.1	11.1	0.407 (89.0 by 41.0)	1,241.4	28.5	42.5	50.0
Yellow poplar	5	116.6	21.3	0.451 (105.0 by 43.5	843.7	22.0	66.0	75.0
Yellow birch	5	99.3	8.7	0.247 (75.4 by 36.2)	1,289.9	35.0	55.0	53.6
Blackgum	4	95.2	14.7	0.146 (41.8 by 35.0)	962.4	27.3	31.3	54.5
Red maple	4	97.1	9.2	0.497 (118.0 by 44.8)	1,232.9	34.0	6.0	13.3
Black cherry	1	123.5	—	—	975.4	30.0	80.0	50.0
Scarlet oak	1	81.8	11.5	0.240 (80.0 by 30.0)	1,219.2	20.0	5.0	0.0
Yellow buckeye	1	94.9	19.8	0.130 (48.0 by 27.0)	1,438.7	32.0	7.0	88.0
Chestnut snag	1	101.9	11.4	0.095 (28.0 by 34.0)	1,194.8	31.0	17.0	4.0
Mean for all dens		100.7	12.1	0.402 (105.6 by 37.2)	1,006.7	29.9	33.9	41.5
F		1.60	4.35	0.88	4.94	1.05	2.05	2.71
$P <$		0.1406	0.0006	0.5528	0.0001	0.4210	0.0551	0.0132

In certain regions of black bear range, particulary those with severe winters, den entrance aspect may be important in den selection. Beecham (1980) found that most dens in Idaho faced west, northwest, or north, and believed that these exposures allowed deeper snow accumulation and better insulation. Tietje and Ruff (1980) found that most dens in Alberta faced north and west, but believed that den entrance aspect was not a primary factor in site selection. Other investigators have proposed that entrance aspect was minimally important in den selection (Lindzey and Meslow 1976, Johnson and Pelton 1981). Johnson and Pelton (1981) indicated that protection from wind and precipitation was adequate when the tree cavity was well below the entrance. Our study indicates that entrance aspect was of little importance in den selection, but it likely reflects den availability.

Site and Vegetative Characteristics of Dens

The average slope of all den sites was 31.3° with ground dens ($\bar{x}$ = 33.3°; Table 2) occurring on steeper slopes ($P < 0.04$) than tree dens ($\bar{x}$ = 29.9°; Table 1). The slope aspects on which dens occurred were evenly distributed among northeast ($N = 29$), northwest ($N = 28$), and southwest ($N = 21$) exposures, with fewer ($N = 10$) on southeast slopes. This relationship was consistent for both tree and ground dens and likely reflects study area topography, with the major ridge (Tenn.-N. Carol. border) running northeast to southwest (Fig. 1).

The average elevation of all dens was 962.7 m. No significant differences were noted between ground and tree dens with respect to micro- ($P < 0.60$) or macro- ($P < 0.13$) positions on slopes. However, the micro-position of ground and tree dens was higher than the macro-position. Most dens (84.1%) occurred on the upper half (0–50%) of the micro-position (G = 43.2, $P < 0.0005$). This significant relationship existed for ground (G = 14.9, $P < 0.0005$) and tree dens (G = 27.0, $P < 0.0005$). Most tree dens (62.7%) were also on the upper half of the macro-position, although the relationship was not significant (G = 3.4, $0.05 < P < 0.10$). Ground dens were evenly distributed between the upper ($N = 19$) and lower halves ($N = 18$).

Tree den species differed with elevation ($P < 0.0001$) and macro-position ($P < 0.01$; Table 1); micro-position differences were nearly significant ($P < 0.06$). Chestnut oak ($\bar{x}$ = 771.4 m) and yellow poplar ($\bar{x}$ = 843.7 m) dens occurred at low elevations; red maple ($\bar{x}$ = 1,232.9 m), eastern hemlock ($\bar{x}$ = 1,214.4 m), and yellow birch ($\bar{x}$ = 1,289.9 m) dens were at high elevations. Yellow poplar ($\bar{x}$ = 75.0%) and yellow buckeye ($\bar{x}$ = 88.0%) den macro-position was low, whereas red maple ($\bar{x}$ = 13.3%) and chestnut oak ($\bar{x}$ = 23.9%) den macro-position was high. The micro-position patterns of den tree species was similar to macro-position; yellow poplar dens ($\bar{x}$ = 66.0%) occurred low, and red maple ($\bar{x}$ = 6.0%) and chestnut oak ($\bar{x}$ = 23.8%) dens occurred high.

The relationship of site characteristics to den selection by black bears is complex and likely related to availability. For instance, ground dens were distributed over a wide range of elevational and topographical situations, although there was some variation among ground den types with respect to slope and elevation (Table 2). The predominance of ground dens on the upper half of the micro-position may reflect a tendency of bears to select ground dens on drier and better-drained soils on upper slopes. Also, the importance of large trees and wind damage (Johnson and Pelton 1981) to cavities associated with the root systems of wind-tilted trees probably increases their availability higher on slopes.

Den tree species were more closely related to elevation, and micro- and macro-position than were ground dens. Differences are largely related to specific growth requirements of the den tree species associated with elevation and soil characteristics (micro- and macro-position). Furthermore, the high micro-position of most den trees apparently reflected the susceptibility and increased availability of these trees to ice and wind damage and subsequent cavity formation.

The density of understory vegetation was greater (G = 14.3, $P < 0.0005$) around ground dens than tree dens. Most ground dens (87.2%) had dense or moderate understories, whereas most tree dens (66.0%) were associated with moderate and light understories. Five tree dens had no understory, but no ground dens lacked understory. Predominant understory species associated with ground dens with dense understories included rhododendron (*Rhododendron maximum*) (47.6%), wild grape (*Vitis* sp.) and greenbriar (*Smilax* sp.) (38.1%), and mountain laurel (*Kalmia latifolia*) (14.3%). Lentz and Marchinton (1983) also found that rhododendron and mountain laurel offered concealment and wind protection to dens in northeastern Georgia.

The relationship of understory density to ground dens may be a function of past disturbances such as

Table 2. Mean physical and site characteristics of black bear ground dens in the Southern Appalachian Region.

Den type	*N*	DBH (cm)	Entrance size (m^2) (H[cm] by W[cm])	Elevation (m)	Slope (degrees)	Microtopographic position (%)	Macrotopgraphic position (%)
Cavity associated with root system	12	—	0.277 (45.8 by 57.7)	934.5	35.2	31.5	56.5
Rock crevice	10	—	0.362 (45.5 by 82.9)	1,035.6	34.4	26.1	51.6
Tree stump	9	112.4	0.382 (53.9 by 70.8)	927.9	36.0	37.6	41.1
Overblown logs	4	—	0.105[a] (27.0 by 39.0)	594.4	32.0	26.7	67.3
Ground nest	4	—	—	809.2	28.3	21.3	62.5
Cavity at base of live tree	3	102.7	0.180 (43.7 by 42.7)	792.5	25.3	31.7	35.0
Mean for all dens		109.9	0.316 (47.1 by 66.7)	903.8	33.3	30.2	51.5
F		0.10	1.51	2.03	2.34	0.18	0.83
P <		0.7632	0.2254	0.1003	0.0661	0.9679	0.5379

[a] Entrance size based on 1 measurement; other entrances were immeasurable.

logging (tree stump cavities) or wind damage (overblown logs, root systems of wind-tilted trees) opening the canopy and creating seral vegetation stages. The dense understory typical around ground dens likely conceals black bears (Johnson and Pelton 1981), but apparently was not as important to bears in rock crevices or cavities at the base of live trees. In these dens, small openings and enclosed cavities probably provide adequate concealment and protection.

Ground dens occurred in a variety of vegetation types including open oak-pine (27.5%), wild grape and greenbiar (22.5%), other early successional stages (12.5%), cove hardwood (12.5%), closed oak (10.3%), northern hardwood (7.7%), eastern hemlock (5.1%), table mountain pine (*Pinus pungens*) (2.6%), and a clear-cut area (2.6%). Tree dens occurred in northern hardwood (26.4%), open oak (22.6%), cove hardwood (18.9%), closed oak (17.0%), eastern hemlock (11.3%), and early successional (3.8%) forest types. We did not find general patterns associating certain types of ground dens with specific vegetation types. However, most (78%) tree stump cavities occurred in early successional ($N = 2$) or wild grape ($N = 5$) vegetation types. The disturbance from earlier logging activities in these areas probably resulted in the influx of these early seral stages. Den tree species were largely restricted to specific forest types, with yellow poplar and yellow birch occurring exclusively in cove hardwood and northern hardwood forest types, respectively.

The relationship of black bear dens to site and vegetative characteristics is complex, especially in areas of less severe winters. Lindzey and Meslow (1976) found no evidence of slope aspect influencing den selection in Washington, but noted that adults selected dens in secure timbered areas, whereas yearlings tended to den in open, less secure areas. Black bears in southern California selected dens associated with the Canyon Oak Series vegetation type which offered thermal advantages (cooling) compared to dens in less protected areas (Novick et al. 1981). In Arizona, black bear dens were surrounded by dense vegetation and occurred on north- or west-facing slopes between 1,300 m and 1,500 m (LeCount 1980). Black bears of North Carolina's coastal plain denned in Carolina bays surrounded by dense vegetation (Hamilton and Marchinton 1980).

In the Southern Appalachian Region, black bears appear to prefer tree dens over ground dens. Eiler (1981) and Johnson and Pelton (1981) found a disproportionate use of tree dens, especially by female bears, even in areas that had been subjected to clear-cut logging operations (Tremont) or to even-age timber management (CNF). Apparently, site and vegetative characteristics had little influence on the actual selection of a tree den, but was more related to that tree's specific site requirements. Although tree dens offer better protection than ground dens, results of this study indicated that selection of certain den tree species was a function of availability rather than superior protection afforded by specific tree den species.

Area Differences

A wider variety of den types was used in the interior ($N = 15$) of the study area than in the exterior ($N = 6$, $G = 3.126$, $0.05 < P < 0.10$), probably because of elevational differences between the 2 areas. Dens in the interior occurred from 518 m to 1,036 m ($\bar{x} = 770$ m). The greatest number of den types ($N = 15$) occurred between 915 m and 1,219 m because of the increased availability of different den tree species at higher elevations. All types of ground dens were used at elevations below 762 m. Increased diversity of interior den types was also a result of increased habitat complexity.

The relative lack of den type diversity in the exterior of the study area magnifies the importance of chestnut oak and northern red oak as den tree species. Chestnut oak and northern red oak comprised 4 of 8 tree dens in the PBR area and 6 of 7 tree dens in the CNF. The availability and use of yellow poplar ($N = 3$) and black cherry ($N = 1$) in the PBR are probably related to the lack of logging activities. The yellow poplar used as a den in the CNF area was in a virgin timber stand in North Carolina. Therefore, chestnut oak and northern red oak dens appear to be extremely important in low elevation areas undergoing timber management in the Southern Appalachian Region.

Characteristics of Chestnut Oak and Northern Red Oak Tree Dens

The DBH of chestnut oak dens ($\bar{x} = 91.5$ cm) and northern red oak dens ($\bar{x} = 99.4$ cm) was similar ($P < 0.33$) as were entrance sizes ($\bar{x} = 0.566$ m^2 and 0.351 m^2, respectively; $P < 0.25$). However, entrances to northern red oak dens ($\bar{x} = 13.3$ m) were significantly higher ($P < 0.03$) than chestnut oak dens ($\bar{x} = 9.5$ m). Nine of 13 entrances to chestnut oak dens had southeast or southwest aspects, whereas most entrances to northern red oak dens had northwest or southeast aspects. Northern red oak dens ($\bar{x}$ = 982.1 m) occurred at higher elevations ($P < 0.02$) than chestnut oak dens ($\bar{x}$ = 771.4 m). Both species were used at elevations between 610 and 1,219 m, but chestnut oak dens were apparently the only species used below 610 m. Both chestnut oak and northern red oak dens ($\bar{x}$ = 23.9% and 29.2%, respectively) had high micro-positions, but northern red oak dens ($\bar{x}$ = 44.0%) had lower macro-position than chestnut oak dens ($\bar{x}$ = 23.9%). The micro- and macro-position patterns demonstrated by these 2 species probably reflect the importance of wind damage to cavity formation resulting on high micro-position sites (Johnson and Pelton 1981), and general soil and topography requirements of the respective species. Chestnut oaks are typically found in dry, sandy, and rocky soils characteristic of ridges of the Southern Appalachian Region (Fowells 1965:574, Harlow and Harrar 1969:308-309), whereas northern red oaks grow on sandy loam soils from middle to lower slopes (Fowells 1965:589, Harlow and Harrar 1969:315). Both chestnut oak (9 of 13) and northern red oak (7 of 9) tree dens were predominantly on northern aspects.

Most (9 of 10) northern red oak dens were found in closed oak (N = 6) or northern hardwood (N = 3) forest types, whereas most (10 of 13) chestnut oak dens occurred in open oak-pine. Predominant understory species associated with chestnut oak dens included mountain laurel, rhododendron, hardwood tree saplings, hemlock, blueberries (*Vaccinium* spp.), and huckleberries (*Gaylusaccia* spp.) characteristic of drier sites. Eight of 13 chestnut oak dens were associated with moderate understories. Northern red oak dens occurred in understories classified as none (N = 13), light (N = 3), or moderate (N = 4), consisting primarily of hardwood saplings, rhododendron, and wild grape—species characteristic of more mesic sites.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Black bears prefer tree cavities above ground as winter dens in the Southern Appalachian Region. Chestnut oaks and northern red oaks are the primary species used as den trees outside the GSMNP. The availability of tree dens on national forests is largely unknown, but projected increases in timber production, use of cable logging, and conversion of "poor " quality sites to white pine (*Pinus strobus*) will reduce available den trees on national forests in the Southern Appalachian Region. Therefore, timber management should be coordinated with den tree requirements and based on short-term and long-term management strategies.

Short-term management should assess the availability of den trees on USFS lands, and ensure preservation of individual den trees through careful coordination with logging activities. Long-term considerations should include initiating research to determine site and vegetative characteristics useful in quantitatively classifying and mapping areas with high potential for den tree production. Areas with high potential should be placed in old-growth management compartments or wilderness areas.

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THE DEVELOPMENT OF OLD-GROWTH STRUCTURAL CHARACTERISTICS IN SECOND-GROWTH FORESTS OF THE CUMBERLAND PLATEAU, KENTUCKY, U.S.A.

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THE DEVELOPMENT OF OLD-GROWTH STRUCTURAL CHARACTERISTICS IN SECOND-GROWTH FORESTS OF THE CUMBERLAND PLATEAU, KENTUCKY, U.S.A.

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December, 2012

DEDICATION

This work is dedicated to all of the individuals and organizations whose tireless efforts to protect and preserve our forests has allowed us to experience the beauty and wonder of the deciduous forests of eastern North America.

And

To the Great Forest, who's resiliency speaks volumes of the richness of the past and gives hope for the future. May she return in all her greatness.

ACKNOWLEDGEMENTS

I would first like to thank the members of my thesis committee, Dr. Neil Pederson, Dr. Ronald Jones, Dr. Jennifer Koslow, and Dr. Charles Elliot. I would like to express particular gratitude to Dr. Neil Pederson for taking me on as a student during a period of transition, and for remaining a mentor throughout this process, and to Dr. Ronald Jones for stepping in as committee Chair and advisor. Thanks also to Dr. Tyler Smith for assistance during his time at EKU.

I could not have completed this research without the help of the many field assistants willing to volunteer their time and brave the poison ivy, ticks, chiggers, and other challenges of traversing Kentucky forests in summer. In particular, I have the utmost gratitude for Brad Catron and Robert Ukeiley, each of whom accompanied me on many occasions and helped to make my many trips into the woods all the more enjoyable.

Thanks to the Eastern Kentucky University Division of Natural Areas and Dr. Ryan McEwan for sharing data from Lilley Cornett Woods, to the Daniel Boone National Forest for providing GIS data, and to David Taylor for assisting me in acquiring the necessary permits. Greatly appreciated financial assistance came from the Kentucky Academy of Science. Thanks as well to Kentucky Heartwood, my employer these last several years, for ongoing support, encouragement, and inspiration.

And, finally, to my wife and partner, Tina Marie Johnson, for your help in the field and at home, for your patience throughout this endeavor, and for sharing with me your love of forests and all those little things that escape my notice.

ABSTRACT

Prior to Euro-American colonization beginning in the late 1700s and subsequent periods of land conversion and intensive resource extraction, most forest on the Cumberland Plateau in Kentucky would have existed in a state meeting one or more of the definitions of old-growth forest in use today. However, many recovering, mature forests currently exist that might be redeveloping old-growth structure and function. To assess the development of old-growth forest characteristics in second-growth forests, 70 – 90 year old (young) and 140 – 160 year old (old) hardwood forests in the Daniel Boone National Forest were examined for a suite of structural characteristics to discern patterns of structural and successional development. Old forest was distinguishable from young forest, having reached thresholds similar to old-growth for presence of large canopy trees, coarse woody debris volume and size distribution, multi-age distribution, age of oldest trees, and complex canopy structure. Both ages of forest met thresholds for total basal area and met some proposed thresholds for stem density. Neither age of forest met suggested minimum densities for old-growth for snags > 30 cm DBH, though old forest had almost three times that of young forest, and nearly approached values reported for old-growth forest. Young and old forest also exhibited different patterns in oak and maple dynamics. Understory maples and overstory oaks recruited synchronously in young forest during the 1920s and 1930s, while recruitment of both species in old forest was temporally more broadly distributed.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

1. INTRODUCTION

Prior to Euro-American colonization beginning in the late 1700s and subsequent periods of land conversion and intensive resource extraction, the forests of eastern Kentucky's Cumberland Plateau were part of a nearly contiguous forest covering much of the eastern United States. The Eastern Deciduous Forest, sometimes called "The Great Forest," was estimated to have covered as much as 380 million hectares (Leverett 1996; Bolgiano 1998), including an estimated 85 – 90% of Kentucky's total land area (Evans and Abernathy 2008). While those forests would have fluctuated within a range of community associations, structural relations, and successional states, most forest on the Cumberland Plateau would have existed in a state meeting one or more of the definitions of old-growth forest in use today.

Forest clearing for agricultural and industrial use in the Cumberland Plateau from around the mid-1800s to 1930 left little forest untouched, and only a few examples of relatively intact old-growth forests remain in Kentucky (Jones 2005). However, many recovering, mature forests currently exist that might be redeveloping old-growth structure and function. Many existing old-growth forests are recognized as having initiated following major disturbance (Whitney 1994), and models of forest structural development describe forests as proceeding from a regenerating, even-aged distribution toward a multi-aged, old-growth architecture given sufficient time (Oliver and Larson 1996; Frelich 2002). While the specifics may vary by disturbance intensity, species composition, climate, and edaphic conditions, the natural redevelopment of old-growth forest structure, composition, and processes is expected (Frelich 2002).

The purpose of this investigation was to assess the development of old-growth structural characteristics in some of the oldest second-growth hardwood forests of eastern Kentucky.

1.1 DEFINING OLD-GROWTH FOREST

While the term “old-growth forest” itself may be in common use and evocative of some archetypal visage, it is too general from a scientific or operational perspective to be used without further clarification (Wirth et al. 2009). Generally, most definitions or criteria for assigning or assessing a forest as old-growth can be divided into structural, successional, or age-related considerations (Wirth et al. 2009; Cooper 2011). Frelich and Reich (2003) offer several ecological definitions for old-growth forest that are useful in considerations for the Cumberland Plateau and other regions.

Climax Old-Growth

The climax definition of old-growth forest references the final stage in successional development of the community (Clements 1936; Braun 1950). Hypothesized to be a steady state of community organization in the absence of disturbance, the existence of a true climax community has come into question as the integral relationship between climate change, disturbance, and community structure has come to be better understood.

In terms of forest development, a climax old-growth forest is one that is dominated by shade-tolerant, self-replacing species, and occurs in the absence of significant disturbance that would otherwise allow for more influence by shade-intolerant or mid-tolerant species (Frelich 2002). Understory and midstory species are essentially the same as those in the canopy, such that turnover in the canopy results in a continuity of species composition.

In the Appalachian region, species typifying climax old-growth are sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and black gum (*Nyssa sylvatica*) (Lorimer 1980).

Sub-Climax or Seral Old-Growth

Sub-climax or seral old-growth forests are those that are composed of shade-intolerant or mid-tolerant species, such white oak (*Quercus alba*), tulip poplar

(*Liriodendron tulipifera*), and mockernut hickory (*Carya tomentosa*), but otherwise exhibit age and structural characteristics associated with old-growth (Frelich and Reich 2003). Species composition in these forests is understood to be maintained by periodic disturbance, without which the forest succeeds to shade-tolerant, climax-associated species.

Primary Forest

Primary forests are those that have developed in the absence of significant interference from humans through logging, agricultural clearing, or other major manipulation. Structure in primary forests results from a continuous legacy of natural disturbance, regeneration, and stand development (Frelich and Reich 2003). The term *virgin forest* can be considered synonymous with primary forest.

Typically, forests initiating prior to settlement by Euro-Americans are considered primary forests. However, the applicability of this definition can become muddied when considering the role of anthropogenic fire prior to Euro-American colonization or the loss of species like American chestnut (*Castanea dentata*) from a human-introduced blight in forests otherwise undisturbed by modern humans.

Secondary Old-Growth

Forests that have been heavily logged or cleared at some time in the past, and in particular since Euro-American settlement, but have redeveloped structural or age characteristics similar to old-growth under one of the above definitions are considered secondary old-growth (Frelich 1995; Frelich and Reich 2003). Many secondary forests in New England are considered secondary old-growth on account of the amount of time of regrowth since initial disturbance associated with European colonization of the region (Dunwiddie et al. 1996). The question of whether old second-growth forests in the Cumberland Plateau region in Kentucky can or should be considered secondary old-growth is unclear and the purpose of this investigation.

1.2 STRUCTURAL CHARACTERISTICS

Structural characteristics of old-growth forests can vary widely depending on forest type, disturbance regime, climate, edaphic conditions, and other variables. For example, an old-growth boreal forest will have a substantially different structure than an old-growth tropical forest, yet both may be validly considered old-growth (Wirth et al. 2009). Still, a great deal of consistency has been found in the structural characteristics associated with old-growth forests across the Eastern Deciduous Forest and the Central Appalachians (Parker 1989; Martin 1992; Tyrrell and Crow 1994), suggesting a certain unity in pattern and process across the Eastern Deciduous Forest as a whole.

Accepting natural variation and differing ranges of values depending on species composition, forest productivity, and other factors, this suite of characteristics can be used to assess old-growth status or degree of "old-growthness," which describes the extent to which a forest exhibits the structural and functional characteristics associated with old-growth forests (Bauhus et al. 2009). While the following characteristics are often indicative of old-growth, it is important to note that the presence or absence of some characteristics does not necessary mean that the forest is or is not de facto old-growth per any given definition. Subsequent use of the term "old-growth forest" herein refers to that which is found primarily in the Eastern Deciduous Forest region of North America.

Canopy Age

Canopy age is often used as a criterion for determining old-growth forest status. In some cases, the age approach is somewhat arbitrary and can be based more on socio-political rather than ecological considerations (Frelich and Reich 2003). In Kentucky, forest stands are generally considered old-growth if the dominant canopy is older than the period of initial colonization by Euro-Americans near the end of the 1700s. Martin (1992) suggested that to be considered old-growth, the oldest trees in mixed mesophytic forest communities should be at least 200 years old based on the average life expectancy of canopy dominants, while

Parker (1989) similarly suggests that old-growth structure in the central hardwood region on the whole should develop by the time the canopy reaches 150 – 200 years. However, forests recovering from a stand-replacing event may need longer than the above time frames to fully recover some old-growth characteristics, and in particular may need much longer to develop a true multi-age canopy structure (Oliver and Larson 1996; Frelich 2002).

Large Diameter Trees

While old trees aren't necessarily large, nor large trees old (Pederson 2010), old-growth forests tend to contain trees that are relatively large for given site and species constraints. Martin (1992) reported at least seven trees per hectare >75 cm DBH (diameter at breast height, 1.3 m) in the mixed mesophytic forests at Lilley Cornett Woods in Letcher County, Kentucky. Large diameter trees may be larger and more abundant in increasingly mesic, protected cove forests (e.g., coves of the Great Smoky Mountains), while tree size is typically more restricted on xeric, drought-prone, and exposed sites (Stahle and Chaney 1994). Much of the remaining old-growth forest in the eastern U.S. is exemplified by these low-productivity sites, as they were often ignored for timber or agricultural production (Stahle and Chaney 1994).

Large trees play an important role in the ecology of many forests, and can have a major influence on a number of ecosystem processes, including competitive relationships, nutrient dynamics, biomass allocation, and others (Lutz et al. 2012). It is also notable that many of the structural and functional characteristics that distinguish old-growth forests from younger forests, as discussed below, derive from the presence of large trees (Runkle 1991).

Coarse Woody Debris

Coarse woody debris (CWD), also referred to as "coarse woody detritus" or "coarse woody material," is dead, downed woody material usually delineated as being >10 cm diameter and >1 m in length. On occasion CWD is used to refer to both down and standing dead wood (snags), though I treat the two separately here.

Smaller diameter woody material is usually referred to as “fine” woody detritus, material, or debris.

The presence of relatively high volumes of CWD, particularly in larger diameter classes and later stages of decay, is likely one of the characteristics that most distinguishes old-growth forests from second-growth forests (Parker 1989; Martin 1992; Hale et al. 1999; Spetich et al. 1999; Harmon 2009). The larger volumes of CWD observed in old-growth forests are typically the result of the contributions of a few large-diameter trees to the total pool (Shifley et al. 1997). However, distribution and total volume of CWD in a forest can fluctuate considerably based on disturbance history, mortality, and climate (Brown and Schroeder 1999; Harmon 2009), and often increases with forest productivity (Spetich et al. 1999). While old-growth forests are generally assumed to have a greater representation across decay classes than their younger counterparts (Martin 1992; Goodburn and Lorimer 1998), this is not always the case (Shifley et al. 1997; Haney and Lydic 1999).

Coarse woody debris in forests that have been subject to stand replacing events without the removal of logs (e.g., tornados) show a marked spike in CWD volume that decreases with time as decomposition proceeds, and eventually plateaus when background inputs from mortality approximate decomposition (Harmon 2009). Forests subject to logging, either as the primary disturbance or through post-disturbance salvage logging, will similarly exhibit a spike in CWD from logging slash and other residue. However, due to the absence of large decomposing boles, decomposition of the smaller diameter slash will be more rapid and result in a period of very low total CWD until trees grow large enough to provide significant CWD inputs (Spetich et al. 1999).

Coarse woody debris is involved in many ecological processes, including energy flow, nutrient cycling, soil and sediment transport, moisture retention, and providing habitat for a wide array of species, including arthropods, birds, small mammals, herptiles, fungi, and microorganisms (Harmon et al. 1986; Goodburn and Lorimer 1999; McGee et al. 1999; Muller 2003).

The comparatively warmer upper surface, cooler underside, and relative stability of internal moisture and temperature conditions provided by CWD allow for a variety of herpetofauna to utilize CWD for a number of important life history activities, including thermoregulation (both warm and cold-season), avoidance of desiccation, predator avoidance, and successful egg laying and hatching (Whiles and Grubaugh 1993).

At least 55 mammal species use downed logs in the southeastern U.S., and CWD may be critical habitat for some small mammals including shrews (Loeb 1993). Logs are used as travel corridors and provide cover for predator avoidance, and, by providing habitat for macroinvertebrates and fungi, are important for feeding and foraging. Several mammal species also use CWD for nesting and denning, including striped skunks (Mephitis mephitis), gray fox (*Urocyon cinereoargenteus*), weasels (*Mustela* spp.), black bears (*Ursus americanus*), and a variety of mice (*Mus* spp.) and shrews (*Soricidae*) (Harmon et al. 1986; Wathen et al. 1986; Loeb 1993).

Few birds use downed CWD, with the notable exception of ruffed grouse use of logs for "drumming" (Gullion 1967; Harmon 1986). CWD is also important habitat for a wide array of micro- and macroinvertebrates and fungi that both provide food for a number of taxa and play vital roles in forest nutrient and energy cycling (Harmon et al. 1986; Hanula 1992; Johnston and Crossley 1993).

Large-Diameter Snags

Large-diameter snags (standing dead trees) are frequently missing from young and maturing second-growth forests, but are often typical of old-growth forests (Goodburn and Lorimer 1999; McGee et al. 1999), excepting for low productivity forests where tree diameter may be truncated by edaphic or other conditions. Some studies have found larger frequencies of small-diameter snags in younger forests, most likely related to density-dependent mortality from competition during stem exclusion and demographic transition phases stand development (McComb and Muller 1983; Goodburn and Lorimer 1999; Frelich 2002). The total density or volume of snags can be similar in old-growth and second-growth forests, but this is often due to either residual trees remaining from past partial harvests or the cumulative basal area of smaller snags in the younger forests (McComb and Muller 1983; Goodburn and Lorimer 1999; Hale et al. 1999).

Cavity Trees

Related to snags are cavity trees. While snags are more likely to have cavities than live trees, the latter typically provide more cavities in a forest because live trees are much more frequent (Goodburn and Lorimer 1999; Fan et al. 2003). Cavity formation often occurs through a succession of dead wood utilization by a variety of taxa. Heart rotting fungi create conditions that facilitate wood-eating insects and other fungi, which further provide food for a range of vertebrates. As the wood softens, primary cavity species, usually cavity nesting birds, excavate an initial cavity for use, while secondary cavity species, including birds, bats, squirrels, bees, chipmunks, raccoons, and other taxa, use or enlarge existing cavities (Harmon et al. 1986; Gysel 1961).

Old-growth forests tend to have more cavity trees, and substantially more cavities in trees of larger size classes, than younger forests (Fan et al. 2003; 2005). Large tree cavities are important as the initial diameter of the tree and cavity can be a limiting factor for some cavity nesting birds and other taxa. The greater number and range of sizes of cavities may be why old-growth forests, in general, have a greater number of cavity nesting birds than their younger counterparts (Harmon et al. 1986; Haney and Lydic 1999). Large diameter cavities around 100 cm DBH and greater, which are typically absent in younger forests, have been found to be preferred den sites for black bears (*Ursus americanus*) in the Southern Appalachians, suggesting the importance of old forests for this species (Wathen et al. 1986, White et al. 2001).

Uneven Age Distribution

Trees in old-growth forests often follow a multi-age distribution, with recruitment either continuous or occurring through multiple recruitment events, or both, depending on the spatial scale under consideration. An uneven-aged distribution results when stand development proceeds in the absence of major disturbance, with tree mortality occurring individually or in small groups (Oliver and Larson 1996; Frelich 2002).

Trees in Multiple Size Classes and the "Reverse-J" Diameter Distribution

Diameter distributions in old-growth forests typically follow a "reverse-J," roughly inverse exponential distribution, where a large frequency of small diameter trees tapers off to an increasingly lower frequency of large diameter trees, and plot on a log scale as a straight line (Frelich 2002; Gove et al. 2008). Some old-growth forest and other uneven-aged forests have been found to exhibit a "rotated sigmoid" distribution, where the diameter distribution has a hump or plateau in the mid-diameter range (Gove et al. 2008). It has been suggested that this distribution reflects past intermediate-scale disturbance in the stand (Lorimer and Frelich 1984; Leak 1996). While many old-growth forests follow the reverse-J distribution, some even-aged second-growth forests have been found to similarly follow this pattern (Goodburn and Lorimer 1999).

Multi-layered Canopy

Generally speaking, canopy stratification describes the relative vertical distribution or layering of trees within the forest canopy (Parker and Brown 2000). The vertical and horizontal structure of the canopy, together, are important determinants in growing space availability and light penetration through the canopy (Jennings et al. 1999). Old-growth forest and other uneven-aged forests tend to have greater stratification of their canopies contributing to their greater structural diversity over younger even-aged forests (Frelich 2002).

Large Overstory Basal Area

The basal area (BA) of a stand is the sum of cross-sectional areas of all trees at 1.3 m, or breast-height, over a given area and expressed in m^2/ha (or ft2/ac in American forestry). Basal area tends to increase with stand maturity and inversely with stand density, and can vary considerably by forest type with drier or more disturbance-prone forests having lower basal areas than more productive and sheltered forests. Martin (1992) provided a lower threshold for old-growth forests of 25 m^2/ha based on values from Lilley Cornett Woods, where BA values ranged from 20.6 to 42.4 m^2/ha across all communities. However, total forest BA for mature, and even young, second-growth forests sometimes falls within this same range (Goebel and Hix 1996; Hale et al. 1999).

Overstory Density

Stem density tends to decrease with age as a function of stand development as basal area is redistributed to increasingly larger diameter trees. Martin (1992) proposed 250 stems/ha > 10 cm DBH as a threshold for old-growth forests based on values ranging from 160 to 315 stems/ha at Lilly Cornett Woods. Parker (1989) found similar values for old-growth throughout the eastern hardwood region ranging from 161 to 427 stems/ha. However, Hart et. al (2012a) found 620 stems > 10 cm DBH/ha in an oak-pine upland forest at Savage Gulf, an old-growth forest on the Cumberland Plateau in Tennessee, and unpublished data from a 2010 inventory of Lilley Cornett Woods found a density of 536 trees > 10 cm DBH/ha (McEwan and Richter 2010), calling into question the usefulness of this metric for assessing old-growth condition.

Herbaceous Diversity

Herbaceous diversity may be greater in old-growth forests (Martin 1992), with incomplete recovery in second-growth stands over the historical period (Duffy and Meier 1992). Several factors may contribute to diminished herbaceous diversity following logging, including many species' short dormancy and consequent lack of persistence in the seed bank, limitations on dispersal (with forest herbs often clonal, gravity-dispersed, or ant-dispersed), inability to compete with r-selected plant species, and changes in microhabitat, among others (Meier et al. 1995; Whigham 2004). However, for considerations of herbaceous diversity in comparisons of forests, differences in community type need to be taken into consideration and not be confounded with differences related to stand age (Harrelson and Matlack 2006).

Pit and Mound Topography

When a large tree falls, its root mass is usually pulled from the soil and lifted perpendicular to the ground along with humus, mineral soil, and rock fragments (Schaetzel et al. 1989). The resulting formation is referred to as a "tip-up mound" or, at a larger scale, "pit and mound topography," and can be an indicator of old-growth forests. The process occurs relative to disturbance frequency, with pits and mounds often evident for centuries after formation (Peterson and Campbell 1993). Tip-up mounds can be missing from second-growth forests due to removal as part of agricultural use prior to abandonment (Whitney 1994). They may also be infrequent as a result of logging alone, where trees large enough to leave substantial tip-up mounds have been missing from the forest during stand development and recovery, creating a lapse in formation. However, there can be a great deal of variability depending on site-specific conditions and history.

Tip-up mounds are important because they create varying moisture, temperature, and nutrient conditions, including the exposure of bare mineral soil, that can affect species richness and distribution by allowing for a diversity of microsites for seedling germination (Schaetzel et al. 1989; Peterson and Campbell 1993; Clinton and Baker 2000). When considered as an ongoing process over the course of millennia, tree uprooting may have important consequences for soil structure, the mixing of soil horizons, and soil carbon and nutrient dynamics.

Canopy Gaps

Gaps in the canopy created by mortality or blow-down of individuals or small groups of trees is a characteristic strongly associated with old-growth forests (Runkle 1985; Martin 1992). The pattern of gaps reflects a history of small-scale disturbance and relates to the development of uneven-aged canopy distributions, canopy layering, coarse woody debris, and other structural elements (Runkle 1985; Frelich 2002). Canopy gaps and gap dynamics are discussed more thoroughly later in this document.

1.3 REGION 8 GUIDANCE ON OLD-GROWTH

The U.S. Forest Service published in 1997 its *Guidance for Conserving and Restoring Old-Growth Forest Communities on National Forests in the Southern Region: Report of the Region 8 Old-Growth Team* (hereafter referred to as the "Region 8 Guidance") (USDA FS 1997). The purpose of the document was to aid national forests in the southern region (Region 8) in "developing a network of old-growth areas of varying sizes to provide for the distribution, linkages, and representation of all old-growth forest community types on national forest lands." The authors also recognized the importance of recovering old-growth, stating "Since very little old growth currently exists, managers will emphasize areas for developing or restoring old growth."

The Region 8 Guidance provides operational definitions for old-growth forests based primarily on broad structural and age considerations across a variety of forest types in the southeastern U.S. While some of the definitions provided are arguable and should not replace more detailed ecological considerations, the Guidance is nevertheless important in that it helps to guide old-growth delineation and management on fourteen southeastern national forests, including the Daniel Boone National Forest which incorporated this guidance into the 2004 Forest Plan (USDA FS 2004).

The two communities described that are most pertinent to this research are the Mixed Mesophytic (Type 5) and Dry-Mesic Oak (Type 21), though the latter better describes most of the study sites. The four operational criteria are as follows:

1) **Minimum Age of Oldest Age Class:** The Guidance suggests at least 74 trees/ha (30 trees/ac) in the oldest age class, but recognizes a need for flexibility in applying this criterion. Minimum ages provided are 140 years for mixed mesophytic and 130 years for dry-mesic oak.

2) **Disturbance Criteria:** The disturbance criteria in the Region 8 Guidance are flexible. Rather than setting a 'virgin' condition for validating old-

growth, the guidance states "for a stand to be considered as existing old growth, no obvious evidence of past human disturbance which conflicts with the old-growth characteristics of the area should be present." The definition explicitly allows for management activities to have taken place, including limited tree cutting, midstory treatments, and prescribed fire, as long as they don't interfere with overall old-growth characteristics.

3) **Minimum Basal Area:** The minimum basal area set for both old-growth mixed mesophytic and dry-mesic oak communities is about 10 m^2/ha (40 ft2/ac). This value is much lower than that found in the literature for these forest types, and is explained by stating that the value "is a conservative estimate to ensure that stands are not excluded due to the variety of ecological conditions which exist."

4) **Diameter at Breast Height (DBH) of the Largest Trees:** This criterion recommends that there be at least 6 to 10 trees > 76.2 cm (30 in) DBH for mixed mesophytic communities or > 50.8 cm (20 in) DBH for dry-mesic oak forests.

1.4 STAND DEVELOPMENT

Stand development describes the procession of structural arrangements in a forest following major disturbance, and is a distinct, though related process, from forest succession — the latter describing the changes in species composition based on relative light conditions. Stand development occurs through the interplay of species' life history traits, inter-tree competition, and small-scale natural disturbance.

A series of four stages of stand development was initially described by Oliver (1981) and Oliver and Larson (1996) and modified by Frelich (2002)(Figure 1). I use the latter sequence here. Both models assume beginning with a stand-replacing

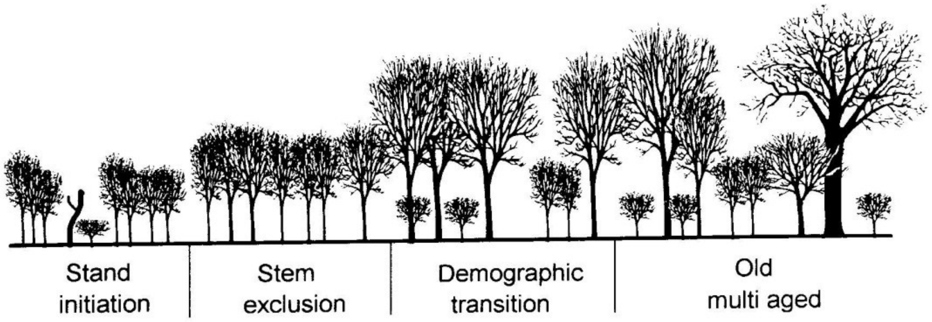


Figure 1: Sequence of structural phases in stand development.

Source: Frelich, L.E. 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge University Press, Cambridge.

event, though regeneration within forest gaps of sufficient size should still follow this same pattern of development (Frelich 2002). However, it has also been noted that intermediate levels of disturbance can result in more varied trajectories of structural development and succession than that described by the standard, cohort-driven model (Hanson and Lorimer 2007).

Stage 1. Stand Initiation: Stand initiation follows a major, stand-replacing disturbance such as a tornado or clearcut. Most or all canopy trees are leveled or removed, with advance regeneration, root sprouts, and seed sprouting leading to the development of a new cohort of trees.

Stage 2. Stem Exclusion: During this second stage, the young trees form a dense, codominant canopy with a unimodal diameter distribution. Inter-tree, density-dependent competition drives self-thinning in the stand, while remaining trees rapidly fill in gaps through lateral growth. Tree density decreases while tree diameters, stand basal area, and crown height increase. Light exclusion inhibits growth of seedlings and saplings.

Stage 3. Demographic Transition: As canopy trees become larger and taller, large and small gaps form in the canopy, allowing sufficient light conditions in the understory for a new cohort of trees to grow. The unimodal peak evident during stem exclusion has transitioned into larger sizes classes with a lower density, while a new peak in the smaller diameter classes emerges. This particular diameter distribution has been called a 'compound diameter distribution.' During demographic transition, tree mortality is driven mainly by density-independent phenomena, including small scale natural disturbance. Large coarse woody debris and an increasingly uneven canopy begin to accrue. This stage was considered the 'understory reinitiation phase' by Oliver and Larson (1996).

Stage 4. Old Multi-Aged: In the old multi-aged forest, the forest stand has transitioned into an uneven-aged distribution with varying sizes of trees in the canopy. The formerly uniform, codominant canopy has given way to a mix of dominant and codominant canopy trees, with few trees from the initial cohort still present. The diameter distribution follows a "reverse-J" distribution, with numerous trees in the small diameter classes dropping off sharply then trailing off into the largest diameter classes. Tree mortality occurs primarily through individuals or small gaps, with self-thinning occurring in small patches that have undergone stand initiation within larger gaps. The "old multi-aged" stage of development was previously described as the "old-growth stage" by Oliver (Oliver 1981, Oliver and Larson 1996), though modified by Frelich to avoid complications arising from the myriad uses of the term.

1.5 NATURAL DISTURBANCE

Natural disturbance is a major driver of forest structure. Exogenous natural disturbance describes forces coming from outside the community as the agents of change, and include disturbance events such as wind, fire, and ice (Picket and White, 1985). Endogenous disturbance, alternatively, arises from within the community and is typically relegated to factors such as competition or decline from disease or other factors. While the distinction can be useful, the differences between the two can be fine and has been called into question (Runkle 1985).

Natural disturbance occurs on a continuum with a generally inverse relationship between event severity and return interval (Seymore et al. 2002), with stand-replacing events relatively uncommon in the central Appalachians. Overall, canopy turnover in the Eastern Deciduous Forest is estimated to occur at a rate of 0.5% to 2.0% per year, with most of this turnover in the form small to mid-sized gaps in the canopy (Runkle 1985).

Wind

Wind events, including tornados, derechos, and storm microbursts often provide the most dramatic changes in forest structure. Hurricanes, while able to cause large-scale canopy disturbance in some eastern oak and hardwood forests, are not an important disturbance regime in the Allegheny and Cumberland Plateau regions (Lorimer and White 2003).

Seymore et al. (2002) aggregated information on natural disturbance in forests of the northeastern United States and estimated that stand-replacing wind events affected patches with a mean size of 14 ha to 93 ha with a return interval of 855 to 14,300 years. Low to moderate severity disturbance resulting in canopy gaps affected patches with mean size ranging from 24 m^2 – 126 m^2, and occurred with return intervals ranging from 50 – 200 years (Seymore et al. 2002). The former value is consistent with the range in regional values summarized by Whitney (1994), while the latter aligns well with rates of gap formation reported by Runkle (1985).

While severe wind events, such as tornadoes and derechos, can remove most or all of a forest canopy, particularly over small or narrow areas (Peterson and Pickett 1995), this is frequently not the case (Held et al. 1998; Marks et al. 1999; Arevalo et al. 2000; Lorimer and White 2003; Held et al. 2006). The impact of tornados is further moderated by a relatively low frequency of occurrence, with a mean point reoccurrence in the Appalachian Plateau estimated from 5,000 to 20,000 years (Whitney 1994). Between 1961 and 1990, Kentucky had an average of 10-13 tornados/year, with frequency decreasing from west to east, and becoming increasingly uncommon in the Appalachian mountain region (NOAA 2012a & 2012b; Runkle 1985). Derechos can have significant landscape effects, with individual downbursts ranging from 4 km to 40 km in length over a front of at least 400 km (Coniglio and Stensrud 2004). However, severe derecho events are infrequent, and the canopy impacts are often patchy (Lorimer and White 2003). More frequent, intermediate severity natural disturbance events can potentially increase overall heterogeneity of stand structural and species composition (Hanson and Lorimer 2007).

Gap Dynamics

Most canopy disturbance in forests of the eastern deciduous forest region occurs through the death of individual or small groups of trees from disturbance, disease, or other factors. These small, within-community patches of disturbance are termed “gaps” (Watt 1947; Runkle 1985). The size of the gap can have a profound effect on the environmental conditions within the gap and, consequently, future forest structure. Within a forest gap, both light and soil moisture increase while humidity decreases. Increased light conditions reach a maximum where the gap diameter (D) equals or exceeds approximately twice the height (H) of the surrounding canopy, or where $D/H \approx 2$ (Runkle 1985). Gaps of sufficient size can support regeneration of shade intolerant or mid-tolerant species, while smaller gaps will limit regeneration to more shade tolerant species (Runkle 1982).

Small gaps close rapidly through lateral growth of edge trees and effectively return the forest patch to a closed canopy condition in a few years. Gaps of sufficient size, however, close more slowly through vertical growth of released understory trees or development of a new cohort from advance regeneration or seed bank. Further, Runkle (1998) found increased rates of mortality among edge trees in larger gaps, leading to further enlargement of the gap environment and longer persistence.

Prior to the formation of a new canopy within a gap, the gap environment plays an important role as early seral habitat within an otherwise closed-canopy forest. These conditions allow for the growth and fruiting of important forage for black bears (*Ursus americanus*), such as blackberries (*Rubus* spp.), blueberries (*Vaccinium* spp.), huckleberries (*Gaylusaccia* spp.), and grapes (*Vitis* spp.) (Mitchell and Powell 2003), as well as habitat for many disturbance-dependent bird species (Hunter et al. 2001).

Large trees confer characteristics relating to gap formation that can be missing from younger forests (Runkle 1991). Large, dominant trees, for example, have their crowns exposed above the general canopy and are more susceptible to wind disturbance. And large tree-fall gaps are more likely to occur as the result of a large tree falling than a small one (Runkle 1991). In addition to the greater canopy area typically occupied by larger trees, the combination of height and mass make it more likely that the falling tree will knock down several others in its path. As a result, the presence of larger trees can lead to a greater amount of early seral habitat within the forested landscape (Hunter et al. 2001). Overall, the structural legacy of gap dynamics is the creation or maintenance of a complex forest architecture, with multiple age groups, canopy classes, and seral states coexisting within the forest matrix.

Ice

Ice storms are a periodic disturbance of intermediate severity in forests of the Cumberland Plateau. Glazing of ice on limbs can lead to limb breakage, stem snapping, and uprooting of trees (Lafon 2006). Ice damage can have a differential effect across species, thereby affecting species distributions in forests. Oak species, including *Quercus alba*, *Q. montana*, and *Q. rubra*, along with many *Pinus* species (except *P. strobus*) are generally more resistant to ice damage than *Acer* species, which are, in turn, more resistant than basswood (*Tilia americana*), elm (*Ulumus americana*), black cherry (*Prunus serotina*), and other light-wooded trees.

Depending on the severity of the event, ice storms can cause significant mortality and changes to stand structure. Lafon (2006) reported for a *Quercus* forest in southwestern Virginia that roughly 30% of all canopy trees had died within 4 years of an ice storm, leading to changes in overall forest structure and patterns of recruitment.

Large Herbivores

Large herbivores can have significant short and long-term impacts on temperate forest ecosystem structure, composition, and productivity (Kowalczyk et al. 2011; White 2012), with vegetation responses varying based on the species of herbivores present, forage preferences and availability, population size and distribution, temporal variation of herbivore populations, and other factors (Kuijper et al. 2010). Herbivores drive changes in forest structure and composition by decreasing seedling and sapling densities, with particular reductions in preferred forage species (Kowalczyk et al. 2011; White 2012), which can, in-turn, drive long-term changes in species composition and canopy structure (Didion et al. 2009).

The paleohistory of Kentucky is intricately linked to large herbivores that likely had a substantial impact on the structure and function of forests and other native communities. Pleistocene-aged fossils from a wide variety of megafauna have been identified at Big Bone Lick in north-central Kentucky, including mastodon (*Mammut americanum*), mammoth (*Mammuthus* spp.), bison (*Bison antiquus*), caribou (*Rangifer tarnadus*), helmeted musk ox (*Bootherium bombifrons*), stag moose, (*Cervalces scotti*), complex-tooth horse (*Equus complicatus*), Harlan's ground sloth (*Paramylodon harlani*), and Jefferson's ground sloth (*Megalonyx jeffersonii*) (Tankersley et al. 2009). However, a mass extinction at the end of the Pleistocene, possibly associated with the Younger Dryas cooling event, saw these species disappear from the landscape (Firestone et al. 2007).

Still, several large, native herbivores have been significant in Kentucky's ecology for most of the Holocene, including white-tailed deer (*Odocoileus virginianus*), modern bison (*Bison bison*), and elk (*Cervus canadensis*). The latter two were effectively extirpated in Kentucky by the modern era (Tankersley et al. 2009), though recently Rocky Mountain elk (*Cervus elaphus*) have been introduced. Livestock grazing, particularly cattle and hogs, can also have significant impacts on forest structure, though the effects of livestock may be somewhat different from those of native herbivores as a result of differences in forage preferences, animal density, and enclosure (Apsley et al. 1984).

Drought

While not regularly considered a form of natural disturbance, episodic, severe drought may be an important disturbance regime affecting forest structure and species composition (Hursh and Haasis 1931). Haasis (1923) studied tree rings from stumps of logged old-growth forests in Letcher County, Kentucky, and found that 82 percent of the trees observed initiated at about the same time following 1660. Hassis (1923) noted that records for an adjacent region document a major drought in 1662, and that trees in the study area that predated this period exhibited a marked decrease in growth rates prior to a release event coinciding with the period of drought and regeneration. More recent dendrochronological analyses suggest that major drought events more severe than those typifying the twentieth century were more common in previous centuries (McEwan et al. 2010; Pederson et al. 2012).

1.6 ANTHROPOGENIC DISTURBANCE

Anthropogenic disturbance to forest ecosystems in Kentucky and the Central Appalachians has been occurring for at least 11,000 years (Pollock 2008). While the direct effects of human habitation and use for much of the Holocene may have been localized, the cumulative effects of anthropogenic fire, horticulture, and hunting over millennia likely had major ramifications on forest and other community structure and function at the landscape scale. However, in the modern era, human activities have radically altered the forest landscape (Abernathy et al. 2010).

Fire

Fire is a recurring source of disturbance that can affect forest structure (Abrams 1992). On the Cumberland Plateau, lightning-caused fires are estimated to occur at a rate of less than five per one million acres annually (Ison 2000). As such, the existence and effects of fire on the landscape, in both the historic and prehistoric periods, should be considered anthropogenic forms of disturbance (Lynch and Hessl 2010). While the frequency and extent of fire is related to human population and cultural practices (Guyette et al. 2002), its prevalence and extent generally increase during dry years (Lynch and Hessl 2010). While several hardwood species, and oaks in particular, are somewhat resistant to fire damage (McEwan et al. 2007), fire can result in mortality or decreased vigor in individual trees as a result of heat damage to the cambium (Jones et al. 2006). The extent of mortality at the stand level is largely dependent on the severity of the fire, which is in turn affected by vegetation type, topography, and other factors (Wimberly and Reilly 2007), and can range from just a small percentage of trees in low-severity fires to a majority of trees in high-severity fires (Regelbrugge and Smith 1994). Because burn severity is often patchy at large and small scales, the resulting legacy tends toward a mosaic of vegetation patterns (Ford et al. 1999). Repeated fires of sufficient intensity and frequency can result in significant impacts to forest structure and herbaceous community composition (Peterson and Reich 2001).

Fire is hypothesized to be an important driver of species dynamics in eastern forests — particularly as relates to the issue of oak dominance (Abrams 1992; McEwan et al. 2007). Throughout oak-dominated forests of the eastern U.S. there has been an observed pattern of poor oak establishment or success in the understory, countered by a concomitant, and marked, increase in maple abundance (particularly red maple, *Acer rubrum*)(Lorimer 1984). The “fire and oak hypothesis” suggests that this apparent shift in species dominance is a direct result of fire suppression beginning ca. 1930 (Abrams 1992). While there is some evidence supporting this hypothesis, a review of the literature suggests that the observed oak-maple dynamics may reflect a more complicated suite of ecological drivers, including changes in herbivore populations, loss of the American chestnut (*Castanea dentata*), climate patterns, and other factors (McEwan et al. 2010).

Fire is also believed to have been important in maintaining open oak woodland or savannah communities in Kentucky (Ison 2000). Such communities would have been characterized by greater spacing between trees, little or absent midstory and understory, and a greater abundance of grasses and other sun-loving, heliophytic forbs than is common in closed canopy and mesic forests (Davis et al. 2000; Peterson and Reich 2001). While historical and botanical records attest to the presence of these communities in the Cumberland Plateau and the central and southern Appalachians (Ison 2000), the historical frequency and extent of these woodland and savannah communities in the region is unknown and a matter of active debate. Greater regions of woodland and savanna are believed to have existed in the Bluegrass and Big Barrens regions of Kentucky (McInteer 1952), but few remnants remain today for study (McEwan and McCarthy 2008).

Logging

Other than the complete removal of forests through agricultural conversion, surface mining, or development, logging has provided the most intensive, and certainly widespread, impacts to forests in the Eastern Deciduous Forest during the modern era. Logging historically has taken many forms resulting in a wide range of secondary forest conditions. In many cases, the practice of selective cutting of the most valuable trees, particularly over multiple entries, resulted in a shift in species composition while leaving trees that, from a timber perspective, are of poor form, quality, or health (Roach and Gingrich 1968, Kentucky Division of Forestry 2010). Modern forestry, beginning in the mid-20th century, emphasized even-aged methods of forest management, including clearcutting, seed-tree, and shelterwood methods with an emphasis on the regeneration of commercial species and high-value timber (Roach and Gingrich 1968; Wenger 1984), though uneven-aged approaches have also been applied (Smith 1980; Wenger 1984) . More recently, selective approaches have been designed to enhance or better mimic old-growth forest conditions (Runkle 1991; Lorimer and Frelich 1994; Keeton 2006; Bauhus et al. 2009). However, most forest land in Kentucky is privately owned, with logging practices essentially unregulated and often carried out in the absence of a certified forester or management plan (Kentucky Division of Forestry 2010).

Logging can create canopy disturbances similar to some types of natural disturbance (Larsen and Johnson 1998), though often at scales significantly larger than those occurring from most natural processes (Seymour et al. 2002). While removal of the canopy from logging or natural disturbance induces a loss of dissolved nutrients from decomposition-nitrification processes, the removal of biomass from logging can cause a loss of several times this amount (Borman and Likens 1979). And unlike natural processes, surface disturbance from logging roads, skid trails, and dragging logs can both increase erosion and create conditions promoting the establishment of non-native invasive plants (Patric 1976; Wenger 1984; Marshall and Buckley 2008).

1.7 AMERICAN CHESTNUT (*CASTANEA DENTATA*)

Any discussion of the current structure and function of Appalachian forests would be remiss to omit addressing the loss of the American chestnut (*Castanea dentata*). While its prevalence was variable, American chestnut was a dominant species in many forests throughout the Appalachian region and Cumberland Plateau (Braun 1950). Prized for its rot-resistant timber and abundant, nutritious nuts, American chestnut was effectively extirpated as the result of the introduction of the Asian fungus *Cryphonectria parasitica*. First identified in New York in 1904 (Griffin 2000), the blight reached Kentucky by 1930 and quickly spread throughout the state. The fungus attacks the trees' vascular tissue, effectively girdling the tree and choking off the flow of nutrients and water. However, the rootstock can survive and send up new stems, which are frequently observed in Appalachian forests, though rarely larger than saplings. Several efforts to develop and deploy resistant strains of American chestnut show promise (Griffin 2000; Jacobs 2007). American chestnut was able to survive a wide range of edaphic conditions, and replacement in the canopy following blight appears to have been strongly related to whichever species were both present at a given site at the time of decline and physiologically capable of exerting dominance (Elliot and Swank 2008). While an occasional chestnut stump can still be found, because of the > 70 years since chestnut decline in Kentucky, no direct, American chestnut-related structural impacts, such as gaps, down logs, etc, are common in present-day forests.

1.8 STATUS OF OLD-GROWTH FORESTS IN KENTUCKY

By 1930, nearly all of Kentucky's forests had been logged or converted to agricultural use (Braun 1950; Jones 2005). However, a small sample of old-growth forests were left largely untouched and remain today for study and enjoyment. These remaining old-growth forests can be considered as existing within a continuum of old-growth quality or relative pristineness, with some affected only by Chestnut blight or episodic grazing, others subjected to the selective removal of a small number of high-value trees, and still others that retain significant numbers of old-growth trees and structure but show signs of moderate levels of timber removal, grazing, or other human disturbance (Cooper 2011).

Lilley Cornett Woods

Lilley Cornett Woods in Letcher County is a 224 ha (554 ac) preserve that includes 101 ha (252 ac) of old growth forest in the Mixed Mesophytic region of southeastern Kentucky. The forest is managed by the Eastern Kentucky University Division of Natural Areas and has been the subject of intensive study for several decades (Martin 1975, 1992; McComb and Muller 1983; McEwan et al. 2005; McEwan and Muller 2006). Because of its proximity to the study area, similarity of forest types, and large pool of available data, Lilley Cornett Woods was used in this study as a benchmark for comparing structural characteristics of second-growth and old-growth forests.

Blanton Forest

Blanton Forest is a 1,254 ha (3,100 ac) preserve including 951 ha (2,350 ac) of old-growth on Pine Mountain in Harlan County, and is the largest old-growth forest in Kentucky. The forest is managed cooperatively between the Kentucky State Nature Preserves Commission and Kentucky Natural Lands Trust. The forest was initially protected by its namesake family, with acquisitions by the Kentucky Natural Lands Trust beginning in 1995. Despite its potential, the forest has so far been the subject of little scientific research (Weckman 1999; Barnes 2002; Pederson et al. 2012).

Rock Creek Research Natural Area

Rock Creek Research Natural Area (RNA) is a 77 ha (190 ac) old-growth hemlock-mixed mesophytic forest in Laurel county managed as a Research Natural Area by the Daniel Boone National Forest (Thompson and Jones 2001). The old-growth forest remained largely intact due to its relative inaccessibility within a cliff-bound tributary of the Rockcastle River. Rock Creek RNA has been the subject of several scientific inventories and studies (Braun 1950; Winstead and Nicely 1976; Cameron and Winstead 1978; Thompson et al. 2000; Thompson and Jones 2001; Tackett 2012).

Mammoth Cave Big Woods

The Big Woods of Mammoth Cave National Park is a 121 ha (300 ac) section of old-growth forest in the Interior Low Plateau of the Western Mesophytic forest region in Kentucky (Braun 1950; Jones 2005). The Big Woods are designated as a Natural Area by the Kentucky State Nature Preserves Commission, while the entirety of Mammoth Cave National Park is designated a UNESCO World Heritage Site and Biosphere Reserve. Recent unpublished work suggests that the forest may meet some definitions of old-growth forest but may have been impacted by some logging and other activities in the past (Neil Pederson, Lamont-Doherty Earth Observatory, personal communication 2012).

Tight Hollow

Tight Hollow is a barely accessible 29 ha (72 ac) cliff-bound ravine on a headwater tributary of the Red River in the Red River Gorge Geological Area of the Daniel Boone National Forest. The forest is a mixed-mesophytic forest dominated by tulip poplar (*Liriodendron tulipifera*), eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*), with a dense understory of rhododendron. Tight Hollow currently has some of the oldest dated trees in Kentucky, with at least one tulip poplar over 400 years in age (Scheff, unpublished data). The forest has been the subject of at least two studies (Hendrix et al. 1971; Herman and See 1973) and is listed as a candidate Research Natural Area in the Daniel Boone National Forest Land Resource Management Plan (USDA FS 2004).

Beaver Creek Wilderness

Beaver Creek Wilderness is a 1,923 ha (4,753 ac) designated Wilderness Area in the Daniel Boone National Forest in McCreary County. The central part of the wilderness, which is entirely within a cliff-bound ravine, contains extensive old-growth forest. While apparent that the forest has been impacted by some logging, the full extent and quality of old-growth forest in Beaver Creek does not appear to have been delineated or studied.

Other Old-Growth Forests

Other, more substantially impacted old-growth sites have been recognized across Kentucky, including Angel Hollow, Gladie Creek, Hensley Settlement, Cane Creek, and others (Cooper 2011; Tackett 2012). Numerous undocumented small patches of old-growth forest likely remain in Kentucky.

2. STUDY AREA

2.1 ECOLOGICAL SETTING

The study area was located within the Daniel Boone National Forest (DBNF) in eastern Kentucky (Figure 2). The DBNF consists of 286,000 ha (706,000 ac) within a 850,000 ha proclamation boundary, a majority of which spans a narrow strip roughly 140 miles long in a generally northeast to southwest orientation along the western escarpment of the Cumberland Plateau. The area is part of the Appalachian Plateau physiographic province, and includes portions of the Southwestern Appalachians and Western Allegheny Plateau Level III ecoregions (Jones 2005).

The DBNF lies within the Mixed Mesophytic forest region (Braun 1950; Jones 2005), and includes a variety of forest types ranging from mixed mesophytic communities in sheltered ravines to xeric oak and oak-pine communities along ridges and exposed cliffline. The most common forest communities in the DBNF are upland hardwoods of primarily oak-hickory forest associations that include an admixture of both mesic and xeric species depending on topographic position, edaphic conditions, and aspect.

The landscape is predominantly a dissected plateau of hilly to mountainous terrain, including steep ravines, narrow stream channels, rolling hills, and more than 5,000 km of cliffline on national forest system lands alone (USDA FS 2004). Bedrock is a mix of sandstone, shale, siltstone, and limestone, and soils are generally acidic and of moderate to low fertility (USDA FS 2004). Average precipitation ranges from about 116 to 132 cm annually, generally increasing from north to south (Abernathy et al. 2010). By age, approximately 68,800 hectares (24%) is over 100 years old and 1,630 hectares (0.6%) over 140 years old. Of the latter, only an estimated 308 hectares is hardwoods, with the remainder mostly hemlock forests (USDA FS 2009).

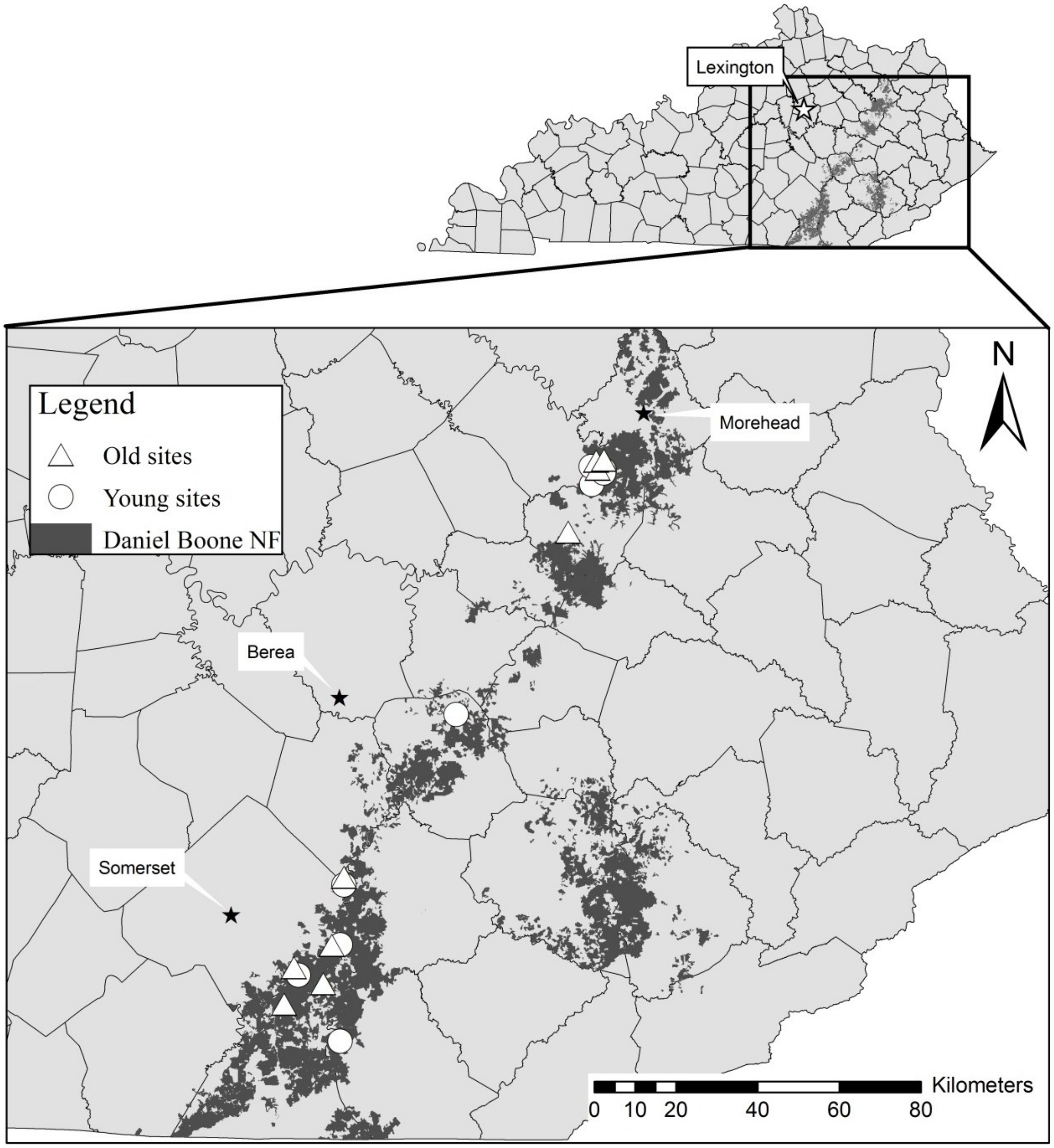


Figure 2: Map depicting study sites in the Daniel Boone National Forest, Kentucky. Circles indicate young study sites (70-90 years old); triangles indicate old study sites (140-160 years old).

2.2 DISTURBANCE REGIMES

Natural disturbance events in the DBNF are typical of the region, and include thunderstorms and microbursts, tornadoes, derechos, and ice-storms, with fire, logging, and historic coal mining and conversion to agricultural use being the main forms of anthropogenic disturbance. Drought may also be a significant form of natural disturbance in the area, albeit on longer time-frames, and with the capacity to drive major regeneration events (Haasis 1923). Depending on the severity and spatial scale of the disturbance event, the effects can be minimal, gap-scale canopy disturbance affecting only individual or small groups of trees, or so severe as to cause near-complete removal of the canopy. Other than the regional information concerning natural perturbations discussed previously, little reliable data on rates of natural disturbance exist for the study area.

2.3 LAND USE HISTORY

Humans have inhabited the Appalachian forest for the duration of the post-glacial Holocene (Pollack 2008). While the direct relationship between humans and impacts on the forest during the last 200 years are evident, elucidating the effects of human activities over the preceding 10,000 years is more speculative. Still, it is certain that humans interacted with their environment, and through practices like hunting and burning may have had significant short- and long-term impacts on the structure and distribution of natural communities (Delcourt et al. 1998). A better understanding of past natural community structure, including the range of temporal and spatial variability, will require an increased depth of knowledge of human populations and cultural practices.

Native American Use

Archeological evidence suggests that human habitation of the Cumberland Plateau extends to at least 11,000 to 14,000 years before present (B.P.) (Pollock

2008). During the Paleoindian period and throughout most of the Archaic period, humans are believed to have inhabited the Cumberland Plateau at relatively low populations, utilizing hunter-gatherer subsistence practices. From about 9,500 to 7,300 B.P., cool-temperate to boreal forests including spruce (*Picea* spp.) and white cedar (*Thuja occidentalis*) characterized the area (Delcourt et al. 1998). Forests then shifted to a mixed mesophytic forest assemblage until around 4,800 years B.P., when eastern hemlock (*Tsuga canadensis*) disappeared and eastern red cedar (*Juniperus virginiana*) increased (Delcourt et al. 1998). Archeological and paleoecological evidence, including charcoal and pollen from pond sediments, suggests that around 3000 years ago, concomitant with the shift from the Terminal Archaic to Early Woodland periods, native inhabitants began using fire as a tool to clear areas around settlements for growing cultivated, annual plants (i.e., "forest gardening") near cliff dwellings (Delcourt et al. 1998; Ison 2000). The development of fire as a cultural practice coincides with a larger ecological shift evidenced in pollen records toward more fire-tolerant taxa, including oaks (*Quercus* spp.) and chestnut (*Castanea*) (Delcourt et al. 1998, Ison 2000), though the causal link is not entirely clear.

Around 1000 A.D., two separate agriculturally-based societies defined Kentucky. Western and southern Kentucky, and extending up the Cumberland river valley, were part of the large Mississippian complex that extended well to the west and south (Pollack et al. 2002). Mississippian society was organized in chiefdoms, and was concentrated in large towns and mound complexes and associated smaller settlements. Subsistence was based on farming of maize, squash, and beans, and supplemented with hunting and gathering. Many Mississippian communities are distinguished by the presence of flat mounds that are understood to be related to the hierarchical power structure that is frequently attributed to the culture (Polluck 2008). Mississippian habitation in southeastern Kentucky appears to have been mostly associated with small communities along the Cumberland river floodplain, with rockshelters accounting for 55% of known sites and mostly attributed to hunting camps (Pollack 2008). By the mid-fifteenth century, the Mississippian culture collapsed in an episode of widespread abandonment that included the lower

Ohio river valley and the western half of Kentucky, referred to as the "Vacant Quarter" (Cobb and Butler 2002).

Fort Ancient societies were contemporary with their Mississippian neighbors, occupying a region that included most of Kentucky's Bluegrass region and the Kentucky, Licking, and Big Sandy river watersheds, and extended as far as southern West Virginia and southeast Ohio (Lewis 1996; Pollack et al. 2002). While the Fort Ancient peoples subsisted in a manner similar to the Mississippian peoples, communities were generally smaller and their social organization is believed to have been much more decentralized and egalitarian (Lewis 1996). For the earlier periods of Fort Ancient culture, communities and farms were established and then abandoned after one or two generations as resources were depleted (Pollack et al. 2002). In Kentucky, larger settlements were concentrated in the larger river valleys, with evidence of habitation in the more mountainous regions appearing to be restricted to small hunting camps and rock shelters, a pattern similar to that of the Mississippian culture. Unlike their Mississippian neighbors, the Fort Ancient communities persisted into the 1700s (Pollack et al. 2002).

Euro-American Settlement

From the late 1600s into the early and mid-1700s, Kentucky is considered to have been largely depopulated (Henderson et al. 1986; Aron 1996). While it has been suggested that this apparent low in resident population was a result of Iroquois attacks on the Shawnee in order to lay claim to game-lands in Kentucky and along the middle Ohio river valley (Aron 1996), it is probable that depopulation was driven more by pandemics and attendant social reordering (Henderson et al. 1986). The relationship between depopulation and evidence of extreme drought around 1660 (Haasis 1923) has not been explored. Regardless of why, eastern Kentucky seems to have remained sparsely populated throughout the eighteenth century, with Shawnee, Cherokee, and other peoples gradually moving back into the area as a seasonal hunting ground (Aron 1996). However, while the French and English had long travelled the Ohio river corridor, it wasn't until the late eighteenth century that Anglo-American long hunters, including Daniel Boone, began pressing into Appalachian Kentucky in search of both game for the fur trade and land interests. Despite ongoing conflicts with Native American groups, by the late 1770s the first mass-migrations of white settlers through the Cumberland Gap and into Kentucky via the Wilderness Road began (Aron 1996). While the first migrants into Kentucky settled in the Bluegrass Region in central Kentucky, it was not until the first quarter of the nineteenth century that immigrants settled the more rugged lands of the Cumberland Plateau (Pudup 1990).

Early Euro-American settlement of the Cumberland Plateau was characterized by forest clearing for subsistence agricultural production and forest grazing of livestock, particularly hogs, for both family use and market sale (Pudup 1990). Forest clearing took many forms, but usually included some version of cutting and burning trees followed by digging or burning out stumps to prepare the land for planting (Whitney 1994). Where trees were too large to cut, particularly in bottomlands, they were sometimes girdled and left to die standing, with crops planted underneath the newly bare canopy (Collins 1975). Availability of soil nutrients from the removal of vegetation and mineralization from burning allowed for abundant crop yields, though usually for only a short period of time. Within 2 – 10 years productivity at a given site would be depleted and the plot abandoned in a practice known as “forest fallowing,” while other areas were cleared and put into production (Otto 1989; Pudup 1990).

While a great deal of timber was burned as waste, small-scale logging was also taking place during the mid-nineteenth century, with trees felled and dragged to the nearest stream to be floated to market with spring floods (Pudup 1990). However, after the Civil War, technological developments, including steam power, along with westward American expansion, urban growth, and diminishing timber supplies in the east, created a new timber economy driven by large timber and land-holding companies (Whitney 1994). By the 1880s the lumber industry in Kentucky became more fully developed, and forest exploitation expanded at a dramatic rate (Collins 1975; Pudup 1990). By 1930, nearly all of Kentucky’s original forest had been logged (Braun 1950; Jones 2005).

National Forest Establishment

Beginning in the late nineteenth century, a series of laws were passed that paved the way for the establishment of the Daniel Boone and other national forests. Most important were the Creative Act of 1881, authorizing the setting aside of public lands as forest reserves, the Organic Administration Act of 1897, which established a system of National Forests, and the Weeks Law of 1911, which authorized the federal government to purchase forest lands, especially degraded lands, "for the purpose of conserving the forests and the water supply of the States" (Granger 1949; USDA FS 1993).

In 1937 the Cumberland National Forest was established in Kentucky, with the federal government purchasing 136,254 ha (336,692 acres) within an established proclamation boundary of 541,556 ha (1,338,214 ac). In 1966 the name of the forest was changed to the Daniel Boone National Forest to address long-held opposition in Kentucky over the original naming (Collins 1975). Currently, the federal government manages a highly fragmented 286,000 ha (706,000 acres) within a 850,000 ha (2,100,000 ac) proclamation boundary under a multiple use framework that includes various forms of recreation, ecosystem management, commercial logging, mining, and oil and gas development. Logging during the national forest period has varied in method and scope, with a major boom occurring during the 1980s and 1990s, during which approximately 100,000 acres was logged (USDA Forest Service 2009). The long-term legacy has left a mix of primarily second- and third-growth forests on the DBNF with small amounts of old-growth mostly found in isolated and difficult to access ravines.

3. METHODS

3.1 SITE SELECTION

Study sites for this project were initially derived using data in the Daniel Boone National Forest Stands GIS database (USDA Forest Service 2009). The database provides basic spatial and inventory information for nearly all stands in the DBNF, including age and forest type. A series of queries were used to select 70 – 90 year-old (hereafter "young") and 140 – 160 year-old (hereafter "old"), predominantly hardwood stands absent significant quantities of eastern hemlock (*Tsuga canadensis*) and shortleaf pine (*Pinus echinata*). Eliminating these two species was done for several reasons. Firstly, the two species were removed to better isolate for study oak-dominated and other hardwood stands from the more restricted mixed-mesophytic and xeric pine and oak-pine community associations, with hemlock and shortleaf pine, respectively, being strong indicators for these communities.

In addition to filtering for community type, shortleaf pine was avoided because forests in the DBNF were subject to a major outbreak of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) from 1999 – 2002 that killed an estimated 61% of shortleaf and Virginia pines (*Pinus virginiana*) in the DBNF (Maingi and Luhn 2005). It was assumed that structural changes resulting from pine beetle induced mortality in mixed stands would represent a level and type of exogenous disturbance that would affect forest stand development in a manner outside the scope of this investigation, and possibly skew values obtained for various structural metrics. Stands with significant eastern hemlock were similarly removed from the study because of the recent arrival of the hemlock wooly adelgid (*Adelges tsugae* Annand), an invasive, aphid-like insect that infests eastern hemlocks resulting in mortality of hemlocks in about 4-6 years (Eschtruth et al. 2006). It was assumed that the structural and successional trajectories soon to be seen in hemlock forests across the study area would make investigating the development of old-growth characteristics in these particular stands somewhat moot and limit the applicability of this study's findings for future management decisions.

Nine old sites in the DBNF were located that met age and species criteria and were reasonably accessible. Young sites, which were much more abundant, were matched to old sites based on proximity and, where possible, aspect and elevation (Figure 2). Sampling occurred from June 2010 through October 2011 while leaves were on trees to aid in identification. A total of 1 – 3 plots were sampled at each site. Sites limited to one sample plot either had only one suitable forest patch per study criteria or had access constraints or other difficulties limiting my ability to sample more plots.

Plot Location

Age data provided by the Stands GIS database were frequently inaccurate in the field, often describing only small patches within delineated stand boundaries. To locate forest patches meeting the appropriate age criteria, canopy trees were selectively cored with an 18" increment borer and growth rings field counted. Once a forest patch > 0.5 ha meeting study criteria was identified, a study plot was randomly sited within the forest patch. Plot location was randomized by picking a location roughly in the middle of the forest patch and spinning a standard board-game style spinner and walking 10 paces in the direction of the arrow. This was repeated a total of 3 times to minimize selection bias for or against the starting location. The ending location was then used as the center of the study plot.

Sampling

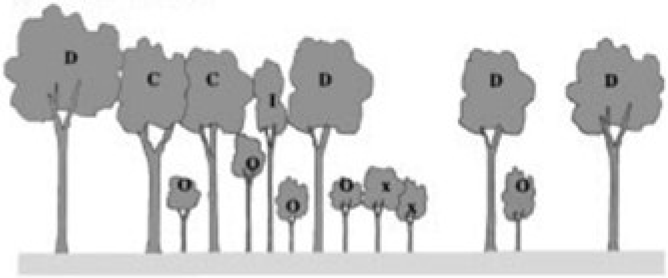
For each plot, a 10 x 10 m quadrat was set on the cardinal directions. The species, diameter at breast height (DBH; 1.3 m above the ground), crown position (overtopped, intermediate, codominant, or dominant; Table 1 & Figure 3), and illumination index (1-5) (modified from Jennings et al. 1999; Table 1) of each tree > 10 cm DBH was recorded. The number and species of all saplings (trees < 10 cm DBH and > 1 m tall) and seedlings (trees < 1 m tall) in nested subplots of 5x5 m and 3 x 3 m, respectively, in the NE corner of each plot were recorded. Coarse woody

Table 1: Criteria used to assign canopy position and illumination index values to trees within study plots in the Daniel Boone National Forest, Kentucky.

Crown Position		Dawkins Crown Illumination Index	
Class	Definition	Class	Definition
Overtopped (O)	Shorter than the canopy level and receiving no illumination from above	1	No direct light (crown not lit directly either vertically or laterally
		2	Lateral light (<10% of the vertical projection of the crown exposed to vertical light, crown lit laterally
Intermediate (I)	Shorter than the general canopy level, tree crown reaches into lower foliage of canopy trees	3	Some overhead light (10-90% of the vertical projection of the crown exposed to vertical illumination)
Codominant (C)	Crown within the general level of the canopy	4	Full overhead light (≥90% of the vertical projection of the crown exposed to vertical light, lateral light blocked within some or all of the 90° inverted cone encompassing the crown)
Dominant (D)	Crown above the general level of the canopy	5	Crown fully exposed to vertical and lateral illumination within the 90° inverted cone encompassing the crown

Source: Modified from Jennings, S.B., N.D. Brown, and D. Sheil. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover, and other measures. Forestry 72(1): 59-73.

(a) Crown position score



(b) Dawkins crown illumination index

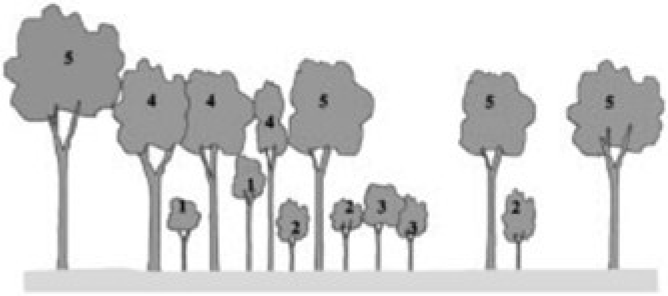


Figure 3: Diagram showing crown position (a) and illumination index (b) scores used to assess canopy structure in forests in the Daniel Boone National Forest, Kentucky.

Source: Reprinted from Jennings, S.B., N.D. Brown, and D. Sheil 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover, and other measures. Forestry 72(1): 59-73.

debris (CWD) was defined as downed dead wood > 10 cm diameter and > 1.0 m long, with the volume determined by the equation $V = [\pi h(R_1^2 + R_1R_2 + R_2^2)]/3$, where h is the within-plot length of the segment, and R_1 and R_2 are the end radii of each segment (Rubino and McCarthy 2003). In cases where the segment diameter tapered to < 10 cm, h was measured only to where the diameter equaled 10 cm. Where the segment crossed the plot boundary, the diameter was recorded at the boundary. Snags were recorded for DBH and height using a clinometer within a 20 x 20 m plot centered on the 10 x 10 m quadrat. Decay class (1-5) of both CWD and snags was assigned following Rubino and McCarthy (2003) (Table 2).

To assess age structure, an 18” increment borer was used to remove two cores from one tree in each of three size classes (10 cm < DBH < 25 cm, 25 < DBH < 50 cm, and DBH > 50 cm) in each plot. Where a tree of a particular diameter class was not available within the plot, the nearest tree to the plot in the respective diameter class was cored for age structure but excluded from other vegetation analyses.

Table 2: Criteria used to assign decay class to coarse woody debris in the Daniel Boone National Forest, Kentucky.

Decay Class	Criteria
I	Bark intact, small branches present
II	Bark loose or sloughing, small branches present, no sapwood degradation
III	Little to no bark, sapwood degradation, not punky
IV	No bark, mosses present, distinct sapwood degradation, punky
V	No bark, loss of circular shape, portions of log incorporating into humus layer, high fragmentation and moss cover

Source: Rubino, D.L. and B.C. McCarthy. 2003. Evaluation of coarse woody debris and forest vegetation across topographic gradients in a southern Ohio forest. Forest Ecology and Management 183: 221-238.

3.2 ANALYSIS

Data were analyzed by scaling values for each plot to per-hectare values, and aggregating plots within each age cohort to calculate means for given structural metrics. Graphical interpretation and statistical analyses were used to assess structural patterns. Because of high variance, non-parametric distributions of most data, and the failure of logarithmic transformations to adequately establish parametric distributions, I relied primarily on the Mann-Whitney *U* test for testing significance. The Mann-Whitney *U* test is a non-parametric significance test that looks for differences in the central tendency of a range of values by transforming values to ranks, thus minimizing the effect of outliers in determining statistical significance (Zar 2010). Where data were distributed normally, I used a standard *t* test. It is possible that a larger sample size would have resulted in a more parametric distribution of values for some of the characteristics studied. However, resource limitations did not make this possible.

Low sample size has been recognized as resulting in larger *P*-values, which can obscure biological significance (Yoccoz 1991; Johnson 1999). Confidence intervals have been proposed as a more valuable alternative to relying on *P*-values (Yoccoz 1991; Johnson 1999). However, non-parametric alternatives for calculating confidence intervals were not readily apparent for this study. Therefore, to better balance Type I and Type II error, significance was set at $P < 0.1$ instead of the conventional $P < 0.05$, with *P*-values reported and analyzed in context with graphical interpretation of sample means and discussions of forest processes. It is also important to note that outliers of relatively infrequent phenomena, such as large-diameter snags, could be biologically significant, but not result in statistical significance due to the ranking nature of the Mann-Whitney *U* test.

Tree ages where cores were oblique to, but < 3 cm from the pith were estimated by fitting a circle of known radius to the curvature of existing rings and estimating the missing rings by applying the average number of rings in the last evident centimeter to the missing distance to the pith. Where trees were hollow and cores oriented toward the pith, or oblique and > 3 cm from the pith, no age estimate was made. Unlike other metrics in this study, tree age data are provided as counts rather than means.

Where applicable, results were compared with data from Lilley Cornett Woods from unpublished 2010 survey data (McEwan and Richter 2010) and previously published literature (Parker 1989; Muller and Liu 1991; Martin 1992). Because of differences in data collection and methodology, statistical comparison was not appropriate, with graphical and numerical data standing on their own. Data were also compared to values in the Region 8 Guidance to assess the status of forests studied relative to administrative considerations (USDA Forest Service 1997).

4. RESULTS

Age Distributions

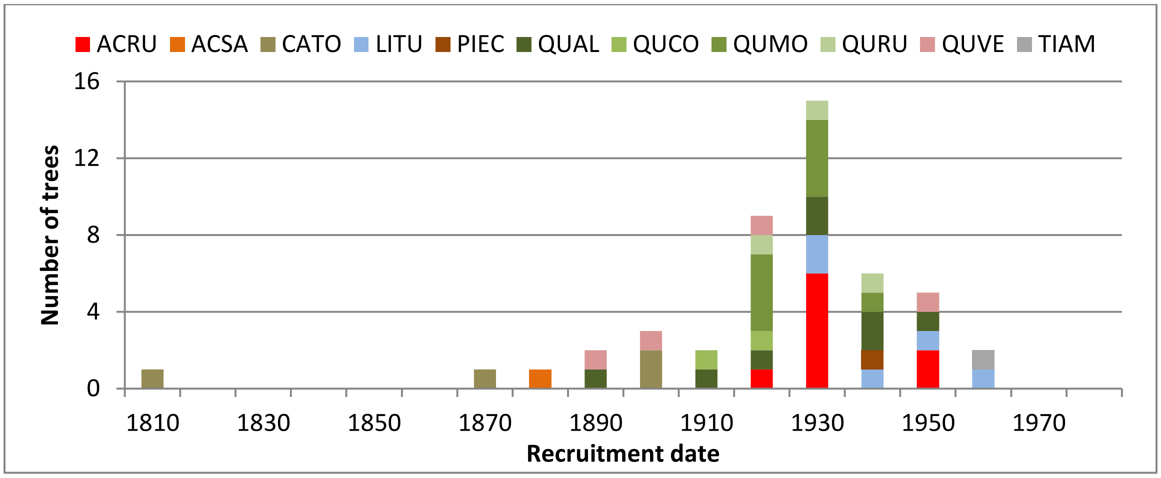
Tree age distribution in young forest was clumped around the 1920s through 1940s, consistent with the target stand age (Figure 4a). Several trees older than general stand age were present, represented by oaks (*Quercus* spp.) and mockernut hickory (*Carya tomentosa*). Regeneration was primarily oaks and tulip poplar (*Liriodendron tulipifera*), with a spike of red maple (*Acer rubrum*) in the 1930s and, to a lesser extent, in the 1950s (Figure 4a). No trees recruiting after the 1960s were found to have reached the 10 cm minimum diameter range for sampling.

Old forest had a much broader age distribution than young forest, showing near-continuous recruitment from the 1840s through the 1980s, with several trees over 200 years in age, including white oak (*Quercus alba*), chestnut oak (*Q. montana*), pignut hickory (*Carya glabra*), and tulip poplar (*Liriodendron tulipifera*) (Figure 4b). Oaks and pignut hickory (*C. glabra*) dominated recruitment from the 1840s through 1870s, with oak recruitment sporadic until the 1930s. Sugar maple (*Acer saccharum*) and tulip poplar were strong recruiters during the 1890s and 1900s, with red maple entering the mix beginning in the 1910s through the 1930s (Figure 4b). Recruitment from 1940 onward was characterized by largely shade-tolerant species, including eastern hemlock (*Tsuga canadensis*), cucumber magnolia (*Magnolia acuminata*), American beech (*Fagus grandifolia*), black gum (*Nyssa sylvatica*), and sugar maple.

Coarse Woody Debris

Total coarse woody debris (CWD) was 23.0 m^3/ha in young forest and 84.9 m^3/ha in old forest (Mann-Whitney $U = 165.5$, $n_1 = 17$, $n_2 = 15$, $P \approx 0.1$, one-tailed) (Figure 5). CWD in young forest was restricted to logs < 30 cm diameter, with more volume in this size range than in old forest (Mann-Whitney $U = 194$, $n_1 = 17$, $n_2 = 15$, $P < 0.01$, one-tailed), while in old forest CWD volume was dominated by logs between 40 cm and 79 cm diameter (Figure 6). CWD in old forest was mostly in

a.



b.

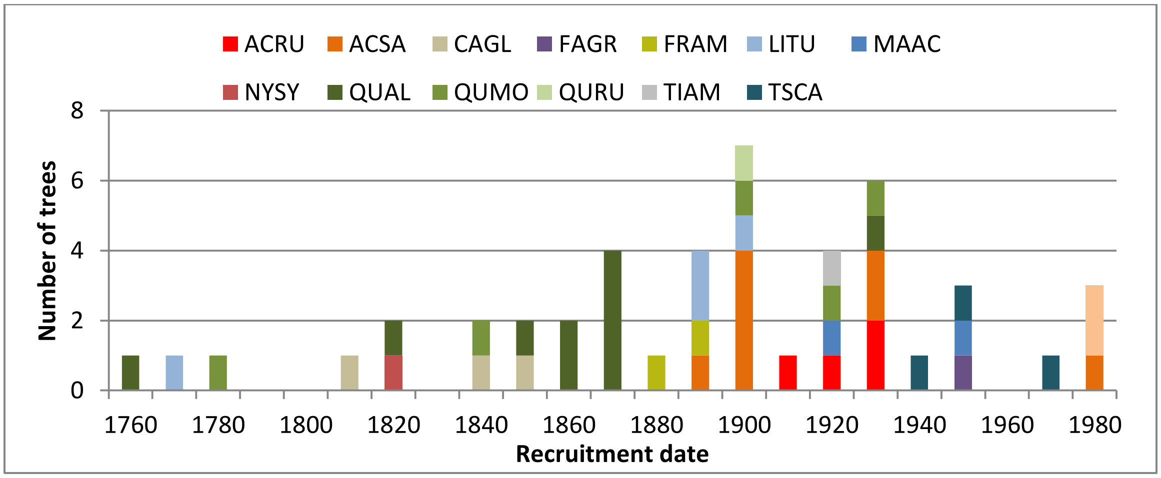


Figure 4: Age distribution of trees in young (a) and old (b) forest. Abbreviations as follows: ACRU = red maple (*Acer rubrum*); ACSA = sugar maple (*Acer saccharum*); CATO = mockernut hickory (*Carya tomentosa*); FAGR = American beech (*Fagus grandifolia*); FRAM = white ash (*Fraxinus* americana); LITU = tulip poplar (*Liriodendron tulipifera*); MAAC = cucumber magnolia (*Magnolia acuminata*); NYSY = black gum (*Nyssa sylvatica*); PIEC = shortleaf pine (*Pinus echinata*); QUAL = white oak (*Quercus alba*); QUCO = scarlet oak (*Quercus coccinea*); QUMO = chestnut oak (*Quercus montana*); QURU = northern red oak (*Quercus rubra*); QUVE = black oak (*Quercus velutina*); TIAM = basswood (*Tilia americana*); TSCA = eastern hemlock (*Tsuga canadensis*).

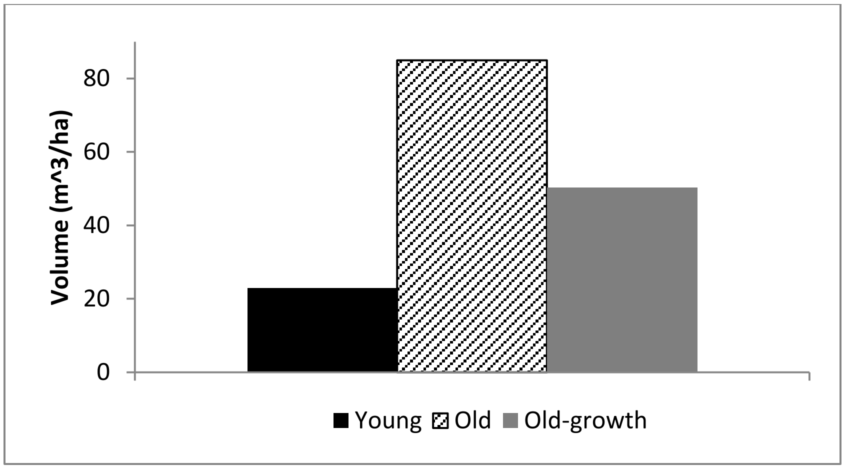


Figure 5: Coarse woody debris volume for young (70-90 years old), old (140-160 years old), and old-growth forest (Lilley Cornett Woods) in the Cumberland Plateau of Kentucky.

Source: Old-growth value from Muller, R.N. and Y. Liu. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Canadian Journal of Forest Research 21(11): 1567-1572).

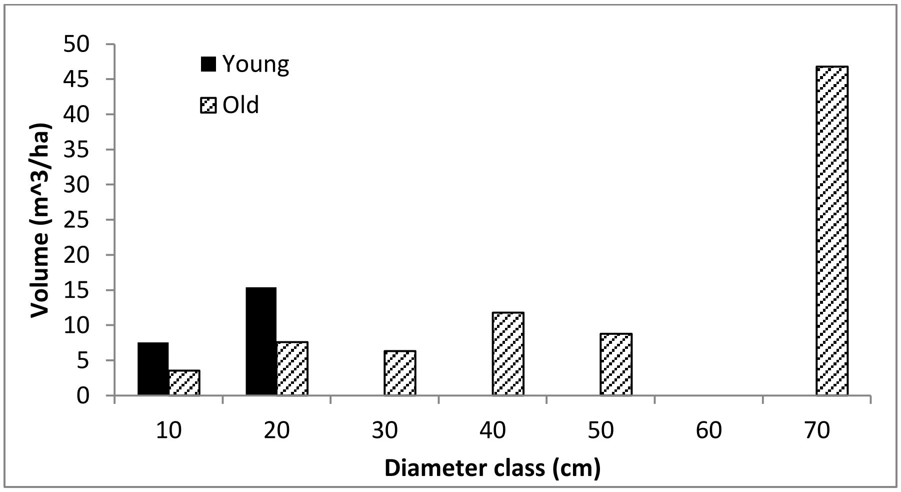


Figure 6: Coarse woody debris volume by diameter class in young (70-90 years old) and old (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

decay classes 1 and 4, while young forest had CWD spread somewhat evenly from classes 2 through 5 (Figure 7).

Snags

Young forest had 32.8 snags/ha in the 10 cm diameter class, compared to only 7.4 snags/ha in this diameter in old forest (Mann-Whitney $U = 195.5$, $n_1 = 17$, $n_2 = 16$, $P < 0.025$, one-tailed) (Figure 8). Values were similar for snags in the 20 cm through 40 cm diameter classes. Old forests had 5.9 snags/ha > 50 cm diameter compared to 1.6 snags/ha in young forest, though the difference was not statistically significant (Mann-Whitney $U = 163$, $n_1 = 17$, $n_2 = 16$, $P \approx 0.15$, one-tailed).

Crown Position

While old forest appeared to have more overtopped (O) trees (644.4/ha versus 446.7/ha in young forest) (Figure 9), this difference was not statistically significant (Mann-Whitney $U = 153$, $n_1 = 18$, $n_2 = 15$, $P > 0.2$, one-tailed). Young and old forests had similar values for intermediate trees (146.7 trees/ha in young and 166.7 trees/ha in old forest), though the pattern for codominant and dominant trees was quite different. Young forest had 233.3 codominant (C) trees/ha compared to 88.9 trees/ha in old forest. Old forest had 55.6 dominant (D) trees/ha, while young forest had none.

In both young and old forest, oaks were predominant in the overstory (codominant and dominant crown positions), while nearly absent in the overtopped (O) layer. Maples followed an opposite pattern, dominating the overtopped layer while nearly absent in the codominant and dominant layers. Oak density was about the same as maple in the intermediate (I) position for young forest, though oak was barely represented in this layer in old forest. No other species represented more than 10% of any given crown position in young or old forest.

Illumination Index

Indices 1, 4, and 5 of the illumination index followed a nearly identical pattern to the overtopped (O), codominant (C), and dominant (D) crown positions,

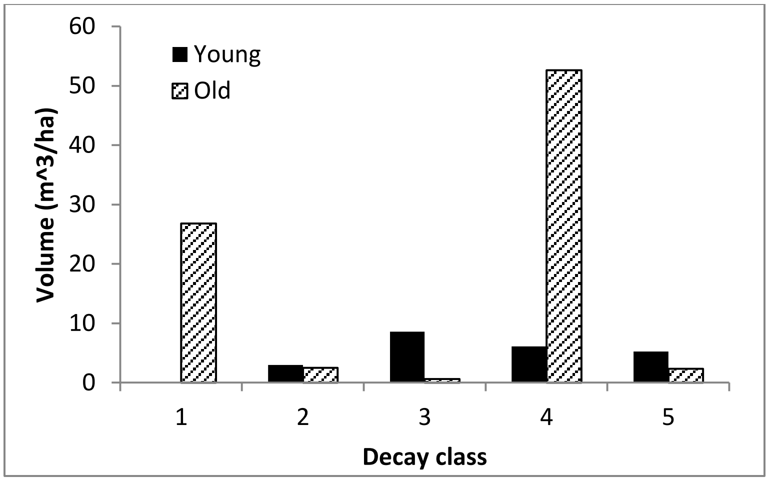


Figure 7: Coarse woody debris volume by decay class in young (70-90 years old) and old (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

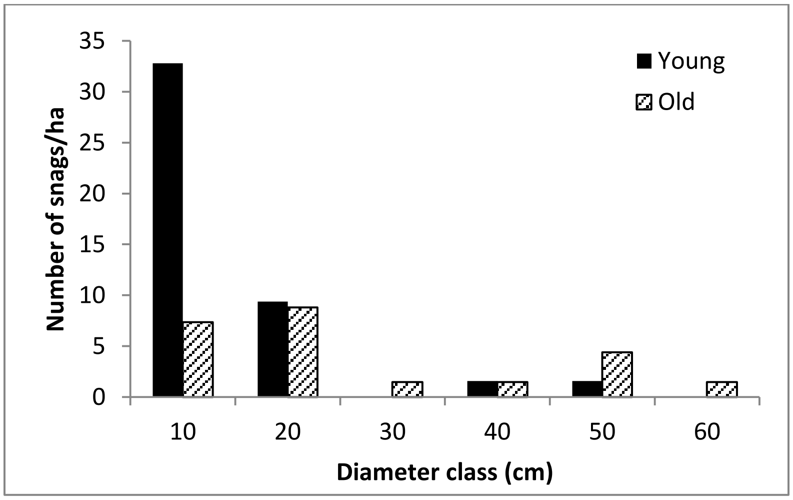


Figure 8: Snag density by diameter class in young (70-90 years old) and old (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

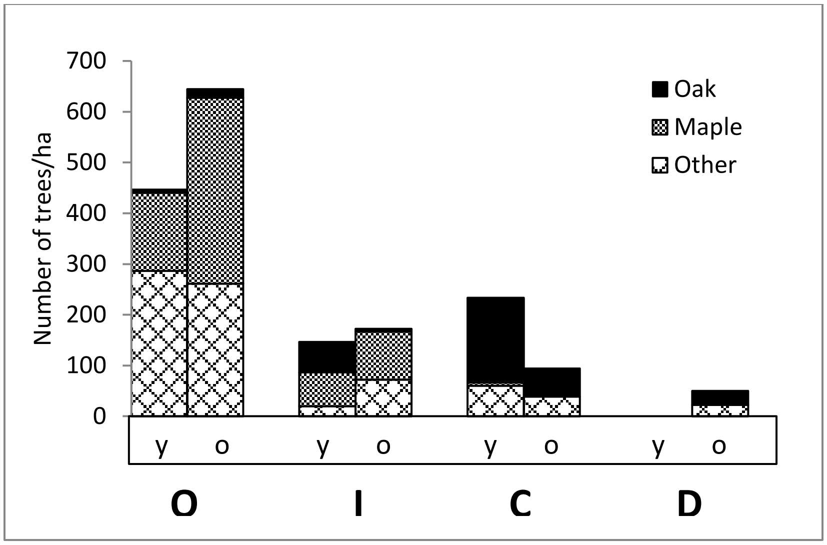


Figure 9: Crown position in young (y) (70-90 years old) and old (o) (140-160 years old) forest in the Daniel Boone National Forest, Kentucky. Categories are overtopped (O), intermediate (I), codominant (C), and dominant (D).

Source: Modified from Jennings, S.B., N.D. Brown, and D. Sheil. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover, and other measures. Forestry 72(1): 59-73.

respectively, in both absolute density and density of oak and maple species in young and old forest (Figure 10). For illumination index 2, young forest had 33.3 stems/ha while old forest had 83.3 stems/ha, though statistical significance is arguably lacking (Mann-Whitney $U = 169$, $n_1 = 18$, $n_2 = 15$, $P \approx 0.12$, one-tailed). Nearly all differences between young and old forest for illumination index 2 resulted from more maples in the older forest.

For illumination index 3, young forest had 46.7 stems/ha compared to 166.7 stems/ha in old forest (Mann-Whitney $U = 186$, $n_1 = 18$, $n_2 = 15$, $P < 0.05$, one-tailed). As with illumination index 2, the increase observed in old forest was driven largely by maples, though other species also contributed to this difference.

Canopy Species

The relative frequencies of canopy species (codominant or dominant trees) show a predominance of white oak (*Quercus alba*) followed by chestnut oak (*Q. montana*) and tulip poplar (*Liriodendron tulipifera*) in both young and old forest plots sampled (Figure 11). Young forest had more hickories (*Carya* spp.) and red oak (*Q. rubra*). Red maple (*Acer rubrum*), shortleaf pine (*Pinus echinata*), scarlet oak (*Q. coccinea*), and black oak (*Q. velutina*) appeared only in the canopies of young forest plots. Unique to old forests canopies were basswood (*Tilia americana*), American beech (*Fagus grandifolia*), black gum (*Nyssa sylvatica*), and eastern hemlock (*Tsuga canadensis*).

Basal Area and Density

Total basal area was greater in old forest, with 31.5 m^2/ha in young forest and 41.0 m^2/ha in old forest ($t(31) = 1.50$, $P = 0.072$) (Figure 12). The density of trees > 10 cm DBH in young and old forest was 420 stems/ha and 378 stems/ha, respectively, with differences not significant (Mann-Whitney $U = 145$, $n_1 = 18$, $n_2 = 15$, $P > 0.2$, two-tailed). This compares to 536 stems/ha from the 2010 Lilley Cornett Woods data and the 250 stems/ha average reported for the same forest by Martin (1992) (Figure 13).

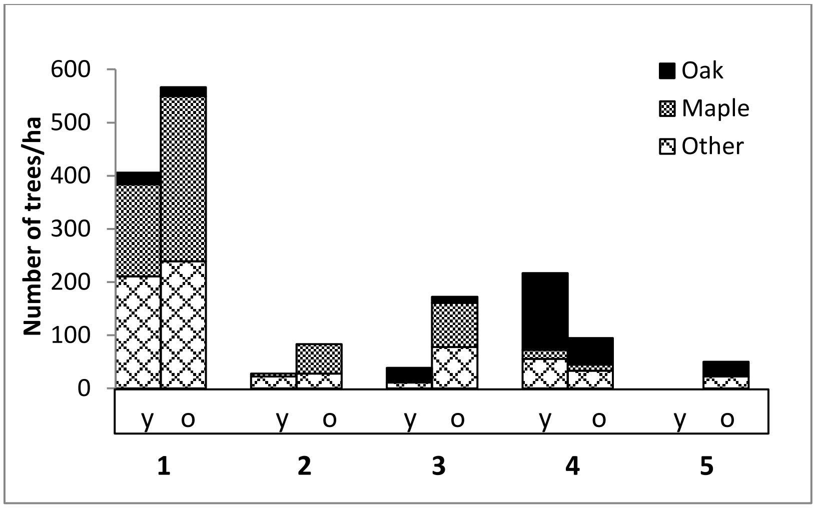


Figure 10: Illumination indices (1-5) for young (y) (70-90 years old) and old (o) (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

Source: Jennings, S.B., N.D. Brown, and D. Sheil. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover, and other measures. Forestry 72(1): 59-73.

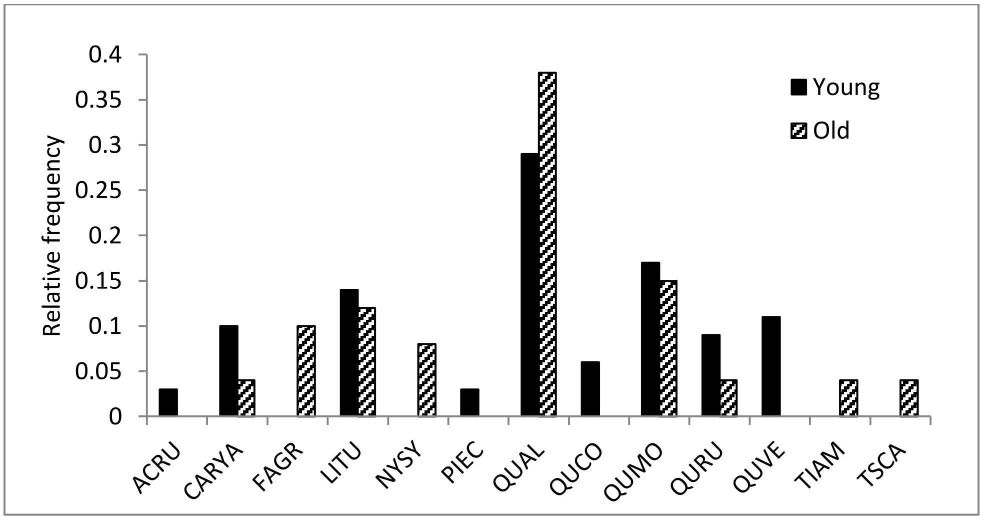


Figure 11: Canopy species in young and old forest, including codominant and dominant trees in young (70-90 years old) and old (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

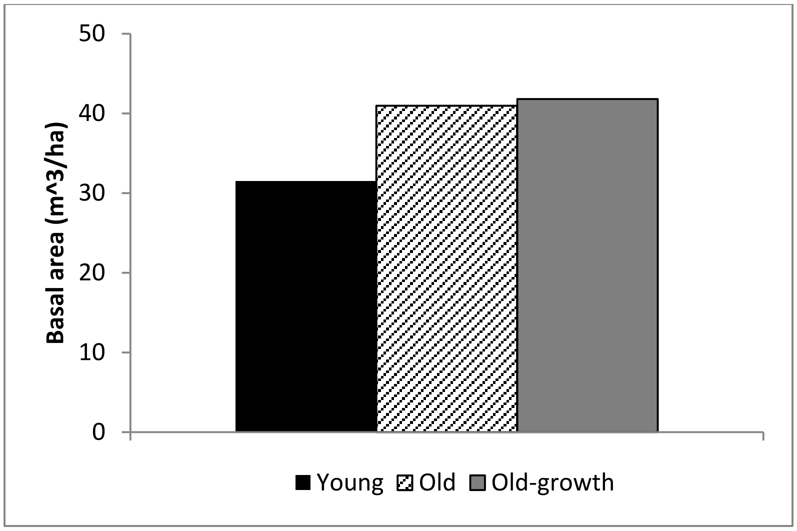


Figure 12: Basal area in young (70-90 years old), old (140-160 years old), and old-growth forest (Lilley Cornett Woods) in the Cumberland Plateau of Kentucky.

Source: Old-growth value is calculated from McEwan, R.W. and S. Richter. 2010. Lilley Cornett Woods long-term data. Division of Natural Areas, Eastern Kentucky University, Richmond, KY.

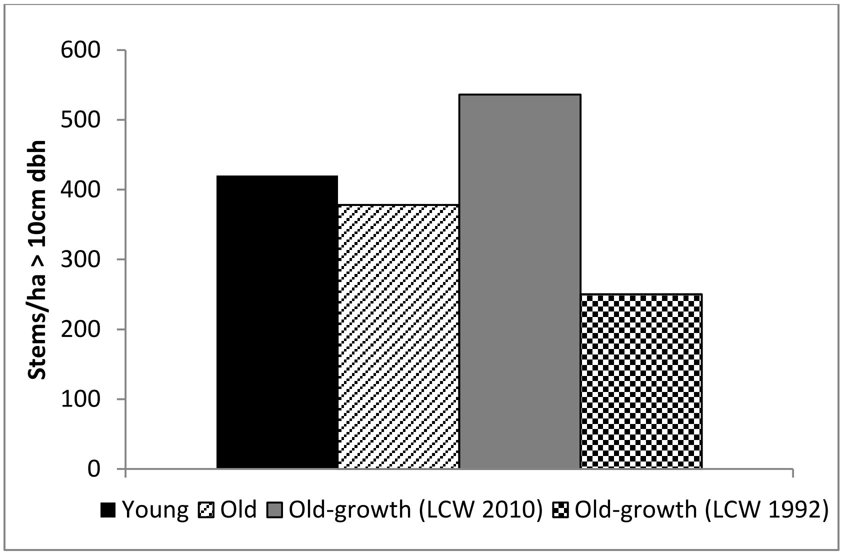


Figure 13: Density of trees > 10 cm DBH in young, old, and old-growth forests (Lilley Cornett Woods) in the Cumberland Plateau of Kentucky.

Source: Old-growth values are from Lilley Cornett Woods. LCW 2010 data are derived from McEwan, R.W. and S. Richter. 2010. Lilley Cornett Woods long-term data. Division of Natural Areas, Eastern Kentucky University, Richmond, KY. LCW 1992 data are from Martin, W.H. 1992. Characteristics of old-growth mixed mesophytic forests. Natural Areas Journal 12(3): 127-135.

Diameter Distributions

Maximum diameters in young, old, and old-growth forests (McEwan and Richter 2010) were 55.6 cm, 88.9 cm, and 124.0 cm, respectively, showing a clear trend of increasing maximum diameter with time (Figure 14). The diameter distribution for the 140–160 year-old, old forest followed close to a reverse-J distribution, with a slight plateau through the 20 cm and 30 cm diameter classes reminiscent of a rotated sigmoid distribution. The diameter distribution for young forest shows a hump in the mid-diameter (20–49 cm) range where the old forest appears to plateau and drop. Differences between age groups in the 30–49 cm range were significant (Mann-Whitney $U = 211$, $n_1 = 18$, $n_2 = 15$, $P < 0.005$, one-tailed). By comparison, the Lilley Cornett Woods data from 2010 followed a smooth reverse-J, long-tailed distribution (Figure 14).

Despite the appearance of a trend in the 2.5 cm diameter cohort of increasing density with age, results of a Mann-Whitney *U*-Test indicated a lack of significant differences between young and old forest (Mann-Whitney $U = 157$, $n_1 = 18$, $n_2 = 15$, $P > 0.1$, two-tailed).

Seedlings and Saplings

Total seedlings were greater in young than old forest, with 31,630 stems/ha and 14,127 stems/ha, respectively, though the difference was not statistically significant (Mann-Whitney $U = 151$, $n_1 = 18$, $n_2 = 15$, $P > 0.2$, one-tailed). Saplings followed a similar, though statistically significant, pattern of 2,987 stems/ha in young and 1,689 stems/ha in old forest (Mann-Whitney $U = 178$, $n_1 = 18$, $n_2 = 15$, $P < 0.1$, one-tailed)(Figure 15a).

There were more maple (*Acer*) seedlings in young forest than old forest (9,259 stems/ha and 3,810 stems/ha, respectively; Mann-Whitney $U = 177$, $n_1 = 18$, $n_2 = 15$, $P < 0.1$, one-tailed). Oak (*Quercus*) seedling densities were greater in young forest (14,519 stems/ha) than in old forest (2,037 stems/ha) (Mann-Whitney $U = 229.5$, $n_1 = 18$, $n_2 = 15$, $P < .01$, one-tailed). The large number of oak seedlings in the young forest was driven, in large part, by a single plot that had a very large number of very small chestnut oak (*Q. montana*) seedlings. Removing this plot resulted in a

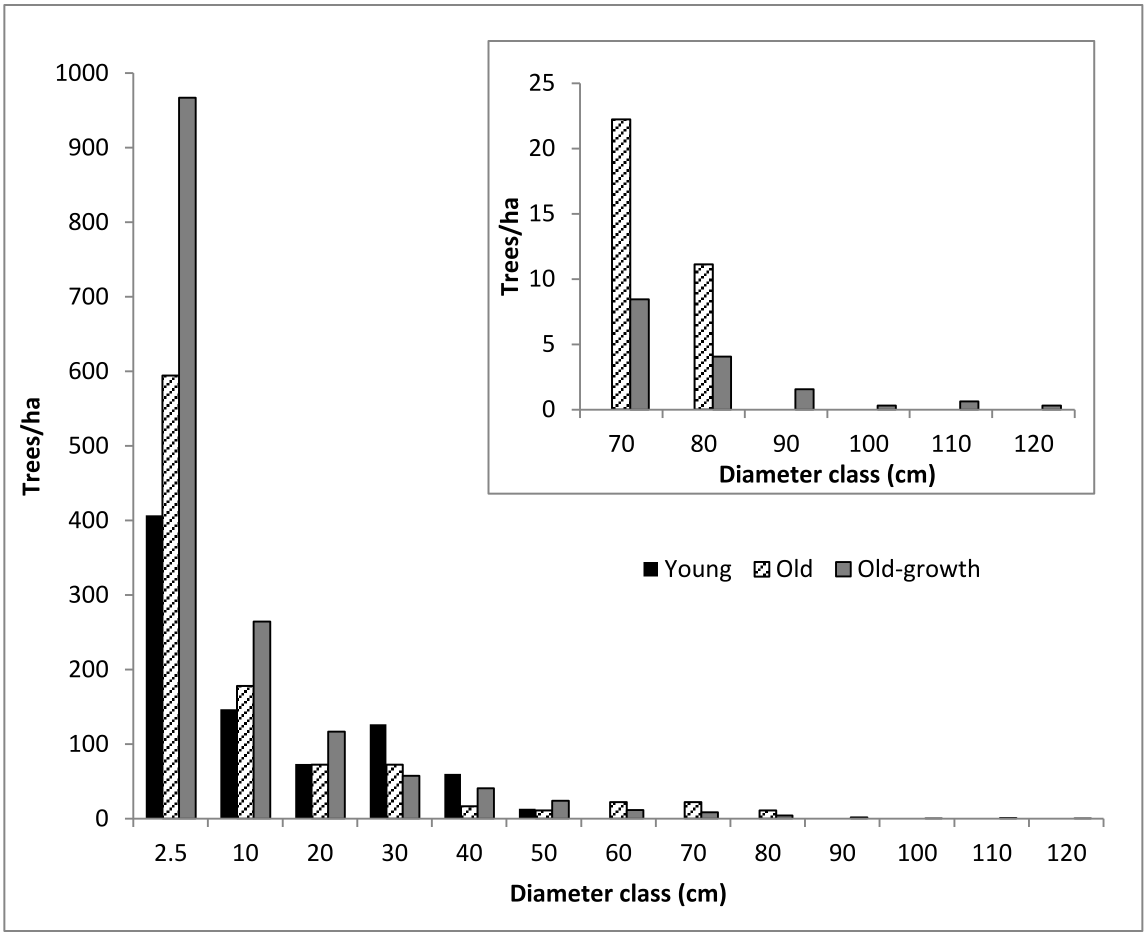


Figure 14: Diameter distributions of live trees in young (70-90 years old), old (140-160 years old), and old-growth forest (Lilley Cornett Woods) in the Cumberland Plateau of Kentucky.

Note: Inset shows diameters >70 cm dbh.

Source: Old-growth values calculated from McEwan, R.W. and S. Richter. 2010. Lilley Cornett Woods long-term data. Division of Natural Areas, Eastern Kentucky University, Richmond, KY.

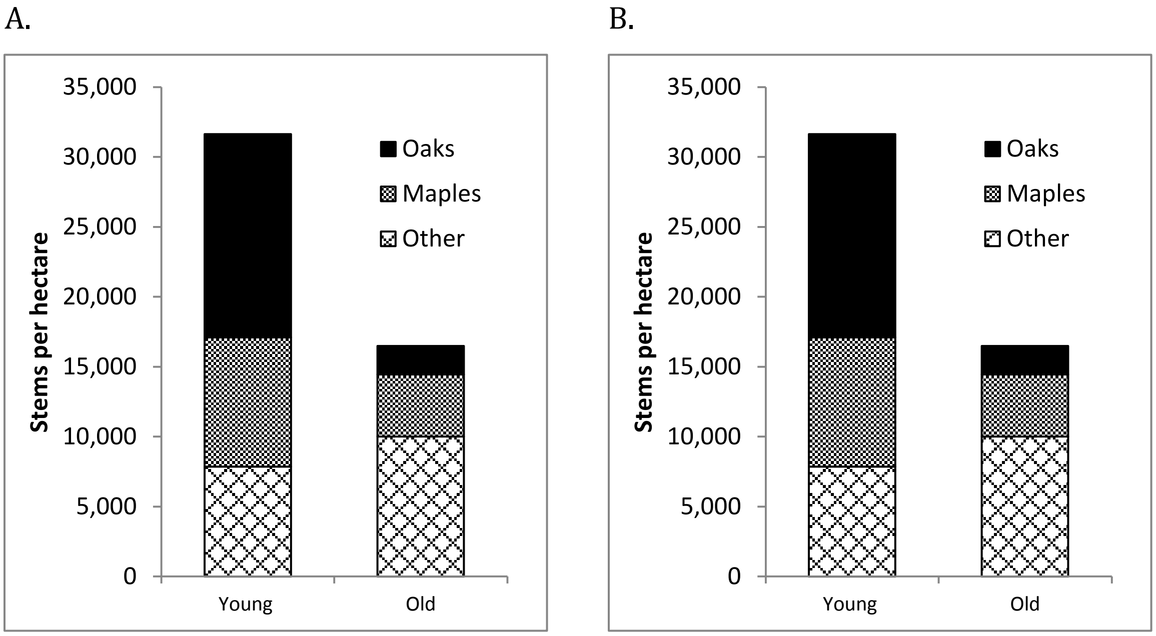


Figure 15: Density of seedlings (A) and saplings (B) in young (70-90 years old) and old (140-160 years old) forests in the Daniel Boone National Forest, Kentucky.

density of 9,603 stems/ha for young forest, with the difference in oak seedling density remaining significant (Mann-Whitney $U = 211.5$, $n_1 = 18$, $n_2 = 14$, $P < .01$, one-tailed). Old forest had more maple than oak seedlings (Mann-Whitney $U = 206$, $n_1 = 18$, $n_2 = 18$, $P < 0.1$, one-tailed), while young forest showed no differences (Mann-Whitney $U = 135.5$, $n_1 = 15$, $n_2 = 15$, $P \approx 0.2$).

Young forest had more oak saplings than old forest (373 stems/ha and 0 stems/ha, respectively; Mann-Whitney $U = 171$, $n_1 = 18$, $n_2 = 15$, $P \approx 0.1$, one-tailed), while maple sapling density was also greater in young forest (1,227 stems/ha and 600 stems/ha, respectively; Mann-Whitney $U = 179$, $n_1 = 18$, $n_2 = 15$, $P < 0.1$, one-tailed)(Figure 15b). Old forest had significantly more maple than oak saplings (Mann-Whitney $U = 261$, $n_1 = 18$, $n^2 = 18$, $P < 0.001$, one-tailed), while young forest had nearly twice as many maple as oak saplings (Mann-Whitney $U = 179$, $n_1 = 15$, $n_2 = 15$, $P = 0.0025$).

5. DISCUSSION

The data presented here represent a composite of plots from similar forests in two age classes across the Daniel Boone National Forest and the Western Escarpment of the Northern Cumberland Plateau of Kentucky. The wide-ranging, low-density sampling employed in this study limits the capacity for site-specific interpretation, and instead offers insight into broad patterns of forest development. This study was designed as a chronosequence investigating the development of old-growth characteristics with time based upon existing forest inventory age data. However, dendrochronological analysis suggests that historical contingencies, especially of differences in disturbance intensity, may also have a bearing on current forest structure.

While some individual characteristics examined in this study were found to be of marginal or lacking of statistical significance, overall results show that the old forests sampled are approaching old-growth conditions (Table 3). Trends in the data indicated that old forest had more large trees, large snags, coarse woody debris, canopy gaps, canopy stratification, and overall basal area, along with a more uneven age distribution, than young forest. While old forest was generally intermediate between young and old-growth forest conditions, it more closely resembled old-growth forest than young forest which, at 70-90 years, would typically be considered “mature” and ready for harvest by many silvicultural standards (Miller et al. 1995).

Old forest in this study was defined as forests between 140 and 160 years in age, reflecting the oldest second-growth hardwood stands as provided in the DBNF Stands GIS database (USDA FS 2009). As discussed in the methods section, field examination of inventoried stands most often revealed that stands ostensibly within the sought after age bracket were predominantly of a younger age—typically between 110 and 130 years of age, and that older forest was relegated to small patches within these decades-younger forests. It is also probable that, despite great care, errors occurred in field-counting tree cores when confirming forest age, and

Table 3: Comparison of selected old-growth benchmarks in young (70-90 years old) and old (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

Source	**Characteristic**	**Benchmark**	**Young forest**	**Old forest**
Martin (1992) R8 Guidance	Large canopy trees	> 7 trees/ha > 75cm DBH Canopy trees > 50 cm DBH	No; (0/ha) Few (13.3/ha)	Yes (16.7/ha) Many (66.7/ha)
Martin (1992) R8 Guidance	Tree ages	Oldest trees > 200 years Canopy > 150 years	No No	Yes Yes
Martin (1992) Parker (1989)	Stem density	160-315 stems >10 cm DBH/ha 161-427 stems > 10 cm DBH/ha	No (420/ha) Yes	No (378/ha) Yes
Martin (1992) R8 Guidance	Total basal area	Total basal area > 25 m^2/ha Total basal area > 10 m^2/ha	Yes Yes	Yes Yes
Martin (1992)	Snag density	Ave. 10 snags > 30 cm DBH/ha	No (3/ha)	No (8.82/ha)
Muller & Liu (1991)	Coarse woody debris	More in old –growth; 50.4 m^3/ha in LCW	23.0 m^3/ha	84.9 m^3/ha
Oliver and Larson (1996), Frelich (2002)	Age distribution	Uneven age distribution	No	Yes
Frelich (2002)	Canopy Structure	Vertical and horizontal structural complexity	Less	More

Sources: Martin, W.H. 1992. Characteristics of old-growth mixed mesophytic forests. Natural Areas Journal 12(3): 127-135.

USDA FS. 1997. Guidance for Conserving and Restoring Old-Growth Forest Communities on National Forests in the Southern Region. Report of the Region 8 old-Growth Team. United States Department of Agriculture Forestry Report R8-FR, 56.

Parker, G.R. 1989. Old-growth forests of the central hardwood region. Natural Areas Journal 9(1): 5-11.

Muller, R.N. and Y. Liu. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Canadian Journal of Forest Research 21(11): 1567-1572.

Oliver, C.D. and B.C. Larson. 1996. Forest Stand Dynamics, Update Edition. John Wiley & Sons, Inc., New York.

Frelich, L.E. 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge University Press, Cambridge.

plots may have represented forest patches slightly older or younger than the target age.

Patches of forest 140 to 160 years old at the time of this study initiated between 1850 and 1870, during the homesteading period and just prior to the major logging era (roughly 1870 to 1930) (Braun 1950; Collins 1975; Pudup 1990). These older areas of forest represent small patches that were likely disturbed within an otherwise intact, or mostly intact, forest. Whether the initiating disturbances were natural or anthropogenic in origin, or both, is not clear, and likely vary by site. However, the number of residual trees > 160 years in these older forest patches suggest that the intensity of disturbance was intermediate for at least some sites.

The most likely candidates for the disturbances that initiated the old forest sites are logging or small-scale natural disturbance with localized effects (e.g., microbursts). This latter assumption is based on the fact that most forest surrounding the old forest patches was only a few decades younger (i.e., regenerated c.a. 1880-1900) and likely regenerated by being logged, suggesting that surrounding forest was substantially intact with merchantable trees when the old forest patches were initially disturbed. Some stands had more area of forest initiating during the target period, and may have been subject to larger disturbance events (e.g., tornados, straight-line winds, or logging), but still within a matrix of intact forest. Still larger-scale disturbances, such as ice storms, derechos, or extreme drought, would most likely have caused more forest to be synchronously initiated than was found. Based upon observations of the landscape and setting of the older stands sampled here, clearing for homestead sites or small-scale agricultural use are unlikely to have occurred at most sites because of steep slopes and the presence of residual trees. Steep slopes, especially south-facing slopes, are less likely to be productive and more likely to have older trees (Stahle and Chaney, 1994).

It is also notable that the oldest trees in the old forest were often not the largest (Figure 16), suggesting that larger old-growth trees were removed. It may also be that selectively removing the largest trees would have been extremely difficult this early in settlement, when major infrastructure to support large-scale

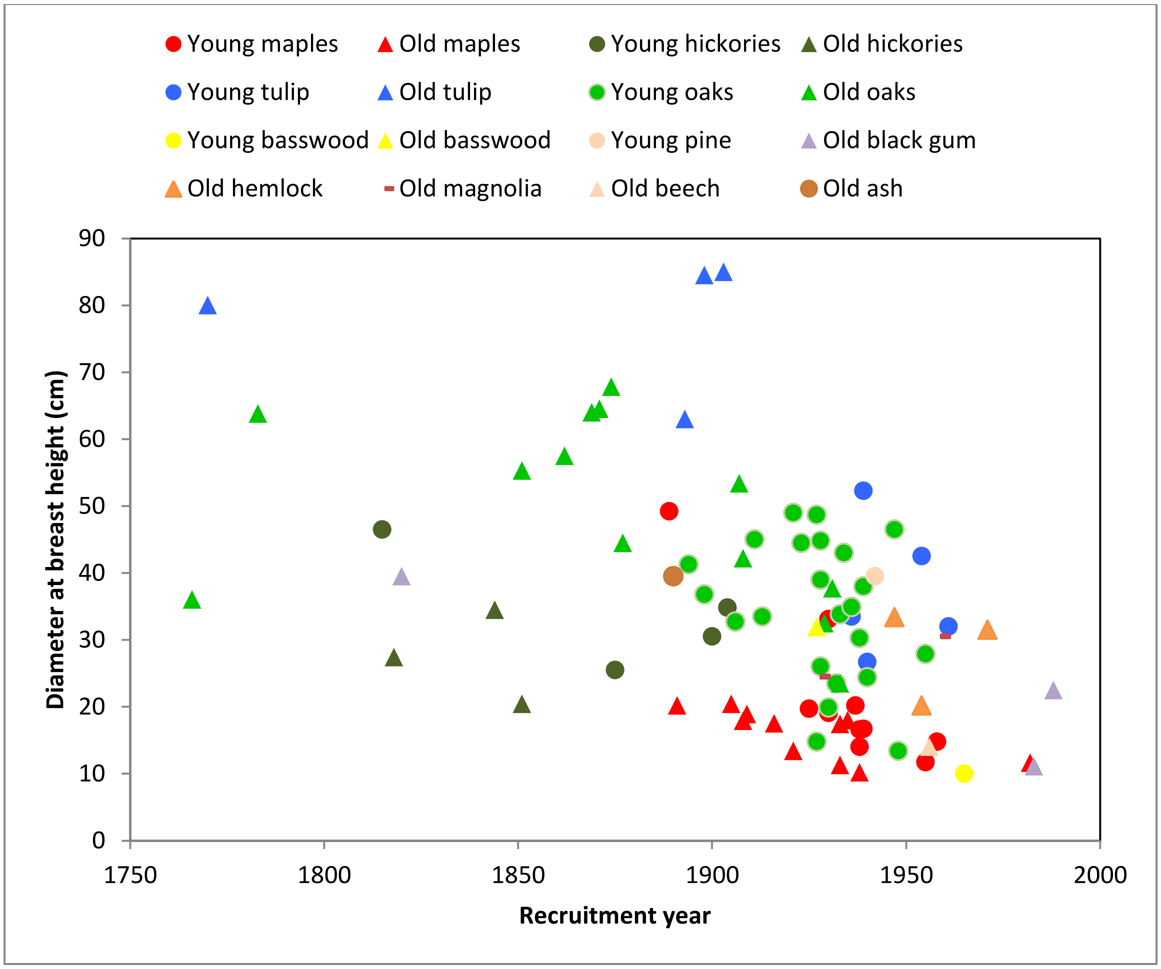


Figure 16: Size vs. age relationships for trees by species in young (70-90 years old)(triangle) and old (140-160 years old)(circle) forests in the Daniel Boone National Forest, Kentucky.

logging was just entering the region, again suggesting that natural disturbance may have been the cause of initiation. Ring patterns in residual old-growth trees often indicated that they were suppressed and likely in the mid- or understory trees, or otherwise of modest diameter at the time of disturbance. As such, basal area and frequency after the initial disturbance was probably low, and comprised of scattered, relatively small trees < 20 cm DBH. The initial forest structure in the young forest cohort was probably similar to that of old forests, as evidenced by the similar frequency of residual trees older than the dominant cohort.

Despite the unknowns associated with the history of individual forest stands, the likelihood that initial forest structure following disturbance was probably similar in young and old forests still allows for the elucidation of the development of old-growth structural characteristics with time.

5.1 OLD-GROWTH CHARACTERISTICS

Age Distributions

Emerging patterns from the examination of age data show a wide and nearly continuous distribution of ages in old forest ranging from around 1760 into the 1980's, with ongoing recruitment from stand initiation until 1983 (and presumably beyond, represented by seedlings and saplings). Within this age continuum, the old forest cohort shows two pronounced episodes of recruitment after the major disturbance event, from about 1890-1909 and then 1920-1929 that include shade intolerant, mid-tolerant, and tolerant species. These episodes probably represent a combination of natural and anthropogenic disturbances (i.e. selective logging) of varying intensities, resulting in a range of light conditions and consequently differences in species recruitment (Runkle 1982; Runkle and Yetter 1987; Tackett 2012). The age structure of the older forest in this study is similar to the general patterns in old-growth forests, which are often uneven- or multi-aged, with continuous or multiple periods of episodic recruitment (Martin 1992; Oliver and Larson 1996; Frelich 2002; Tackett 2012). While there is some uncertainty about whether recruitment from about 1840 to 1900 represents continuous recruitment in individual stands or instead reflects error in canopy age determination, ongoing recruitment after 1900 was common in old forest plots. This, along with the presence of several trees > 200 years old, lends legitimacy to the determination that the old forests in this study are indeed mixed-aged forests.

The age distribution of the old forest cohort also bears a striking resemblance to those recently published for Rock Creek Research Natural Area (RCRNA) and Cane Creek in the Cold Hill Area (CHA), both hemlock-mixed mesophytic forests in the DBNF (Tackett 2012). Rock Creek RNA was confirmed as old-growth, though with some limited, selective cutting at one end of the ravine. Cold Hill, in contrast, contained old-growth trees but was determined to have had more intense selective cutting. Both forests were multi-aged and included the presence of old-growth trees > 200 years old.

In contrast, young forest shows a more truncated age distribution, with little recruitment following the initial disturbance peak from 1920–1939, and no trees at 10 cm DBH or larger having recruited after 1960. It is important to note here that, since only trees > 10 cm DBH were cored, and because some tree species can remain in the seedling or sapling stages for decades (Marks and Gardescu 1998), any lack of a species during the past several decades from the dendrochronological record presented here should not infer a lack of reproduction or persistence, but rather a lack of trees growing to 10 cm or greater over the interval of time after disturbance and prior to sampling.

While some trees older and younger than the dominant cohort are present, young forest in this study was predominantly even-aged, though about 20 percent of the trees in young forest were recruited prior to the initial disturbance peak, compared to about 10 percent in the old forest. However, these percentages need to take into account that some trees for both types of forest, and more in old forest, were hollow and impossible to date accurately. Therefore, while old forest contains more residual trees > 200 years old, the relationship between the ages and numbers of residual trees to the period of initial disturbance is similar. In both young and old forest, residual trees appear to have been mainly suppressed or midstory trees of modest size (< 20 cm DBH) at the time of disturbance. Therefore, in an absolute sense, the old forest had more old trees, but in a relative sense of forest development they are similar.

It is also notable that most residual trees in the young forest were < 50 years older than the initial disturbance, while in old forest several of the residual trees were 50-100 years older than the initial disturbance. If old forest was regenerated by logging, this difference could be attributable to changes in the technology and economics of logging between the mid-nineteenth century, when the old forest was logged, and the latter period of the 1920s and 1930s, when the young cohort was regenerated. As stated above, the tree-ring pattern in the residual trees suggests that they were suppressed, relatively small trees when the forest was logged. By the end of the logging boom in the 1920s and 1930s, the presence of established infrastructure, a greater ease of cutting and hauling timber, and the fact that by this time timber resources were dwindling in the region, all may have contributed to the cutting of smaller trees that, 70 years earlier, may have been left in the forest.

While it is difficult to parse the influences of stand development from the unknown history of anthropogenic disturbance at the patch and stand level with such a limited data set, the overall pattern of age structure between older and younger forest substantiates the presumption of similarity. Regardless of specific land-use history, old and young forest had a considerably similar structure at the time of initiation, validating that differences between to the two forest types are substantially related to changes with time.

Succession

The distribution of canopy species shows that, while the two cohorts are substantially similar, the old forest contains a handful of more mesic or shade-tolerant species. One interpretation of this discrepancy is that the old sites, despite efforts to obtain data from similar forest types, skewed toward more mesic conditions. However, the dendrochronological analysis suggests that successional processes may be responsible for the observed differences.

While the young forest is mostly limited to shade-intolerant and mid-tolerant species throughout the chronology, age reconstruction in the old forest shows that, prior to about 1900, regeneration was dominated by mid-successional, shade-intolerant or mid-tolerant species, including pignut hickory (*Carya glabra*), tulip poplar (*Liriodendron tulipifera*), chestnut oak (*Quercus montana*), white oak *(Q. alba*), and northern red oak (*Q. rubra*). From 1890 until 1930, shade-tolerant sugar maple (*Acer saccharum*) and mid-tolerant red maple (*A. rubrum*) appear in the record, while the oaks and tulip poplar continue to recruit. From 1940 onward, recruitment was limited to shade-tolerant species, including eastern hemlock (*Tsuga canadensis*), cucumber magnolia (*Magnolia acuminata*), American beech (*Fagus grandifolia*), black gum (*Nyssa sylvatica*), and sugar maple. While other species may have recruited post-1940, none were sampled that had reached the minimum coring diameter. This pattern of increasing shade tolerance suggests, in the absence of substantial disturbance events that can reset or accelerate succession (Abrams and Scott 1989), a migration toward a late-successional structure with age. It is possible that this could suggest progression toward a climax old-growth community (Braun 1950; Frelich and Reich 2003), though natural disturbance and drought may maintain the forest as seral old-growth over the long-run (McEwan et al. 2010). Further, a trend towards increased mesic species could also be following a centennial-scale trend towards wetter conditions in the eastern US (Pederson et al. 2012).

While oak and maple dynamics will be discussed more thoroughly later, it is worth noting here that in neither young nor old forest do hickories (*Carya* spp.) recruit much into the twentieth century, with the youngest hickory in the young forest recruiting around 1904 (before stand initiation), and 1851 in the old forest. In both forest cohorts, hickories stop appearing in the record either at or before the initial disturbance while oaks, a common associate, continue to recruit. Hickories were present in both seedling and sapling layers, suggesting difficulty transitioning from seedling and sapling stages to a tree in the lower canopy. This pattern may be, in part, because hickories often grow very slowly (Figure 16), and so may not have yet had time to progress into larger size classes.

Coarse Woody Debris

Old-growth forests typically have a marked increase in coarse woody debris (CWD) over younger forests (Parker 1989; Martin 1992; Hale et al. 1999; Spetich et al. 1999; Harmon 2009). In this study, old, second-growth forest had substantially more CWD than younger forest (84.9 m^3/ha and 23.0 m^3/ha, respectively), with the difference driven by logs in upper diameter classes. Following a similar pattern, Shifley et al. (1997) found 35.9 m^3/ha in old-growth versus 17.5 m^3/ha in second-growth Missouri forests, with the differences being driven by logs in the larger diameter ranges. Further, the old forest CWD volume exceeds several published values for old-growth forests. Muller and Liu (1991) reported an estimated 50.4 m^3/ha of CWD in Lilley Cornett Woods (Muller and Liu 1991). Importantly, the total value for standing and down CWD in that study is given as 66.3 m^3/ha, with 24% by mass from snags. Reducing volume by 24% provides an estimate for downed CWD of 50.4 m^3/ha. This suggests that 140 -160 years is enough time for forests in this region to develop a pool of CWD similar to that found in old-growth forests, and that 140 – 160 year old forests exhibit important functional and habitat differences from their younger, 70 – 90 year old counterparts.

The distribution of decay classes in the old forest cohort indicated a discontinuous input of CWD. While Martin (1992) suggested that CWD in various stages of decay is a characteristic of old-growth forests, similarly discontinuous distributions have been found in some old-growth forests (Shifley et al. 1997; Haney and Lydic 1999). Therefore, the lack of continuity of decay classes does not necessarily imply a substantial deviation from old-growth structure with respect to CWD, nor does the relatively continuous distribution of CWD decay classes in the young forest in this study suggest that it is similar to old-growth forest. Further, it may be that the skewed distribution is an artifact of low sample size. Muller (2003) showed that CWD at Lilley Cornett Woods followed a highly skewed distribution, with low volumes of CWD in a large number of plots and large volumes in a small number of plots. Because large pieces of CWD are uncommon and can have a large effect on sample means, it may be that a greater number of sample plots are needed to capture large pieces of CWD in various stages of decay.

The presence of large-diameter coarse woody debris is also a useful proxy for gap formation (Harmon 2009), which I was unable to measure directly in this study. Where small-diameter CWD reflects the death of small or mid-sized trees or the loss of branches, the presence of large-diameter CWD signifies a legacy of the falling of large trees from the canopy. Thus, while canopy gaps were not directly studied here, the marked differences in diameter classes for CWD suggest that gap formation was more prevalent in old forest, which is of ecological and biological importance in the dynamics and habitat quality of old, second-growth forests.

Snags

The distribution of snags in the lower diameter range followed the expected pattern of more small snags in young forest than old forest. Examining the ratio of snags to live trees in the 10 cm DBH class, we find 0.22 for young forest and 0.042 for old forest, or a 5-fold increase by percentage of mortality in this diameter class in young forest. Interestingly, the ratio of snags to trees in this diameter range is similar to the 0.056 value for Lilley Cornett Woods derived from McComb and Muller (1983). This same pattern was not seen in the 20 cm DBH class, with young and old forests having a ratio of snags to live trees of 0.13 and 0.12, respectively.

The relatively large number of snags in the 10 cm DBH cohort in the young forest was driven in-part by what appeared to be a recent fire in one plot causing high mortality of red maple (*Acer rubrum*), as evidenced by burn marks on trees in the stand. However, because of the utilization of ranks, rather than means, in the Mann-Whitney U test, this outlier did not drive the statistical differences found between the age classes. The comparatively high level of mortality in this diameter class suggests ongoing processes in the young forest that are different from the old forest. While the young forest appears in some respects to be in the demographic transition phase, it may be that this increase in small diameter tree mortality is related to density-dependent self-thinning from the stem-exclusion phase. This possibility is corroborated by the dendrochronological analysis that showed how many of the smaller midstory trees (which comprise the pool contributing to small diameter snag density), and maples in particular, are actually part of the original, stand-replacing cohort. If these trees are dying as a result of long-term suppression it could signify that young forest in this study is in a late stage of stem exclusion or transitional between stem exclusion and demographic transition.

The lack of statistical significance between young and old forest for snags > 50 cm DBH was unexpected, particularly since old forest has many more trees in this size range. Martin (1992) reported at least 3 snags/ha >60 cm DBH, while old forest in this study had 1.47 snags/ha and young forest had none. However, as measured, the number of snags > 50 cm DBH in this study were 1.56/ha in young forest and 5.88/ha in old forest, with respective snag to live tree ratios of 0.088 and 0.12. The young forest value was similar to the 1.3 snags/ha > 50 cm DBH reported for 90–100 year-old hemlock-northern hardwood forests in the Adirondacks (McGee et al. 1999), though the northern forests are likely less productive, limiting maximum tree and snag diameters. It is entirely possible that a Type II statistical error resulted in an erroneous determination of no significant differences. However, it may be that more time is needed to drive large snag formation at the level of old-growth forest. Regardless, the nearly four-times greater density of snags > 50 cm DBH in old forest seemingly conveys a biologically and ecologically important difference between the two kinds of forest, as large snags provide habitat for a variety of taxa that is lacking in forests limited to small-diameter trees and snags (Harmon et al. 1986; Wathen et al. 1986; Goodburn and Lorimer 1998; White et al. 2001; Fan et al. 2003). As such, old second-growth forests are potentially more valuable from a habitat perspective for snag and cavity-using species.

Crown Position and Illumination Index

The measures of crown position and illumination index show that the old forest canopy had greater vertical and horizontal structural diversity than the young forest, and is therefore more suggestive of old-growth forest conditions (Messier et al. 2009). In the understory, the greater frequency in old forest of trees with illumination indices of 2 and 3 indicates that more light is reaching the understory through gaps in the canopy than in young forest. This increased variability in understory light conditions is hypothesized to drive further stratification of the canopy as well as allow for increased species diversity through partitioning of a greater number of environmental microsites (Messier et al. 2009).

Additionally, while the young forest overstory consisted entirely of codominant trees, the old forest contained several dominant trees (55.6 dominant trees/ha) extending above or standing apart from the general level of the canopy. This value is greater than the 11 dominant trees/ha reported for Savage Gulf, a similar, but old-growth forest on the Cumberland Plateau in Tennessee (Hart et al. 2012a).

The overall pattern with respect to canopy structure in the young forest in this study is somewhat consistent with the demographic transition stage of forest development, while the old forest appears more similar to the old-growth or multi-aged stage of forest development (Oliver and Larson 1996; Frelich 2002). This significant difference in structural complexity between old and young forests again conveys a biologically and ecologically important difference, with increased structural diversity in old, second-growth forests providing likely differences in habitat and processional characteristics (Haney and Lydic 1999).

Basal Area and Density

Total basal area for both young and old forests (31.5 m^2/ha and 41.0 m^2/ha, respectively) were well above the lower thresholds of 25 m2/ha suggested by Martin (1992) and 10 m^2/ha for the U.S. Forest Service Region 8 Guidance on Old-Growth. By comparison, Hart et. al (2012a) found a total basal area for all stems > 5 cm DBH of 26 m^2/ha in the upland old-growth oak-pine forests at Savage Gulf, in the Cumberland Plateau in Tennessee. That both age cohorts meet or exceed lower thresholds reported for old-growth forest is consistent with other published data, and may suggest that basal area is not, in itself, a good indicator of old-growth status. Goebel and Hix (1996) suggested as much, finding no differences in basal area in a chronosequence of forests in southeastern Ohio ranging from 70 years to presumed old-growth > 150 years, with values all around 25 m^2/ha.

The data here, however, do suggest that stand-level basal increases with age, with both old and old-growth forest basal areas greater than that found in young forest. In this case, old forest appears to have reached approximately the same basal area as old-growth. The value of 41.0 m^2/ha for old forest is nearly identical to the 41.8 m^2/ha for Lilley Cornett Woods in 2010, and toward the upper range value of 42.4 m^2/ha for Lilley Cornett Woods reported by Martin (1992), who provided a range of 20.6 m^2/ha to 42.4 m^2/ha across all community types in that forest. Alternatively, it may be that the differences in basal area in this study are an artifact of differences in site productivity. Despite having chosen sites to maximize similarity in community type, the species distribution of canopy trees does suggest the possibility that the pool of old sites may have skewed more mesic than mature sites, affecting overall values (Figure 11). However, even if this were partly true, the major differences here still suggest increasing BA, and therefore biomass, with time well into old-growth phases of forest development, an observation now frequently found globally (Luyssaert et al. 2008; Keeton et al. 2011).

As stated previously, basal area and tree density typically are inversely related, with density decreasing and basal area increasing as stand development proceeds (Runkle 2000; Frelich 2002). Therefore, the larger basal area found in old forest should translate to a lower density of trees. Martin (1992) reported a range of 160 to 315 trees > 10 cm DBH/ha for mesic sites at Lilley Cornett Woods, while Parker (1989) reported a range of 161 to 427 stems/ha > 10 cm DBH for the central hardwood region. However, differences between young and old second-growth forest here were nominal and not statistically significant (420 stems/ha > 10 cm DBH in mature forest and 378 stems/ha > 10 cm DBH in old forest). Two possible explanations are that 1) the difference is real, and that a Type II statistical error has occurred, or 2) the old forest plots were generally more productive, per the discussion above.

Neither young nor old forest fits within Martin's (1992) reported values for Lilley Cornett Woods, though both fall within Parker's (1989) range for Midwestern old-growth forests. Notably, the 2010 Lilley Cornett data fits neither, with a density of 536 trees/ha > 10 cm DBH, and Hart et. al (2012a) similarly reported 620 stems/ha >10 cm DBH at Savage Gulf. Both Lilley Cornett Woods and Savage Gulf are old-growth forests on the Cumberland Plateau, yet both exhibit a density well over that for both young and old second-growth forests in this study. Hart et. al (2012) suggested that the higher density in upland forests at Savage Gulf may be driven by lower site productivity, but this does not explain the results for Lilley Cornett Woods.

Diameter Distributions

When considering the distribution of diameters, it is useful to consider again how diameter distributions tend to change with the progression of stand development. After a stand-replacing disturbance, an initial peak in the lowest diameter classes signals the initiation of the new canopy. During the stem exclusion phase, a unimodal, leptokurtic peak gradually shifts toward the right with increasing diameters and a concomitant decrease in density. This unimodal peak gradually transitions to a platykurtic, or increasingly flat, distribution as inter-tree competition and species' life history traits play out in the spread of diameters amongst same-aged trees. During demographic transition, the original peak continues along its rightward and flattening trajectory, while a new cohort of understory trees appears in the lower diameter classes to create a 'compound DBH distribution' (Frelich 2002). Given sufficient time, the original peak disappears, diameters reach a maximum for species and site constraints, and ongoing transition in the understory continually moves trees in to larger diameters, resulting in a reverse-J, inverse exponential diameter distribution.

The results in this study appear to present an illustrative chronosequence for young, old, and old-growth forests with respect to diameter distributions and stand development. The Lilley Cornett Woods 2010 data has the 'quintessential', smooth reverse-J, long-tailed diameter distribution extending into a low frequency of very large diameter trees, extending up to 124.0 cm, and reflect well the expectations of an old-growth diameter distribution.

By contrast, the diameter of young forest trees did not reach beyond 55.6 cm, which was less than half that of the old-growth forest, and exhibited a secondary peak around 30 cm DBH in an otherwise truncated, reverse-J distribution. This secondary peak suggests the initial, 70-90 year old stand-replacing cohort having increased in diameter and decreased in frequency, as suggested by the model. It is worth noting here that the dendrochronological analysis shows that many of the trees in the 10 cm and 20 cm DBH cohorts were of the same age as those of larger diameters, and exhibiting suppression. The peak in small diameter trees at the left of the distribution (2.5 cm and 10 cm cohorts, though particularly the former) may appear to suggest that a new cohort of trees has developed in the understory, though without age data in these size classes it is impossible to say whether these small trees represent regeneration in the understory or long-term suppression. Further dendroecological investigation of small diameter trees in these forests could be illuminating. The compound DBH distribution exhibited suggests that these 70-90 year old forests are in the demographic transition, or understory reinitiation, phase of stand development (Oliver and Larson 1996, Frelich 2002), but again this cannot be confirmed without a better understanding of the ages of small trees and saplings.

The diameter distribution for the old second-growth forest appears intermediate between young and old-growth forest, with a maximum diameter of 88.9 cm and a near reverse-J distribution with a slight plateau in the 20 cm and 30 cm diameter classes. The location of this plateau suggests that, unlike the young forest, this is not a remnant of the stand initiating cohort. If a signal from the stand-initiating cohort was visible, it would most likely be centered on a higher range of diameters. A plausible explanation is that the plateau is a result of the merging of distributions of both the stand-initiating cohort and the secondary peak associated with demographic transition, resulting in an increased density of trees in this diameter range. However, it may also represent an episode of low or intermediate disturbance (Lorimer and Frelich 1984; Leak 1996), which would be consistent with the peaks in recruitment from about 1890–1909 and then 1920–1929 seen in the dendrochronological analysis.

While the appearance of a trend in the 2.5 cm diameter cohort of increasing density with age proved statistically insignificant, the pattern may warrant further investigation. It could suggest a transition from the understory reinitiation or demographic transition phase into the multi-aged or old-growth phase of stand development. While greater number of seedlings and saplings in the young forest noted previously implies a greater capacity for advance regeneration than in the old forest, an alternative hypothesis is that the increased understory light conditions observed in old forest are allowing more seedlings and saplings to advance into larger diameter cohorts, thus decreasing the bank of seedlings and saplings. While speculative, this would be a logical extrapolation from what is generally understood about forest development.

Notably, while trees in the old second-growth forest were not as large as some of those inventoried at Lilley Cornett Woods, the density of large trees > 75 cm DBH was 16.7 tree/ha, which is greater than the minimum density 7 trees > 75 cm DBH/ha suggested by Martin (1992) as a minimum for old growth, mesic forests, as well as that for mixed mesophytic forest in the Region 8 Guidance (USDA Forest Service 1997). Large tree density surpassed substantially the threshold for dry-mesic oak communities in the Region 8 Guidance, with 66.7 trees/ha > 50 cm. The presence of these large trees could convey differences in habitat suitability for a number of vertebrate species, particularly cavity users (Harmon et al. 1986; Wathen et al. 1986; Goodburn and Lorimer 1998; White et al. 2001; Fan et al. 2003). However, the effects of site productivity on tree size cannot be stressed enough. Hart et. al (2012a) reported only 1 tree > 75 cm DBH/ha in the upland forests at Savage Gulf, despite its being an old-growth forest. This relatively low maximum threshold is likely a result of the forest's modest productivity.

Both Frelich (2002) and Oliver and Larson (1996) suggest that the multi-aged or old-growth stage of development only occurs after few or all remnants of the stand initiating cohort no longer remain. However, it appears in this study that a forest can develop a reverse-J distribution approximating an old-growth distribution prior to the loss of the stand initiating cohort. In the case of the old forest cohort, this could be explained, in part, by the multi-age distribution that I attribute to incomplete initial disturbance followed by periods of low or intermediate severity disturbance. However, the young forest was predominantly even-aged, and yet still approximated the reverse-J distribution seen in the old-growth forest. It may be that, in some forests, the reverse-J diameter distribution is approached through the interplay of competition and species-specific growth characteristics, with absolute age and canopy turnover less important.

Perhaps the most significant difference in this study between the young, old, and old-growth diameter distributions is the presence of the long-tail of especially large-diameter trees in the old-growth forest, albeit at low frequencies. It may be that after 140–160 years, forests in the study area are able to develop a continuous distribution of diameters, and a significant density of trees > 75 cm DBH, but have yet to reach a full distribution of potential maximum size classes, while young forest (70-90 years) has yet to develop trees in this diameter range. This suggests that managed forests could potentially retain or more rapidly recover an old-growth type diameter distribution through the retention of at least some large canopy trees that will be able to move into the largest diameter classes as the forest recovers.

5.2 OAK AND MAPLE DYNAMICS

The pattern of oak (*Quercus* spp.) dominance in the overstory and seemingly attendant dominance of maple (*Acer* spp.) in the understory has been widely observed across the eastern deciduous forest (Lorimer 1984; Abrams 1992; McEwan et al. 2010), and is apparent in this study. Across all plots for both age groups, oaks were the predominant species in the canopy (codominant and dominant), while maples were nearly absent. In the overtopped crown position, maples were the predominant species with very few oaks present, while in the intermediate layer, oaks and maples were about equal in the young forest with nearly all maples in the intermediate layer for old forest. Both young and old forest had more maple than oak saplings, and old forest had more maple than oak seedlings, while young forest exhibited no difference between maple and oak seedlings.

While the above implies an overall pattern of shifting recruitment and dominance with time, the dendrochronological analysis reveals more complex and nuanced patterns. Oak recruitment peaks with both age groups around the period of stand initiation, and continues in an episodic fashion in the old forest from 1900 through 1940 and through the 1950s in young forest. However, whether the post-regeneration, episodic recruitment of oaks is related to natural disturbance, selective logging, or is independent of disturbance is unclear from the data. Regardless of the initiator, the timing suggests that intense disturbance may be an important aspect of successful oak recruitment.

In the young forest, most red maples (*A. rubrum*) recruited synchronously with the oak overstory, but have remained suppressed, with diameters of all but one maple used in the dendrochronological analysis ranging between 10 cm and 20 cm DBH. In contrast, oaks of the same generation have maintained canopy dominance and added girth accordingly. The peak of red maple recruitment in young forest around 1930 aligns closely with the peak for this species detected in old forest during the same period of time, suggesting that the peak influx of maple is not correlated with time since disturbance, but instead other exogenous factors.

Most commonly, this synchronous influx of red maple recruitment is attributed to the beginning of fire suppression policies. A shift from the long-held cultural practice of burning forests began in 1912 with the establishment of the Kentucky Division of Forestry, which soon began implementing a policy of fire control (Kentucky Division of Forestry 2010). However, after initial progress, a lack of funding through the 1920s halted advancement in fire suppression and other activities by the Kentucky Division of Forestry until the 1930s (Kentucky Division of Forestry 2010; Blankenship and Arthur 1999). The federal government made fire suppression a national policy with the passage of the Clarke-McNary Act in 1924, which tied federal appropriations to requirements that states adopt fire-suppression policies (Stephens and Ruth 2005).

The oldest red maple in the young forest dates to 1924, aligning with passage of the Clarke-McNary Act, though the oldest red maples in the old forest date to 1916 and 1921, just prior to the recognized period of fire suppression. Cooper (2011) and Tackett (2012) show the period of red maple recruitment in various old and old-growth forests around the Cumberland Plateau predating the period of fire suppression, with red maples initiating as early as the 1860s. It may be that the peak influx of red maple is attributable to something other than fire suppression.

In the old forest, sugar maple (*A. saccharum*) followed a different pattern from red maple, with most recruitment between 1891 and 1910, followed by another flux of recruitment in the 1930s. McEwan et al. (2010) reported that, prior to 1900, climatic conditions in the central portion of the Eastern Deciduous Forest shifted to a pattern of increasing moisture availability and reduced drought compared to the previous several hundred years. This pattern of increasing moisture is now seen all across the Eastern Deciduous Forest (Pederson et al. 2012). As both red maple and sugar maple are associated with more mesic conditions than oaks, it is possible that the influx of maples is partly driven by increasing moisture availability.

The dendrochronological and canopy analysis in this study shows that maples recruited after the 1930's have, in large part, failed to advance in their development from seedlings and saplings into understory or midstory trees. Despite the relative abundance of maples in the seedling and sapling layers in both mature and old forest, some combination of conditions in both ages of forest studied appear to be suppressing the development and growth of maples in all stages of development.

Maples, and especially red maples, have been predicted to eventually attain canopy dominance (Lorimer 1984; Hart et al. 2012b). In this study, illumination indices show that maples are in a position to take advantage of increased light conditions in the understory in old forest stands (index ratings 2 and 3). Through the process known as 'disturbance-mediated accelerated succession,' the successional transition toward dominance of increasingly shade-tolerant species can proceed more rapidly in the presence of disturbance, whereby shade-tolerant trees are released and attain codominant or dominant status (Abrams and Scott 1989). Hart et al. (2012b) found that 61% of red maples in the canopy at Savage Gulf originated in gaps and reached the canopy without exhibiting periods of suppression. However, only 24% of red maples established in the understory and reached the canopy after one or more gap releases. For trees following this strategy, the mean age of trees upon ascent to the canopy was 20 years, with the longest duration suppressed in the understory being 71 years. In my study, the two oldest red maples were a 92 year old, 17.5 cm DBH tree with an intermediate (I) crown position and illumination index of 2 (receiving some lateral light exposure) and an 89 year old, 13.4 cm DBH tree with an overtopped (O) crown position and illumination index of 1 (no direct light exposure), suggesting that red maple can stay in the lower strata of forests for nearly a century. It may be that small-scale, gap creating disturbances will produce the necessary conditions to release maples from their currently suppressed state and allow them to eventually attain canopy dominance. However, it is not clear how long red maples can persist in a suppressed state in the understory. Since many oaks can live for 300 to 500 years, in the absence of widespread disturbance, it might be that red maples will continue to be relegated to suppressed understory status and could eventually drop in importance as individuals decline due to insufficient resources.

The concept of the 'storage effect' suggests that long-lived species with high adult survival rates can maintain their status in a community despite having only infrequent periods of successful reproduction (Warner and Chesson 1985). Recent dendroclimatalogical reconstructions suggest that, prior to the twentieth century, eastern North America was subject to longer and more extreme droughts (Pederson et al. 2012). While Lorimer (1984) determined that drought was not sufficient to induce decline in red maples relative to oaks, his results were based on the northeastern drought of 1962-1966. Pederson et. al (*In Press)* showed that this drought event was relatively short in duration and buffered by unusually wet periods before and after, compared to the more frequently dry centuries from 1500–1899. As such, it may be that oak recruitment and maple decline are promoted through dry climatological conditions that would otherwise be considered exceptional by twentieth century standards, and that oaks maintain dominance in the interim by suppressing maples through their longevity and relative resilience to drought.

Further, because of the association between dry climatological conditions and fire regimes (Lynch and Hessl 2010; Lafon and Quiring, 2012), it stands to reason that the above proposed mechanism for oak persistence and dominance would include fire, as suggested by the oak and fire hypothesis (Abrams 1992). And while severe drought conditions can cause decline in oaks, particularly the red oak group (*Erythrobalanus* subgenus)(Hursh and Haasis 1931), some level of canopy mortality from drought stress, fire, and other causes may be necessary for fire to be effective in promoting oak establishment and recruitment (Arthur et al. 2012).

Therefore, while the data for this study with respect to oak and maple dynamics reflect similar patterns observed in the Cumberland Plateau and elsewhere, the long-term trajectory will likely depend on climatological and other disturbance factors over the coming decades and centuries, and could result in continued oak dominance, a transition to maple dominance, or a more mixed canopy inclusive of both genera.

5.3 PROSPECTS FOR OLD-GROWTH RECOVERY

The results of this study suggest that older second-growth forests in the Cumberland Plateau region of Kentucky are developing characteristics reminiscent of old-growth forests, and, in the absence of major disturbance, will continue to more closely approximate old-growth forest conditions in the coming decades. While Kentucky has more than 5 million ha of forest, 78% is owned by private individuals with 46% in patches < 400 ha (Kentucky Division of Forestry 2010). Conversion of forest land to other uses leads to a loss of more than 40 ha per day, while logging to meet economic or other purposes continues to impede the development of old-growth structure across much of the state (Kentucky Division of Forestry 2010). However, several public and private land-holdings in Kentucky offer substantial opportunities for the recovery of old-growth structure and function at the landscape scale. The following represent some of the more prominent examples, though others certainly exist.

Daniel Boone National Forest

The Daniel Boone National Forest (DBNF) offers the greatest opportunities for recovering old-growth in Kentucky. Of the 286,000 ha of forest in the DBNF, 68,818 ha, or 24%, is inventoried as over 100 years old (USDA FS 2009) and could develop substantial old-growth structure and function over the coming decades. While most of the national forest is managed under a “multiple use” program that includes commercial logging for a variety of economic and ecosystem goals (USDA FS 2004), opportunities clearly exist to recover a suite of old-growth characteristics at multiple scales should this become a management priority.

Currently, the Old-Growth management prescription (1.I) in the DBNF Forest Plan includes 6,248 ha (15,440 ac) designated for the development of old-growth characteristics. These allocations include primarily mature second-growth forest with some young third-growth areas clearcut in the past 30 years. Designated Wilderness, where logging is strictly prohibited, represents 7,057 ha (17,437 ac), and includes the Clifty Wilderness (approximately 4,850 ha) and Beaver Creek Wilderness (approximately 2,020 ha). The national forest also includes one Research Natural Area (RNA), Rock Creek RNA, and two proposed RNA’s, Tight Hollow and Right Fork of Elisha Creek, which total 266 ha and are off limits to logging. Several other smaller areas and corridors exist where logging is limited or prohibited, including several designated and proposed Wild and Scenic River corridors, recreational areas, and buffers around cliffline.

Kentucky State Nature Preserves and Natural Areas

The Kentucky State Nature Preserves Commission (KSNPC) manages nearly 7,600 ha on 45 forest reserves for the purpose of protecting rare species and natural communities in Kentucky (Kentucky Division of Forestry 2010). Managed primarily for preservation and permanently protected from logging, many of these forests hold potential for recovering old-growth in the future. Further, some forests managed by KSNPC contain remnant or extant old-growth, including Blanton Forest, Kentucky’s largest existing old-growth forest.

Kentucky Natural Lands Trust

The Kentucky Natural Lands Trust (KNLT) is a privately held land trust "committed to preserving, restoring and connecting the state's remaining wildlands." While active in conserving forests throughout the state, the main focus of KNLT is the Pine Mountain Wildlife Corridor, which seeks to connect existing protected forests on Pine Mountain and create a contiguous forest corridor along the 193 km mountain ridge, including Blanton Forest.

Bernheim Arboretum and Research Forest

Bernheim Arboretum and Research Forest is a 5,665 ha holding including 4,856 ha of forest in Bullitt County, Kentucky. It is one of the largest blocks of protected forest in the western portion of Kentucky and is managed for educational and research purposes. Because of its large size and preservation emphasis, Bernheim offers one of the greatest opportunities for old-growth recovery at a landscape-scale in west-central Kentucky.

Robinson Forest

Robinson Forest is a nearly 6,000 ha research forest in Breathitt, Knott, and Perry Counties, Kentucky, managed by the University of Kentucky. A mostly mature, second-growth forest, parts of Robinson Forest have been subject to surface mining and logging in recent decades. While the forest is not managed under an ethic of preservation, its size and ownership could allow for the long-term study of the redevelopment of old-growth characteristics under active and passive management approaches in a region heavily impacted by surface mining and logging.

Land Between the Lakes

Land Between the Lakes National Recreation Area (LBL), also called Land Between the Rivers by former residents, is a nearly 70,000 ha peninsula in western Kentucky bound by impoundments on the Cumberland River (Lake Barkley) and the Tennessee River (Kentucky Lake). It is the second-largest public land holding in

Kentucky and is managed by U.S. Forest Service under a multiple-use mandate similar to that of the Daniel Boone National Forest, with an emphasis on recreation.

Mammoth Cave National Park

Mammoth Cave National Park is a 21,380 ha national park along the Green River in central Kentucky, in Edmonson, Hart, and Barren Counties. The forest is mostly mature second-growth, with some old-growth remnants, most notably the Big Woods. Logging is prohibited in National Parks, though prescribed fire has been introduced as a management tool.

Big South Fork National Recreation Area

Big South Fork National Recreation Area is a 50,710 ha area of forest on the Cumberland Plateau including portions of Tennessee and Kentucky. The forest is mostly mature second-growth forest characteristic of the Cumberland Plateau. As with Mammoth Cave National Park, logging is prohibited though prescribed fire is used for management.

5.4 SILVICULTURE FOR OLD-GROWTH CHARACTERISTICS

While this study focused on the development of old-growth characteristics with time, an emerging body of research is looking at adapting silvicultural methods to mimic or accelerate the development of some old-growth forest characteristics in second-growth forests (Runkle 1991; Lorimer and Frelich 1994; Keeton 2006; Bauhus et al. 2009). Generally, these approaches to old-growth structural development differ from traditional uneven-aged management or selective harvesting approaches. While long-term studies in this field are still lacking, Keeton (2006) proposed a suite of silvicultural techniques termed structural complexity enhancement (SCE) (Table 4). Early implementation of SCE treatments as part of the Vermont Forest Ecosystem Management Demonstration Project suggest that SCE can more rapidly increase CWD volume, large tree recruitment, and total basal area

Table 4: Structural objectives and corresponding silvicultural techniques used to promote targeted old-growth characteristics in structural complexity enhancement (SCE).

Structural objective	Silvicultural technique
Vertically differentiated canopy	• Single tree selection using a target diameter distribution • Release advanced regeneration • Regenerate new cohort
Elevated large snag densities	• Girdling of selected medium to large sized, low vigor trees
Elevated downed woody debris densities and volume	• Felling and leaving trees, or • Pulling over and leaving trees
Variable horizontal density, including small canopy gaps	• Harvest trees clustered around "release trees" • Variable density marking
Re-allocation of basal area to larger diameter classes	• Rotated sigmoid diameter distribution • High target basal area • Maximum tree size set at 90 cm dbh
Accelerated growth in largest trees	• Full and partial crown release of largest, healthiest trees

Source: Keeton, W.S. and A.R. Troy. 2006. Balancing ecological and economic objectives while managing for old-growth forest characteristics. Pages 21-33 in: L. Zahoyska, editor. Ecologisation of economy as a key prerequisite for sustainable development. Proceedings of the international conference, Sept. 22-23, 2005, Ukrainian National Forestry University, L'viv, Ukraine.

and above-ground biomass than passive treatments alone (Keeton 2006). While forests in the Vermont Forest Ecosystem Management Demonstration Project are characteristic of northern hardwood forests and generally composed of more shade-tolerant species than those typical of the Cumberland Plateau, I suggest that SCE could be modified for forests in the study area to facilitate oak recruitment by incorporating group selection harvests targeted in forest patches with ample advanced oak regeneration. Mimicking gap-scale natural disturbance in a limited and highly targeted manner would fall within the range of disturbance intensities consistent with developing and maintaining old-growth structure while assisting in the regeneration and recruitment of oaks and other shade mid-tolerant species.

The advantages of applying SCE or similar silvicultural approaches may be moot for forests within or approaching the 140-160 year age range of old forests in my study, since these forests have largely developed the targeted characteristics on their own with time. However, in the absence of low or intermediate intensity natural disturbance (which may advance structural development without human intervention), appropriate management of young forests (i.e., 70-90 years old, or thereabouts), could accelerate the development of important old-growth characteristics while allowing for an economic return that may make it a viable management option for some land owners and managers (Keeton and Troy 2006). Still, the potential negative impacts of logging should be weighed in any management consideration. While studies similar to the Vermont Forest Ecosystem Management Demonstration Project are not apparent in the Central or Southern Appalachian region, such experiments could be worthwhile in an effort to bridge the often competing goals of forest preservation and economic return.

6. CONCLUSION

The results of this study confirm models and observational evidence that many of the structural characteristics associated with old-growth forest can and do return to forests given time. With more large trees, large snags, coarse woody debris, and a more complex canopy and age structure, the oldest second-growth hardwood forests in the Cumberland Plateau of Kentucky are developing a suite of characteristics reminiscent of old-growth forests that make them distinguishable from younger and more abundant 70-90 year-old forests that are frequently seen as having reached their maximum potential from a silvicultural perspective.

With the recovery of old-growth structure and function eminently possible, the prospects for old-growth recovery in Kentucky and elsewhere are ultimately a social phenomenon. Whether or not we allow or assist the redevelopment of this once-prominent suite of forest conditions on the landscape will depend largely on the degree to which old-growth forests are seen as valuable to both forest managers and the broader public, and the extent to which we are able to balance the utilitarian ethic that dominates forest management today with a preservationist vision of the return of the Great Forest.

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Forest Ecology and Management 503 (2022) 119757

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Endangered *Myotis* bats forage in regeneration openings in a managed forest

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ARTICLE INFO

Keywords:
Bats
Foraging
Forest management
Myotis sodalis
Myotis septentrionalis
Timber harvest

ABSTRACT

Bat populations face numerous threats, including the loss of forests in which they roost and forage. Present-day forests are commonly managed for timber harvesting, recreation, and wildlife. Understanding bat responses to forest management is crucial for balancing the conservation of endangered bats and forest restoration. We used radio telemetry to study nocturnal movements and habitat selection patterns of female and juvenile bats of two forest-dependent, federally listed bat species in an oak-dominated managed forest. We estimated foraging space use and assessed habitat selection for 33 northern long-eared bats (*Myotis septentrionalis*) and 25 Indiana bats (*Myotis sodalis*) from May to August 2014–2017 in south-central Indiana, USA. *Myotis septentrionalis* space use averaged 176 ha and bats selected water, historic thinning, and patch cuts ($\leq$4 ha) over other habitats, with all but one bat avoiding larger openings ($\geq$4-ha clearcuts). *Myotis sodalis* space use averaged 343 ha and bats selected 4-ha patch cuts, historic openings, and historic thinning over other habitats. In contrast to *M. septentrionalis*, one-third of the *M. sodalis* foraged over larger clearcuts, while two-thirds foraged over smaller openings and thinnings. We showed that bats were attracted to small regeneration harvests of varying structural ages. Forests maintained for a mix of mature stands, thinned stands, shelterwoods, small regenerative cuts ($<$7 ha), and small water sources should provide suitable foraging habitat for these endangered *Myotis* species, while also promoting forest regeneration.

1. Introduction

Bat populations face numerous threats worldwide. Loss of habitat is a major threat shared by nearly all bats (Frick et al., 2019) and, in North America, many bats are experiencing population-level declines due to white-nose syndrome (Frick et al., 2015). Globally, many bat species are dependent on forests for habitat during some portion of the year and forest management could impact habitat suitability or availability (Law et al., 2016). Alternatively, forest management could also benefit bats by creating roosting and foraging opportunities (Wright et al., 2021). Effects of forest management vary across bat species with different eco-morphological adaptations and with the degree of overstory removal (Loeb, 2020). Understanding bat responses to silviculture is crucial for balancing the conservation of imperiled bats and forest restoration (Russo et al., 2016).

Our study focuses on the federally endangered Indiana bat (*Myotis sodalis*) and federally threatened northern long-eared bat (*Myotis septentrionalis*), which are sympatric in oak-dominated forests of the Central Hardwoods region (Loeb and O'Keefe, 2011). This region has a diverse assemblage of oaks, which support diverse wildlife, insect, and plant communities; however, sustaining oak forests requires active timber management such as harvest and prescribed fire (Fralish 2004). During the non-hibernation season (April to September for *M. sodalis*, (Pettit and O'Keefe, 2017), reproductive females and pups roost in large dead or damaged trees (Lacki et al., 2009; Drake et al., 2020), including oaks and hickories (Bergeson et al., 2018; Bergeson et al., 2021). Roost solar exposure is important for energetic savings and pup growth, so forest-dwelling bats select tall trees with open canopy (Kalcounis-Rüeppell et al., 2005), conditions achieved by senescence of mature trees or by disturbance factors like fire, silviculture, wind, insects, and flooding (reviewed by (O'Keefe and Loeb, 2017). *Myotis sodalis* and *M. septentrionalis* are most likely to select roosts in or near continuous

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https://doi.org/10.1016/j.foreco.2021.119757
Received 20 July 2021; Received in revised form 28 September 2021; Accepted 30 September 2021

forest (Carter and Feldhamer, 2005; Pauli et al., 2015a), possibly for access to preferred foraging habitat. Although roosting habitat is critical, roosting and foraging areas are linked (Brigham, 1991; Whitaker, 1994), and we should consider the entire spatial footprint of roosting (roost to plot scale) and foraging (stand to landscape scale) areas in habitat assessments (Pauli et al., 2015b; Perry, 2011).

Both *M. sodalis* and *M. septentrionalis* are more likely to occur in closed canopy forest (Ford et al., 2005) and thus may respond negatively to large regeneration harvests (e.g., as predicted by Loeb, 2020); however, they may respond positively to fine-scale disturbances within larger forest patches (e.g., Loeb and O'Keefe, 2006). Both species are small (<8 g), with high-frequency echolocation calls and low wing loading, which facilitates foraging in cluttered, closed-canopy hardwood forests (Owen et al., 2003). An understanding of how these species forage in heterogeneous forests requires landscape context, as demonstrated by acoustic surveys in the Central Hardwoods region of USA (Caldwell et al., 2019; Pauli et al., 2017; Starbuck et al., 2015). Although such acoustic studies have provided valuable data on bat activity in forested landscapes, they lack fine-scale resolution on the variability in space use or habitat selection between individuals. In contrast, radio telemetry is specific to individual bats and, with sufficient sampling, can yield data for quantifying habitat preferences (Miller et al., 2003).

Radio telemetry demonstrates that *M. sodalis* and *M. septentrionalis* forage mainly in forested areas, including areas with low levels of active timber management (Table S1; Lacki et al., 2009; Owen et al., 2003). Individuals respond to management that reduces forest clutter—e.g., *M. septentrionalis* forage closer to burned areas after prescribed fires in pine-hardwood forests (Lacki et al., 2009) and prefer thinned stands in northern hardwood forests (Owen et al., 2003). With data quantified from known individuals, we can better assess the variability in space use and habitat selection to inform management practices that can consider different foraging strategies. Currently, we lack large, multi-year datasets on individual behaviors and comparable data for these two species in the same landscape; thus, we may base management decisions only on the most commonly observed foraging behaviors across species. We expect different responses to forest management for the two species, as *M. septentrionalis* have foraging ranges an order of magnitude smaller than *M. sodalis* (Table S1). In this study, we define a foraging range as the space used by a bat while roosting and hunting insects in summer habitat, in contrast to the more ambiguous term 'home range' that should also include migratory pathways and winter habitat.

We conducted a 4-year study using radio telemetry to track individuals of both species, focusing on adult females, as they foraged over mixed-oak forests managed with thinning, patch and shelterwood cuts, prescribed fire, and small clearcuts. Our goal was to identify commonalities and quantify differences in foraging space use and habitat selection to yield information on the effects of forest management practices on both species.

2. Materials and methods

2.1. Study site

We worked across an 18,000-ha area (Fig. S1) mostly including Morgan-Monroe and Yellowwood state forests in south-central Indiana, USA. State forests were managed by the Indiana Department of Natural Resources (INDNR); a 25.1 ha inholding was managed by The Nature Conservancy (TNC). Elevation ranged from 540 to 970 m. Dominant overstory tree species included white and red oaks (*Quercus alba, Q. montana, Q. velutina, Q. rubra*), hickory (*Carya* spp.), and other hardwoods. The midstory was mainly sassafras (*Sassafras albidum*), elms (*Ulmus* spp.), maples (*Acer* spp.), and American beech (*Fagus grandifolia*). Nearby agricultural areas contained row crops or hay/pasture, and developed areas included sparse buildings and paved roads. There were few perennial and intermittent streams, which dried by midsummer; 73 human-made ponds (~0.2 ha each, widely distributed across space) were the primary water sources for bats.

The larger landscape consisted of mostly intact forest intermittently treated with single-tree selection harvest (91% of landscape; Bergeson et al., 2018). For some of the forest, INDNR applied regenerative harvests such as group selection cuts, patch cuts, clearcuts, and shelterwoods. However, most state forest acreage is harvested via thinning and improvement harvests (Haulton, 2013). Embedded within state forest land were nine 81-ha units (Fig. S1, mix of controls and harvest treatments) delineated for the Hardwood Ecosystem Experiment (HEE) project, a collaborative 100-year project studying social and wildlife responses to timber harvesting (see Kalb and Mycroft, 2013).

From 15 May to 31 July 2014–2017, daily air temperature ranged from 3.9 to 35.0 °C with a mean minimum of 15.6–16.6 °C and mean maximum of 26.6–28.3 °C. Total precipitation during each sampling period was 324 mm in 2014, 410 mm in 2015, 342 mm in 2016, and 273 mm in 2017 (NOAA station GHCND:USC00120784 in Bloomington, Indiana, USA).

2.2. Bat capture and radio telemetry

From May to August 2014–2017, we captured bats near ponds, streams, or unpaved roads. We recorded species, sex, age, and reproductive condition, and banded bats with aluminum forearm bands (2.9 mm; Porzana, Ltd., East Sussex, UK). Sampling was conducted under federal and state permits, following recommended guidelines (Sikes et al., 2016) and institutional animal care and use protocols (Indiana State University # 559972–1:JO, Ball State University # 109929–5). All equipment was decontaminated nightly (USFWS, 2018).

We used surgical cement (Perma-Type, Plainville, CT, USA) to attach radio transmitters (0.25–0.35 g Blackburn, Nagadoches, TX, USA—or similar) between the scapulae of 38 *M. sodalis* and 57 *M. septentrionalis*. Most bats were adult females except for three juvenile female *M. septentrionalis* and two juvenile *M. sodalis*. We assumed that juvenile bats selected habitat similar to intraspecific adult females, regardless of sex, for local enhancement of foraging. Tags weighed $\leq$ 5% of body mass (Aldridge and Brigham, 1988) and stayed attached 1–23 days. We searched for roosts daily (see Bergeson et al., 2018), and tracked bats at night for four hours post-emergence. We positioned 3–5 trackers with receivers (Advanced Telemetry Systems, Isanti, MN, USA) and 5-element yagi antennas on ridgetops ~ 500–900-m apart, collecting azimuths in the direction of the strongest signal for 2–3 bats/night every 2–5 min ($\geq$5 min intervals per bat). When bats were stationary in roosts before emergence, we estimated an average linear triangulation error of 239 m (n = 84 tests; 340 m in 2014, 159 m in 2017).

2.3. Foraging space-use estimation

We calculated maximum likelihood estimates for foraging locations using 2–5 contributing azimuths in LOAS 4.0 software (Sallee et al., 2010), only using bi-angulations when crossing azimuths resulted in angles 45–135°. We used an R script (Supporting Information) to create kernel density estimates (KDEs) with a cross-validated smoothing parameter (Horne and Garton, 2006) and interpolated foraging ranges for bats with $\geq$ 30 relocations in Geospatial Modeling Environment software (Beyer, 2012); this process incorporated sampling and spatial errors across a probability density surface, with a focus on foraging relocations in close proximity rather than treating each relocation independently. In ArcMap 10.7 (ESRI, Redlands, CA, USA), we measured space use within polygons corresponding to 50% core-use and 95% foraging-extent KDEs. We tested for second-order habitat selection within 95% KDEs relative to land cover availability in the overall population foraging extent (Thomas and Taylor, 2006). For each species, the foraging extent was two disjunct polygons, one per state forest (Fig. S1); each polygon covered the species' roosting area buffered by the mean maximum foraging distance for that species (all bats tracked in this study: 2.0 km for *M. septentrionalis*, 2.9 km for *M. sodalis*). We assumed individual bats were capable of foraging at least as far away from roosts as the mean observed distances. We used Wilcoxon ranked sum tests to compare non-normal maximum distances traveled and 95% foraging range size between species.

2.4. *Converting land cover to available foraging habitat types*

To create annual habitat maps, we reclassified annual 30-m^2 National Agriculture Statistics Survey layers into four categories: water, developed, agricultural, and forested. We converted vector layers for forest ponds and timber harvest areas, from INDNR, TNC, and HEE, to 30-m raster cells. Divoll (2020) describes GIS data processing in more detail, and final foraging land cover categories are in Table 1. In most cases, regenerative treatments were assigned to patch cut, clearcut, or historic opening categories. Traditionally, shelterwoods are considered regenerative; however, during our study, they were in early stages that more structurally resembled a thinning or selection harvest and, thus, we included them in recent thinnings (Table 1). We assumed management treatments in each category were coarsely similar in structural density, height, and canopy closure, as potentially perceived by foraging bats. We equated these land cover types with potential foraging habitats that bats may choose from and, therefore, refer to them as habitats. We developed six habitat availability layers for each species; one for each state forest in each of three periods: 2014/2015 (no major landscape changes between years), 2016, and 2017.

We quantified availability of habitats at the population level, assuming all animals in a population had access to the same area (Design 2; Thomas and Taylor, 2006). To test for habitat selection, we used a weighted compositional analysis (Millspaugh et al., 2006) with foraging density values (95% KDEs) and the habitat types in Table 1. We summed values of each habitat type and derived proportions of habitats available to bats during each period. We used a Python 2.7 script (Supporting Information) to sum foraging density values per bat per habitat and calculated proportions used by each bat, assuming more importance in habitats with greater density of foraging (Millspaugh et al., 2006).

2.5. *Habitat selection analyses*

We took a multifaceted approach to test for intra-specific consistency and population-level habitat selection (adehabitatHS package in R; Calenge, 2011; R Core Team, 2018). We first used an eigenanalysis to measure intra-specific variation in habitat selection (Calenge and Dufour, 2006; Nelson and Gillam, 2017). We visually compared patterns among individuals with a Principal Components Analysis (PCA) plot of the first two factorial axes. Individuals in close proximity were assumed to exhibit similar foraging behaviors, whereas clustering along more than one PCA axis indicated different intra-specific foraging behaviors. Next, we used a Wilk's lambda statistic to establish overall population-level selection relative to respective habitat availability. Finally, we used multivariate analysis of variance with log-odds ratios to rank species-level habitat selection (Aebischer et al., 1993).

3. Results

3.1. *Radio telemetry*

Bats were captured at forest ponds or over two-track roads. We obtained 30–114 relocations for 33 *M. septentrionalis* over 1–6 (3.1 ± 1.3) nights and 30–129 relocations for 25 *M. sodalis* over 1–6 (3.4 ± 1.2) nights (Table 2). *M. septentrionalis* proved easier to track (84% triangulation success rate) compared to *M. sodalis* (69% success rate).

3.2. *Foraging ranges and space use*

Kernel density estimates (95%) for *M. sodalis* s (343 ± 70 ha) were nearly double the size of 95% KDEs for *M. septentrionalis* (176 ± 25 ha; Wilcoxon test, $P = 0.02$; Table 2). *Myotis sodalis* also traveled farther from roost trees to forage, averaging 2.9 km versus 1.6 km for *M. septentrionalis* (Wilcoxon test, $P < 0.05$). Differences in space use between species were consistent across reproductive periods, with lactating bats traveling the furthest. However, the maximum observed foraging distance from a roost was 5.6 km for a post-lactating *M. sodalis* and 3.4 km for a pregnant *M. septentrionalis*. Most (99%) *M. septentrionalis* roosts were within 95% KDE foraging areas and 68% were in 50% KDE core use areas; in contrast, only 60% of *M. sodalis* roosts were located inside 95% KDEs and 18% were in 50% KDEs. Thus, *M. sodalis* tended to forage away from roosts, whereas *M. septentrionalis* foraged proximal to roosts (Fig. 1).

Table 1

Derived habitat categories for habitat selection analyses. Percentages available to bats were calculated from the sum of cells in each habitat category, averaged across populations sampled across two areas and over four years. We did not calculate agricultural, developed, and water patch areas due to their irregular shapes and high variability.

Habitat category	Cutting age (yrs)	Patch size (ha)	Treatment	Structural description	Percent available to *Myotis septentrionalis*	Percent available to *Myotis sodalis*
Patch cut	≤10	0.08–4.04	Small regenerative harvests	Canopy open; high stem volume removal; low to moderate regrowth height; vertical edge	1.08	0.86
Clearcut	≤10	4.05–7.08	Large regenerative harvests	Canopy open; high stem volume removal; low to moderate regrowth height; vertical edge	0.05	0.18
Historic opening	>10	0.4–5.6	Historic regenerative harvests	Open at high canopy, with developing subcanopy from regeneration; high stem volume removal; tall regrowth; vertical edge	1.04	0.59
Recent thinning	≤10	0.4–105	Mostly non-regenerative; includes thinning/single-tree selection, early shelterwood stages, fire, and selective timber salvage	Canopy intact to partially open; low to moderate stem volume removal	6.52	4.33
Historic thinning	>10	0.4–86.2	Non-regenerative; thinning/single-tree selection, selective timber salvage	Canopy intact/recovered; low to moderate stem volume removal; various levels of stand ingrowth	86.78	82.47
Agriculture	NA	–	Corn, soy, hay, pasture	C4 plants only; horizontal edge	2.55	8.05
Developed	NA	–	Paved roads, residential	Potential barriers	1.73	2.96
Water	NA	–	0.02-ha ponds, lakes, streams	Water sources for drinking/foraging	0.25	0.57

Table 2
Radio-tracking and space use data for northern long-eared bats (*Myotis septentrionalis*) and Indiana bats (*Myotis sodalis*). Tracking success rate equals successful relocations divided by attempted triangulations. Kernel Density Estimates (KDEs) were generated from point relocations in core use and total foraging areas (50% and 95%). Maximum travel distance is from roost trees to the farthest extent of each bat's 95% KDE polygon. We calculated the area in hectares of each bat's corresponding polygon (50% and 95% contours).

	Number of bats	Mean number of relocations	Mean track success rate (%)	Mean nights tracked	Mean area (ha) of 95% KDE foraging	Range of area (ha) of 95% KDE foraging	Mean maximum travel distance (m)	Mean % of roosts in 50% KDE	Mean % of roosts in 95% KDE
Myotis septentrionalis									
♀ Pregnant	14	60	79	4	171	23–624	1553	67	98
♀ Lactating	10	61	87	3	218	80–605	1769	70	100
♀ Post-lactating	6	66	87	2	146	44–272	1574	69	100
♀ Juvenile	3	77	91	3	118	29–230	1060	67	100
Total or mean	33	63	84	3	176	44–433	1577	68	99
Myotis sodalis									
♀ Pregnant	7	61	65	3	247	76–551	2336	29	76
♀ Lactating	4	76	84	4	214	118–268	3889	20	30
♀ Post-lactating	9	65	62	3	327	79–818	3020	13	69
♀ Non-reproductive	3	82	79	4	423	97–778	2517	0	20
♂ Juvenile	2	43	62	3	890	152–1629	2920	0	100
Total or mean	25	66	69	3	343	104–809	2899	18	60

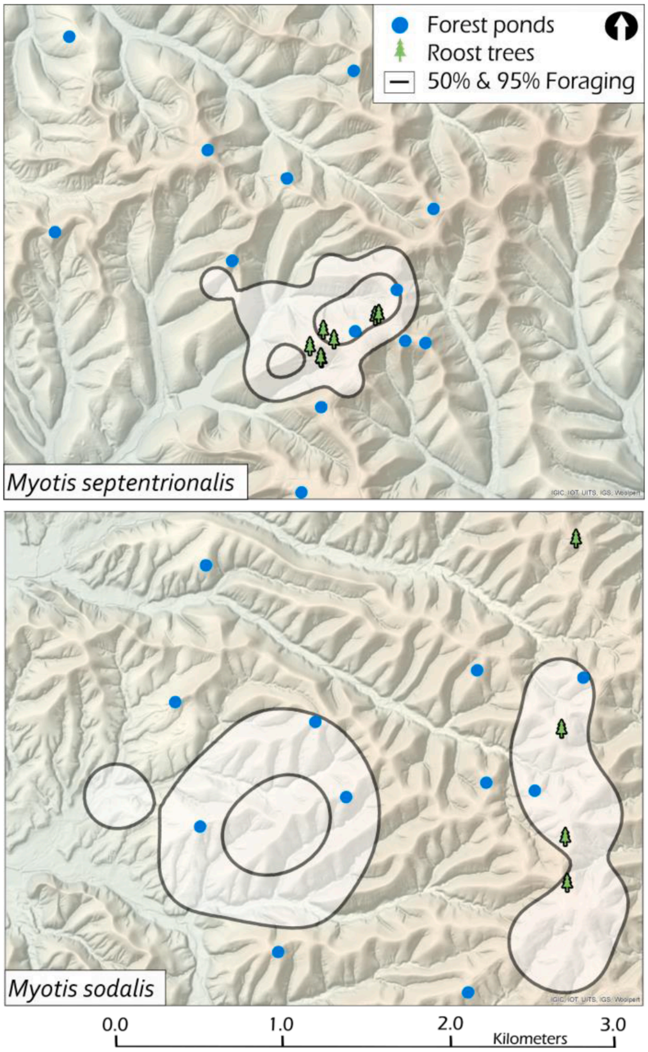

Fig. 1. Examples of roosting-foraging proximity. Northern long-eared bat (*Myotis septentrionalis*) roosts were typically near the center of foraging areas, as shown for one pregnant *M. septentrionalis* (top panel). Indiana bat (*Myotis sodalis*) roost sites were often disjunct from foraging areas, as shown for one pregnant *M. sodalis* (bottom panel). Foraging polygons represent 95% (extent) and 50% (core use) areas, which included 0.2-ha forest ponds.

3.3. Habitat selection within a managed forest

Both species displayed intra-specific variation in habitat selection. The first two factorial axes of the eigenanalysis explained 87.2% of the chi-square variation for *M. septentrionalis* and 96.6% for *M. sodalis*. Recent thinning drove factor loading on Axis 1, and clearcuts drove factor loading on Axis 2 (Figs. 2 and 3). Most *M. septentrionalis* clustered along Axis 1, foraging in recently thinned areas, patch cuts, and water (forest ponds); this axis explained 56.0% of the variation (Fig. 2). However, one pregnant *M. septentrionalis* used a clearcut more than expected in early June 2014 (explaining 31.2% of the variation; Bat 28, Fig. 2). *Myotis sodalis* used either recent thinning or patch cuts, which explained 58.9% of chi-square variation, or they used clearcuts (37.7% of the variation); these patterns are evident in Fig. 3. Although each species used multiple strategies of structural habitat selection, *M. septentrionalis* were more selective and showed greater consistency than *M. sodalis* (Figs. 2 and 3).

From weighted compositional analysis, we observed evidence of population-level habitat selection for both species. *Myotis septentrionalis* did not use available habitat randomly (Wilk's lambda = 0.079, P =

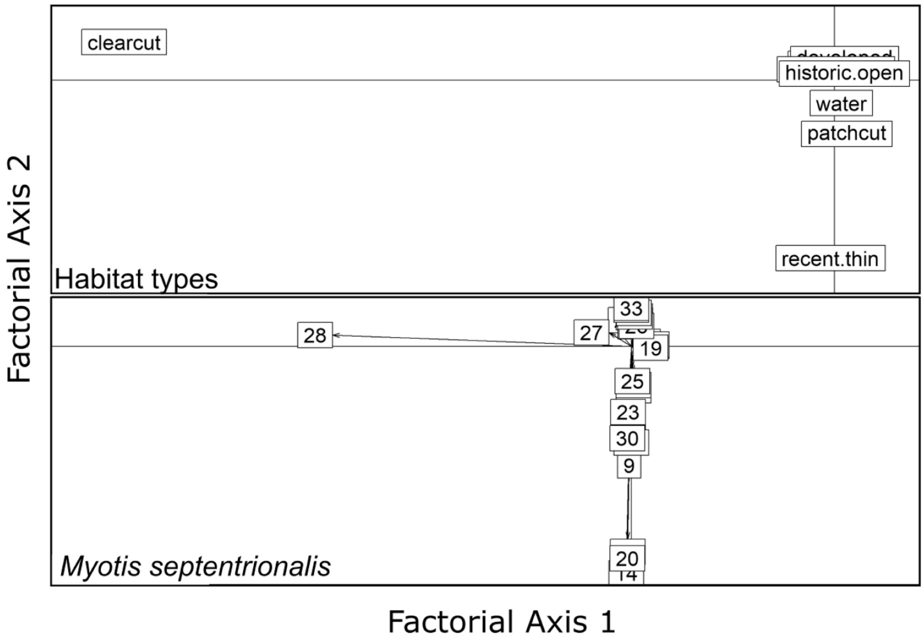

Fig. 2. Eigenanalysis of habitat selection ratios for 33 northern long-eared bats (*Myotis septentrionalis*). The top panel displays habitat loadings along the first two factorial axes and the bottom panel displays habitat preferences of individual bats in the same factorial space.

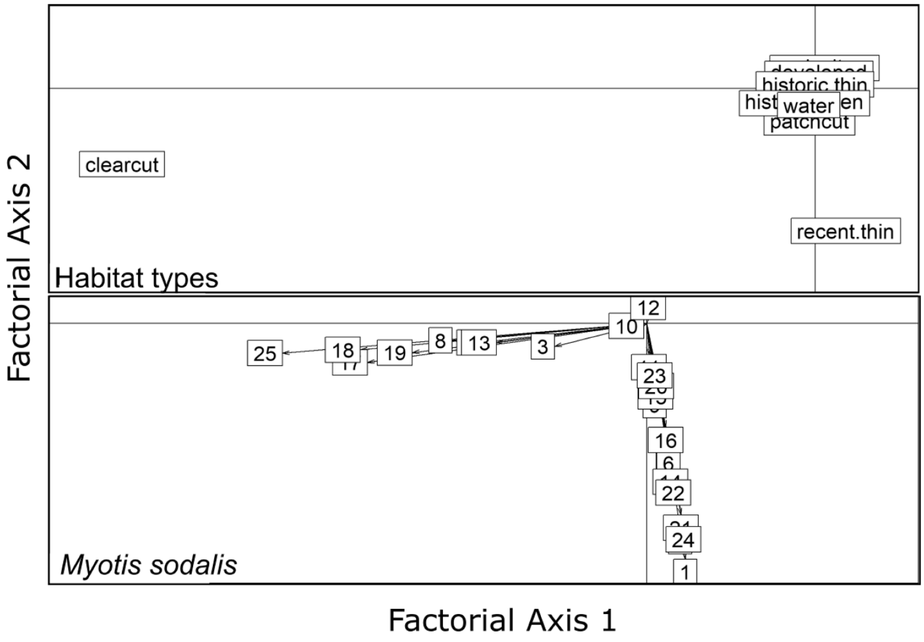

Fig. 3. Eigenanalysis of habitat selection ratios for 25 Indiana bats (*Myotis sodalis*). The top panel displays habitat loadings along the first two factorial axes and the bottom panel displays habitat preferences of individual bats in the same factorial space.

0.001); water (0.25% available, see Table 1) and historically thinned forest (87% available) were used significantly more than other categories (Table 3). For *M. septentrionalis*, the order of selection was water > historic thinning > patch cuts > recent thinning > historic openings > clearcut > developed > agriculture. *Myotis sodalis* exhibited a similar non-randomness (Wilk's lambda = 0.098, $P = 0.001$). Patch cuts (0.86% of available, see Table 1), historic openings (0.59% available), historic thinning (82% available), water (0.57% available), clearcuts (0.18% available), and recent thinning (4.33% available) were used significantly more than developed or agriculture lands (Table 3), and the order of selection was patch cuts > historic openings > historic thinning > water > recent thinning > clearcut > developed > agriculture. Patch cuts and historic thinning were in the top three most important categories for both species, but harvested openings ranked higher for *M. sodalis* than for *M. septentrionalis*.

4. Discussion

Over four years, we tracked the movements of two endangered, forest-dwelling *Myotis* in a large Central Hardwoods forest in Midwestern USA. *Myotis sodalis* covered twice as much area during their nightly forays, whereas *M. septentrionalis* tended to forage closer to roosts and use less area. Both bats selectively foraged in recent patch cuts, and small ponds were preferred by *M. septentrionalis*. Clearcuts were not

Table 3
Pairwise comparisons from multivariate analysis of variance (MANOVA) of habitat selection for northern long-eared bats (*Myotis septentrionalis*) and Indiana bats (*Myotis sodalis*). Positive (+) or negative (−) signs indicate whether habitats in each row were selected more or less than habitats in corresponding columns; triple signs indicate statistical significance ($P < 0.05$). Habitats are ranked by the number of positive selection values (0 is least selected); bolded rows are the three most important habitat types for each species.

	Agriculture	Clearcut	Developed	Historic thin	Patch cut	Recent thin	Historic open	Water	Rank
Myotis septentrionalis									
Agriculture	0	—	—	—	—	—	—	—	0
Clearcut	+++	0	+	—	—	–	–	—	2
Developed	+++	–	0	—	—	–	–	—	1
Historic thinning	**+++**	**+++**	**+++**	**0**	**+**	**+++**	**+++**	**–**	**6**
Patch cut	**+++**	**+++**	**+++**		**0**	**+++**	**+++**	**–**	**5**
Recent thinning	+++	+	+	—	—	0	+	—	4
Historic opening	+++	+	+	—	—	–	0	—	3
Water	**+++**	**+++**	**+++**	**+**	**+**	**+++**	**+++**	**0**	**7**
Myotis sodalis									
Agriculture	0	—	—	—	—	—	—	—	0
Clearcut	+++	0	+	–	–	–	–	–	2
Developed	+++	–	0	—	—	—	—	—	1
Historic thinning	**+++**	**+**	**+++**	**0**	**—**	**+**	**–**	**+**	**5**
Patch cut	**+++**	**+**	**+++**	**+++**	**0**	**+**	**+**	**+**	**7**
Recent thinning	+++	+	+++	–	–	0	–	–	3
Historic opening	**+++**	**+**	**+++**	**+**	**–**	**+**	**0**	**+**	**6**
Water	+++	+	+++	–	–	+	–	0	4

selected at large, but one-third of the *M. sodalis* used them. We showed that silvicultural practices important to oak restoration should be compatible with management objectives designed to create suitable foraging habitat for these imperiled bats. However, these two closely related bat species responded differently to forest management; understanding differences in foraging space use and habitat selection may be informative for forest management when the objective is support bat assemblages rather than single species. Despite their differences, for both species responses to harvest were neutral or positive. These findings may be transferable to other insectivorous, temperate bat assemblages in which multiple species share roosting or foraging areas in managed forest.

4.1. Differences in space use during summer

We showed that *M. sodalis* use more space for roosting and foraging compared to *M. septentrionalis*. Across known *M. sodalis* colonies, the largest foraging ranges average > 1,000 ha, 10 times larger than the average foraging range for *M. septentrionalis* (Table S1). In our study, roosting ranges for female *M. sodalis* covered a smaller area (mean = 135 ha, 0.3–1035 ha; S. Bergeson, unpublished data) than their foraging ranges (mean = 343 ha, this study). However, roosting ranges for female *M. septentrionalis* in this same area average only 5.4 ha (range 1–9.3 ha, Badin, 2014), a much smaller fraction of their foraging area (mean = 176 ha, this study). As predicted, *M. sodalis* tended to forage away from their roosts, whereas *M. septentrionalis* tended to forage and roost in the same areas (Fig. 1). However, space needs will vary with landscape composition. Amount of available forest is a strong predictor of space use for *M. sodalis*; in landscapes with small, disjunct forest fragments, *M. sodalis* have large foraging ranges—e.g., up to 1,339 ha in a landscape that is only 9% forested (Kniowski and Gehrt, 2014) and up to 3,812 ha in a landscape that is 27% forested (Womack et al., 2013). With less forest available, bats require more space, but *M. sodalis* decrease space use in response to greater forest availability, even in young, second-growth forests (Divoll and O'Keefe, 2018).

4.2. Summer foraging habitat use in a managed forest

Water, which was primarily available at small forest ponds, was the most important feature for *M. septentrionalis* and ranked fourth for *M. sodalis*. Ninety-three percent of bats we tracked included 1–10 forest ponds (mean = 3 ponds) within their foraging ranges, more than would be expected by chance (Divoll, 2020). In addition, ponds were centrally located in *M. septentrionalis* foraging areas (Fig. 1). Small ponds may function as critical water sources for lactating females, (Adams & Hayes, 2008), but bats may also perceive ponds as small openings in the forest canopy that facilitate access to prey. Supporting this, Huie (2002) showed that bat captures were higher than expected at small ponds within mature forest and lower than expected for small ponds within clearcuts in Kentucky, and Gallagher et al. (2021) found greater *Myotis* activity closer to waterbodies in New York.

Myotis septentrionalis may have low tolerance for large open areas (Henderson and Broders, 2008), including clearcuts. Because they have such small roosting ranges (~5 ha in Indiana, Badin, 2014, and North Carolina, O'Keefe, 2009) and foraging ranges (6–433 ha, Table S1, Table 2), they may only forage in large openings near their roosts. Indeed, the one *M. septentrionalis* that used a clearcut in our study roosted at the edge of an unpaved road alongside the clearcut. In our study area, female *M. septentrionalis* roost in live or dead trees in the forest interior with 40–60% canopy closure (stands with single-tree selection ≤ 10 years before; S. Haulton, personal observation), occasionally using trees within harvest openings (6% of roosts) or initial-stage shelterwoods (2%; Bergeson et al., 2021). When foraging, *M. septentrionalis* respond positively to disturbance that reduces clutter in mature forest (e.g., thinning or prescribed fire; Owen et al., 2003; Lacki et al., 2009), like the < 4-ha patch cuts and thinned stands used in our study. While *M. septentrionalis* tended to avoid ≥ 4-ha clearcuts (Fig. 2), this does not mean these openings are wholly unsuitable. At our site, Caldwell et al. (2019) showed that *M. septentrionalis* have similar acoustic activity in thinned forest and clearcuts. We contend that regenerative clearcuts will be perceived differently by bats than large-scale disturbances that remove forest altogether, such as conversion to crops or development. During our study, regenerating clearcuts were characterized by dense layers of saplings, thorny shrubs, and herbaceous plants, and these patches sustain a rich invertebrate community dominated by Diptera, Hymenoptera, Araneae, and Coleoptera (Ruhl et al., 2020), which are commonly eaten by bats at this site (Divoll, 2020).

While the distribution of *M. sodalis* is linked to forest cover (Cable et al., 2021), this species showed a greater affinity for forest openings than *M. septentrionalis* in this study. *Myotis sodalis* foraged over small patch cuts and historic openings more than expected and favored historically thinned (i.e., relatively intact canopy) forest over larger clearcuts. Lower preference for clearcuts does not mean *M. sodalis* will not use large forest openings; in fact, the eigenanalysis showed that one-third used clearcuts more than expected (Fig. 3). Their capacity for moving longer distances while foraging has allowed *M. sodalis* to subsist where forest patches are small, such as narrow riparian buffer strips and scattered woodlots (e.g., central Illinois, Gardner et al., 1991; central Ohio, Kniowski and Gehrt, 2014). One *M. sodalis* maternity colony has shown fidelity to a central Indiana landscape with $<$ 25% forest cover (Divoll and O'Keefe, 2018) for decades; the colony is able to forage successfully where forests are scarce. In Illinois, *M. sodalis* maternity colonies occupy landscapes with $\geq$ 40% forest cover but are most likely to occur with 60–80% forest cover (Cable et al., 2021). In heavy forest cover, *M. sodalis* likely tolerate larger forest openings that are a small portion of the landscape and may find foraging opportunities along their edges.

4.3. Implications for forest management and bat conservation

Sustaining forests for wildlife, carbon offsetting, timber production, and recreation may require various forms of harvest and prescribed fire. Will these disturbances be beneficial, neutral, or harmful to forest-dwelling bats? We showed that two *Myotis* species selectively used small regeneration harvests, which suggests such openings may benefit even small bats. Bats may be attracted to harvested patches when they represent a small portion of a spatially homogeneous forest (Grindal and Brigham, 1998). Smaller regeneration openings have greater edge relative to their size, which promotes plant and insect diversity (Taylor et al., 2020). While small openings and adjacent forest have similar levels of insect biomass (Grindal and Brigham, 1998), bats may be attracted to the hard vertical or horizontal edges of harvests if it is more efficient to capture prey there (Caldwell et al., 2019; Jung et al. 2012).

It is crucial to maintain roost trees and foraging areas to support both short- and long-term habitat requirements of bats. Oaks and hickories are important roost types for our study species (Bergeson et al., 2018, 2021) and other bat species across North America (Luna et al., 2014). As such, conservation plans should include measures to promote mature trees of these taxa, which are most likely to contain large hollows or cavities (Law et al., 2016). Shelterwood harvest, a management type preferred by foraging bats in this study, also promotes mature seed trees that may become roosts and is an effective strategy for oak regeneration during hot, dry summers (Kellner and Swihart, 2016). Our study species responded positively to thinning, which can yield forest structure like initial shelterwood stages, though both species used small patch cuts more than recently thinned stands (Table 3). Although there is general global movement away from even-aged management strategies to promote bat conservation (Law et al., 2016), we note that some individuals repeatedly foraged near small clearcuts ($<$7 ha, Fig. 3) in addition to even smaller patch cuts. Our observations suggest a need to reevaluate the value of even-aged treatments; thus, we recommend additional work to measure the utility of $<$ 7 ha regenerative harvests to forest *Myotis*.

Maintaining heterogeneous forests composed of mature stands, thinned stands, shelterwoods, and small regenerative harvests ($<$7 ha) will allow foraging bats to exploit patch types of varying ages and structure. This approach should directly apply to bat assemblages in managed forests worldwide. A holistic approach to forest–bat management should also consider perennial water sources, roosting habitat requirements, long-term patterns in habitat use, and responses to forest management outside of the summer maternity period (Loeb, 2020).

Authors' Contributions

JMO and GSH conceived the ideas and designed methodology; TJD collected the data; TJD and SPA analyzed the data; TJD and JMO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

Data from this study are publicly available and stored in the Illinois Data Bank at the University of Illinois at Urbana-Champaign.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This paper is a contribution of the Hardwood Ecosystem Experiment, a partnership of the Indiana Department of Natural Resources, Purdue University, Ball State University, the University of Indianapolis, Indiana State University, and Drake University. Funding for the project provided by the Indiana Division of Forestry [HEE: 4201-61398] and the US Fish & Wildlife Service and Wildlife Management Institute [WNS 2015-7]. We thank many technicians and these colleagues for assistance with mist netting and tracking: T. C. Carter, K. L. Caldwell, J. C. Karsk, K. L. Titus, and E. A. Beilke.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119757.

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PLOS ONE

Effects of Hierarchical Roost Removal on Northern Long-Eared Bat (*Myotis septentrionalis*) Maternity Colonies

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Published: January 22, 2015 • https://doi.org/10.1371/journal.pone.0116356

Abstract

Forest roosting bats use a variety of ephemeral roosts such as snags and declining live trees. Although conservation of summer maternity habitat is considered critical for forest-roosting bats, bat response to roost loss still is poorly understood. To address this, we monitored 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies on Fort Knox Military Reservation, Kentucky, USA, before and after targeted roost removal during the dormant season when bats were hibernating in caves. We used 2 treatments: removal of a single highly used (primary) roost and removal of 24% of less used (secondary) roosts, and an un-manipulated control. Neither treatment altered the number of roosts used by individual bats, but secondary roost removal doubled the distances moved between sequentially used roosts. However, overall space use by and location of colonies was similar pre- and post-treatment. Patterns of roost use before and after removal treatments also were similar but bats maintained closer social connections after our treatments. Roost height, diameter at breast height, percent canopy openness, and roost species composition were similar pre- and post-treatment. We detected differences in the distribution of roosts among decay stages and crown classes pre- and post-roost removal, but this may have been a result of temperature differences between treatment years. Our results suggest that loss of a primary roost or ≤ 20% of secondary roosts in the dormant season may not cause northern long-eared bats to abandon roosting areas or substantially alter some roosting behaviors in the following active season when tree-roosts are used. Critically, tolerance limits to roost loss may be dependent upon local forest conditions, and continued research on this topic will be necessary for conservation of the northern long-eared bat across its range.

Citation: Silvis A, Ford WM, Britzke ER (2015) Effects of Hierarchical Roost Removal on Northern Long-Eared Bat (*Myotis septentrionalis*) Maternity Colonies. PLoS ONE 10(1): e0116356. https://doi.org/10.1371/journal.pone.0116356

Academic Editor: Michelle L. Baker, CSIRO, AUSTRALIA

Received: July 11, 2014; **Accepted:** November 20, 2014; **Published:** January 22, 2015

Data Availability: Data used in this study are archived in the Virginia Polytechnic Institute and State University VTechWorks institutional repository (doi: 10.7294/W4H41PBH).

Funding: Funding for this research was provided through a United States Army 6.1 basic science grant. One of the authors in this manuscript works for the United States Army Corps of Engineers, but we have no conflicts of interest with the United States Army. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. This research was conducted on an active military installation, and accordingly, our field sites were positioned within areas of the installation that were not used for active training. We, the authors, selected these sites from a list of several safe operation zones on the installation.

Competing interests: The authors have declared that no competing interests exist.

Introduction

Roosts provide bats with sites for day-time sheltering as protection from weather and predators, mating, and social interaction. For species in temperate areas that form maternity groups in forested landscapes, roosts also provide thermal benefits for successful juvenile development [1–4]. Because of their importance in both survival and recruitment, roosts long have been considered a critical habitat feature for bats [5, 6]. Approximately half of all known bat species use plants as roosts [6]; in North America, roosts most commonly are found in snags or live trees with cavities or defects. Roosts such as snags in forests are ephemeral [7, 8]. Ephemerality of the roost resource strongly suggests that bats experience roost loss at some low constant background level, with periodic pulses of increased roost loss after intense disturbances from fire, wind throw, ice damage, insect outbreak, or certain types of forest management actions [9–12]. It seems likely, therefore, that bats are adaptive to roost loss. This plasticity often is ignored as many managers tasked with bat conservation often view roosts and roosting areas as fixed landscape elements that are decoupled from stochastic environmental processes [13, 14].

Bat conservation in forested landscapes often involves identification of roost sites with subsequent limitations on management activities (e.g., forestry) within these areas. Conservative approaches to roost habitat management may seem warranted, but this strategy may interrupt natural processes or anthropogenic management actions that are vital to create suitable roosts in the present or provide roosts in the future. Impacts of management actions that result in roost loss are unknown as few studies directly have assessed the effect of roost loss on bat roosting behavior in controlled, manipulative studies. Evidence from roost exclusion studies suggests that exclusion from permanent structures can decrease site fidelity, alter home range size, lower reproductive recruitment, and reduce colony size and the strength of association among individuals [15–18]. Conversely, several lines of evidence suggest that tree roosting bats may be tolerant of roost loss up to some threshold point. For example, bats have exhibited positive roosting responses to prescribed fire at short-term and long-term temporal scales [19–23]. Positive responses to prescribed fire may be due to rapid, increased snag recruitment that offsets the loss of existing snags [24–26]. Clearly, natural forest disturbance processes also can remove and create bat roosts. Natural forest disturbance processes contrast with many types of forest harvest that remove potential and available roosts without creating new roosts in the short-term. However, if applied on the landscape properly, it is possible that forest harvesting may mimic natural processes that also create suitable roosting areas or possibly enhance the quality of existing roosts, i.e., reduce canopy shading of remaining boles.

Tolerance limits to roost loss are unclear and probably highly variable among bat species and the forest systems wherein they reside [15–18, 27, 28]. For colonial species, insight into the impacts of roost loss will require understanding both of individual and colony level factors [29]. Responses to roost loss may be apparent in demographics, survival, roost use, space use, and sociality. Unfortunately, demographic changes are exceedingly difficult to ascertain for bats that roost-switch frequently and exhibit fission-fusion behavior. Within the context of roost use, resilience to roost loss generally may be visible as either a shift in overall uses of individual roosts without a change in overall space use or social structure, or alternatively, as a shift in roosting area and roosts without a change in social structure. Conversely, if colonies are not robust to disturbance, the colony may either dissolve such that social structure at the site is not maintained, or dissolve to the point where no bats are present on the site [27]. Within the network of roosts used by colonies of bats, individual roosts frequently are used differentially, with some receiving intense use (primary roosts) and others limited use (secondary roosts) [29–31]. Roost switching studies have provided insight on why bats may switch roosts, but the underlying causes for differences in the relative level of roost use have not been investigated widely. Regardless, differential roost use suggests that individual roosts may either serve different functions for colonies and individual bats therein or vary in their value. If so, loss of heavily used or primary roosts may impact colonies more strongly than loss of less frequently used roosts [28, 29].

Our objective was to experimentally examine how hierarchical loss of roosts affects roosting social structure along with roost and space use by female northern long-eared bats (*Myotis septentrionalis*) during the maternity season at both the colony and individual level. Northern long-eared bats occur in forests throughout the eastern United States and southern Canada [32–38], but foraging activity consistently is greatest in closed-canopy forests [34, 39–44]. During the maternity season (May-July), female northern long-eared bats form non-random assorting colonies in upland forests under the exfoliating bark or within cavities of snags or declining live trees [10, 33, 36, 44]. This species is a proposed for listing as endangered and currently of high conservation concern in North America (*Federal Register* § 78:61045–61080) due to severe population declines following the onset and spread of White-nose Syndrome in eastern North America. An improved understanding of the effects of roost loss on this species will be important for development of future conservation efforts.

Accordingly, we evaluated the impacts of primary and multiple secondary roost loss specifically to reflect discussion in the literature by Rhodes et al. [29] and Silvis et al. [27] that suggests that loss of either a single primary of >20% of total roosts might result in colony fragmentation, a negative conservation outcome of substantial concern. We assessed changes in colony roost and space use, roost selection, and social structure, as well as changes in individual behaviors related to roost switching. We specified several *a priori* hypotheses related to the differing levels of roost site disturbance based on previous research on multiple species [15, 16, 18, 27, 29]. For primary roost tree removal, we proposed 2 hypotheses:

1. H_1: At the colony level, loss of the primary roost will result in an alternate tree receiving increased use, subsequently causing a previously less-used roost to become the primary roost [15, 16]; bats will not display evidence of roost seeking behavior. Bats will display an affinity for the same roosting area, but the core use area would re-center around the new primary roost, and roost selection would be consistent. At the individual level, loss of the primary roost will not impact roost switching behavior or distances moved between sequentially used roosts.
2. H_2: At the colony level, loss of the primary roost will result in dissolution of the colony [29]. Space use will either be random across the former roosting area or will be nonexistent. Bats will display characteristics of roost searching, and the characteristics of selected roosts will differ [18]. At the individual level, loss of the primary roost will increase roost switching frequency and the distances moved between sequentially used roosts.

For secondary roost loss, we proposed three hypotheses:

1. H_1: At the colony level, loss of multiple secondary roosts will not impact roosting behavior, social structure, space use, or roost selection by northern long-eared bat maternity colonies [27]. At the individual level, loss of multiple secondary roosts will not impact roost switching behavior or distances moved between sequentially used roosts. Roost characteristics will not differ.
2. H_2: At the colony level, loss of multiple secondary roosts will result in dissolution of the colony [27]. Space use will either be random across the former roosting area or will be nonexistent. Bats will display characteristics of roost searching and roost characteristics will differ [18]. At the individual level, loss of multiple secondary roosts will increase roost switching frequency and the distances moved between sequentially used roosts.
3. H_3: At the colony level, loss of multiple secondary roosts will result in increased social cohesion and increased use of the primary roost, and roosting area will decrease. Roost characteristics will not differ. At the individual level, loss of multiple secondary roosts will decrease the number of roosts used by individual bats and the distances moved between roosts.

Methods

We conducted our study at 3 sites on the Fort Knox military reservation in Meade, Bullitt, and Hardin Counties, Kentucky, USA (37.9°N, −85.9°E, WGS84). Our sites lie in the Western Pennyroyal subregion of the Mississippian portion of the Interior Low Plateau physiographic province of the upper South and lower Midwest portion of the USA [45]. Forest cover is predominantly a western mixed-mesophytic association [46], with second- and third-growth forests dominated by white oak (*Quercus alba*), black oak (*Q. velutina*), chinkapin oak (*Q. muehlenbergii*), shagbark hickory (*Carya ovata*), yellow poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), and American beech *(Fagus grandifolia*) in the overstory, and sassafras (*Sassafras albidum*), redbud (*Cercis canadensis*), and sugar maple (*Acer saccharum*) in the understory [47].

We initially captured northern long-eared bats over small woodland pools from May through July 2011 (pre-roost removal) and 2012 (post-roost removal). We attached a radiotransmitter (LB-2, 0.31 g: Holohil Systems Ltd., Woodlawn, ON, Canada) between the scapulae of each female bat using Perma-Type surgical cement (Perma-Type Company Inc., Plainville, CT, USA). A uniquely numbered lipped band was attached to the forearm of all captured bats. After identifying a small number of roosts, we maximized number of bats captured by erecting mist nets around roosts located while radiotracking bats. Captured bats were released within 30 minutes of capture at the net site. Using TRX-1000S receivers and folding 3-element Yagi antennas (Wildlife Materials Inc., Carbondale, IL, USA), we attempted to locate radio-tagged bats daily for the life of the transmitter or until the unit dropped from the bat. For each located roost, we recorded tree species, diameter at breast height (dbh; cm), height (m), canopy openness (%), decay class ([48]; live [1], declining [2], recent dead [3], loose bark [4], no bark [4], broken top [6], broken bole [7]) and crown class ([49]; i.e., suppressed [S], intermediate [I], codominant [CO], dominant [D]). We estimated size of individual colonies by performing 5 exit counts per colony at day-roosts used by radiotracked bats.

We followed the methods of Silvis *et al.* [27] in defining a northern long-eared bat maternity colony as all female and juvenile bats connected by coincident roost use. We represented colonies graphically and analytically as two-mode networks that consisted of bats and roosts (hereafter “roost network”) [30, 31]. We used these roost network representations to describe patterns of roost use by colonies and to identify roosts for our removal treatments. To reduce bias resulting from uneven tracking periods and observing only a portion of each colony, we considered relationships to be binary (i.e., presence or absence of a connection) [50]. We assessed roost network structure using mean degree, network degree centralization, network density, and clustering. Within networks, degree is a count of the number of edges incident with a node [51]; high degree values indicate a large number of connections to a node. Network degree centralization, density, and clustering all have values between 0 and 1 (0 = low, 1 = high). Network degree centralization describes the extent that a network is structured around individual nodes, whereas network density and clustering describe the distribution of connections among nodes [52–56]. We calculated two-mode degree centralization and density using the methods of Borgatti and Everett [52] and clustering using the method of Opsahl [57] for our roost network. To determine whether our observed network values differed from those of random networks, we performed 999 Monte Carlo simulations and compared observed network metrics to random network metrics using two-tailed permutation tests [58, 59]; random networks [60] were generated with the same number of nodes as our observed networks and with a constant probability of link establishment. We then compared the relative difference from random networks pre-post treatment to assess whether colony social dynamics and roost use patterns were disrupted.

In February 2012 when bats were hibernating and not occupants of trees and snags, we implemented two roost removal treatments and one control following the identification and delineation of 3 colonies in 2011. For our primary roost removal treatment, we felled the single roost with the highest degree centralization value via chainsaw. For the secondary roost removal treatment, we similarly felled 5 randomly selected roosts (24% of colony total) with degree centralization values less than the colony maximum, but greater than the colony minimum in our secondary roost removal treatment group. This number was selected to specifically test the simulation-based predictions of Silvis *et al.* [27] that colonies may fragment with loss of >20% of roosts.

We used conditional Wilcoxon 2-sample tests and conditional Chi-squared tests to compare continuous (height, dbh, and canopy openness) and categorical roost characteristics (species composition, decay stage, and crown class) pre- and post-treatment and among groups; we corrected for multiple comparisons using the Bonferroni method. Conditional tests were performed using Monte Carlo simulations with 999 permutations. We examined the roost switching behavior of individual bats by creating a Poisson regression model describing the number of roosts used by a bat relative to the total number of relocations, reproductive condition, and interaction of treatment identity and year. We used this Poisson model to conduct general linear hypothesis tests with Tukey’s adjustment for multiple comparisons to determine whether the number of roosts used by bats differed within or among treatment areas. We evaluated the fit of our Poisson model using maximum-adjusted D^2 [61]. We assessed the spatial component of roost switching behavior by individual bats by comparing the distances that bats within treatment areas moved between sequentially used roosts with general linear hypothesis tests, also with Tukey’s adjustment for multiple comparisons. We performed our general linear hypothesis tests for distances moved on a linear mixed model containing year, group, their interaction term, and reproductive condition as fixed effects, and bat identity as a random effect; we used a log transformation to normalize distance data. We assessed the fit of our linear mixed model using the conditional (R^{2c}) and marginal (R^{2m}) coefficients of determination [62].

We evaluated roost removal impacts on colony roosting area space use for each treatment group using Bhattacharya’s affinity (BA) [63] and the difference in roosting area centroids between years. The BA uses the joint distribution of 2 utilization distributions to quantify similarity between utilization distributions and is appropriate for comparisons of utilization distributions for the same individual or group [63]. These values range from 0 to 1, with values close to 1 indicating highly similar utilization distributions [63]. We calculated 95% utilization distributions from the pooled locations of all bats within a colony using bivariate normal fixed kernel methodology. To reflect the concentration of roost use, we weighted roost locations by the number of times a roost was used by radio-tagged bats [64]. We used the reference method for smoothing parameter estimation as appropriate for weighted locations [65]; that also allowed us to consider our estimates of colony space use as liberal. In cases where roosting areas of separate colonies overlapped to an appreciable extent, we calculated the utilization distribution overlap index (UDOI) to determine if space use was independent; UDOI values range from 0 to infinity, with values <1 indicating independent space use, and values >1 indicating non-independence [63].

We assessed overall changes in colony roost use patterns by comparing pre- and post-roost removal network degree centralization, density, and clustering for the roost networks. We used this same comparative network approach to assess changes in colony roosting social structure for the single mode projections of our 2-mode roost networks [66]. This projection allowed us to focus on existing direct and indirect connections among bats in a colony. Because comparing values from networks of differing size may yield inappropriate inferences [67], we used indirect comparisons of network characteristics. In these, we compared the relative difference between a roost or social network and its equivalent random network pre- and post-treatment. All analyses were performed in the R statistical program version 3.0.2 [68]. We calculated conditional tests using the *coin* package [69], linear mixed models using *lme4* [70], and utilization distributions, BA, and UDOI values using the *adehabitatHR* package [71]. We used the *igraph* [72] and *tnet* libraries [57] to visualize networks and calculate metrics. Lastly, network Monte Carlo simulations were performed using a custom script with dependencies on the *igraph* and *tnet* libraries. We used an $\alpha = 0.05$ for all tests of statistical significance.

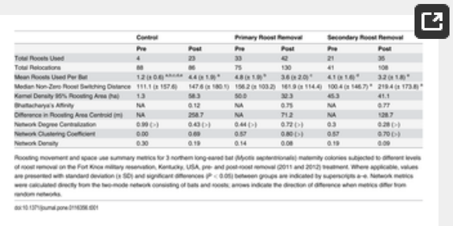
Ethics statement

Our study was carried out in accordance with state requirements for capture and handling of wildlife (Kentucky Department of Fish and Wildlife Resources permit numbers SC1111108 and SC1311170) and did not involve any endangered species at the time of the study. Capture and handling protocol followed the guidelines of the American Society of Mammalogists [73] and was approved by the Virginia Polytechnic Institute and State University Institutional Animal Care and Use Committee (protocol number 11–040-FIW). We received explicit permission to conduct work on the Fort Knox military reservation from the reservation staff biologists and Fort Knox Range Control. Data used in this study are archived in the Virginia Polytechnic Institute and State University VTechWorks institutional repository (DOI: 10.7294/W4H41PBH).

Results

We captured 58 female northern long-eared bats pre-treatment in 2011. Based on patterns of coincident roost use, we assigned 36 of these bats (11 gestating, 20 lactating, 1 post-lactation, and 4 non-reproductive) to 3 colonies. Exit counts for these 3 colonies generated minimum estimated colony sizes of 13, 18, and 14 bats, respectively. We captured 67 bats post-treatment in 2012, 62 of which (4 gestating, 45 lactating, 10 post-lactation, and 3 non-reproductive) we were able to assign to the 3 colonies identified in 2011. We recaptured only 3 individuals banded in 2011 during 2012. Exit counts indicated that the 2012 colonies contained a minimum of 24, 20 and 25 bats, respectively. We located 58 roosts over 204 relocation events for the 3 colonies identified in 2011 and 100 roosts (7 of which were used in 2011) over 324 relocation events in 2012. We recorded a mean (± SD) of 5.7 (± 1.5) locations per bat in 2011 and 5.2 (± 2.9) in 2012.

We identified between 4 and 33 roosts per colony pre-roost removal, and between 23 and 42 roosts per colony post-removal (Table 1). When controlling for the total number of relocations of an individual bat and reproductive condition, the number of roosts used by individual bats was similar between pre- and post-treatment and among colonies, with the exception of the control colony, pre-removal, that differed from all other groups (model $D^2 = 0.74$; Tables 1, 2).



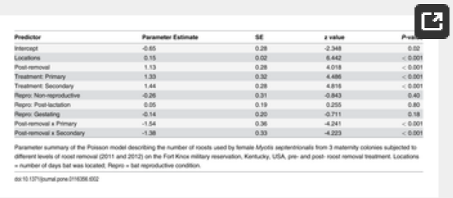
	Control		Primary Roost Removal		Secondary Roost Removal	
	Pre	Post	Pre	Post	Pre	Post
Total Roosts Used	4	23	33	42	21	35
Total Relocations	88	86	75	130	41	108
Mean Roosts Used Per Bat	1.2 (± 0.6)	4.4 (± 1.9)	4.8 (± 1.9)	3.6 (± 2.0)	4.1 (± 1.6)	3.2 (± 1.8)
Median Non-Zero Roost Switching Distance	111.1 (± 157.6)	147.6 (± 180.1)	156.2 (± 103.2)	161.9 (± 114.4)	100.4 (± 146.7)	219.4 (± 173.8)
Kernel Density 95% Roosting Area (ha)	1.3	58.3	50.0	32.3	45.3	41.1
Bhattacharya's Affinity	NA	0.12	NA	0.75	NA	0.77
Difference in Roosting Area Centroid (m)	NA	258.7	NA	71.2	NA	128.7
Network Degree Centralization	0.99 (>)	0.43 (>)	0.44 (>)	0.72 (>)	0.3	0.28 (>)
Network Clustering Coefficient	0.00	0.69	0.57	0.80 (>)	0.57	0.70 (>)
Network Density	0.30	0.19	0.14	0.08	0.19	0.09

Roosting movement and space use summary metrics for 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies subjected to different levels of roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post-roost removal (2011 and 2012) treatment. Where applicable, values are presented with standard deviation (± SD) and significant differences ($P < 0.05$) between groups are indicated by superscripts a–e. Network metrics were calculated directly from the two-mode network consisting of bats and roosts; arrows indicate the direction of difference when metrics differ from random networks.

doi:10.1371/journal.pone.0116356.t001

Table 1. Summary of female northern long-eared bat roost use patterns.

https://doi.org/10.1371/journal.pone.0116356.t001



Predictor	Parameter Estimate	SE	z value	P-va
Intercept	-0.65	0.28	-2.348	0.02
Locations	0.15	0.02	6.442	< 0.001
Post-removal	1.13	0.28	4.018	< 0.001
Treatment: Primary	1.33	0.32	4.486	< 0.001
Treatment: Secondary	1.44	0.28	4.816	< 0.001
Repro: Non-reproductive	-0.26	0.31	-0.843	0.40
Repro: Post-lactation	0.05	0.19	0.255	0.80
Repro: Gestating	-0.14	0.20	-0.711	0.18
Post-removal x Primary	-1.54	0.36	-4.241	< 0.001
Post-removal x Secondary	-1.38	0.33	-4.223	< 0.001

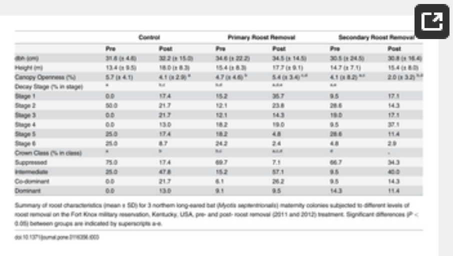
Parameter summary of the Poisson model describing the number of roosts used by female *Myotis septentrionalis* from 3 maternity colonies subjected to different levels of roost removal (2011 and 2012) on the Fort Knox military reservation, Kentucky, USA, pre- and post- roost removal treatment. Locations = number of days bat was located; Repro = bat reproductive condition.

doi:10.1371/journal.pone.0116356.t002

Table 2. Factors influencing the number of roosts used by individual female northern long-eared bats.

https://doi.org/10.1371/journal.pone.0116356.t002

Neither roost dbh nor height differed between treatments or among colonies (Table 3). Canopy openness was similar between pre- and post-treatment, but some individual colonies differed from one another (Table 3). Distribution of roosts among decay stages differed pre- and post-treatment within the primary removal colony but not in the control colony or the secondary removal colony (Table 3). Distribution of roosts among crown classes differed pre- and post-treatment for the primary removal colony but not in the control or secondary removal colony (Table 3). Distribution of roosts among decay stage and crown classes did differ among colonies in some cases (Table 3). We found no difference in roost species composition between pre- and post-treatment or among any of our groups (Table 3). Sassafras (*Sassafras albidum*) trees or snags were the most commonly used roost species, accounting for between 43 and 57% of roosts used in each group.



	Control		Primary Roost Removal		Secondary Roost Removal	
	Pre	Post	Pre	Post	Pre	Post
dbh (cm)	31.6 (± 4.6)	32.2 (± 15.0)	34.6 (± 22.2)	34.5 (± 14.5)	30.5 (± 24.5)	30.8 (± 16.4)
Height (m)	13.4 (± 9.5)	18.0 (± 8.3)	15.4 (± 8.3)	17.7 (± 9.1)	14.7 (± 7.1)	15.4 (± 8.0)
Canopy Openness (%)	5.7 (± 4.1)	4.1 (± 2.9)	4.7 (± 4.6)	5.4 (± 3.4)	4.1 (± 8.2)	2.0 (± 3.2)
Decay Stage (% in stage)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
Stage 1	0.0	17.4	15.2	35.7	9.5	17.1
Stage 2	50.0	21.7	12.1	23.8	28.6	14.3
Stage 3	0.0	21.7	12.1	14.3	19.0	17.1
Stage 4	0.0	13.0	18.2	19.0	9.5	37.1
Stage 5	25.0	17.4	18.2	4.8	28.6	11.4
Stage 6	25.0	8.7	24.2	2.4	4.8	2.9
Crown Class (% in class)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	-
Suppressed	75.0	17.4	69.7	7.1	66.7	34.3
Intermediate	25.0	47.8	15.2	57.1	9.5	40.0
Co-dominant	0.0	21.7	6.1	26.2	9.5	14.3
Dominant	0.0	13.0	9.1	9.5	14.3	11.4

Summary of roost characteristics (mean ± SD) for 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies subjected to different levels of roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post- roost removal (2011 and 2012) treatment. Significant differences ($P < 0.05$) between groups are indicated by superscripts a-e.

doi:10.1371/journal.pone.0116356.t003

Table 3. Summary of female northern long-eared bat roost characteristics.

https://doi.org/10.1371/journal.pone.0116356.t003

Distances moved between sequentially used roosts were non-normally distributed with right skew; median distances were between 111.1 and 219.4 m (Table 1). Distances between sequentially used roosts differed only pre- and post-roost removal in our secondary roost removal treatment group (model $R^{2c} = 0.18$, $R^{2m} = 0.08$; Tables 1, 4). Overall colony roosting areas were between 1.3 and 58.5 ha (Table 1). Patterns of roosting area space use largely were consistent between pre- and post-treatment in our primary and secondary roost removal treatment groups, particularly evident in the distances between weighted colony roosting area centroids (Table 1, Fig. 1). However, space use by and roosting area centroids of our control colony differed substantially between years (Table 1).

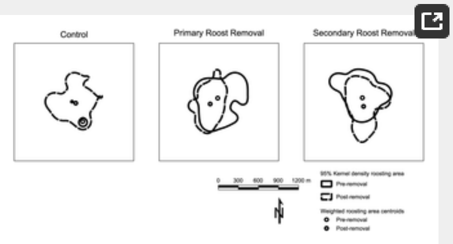
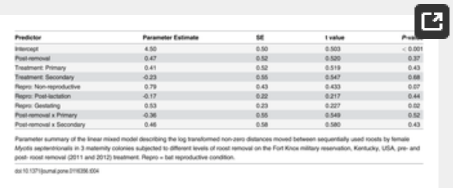


Figure 1. Northern long-eared bat maternity colony roosting areas.

Roosting areas (95% utilization distribution) of 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies subjected to different levels of roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post- roost removal (2011 and 2012)

https://doi.org/10.1371/journal.pone.0116356.g001



Predictor	Parameter Estimate	SE	t value	P-value
Intercept	4.50	0.50	0.503	< 0.001
Post-removal	0.47	0.52	0.520	0.37
Treatment: Primary	0.41	0.52	0.519	0.43
Treatment: Secondary	-0.23	0.55	0.547	0.68
Repro: Non-reproductive	0.79	0.43	0.433	0.07
Repro: Post-lactation	-0.17	0.22	0.217	0.44
Repro: Gestating	0.53	0.23	0.227	0.02
Post-removal x Primary	-0.36	0.55	0.549	0.52
Post-removal x Secondary	0.46	0.58	0.580	0.43

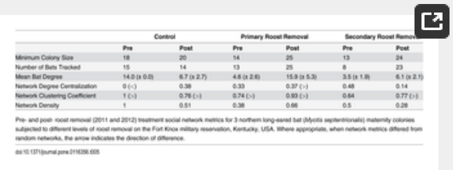
Parameter summary of the linear mixed model describing the log transformed non-zero distances moved between sequentially used roosts by female *Myotis septentrionalis* in 3 maternity colonies subjected to different levels of roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post- roost removal (2011 and 2012) treatment. Repro = bat reproductive condition.

doi:10.1371/journal.pone.0116356.t004

Table 4. Factors influencing distances moved between roosts by female northern long-eared bats.

https://doi.org/10.1371/journal.pone.0116356.t004

Roost network degree centralization significantly was greater than random for primary removal and control colonies, but not the secondary roost removal colony pre-treatment (Table 1). Roost network clustering differed from random networks in both the primary and secondary roost removal colonies post-treatment, but, for all other colonies, there was no difference from random networks (Table 1). Roost network density did not significantly differ from random networks for any group (Table 1). As represented in the social networks, bats shared between 3.5 and 15.9 social connections with other bats within colonies (Table 5). Social network degree centralization differed from random networks only for the control colony pre-treatment and the primary roost removal treatment post-treatment; the former was significantly less than and the latter significantly greater than equivalent random networks (Table 5). Social network clustering significantly was greater than that of random networks for colonies except the secondary roost removal treatment colony pre-treatment (Table 5). Social network density did not differ from random networks pre-treatment, but was greater in all other cases (Table 5).



	Control		Primary Roost Removal		Secondary Roost Removal	
	Pre	Post	Pre	Post	Pre	Post
Minimum Colony Size	18	20	14	25	13	24
Number of Bats Tracked	15	14	13	25	8	23
Mean Bat Degree	14.0 (± 0.0)	6.7 (± 2.7)	4.6 (± 2.6)	15.9 (± 5.3)	3.5 (± 1.9)	6.1 (± 2.1)
Network Degree Centralization	0 (<)	0.38	0.33	0.37 (>)	0.48	0.14
Network Clustering Coefficient	1 (>)	0.76 (>)	0.74 (>)	0.93 (>)	0.64	0.77 (>)
Network Density	1	0.51	0.38	0.66	0.5	0.28

Pre- and post- roost removal (2011 and 2012) treatment social network metrics for 3 northern long-eared bat (Myotis septentrionalis) maternity colonies subjected to different levels of roost removal on the Fort Knox military reservation, Kentucky, USA. Where appropriate, when network metrics differed from random networks, the arrow indicates the direction of difference.

doi:10.1371/journal.pone.0116356.t005

Table 5. Northern long-eared bat maternity colony social network metrics.

https://doi.org/10.1371/journal.pone.0116356.t005

Visual inspection of the roost network maps indicated that the secondary roost removal colony was split into 2 groups connected only by a single roost post-treatment (Fig. 2). Because these 2 halves possibly represented 2 separate colonies connected by a single ‘chance’ roost use, we conducted a *post-hoc* analysis wherein we removed the roost connecting the 2 network sections (subcolony 1 and subcolony 2) and re-calculated spatial metrics. Roosting area was 46.37 ha for subcolony 1 and 27.43 ha for subcolony 2. Roosting areas of these 2 sections overlapped substantially (UDOI = 1.26).

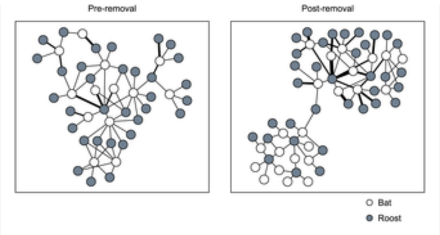


Figure 2. Northern long-eared bat maternity colony roost network map.

Pre- and post- roost removal treatment (2011 and 2012) 2-mode roost network map of a northern long-eared bat (*Myotis septentrionalis*) maternity colony subjected to removal of 5 secondary roosts on the Fort Knox military reservation, Kentucky, USA. Edge width is scaled by the number of connections between a bat and an individual roost.
https://doi.org/10.1371/journal.pone.0116356.g002

Discussion

In our manipulative roost removal experiment, treatments did not result in abandonment of roosting areas by northern long-eared bats. Persistence after exclusion from a roost also has been observed in big brown bats (*Eptesicus fuscus*) in northern forest-prairie transitions zones in Canada [15] and disc-winged bats (*Thyroptera tricolor*) in Costa Rican tropical forests [18], species that both exhibit relatively frequent roost switching. In contrast, syntopic little brown bats (*Myotis lucifugus*), that form larger colonies and roost-switch less than northern long-eared bats, appear to abandon roosting areas after exclusion [16]. Persistence after roost loss may be related to the greater number of roosts used by colonies and to roost ephemerality. Roost fidelity is less in species with more ephemeral roosts [74], therefore, having a variety of alternate roosts or some degree of flexibility in what roosts may be selected may be an adaptation for tolerating roost loss for the northern long-eared bat.

Northern long-eared bat maternity colony roosting areas did not appear to change as a result of either of our roost removal treatments. In contrast, Chaverri and Kunz [18] found that exclusion resulted in larger individual roosting home ranges in disc-winged bats [18] and Borkin et al. [17] found that roost loss resulted in smaller home ranges in New Zealand long-tailed bats (*Chalinolobus tuberculatus*) [17]. Increased home range size in disc-winged bats was related to the need to locate a limiting resource—suitable roosts [18]. However, northern long-eared bats are not extreme roost specialists [32, 75, 76] and potential roosts are not limited on our sites [77]. On the other hand, decreased home range size in New Zealand long-tailed bats as a result of roost loss following clear-cutting, reflected the lack of available roosts and alternative roosting areas in the harvested areas [17]. Locally, large numbers of available roosts may explain why so few roosts were used in both years of our study and why colony locations did not change.

It was surprising that so few roosts were used both pre- and post-treatment, but could be the result of tracking different bats in each year. We captured a substantial proportion of the bats within individual colonies (range 0.62–1.0, $\bar{x} = 0.84$). As such, it is unlikely that our low recapture rate was due to sampling effort. Regardless, roost removal treatments did not impact the number of roosts used by individual bats within treatment areas when controlling for the number of total locations and reproductive condition. The lack of difference in the number of roosts used differs from Borkin *et al.* [17], who found that bats used fewer roosts post-roost loss. The number of roosts used per bat was fewer in 2011 than in 2012 in our control colony, but this is likely due to the fact that the colony was captured and tracked during parturition in 2011 [78]; the number of roosts used per bat in the control colony in 2012 was consistent with that of all other groups. Given the positive relationship between the number of roosts located and the number of days a bat was tracked, differences in the total number of roosts located per colony were not unexpected.

Northern long-eared bats are known to exhibit inter-annual site fidelity of at least 5 years in a mixed pine-deciduous system in Arkansas [79], but our low recapture rates relative to our sampling effort suggest that bats marked during the first year of our study largely were not present in the second. Whether this is due to high annual adult mortality or some other socio-spatial assortment dynamic is unknown, but Perry [79] also recaptured few banded individuals. Consistent patterns of space use between years suggest that, although colony composition changed, colony identity did not. Northern long-eared bat maternity colonies [80] as well as those of some other species [81] contain maternally-related individuals, and it is possible that primarily juveniles from the first year returned in the second. In the context of having tracked different bats within colonies, our data may be interpreted best not as changes in behavior of individual bats resulting from removal treatments, but as differences in patterns of colony behavior at our treatment sites.

In contrast to Chaverri and Kunz [18], we observed no change in roost species selection post-roost removal. This is consistent with the high roost availability at our sites [27]. Roost decay stage and crown class in the primary removal colony were the only roost characteristics to differ between pre- and post-treatment. Selection for more advanced stages of decay in 2011 appears to be correlated with crown class, as trees in advanced stages of decay at our sites are primarily in suppressed crown classes. Although the difference in decay stage and crown class pre- and post-treatment is statistically significant only for the primary removal colony, a similar trend in reduced selection for suppressed roosts in later stages of decay was visible across all colonies in 2012. It is possible that by random chance roost removal caused the difference in roost decay stage and crown class in our findings, but given the lack of difference between roost dbh, height, and canopy openness in the primary removal colony, this seems unlikely. Higher summer temperatures in 2011 than in 2012 on our study site may have caused bats to select trees in more suppressed crown classes, thereby reducing solar heating of roosts. Mean minimum temperature during June–July was 1.78 C° greater in 2011 than in 2012 (National Oceanic and Atmospheric Administration station GHCND: USC00154955); similarly small temperature differences have been found to affect roost selection by Bechstein's bats (*Myotis bechsteinii*) [82] and development of juvenile greater mouse-eared bats (*Myotis myotis*) [83].

Patterns of northern long-eared bat roost use and association, as assessed through roost and social networks, displayed a mix of random and non-random characteristics. The overall character of roost networks relative to random networks was similar within and among treatments. Although there were minor differences in roost and social networks pre- and post-treatment, northern long-eared bat social network structure changes with reproductive condition [84, 85]. After accounting for reproductive condition, the character of the roost networks post-treatment differed only for roost network clustering. The change in roost network clustering from not significantly different from random networks to significantly greater than random networks also was reflected through increased social network density. An increase in roost network clustering and social network density may be an adaptive response to maintain colony stability after roost loss. Such an adaptive response to roost loss could suggest co-evolution between northern long-eared bats and these mixed mesophytic forests and other systems with similar stand dynamics and disturbance patterns, but replication of our study across more regions and forest types is required to document this.

For the secondary roost removal colony, we observed a segmented roost network and the only statistically significant difference in the distance moved between sequentially used roosts. Division of this network into 2 halves as a result of the removal of 24% of roosts would be consistent with previous simulation based outcomes showing that loss of approximately 20% of roosts generates a 50% chance of colony fragmentation [27]. Connection of the 2 halves of this network by a single roost may reflect an incomplete division of the colony. An incomplete division may indicate that colony fragmentation occurs incrementally as roosts are lost, an outcome that theoretically should be most likely to occur if individual roosts are important locations for social interaction. Incomplete colony fragmentation is consistent with our finding that the 2 sections of this colony shared a single roosting area—an observation that was contrary to our *a priori* prediction that colony fragmentation would result in random use of the roosting area, but that may be related to the difference in distances moved between roosts by bats in this colony. Alternately, apparent division also could be the result of unwarranted joining of two separate neighboring colonies as a result of chance use of single roost. Silvis *et al.* [27] speculated that roost sharing may be infrequent and inconsequential at the periphery of the roosting area for northern long-eared bats. In this case, the shared roost was not at the periphery of the colony roosting area and the roosting areas of the 2 sections of the colony overlapped extensively in terms of both extent and concentration of use. Research from other bat species in both temperate and tropical regions suggests that roosting areas are exclusive relatively to individual colonies [17, 30, 31]. Whether this apparent fragmentation is a result of roost removal treatments or some other process remains speculative.

Conclusions

In their review of conservation concerns for bats in the United States, Weller et al. [86] identified a need to transition conservation priorities from focal threats to diffuse threats. In the context of the White-nose Syndrome enzootic that is threatening many species, including the northern long-eared bat, with widespread extirpation, it is necessary to link focal and diffuse threats through understanding of the impacts of specific changes to roosting habitats. Although our study contains limited replicates of our individual treatments, it is to our knowledge the only study to perform targeted roost removal treatments for colonial bats in a temperate forest ecosystem. Clearly, caution should be taken in interpreting the results of individual treatments, particularly with regard to changes in roost and social network structure. However, our results are consistent with previous predictions and anecdotal observations that northern long-eared bats would be robust to low levels of roost loss [20, 22] particularly if loss of these naturally ephemeral roost resources are lost at or below rates of tree mortality / snag loss in temperate forests. Clearly, the maximum levels of annual or cumulative multi-year roost loss that northern long-eared bats can tolerate remains to be determined. It is important to consider that roosts were not limiting at our study sites similar to much of the temperate forested environments where northern long-eared bats occur [10, 87]. However, in more roost limited areas, e.g., in agricultural landscapes with greater forest fragmentation or in industrial forest settings skewed towards younger forest age classes, roost loss may have different consequences for northern long-eared bats.

Monitoring of sufficient numbers of colonies for robust inference is largely infeasible within a single study. Therefore, replication across studies is needed to better confirm or modify the patterns we have observed. With the ongoing spread of White-nose Syndrome in North America, and continued rapid declines in northern long-eared bat populations, replication of this study in disease-free areas is urgently needed. Moreover, a better understanding the impacts of roost loss, whether natural or anthropogenic, on survival and recruitment remains a critical gap in our knowledge of bat ecology.

Acknowledgments

We thank Jimmy Watkins, Mike Brandenberg, and Charlie Logsdon for their assistance in supporting this project. The Kentucky Department of Fish and Wildlife Resources graciously provided field housing for this project. We thank James Fraser, James Parkhurst, Tim Carter, Steven Castleberry and an anonymous reviewer for comments that improved this manuscript. Use of trade, product, or firm names does not imply endorsement by the US government.

Author Contributions

Conceived and designed the experiments: WMF ERB AS. Performed the experiments: AS WMF ERB. Analyzed the data: AS WMF ERB. Contributed reagents/materials/analysis tools: WMF ERB. Wrote the paper: AS WMF ERB.

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Forest Management and Female Black Bear Denning
Author(s): Thomas H. White, Jr., Jacob L. Bowman, Harry A. Jacobson, Bruce D. Leopold, Winston P. Smith
Source: *The Journal of Wildlife Management*, Vol. 65, No. 1 (Jan., 2001), pp. 34-40
Published by: Allen Press
Stable URL: http://www.jstor.org/stable/3803274
Accessed: 02/03/2011 15:46

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Received 4 November 1998.
Accepted 5 June 2000.
Associate Editor: Hellgren.

FOREST MANAGEMENT AND FEMALE BLACK BEAR DENNING

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Abstract: Most habitats available to black bear (*Ursus americanus*) in the Mississippi Alluvial Valley (MAV) consist of seasonally flooded commercial forests where lack of suitable dens may limit population growth. We studied interactions between forest management and flooding relative to female black bear denning. Denning behavior differed between commercial and noncommercial forests. Females used tree dens exclusively on noncommercial forests, whereas on commercial forests, most (83%) were ground dens. Variations in ground den elevation resulted in differing inundation probabilities, altering survival probabilities for neonates. On commercial forests, ground dens with similar inundation probabilities as tree dens allowed successful reproduction to occur. Management practices that enhance suitable cover in areas of minimal inundation probability may mitigate for lack of den trees in flood-prone landscapes.

JOURNAL OF WILDLIFE MANAGEMENT 65(1):34–40

Key words: batture, black bear, denning, elevation, flooding, forest management, Misissippi Alluvial Valley, reproduction, topography, *Ursus americanus*.

Hibernation is a key segment of the black bear life cycle because this is when parturition occurs (Aldous 1937, Hellgren 1988, Eiler et al. 1989). For parturient females, denning also provides a secure setting for early maternal care. Black bears use a variety of den sites and preference appears to be sex-specific. In bottomland hardwoods, Smith (1985) found that only males used ground dens (e.g., brushpiles). In the southern Appalachians, Carlock et al. (1983) reported 67% of 112 dens were in trees and that adult females accounted for 64% of tree den use, whereas only 10% of adult males denned in trees. Cahalane (1947), Erickson (1964) and Pelton et al. (1980) reported similar findings. By using tree dens, bears increase endogenous energy savings by >15% (Johnson et al. 1978), minimized likelihood of disturbance (Johnson

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and Pelton 1981), and may enhance neonate survival.

Natural mortality is typically greatest for black bears during the first year of life (Rogers 1977, LeCount 1987, Eiler et al. 1989, Elowe and Dodge 1989), although Jonkel and Cowan (1971) found that mortality was greatest for yearlings following independence. Because black bears exhibit slow reproductive maturity, a prolonged reproductive cycle, and small litter sizes (Erickson 1964, Rogers 1977, Ruff 1978), cub mortality can significantly affect productivity. In southeastern U.S. wetlands, neonatal drowning may be a particular hazard due to limited availability of dry den sites (Hellgren and Vaughan 1989, Weaver and Pelton 1994, White 1996, Oli et al. 1997). In flood-prone areas selection for higher ground (Hellgren and Vaughan 1989, Marchinton 1995) or for above-ground tree cavities (Smith 1985, Oli et al. 1997) may help reduce this hazard.

Intensive forest management practices coupled with past reductions in bottomland hardwood forests may substantially impact black bear populations throughout the southeastern United States. Moreover, normal forestry operations in habitats that the federally threatened Louisiana black bear occupy are not regulated (U.S. Department of Interior 1991). This exemplifies the need to examine influences of bottomland hardwood forest management on black bear populations in the Mississippi Alluvial Valley. Our objectives were to determine if timber management, elevation, or bear age affected den selection.

STUDY AREA

The study area included 2 sites of similar habitat located within the batture at the confluence of the White, Arkansas, and Mississippi River systems, in Desha and Phillips counties, Arkansas (Fig. 1). The Big Island and Montgomery Island site encompassed 12,340 ha of privately owned land that is intensively managed for commercial production of hardwood sawtimber. Our second site was 11,480 ha of the southeastern portion of the White River National Wildlife Refuge. White River National Wildlife Refuge supports more den trees because of conservative timber management (U.S. Fish and Wildlife Service unpublished forest management plan White River National Wildlife Refuge 1980, Smith 1985).

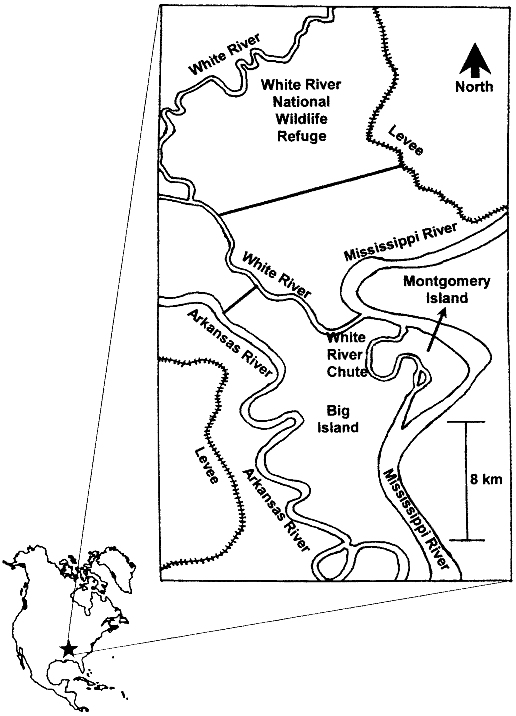

Fig. 1. Map of study sites for black bear denning study on Big Island and Montgomery Island, and White River National Wildlife Refuge, Arkansas, 1992–94.

Elevation ranged from 40.8 to 48.2 m above mean sea level. However, the average elevation was 0.7 m greater on Big Island and Montgomery Island than White River National Wildlife Refuge because of its close proximity to the Mississippi River main channel. This proximity caused the area to have more ridge and swale topography because of the alternate scouring and deposition action of floodwaters. Rivers separating study areas were from 200 to 1,600 m wide. The White River, about 200 m wide, was the only river adjacent to White River National Wildlife Refuge. In contrast, Big Island and Montgomery Island were adjacent to the Arkansas, Mississippi, and White Rivers. River depths, widths and current velocities varied seasonally, with a distinct spring flood pulse (Junk et al. 1989). Significant flooding occurred during 16.9% (185 days) and 22.3% (244 days) of study duration (1993–95) on Big Island and Montgomery Island, and White River National Wildlife Refuge, respectively. Duration of flooding was 31.9% greater on White River National Wildlife Refuge compared to Big Island and Montgomery Island because of the difference in mean elevations.

Principal overstory species on both sites included sugarberry (*Celtis laevigata*), American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*), sweet pecan (*Carya illionensis*), bitter pecan (*C. aquatica*), cottonwood (*Populus deltoides*), overcup oak (*Quercus lyrata*), nuttall oak (*Q. nuttallii*), black willow (*Salix nigra*), sycamore (*Platanus occidentalis*), persimmon (*Diospyros virginiana*), sweetgum (*Liquidambar styraciflua*), and bald cypress (*Taxodium distichum*; Wiseman 1982, Smith 1985). On White River National Wildlife Refuge, overcup oak and bitter pecan predominated, primarily because of their tolerance to frequent, prolonged flooding and heavy clay soils (Smith 1985). On Big Island and Montgomery Island, sassafras (*Sassafras albidum*) and honey locust (*Gleditsia triacanthos*) were locally abundant on sandy, well-drained ridges.

METHODS

Black bears were captured with modified Aldrich spring-activated foot snares (Johnson and Pelton 1980) during June–August from 1992 to 1994. Bears were equipped with mortality-sensitive radiocollars (Advanced Telemetry Systems, Isanti, Minnesota, USA) and released at the capture site. An upper first premolar was extracted from each bear and sent to Matson's Laboratory (Milltown, Montana, USA) for age estimation (Willey 1974). We tracked radiocollared females (n = 21) to winter dens and determined den type (tree or ground).

Dens were pooled by study area for statistical analyses. Difference in proportions of den types per study area was evaluated using a binomial Z-test for small samples (Siegel 1956). We used this test to determine if use of tree versus ground dens differed by area. Difference in proportions of den types between study areas was evaluated using a G-test (Sokal and Rohlf 1981).

We measured distance and bearing from distinct topographic features (e.g., road intersections, bayous) to plot den locations on U.S. Geological Survey 1:24,000 topographic maps and to determine den site elevation. We compared mean elevation of tree dens and ground dens using 2-sample t-tests. The relation between ground den elevations and age of ground-denning females was determined using Pearson product-moment correlation. We transformed age using natural logarithms (Sokal and Rohlf 1981:541).

Mississippi River stage data were acquired from the U.S. Army Corps of Engineers office in Vicksburg, Mississippi. We used data from the gauging station at Rosedale, Mississippi, located opposite the Big Island and Montgomery Island study areas about 20 km downstream from White River National Wildlife Refuge. The river bed slope from Rosedale, Mississippi, to the White River National Wildlife Refuge study area was negligible; thus, gauge reading from Rosedale provided an accurate measure of river stage of the White River at White River National Wildlife Refuge (W. Hill, US Army Corps of Engineers, Vicksburg, Mississippi, personal communication). Flood water elevations were derived from stage elevations and simultaneously adjusted for a low water reference plane of +1.34 m and gauge elevation of 33.15 m by adding 34.49 m to stage elevations. Based on river stage data and den elevation, the probability of inundation was calculated for each ground den during December–April (White 1996).

We used inundation probabilities as an index to survival because cub and den survival are likely correlated. We assumed that helpless cubs in an inundated den would perish. However, we acknowledge that as cubs age their vagility increases and that by mid- to late-April most cubs can escape flooding. The elevation at which survival probability for April asymptotically approached 0.90 was considered the critical elevation, below which ground dens were subject to inundation. We used April because for any given elevation, it had the greatest probability of inundation. Elevations with minimal April inundation probabilities provide greater protection from inundation during the remainder of the denning period. Finally, mean annual maximum and monthly maximum mean river stages were derived from historical river stage data and a stage duration table, respectively (U.S. Army Corps of Engineers, Vicksburg, Mississippi).

We determined mean elevation of White River National Wildlife Refuge, and Big Island and Montgomery Island by averaging point elevations at section centers and corners on 1:24,000 U.S. Geologic Survey topographic maps. We determined point elevations every 402 m along a north-south transect through the geographic center of each study site, then plotted comparative topographic profiles, and mean annual maximum and mean monthly maximum inundation levels.

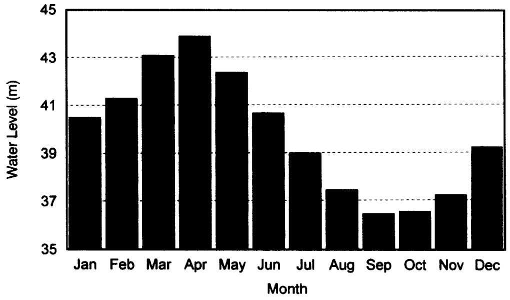

Fig. 2. Mean monthly stage of the Mississippi River at Rosedale, Mississippi, 1945–95.

RESULTS

We documented 35 female black bear dens on Big Island and Montgomery Island ($n = 12$), and White River National Wildlife Refuge ($n = 23$). Mean litter size was 2.6 cubs (range 1—3; 4 at Big Island and Montgomery Island; 3 at White River National Wildlife Refuge). Ground denning was more frequent ($G_1 = 31.06$, $P < 0.001$) on Big Island and Montgomery Island (83%) than on White River National Wildlife Refuge where females used tree dens exclusively. Use of the same cypress tree by the same female during 2 consecutive winters (1993, 1994) accounted for all observed Big Island and Montgomery Island tree dens. Most (9/10) ground dens were in debris (e.g., cut tree tops, log piles) resulting from timber harvests. All ground dens were excavated depressions (ca. 15–20 cm deep × 65–70 cm diam) lined with leaves, twigs, and other ground litter raked from the surrounding area.

Mean elevation differed between White River National Wildlife Refuge ($\bar{x} = 44.3$, SE = 0.15 m), and Big Island and Montgomery Island ($\bar{x} = 45.0$, SE = 0.18 m). Ground dens were located at higher ($t_{13} = -7.23$, $P < 0.001$) elevations ($\bar{x} = 46.5$, SE = 0.34 m) than ground level of tree dens ($\bar{x} = 43.7$, SE = 0.15 m). Moreover, ground den elevations ($\bar{x} = 46.5$, SE = 0.34 m) differed ($t_{73} = 2.92$, $P = 0.004$) from mean Big Island and Montgomery Island elevation ($\bar{x} = 45.0$, SE = 0.18 m). There was a positive relationship ($r = 0.71$, $P = 0.03$) between female age and ground den elevation.

The mean annual maximum and mean monthly maximum river stages for the study areas were 46.2 m and 44.0 m, respectively. Mean maximum monthly river stage occurred during April. Mean annual maximum river stage could occur during any month, but was most likely to occur during April based on historical data (1945–95; U.S. Army Corps of Engineers, Vicksburg, Mississippi). Inundation probability increased monthly during the denning period (Fig. 3). On both study sites, the critical elevation (90% probability of den survival), below which the probability of den inundation increased rapidly, was 47.0 m (Fig. 4).

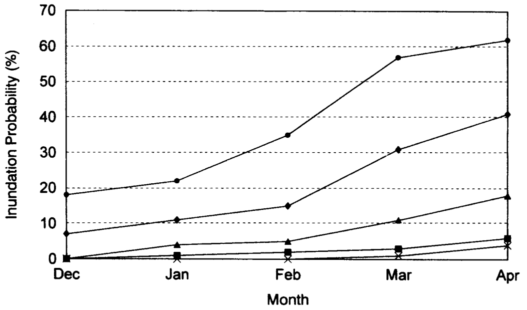

Fig. 3. Denning period inundation probabilities by month for 42.7 m (●), 44.2 m (♦), 45.7 m (▲), 47.2 m (■), and 48.8 m (x) on Big Island and Montgomery Island, and White River National Wildlife Refuge, Arkansas, 1992–94.

DISCUSSION

Smith (1985) and Oli et al. (1997) suggested that White River National Wildlife Refuge female black bears use aboveground tree cavities as natal dens to escape from seasonal flooding, and that den trees were vital to their reproductive fitness in bottomland hardwood forests. We found that successful black bear reproduction can also occur in bottomland hardwood forest that lack aboveground tree dens.

We identified 2 factors that were primarily responsible for differences in denning behavior and successful reproduction in both areas. First, because Big Island and Montgomery Island are intensively managed for timber production, few,

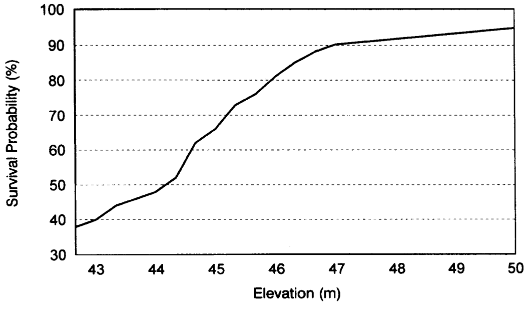

Fig. 4. Survival probabilities for ground dens during April at elevations of 43—50 m on Big Island and Montgomery Island, and White River National Wildlife Refuge, Arkansas, 1992–94.

if any, merchantable trees are allowed to develop decay-induced cavities. Exceptions included occasional large, hollow bald cypress trees scattered throughout Big Island. Conversely, management at White River National Wildlife Refuge focuses on wildlife habitat; thus, large cavity trees, particularly overcup oaks, are abundant (Smith 1985, Oli et al. 1997). It appears that female black bears chose tree dens when available. Alternatively, if tree dens are unavailable, female bears select ground-level dens in cover, such as logging debris.

Secondly, although the mean elevation difference was only 0.76 m, this was sufficient to increase ground-level inundation probability at White River National Wildlife Refuge by 42%. Mean ground elevation at White River National Wildlife Refuge den tree locations was 2.7 m lower than at Big Island and Montgomery Island ground dens. Accordingly, probability of ground-level inundation at White River National Wildlife Refuge was 3.6 times greater than at Big Island and Montgomery Island ground dens.

Although areas around tree dens are flood-prone, Smith (1985) found that the elevation of den chambers at White River National Wildlife Refuge ($\bar{x}$ = 47.0m) provided protection from flooding. Big Island and Montgomery Island ground dens at ≥46.3 m approximated the level of flood protection of tree dens at White River National Wildlife Refuge, and may facilitate similar reproductive success in each area. Tree dens may provide additional protection from extreme environmental conditions (Johnson et al. 1978, Smith 1985), human disturbance (Johnson and Pelton 1981), and intraspecific molestation (Lindzey and Meslow 1976) that ground dens do not provide.

The relationship between female age and elevation of ground dens suggested that successful ground denning involved a learned behavioral response to a variable environment. Therefore, younger, less experienced females may suffer more frequent losses of litters to inundation than older females. This could slow population growth by extending age of effective primiparity (Caughley 1977) and increasing the mean age of first successful reproduction. This effect may be especially pronounced in K-selected species such as black bear (Craighead et al. 1974, Eiler et al. 1989). For example, in this study, a primiparous 4-year-old female on Montgomery Island used a ground den at 44.8 m elevation that was inundated during early April 1993. The litter of ambulatory cubs survived, although elevations of her subsequent ground dens (n = 2) exceeded 46.3 meters. A 3-year-old female chose a ground den on the bank of the Mississippi River at 44.5 m elevation that was inundated during late February 1994. Although reproduction was not confirmed in the flooded den, her subsequent den sites (n = 2) were at elevations ≥46.3 m. Further, females >10 years old did not select any ground den site <46.3 m elevation.

Topographic differences unrelated to inundation may affect reproductive success on White River National Wildlife Refuge, and Big Island and Montgomery Island. Smith (1985: 106) documented the stranding of a female bear and her cubs in a tree for 2–4 weeks following a late-spring flood. Such floods also can delay development of important food plants (Noble and Murphy 1975, Smith 1985). At White River National Wildlife Refuge extensive areas were inundated with relatively small increases in river stage, whereas on Big Island and Montgomery Island, more of the area was above both the maximum monthly mean and mean annual maximum river stages (Fig. 3). At a river stage of 44.0 m (maximum monthly mean), Big Island and Montgomery Island was barely inundated, whereas nearly 40% of White River National Wildlife Refuge was flooded. The greater topographic relief at Big Island and Montgomery Island provided more and larger emergent ridges during flooding, which reduced the probability that post-emergent litters on Big Island and Montgomery Island would be stranded and provided access to spring vegetation before bears on White River National Wildlife Refuge.

MANAGEMENT IMPLICATIONS

In flood-prone habitats, forestry practices may influence denning ecology of female black bears. On Big Island and Montgomery Island logging reduces availability of potential den trees, but leaves cut tree tops, cull piles, and slash that can be used by bears for dens. To minimize the likelihood of den inundation on Big Island and Montgomery Island, loggers should concentrate slash at or above 46.3–47.0m. Minimizing logging debris at low (i.e., ≤45.1 m) elevations should reduce the probability that bears will choose flood-prone den sites. These management practices can be optimized by combining river stage, elevation, and forest planning data in a Geographic Information System (White et al. 1996). This would enable managers to rapidly and accurately identify optimal and suboptimal ground-denning sites. On flood-prone sites such as White River National Wildlife Refuge, maintaining and perpetuating extensive stands of overcup oak may be critical to long-term fitness of local black bear populations.

ACKNOWLEDGMENTS

This study was made possible by financial contributions of the U.S. Forest Service—Southern Hardwoods Lab, Mississippi Department of Wildlife, Fisheries and Parks through Federal Aid in Wildlife Restoration Funds (W-48, Study XXXXIII), Anderson-Tully Company, Boone and Crockett Club, U.S. Fish and Wildlife Service (Fish and Wildlife Foundation), Arkansas Nature Conservancy, Delta Wildlife Foundation, Tara Wildlife, and the Department of Defense (Mississippi Army Ammunition Plant). Anderson-Tully Company, Montgomery Island Hunting Club, and White River National Wildlife Refuge provided access to study sites and logistical support. The Norris Hunting Club and Donaldson Point Hunting Club provided additional field facilities. We thank N. Hunter of White River National Wildlife Refuge and M. Staten of Anderson-Tully Company for assistance. We also thank D. Jackson, S. Kaplan, D. Miller, M. Oli, C. Shropshire, B. Wade, and M. Weinstein for assistance with field work, and M. Chamberlain and B. Strickland for reviewing this manuscript. This manuscript (MS #—WF142) is a contribution of the Forest and Wildlife Research Center at Mississippi State University. We thank the Delaware Agricultural Experiment Station, Department of Entomology and Applied Ecology in College of Agricultural and Natural Resources at the University of Delaware for support during the editing phase of publication. Published as Paper No. 00-10-1682 in the Journal Series of the Delaware Agricultural Experiment Station.

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Received 1 October 1999.
Accepted 17 July 2000.
Associate Editor: Maehr.

EFFECTS OF TILLAGE ON LEAD SHOT DISTRIBUTION IN WETLAND SEDIMENTS

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Abstract: At Sacramento National Wildlife Refuge, California, we examined 2 types of deep tillage (disking and plowing) as possible management options for reducing lead pellet densities in wetlands. In addition, we examined the vegetation changes that resulted from tilling. Both disking and plowing moved lead pellets below the zone of availability for dabbling ducks (>10 cm). However, plowing moved a higher percentage of pellets into the 15–20-cm layer of sediment ($P = 0.02$). Similarly, plowing was more effective ($P = 0.04$) than disking or controls in redistributing pellets below the deeper zone of availability (>20 cm) for tundra swans (*Cygnus columbianus*). Maximum height of vegetation increased ($P < 0.001$) on tilled plots during the first and second year after treatment. Tillage initially reduced percent cover ($P = 0.03$) and density ($P < 0.001$) of swamp timothy (*Crypsis schoenoides*), but resulted in increased swamp timothy cover and stem density by the second year posttreatment. Percent cover by California loosestrife (*Lythrum hyssopifolium*) showed the opposite trend, with an initial increase ($P < 0.001$), followed by a decrease to levels similar to control plots in the second year. In certain managed wetlands, disking and plowing can be effective management tools for redistributing residual lead shot deeper into wetland sediments and potentially reducing waterbird mortality due to lead poisoning.

JOURNAL OF WILDLIFE MANAGEMENT 65(1):40–46

Key words: lead poisoning, lead shot, Sacramento National Wildlife Refuge, tillage, waterfowl, wetlands.

Avian lead poisoning has been a recognized problem for >100 years (U.S. Geological Survey 1999). Shot ingestion usually occurs when birds feed in hunted areas and inadvertently ingest spent lead pellets (Sanderson and Bellrose 1986). Diving ducks typically have the highest rates of lead pellet ingestion, followed by dabbling and grazing waterfowl (Sanderson and Bellrose 1986, Pain 1990). In some wetlands with soft sediments, little residual lead shot (at depths available to waterfowl) has been found from 1 year to the next (Mudge 1984). In areas underlain by hardpan clay layers, pellets are prevented from settling beyond the level of availability to ducks and swans, and may result in continued lead poisoning in these areas (Mudge 1984, Pain 1991). One such area appears to be the Sacramento National Wildlife Refuge in northern California.

Although non-toxic shot has been required

Forests of the Cumberland Mountains
Author(s): E. Lucy Braun
Source: *Ecological Monographs*, Vol. 12, No. 4 (Oct., 1942), pp. 413-447
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1943039
Accessed: 16-08-2014 20:30 UTC

FORESTS OF THE CUMBERLAND MOUNTAINS[1]

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University of Cincinnati

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[1] Abnormal cost of illustrations borne by author.

TABLE OF CONTENTS

FORESTS OF THE CUMBERLAND MOUNTAINS

INTRODUCTION

Mixed deciduous forest covers (or originally covered) almost all of the higher mountain section of southeastern Kentucky. This part of Kentucky, and smaller areas adjacent in Virginia and to the southwest in Tennessee comprise the Cumberland Mountains physiographic section, at the southeastern margin of the Appalachian Plateaus province. This is a strip nearly 150 miles long in a northeast-southwest direction, from about the Breaks of Sandy on Russell Fork of the Big Sandy River at the Kentucky-Virginia line, southwestward into Tennessee (see map, Fig. 1). The highest and most characteristic part is carved from a large block fault with more or less upturned edges which form the monoclinal mountains bordering this section—Pine Mountain along the northwest side and Cumberland and Stone Mountains on the southeast. The interior strongly dissected part, the syncline, includes Black Mountain and Little Black Mountain, the Log Mountains near Middlesboro, and other lesser mountains. The western (or northwestern) limits are fairly distinct in the northern half of the section where Pine Mountain prominently overlooks the adjacent Cumberland Plateau. Southward, the strongly dissected plateau rises to elevations approximately equal to those of the fault block mountains to the east, thus obscuring the structural limits. This higher exterior section may be included in the Cumberland Mountains.[2] In Kentucky, the boundary begins to diverge slightly from Pine Mountain south of Whitesburg, then swings westward from Pine Mountain between the Kentucky and Cumberland River drainage to about Williamsburg, including "Williamsburg Mountain" and "Jellico Mountain." The northeastern boundary of the Cumberland Mountains (from east of Norton to the Breaks of Sandy) is rather indefinite; there the Cumberlands merge into the high dissected plateau. The boundary between this northeastern part of the Cumberlands (and adjacent plateau) and the Ridge and Valley Province is, however, very pronounced.

Because of the structural features of the area and its physiographic history, a great variety of topographic situations and hence of habitats are included. Longitudinal streams have cut deep valleys paralleling the main structural features; most important of these is the Cumberland River and its major tributaries, Poor Fork, Martins Fork and Yellow Creek, and on the east side, Pound and Powell Rivers. Into these flow short lateral tributaries with steep gradients, streams which indent the mountain slopes, some forming broad and shallow coves, others, deep and narrow gorges. Such detail depends to a considerable extent upon the nature of the rock which is cut (and its dip); it affects the composition of the occupying forest. The strata of Cumberland and Stone Mountains on the one side, and of Pine Mountain on the other side, are dipping; those of the central mountain masses (Black and Log Mountains) and of the outlying section are nearly horizontal. The whole area, then, is a complex of mountains carved by erosion from horizontal strata (as Black and Log Mountains) and from more or less strongly dipping strata (Pine and Cumberland Mountains); of valleys worn down on weaker rocks between the principal mountains, valleys in which there are incipient floodplains and valley flats (Cumberland valley and its major tributaries); of short tributary valleys of steep gradient indenting the mountain slopes. Elevations range from about 1,000 feet along the Cumberland River near Pineville, 1,200 feet at Harlan, and 1,700 feet near Eolia in the upper Cumberland valley, to 3,100 feet on the Log Mountains, 3,000 to 3,400 on Cumberland Mountain, 2,500 to 3,000 or over on Pine Mountain (3,200 feet at High Rock), and up to 4,250 feet on Black Mountain at the Doubles in Harlan County (indicated by ∆ on map, Fig. 1).

The underlying rocks of the area all belong to the Pottsville series of the Pennsylvanian, with the exception of small areas along or near the Pine Mountain fault where older strata may be exposed. Limestone outcrops midway on the northwesterly slope of Pine Mountain and along the valleys bordering the area on the east. Eleswhere are sandstones and shales, and interbedded coal seams.

In valleys, and on the slopes of the mountains where the underlying rock is horizontal, is a deep soil mantle in most places scarcely or not at all reflecting the character of the underlying rock. Such soils generally are graybrownerths, the zonal soil type for the latitude. The humus layer is mull. Where sandstones outcrop on ridge crests or on the dip slope of Pine Mountain or of Cumberland Mountain, shallow sandy soils prevail, generally with a thin covering of mor (duff). Such soils are immature, and pronounced departure from the climatic vegetation type is seen.

No adequate picture of the climate of the area may be had from available weather data. Weather stations are few, and records have, with few exceptions, been kept but a short time. Middlesboro (with record for 40 years) would appear to be representative if one judged from its location within the area; however, the 51 inches annual precipitation there recorded gives no idea of what the rainfall on the Log Mountains but a few miles away and about 2,000 feet higher may be. On many a summer day when there is *no* rain at Middlesboro there is heavy rain on the mountains, sometimes even enough to

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[2] The term "Cumberlands" is often popularly used to include the entire Cumberland Plateau. The limits used in this paper are essentially those of the Cumberland Mountains physiographic section as defined by Fenneman, 1938.

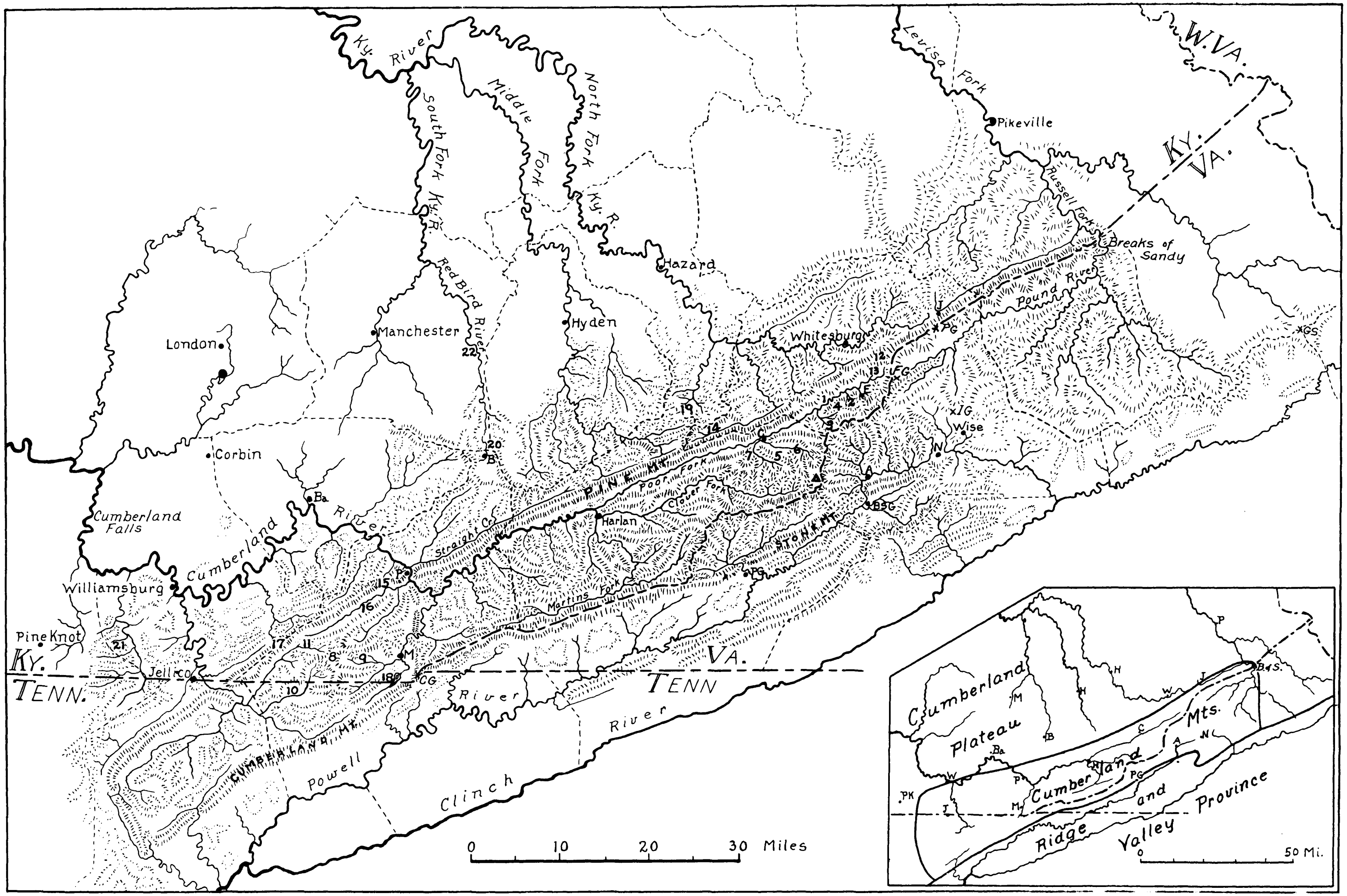

FIG. 1. Map of Cumberland Mountains and adjacent area. Inset map shows boundaries of physiographic provinces (after Fenneman). Δ—The Doubles, 4,250 ft.; *PG*—Pound Gap; *FG*—Flat Gap; *IG*—Indian Gap; *GS*—Gap of Sandy; *CG*—Cumberland Gap; A—Appalachia; B—Beverly; Ba—Barbourville; BSG—Big Stone Gap; C—Cumberland; E—Eolia; J—Jenkins; M—Middlesboro; N—Norton; P—Pineville (and Pine Gap); PG—Pennington Gap. Numbers refer to locations mentioned in the text.

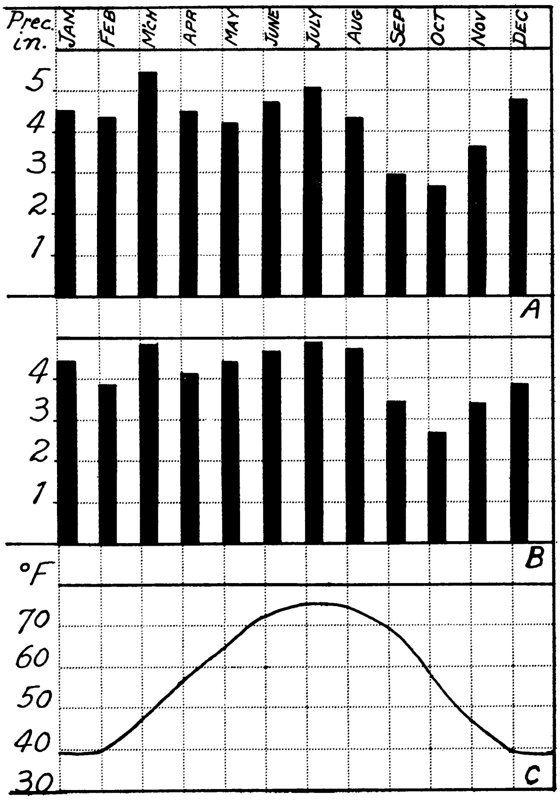

FIG. 2. A. Mean monthly precipitation at Middlesboro. B. Mean monthly precipitation at Williamsburg. C. Mean monthly temperature at Middlesboro.

bring streams out of their banks. As all stations in or at the borders of the Cumberland Mountains are in valleys, the data compiled in Figure 2, for Middlesboro and Williamsburg, are suggestive only. Middlesboro, at an elevation of 1,128 feet, has average annual precipitation of 50.92 inches; average annual temperature, 57° F.; highest and lowest recorded temperatures, 112° and —20° F.; average minimum for January, 27.5° F.; average maximum for July, 87.2° F.; frostless season, April 18 to October 18. Williamsburg, elevation 939 feet, has average annual precipitation of 49.12 inches; average annual temperature, 56.8° F.; highest and lowest recorded temperatures, 105° and —19° F.; average minimum for January, 27.3°; average maximum for July, 89°; frostless season, April 17 to October 21.

VEGETATION

The deciduous forest of the Cumberland Mountains is outstanding in its superlative quality. In number of tree species, in size of individuals, in variety of forest types it ranks as one of the finest deciduous forest areas of North America. The mixed mesophytic forest association is here at its best; nowhere else is it as well developed (Braun 1941). Variations in forest composition are related to differences in topography, elevation and soils and portray in greater or less degree the influence of these factors.

The extent of the area included here for consideration is not determined alone by physiographic boundaries, but also by vegetation. There are differences in complexity and luxuriance which affect the aspect of the forests of the Cumberland Mountains and adjacent Cumberland Plateau. Eastward, the transition to the Ridge and Valley Province is in places as sharp as the physiographic boundary. Agricultural utilization, because of fertile limestone soils in many of the valleys, accentuates the change in aspect.

The vegetation of the major topographic areas of the Cumberland Mountains will be considered separately.

The rapid decimation of forests due to recent increase in logging operations impels the writer to make available data on forest composition, for it is a matter of but very few years before no more can be obtained. Most of the area described by Braun (1940) in "An ecological transect of Black Mountain, Kentucky," has since been logged. Most of the areas for which percentage composition of canopy is given in this paper are no longer uncut; this is noted in each case. Virgin forest of any extent is all but gone. The present paper is extensive rather than intensive. It includes observations made during ten field seasons, comprising over twenty weeks in the field.[3] Although there are sections in the 5,000 or more square miles included in the Cumberland Mountains which were not visited, most of the area was traversed. The examples used for illustration are selected from the best and most representative areas. The emphasis throughout is on *original* forest. The desirability of more detailed statistical studies than are included here is recognized; the extent of the area and the inaccessibility of the best sites (and later their destruction) precluded this. Frequent visits to places 5 or 10 miles from any highway are difficult; when highways came, the forest went.

THE CENTRAL MOUNTAIN AREA: BLACK MOUNTAIN AND LOG MOUNTAINS

The dominant feature of both Black and Log Mountains is the splendid mixed deciduous forest of the mountain slopes. Apparently the whole synclinal area is mixed forest, for here where underlying strata are horizontal there is generally deep soil, in contrast to the shallow soil over the dipping strata of the bordering mountains. Composition of the forest varies in relation to slope exposure and, to some extent, to altitude. On southerly exposures, especially at low elevations, white oak and beech are numerically most important; on narrow ridge crests or very steep south or southwesterly slopes, some variant of an oak-chestnut community may prevail; elsewhere the mixed mesophytic forest in which bass-

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[3] Grateful acknowledgment is made for grants, from the American Association for the Advancement of Science in 1932 and the National Research Council in 1934-35, for aid in these field studies.

wood, sugar maple, tulip tree, buckeye, beech, chestnut, and red oak are most abundant is seen. Even on south slopes, unless convex, or at very low elevation, enough of the characteristic trees of the mixed mesophytic forest occur to give a decidedly mixed aspect. This is most strikingly seen during the period of fall coloration when the great number of species of the mixed forest assume different hues. Then, the small area occupied by the oak-chestnut forest is most apparent.

Some altitudinal sequence of forest types is discernible. Beech and white oak may be numerically important constituents of forest communities at elevations below about 2,000 feet. Above this elevation they are absent (except that they reappear at nearly 4,000 feet), and other constituents of the mixed mesophytic forest, especially basswood, buckeye, sugar maple, and tulip tree, are proportionately more abundant. Above 2,000 feet, sugar maple becomes increasingly abundant (Fig. 8). At elevations of about 3,700 feet, the admixture of birch and cherry and the reappearance of beech, introduce a new forest aspect. This may be seen only on the highest slopes of Black Mountain (Fig. 7).

Studies made in various parts of the mountains serve to demonstrate the variations in type of forest developing in different habitats. The central mountain area may be divided conveniently into two sections, separated by the north-south line connecting Pineville (or Pine Gap in Pine Mountain) and Cumberland Gap (see map, Fig. 1). To the northeast are the Black Mountains of which Black Mountain and Little Black Mountain are most important (Fig. 3). To the west are the Log Mountains (Fig. 11).

BLACK MOUNTAIN

In a previous paper, most of the forest communities of Black Mountain have been considered (Braun 1940). There remain, however, a few distinct communities poorly or not at all represented in the area there treated (those of lowest and of highest slopes) and certain areas of lesser importance, topographically young, and hence vegetationally different.

Forests of Low Elevations

On southerly slopes (southeast to southwest), a beech-white oak forest type prevails. This generally is poorly preserved, for it is adjacent to cleared and farmed valleys; its white oak generally was cut for farm buildings or for mine props; it now is often overrun with hogs. There are remnants, however, which clearly indicate the widespread occurrence in suitable habitats of this forest type, a type considered in greater detail in connection with the vegetation of the "Monoclinal Borders," where, on the slopes

FIG. 3. View of Black Mountain from Pine Mountain about ten miles above Cumberland. Pines in foreground on a sandstone outcrop; the valley indenting the slopes of Black Mountain is that of Colliers Creek.

of Limestone Creek (location 17 on map, Fig. 1) good examples remain and in the "Vegetation of Pine Mountain" (Braun 1935), along Line Fork on slopes opposing Pine Mountain (location 14 on map). In places beech is dominant, and Rhododendron and Kalmia form a lower layer. This variant, which appears on the lower slopes of Benham Spur, may be related to a sandstone horizon.

White oak is abundant at the lower elevations not only in the white oak-beech type of warmer slopes, but also in ravine and cove forests with hemlock. This is well illustrated in the lower part of the valley of Colliers Creek in Letcher County.

Lower elevation cove forest; hemlock and white oak abundant; Colliers Creek, Letcher County.

	Percent
Tsuga canadensis, hemlock	42
Quercus alba, white oak	28
Acer rubrum, red maple	11
Quercus borealis maxima, northern red oak	6
Fagus grandifolia, beech	5
Magnolia Fraseri, mountain magnolia	3
Aesculus octandra, buckeye	2
Castanea dentata, chestnut	2
Betula allegheniensis,[4] birch	1

Mixed mesophytic forest of lower elevations of valleys; white oak one of the important species; Colliers Creek.

	Percent
Liriodendron tulipifera, tulip tree	17
Fagus grandifolia, beech	16
Castanea dentata, chestnut	16
Tsuga canadensis, hemlock	13
Acer rubrum, red maple	10
Quercus alba, white oak	7
Quercus borealis maxima, northern red oak	5
Juglans nigra, walnut	3
Juglans cinerea, butternut	3
Nyssa sylvatica, sour gum	3
Magnolia Fraseri, mountain magnolia	3
Betula allegheniensis, birch	2
Aesculus octandra, buckeye	1
Carya sp., hickory	1

In the first of these examples, white oak is an important constituent in the cove hemlock forest, where the great density of canopy almost eliminates ground vegetation. In the second, it is one of the important constituents of the mixed mesophytic forest of the lower elevations of valleys on the slopes of Black Mountain.[5]

On northerly slopes, at low elevations, white oak is absent; beech is proportionately more abundant, generally constituting about 50 percent of a forest in which several other mesophytes make up most of the rest of the canopy. In one place, on lower north slopes in Cave Branch of Cloverlick Creek (location 7 on map), sugar maple is second in abundance to beech, although certainly not of sufficient abundance to be thought of as codominant with the beech. This is the only place seen in the entire Cumberland Mountains in which there is any approach toward what could be termed a beech-maple forest.

Forest of Cave Branch of Cloverlick Creek, Harlan County.

	Percent
Fagus grandifolia, beech	50
Acer saccharum, sugar maple	16
Liriodendron tulipifera, tulip tree	10
Tilia heterophylla, basswood	8
Aesculus octandra, buckeye	5
Castanea dentata, chestnut	5
Magnolia acuminata, cucumber tree	6
Betula allegheniensis, birch	
Betula lutea, yellow birch	
Carya sp., hickory	
Nyssa sylvatica, sour gum	

Many constituents of the mixed forest are present, including the highly characteristic *Tilia heterophylla* and *Aesculus octandra,* and in both canopy and understory there are species of southerly range. The herbaceous layer of this forest is the rich and varied sort with an abundance of ferns, which is found in all good areas of mixed mesophytic forest.

In secondary areas at lower elevations, white oak is often very prominent on southerly slopes. Tulip tree generally forms pure stands on northerly and easterly slopes, unless erosion has been active.

Forests of High Elevations

The highest elevation in the Cumberland Mountains, 4,250 feet, is reached at the Doubles on Black Mountain in Harlan County (Δ on map, Fig. 1). At these highest elevations, the admixture of birch gives a different aspect to the forest. Topographic situation—flat or narrow ridge top, or slope—and direction of slope greatly affect the composition of forest canopy and understory. (For composition of summit types, other than those of highest elevations, see Braun 1940, p. 229, Fig. 20.)

The summit forest was[6] prevailingly oak-chestnut, with *Castanea dentata, Quercus borealis maxima,* and *Quercus montana* the dominant trees (Fig. 4). Red oak is much more abundant in this summit oak-chestnut forest than in the oak-chestnut of lower elevations. It reaches larger size than other trees of the summit forest, sometimes 4 feet or more in diameter. Locally, sugar maple, birch, cucumber, red maple, and occasional beech were also present. Parts of this summit oak-chestnut forest had a prominent heath layer with the evergreen *Kalmia latifolia* abun-

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[4] It is possible that some *B. lenta* is included; however, those trees of which fruiting branches were obtained are best referred to *B. allegheniensis* on a basis of fruit-bract characters.

[5] This is somewhat comparable to area I of the ravine slopes of Joe Day Branch, previously considered, *loc. cit.,* 1940, p. 209.

[6] The word "was" is used intentionally. When the area was first visited in August, 1931, there was no indication of disturbance of any sort. The chestnut blight was not apparent. The next year, its presence was noted, and by 1935, when the area was next visited, all the chestnut was about dead. Then, the dead chestnut was cut out. The added light reaching lower layers of the forest was soon reflected in vigorous growth of chestnut sprouts, of young chestnut oak, and other saplings, and in many places of blackberries. The aspect was greatly changed, for instead of the rather open growth of reproduction and luxuriant shrub and herbaceous layers, there came to be a dense low woody growth which greatly crowded the forest shrubs and herbs. Recently, the entire area has been logged. Hence no high elevation forest remains. For this reason, more details concerning lower layers of these summit and upper slope forests is given than for other Black Mountain areas treated in this paper. The dominance of the three tree species mentioned was so obvious, that unfortunately no counts were made from which to determine actual percentage composition of canopy.

FIG. 4. Oak-chestnut forest of summit of Black Mountain near the Doubles. Photograph taken Oct. 6, 1931, before blight affected chestnut.

FIG. 5. Red azalea (in bloom) and cinnamon fern in oak-chestnut forest of summit of Black Mountain near the Doubles. June 30, 1932.

dant; in places was a dense shrub layer in which the deciduous heaths, *Vaccinium pallidum, V. simulatum,* and especially the red azalea *(Rhododendron cumberlandense)*[7] prevailed, along with other shrubs and understory trees (Fig. 5). Elsewhere, there was no shrub layer, although of course scattered shrubs were present. In places, particularly on spur ridges, a massive sandstone outcrops; this locally affects the vegetation.

Shrubs and small tree species of the summit forest are:

Pyrularia pubera
Hydrangea arborescens
Hamamelis virginiana
Amelanchier canadensis
Amelanchier laevis
Crataegus macrosperma
Rubus canadensis
Ilex monticola
Acer pennsylvanicum
Kalmia latifolia
Rhododendron cumberlandense
Rhododendron maximum
Vaccinium pallidum
Vaccinium simulatum
Sambucus racemosus
Viburnum acerifolium

The herbaceous layer contains a large number of species, some of which are generally distributed, others very local. The spring (late May) aspect of the summit was emphasized by the many flowers of which *Geranium maculatum* and *Ranunculus hispidus* are very abundant. Later the abundance of cinnamon fern *(Osmunda cinnamomea)* is striking (Fig. 5). Locally, in or near heath areas, *Trillium undulatum* is found.

Herbaceous plants of the summit oak-chestnut forest are:

Aspidium marginale
Aspidium noveboracense
Aspidium spinulosum
Asplenium acrostichoides
Asplenium angustum
Dicksonia punctilobula
Osmunda cinnamomea
Osmunda Claytoniana
Polystichum acrostichoides
Pteris aquilina
Agrostis perennans
Panicum latifolium
Poa cuspidata
Carex aestivalis
Carex allegheniensis
Arisaema triphyllum
Clintonia umbellulata
Disporum lanuginosum
Erythronium americanum
Lilium canadense
Lilium superbum
Medeola virginiana
Smilacina racemosa
Smilax herbacea
Trillium erectum
Trillium grandiflorum
Trillium undulatum
Uvularia perfoliata
Cypripedium acaule
Cypripedium parviflorum var. *pubescens*
Stellaria pubera
Anemone lancifolia
Cimicifuga americana
Cimicifuga racemosa
Clematis viorna
Ranunculus abortivus
Ranunculus hispidus
Ranunculus recurvatus
Thalictrum dioicum
Caulophyllum thalictroides
Podophyllum peltatum
Sanguinaria canadensis
Dentaria laciniata
Sedum ternatum
Aruncus sylvester
Amphicarpa monoica
Geranium maculatum
Impatiens pallida
Hypericum pseudomaculatum
Viola blanda
Viola canadensis
Viola emarginata acutiloba
Viola hastata
Viola palmata
Viola rotundifolia
Viola scabriuscula
Aralia racemosa
Angelica Curtisii
Thaspium aureum atropurpureum
Lysimachia quadrifolia
Steironema intermedia
Gentiana decora
Asclepias phytolaccoides
Hydrophyllum virginianum
Monarda clinopodia
Pedicularis canadensis
Conopholis americana
Houstonia purpurea
Campanula divaricata
Lobelia inflata
Aster cordifolius
Aster divaricatus
Eupatorium purpureum
Eupatorium urticaefolium
Helianthus microcephalus
Solidago Curtisii

The oak-chestnut summit forest extended a short distance down southwesterly slopes (toward head of Clover Fork) before giving way to the mixed forest of upper slopes.

	Percent
Castanea dentata	47
Quercus borealis maxima	21
Magnolia acuminata	11
Acer rubrum	7
Quercus alba	6
Nyssa sylvatica	3
Fagus grandifolia	3
Betula allegheniensis	2

In the understory were the same species (again with red oak and chestnut most abundant) and wild cherry *(Prunus serotina)* and sourwood *(Oxydendrum arboreum),* the former of which happened to be lacking in the canopy in this area. Slightly lower, the aspect becomes more mesophytic, although the forest is very similar. Beech is generally a constituent of this forest.

On northerly slopes, at the head of Looney Creek (location 6 on map), a mixed mesophytic forest in which sugar maple is abundant ascends to the summit (Fig. 6). Here birch is also a frequent constituent of the forest (Fig. 7). The admixture of black cherry suggests the approach here to the altitudinal band in the Great Smoky Mountains in which cherry is so important as to be referred to locally as the "cherry orchards."

	Percent
Acer saccharum	46
Betula allegheniensis	18
Aesculus octandra	7
Tilia heterophylla	6
Castanea dentata	6
Fagus grandifolia	4
Prunus serotina	3
Quercus borealis maxima	3
Fraxinus americana	2
Acer rubrum	2
Magnolia acuminata	2

This upper north slope forest was a magnificent forest of large trees, many reaching heights well over 100 feet and trunk diameters of 3 or 4 feet.[8] Tree branches above about 50 feet are covered with lichens, especially conspicuous being *Usnea barbata.* This reflects the influence of the band of mist which

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[7] The azalea referred to in previous papers (Braun 1935, 1940) as "red azalea" has since been described as *Rhododendron cumberlandense* (Braun 1941a).

[8] A fallen ash 40 inches d.b.h. was measured which was 70 feet to the first small branch, and 100 feet to where the trunk gave off the first large branches; a fallen birch measured 100 feet from base into small branches.

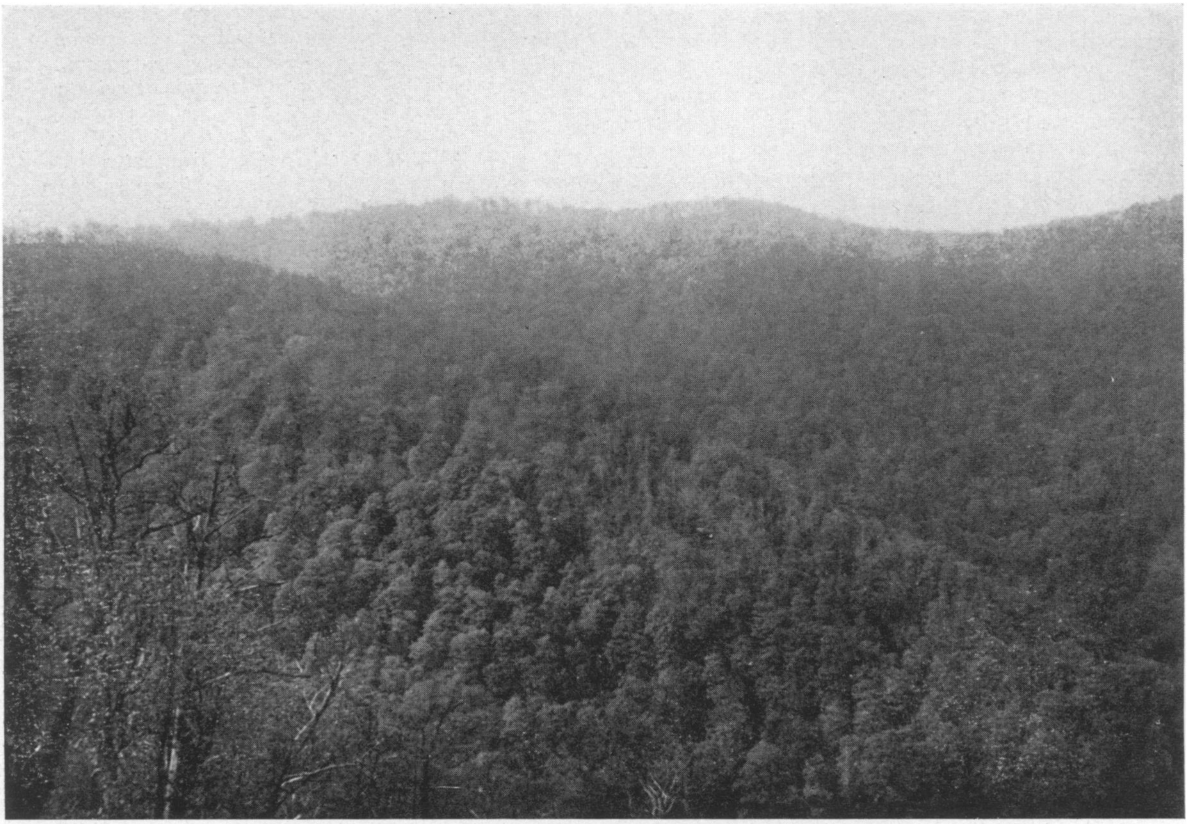

FIG. 6. View of Black Mountain at the head of Looney Creek. All slopes covered with mixed mesophytic forest. The open appearance of the forest along the skyline is due to season; the oaks and chestnut of the summit forest at 4,000 ft. have not come into leaf, although the slope forests are in full leaf. May 24, 1932.

FIG. 7. Forest of the north slope at the head of Looney Creek. The nearer trees are birch. May 23, 1932.

frequently hangs about the upper mountain slopes. A luxuriant and beautiful herbaceous layer, in which are included a few northern and high Alleghenian species, helped to make this one of Black Mountain's most beautiful forests. Here was the only known Kentucky station for *Streptopus roseus* var. *perspectus*. This herbaceous layer included:

Adiantum pedatum
Aspidium noveboracense
Aspidium spinulosum
Asplenium acrostichoides
Phegopteris hexagonoptera
Arisaema triphyllum
Allium tricoccum
Disporum lanuginosum
Disporum maculatum
Erythronium americanum
Medeola virginiana
Melanthium parviflorum
Smilacina racemosa
Streptopus roseus perspectus
Trillium erectum
Trillium grandiflorum
Habenaria psycodes
Orchis spectabilis
Laportea canadensis
Asarum canadense
Stellaria pubera
Actaea alba
Anemone quinquefolia
Delphinium tricorne
Hepatica acutiloba
Caulophyllum thalictroides
Podophyllum peltatum
Dicentra canadensis
Dentaria diphylla
Dentaria laciniata
Mitella diphylla
Tiarella cordifolia
Oxalis montana
Impatiens pallida
Viola affinis
Viola blanda
Viola canadensis
Viola scabriuscula
Osmorhiza longistylis
Hydrophyllum virginianum
Collinsonia canadensis
Monarda clinopodia

The dominance of plants belonging in a mull humus layer is evident.

With only slight variations, this forest extends down to the sugar maple-basswood-buckeye forest which is so predominant at middle elevations in the Cumberland Mountains (see forest of Joe Day Branch, Black Mountain, *loc. cit.*, pp. 212, 213; location 2 on map, Fig. 1 of this paper).

Transition to sugar maple-basswood-buckeye forest, near summit at head of Rogers Fork of Colliers Creek (location 3 on map).

	Percent
Acer saccharum	40
Tilia heterophylla	19
Quercus borealis maxima	13
Aesculus octandra	7
Prunus serotina	7
Castanea dentata	7
Betula allegheniensis	3
Magnolia acuminata	3
Fraxinus americana	1

Typical sugar maple-basswood-buckeye forest, Colliers Creek.

	Percent
Acer saccharum	36
Aesculus octandra	25
Tilia heterophylla	23
Liriodendron tulipifera	4
Carya sp.	3
Fraxinus americana	3
Quercus borealis maxima	2
Castanea dentata	4
Magnolia acuminata	
Juglans cinerea	
Juglans nigra	
Betula allegheniensis	
Magnolia Fraseri	

FIG. 8. Sugar maple is dominant in this forest on the upper slopes of Black Mountain near the head of Colliers Creek. May 4, 1934.

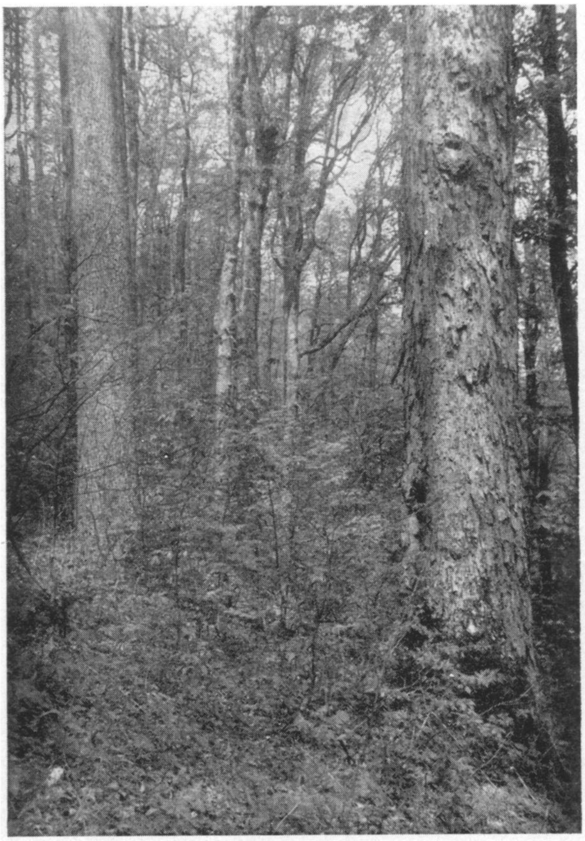

FIG. 9. Sugar maple-basswood-buckeye forest of middle elevations on Black Mountain, near the head of Colliers Creek. Large sugar maple to right, tulip tree to left, and buckeye and sugar maple beyond. May 4, 1934.

The aspect of the transition forest, in which sugar maple may be dominant, and of the sugar maple-basswood-buckeye forest is illustrated by Figures 8, 9 and 10.

River Bluffs

As a result of lateral planation, spurs of Black Mountain are in places truncated, and a topographically young habitat produced. Where actual cliffs are formed, various rock plants occur. Even the steepest slopes, if a little soil has accumulated, support an assemblage of tree species—usually young individuals—indicating the early establishment of mixed mesophytic forest. Hemlock is generally a constituent of the forest of these truncated faces. Where more massive rock is exposed, heath shrubs are conspicuous.

LOG MOUNTAINS

To the west of Middlesboro the Log Mountains rise to elevations a little over 3,000 feet (Fig. 11). As on Black Mountain, some phase of mixed mesophytic forest prevails except on the most xeric situations. The highest altitude types of Black Mountain are lacking, the sugar maple-basswood-buckeye type extends almost to the top on mesic slopes. Locally, red oak is abundant, especially at the highest eleva-

FIG. 10. Basswood and sugar maple in the sugar maple-basswood-buckeye forest on Black Mountain near the head of Colliers Creek.

FIG. 11. View of the Log Mountains with the cleared valley of Laurel Fork in the foreground. The forest areas represented by chart, Figure 12, are on the upper slopes.

tions where it mixes with the sugar maple-basswood-buckeye forest and with the chestnut of the summit ridges, and on mesic southerly slopes above about 2,500 feet. The accompanying chart, Figure 12, is designed to show the shift in dominance with changing slope exposure, and the abundance of white oak and beech on south slopes (7 of chart) at slightly lower elevations (location 8 on map, Fig. 1).

In luxuriance of herbaceous layer the mixed mesophytic forest of the Log Mountains is comparable to that of Black Mountain. Apparent exceptions are due to the rooting by hogs, which in many sections of the mountains have roamed more or less at will for perhaps a century or more. Where the herbaceous layer appears poor, if a habitation is near (within a half-mile or a mile), and if there is no "hog law" which requires confinement of these animals, hogs are the cause.

The forest of the lower mountain slopes is, on the drier southern exposures, the beech-white oak type (seen along the slopes of Yellow Creek, location 9, and of Clear Fork, location 10). On more mesic lower slopes is a more typical mixed mesophytic association with beech, white oak, sugar maple, basswood, buckeye, tulip tree, and a sprinkling of other species. Wherever white oak becomes abundant, basswood is less prominent.

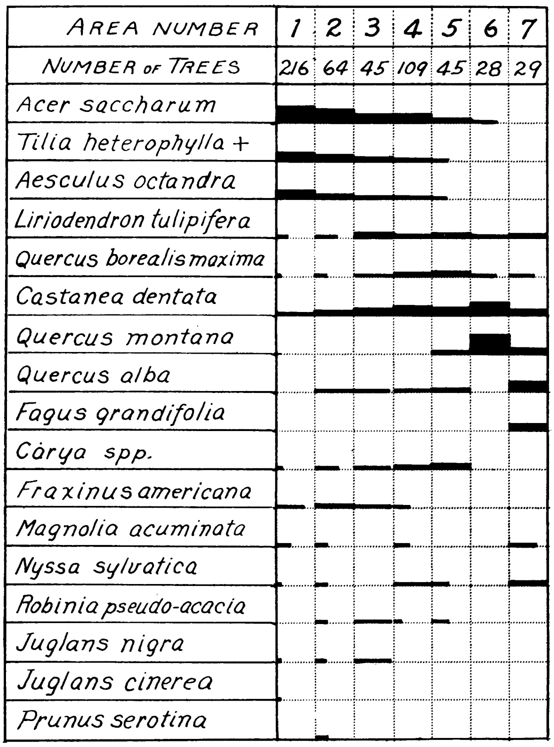

FIG. 12. Percentage composition of canopy of forest communities on Log Mountains near head of Laurel Fork (location 8 on map, Fig. 1). The direction of slope shifts around the head of the valley, from north in areas 1 and 2 to south in area 7. Area 4 extends higher up the slopes than do other areas, approaching a ridge crest; area 6 illustrates a convexity of slope; area 7 is nearly 1,000 ft. lower than the upper part of area 4. (In all the charts, percentages are shown by solid black portion of square; percentages less than 5, by bars reaching a proportionate distance across the base line.)

On lower northerly exposures, where slopes are very gentle, beech may be dominant and the aspect approach that of the beech consociation of valley flats which is of frequent occurrence in the area of the mixed mesophytic forest. A forest in Laurel Fork (location 11 on map) is of this type (Fig. 13).

	Percent
Fagus grandifolia	58
Quercus alba	9
Liriodendron tulipifera	8
Acer rubrum	7
Castanea dentata	6
Nyssa sylvatica	5
Tilia heterophylla	7
Tsuga canadensis	
Quercus borealis maxima	
Acer saccharum	
Magnolia acuminata	
Carya ovata	

Rhododendron maximum is prominent near the streams. In some ravines, hemlock is abundant; its occurrence bears little or no relation to slope exposure.

In general the forest of the Log Mountains, like that of Black Mountain, is mixed mesophytic throughout, except as interrupted by tongues of oak-chestnut forest on the driest ridges. The mixed mesophytic forest with beech prevails at lower elevations; higher, the sugar maple-basswood-buckeye type prevails.

THE MONOCLINAL BORDERS: PINE, CUMBERLAND, AND STONE MOUNTAINS

The most striking feature of the inner (dip) slopes of Pine and Cumberland Mountains is the large amount of pine in some parts of the forest. This interruption to the prevailing deciduous forest is correlated with shallow sandy soils overlying the dipping sandstone strata. Pine is more conspicuous on Pine Mountain, where the direction of the dip slope is southeast, than on Cumberland Mountain, where the northwesterly direction of the slope to a slight extent offsets the effect of shallow soils. Wherever deeper soils accumulate, deciduous forest dominates.

The steeper scarp slopes of both these mountains, the northwest slope of Pine Mountain, the southeast slope of Cumberland Mountain, support deciduous forest. That on Pine Mountain is of a more luxuriant type, due to the northwesterly direction of the slope which increases its mesophytism. However, the southeast slope of Cumberland Mountain appears to have been covered with mixed mesophytic forest, perhaps with a higher percentage of oaks and hickories. In contrast to the corresponding scarp slope of Pine Mountain, forests of Cumberland Mountain are almost entirely secondary, due doubtless to ease of access from the adjacent agricultural valleys.

PINE MOUNTAIN

The dip slope of Pine Mountain almost everywhere descends to longitudinal valleys skirting its southeastern base. From the valley, or from the opposing mountain sides, this slope of Pine Mountain seems to be very uniform, and more or less horizontally banded with pine and deciduous forest. However, it is deeply cut by transverse streams whose valleys in places are deep gorges, in others widen into deep pockets or even open troughs. Although such valleys open to the south, they are always well watered and their forests present astounding contrasts to the apparently continuous xeromesophytic forest of the dip slope. Many of the features of the vegetation of Pine Mountain have already been treated by the writer.[9] Additional studies south of the gap at Pineville substantiate the general features previously described and add new data. In Kentucky Ridge State Park[10] are some remarkably well preserved remnants of forests in ravines of the dip slope. It is possible, with few interruptions, to get the sequence from mountain summit down into deep hemlock gorges (location 15 on map). Minor streams here do not have longitudinal sections in troughs high on the mountain as is more generally true farther north on Pine Mountain (Braun 1935). Instead, they may follow a fairly direct course down the mountain. Near the head of such a stream, the ravine is little more than a concavity on the south slope. Lower, it cuts into the sandstone, which in places stands as almost vertical cliffs. There is a pronounced change in forest composition correlated with this change in character of the ravine, a change from oak forest to one in which hemlock is the most abundant species. Occasional forest areas of south exposure on the slopes of the ravine are comparable in composition to the forest of the ravine head. In the deeper parts of such ravines are magnificent forests, about half hemlock, with a wealth of *Rhododendron maximum*. *Stewartia pentagyna* is abundant anywhere that hemlock and Rhododendron do not prevail. One of these areas is known as "Hemlock Gardens." From the lower opposing slopes of Clear Creek (location 16 on map) none of these features are noticeable. There seems to be scarcely a break in the oak-pine slope.

A study of representative areas in the several communities distinguished illustrates the differences in canopy composition and the change from the oak-chestnut forest of the upper mountain slopes to the hemlock forest of gorges (Fig. 14). The understory

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[9] "Vegetation of Pine Mountain, Kentucky" (1935). The specific features of vegetation described in this paper are based on observations in Letcher and Harlan counties.

[10] Kentucky Ridge State Park is on Pine Mountain south of Pineville, *not* on "Kentucky Ridge" which extends north and west from Pine Mountain north of Pineville and is the divide between the Kentucky and Cumberland River drainage.

FIG. 13. Beech forest of Laurel Fork in the Log Mountains. June 23, 1935.

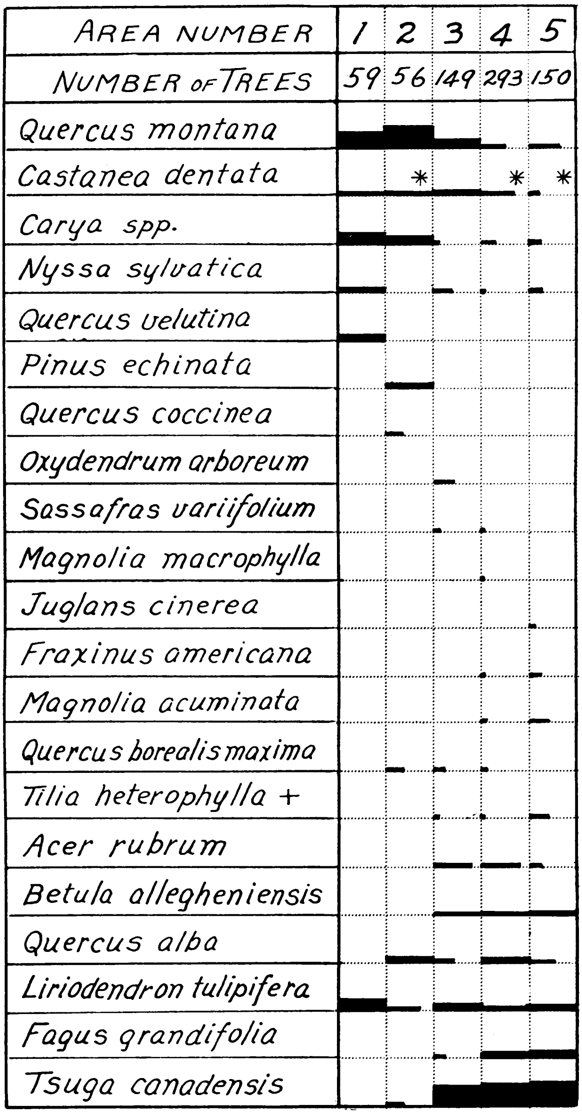

FIG. 14. Percentage composition of canopy of forest communities in Kentucky Ridge State Park on Pine Mountain near Pineville (location 15 on map). Illustrates change from oak-chestnut forest of upper mountain slopes to hemlock forest of gorges. Areas 1 to 4 in sequence from head of ravine down into "Hemlock Gardens"; area 5 in another nearby ravine. Asterisk in chart indicates that dead chestnut may have been removed. See also Table 1.

in all cases is similar to the canopy. The great difference between shrub and herbaceous layers of the several communities is evident from the lists (Table 1); areas 1 and 2 belong to the oak-chestnut forest and have nothing in common with the more mesophytic communities, areas 3, 4, and 5. However, these mesophytic forest communities differ strikingly in their herbaceous layer from the luxuriant mixed mesophytic forests of Black and Log Mountains (*cf.* lists, pp. 421, 422 and Braun 1940).

The "summit" of Pine Mountain is almost everywhere the broken edge of a dipping stratum which forms cliffs at the top of the scarp slope. There are no summit ridges in the same sense that these occur on Black and Log Mountains. There is, of course, variation in the sharpness of this contact between dip and scarp slopes, and there are few nearly level summit areas, generally in the vicinity of gaps (Fig. 15). Where prominent cliffs occur, there may be almost no forest vegetation along the mountain crest (as at High Rock, location 12 on map; *loc. cit.* 1935). Generally, however, there is an open oak or oak-pine forest in which the following trees may occur:

Quercus coccinea
Quercus falcata
Quercus marilandica
Quercus montana
Quercus stellata
Quercus velutina
Castanea dentata
Pinus rigida
Pinus virginiana
Carya alba
Carya glabra
Oxydendrum arboreum

Every crack in the cliffs is occupied by shrubs, most prominent of which are *Rhododendron maximum, Rhododendron catawbiense, Kalmia latifolia, Vaccinium* spp., *Gaylussacia baccata,* and in places, *Philadelphus hirsutus.* On less extreme parts of the summit, tulip tree, walnut and shell-bark hickory occur in a chestnut oak forest.

The scarp slope (northwest slope) of Pine Mountain is almost an unbroken slope, everywhere sup-

FIG. 15. Open chestnut oak forest of flat-topped part of summit of Pine Mountain about 15 miles southwest of Pineville.

TABLE 1. Undergrowth of forest communities shown in Figure 14, illustrating contrast between oak-chestnut communities of upper slopes (areas 1, 2) and ravine forests in which hemlock is a dominant (areas 3, 4, 5).

UNDERSTORY TREES, CANOPY SPECIES	1	2	3	4	5
Quercus montana	X	X	X		
Castanea dentata	X	X			
Carya spp.	X	X	X		
Nyssa sylvatica	X	X			
Quercus velutina	X				
Pinus echinata		X			
Quercus coccinea		X			
Quercus borealis maxima		X	X		X
Oxydendrum arboreum	X	X		X	X
Sassafras variifolium		X	X		
Magnolia macrophylla				X	X
Juglans cinerea					X
Fraxinus americana					X
Magnolia acuminata			X	X	X
Tilia heterophylla					X
Acer rubrum	X	X			X
Betula alleghaniensis			X	X	X
Quercus alba		X			
Liriodendron tulipifera		X	X	X	
Fagus grandifolia				X	X
Tsuga canadensis			X	X	
UNDERSTORY TREES, NOT IN CANOPY					
Robinia Pseudo-Acacia	X	X	X		
Diospyros virginiana		X			
Amelanchier canadensis		X	X		
Cornus florida		X	X	X	X
Ilex opaca			X	X	
Magnolia tripetala			X	X	X
Juglans nigra					X
Cladrastis lutea					X
SHRUBS AND WOODY CLIMBERS					
Aralia spinosa				X	X
Benzoin aestivale					X
Bignonia capreolata					X
Ceanothus americanus		X			
Clethra acuminata			X	X	X
Evonymus americanus					X
Hamamelis virginiana			X		X
Hydrangea arborescens			X		X
Kalmia latifolia		X	X	X	
Psedera quinquefolia					X
Rhododendron cumberlandense	X		X		
Rhododendron maximum			X	X	X
Rhus Toxicodendron					X
Rubus sp.			X		X
Sambucus canadensis					X
Smilax glauca	X				
Stewartia pentagyna			X	X	X
Vaccinium sp.	X	X			
Vaccinium stamineum	X	X	X		
Vaccinium vacillans	X	X	X		
Viburnum acerifolium					X
Vitis aestivalis		X			
Vitis bicolor			X		
GROUND HEATHS					
Chimaphila maculata			X		X
Epigaea repens	X		X		
Gaultheria procumbens			X		
Galax aphylla	X		X	X	

FERNS	1	2	3	4	5
Adiantum pedatum				X	
Aspidium noveboracense			X	X	X
Aspidium marginale			X		X
Aspidium spinulosum			X		X
Asplenium acrostichoides					X
Asplenium angustum			X	X	X
Dicksonia punctilobula			X		X
Osmunda cinnamomea			X	X	
Phegopteris hexagonoptera					X
Polypodium virginianum			X	X	
Polystichum acrostichoides			X	X	X
Pteris aquilina	X				
HERBS					
Andropogon scoparius	X				
Panicum spp.		X			
Sorghastrum nutans	X				
Arisaema quinatum					X
Arisaema triphyllum			X	X	X
Aletris farinosa	X				
Clintonia umbellulata			X		X
Disporum lanuginosum					X
Medeola virginiana			X	X	X
Trillium erectum					X
Dioscorea quaternata			X		X
Iris cristata			X	X	X
Calopogon pulchellus			X		
Cypripedium acaule				X	X
Epipactis pubescens			X		X
Microstylis unifolia			X		
Laportea canadensis					X
Pilea pumila				X	X
Asarum arifolium				X	X
Stellaria pubera				X	
Actaea alba					X
Clematis virginiana			X		
Ranunculus recurvatus					X
Corydalis sempervirens			X		
Heuchera longiflora			X		
Tiarella cordifolia					X
Desmodium nudiflorum	X				
Desmodium pauciflorum			X		
Lespedeza spp.	X	X			
Oxalis montana			X		
Euphorbia corollata	X				
Viola blanda			X	X	X
Viola hastata				X	X
Viola rotundifolia			X	X	X
Circaea lutetiana					X
Aralia racemosa				X	
Panax quinquefolium					X
Osmorhiza longistylis					X
Gerardia laevigata	X				
Houstonia tenuifolia	X				
Mitchella repens			X	X	X
Antennaria plantaginifolia		X			
Aster divaricatus			X	X	X
Aster surculosus	X				
Brachychaeta sphacelata	X				
Chrysopsis graminifolia	X				
Chrysopsis mariana		X			
Elephantopus tomentosus	X				
Eupatorium purpureum					X
Eupatorium urticaefolium					X
Helianthus sp.		X			
Solidago caesia			X		
Solidago odora	X				

porting mixed mesophytic forest. Occasional low limestone cliffs may slightly interrupt this forest. Such breaks are unimportant, although the limestone cliffs do afford local habitats for a variety of plants not found within the forest. If not too steep, the limestone bench is cultivated, and occupied by patches of corn.

Longitudinal creeks generally skirt the northwest base of Pine Mountain and between their headwaters mountain spurs extend out connecting Pine Mountain with adjacent irregular ridges. In the south these ridges are as high or almost as high as Pine Mountain and merge into the extensive exterior section to the west. Near the southern border of Kentucky on Pine Mountain, studies were made on the northwest slope of Pine Mountain and the opposing southeast slopes across Limestone Creek (location 17 on map). Here in absolutely unbroken forest, the entire sequence on both slopes was available.[11]

Viewed from the summit of Pine Mountain (Fig. 16) the forest appears to be entirely mixed mesophytic, except for small patches of pine on cliffs of the opposite mountain face (south slope). Variations in relation to slope exposure and topography are seen, notably the higher proportion of oaks and absence of basswood (except very low) on the south slope; the large amount of beech in the valley of Limestone Creek and extending a short distance up *both* slopes; the abundance of tulip tree on both slopes; the prevalence of the sugar maple-basswood-buckeye-tulip tree forest over much of the northwest slope; and the admixture of chestnut almost throughout the forest.

On the Pine Mountain slope, the change from beech dominance on the lower slope, to the sugar maple-basswood-buckeye-tulip tree association-segregate of the mixed mesophytic forest (Fig. 17) which continues almost to the top, is clearly shown. Tulip tree is an important constituent of the higher part of this community (Fig. 18). On the upper slopes, the greater abundance of chestnut may be noted. The sequence of communities encountered from base to summit on the northwest slope, and from wide ravine floor to headwaters along the longitudinal stream at the base of the mountain are closely comparable (see chart, Fig. 19). It should be noted that the sugar maple-basswood-buckeye-tulip tree forest is here at a lower elevation (1,500-2,000 feet) than it usually occurs on Black or Log Mountain. This entire area of mixed mesophytic forest was a forest striking in the large number of tree species

FIG. 16. View northwest from Pine Mountain (on the Bell-Whitley County line at location 17 on map), showing a portion of the high dissected area of the Cumberland Mountains west of Pine Mountain.

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[11] Much cutting has since been done, and a limestone quarry for road material opened up, where in 1935 there was virgin forest.

FIG. 17. In the sugar maple-basswood-buckeye community of the northwest slope of Pine Mountain above Limestone Creek (area III of chart, Fig. 19). The large tree is buckeye *(Aesculus octandra)*, with papaw *(Asimina triloba)* at its base.

it contained, and the large size attained by many of the individuals.[12]

The herbaceous layer is the luxuriant type so prevalent in the Cumberland Mountains. There is no rhododendron in the valley (probably a reflection of the limestone substratum for which the creek is named), and almost no hemlock. A slight influence of the limestone is seen in the specific content of lower layers.

The forest of the opposing south or southeast slopes (Fig. 20) lacks the luxuriant aspect of the herbaceous layer. The greater proportion of oak increases the exposure to sunlight in spring (due to late leafing of oak), affects the nature of the humus, and hence affects herbaceous growth. Fewer ferns, more legumes (Desmodium and Lespedeza), more xeromesophytes (as *Erigeron pulchellus, Salvia lyrata*), and higher, occasional heaths (Oxydendrum, Vaccinium) emphasize the contrast with the north slopes. Outcropping sandstone layers near the top of the slope (area 6 of chart, Fig. 20) introduce local features.

The contrast in the opposing slopes of Limestone Creek appears to be not entirely due to slope exposure. A resistant sandstone outcropping on the south slope (there is none on the Pine Mountain slope) locally increases the xerophytism and accounts for the occurrence of pines. With this exception, these southerly slopes are essentially like south slopes studied on Black Mountain (Braun 1940).

CUMBERLAND AND STONE MOUNTAINS

No major longitudinal valley skirts the inner base of Cumberland and Stone Mountains; in places there are valleys, but they are not continuous. The inward (northwest) slope of these mountains is much more irregular than is the inner slope of Pine Mountain and in many places there are short more or less parallel ridges between them and the interior area.

The Virginia slope of Cumberland Mountain is occupied by mixed mesophytic forest, but in general lacks the basswood that is so abundant in more typical parts of that forest. On lower hills along the base of the mountain, beech and white oak are abundant; in places, there is basswood. Actually, most of the forest cover is secondary, and only from evidence obtained in scattered stands is it possible to reconstruct something of the general forest type, which seems to accord well with the usual southerly slope aspects of the Cumberland Mountains.

FIG. 18. Tulip trees in the sugar maple-basswood-buckeye-tulip tree community of the northwest slope of Pine Mountain above Limestone Creek.

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[12] A few examples of tree sizes may be of interest: *Magnolia acuminata*, 55 ins., d.b.h.; *Aesculus octandra*, 47 ins., d.b.h.; *Fagus grandifolia*, 49 ins., d.b.h.; *Juglans nigra,*, 36 ins., d.b.h.; *Sassafras variifolium*, 24 ins., d.b.h.

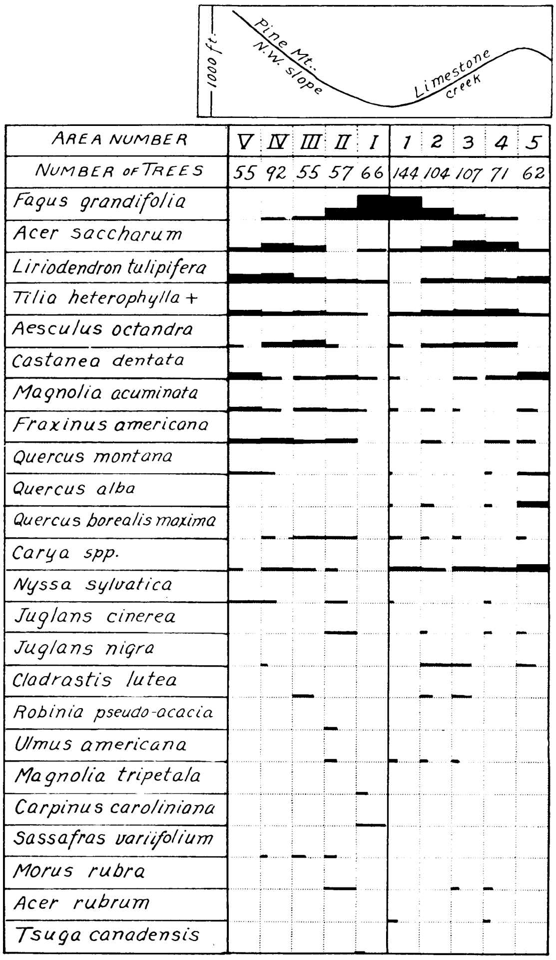

FIG. 19. Percentage composition of canopy of forest communities (at location 17 on map) on the northwest slope of Pine Mountain, and along Limestone Creek, a longitudinal stream at the foot of the mountain. The profiles of the mountain slope and of the stream (steepness exaggerated) suggest the confluence of communities I and 1 in the valley. Area 5, just over the divide from the head of Limestone Creek, is included to show differences in forest due to slope exposure. See also Figure 20.

The dip slope of Cumberland Mountain south of Cumberland Gap descends to the valley of Little Yellow Creek, now Fern Lake (location 18 on map). Although this is a northwesterly slope, the vegetation is remarkably similar to that of the southeast slope of Pine Mountain, with oaks and pines prominent in the canopy, and herbaceous and shrub layers made up of about the same species, although in places they appear to be more luxuriant. Where the dip slope faces almost north, the forest is prevailingly chestnut oak, with chestnut, hickory and tulip tree also abundant. The undergrowth is mesophytic. Ravines are similar to those of the dip slope of Pine Mountain with beech, hemlock, tulip tree, red maple, and white oak, and an undergrowth in which are *Cornus florida, Magnolia tripetala, Rhododendron maximum, Kalmia latifolia* and a variety of deciduous shrubs. Ravine slope forests soon give way laterally to the prevailing oak-pine of the mountain slope. The structural and soil features appear to be more important in their control of vegetation than does slope exposure. All parts of Cumberland Mountain which have been seen are so modified by fire and cutting that no detailed studies were made.

Farther north, on Stone Mountain, the general vegetational features of Pine and Cumberland mountains are seen. Pines prevail wherever there is sandstone outcropping on dry slopes. When, inward, the strata become horizontal, the aspect at once changes, the whole becomes mixed mesophytic forest, for no longer are there shallow soil areas over dipping sandstone rocks.

THE OUTLYING AREA: MOUNTAINS EXTERIOR TO THE FAULT BLOCK

Beyond the limits of the fault block (that is, the highest and most characteristic part of the Cumber-

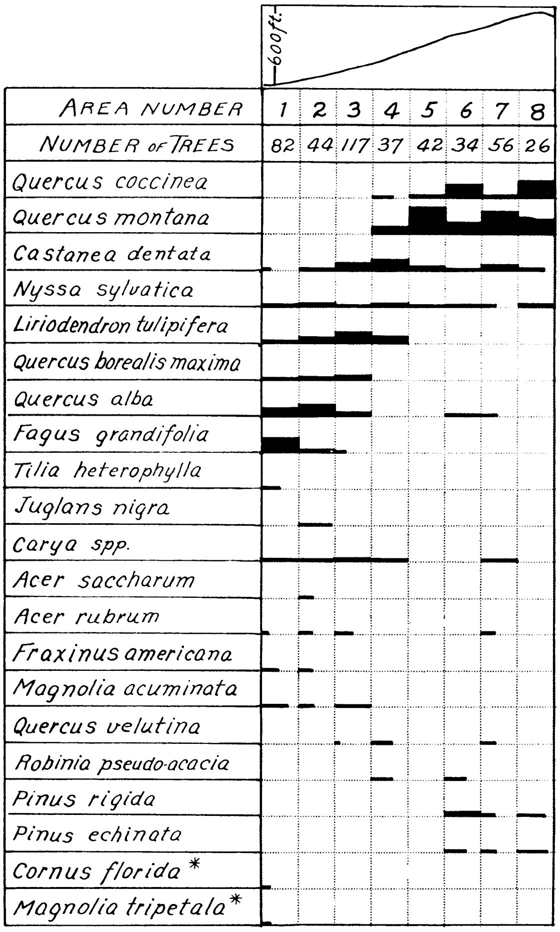

FIG. 20. Percentage composition of canopy of forest communities on the south slope of Limestone Creek. See also Figure 19. *Cornus florida* and *Magnolia tripetala*, usually species of the understory, rarely approach a canopy position.

land Mountains), a large area to the west and southwest is sufficiently similar topographically and vegetationally to be included in the Cumberland Mountains. Mixed deciduous forest prevails throughout this outlying portion of the Cumberland Mountains, except where occasional outcrops of massive sandstone interrupt the otherwise even although steep slopes, or cap high ridges. In such places, pine generally mingles with oaks, although nowhere is it conspicuous as on Pine Mountain. Because of the lesser relief and lower summit altitudes in the outlying area than in most of the more typical parts of the Cumberland Mountains, none of the higher altitude features are seen; the sugar maple-basswood-buckeye-tulip tree community is poorly represented or absent; beech goes nearly to the tops of the ridges, hence is a constituent of most of the forest communities, except those of dry narrow ridge tops.

The mixed mesophytic forest is, then, more homogeneous (if a mixture may be thought of as homogeneous); that is, there is less regrouping of dominants and formation of association-segregates. Individual stands therefore more closely approach the abstract concept of mixed mesophytic forest. Variations in composition in relation to slope exposure are seen, most conspicuous of which is the white oak-beech of south slopes. However, these variations are not often distinct enough to recognize as distinct communities. Altitudinal variations do not complicate those induced by slope exposure.

The western part of the Cumberland Mountains in the vicinity of Williamsburg and east of Pine Knot is a maturely dissected area of strong relief, topographically distinct from the adjacent submaturely dissected Cumberland Plateau. This topographic difference accentuates a vegetational boundary that would otherwise be obscure. Mixed mesophytic forest with almost pure secondary groves of tulip trees on northeast slopes contrasts with the oak, oak-pine or beech woods of the flatter areas of the Plateau.

Northward, however, the Cumberland Plateau is more maturely dissected and rises gradually toward Pine Mountain, although everywhere with summit elevations lower than Pine Mountain. Here there is no other boundary than the structural one which is Pine Mountain. However, the forests of the higher dissected area near to Pine Mountain are distinctly of the Cumberland Mountains type, hence are included here. This will include the headwaters areas of the Kentucky River drainage southwest of Whitesburg, namely, the upper part of Leatherwood Creek, of Middle Fork, and of Red Bird River.

North and east of the northern terminus of Pine Mountain is a high strongly dissected part of the Plateau which extends east between the Cumberland Mountains and the Allegheny Mountains to the Ridge and Valley Province. There, the mixed mesophytic forest of the Cumberlands is continuous with that of the Plateau, and across it into the Allegheny Mountains of West Virginia. This area of dissected plateau is adjacent to and scarcely distinguishable from the northern end of the Cumberland Mountains in Virginia. This area in Virginia to the northeast of Flat Gap is in the drainage basin of Russell and Levisa Forks of the Big Sandy River. Much of it is very deeply dissected and rugged; the ridge-tops are very narrow, and the streams in places are in deep gorges. The whole area is occupied by mixed mesophytic forest. Within the range of the picture (Fig. 21) are:

Fagus grandifolia
Tilia heterophylla
Tilia sp.
Acer saccharum
Liriodendron tulipifera
Quercus borealis maxima
Aesculus octandra
Castanea dentata
Betula allegheniensis
Juglans nigra
Juglans cinerea
Magnolia acuminata
Nyssa sylvatica
Tsuga canadensis
Oxydendrum arboreum
Carya ovata
Acer rubrum
Quercus alba
Carpinus caroliniana
Cornus florida
Magnolia tripetala

Beech goes almost to the top, even on west slopes; in places on southerly slopes the crowns of beech and tulip tree project above the top of the ridge. White oak is more abundant on drier slopes.

Studies in three areas to the west of Pine Mountain are included: the forest of Lynn Fork of Leatherwood Creek, in Perry County (location 19 on map); of Nolans Branch of Red Bird River in Clay County (location 20); and of Buck Branch of Jellico Creek in Whitley County (location 21).[13]

LYNN FORK OF LEATHERWOOD CREEK

The forest of Lynn Fork of Leatherwood Creek was the most magnificent area of deciduous forest, surpassing anything else in the Cumberland Mountains or elsewhere which the writer has ever seen (Figs. 22-30 and Table 2). Here was "a forest of superlative beauty, forest of towering trunks, of luxuriant undergrowth, of exquisite ground cover."

Changes in slope exposure are reflected in changes in relative abundance of the constituent species of the canopy, yet everywhere except on the encircling ridges some phase of mixed mesophytic forest prevails (Fig. 23).

On southerly, southeasterly, and southwesterly slopes, white oak, beech, and in places tulip tree, are most abundant. White oak is here a tree with tall columnar trunks about four feet in diameter. In narrower parts of the valley, and in the vicinity of sandstone ledges, hemlock mingles with the deciduous species, but assumes a position of dominance only in a few places. The influence of the conifer leaf litter and of continuous shade is seen in the changed character of the lower layers of the forest. The mixed mesophytic forest with hemlock has the greatest density of any forest community in the area (Fig. 24).

[13] Lynn Fork of Leatherwood was logged soon after these studies were made and before some additional desirable data concerning white oak reported to be important on another slope were obtained; the forest of Nolans Branch has doubtless been cut as logging operations in upper Red Bird River were almost within hearing distance in 1935; the forest of Buck Branch was intact in the spring of 1939.

Locally, the ravines broaden into small areas known as "bottoms" (Fig. 29). These are not alluvial bottoms, merely nearly level areas. Toward the upper part of the right branch of the Left Fork of Lynn Fork, tulip tree increases in abundance and in size; trees average 14 feet in circumference. Beech and tulip tree (Fig. 25), and higher, sugar maple and tulip tree (Fig. 26) are the dominant species. The largest tulip tree known in or near the Cumberland Mountains grew here (Fig. 27). The undergrowth is exceedingly luxuriant, including a great variety of herbaceous plants and many large ferns (Fig. 26). The humus layer is deep mull.

On the highest slopes and ridges the more characteristic species of the mixed mesophytic forest are rare or absent. The forest is dominantly chestnut oak and chestnut, with an ericaceous undergrowth (Fig. 30).

Studies were made along the route shown on the accompanying map, Figure 22. These illustrate the great amount of variation in composition that is possible with little change in constituent species, except on the highest ridges, and the essential continuity of a mixed mesophytic forest throughout the drainage basin. The accompanying chart (Fig. 23) illustrates the variations in forest composition in the Left Fork of Lynn Fork. A brief characterization of areas distinguished follows:

1. Slope south to southeast; steep.
2. Slope south and less steep.
3. Valley narrower.
4. Low in narrow valley: slope strewn with sandstone blocks; much *Rhododendron maximum.*
5. South slope at fork of creek. A heavy sandstone layer locally affects ground vegetation; Galax and Epigaea abundant.
6. More open valley (Fig. 24); soil of south slope probably shallow because of heavy sandstone layer now beneath surface; trees of slope not so large.
7. South slope; much white oak reproduction in a small area of windfall.
8. Reflects slight influence of a sandstone horizon.
9. Lower ravine slope; soil dark, not sandy.
10. Rich mesophytic aspect (Fig. 25).

11-12. Slopes gentle to steep on sides of cove or valley head; deep mull; very luxuriant aspect, many large ferns (Figs. 26, 27).

13. Upper slopes of cove; less luxuriant aspect.
14. Near 5, and near fork of creek; sugar maple very conspicuous in understory (Fig. 28).

FIG. 21. View in the rugged and deeply dissected portion of the Cumberland Mountains in the Russell Fork drainage northeast of Norton, Va.

15. Higher on slightly convex southeast slope.
16. Slightly concave part of slope.
17. South-southeast slope, slightly convex; white oak appears to be replacing dead chestnut.
18. Lowest ravine slopes and "bottoms" (Fig. 29).
19. Westerly slope, reflected in greater abundance of white oak and beech. Red azalea *(R. cumberlandense)* in full bloom July 12.
20. Higher southwest slope, somewhat transitional to oak-chestnut forest.
21. A south-southwest sloping ridge (not apparent on topographic map); larger proportion of chestnut on less steep parts; Kalmia layer; soil sandy (Fig. 30).
22. Uppermost slopes and ridge-top, divide between Lynn Fork and Oldhouse Branch; shallow soil over slightly dipping sandstone; aspect of southeast slope of Pine Mountain.

The most striking single feature of the Lynn Fork forest is the high percentage of tulip tree in the area as a whole, and especially in the northeast-facing cove which is the head of the right branch of the Left Fork of the creek (Figs. 26, 27). Here the tulip trees tower above all other species, and sugar maple, which anywhere else would look large, forms a second layer in the forest. Beneath these are the usual smaller trees of the understory. Timber cruises show 27 percent of the trees of this drainage basin to be tulip tree, comprising an estimated 58 percent of the board-foot volume of lumber. This latter figure emphasizes the large size of these trees.

Beech is abundant in all communities except those at highest elevations (areas 13, 21 and 22 on chart, which are above 2,000 feet). On southerly slopes, the abundance of white oak, with beech, is evident (areas 2, 6, 7, 17 of chart, Fig. 23). On southwest

TABLE 2. Undergrowth of forest communities of Lynn Fork forest shown in Figure 23. Note that the herbaceous plants of areas 20, 21, and 22 are, with few exceptions, different from those of all other communities. The herbaceous layer is important in distinguishing oak-chestnut communities.

SMALL TREES AND SHRUBS	1	2	3	4	5	6	8	9	10	11	12	13	14	15	18	19	20	21	22
Amelanchier canadensis						x						x					x		x
Asimina triloba	x								x	x	x								
Benzoin aestivale								x		x			x						
Bignonia capreolata	x																		
Carpinus caroliniana	x																		
Cercis canadensis	x		x							x	x	x		x					
Cornus alternifolia	x																		
Cornus florida	x		x						x	x	x		x	x		x		x	
Evonymus americanus	x	x													x	x			
Gaylussacia baccata																			x
Hamamelis virginiana	x		x			x								x					
Hydrangea arborescens				x					x	x	x		x						
Ilex opaca															x				
Kalmia latifolia					x	x	x								x	x	x	x	x
Magnolia Fraseri	x					x		x					x						
Magnolia tripetala			x		x														
Oxydendrum arboreum	x				x	x					x	x					x	x	x
Psedera quinquefolia	x				x				x		x		x						
Pyrularia pubera	x		x			x							x	x		x	x	x	
Rhododendron cumberlandense						x										x		x	
Rhododendron maximum			x	x	x	x									x				
Rhododendron sp.						x										x	x	x	
Rhus Toxicodendron	x							x		x	x		x	x					
Rubus sp.			x																
Smilax Bona-nox	x		x																
Smilax glauca																			x
Vaccinium sp.																		x	
Vaccinium stamineum							x											x	
Vaccinium vacillans						x	x										x	x	
Viburnum acerifolium																			x
Vitis cordifolia	x									x	x	x							
GROUND HEATHS																			
Chimaphila maculata				x	x										x				
Epigaea repens					x												x	x	
Gaultheria procumbens					x														
Galax aphylla					x	x													
FERNS																			
Adiantum pedatum	x		x	x					x	x	x		x	x					
Aspidium Goldianum										x	x								
Aspidium marginale				x															
Aspidium noveboracense	x	x	x		x	x	x	x					x		x	x			
Aspidium spinulosum				x	x								x						
Asplenium acrostichoides				x							x		x						
Asplenium angustifolium	x		x							x	x	x	x						
Asplenium angustum		x	x					x	x	x									
Botrychium virginianum	x								x	x	x	x	x						
Osmunda cinnamomea						x	x	x							x				
Phegopteris hexagonoptera	x		x					x		x			x	x					
Polypodium virginianum	x									x									
Polystichum acrostichoides	x	x	x	x	x	x	x		x	x		x	x	x					
Pteris aquilina																		x	
HERBS																			
Andropogon scoparius																			x
Diarrhena diandra										x	x								
Panicum sp.						x													x
Clintonia umbellulata					x	x													
Disporum lanuginosum									x	x	x		x	x					
Disporum maculatum											x								
Medeola virginiana			x		x										x				
Smilacina racemosa			x																
Trillium erectum										x									
Trillium grandiflorum									x	x	x								
Uvularia grandiflora									x	x			x						
Uvularia perfoliata														x					
Dioscorea quaternata		x	x			x													
Hypoxis hirsuta						x										x			
Iris cristata			x			x													
Cypripedium acaule			x		x														
Cypripedium parviflorum var. pubescens								x		x	x								
Epipactis pubescens															x				
Liparis liliifolia	x																		
Microstylis unifolia						x													
Orchis spectabilis									x	x									
Laportea canadensis	x							x	x	x	x		x						
Pilea pumila	x									x	x								
Aristolochia Serpentaria								x					x						
Asarum canadense	x									x	x		x						
Polygonum virginianum											x		x						
Silene virginica			x																
Stellaria pubera													x						
Anemone quinquefolia															x				
Anemonella thalictroides										x	x								
Cimicifuga racemosa	x		x						x	x			x	x					
Clematis viorna			x																
Clematis virginiana											x								
Hepatica acutiloba										x	x	x							
Ranunculus hispidus			x					x											
Ranunculus recurvatus	x									x									
Menispermum canadense										x									
Caulophyllum thalictroides									x	x	x		x	x					
Sanguinaria canadensis	x		x						x	x	x		x	x					
Astilbe biternata			x	x						x	x		x						
Tiarella cordifolia	x			x					x	x	x		x						
Aruncus sylvester	x																		
Potentilla pumila					x	x													
Amphicarpa monoica	x	x	x			x		x		x	x		x	x					
Desmodium grandiflorum			x			x		x	x	x			x						
Desmodium laevigatum			x																
Desmodium nudiflorum	x					x								x					
Desmodium pauciflorum											x								
Desmodium rotundifolium		x					x										x		
Lespedeza hirta																			x
Tephrosia virginiana																			x
Vicia caroliniana		x	x			x		x									x		
Oxalis grandis	x									x									
Geranium maculatum	x		x			x			x	x	x	x	x	x					
Impatiens pallida										x									
Hybanthus concolor										x									
Viola blanda	x			x	x				x	x	x		x		x				
Viola hastata															x				
Viola palmata													x						
Viola rostrata	x		x						x	x					x				
Viola rotundifolia			x		x										x				
Passiflora lutea	x										x								
Circaea lutetiana	x		x							x	x		x	x					
Aralia racemosa	x							x	x	x	x					x			
Panax quinquefolium											x								
Angelica villosa																			x
Cryptotaenia canadensis										x									
Osmorhiza longistylis											x	x							
Sanicula sp.													x						
Taenidia integerrima																		x	
Thaspium aureum			x																
Monotropa uniflora				x											x				
Lysimachia quadrifolia		x					x											x	
Asclepias quadrifolia											x								
Phlox divaricata	x																		
Hydrophyllum canadense											x								
Hydrophyllum virginianum											x								
Phacelia bipinnatifida										x	x								
Cynoglossum virginianum	x												x	x					
Lappula virginiana			x																
Collinsonia canadensis	x	x	x						x	x	x		x	x					
Monarda clinopodia			x																
Gerardia laevigata						x											x		x
Pedicularis canadensis			x		x											x			
Phryma Leptostachya	x																		
Galium lanceolatum											x								
Houstonia tenuifolia																x			
Mitchella repens	x		x	x	x	x	x	x							x	x			
Triosteum angustifolium									x	x	x								
Campanula americana	x																		
Campanula divaricata																			x
Antennaria plantaginifolia																			
Aster cordifolius	x																		
Aster divaricatus			x								x								
Aster patens																			x
Coreopsis major							x												x
Erigeron pulchellus			x		x														
Eupatorium purpureum			x						x	x	x		x						
Eupatorium urticaefolium	x		x								x								
Hieracium paniculatum			x																
Krigia amplexicaulis		x	x			x													
Polymnia uvedalia											x								
Prenanthes serpentaria																			x
Senecio obovatus	x	x																	
Sericocarpus asteroides																		x	
Solidago caesia	x		x								x								
Solidago latifolia			x						x	x	x		x						

slopes (illustrated by area 20) beech comprises 17 percent of the oak-chestnut forest. In the deepest ravines, beech is associated with hemlock.

Chestnut is present in almost all communities, ranging from the most mesophytic hemlock-beech forest of deep ravines, to the dryest sandstone ridge-tops, where associated with chestnut oak and pine. As in the Black Mountain area (Braun 1940) its presence, even in abundance, can not be taken as an indication of oak-chestnut forest. The lower layers of the forest (shrub and herb) and the nature of the soil and humus layer will distinguish the oak-chestnut communities (Fig. 30 and areas 20, 21, 22 of chart, Fig. 23). Chestnut is, of course, nearly dead as a result of blight. What will take its place in the future forest must be determined for each community separately. Usually it is one of the less tolerant species of the community: chestnut oak *(Quercus montana)* in the oak-chestnut areas; white oak in communities in which this species is well represented (as 17 of chart); sugar maple in the more mesophytic communities.

The undergrowth of the Lynn Fork forest varied from place to place, both in luxuriance and in composition (see Table 2). The species of the last three communities (20, 21, 22 of Fig. 23 and Table 2), which comprise the oak-chestnut forest of the area (Fig. 30), are almost all different from those of the

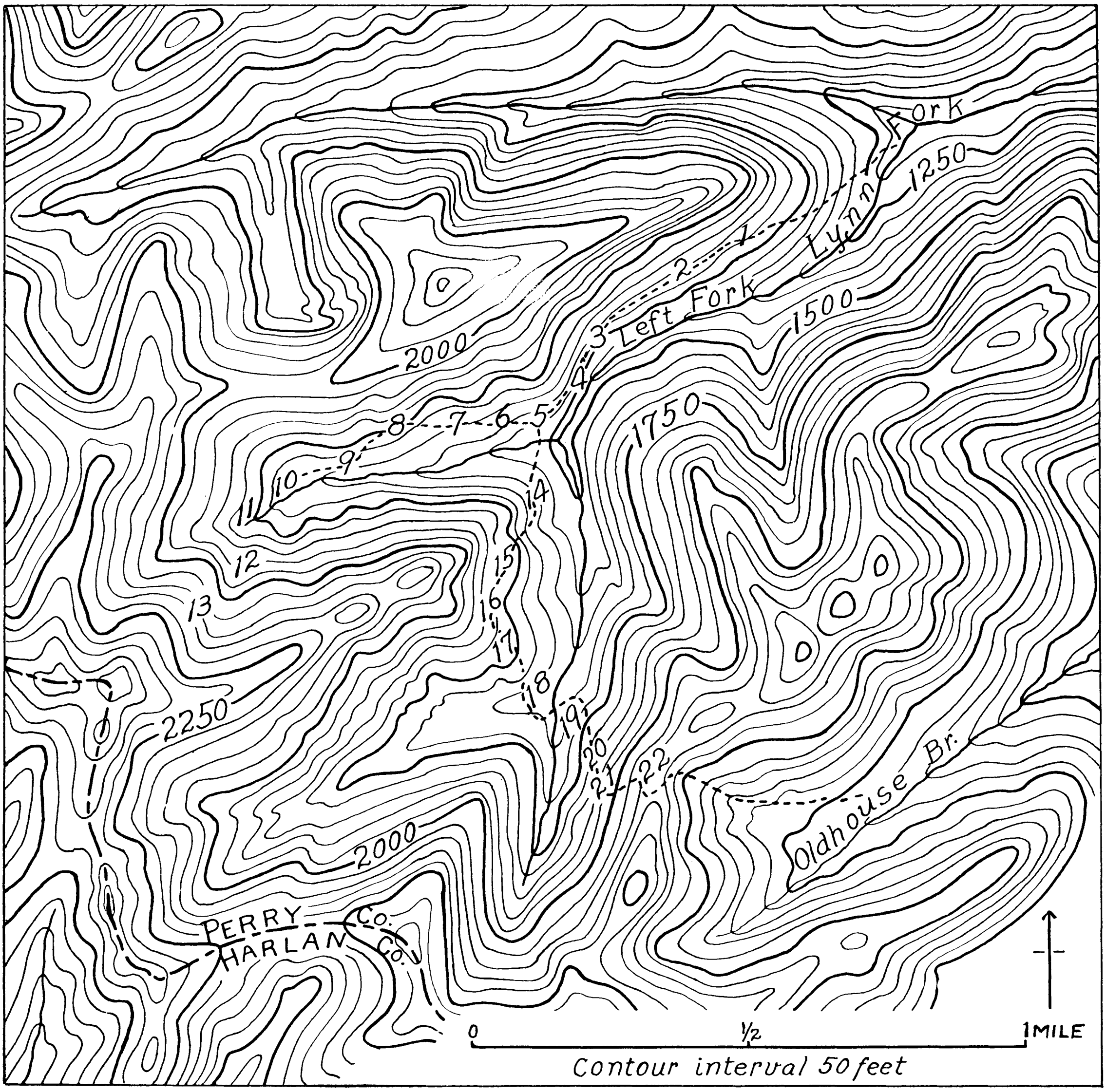

FIG. 22. Topographic map of the drainage basin of Lynn Fork of Leatherwood Creek (location 19 on map, Fig. 1). Numbers give location of forest communities distinguished on chart, Figure 23. Adapted from Cornettsville topographic sheet.

remainder of the forest. Sandy soil (where sandstone substratum is not far below surface) affects to a slight extent the undergrowth of a few communities (for example, 4, 5, 6, 8). The richest undergrowth and the deepest mull is in the tulip tree-sugar maple forest of the right branch of the creek (areas 11, 12), illustrated in Figures 26 and 27. The beech-tulip tree area (area 10 and Fig. 25) is almost as rich.

NOLANS BRANCH OF RED BIRD RIVER

Areas studied on Nolans Branch were less continuous than those in Lynn Fork. The series selected represents differences in slope exposure, with little altitudinal range (see chart, Fig. 31). Regardless of exposure, mixed mesophytic forest prevails. There is no massive rock in the area, hence all slopes are about equally reduced, and nowhere exceedingly steep. One small area on a northerly slope approaches the sugar maple-basswood-buckeye-tulip tree type of the higher Cumberlands. Elsewhere, beech is present, although variable in amount. Every community is mixed, and even on southwesterly slopes where chestnut oak is abundant, all of the more characteristic mesophytic species except buckeye are present.

BUCK BRANCH OF JELLICO CREEK

Buck Branch of Jellico Creek is an eastward-flowing stream only a few miles from the western border of the Cumberland Mountains east of Pine Knot (location 21 on map, Fig. 1). Although the low vegetation has been somewhat affected by hogs and sheep, most of the species are probably represented in sheltered or inaccessible spots. The tops of large sandstone blocks lying on lower slopes (derived from higher strata which form the ridge crests) are veritable flower gardens with *Sedum ternatum, Arisaema triphyllum, Smilacina racemosa, Trillium Hugeri,* plants which should be abundant throughout the ground layer. In respect to canopy, the forest is a virgin stand affording opportunity for study of ravine and slope forests of different exposures. The similarity of the ravine and north slope forests is apparent (Fig. 33). The topographic locations of areas distinguished on the chart are shown in Figure 32. On the lower south slopes, the beech-white oak or beech-white oak-tulip tree forest type prevails, giving way upward to oak-tulip tree and finally, on the rocky very steep uppermost slopes, to chestnut oak forest with an open heath layer and sparse sandy soil herbaceous flora. On these highest slopes the rocky immature soil is covered by a thin layer of mor. Elsewhere the mull humus layer of the mixed forest prevails. These differences are reflected in the composition of lower layers (Table 3). Farther downstream (and below this area of uncut forest)

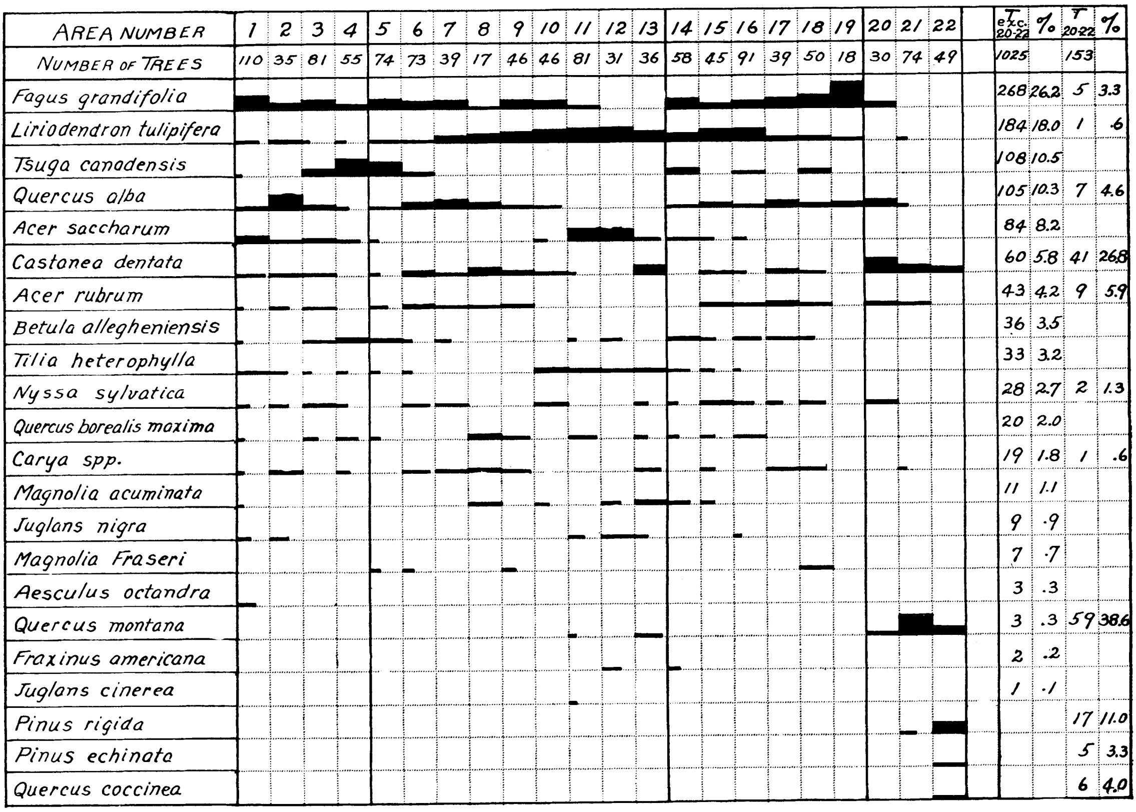

Fig. 23. Percentage composition of canopy of forest communities in Lynn Fork of Leatherwood Creek (location 19 on map, Fig. 1). See also Figure 22 and Table 2.

hemlock occurs locally on low sandstone cliffs near the stream level.

BEYOND THE LIMITS OF THE CUMBERLAND MOUNTAINS

In order to contrast the forests of the Cumberland Mountains with those on the adjacent maturely dissected plateau, Figure 34 is included. Beyond the limits of the Cumberland Mountains (at location 22 on map, Fig. 1), forest composition on various slope exposures, in ravines, and on ridges was determined. This area is representative of a considerable part of the maturely dissected plateau of low relief, about 500 to 700 feet; it is neither representative of the more deeply dissected parts nor of the dissected margin of the plateau, in both of which areas there are typical mixed mesophytic forests.

Local variations occur on the several slope exposures, due to irregularities in steepness and to slight differences of slope exposure introduced by convexities and concavities of slope. Beech extends about half way up south and west slopes and two thirds or more of the way up east and north slopes. Tilia is prominent on north and east slopes, absent from south and west slopes. Ridges vary as to dominance of chestnut oak or scarlet oak; nowhere is chestnut a dominant in the ridge forest. As compared with the Cumberland Mountains, there is a striking increase in the dominance of beech and of white oak, and an equally striking decrease in the proportion of other dominants of the mixed mesophytic forest—basswood, buckeye, sugar maple, tulip tree, red oak—yet all are present, and in actual number of tree species this forest compares favorably with

TABLE 3. Undergrowth of forest communities of Buck Branch forest shown in Figure 33.

UNDERSTORY TREES, CANOPY SPECIES	N3	N2	N1	R1	R2	R3	R4	S1	S2	S3	K
Fagus grandifolia		x	x	x	x	x		x	x	x	
Acer saccharum	x	x	x	x	x	x	x	x	x	x	x
Aesculus octandra	x		x	x		x					
Tilia heterophylla	x	x				x	x				
Castanea dentata								x			
Liriodendron tulipifera		x		x				x	x		
Quercus montana									x	x	x
Quercus alba	x							x	x	x	
Carya alba		x							x		
Carya cordiformis		x	x								
Carya glabra								x	x		
Carya ovata							x		x		
Quercus borealis maxima		x				x		x	x		
Fraxinus americana		x	x	x		x	x	x	x		
Nyssa sylvatica				x				x	x	x	
Quercus velutina									x		
Magnolia acuminata		x				x					
Acer rubrum				x				x	x	x	x
Juglans nigra	x	x		x							
Cladrastis lutea	x	x		x			x				
Juglans cinerea				x							
Ulmus alata					x						
Liquidambar styraciflua				x							
Robinia Pseudo-Acacia									x		
SMALL TREES AND SHRUBS											
Amelanchier canadensis								x			x
Asimina triloba	x	x	x	x	x	x		x	x		
Benzoin aestivale			x	x							
Carpinus caroliniana		x	x	x	x	x		x			
Cercis canadensis	x									x	
Cornus florida	x	x	x	x	x	x	x	x	x	x	x
Crataegus sp.				x							
Gaylussacia baccata											x
Hydrangea arborescens				x	x						
Oxydendrum arboreum								x	x	x	x
Psedera quinquefolia	x						x		x	x	
Rhododendron cumberlandense								x		x	
Rhus Toxicodendron	x								x	x	
Smilax glauca										x	
Smilax Bona-nox									x	x	
Vaccinium arboreum										x	
Vaccinium simulatum								x	x	x	
Vaccinium stamineum									x		x
Vaccinium vacillans								x		x	x
FERNS											
Adiantum pedatum		x	x	x	x		x	x			
Aspidium noveboracense				x				x			
Asplenium acrostichoides			x	x	x						
Asplenium angustifolium			x								
Asplenium angustum									x		
Asplenium platyneuron									x		
Botrychium virginianum			x						x		
Camptosorus rhizophyllus							x				
Phegopteris hexagonoptera			x	x	x		x	x			
Polypodium virginianum										x	
Polystichum acrostichoides			x	x	x			x	x	x	

HERBS	N3	N2	N1	R1	R2	R3	R4	S1	S2	S3	K
Festuca octoflora											x
Poa cuspidata											x
Arisaema triphyllum	x		x	x	x	x	x				
Luzula sp.									x		
Disporum lanuginosum			x								
Erythronium americanum	x	x	x	x	x	x	x				
Medeola virginiana								x			
Polygonatum biflorum		x	x								
Smilacina racemosa					x	x	x	x	x		
Trillium erectum		x	x			x					
Trillium grandiflorum						x	x				
Trillium Hugeri	x	x					x	x			
Uvularia perfoliata									x		
Dioscorea sp.		x	x								
Iris cristata				x	x			x			
Aplectrum hyemale	x										
Tipularia discolor								x			
Laportea canadensis			x			x					
Asarum arifolium									x		
Stellaria pubera		x	x					x			
Claytonia caroliniana	x	x	x	x							
Claytonia virginica											x
Anemone quinquefolia			x								
Anemonella thalictroides	x	x	x		x	x	x	x	x		x
Cimicifuga americana	x										
Cimicifuga racemosa	x	x	x	x	x	x	x				
Hepatica acutiloba				x	x	x	x				
Ranunculus hispidus				x	x			x			
Ranunculus recurvatus			x	x							
Caulophyllum thalictroides		x	x	x	x	x	x				
Podophyllum peltatum			x	x	x	x	x	x			
Sanguinaria canadensis	x	x	x								
Cardamine parviflora									x		
Dentaria diphylla		x									
Dentaria heterophylla	x	x	x	x	x	x	x				
Dentaria laciniata			x	x	x	x					
Sedum ternatum	x		x	x		x	x				x
Heuchera americana	x								x		x
Tiarella cordifolia			x	x	x						
Potentilla canadensis									x		
Potentilla pumila										x	
Dsemodium rotundifolium									x		
Lespedeza spp.									x		
Vicia caroliniana								x	x	x	
Oxalis violacea				x				x	x	x	
Geranium maculatum								x	x		
Impatiens pallida				x							
Ascyrum hypericoides										x	
Viola hirsutula								x			
Viola papilionacea			x								
Viola scabriuscula				x	x						
Panax quinquefolium	x			x							
Panax trifolium			x								
Erigenia bulbosa			x	x	x	x	x				
Chimaphila maculata			x								
Phlox divaricata			x		x	x	x	x			
Cynoglossum virginianum				x				x			
Myosotis macrosperma											x
Cunila origanoides									x	x	
Conopholis americana		x									
Houstonia caerulea				x				x	x	x	
Antennaria plantaginifolia								x		x	
Coreopsis major									x	x	
Eupatorium urticaefolium	x	x		x	x	x	x	x	x		
Hieracium venosum								x	x		
Krigia virginica										x	
Solidago caesia								x			

forests in the Cumberland Mountains. Here also, chestnut is much less abundant, and Carya (all species taken together) is much more abundant than in the Cumberland Mountains.

The topography, and the poorer soil, appear to be related to stratigraphic horizon, and thick shale beds. As a result, a poorer type of mixed mesophytic forest has developed, a forest not referable, however, to any other major association. Because of slower water penetration into the shales and subsoils derived from them, erosion of humus is more rapid after clearing than it is on more porous soils. Secondary forests in such areas are prevailingly oak-hickory. It may be features of this sort which have influenced some to map the plateau as "oak-hickory" (Kendeigh 1934). Only on a few ridge crests is there any primary oak-hickory. There it occupies the same situations as does oak-chestnut and is its ecological equivalent; both are physiographic climaxes in the area of the mixed mesophytic association.

FOREST COMMUNITIES OF LARGER VALLEYS

Although the emphasis in the present paper is upon climax and physiographic climax forest communities, consideration of seral stages of river valleys is of importance, both because there are features here not common to the whole deciduous forest, or even to the whole area of the mixed mesophytic climax, and because successional development demonstrates the establishment of a mixed mesophytic forest on valley floors essentially like that of mountain slopes.

THE VALLEY FLOORS

Few areas of natural vegetation remain on valley floors. There is so little land suitable for cultivation in the Cumberland Mountains, that almost every acre of relatively level land is utilized, unless it is adjacent to streams and subject to frequent overflow, or is swampy or poorly drained. Seral vegetational stages occupy such places. A few very small areas of forested mesic valley flats along small streams have been seen; these always support mixed mesophytic forest. In larger valleys scattered trees or groups of trees left along roads may be used as evidence from which to reconstruct the mesophytic forest types of valley floors.

Stream Margins

In many places, mountain slopes descend directly to stream margins; slope forest with no admixture of river border trees may continue to within a few feet of the stream (Fig. 35). Depositing shores, even if narrow, usually have a fringe of trees of

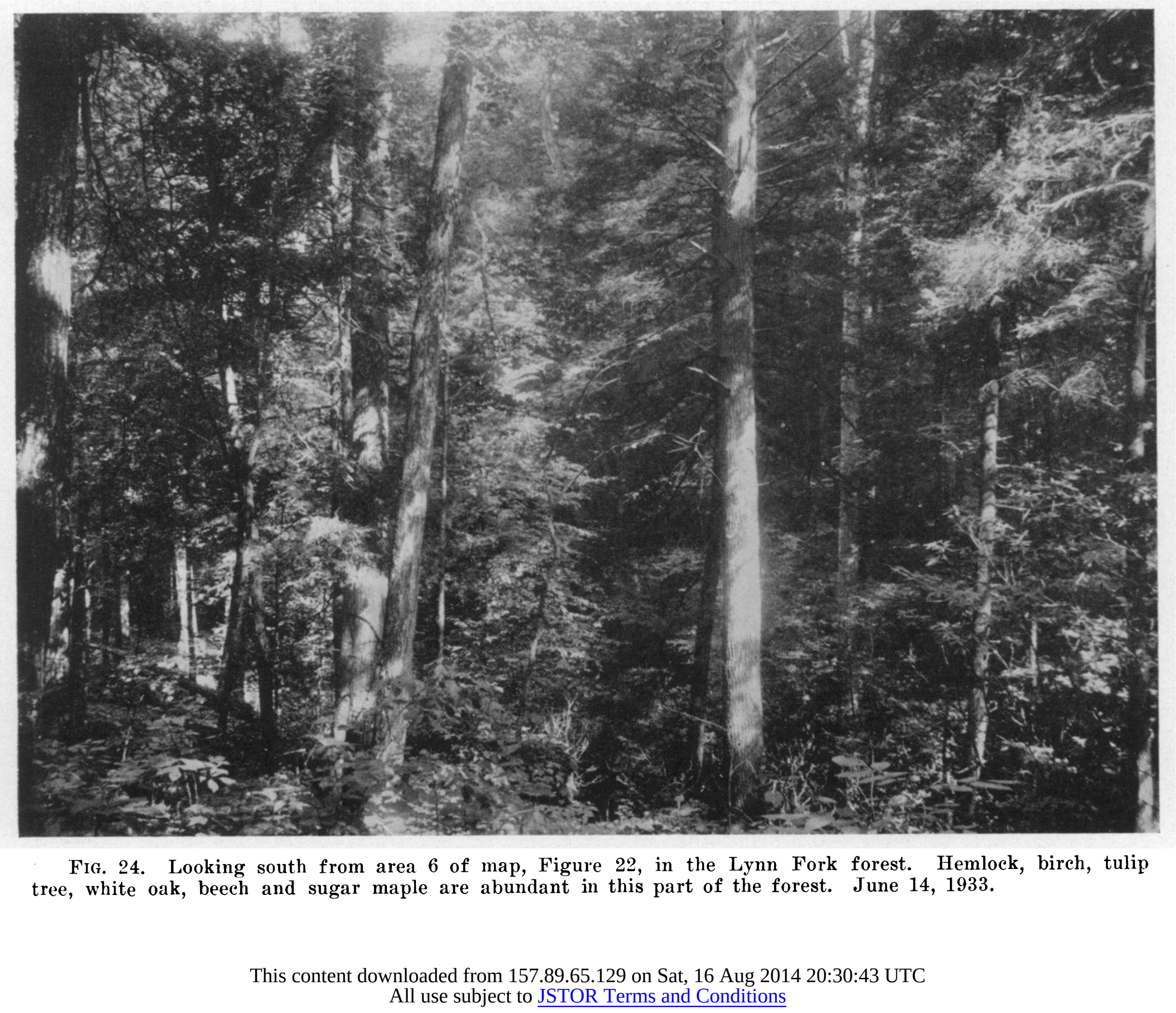

FIG. 24. Looking south from area 6 of map, Figure 22, in the Lynn Fork forest. Hemlock, birch, tulip tree, white oak, beech and sugar maple are abundant in this part of the forest. June 14, 1933.

species not general elsewhere. The widely distributed streamside trees—sycamore, black willow, box elder, white elm and silver maple—are of course present, although not all are to be expected in any one area. River birch *(Betula nigra)* is conspicuous and in many places is the most abundant tree (Fig. 35). Sweet gum *(Liquidambar styraciflua)* is sometimes abundant. *Ulmus serotina* may be present. In places, more or less extensive sycamore flats are seen; sweet gum is usually mingled with the sycamore, and *Magnolia tripetala* may be abundant as an understory tree—flats of Red Bird River below Beverly (Fig. 36). Bamboo *(Arundinaria macrosperma)* is sometimes abundant.

Immediately back of the margin, an admixture of mesophytic species indicates the early replacement of marginal species when habitat conditions permit. In fact, the forest of mesic valley flats may in places have no border of marginal species. If depositing areas are small (and hence shaded by adjacent forest) and variation in stream height little, or periods of overflow of very short duration, as is true of some smaller streams, trees of the climax forest may pioneer in the bare areas of deposition. Young hemlock, beech, tulip tree, red and sugar maple, together with sycamore initiate a new community on the depositing shore.

Swampy or Poorly Drained Flats

West of Pine Mountain and near to the Cumberland River, wide valley flats extend into the mountains from the Cumberland Plateau like narrow tongues. Little of the original forest remains; the scattered trees indicate former occupancy by swamp forest in which sweet gum, willow oak *(Quercus phellos)*, swamp white oak *(Quercus bicolor)*, winged elm *(Ulmus alata)* and red maple were important species. On slightly higher flats, southern red oak *(Quercus falcata)* is common, generally associated with sweet gum and sometimes with beech. Swamp meadows and alder thickets (secondary vegetation) are of frequent occurrence.

Within the Cumberland Valley above Pine Gap, swamps are small and local, confined to cut-offs and seepage areas near the base of mountain slopes. Somewhat larger swamps occur in the valley of Clear Creek. Although adding to the diversity of vegetation and increasing the flora of these mountains, such areas are ecologically unimportant.

FIG. 25. Beech and tulip trees prevail in area 10 (map, Fig. 22). The figure beside tulip tree in center of picture gives some impression of relative sizes. The herbaceous layer and low woody layer are very luxuriant. June 14, 1933.

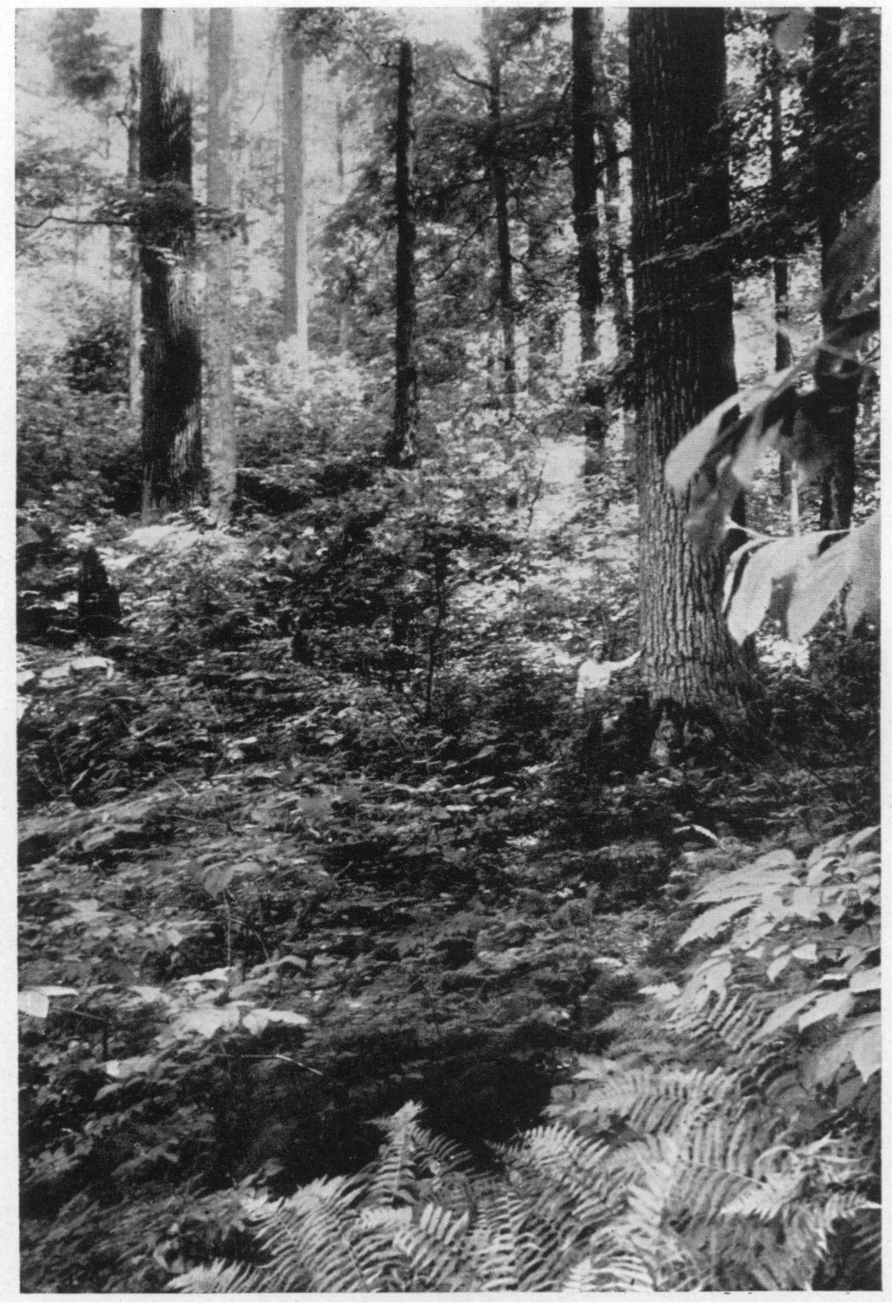

FIG. 26. In a grove of giant tulip trees (area 11); ferns, *Asplenium angustifolium,* are conspicuous in the luxuriant ground cover. June 14, 1933. Courtesy Nature Magazine.

Mesic Valley Flats

Small areas of low alluvial or sandy terraces border the Cumberland River and some of its tributaries above Pine Gap. On a few of the smallest of such areas, secondary forests have developed; elsewhere the land is utilized and only scattered trees along roads remain as evidence of the former mixed mesophytic forest, which contained beech, tulip tree, white oak, chestnut, walnut, butternut, basswood, red maple, sweet birch, hemlock, and doubtless other species. It is said that in some places rhododendron formed impenetrable thickets in this forest. The low slopes leading to such terraces were occupied by mixed forest.

Young secondary forest on small terrace remnants (in the upper Cumberland Valley and along Clear Creek) contains, in addition to a number of the mesophytic tree species mentioned above, *Cornus florida,* *Magnolia tripetala, M. macrophylla, Nyssa sylvatica, Diospyros virginiana, Aralia spinosa, Cercis canadensis, Ilex opaca, Clethra acuminata, Stewartia pentagyna, Hamamelis virginiana,* etc. In places where the soil is very sandy, pines *(Pinus rigida, P. virginiana)* sometimes form dense groves.

LOW HILLS OF THE MIDDLESBORO BASIN

Areally unimportant, but ecologically interesting, are the low hills in the Middlesboro basin. As most of these are occupied by the outskirts of the city of Middlesboro, only fragmentary evidence remains concerning their forest cover. Oaks prevail; the soil is the yellow-red prevalent southward. The combination suggests an outlier here of the oak forest type of the red and yellowerths, the zonal soil type to the south of the area of the mixed mesophytic forest.

DISCUSSION

The Cumberland Mountains are the center of distribution of the mixed mesophytic association of the deciduous forest (Braun 1941). Here variations in composition of the mixed forest due to shifting dominance or changing numerical importance of species give rise to association-segregates, some of which help to demonstrate the relationships and mode of origin of the great climax units of the deciduous forest. Large size attained by individuals, large number of species comprising the forest, and wide range of habitat occupied by many of the climax species further demonstrate that here is the optimum area for mixed mesophytic forest.

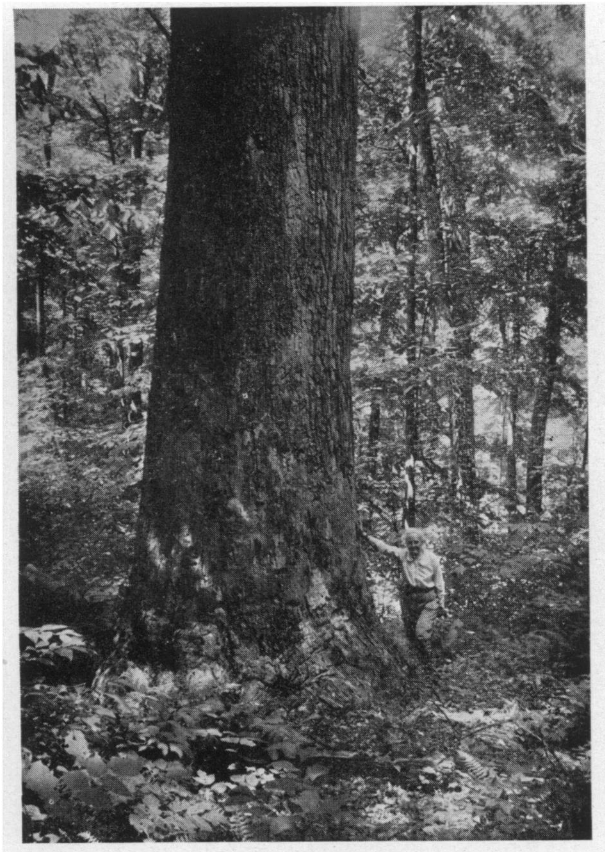

FIG. 27. Tulip tree (area 12), 23 feet in circumference 4 feet above the up-slope side of the base. Ferns and *Aralia racemosa* in foreground. June 14, 1933.

Large size of individuals—a feature of a center of distribution—is apparent from figures of diameters and photographs in this and preceding papers. *Aesculus octandra* (Fig. 17) frequently exceeds the size range of this species given by Sargent (1933), as do also *Magnolia acuminata, Castanea dentata* (straight columnar form), *Quercus borealis* var. *maxima* and others. Tulip tree reaches enormous size (Fig. 27). Sugar maple (Fig. 8) is larger than in the Great Smokies.

The number of species of the forest canopy, often twenty or over, is a feature of the mixed mesophytic forest, a feature strikingly emphasized in October during the period of fall coloration, and evident on all the charts of percentage composition.

The wide range of habitats occupied by climax species in the forests of the Cumberland Mountains is readily ascertained from charts of forest composition in this and previous papers (Braun 1935, 1940). Most conspicuous in this respect is beech. Frequent repetition has been made of the presence of beech in south slope communities and of its higher altitudinal range on warm (south or west) slopes. In addition, beech is a constituent of ravine forests and of many ridge crest communities. Beech in the Cumberland Mountains, the center and optimum area of the mixed mesophytic forest, has a wide habitat range. This is in contrast to the narrower habitat range of this species toward the geographic limits of the mixed mesophytic association (especially in the ecotone between the mixed mesophytic and oak-hickory climaxes). There it is often confined to the most favorable sites. For example, in western Kentucky where oak-hickory forest prevails, beech occurs on the more mesophytic ravine slopes and in gorges where may be seen outliers (relics) of the mixed mesophytic forest. In the Knobs region of Indiana, beech is more generally confined to northerly slopes, while oak-hickory forest occupies the southerly slopes (Potzger & Friesner 1940).

As was pointed out in the Black Mountain area (Braun 1940), chestnut has an exceedingly wide community range. It is present in almost every community in the Cumberlands (see percentage lists and charts) from the drier ridge crests to the most mesophytic ravine communities with hemlock, and on alluvial flats.

The position of tulip tree in the climax mixed mesophytic association of the deciduous forest may be questioned, just as is that of white pine in the northern hardwood or Lake forest (Nichols 1935, Graham 1941). Tulip tree is an abundant species in certain communities, especially in some areas of the sugar maple-basswood-buckeye association-segregate. It occurs commonly in deep ravines with hem-

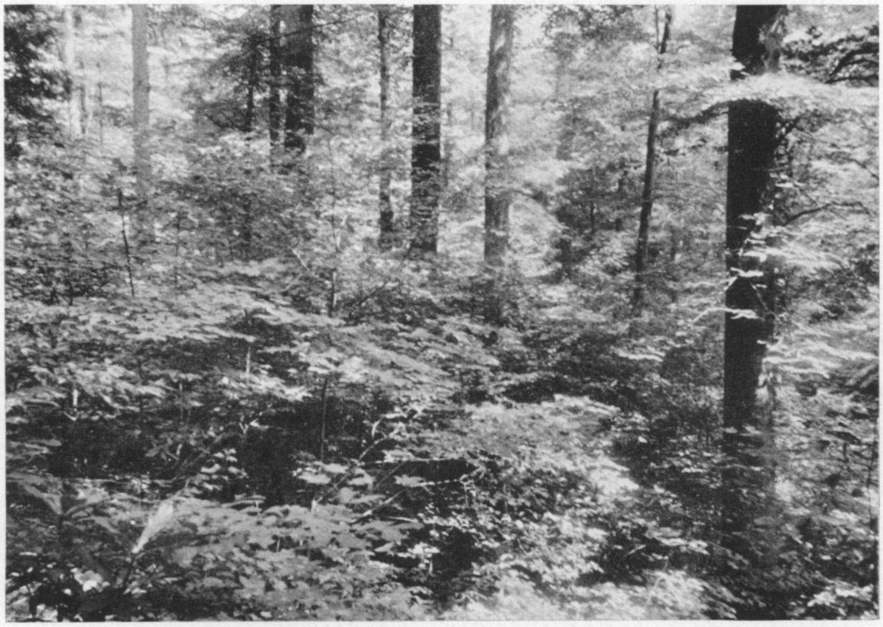

Fig. 28. Beech, tulip tree, and sugar maple (in area 14); sugar maple is very abundant in the understory. July 12, 1935.

Fig. 29. Small more or less flat areas such as this (area 18) are often referred to as "bottoms." Ferns *(Aspidium noveboracense)* and Kalmia beneath the beech, hemlock, and sugar maple. July 12, 1935.

FIG. 30. Chestnut oak-chestnut forest of a south-southwest sloping ridge (area 21) with a small tree layer in which dogwood is a subdominant, and a shrub layer of Kalmia. July 12, 1935.

lock and beech; it is one of the dominants in the chestnut-sugar maple-tulip tree association-segregate. In fact, it is present in most communities but less abundant in the more xeric ones. Apparent tolerance is influenced by favorable habitat factors (Toumey & Korstian 1937). Although generally considered as an intolerant tree, Liriodendron in the Cumberland Mountains reacts to the optimum conditions of this area, thus displaying an apparent tolerance which may largely account for its presence in a wide variety of communities. It may thrive in the open, as demonstrated by the many small secondary stands of this species. These, however, generally occupy sheltered situations—lower ravine slopes or coves on northerly mountain slopes. These cove forests of secondary tulip tree are a conspicuous feature of the Cumberland Mountains. Or, it may reproduce in the shade and in competition with other constituents of the mixed mesophytic forest. In almost every community studied in which it is a constituent of the canopy, thriving young individuals are seen, just as are young sugar maple, beech, and chestnut.

In a few areas of primary forest where Liriodendron is especially abundant, this abundance may be due to accident centuries ago. The secondary cove forests of today, two or three centuries hence, might resemble certain local areas seen in forests of northerly slopes. One such place was seen on Pine Mountain near the head of Limestone Creek (not included in chart). In one area in Lynn Fork where especially abundant, beech and sugar maple (large), together with other species of the mixed forest, might be considered as forming a layer below the canopy of Liriodendron. In such places, it might be considered as a remnant of a seral stage following, for instance, a tornado of the past. However, the general occur-

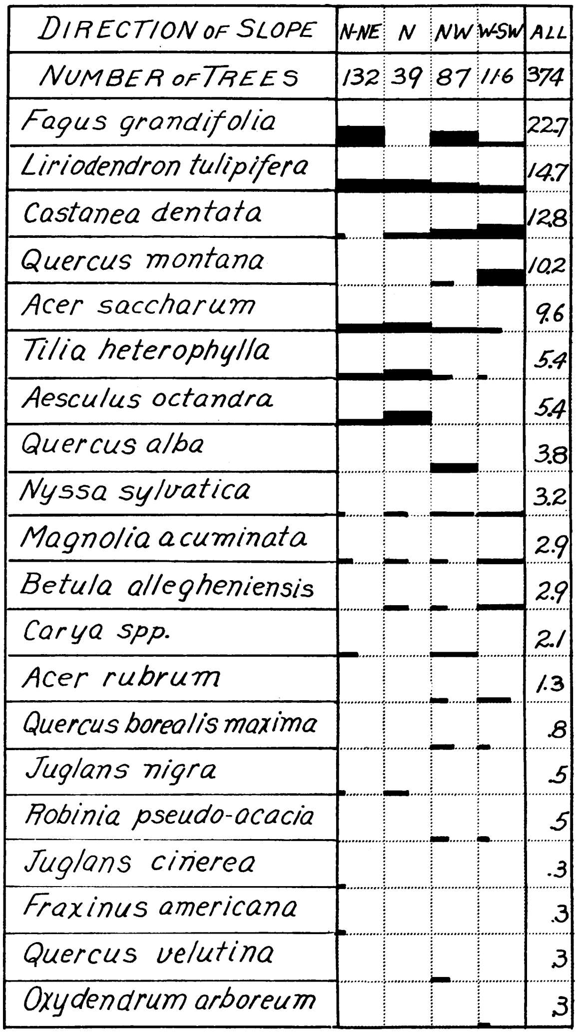

FIG. 31. Percentage composition of forest communities in Nolans Branch of Red Bird River (location 20 on map).

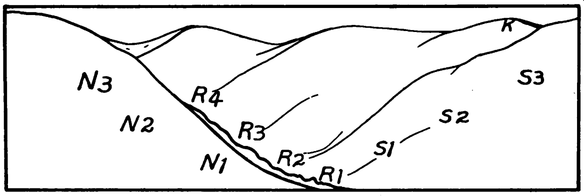

FIG. 32. Sketch designed to show topographic locations, in Buck Branch forest, of areas distinguished in chart, Figure 33.

rence of Liriodendron cannot be explained on a basis of past catastrophe. Neither does it appear that local windfalls, or the dying of canopy species, are necessary for the species to assume a canopy position. It would be difficult to account for its abundance and wide community range by accident alone. In most places, it appears to be as much a true constituent of the climax as do any other of the dominant species.

The most characteristic species of the mixed mesophytic forest appear to be *Tilia heterophylla*[14] and

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[14] Unfortunately, the taxonomic status of forms of Tilia in the mountains seems open to question. *T. heterophylla* is used here in a broad sense, and may include other species (as *T. Michauxii*) with leapes whitened beneath. Still other species of Tilia, with leaves green beneath, also occur. Because of height of trees and inaccessibility of flowering and fruiting branches, no attempt has been made to separate the species or varieties in the determination of percentage composition. The most abundant form is, however, the one with leaves whitened beneath, which appears to be typical *T. heterophylla*.

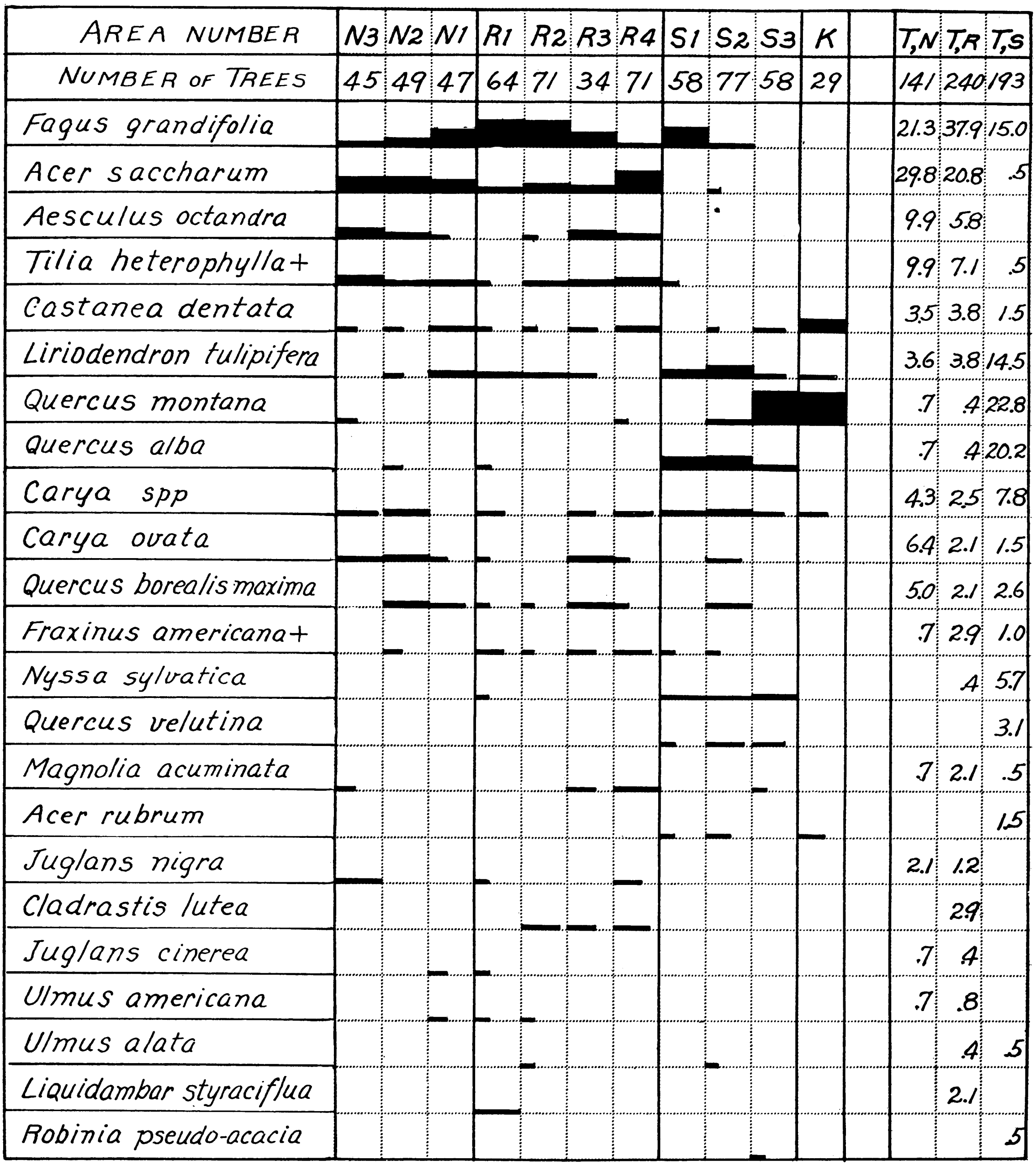

FIG. 33. Percentage composition of canopy of forest communities on Buck Branch of Jellico Creek (location 21 on map). North slope, south slope, and ravine forests distinguished by N, S, and R, respectively; K, knobs. See Figure 32 for topographic locations of communities.

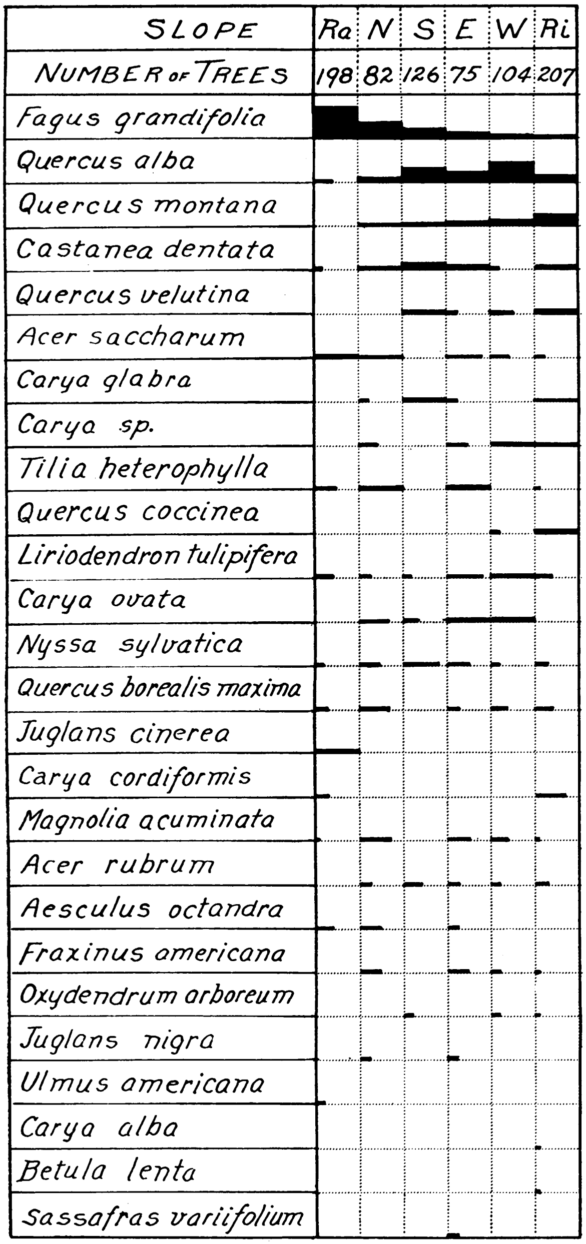

FIG. 34. Percentage composition of canopy of forest communities of different slope exposures, of ravines, and of ridges near Peabody on Red Bird River (location 22 on map).

Aesculus octandra, although either or both may drop out before the geographical limits of this association are reached. Both are numerically important constituents of the mixed mesophytic forest of the Cumberland Mountains. Neither is a constituent of any other than mixed mesophytic forest. That the ranges of these species coincide fairly well with the limits of the mixed mesophytic forest is emphasized by a consideration of the limits of their ranges. Neither is listed by Fosberg and Walker (1941) for the Shenandoah National Park, which is east of the area of dominance of the mixed mesophytic climax. Northward, their ranges terminate about where the mixed mesophytic forest ends (see Schaffner 1932, and map of distribution in Indiana, Deam 1940). Westward, these species drop out in the broad ecotone between the mixed mesophytic and the oak-hickory forests.

Climate alone is not sufficient to account for the dominance of this climax in this area. Past physiographic history, and the influence of the major soil type or zonal soil type (a reflection of climate) must also be considered.

A climate characterized by abundant and well-distributed precipitation and great temperature range with cold winters and hot humid summers marks this area (see Fig. 2). Westward the tendency to summer droughts is greater; southward the winters are more open. Dry summers are detrimental to the most mesophytic species. *Aesculus octandra* is the first of these species to be affected by deficient water; leaf-fall (due to dryness) may occur in July. Obviously, where summer drought is the rule, such a species would be eliminated because of shortness of the vegetative season. Open winters favor leaching of the soil, reducing its fertility. This is reflected in the development of the red-and-yellowerths, less favorable to mixed mesophytic forest, and generally

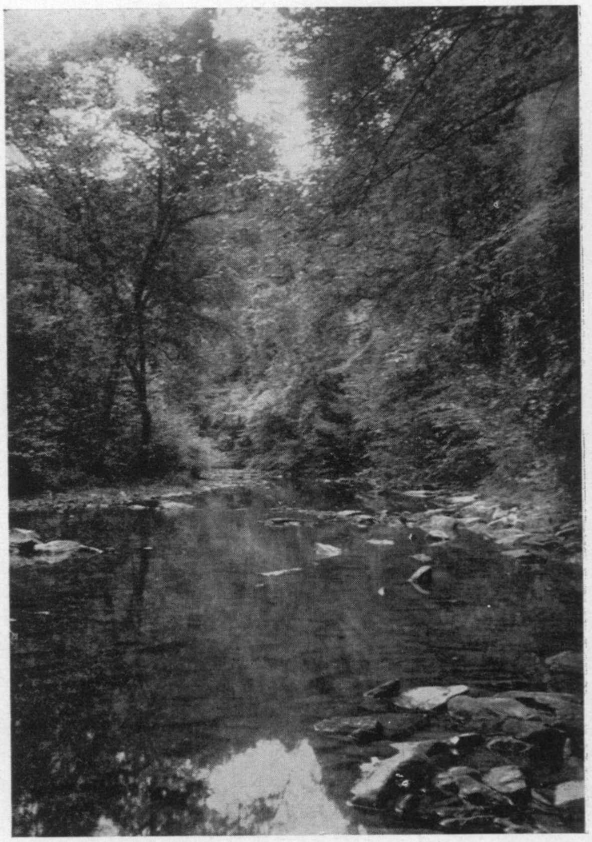

FIG. 35. Poor Fork of Cumberland River above Cumberland. Steep forested slopes of Black Mountain descend to river on the right. On the left, river birch *(Betula nigra)* overhangs the stream.

occupied by some type of oak or oak-pine forest. The development of the mull type of humus layer is inhibited on leached and acid soils. These soil factors, dependent on climate and affected by forest type, are in turn influential in maintaining the mixed mesophytic forest.

Wherever, within the area of the Cumberland Mountains, the optimum area of mixed mesophytic forest, the influence of underlying rock is so strong as to overcome the regional forces (as on dipping sandstone strata of Pine Mountain, and locally on sandstone ridges) the mixed mesophytic forest is interrupted. Some other forest type, generally oak-chestnut or pine, develops, maintaining itself as a physiographic climax on such dry slopes and ridges. Poorer soils, derived from some of the non-calcareous shales of the Pottsville series, sometimes result in an increase in the proportion of beech, if habitat factors are otherwise favorable to the development of the mixed mesophytic forest. The limits of the Cumberland Mountains vegetation are perhaps accentuated in places because of this. As an example, note the composition of forest communities near Peabody (at location 22 on map) a few miles up Red Bird River from Big Creek and some twenty-five miles downstream from its source, and 15 to 20 miles downstream from Nolans Branch (location 20).

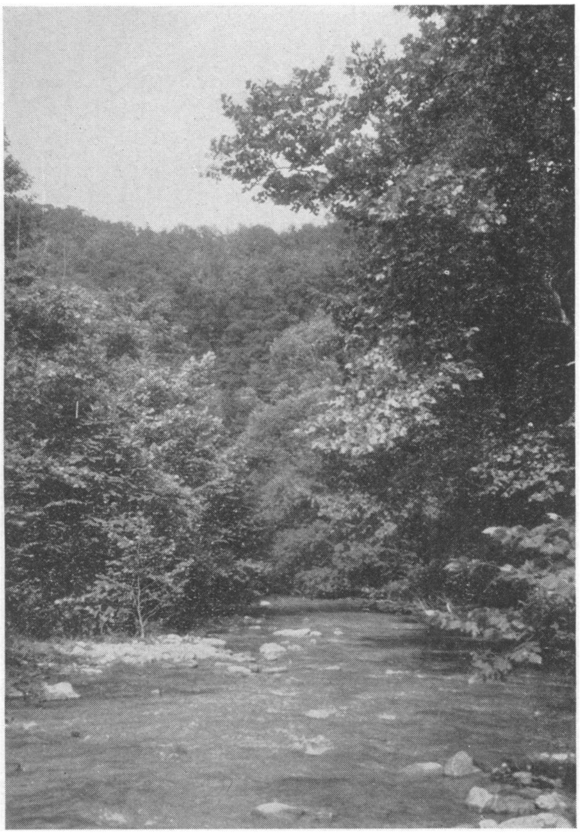

FIG. 36. Red Bird River near Nolans Branch. Mesophytic forest comes almost to the water's edge on the slope in the center of the picture. Sycamore on either side on flatter shores.

Throughout the Cumberland Mountains, the dominance of mixed deciduous forest is evident. From any eminence from which one may view a thousand feet or so of mountain slope with its ravines and ridges, it is the impression of mixed forest which prevails. Some localization of species will appear here and there, but only near the ridge crests does any great change in forest take place. It is only closer observation within the forest that discloses the niceties of variation in composition and makes possible a correlation of these variations with habitat fluctuations. The recognition of association-segregates became a necessity in interpreting the forest as a whole (Braun 1935a). Unless all are recognized as integral parts of the climax, an interpretation of some of them as seral stages would be necessary. There is no evidence for this. If an hypothetical climax is conceived, which approaches in composition some one of the communities actually present, which shall be selected? And if microclimates resulting from the great diversity of topography are to be set aside in picturing a "regional" climate, what shall that climate be? The climate of the peneplain which may presumably some day occupy this location cannot be the climate of a mountainous area. The climate of the area together with the innumerable temperature and moisture variations—the microclimates—is a climate largely affected by the mountains which influence summer rains. The mixed mesophytic forest with its several association-segregates is the response to these conditions. Its areal distribution has been affected in the past by physiographic changes and accompanying climatic changes. It finds, in an area of mature topography resulting from the dissection of the ancient Cumberland peneplain (mid-Tertiary), and unaffected by later peneplains (as was the Ridge and Valley Province) an optimum area where is preserved a mixed forest enriched through the ages by migrations into it, and little affected by the profound changes which affected deciduous forest farther west and farther north.

SUMMARY

The area studied comprises the Cumberland Mountains physiographic section located in southeastern Kentucky and adjacent Virginia and extending into Tennessee; an area of approximately 5,000 square miles. The range of elevation is from about 1,000 feet to 4,250 feet. Subdivisions recognized in the area include (1) the higher and most characteristic central part, Black and Log Mountains; (2) the bordering monoclinal mountains with dipping strata, Pine, Cumberland and Stone Mountains; (3) a large section exterior to the fault block. The vegetation of these subdivisions is discussed separately.

Mixed deciduous forest of superlative quality originally covered most of the area. This is now represented by rapidly diminishing areas of virgin forest

and extensive cut-over and secondary stands. The emphasis throughout this paper is on original forest.

Studies show that forest composition varies with slope exposure and to some extent with altitude. Except in a few habitats, mixed mesophytic forest prevails. The variations in composition and shifting dominance of species of the mixed mesophytic forest are illustrated by charts showing percentage composition of canopy trees. The nature of the undergrowth correlates well with the composition of canopy. In all areas of mixed mesophytic forest, the mull type of humus layer has developed. Locally, departure from mixed mesophytic forest, due to extreme edaphic factors, is seen.

The Cumberland Mountains are the center of distribution of the mixed mesophytic forest. This is emphasized by the large number of association-segregates of the mixed mesophytic association, the large size of trees, large number of species in the canopy, and wide range of habitat of climax species.

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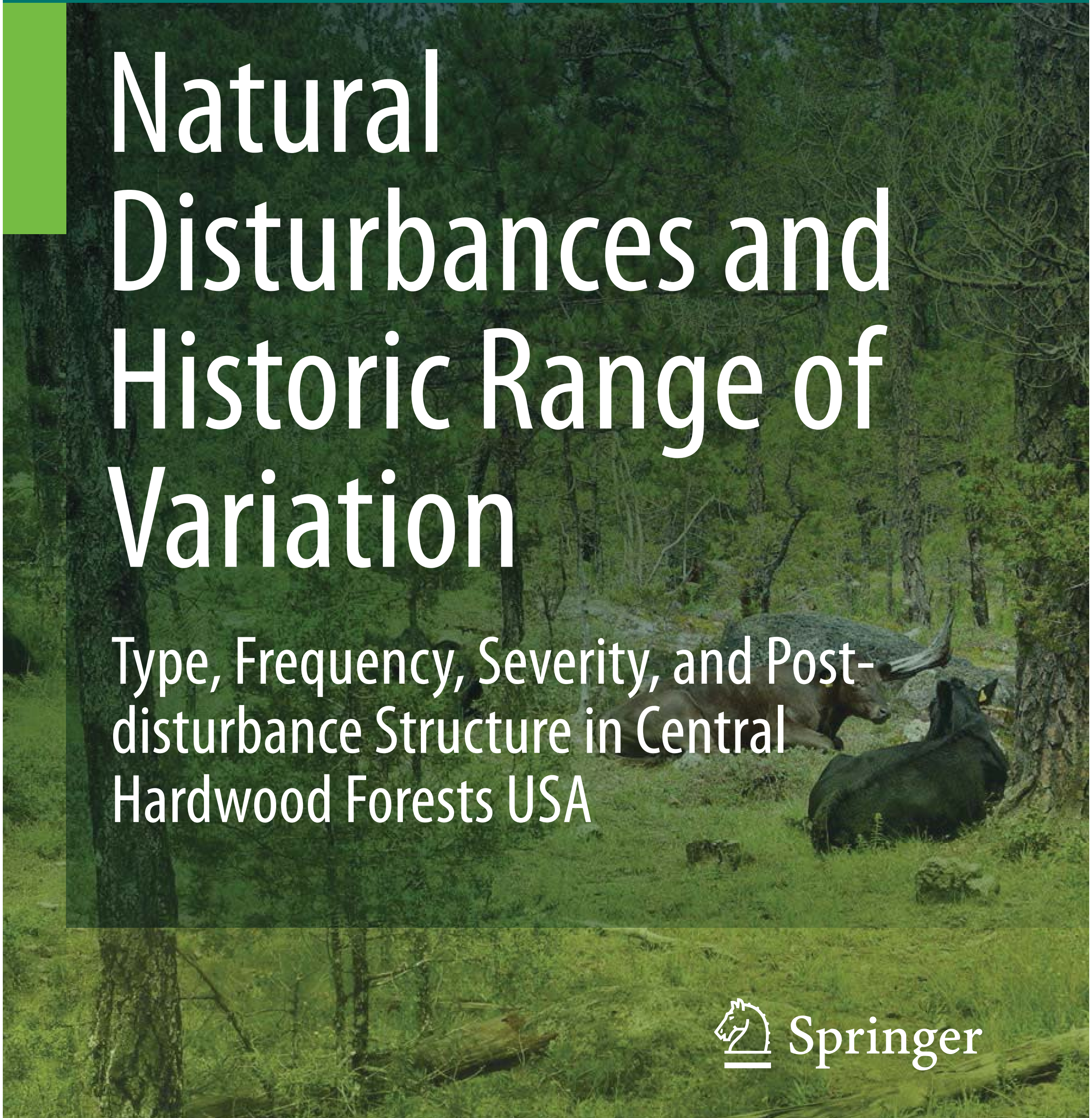

Natural Disturbances and Historic Range of Variation

Type, Frequency, Severity, and Post-disturbance Structure in Central Hardwood Forests USA

Springer

Managing Forest Ecosystems

Volume 32

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Type, Frequency, Severity, and Post-disturbance Structure in Central Hardwood Forests USA

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ISSN 1568-1319 ISSN 2352-3956 (electronic)
ISBN 978-3-319-21526-6 ISBN 978-3-319-21527-3 (eBook)
DOI 10.1007/978-3-319-21527-3

Library of Congress Control Number: 2015953434

Springer Cham Heidelberg New York Dordrecht London
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Preface

This edited volume addresses the historic range of variation (HRV) in types, frequencies, severities, and scales of natural disturbances, and how they create heterogeneous structure within upland hardwood forests of Central Hardwood Region (CHR). The idea for this book was partially in response to a new (2012) forest planning rule which requires national forests to be managed to sustain 'ecological integrity' and within the 'natural range of variation' of natural disturbances and vegetation structure. This new mandate has brought to the forefront discussions of HRV (e.g., what is it?) and whether natural disturbance regimes should be the primary guide to forest management on national forests and other public lands. Natural resource professionals often seek 'reference conditions,' based on HRV, for defining forest management and restoration objectives. A large body of literature addresses changes in forest structure after natural disturbance, but most studies are limited to a specific site, disturbance event, forest type, or geographic area. Several literature reviews address a single natural disturbance type within a limited geographic area (often not the CHR), but do not address others or how their importance may differ among ecoregions. Synthesizing information on HRV of natural disturbance types, and their impacts on forest structure, has been identified as a top synthesis need.

Historically, as they are today, natural (non-anthropogenic) disturbances were integral to shaping central hardwood forests and essential in maintaining diverse biotic communities. In addition to a 'background' of canopy gaps created by single tree mortality, wind, fire, ice, drought, insect pests, oak decline, floods, and landslides recurringly or episodically killed or damaged trees, at scales ranging from scattered, to small or large groups of trees, and across small to large areas. Additionally, some animals, such as beavers, elks, bisons, and perhaps passenger pigeons, functioned as keystone species by affecting forest structure and thus habitat availability for other wildlife species. Prehistoric anthropogenic disturbances – fire and clearing in particular – also influenced forest structure and composition throughout much of the CHR and therefore the distribution of disturbance-dependent wildlife species. The spatial extent, frequencies, and severities differed among these natural disturbance types and created mosaics and gradients of structural conditions and canopy openness within stands and across the landscape.

A full-day symposium, organized by the editors, at the 2014 Association of Southeastern Biologists conference in Spartanburg, South Carolina, was the basis for this book. Our goal was to present original scientific research and knowledge synthesis covering major natural disturbance types, with a focus on forest structure and implications for forest management. Chapters were written by respected experts on each topic with the goal of providing current, organized, and readily accessible information for the conservation community, land managers, scientists, students and educators, and others interested in how natural disturbances historically influenced the structure and composition of central hardwood forests and what that means for forest management today.

Chapters in this volume address questions sparked by debated and sometimes controversial goals and 'reference conditions' in forest management and restoration, such as the following: What was the historic distribution, scale, and frequency of different natural disturbances? What is the gradient of patch sizes or level of tree mortality conditions created by these disturbances? How do gradual disturbances such as oak decline, occurring over a long period of time and across a broad landscape, differ in effects from discrete disturbances such as tornadoes? How does topography influence disturbance regimes or impacts? How do native biotic (insects or fungi, keystone wildlife species) and abiotic (precipitation, drought, temperature, wind, and soil) agents interact to alter disturbance outcomes? What was the diversity of age classes and gradient of forest structure created by natural disturbances alone? How might disturbance-adapted plants and animals have fared in the hypothetical historic absence of anthropogenic disturbances? How might climate change alter disturbance regimes and structure of upland hardwood forests in the future? And finally, should, and how, can land managers manage these forests within the HRV of natural disturbance frequencies, spatial extents, and gradient of conditions they create?

We sincerely thank all those who encouraged and aided in the development of this book. Each chapter was peer-reviewed by at least two outside experts and both coeditors, and we thank these colleagues for their useful suggestions: Chris Asaro, Robert Askins, Francis Ashland, Bart Cattanach, Steven Croy, Kim Daehyun, Dianne DeSteven, Chris Fettig, Mark Harmon, Matthew Heller, Louis Iverson, John Kabrick, Tara Keyser, Scott Lecce, William MacDonald, Henry McNab, Manfred Mielke, Billy Minser, Scott Pearson, Duke Rankin, Jim Rentch, John Stanturf, Scott Stoleson, Ben Tanner, and Thomas Wentworth. We also thank the Association of Southeastern Biologists for allowing us to host a conference symposium on this important topic, and the National Forests of North Carolina for assistance with travel costs for speakers. We especially thank each author for contributing, and for timely chapter revisions, which made this book possible.

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Chapter 12

The Historic Role of Humans and Other Keystone Species in Shaping Central Hardwood Forests for Disturbance-Dependent Wildlife

Cathryn H. Greenberg, Kendrick Weeks, and Gordon S. Warburton

Abstract Multiple natural disturbance types historically created conditions that were suitable for many, but not all, disturbance-dependent wildlife species in the Central Hardwood Region (CHR). In addition, some wildlife species, such as beavers, passenger pigeons, elk, and bison, historically functioned as keystone species by creating or maintaining unique disturbed habitats that otherwise would be rare. For millennia, humans (Native Americans, and later European settlers) also created and maintained early successional habitat variants (estimated at 7–43 % of the CHR landscape in 1500 AD) including farmlands, old fields in different stages of succession, grasslands, and open woodlands by clearing for cultivation and settlements, frequent burning, and old field abandonment. In this chapter, we argue that humans were a keystone species in the CHR, having a major influence on the diversity, distribution, and abundance of many disturbance-dependent wildlife species by creating, maintaining, or greatly expanding specific, unique types of early successional habitats and some mature forest types dominated by shade-intolerant pioneer species, such as yellow pine. Determining the largely unknowable historic range of variation of natural disturbances, selecting an arbitrary moment on a temporally and spatially dynamic landscape as a reference, and subjectively deciding what should

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C.H. Greenberg, B.S. Collins (eds.), *Natural Disturbances and Historic Range of Variation*, Managing Forest Ecosystems 32,
DOI 10.1007/978-3-319-21527-3_12

or should not be included as 'natural' may not serve as the most productive guide for conservation. Alternatively, forest and land use planning for diverse wildlife conservation might more logically start with clear objectives, and proceed with management activities targeted toward attaining them.

Keywords Wildlife • Keystone species • Humans • Ecosystem engineers • Disturbance-dependent birds

12.1 Introduction

Disturbance-dependent wildlife species require open structural conditions created immediately after forest disturbances or at some point early in the dynamic process of recovery and maturation. Historically, natural disturbances (e.g., Chaps. 1, 2, 3, 4, 5, 6, 7, 8, 9, this volume) provided habitats for many disturbance-dependent species by creating patches of young forest structure, from small canopy gaps to large swaths of partial or complete canopy removal, within a mature upland hardwood forest matrix of the Central Hardwood Region (CHR). In addition, some wildlife species, such as beavers (*Castor canadensis*), passenger pigeons (*Ectopistes migratorius*), elk (*Cervus canadensis*), and bison (*bison bison*), historically functioned as keystone species by creating or maintaining unique disturbed habitats such as wetlands or prairies that would otherwise be rare, thereby increasing the abundance, diversity, and distribution of wildlife species that required them. Hence, multiple natural disturbance types historically created conditions that were suitable for many, but not all, disturbance-dependent wildlife species. However, several breeding birds (Askins 2001) and other wildlife species of the CHR such as woodchucks (*Marmota monax*) and rabbits (*Sylvilagus floridanus*) require specific variants of disturbance-created habitats that were created, maintained, or expanded in large part by humans (*Homo sapiens*) through active land management by clearing, frequent burning, and land abandonment in and surrounding inhabited areas, for thousands of years (Delcourt and Delcourt 2004).

In this chapter, we argue that humans were a keystone species in the CHR, having a major influence on the diversity, distribution, and abundance of many disturbance-dependent wildlife species by creating, maintaining, or greatly expanding specific, unique types of early successional habitats and some mature forest types dominated by shade-intolerant pioneer species, such as yellow pine (*Pinus spp*.). Through land use and active land management by clearing, farming, and frequent burning Native Americans (and later European settlers) created settlements, gardens, farmlands, meadows and prairies, open woodlands, [river] canebreaks (*Arundinaria gigantea*), and old fields at varying stages of succession that included successional yellow pine forests (Delcourt and Delcourt 2004). We use results of studies on natural disturbances, paleoecology, archeology, and historical accounts by early explorers to illustrate and discuss likely dynamic scenarios of prehistoric (prior to European settlement) CHR landscapes, and availability of different early successional habitat variants required by disturbance-dependent wildlife. We focus our discussion on disturbance-created habitats rather than wildlife species per se, because habitat availability likely governed the distribution of many disturbance-dependent wildlife species historically, as it does today. We use disturbance-dependent breeding birds to illustrate possible scenarios of historic wildlife distribution because they are among the most thoroughly studied taxa, and many species are specialized in their associations with specific variants of early successional habitat (MacArthur and MacArthur 1961) that include disturbed young forests, but also other land uses and conditions commonly created by humans (Askins 2001).

12.2 Origin and Early History of Central Hardwood Forests: Climate, Megafauna, and Humans

Human arrival in the CHR coincided with retreating ice sheets and a warming climate more than 13,000 years before present (BP), as open tundra-boreal ‘parklands’ dominated by spruce (*Picea* sp.) and jack pine (*P. banksiana*) were slowly being replaced by temperate, deciduous forest migrating north from warmer more southerly refuges (Delcourt and Delcourt 2004). During the last ice age, glaciers in North America extended south as far as the Missouri and Ohio Rivers, and east to New England (Clark et al. 2009), and a colder, drier climate resulted in alpine tundra in the Blue Ridge Mountains above 1,450 m (Delcourt and Delcourt 2004). Between 18,000 years and 5,000 years BP, climate in the CHR shifted from arid-cool to the warm-humid climate of today (Carroll et al. 2002), interrupted by glacial re-advancing with associated cold and drought during the Younger Dryas period (12,800–11,500 years BP) (http://en.wikipedia.org/wiki/Younger_Dryas), and a rapid warming (more than 7° C in 50 years) around 11,500 years BP (the Pre-boreal transition phase) (http://en.wikipedia.org/wiki/Boreal_(age)). Warmer temperatures during the hypsithermal (7,500–5,000 years BP) were followed by a cooling trend (5,000–120 years BP) that included the Little Ice Age (600–120 years BP) (Carroll et al. 2002). Oak-chestnut-hickory (*Quercus-Castanea-Carya*) forests became widespread in the CHR by 3,000 years BP (Dickinson 2000; Delcourt and Delcourt 2004). Past climate change and associated disturbance regimes, even in recent millennia, has been a major ‘background’ natural disturbance in the CHR and resulted in major shifts in forest composition and habitats, as well as extinctions and reassembly of wildlife communities.

When humans first arrived, megafauna including ancient and modern bison (*Bison antiquus* and *B. bison*), elk, primitive horses (*Equus* spp.), wooly mammoths (*Mammuthus* sp.), mastodons (*Mammut* sp.), stag-moose (*Cervalces scotti),* and giant ground sloth (*Megalonyx* sp. and others), as well as extant modern wildlife species associated with boreal forest and tundra, such as muskox (*Ovibos muschatus*) and caribou (*Rangifer tarandus*) inhabited much of the CHR (Carroll et al. 2002; O’Gara and Dundas 2002; http://exhibits.museum.state.il.us/exhibits/larson/ice_age_animals.html; http://parks.ky.gov/parks/historicsites/big-bone-lick/history.

aspx). A mere 14,000 years ago or less, grazing, browsing, and trampling by keystone megafauna herbivores were important natural disturbances, shaping forests and maintaining open habitats (e.g., Svenning 2002) for many disturbance-dependent species.

Most of these megafauna are now extinct; the relative roles of an overall warming climate, associated shifts in vegetation composition and structure, and the arrival of big-game hunting humans (the Clovis culture) to their extinction is hotly debated (Burney and Flannery 2005; Koch and Barnosky 2006; Askins 2014). Theories that extinctions were precipitated through over-hunting by humans are supported by archaeological evidence at multiple sites, showing human arrival just prior to local extinctions of remaining megafauna (many populations collapsed from 14,800 to 13,700 years BP; Gill et al. 2009). Mosimann and Martin (1975) hypothesized and developed simulations illustrating how even a small founding population of humans could multiply quickly enough to extirpate the slow-reproducing megafauna under a steady hunting regime, with extinctions progressing in a front, beginning in Alaska where humans first entered North America, and moving slowly south and east (Burney 1993). The coincidental timing of extinctions of many megafauna species with the arrival humans is corroborated by a study of spores in lake sediments in upstate New York, Ohio, and Indiana (Gill et al. 2009). The study showed that the abundance of *Sporomiella*, a fungus that grows on the dung of herbivorous mammals, declined dramatically between 14,000 and 13,000 years BP, indicating that large mammals also declined during that period and coinciding with human arrival. This decline was followed by an increase in deciduous trees (possibly released by the absence of grazing and browsing by keystone megafauna), and more frequent fires (possibly set by humans and/or fueled by denser vegetation), as evidenced by increased charcoal particles in the sediments (Gill et al. 2009). Many of the mammals that became extinct at the end of the Pleistocene had survived similar glacial-interglacial transitions for hundreds of thousands of years, suggesting that humans may have played an important and perhaps complex role in their demise (Burney and Flannery 2005; Koch and Barnosky 2006).

Whether through their hypothesized role in extinction of megafauna or (and) their documented role in the more recent extinction or local extirpation of modern fauna, the predatory activities of humans have dramatically and directly influenced many wildlife populations in the CHR. In the last 250 years or less, European settlers were directly responsible for the extinction of several species including the Carolina parakeet (*Conuropsis carolinensis*) and passenger pigeon; the regional extirpation of wolves (*Canis lupus*), cougars (*Puma concolor*), bison, elk, and other species; and dramatic population declines of other species such as beavers through excessive and unregulated hunting and trapping. By removing keystone wildlife species such as beaver (wetland creators), or elk and bison (grazers) whose activities historically created or maintained disturbed, open habitats, humans also indirectly influenced the distributions and populations of many disturbance-dependent wildlife species.

Perhaps most importantly, humans themselves have historically functioned as a keystone species through their management and use of land on inhabited landscapes

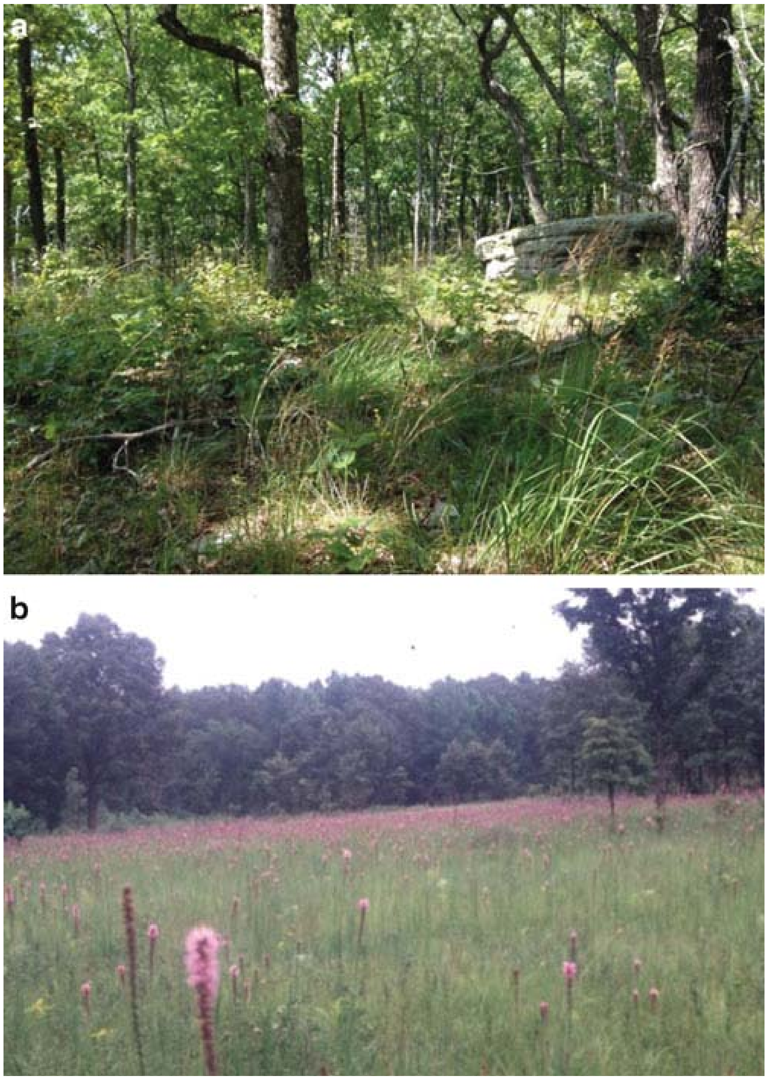

Fig. 12.1 (**a**) Open woodland with grass-forb-woody understory (Similar to descriptions by early explorers in the Cumberland Plateau, Piedmont of the Carolinas and Georgia, and Appalachians on South- and West-facing aspects of the southern Appalachians) on private land in Sequatchie County, Tennessee in 2013. The woodland, initially closed canopy forest, was not mechanically thinned, and was burned every 2–3 years since the late 1970s (Craig Harper pers. comm; photo courtesy of Craig Harper); (**b**) Native prairie vegetation at Ft. Campbell in Kentucky and Tennessee managed with burning or mowing at 1–3 year intervals (Daniel Moss pers. comm.) (Photo courtesy of William Minser)

since before central hardwood forests existed as we know them today. By regularly creating, maintaining, or expanding early successional habitats, including many variants that might rarely be created by natural disturbances alone such as agricultural fields, old fields in different stages of succession, open woodlands (e.g., Fig. 12.1a), meadows or prairies (e.g., Fig. 12.1b), and successional yellow pine-dominated forests, humans historically were a major influence on abundance, distribution, and species diversity of disturbance-dependent fauna.

12.3 Early Successional Habitats: One Size Does Not Fit All

The term 'early successional habitat' is commonly, albeit erroneously, used generically to refer to any open, recently disturbed habitat that is transient unless maintained by recurring disturbances (Greenberg et al. 2011a). Although both young forest and truly early successional habitats share the features of openness in common, they differ considerably in many ways in the structure and composition of plants (Lorimer 2001; Greenberg et al. 2011a) and, because of that, the wildlife species that use them. In the CHR, high-severity natural disturbances such as large blowdowns, or anthropogenic disturbances such as regeneration harvests, create young forest with high woody stem density and thick cover for wildlife, but generally do not create bona fide successional conditions with high plant species turnover. Even after high-severity natural disturbances that substantially reduce canopy cover, plant species composition usually remains similar to the original mature forest, often with a transient addition of blackberry (*Rubus* spp.) or pokeweed (*Phytolacca americana*), as pre-existing shrubs and fallen or damaged trees resprout prolifically and tree seedlings grow from pre-established advance regeneration or seed (Lorimer 2001; Greenberg et al. 2011b). In the CHR open, young forest conditions typically last 8–15 years before canopy closure (Loftis et al. 2011; Thompson and Dessecker 1997).

In contrast, truly successional habitats occur when pioneer plants colonize treeless areas that are no longer disturbed. In the CHR, most successional habitats originate from anthropogenic land uses, such as abandoned pasture or farmlands, as colonizing shade-intolerant pioneer tree species, including yellow pines (e.g., pitch (*P. rigida*), shortleaf (*P. echinata*), or Virginia pine (*P. virginiana*)), yellow-poplar (*Liriodendron tulipifera*), or black locust (*Robinia pseudoacacia*) (Delcourt and Delcourt 2004), and shrubs create conditions suitable for other, later successional species in a relay sequence toward a mature hardwood forest (Lorimer 2001; Greenberg et al. 2011a).

Disturbance-dependent breeding birds are associated with open habitats created by disturbances, but many are relatively specialized, requiring specific but different variants of early successional habitats ranging from young forest to grasslands (Askins 2001; Hunter et al. 2001) (Table 12.1). In this chapter we use the term 'early successional habitat' as it is commonly used and understood in the wildlife literature to denote open conditions created by either natural or anthropogenic disturbances (Greenberg et al. 2011a). However, we emphasize that 'one size does not fit all' for disturbance-dependent wildlife species, and therefore different variants of early successional habitats, created by both natural and anthropogenic disturbances, and interactions between them, are required to maximize diversity and abundance of native, disturbance-dependent breeding birds.

Table 12.1 Associations of select disturbance-dependent breeding bird species of the CHR with different early successional habitat variants[a] created by natural or anthropogenic disturbances

	Early successional habitat variants[a]										
Species	GH	WM	OW	Sa	SS	SF	Pa	Ag	OF	Su	Ur
American goldfinch (*Carduelis tristis*)	X	X	X	X	X	X	X	X	X	X	–
American kestrel (*Falco sparverius*)	X	–	–	X	–	–	X	X	–	–	–
American robin (*Turdus migratorius*)	X	–	X	X	–	–	X	X	–	X	–
American woodcock (*Scolopax minor*)	–	–	X	–	X	X	–	–	–	–	–
Barn owl (*Tyto alba*)	X	–	–	X	–	–	X	X	–	–	–
Barn swallow (*Hirundo rustica*)	X	X	–	X	–	–	–	X	–	X	–
Bewick's wren (*Thryomanes bewickii*)	X	–	X	X	–	–	–	–	–	X	–
Blue grosbeak (*Passerina caerulea*)	–	–	X	–	X	–	–	–	X	–	–
Blue-winged warbler (*Vermivora pinus*)	–	–	X	X	X	–	–	–	X	–	–
Bobolink (*Dolichonyx oryzivorus*)	X	–	–	–	–	–	–	–	–	–	–
Brown thrasher (*Toxostoma rufum*)	–	–	X	X	X	X	–	–	–	X	–
Carolina wren (*Thyrothorus ludovicianus*)	X	–	X	X	–	–	–	–	–	X	–
Chestnut-sided warbler (*Setophaga pensylvanica*)	–	–	X	–	X	–	–	–	–	–	–
Chipping sparrow (*Spizella passerina*)	X	–	X	X	–	–	X	X	–	X	–
Common nighthawk (*Chordeiles minor*)	–	–	X	X	–	–	–	–	–	X	X
Common yellowthroat (*Geothlypis trichas*)	–	–	X	–	X	–	–	–	X	–	–
Dickcissel (*Spiza americana*)	X	–	–	X	–	–	X	X	–	–	–
Eastern bluebird (*Sialia sialis*)	X	–	X	X	–	–	X	X	–	X	–
Eastern kingbird (*Tyrannus tyrannus*)	X	–	–	X	–	–	–	–	–	–	–
Eastern meadowlark (*Sturnella magna*)	X	–	–	–	–	–	X	–	–	–	–
Eastern phoebe (*Sayomis phoebe*)	X	–	X	X	–	–	–	X	–	X	–
Eastern towhee (*Pipilo erythrophthalmus*)	–	–	X	X	X	X	–	–	–	X	–
Field sparrow (*Spizella pucilla*)	–	–	X	X	X	–	–	–	–	–	–
Golden-winged warbler (*Vermivora chrysoptera*)	–	X	X	–	X	–	–	–	–	–	–
Grasshopper sparrow (*Ammodramus savannarum*)	X	–	–	–	–	–	–	–	–	–	–
Gray catbird (*Dumetella carolinensis*)	–	–	X	–	X	X	–	–	–	X	–
Henslow's sparrow (*Ammodramus henslowii*)	X	X	–	–	–	–	X	–	–	–	–
Horned lark (*Eremophila alpestris*)	X	–	–	–	–	–	X	X	–	X	–
House wren (*Troglodytes aedon*)	X	–	X	X	–	–	–	–	–	X	–
Indigo bunting (*Passerina cyanea*)	–	–	X	X	X	–	–	–	–	X	–
Loggerhead shrike (*Lanius ludovicianus*)	X	–	X	X	–	–	X	X	–	–	–
Mourning dove (*Zenaida macroura*)	X	–	X	X	–	–	X	X	–	X	–
Northern bobwhite (*Colinus virginianus*)	X	–	X	X	–	–	–	–	–	–	–
Northern cardinal (*Cardinalis cardinalis*)	–	–	X	–	X	X	–	–	X	X	–
Northern mockingbird (*Mimus polyglotus*)	X	–	X	X	–	–	–	–	–	X	–

(continued)

Table 12.1 (continued)

	Early successional habitat variants[a]										
Species	GH	WM	OW	Sa	SS	SF	Pa	Ag	OF	Su	Ur
Northern rough-winged swallow (*Stelgidopteryx serripennis*)	X	X	–	–	–	–	–	X	–	–	–
Orchard oriole (*Icterus spurius*)	–	–	X	X	–	–	–	–	X	–	–
Prairie warbler (*Setophaga discolor*)	–	–	X	–	X	X	X	–	–	–	–
Purple martin (*Progne subis*)	X	X	–	X	–	–	X	X	X	–	–
Red-headed woodpecker (*Melanerpes erythrocephalus*)	–	X	X	X	–	–	–	–	–	–	–
Red-tailed hawk (*Buteo jamaicensis*)	X	–	X	X	–	–	X	X	X	X	X
Red-winged blackbird (*Agelaius phoeniceus*)	–	X	–	–	–	–	–	–	–	–	–
Ruffed grouse (*Bonasa umbellus*)	–	–	X	X	X	X	–	–	–	–	–
Savannah sparrow (*Passerculus sandwichensis*)	X	–	–	–	–	–	–	–	–	–	–
Song sparrow (*Melospiza melodia*)	X	–	X	X	–	–	–	–	–	X	–
Tree swallow (*Tachycineta bicolor*)	–	X	–	X	–	–	–	X	–	–	–
Vesper sparrow (*Pooecetes gramineus*)	X	–	–	–	–	–	–	–	–	–	–
White-eyed vireo (*Vireo griseus*)	–	–	X	–	X	X	–	–	–	–	–
Yellow-breasted chat (*Icteria virens*)	–	–	X	–	X	X	–	–	X	–	–

[a] *GH* grass-herbaceous, *WM* wet meadow, *OW* open woodland, *Sa* savanna, *SS* scrub-shrub, *SF* sapling forest, *Pa* pasture, *Ag* agricultural, *OF* old field, *Su* suburban, *Ur* urban

12.4 Natural Disturbances and Early Successional Habitats for Wildlife: Severe Weather, Weather-Related, and Biotic Agents

Historically, non-anthropogenic natural disturbances created variable age classes and structural conditions across small- to large areas, at different locations and times in a shifting mosaic of ephemeral patches, with young forest composing varying proportions of the vast CHR landscape at any given time. Mobile, disturbance-dependent wildlife species could use these transient young forest habitats opportunistically. However, in the hypothetical absence of human-caused disturbances, their populations would almost certainly have been variable, fluctuating spatially and temporally as conditions became available for brief periods before becoming unsuitable as forests recovered and matured.

12.4.1 Severe Weather

Based on records over the past 150 years or less, disturbance types, frequencies, and severities historically varied temporally and spatially within and among ecoregions, and locally across topography. For example, in the CHR hurricane-related winds are more frequent in eastern ecoregions, whereas tornados are more frequent in western ecoregions but also commonly occur in the Piedmont, Ridge and Valley, and Southwestern Appalachians ecoregions (see Peterson et al. Chap. 5). Damage from hurricane-related winds is variable. For example in the Blue Ridge Mountains, Hurricane Opal (whose track did not enter the ecoregion despite considerable damage there) caused single- to multiple-tree windthrows from downbursts of wind (McNab et al. 2004), whereas damage from Hurricane Hugo included tens of thousands of hectares rated as "total timberland damaged" (Dogett 1993). Ice storms (Lafon Chap. 7) and landslides (Wooten et al. Chap. 9) are most common on steep slopes in mountainous ecoregions such as the Blue Ridge Mountains. The impacts of severe weather disturbances on central hardwood forests ranged from small gaps (Hart Chap. 2) to large swaths of broken limbs and (or) fallen trees, creating a gradient of young forest conditions potentially suitable for gap, edge, scrub-shrub, or sapling-stage breeding bird species (Table 12.1).

12.4.2 Lightning-Ignited Fire

Lightning-ignited fires are rare in the deciduous forests of the CHR because fuels are generally too moist, discontinuous, or otherwise inadequate to allow spread except under severe drought conditions (e.g., Schroeder and Buck 1970; Barden 1997; Delcourt and Delcourt 1997; Flatley et al. 2013; also see Sect. 12.7.1). Schroeder and Buck (1970) estimated that about 1–5 lightning ignitions occur annually per 4,000 km^2 in the CHR. The wildfire reporting database for National Forests shows that within CHR National Forests, lightning ignites an average of 0.3–7.8 fires per 2,000 km^2 annually; in contrast humans, accidentally or purposefully, ignite an average of 4.8–93.9 wildfires (not including prescribed burns) per 2,000 km^2 annually (Greenberg et al. Chap. 1, Table 1.6). Guyette et al. (2006a) estimated fewer than one in 200 wildfires in the CHR were lightning ignited; the rest were due to arson, cigarettes, unattended campfires, or other anthropogenic causes. Historic fire frequencies positively corresponded with human population densities and far exceeded probable frequencies attributable to lightning ignition (Guyette et al. 2006a, b; Hart and Buchanan 2012; also see Grissino-Mayer Chap. 6; Leigh Chap. 8).

Studies in the Boston Mountains ecoregion suggest that topographic heterogeneity, or 'roughness' reduces fire frequency in general (Guyette et al. 2006b). However, lightning-ignited fires occur more frequently and with higher severity in some topographic positions, such as ridgetops and dry south-, southwest-, or west-facing slopes in the Blue Ridge Mountains ecoregion that tend to be low-quality, drier sites (Flatley et al. 2013). Not coincidentally, these topographic positions are also where Table Mountain pine (*P. rigida*), pitch pine, mountain laurel (*Kalmia latifolia*), and other plant species associated with dry, low-quality sites and occasional fire most commonly occur (Zobel 1969).

Under most conditions, wildfires in hardwood forests of the CHR are low-intensity, and changes to forest structure and breeding bird communities are relatively minor and transient (Greenberg et al. 2013). Exceptions may occur during infrequent, extreme drought conditions, or on steep topography and ridgetops with xeric, low site quality conditions that are more conducive to hot, high-severity fires that result in heavy tree mortality. A combination of low lightning ignition frequency and the relatively random location of lightning strikes across the vast CHR render it unlikely that lightning-ignited fires alone would have repeatedly burned the same landscapes with sufficient frequency needed for the development and maintenance of prairies, savannas, open woodlands, or yellow pine forests (see Sect. 12.4.3) with occasional exceptions. When they did occur, lightning-ignited high-severity fires likely created open, young forest conditions with abundant standing snags potentially suitable for yellow pine regeneration (Jenkins et al. 2011) and for gap-, edge, scrub-shrub, sapling-stage, or open woodland breeding bird species (Table 12.1) (e.g., Greenberg et al. 2013).

12.4.3 *Southern Pine Beetle*

Historically, Native Americans (and later European settlers) promoted the development and maintenance of pine forests over mature, climax upland hardwoods on inhabited landscapes by actively managing with frequent fire, and by abandoning farmlands that were often colonized by yellow pines such as shortleaf, Virginia, and pitch pine (Ashe and Ayers 1901; Mattoon 1915; Ashe 1922; Balch 1928; Delcourt and Delcourt 2004). Such yellow pine-dominated forests are disappearing due to a combination of (1) southern pine beetle (*Dendroctonus frontalis*) attacks on yellow pine forests that established when Native Americans or European settlers (through the mid-1900s) were actively clearing, burning, and abandoning lands (see Nowak et al. Chap. 4), and (2) a dramatic reduction in the frequency of anthropogenic fire ignitions and (or) suppression of wildfires when they do occur (see Sect. 12.7.1). Without active land management by humans, yellow pine-dominated forests would likely have been limited in distribution to low quality sites and topographic positions where hardwood competition is reduced and lightning-ignited fires are more frequent. On a hypothetical CHR landscape without humans, the impact of southern pine beetles may have been minor across much of the landscape, because yellow pine forests would have been much more restricted in their distribution.

12.5 Keystone Wildlife Species: Bison, Elk, and Beaver as Agents of Disturbance and Ecosystem Engineers

Many animal species respond to, rather than drive, forest structure. However, some species were themselves agents of disturbance, functioning as keystone species by helping to create and maintain open, early successional conditions and wetlands that enabled many other wildlife species to thrive. Elk, bison, beaver, and perhaps even passenger pigeons were especially notable ‘ecosystem engineers’ that historically had considerable impacts on the CHR landscape, often in close association with humans. In fact, a mutualism developed between Native Americans, and their large ungulate prey. Native Americans created prairies, open woodlands, and forest edge through frequent burning and clearing that enabled elk and bison to thrive; in turn, their grazing helped to arrest forest succession and maintain these grass-dominated habitats that ignited easily and carried fire across broad areas (Delcourt et al. 1998; McClafferty 2000; Delcourt and Delcourt 2004). This ‘graze and burn’ disturbance regime, co-managed by Native Americans and large ungulates, created structural conditions promoting higher densities and greater distributions of wildlife species requiring open, grassy habitats than would be possible in its absence (e.g., Table 12.1).

12.5.1 *Passenger Pigeon*

Passenger pigeons numbered 3–5 billion in eastern North America until the late 1800s when their population declined until their extinction in 1914 (Yeoman 2014). They ranged throughout most of eastern North America, wintering south of latitude 36° N and breeding in the northern part of the CHR including southern New York, west-southwest across Pennsylvania, northern West Virginia, and Kentucky as well as parts of the midwestern USA (Ellsworth and McComb 2003). Based on their massive numbers and collective mass, passenger pigeon flocks are thought to have been an important agent of low-intensity disturbance throughout much of the CHR, similar to that of ice storms or lower-intensity windstorms, by increasing light levels in forests through limb and tree breakage (Ellsworth and McComb 2003). They also covered the ground with several cm of feces at nesting and roosting sites, killing the understory vegetation and inhibiting plant growth for several years (see Ellsworth and McComb 2003), and potentially altering fuels structure by killing understory plants and creating coarse woody debris (Ellsworth and McComb 2003). Flocks, estimated at 105,000 pigeons per ha, commonly formed columns over 1 km wide and 400–450 km long (King 1866 as cited in Schorger 1955; Ellsworth and McComb 2003) and numbered in the millions (see Yeoman 2014). In 1871, naturalist A.W. Schorger estimated a communal nesting site covering 2,200 km^2 of sandy oak barrens in Wisconsin, with 136 million breeding adults (Yeoman 2014). Roosting and nesting areas, commonly 0.02–10 km^2 but sometimes as large as 130 km^2, were used by an estimated 27,000–36,000 kg per ha of pigeons (Ellsworth and McComb 2003).

Ellsworth and McComb (2003) estimated that historically, passenger pigeons affected approximately 0.5–0.8 % of their total winter range annually through their use of temporary and long-term roosts; breakage of smaller limbs and trees (lower-intensity disturbance) affected an estimated 8 % of their breeding area annually (Ellsworth and McComb 2003). Ellsworth and McComb (2003) suggest that low-intensity damage in nest areas likely resulted in a light environment favoring shade-tolerant tree species such as American beech (*Fagus grandiflora*), eastern hemlock (*Tsuga canadensis*), and sugar maple (*Acer saccharum*), and establishment of intermediate (moderately shade-tolerant) species such as oaks, in gaps. In contrast, severe physical damage in roost areas may have resembled damage from high winds, or even hot fires that top-kill most plants and add nutrients to the soil, resulting in high light levels and release of intermediate tree species such as oaks or eastern white pine (*P. strobus*) (Ellsworth and McComb 2003). The gradient of structural conditions created by passenger pigeons were likely suitable for gap-associated breeding birds such as cerulean warblers (*Setophaga cerulea*) (Perkins 2006) where damage was relatively light, to edge- and open area species such as indigo buntings (*Passerina cyanea*) where damage was more severe. Passenger pigeons also may have played an important role in seed and nut dispersal. Hence, prior to their extirpation by humans, passenger pigeons may have functioned as a keystone species by affecting forest composition as well as forest structure that in turn affected other wildlife species.

12.5.2 Beaver

Historically, beavers inundated riparian forests by damming slow-moving streams, creating large areas of boggy scrub-shrub wetlands with dead standing trees, or beaver meadows (see Greenberg et al. Chap. 1, Fig. 1.2 h) that supported wetland-dependent plants and animals. Beaver populations were estimated at between 60 and 400 million in pre-colonial North America (Seton 1929), and they occurred virtually anywhere with suitable water and food plant resources (Baker and Hill 2003). In his travels, Bartram noted that beaver 'abounded' north of Georgia (Van Doren 1928). Given the extremely high populations of beaver in pre-European times, the entire CHR surely included an extensive mosaic of beaver ponds and swamps of various sizes and configurations. Hey and Phillipi (1995) estimated that 40 million beavers in 1600 would have maintained 206,795 km^2 of water surface in the upper Mississippi and Missouri River basins; current beaver populations there may pond about 2,023 km^2. In the eastern USA, heavy beaver trapping for the fur trade began in the 1600s (Naiman et al. 1988). Between 1853 and 1877 the eastern USA Hudson Bay Company alone shipped three million pelts to England (http://www.ohiohistorycentral.org/w/American_Beaver?rec=1124). Beaver populations nearly vanished throughout North America by the 1900s due to excessive trapping for the fur trade (Naiman et al. 1988; Baker and Hill 2003).

Inundation of dammed waterways provides multiple benefits for wildlife and increases local landscape diversity. Beaver pond complexes provide standing water, edge, standing snags killed by flooding, plant diversity, and vertical stem diversity all in one area (Baker and Hill 2003). Wetland vegetation including sedges (*Carex* spp.), bulrush (*Scirpus* spp.), and cattails (*Typha* spp.) rapidly colonize newly created wetland complexes. Many wildlife species including waterfowl, wading birds, red-winged blackbirds (*Agelaius phoeniceus*), woodpeckers, migrating songbirds, raptors, aquatic furbearers such as mink (*Neovison vison*) and muskrat (*Ondatra zibethicus*), amphibians, and semi-aquatic reptiles such as bog turtles (*Clemmys muhlenbergii*) and water snakes colonize beaver ponds and wetlands, and use them for breeding and habitat (Baker and Hill 2003; Rosell et al. 2005). Historically, when beaver populations were high, at least some beaver ponds may have persisted for over 1,000 years (Ben Tanner unpubl. data). Abandoned beaver ponds eventually drain and are colonized by shrubs and grasses, sometimes lasting for years before eventually reverting to forest (Askins 2000). Historically, these beaver meadows and disturbed areas surrounding beaver ponds were likely extensive along floodplains, and provided habitats for shrub-scrub and some grassland bird species, rodents, lagomorphs, ungulates, and their predators (Askins 2000; Baker and Hill 2003).

Historically, frequent and continual creation and abandonment of beaver ponds across the CHR created diverse wetland habitats that facilitated a much higher local diversity, as well as abundance, landscape distribution and population connectivity for many more wildlife species than today. Some species with poor dispersal ability, such as bog turtles, have reached critically low population levels likely in part because of severely diminished beaver populations and the habitats they engineered (US Fish and Wildlife Service 2001); more than 90 % of mountain bog habitat has been lost (Walton 2006). Thus, prior to their near-extirpation by humans, beaver were historically perhaps one of the greatest animal agents of disturbance given the spatial extent and effects of their habitat alteration activities.

12.5.3 Elk

More than 10 million elk were estimated to have occurred in North America prior to the arrival of Europeans (Seton 1929). Modern elk have occupied the CHR for at least 20,000 years (McClafferty 2000; O'Gara and Dundas 2002), since (and for long after) boreal forest and tundra dominated the landscape (Delcourt and Delcourt 2004). There are many historical reports of large numbers of elk in the CHR. Place names such as Banner Elk, North Carolina (Blue Ridge Mountains ecoregion), Elk River in West Virginia (Central Appalachians and Allegheny Plateau ecoregions), and Elk Creek in Kentucky (Interior Plateau ecoregion) also suggest that elk were once widespread (VDGIF 2010). By the late 1800s or early 1900s they had been eliminated by over-hunting (O'Gara and Dundas 2002; Innes 2011).

Elk are grazers, primarily using grasslands or open prairies, but usually remaining within 400 m of mature forests which they use for cover (Peek 2003). They feed primarily on grasses, shrubs, and forbs depending on the season and location (Peek 2003). Although elk populations were likely controlled by hunting, predation by wolves, black bear (*Ursus americanus*), and cougars, and diseases, their numbers, as seen and reported, were clearly sufficiently high to impact vegetation structure and composition in and around the open areas where they occurred. At high densities elk can alter species composition and structure, reduce or eliminate shrubs or seedlings, decrease plant diversity, and create browse lines (McClafferty 2000).

Even at low to moderate densities, elk browsing can slow the rate of succession (Putnam 1996). Selective grazing can stimulate the growth of palatable grasses at moderate densities or favor undesirable forage species at higher densities (Woodward et al. 1994; Schreiner et al. 1996). Although elk play an important role in maintaining open grasslands by grazing and browsing, it is unlikely that they can create them from a starting point of mature hardwood forest. In all likelihood, Native Americans facilitated the presence of elk in the CHR through frequent burning that created and maintained meadows, prairies and open woodlands.

12.5.4 Bison

Modern bison have been present (until recently) in the CHR since at least the Pleistocene (http://exhibits.museum.state.il.us/exhibits/larson/ice_age_animals.html). As with elk, grasslands created by widespread clearing and frequent burning by Native Americans provided suitable conditions for bison to thrive (Rostlund 1960) for thousands of years (http://exhibits.museum.state.il.us/exhibits/larson/ice_age_animals.html), as the CHR landscape transitioned from boreal parkland to deciduous forest. Reports by early explorers, archeological finds, place names such as Buffalo Lick in the Piedmont ecoregion of northeastern Georgia (http://www.bartramtrail.org/pages/articles.html), and a buffalo wallow in central North Carolina (Simmons 1999), indicate that bison were widespread throughout much of the CHR. Buffalo traces were made and used during their seasonal migrations from the plains of central Illinois, through forests to the salt licks of Kentucky (Interior Plateau and Interior Valleys and Hills ecoregions). These traces were wide enough to be used as travel routes by Native Americans and later by European settlers (http://keithbobbitt.com/Log%20Cabins/NorthCarolinaRoute.htm).

Reports by early explorers indicate that bison were quite numerous, and grasslands and woodlands were sufficiently abundant to support them (Rostlund 1960). In 1722, Catesby noted "The buffalo. They range in droves feeding upon the open savannas morning and evening, and in the sultry time of the day they retire to shady rivulets and streams" in the Piedmont ecoregion (as cited in Rostlund 1960). Michaux (1805) reported seeing bison in groups of 150–200 in his travels through Kentucky in the early 1800s. Ramsey (1853, as cited in Moss 2001) described prairies around Nashville, Tennessee (Interior Plateau ecoregion) "luxuriant growth of native grasses, pastured over as far as the eye could see, with numerous herds of deer [*Odocoileus virginianus*], elk, and buffalo." Captain Timothe de Monbreun, a French hunter and trapper from Illinois, traveling down the Cumberland River near Palmyra, Tennessee (Montgomery County) reported seeing large herds of buffalo in 1777 (Kellogg 1939 as cited in Moss 2001). In 1780, buffalo were killed by Colonel John Donelson and his party near the Cumberland River along the Kentucky-Tennessee line (Williams 1928 as cited by Moss 2001). Bison disappeared from the southeast in the middle 1800s largely due to over-hunting by European settlers (Rostlund 1960). They were extirpated from North Carolina by 1765, Maryland by 1775, and Virginia by 1797 (Rostlund 1960). Michaux (1805) noted that bison were frequently shot by settlers for their tongues, with the remainder of the carcass wasted.

In the CHR, bison used fire-maintained prairies and shrub-grass woodlands for feeding (Tesky 1995). Bison are grazers, eating up to 14 kg of grass daily (Evans and Pobasco 1977), although they may switch to woody browse species if grasses are not available. Similar to elk, bison grazing pressure can lead to changes in plant composition and structure, impede forest succession (Reynolds et al. 1982) and help to maintain the grass-dominated communities they depend on. Bison can also affect local stands of timber by horning and thrashing during the rut (Reynolds et al. 1982). Trails on hillsides can drain upland areas and change vegetative composition (Reynolds et al. 1982), and wallows can become pools of water for other species to use (Tesky 1995). Prior to their regional extirpation by humans, both bison and elk were likely instrumental in retarding forest succession by grazing that, in conjunction with frequent burning by humans, helped to create and maintain open oak woodlands, prairies and savannas.

12.6 Humans as a Keystone Species and Ecosystem Engineer on the Historic Landscape

For millennia, *Homo sapiens* was a predominant keystone species and ecosystem engineer in the CHR that created and maintained many variants of open, early successional habitats and forest age classes for a wide variety of disturbance-dependent species in and surrounding their settlements (Carroll et al. 2002). Native Americans were active land managers, using fire to clear forests for settlements and agriculture, and to improve visibility, facilitate travel, increase native fruit production, and create edge and open, grassy habitats to attract game species (Van Lear and Waldrop 1989; Yarnell 1998; Carroll et al. 2002; Delcourt and Delcourt 2004). Social organization became more centralized and sophisticated over millennia, and by 1,000 BP concentrated settlement patterns and agriculture "generated a landscape patchwork of fragmented forests, cultivated land, and nutrient-depleted old fields abandoned as fallow land" (Delcourt and Delcourt 2004). Habitats created and maintained primarily by Native Americans included settlements, farmlands and gardens, abandoned fields of different age-classes, and forests of pioneer species colonizing abandoned fields including river cane (forming dense canebreaks) and yellow pines (Delcourt and Delcourt 2004). Through their land management activities across large landscapes adjacent to settlements, Native Americans – and later European settlers – created grassland, garden-residential 'suburb,' agricultural field, old-field, yellow pine forest, and open woodland habitats, thereby influencing species diversity, distribution, and abundance of many disturbance-dependent breeding birds with these specific habitat associations (Table 12.1).

12.6.1 *Historic Land Use and Forest Management by Native Americans in the Central Hardwood Region*

As early as 10,000 years BP Native Americans lived in long-term settlements in valleys and lowlands near rivers throughout much of the CHR. Archaeological evidence from the Shenandoah Valley of Virginia, the Little Tennessee River Valley of east Tennessee, eastern Kentucky, Watauga Valley of North Carolina, West Virginia, and the Valley and Ridge province indicate that such settlements were widespread. By the Late Archaic (4,500 years BP) Native Americans cultivated crops and managed forests surrounding and far beyond their settlements by burning frequently to facilitate travel and visibility, promote seed, berry, and nut production, and production of grasses and forage to attract elk, deer, bison, and other game species (Chapman et al. 1982; Williams 1989). These activities increased through the late Holocene, with a substantial increase in burning frequency by 3,000 years BP (Yarnell 1998; Delcourt and Delcourt 2004; Grissino-Mayer Chap. 6; Leigh Chap. 8). Delcourt and Delcourt (2004) suggest that by 3,000 years BP frequent burning by Native Americans promoted upland forests dominated by more fire tolerant oak, chestnut, hickory, and walnut (*Juglans* spp.), even as the prevailing climate would otherwise be expected to promote more fire-intolerant, mesophytic species. Frequent burning promoted the development and maintenance of savannas, prairies, open woodlands and pine forests that were once interspersed throughout the CHR (Flatley et al. 2013). By 1,000 BP Native American social organization was highly sophisticated in the CHR, with widespread dependence on agriculture (Delcourt and Delcourt 2004).

American Indians cleared land for villages and agriculture by girdling trees through peeling or burning away bark, and by burning. Older fields with declining soil fertility and productivity were abandoned to be reclaimed by forest, and new fields were cleared progressively and in rotation (Williams 1989), creating a mosaic of different-aged forests and forest structures in the areas surrounding settlements. Disturbances from agriculture, field abandonment, and frequent burning affected forest composition near settlements. Before agriculture became widespread, only 10 % of wood charcoal from archaeological sites was from pioneer species such as yellow-poplar, pine, red cedar (*Juniperus virginianus*), or river cane; subsequently (and prior to the arrival of Europeans) it rose steadily to 50 % (Chapman et al. 1982; Yarnell 1998).

Wood was used to build structures, and for fuel (Williams 1989). Assuming that fuel wood use by Native Americans was similar to that of European settlers in the Blue Ridge Mountains ecoregion, an average family used about 3.62 m^3 (15 cords) per year for cooking and warmth, which was likely salvaged from cleared land, second growth forest in abandoned fields, cull and undersized trees, or the surrounding forest (Nesbitt and Netboy 1946; Williams 1989). Model simulations for the Little Tennessee River Valley (Baden 1987 as cited in Delcourt and Delcourt 2004) indicate that the area required for growing enough maize for one person increased from 0.1 to nearly 0.4 ha between 1,000 and 250 years BP as dependency on maize increased. Soil fertility and harvest yield generally decline sharply within 10 years on maize fields, forcing abandonment of old and clearing of new fields.

Clearing, agriculture, and widespread burning by Native Americans influenced the forests and early successional habitats, but were almost certainly most pronounced near settlements along valley bottoms and surrounding uplands (Van Lear and Waldrop 1989; Milner and Chaplin 2010). By 3,000 years BP anthropogenic fire resulted in "a fine-grained patchwork of vegetation on upper hillslopes and ridgetops that include prehistoric garden plots, open patches with mixed crops of domesticated species, abandoned Indian old-fields reverting back into early-successional grassland barrens, thickets of shrubs, and even-aged stands of pitch pine or tulip poplar trees" on the Cumberland Plateau with mixed mesophytic forests in more sheltered topographic positions (Delcourt and Delcourt 2004). A schematic representation of land use by Native Americans illustrates the different variants of early successional habitats they created in and surrounding villages by clearing, burning, and agricultural activities (Fig. 12.2).

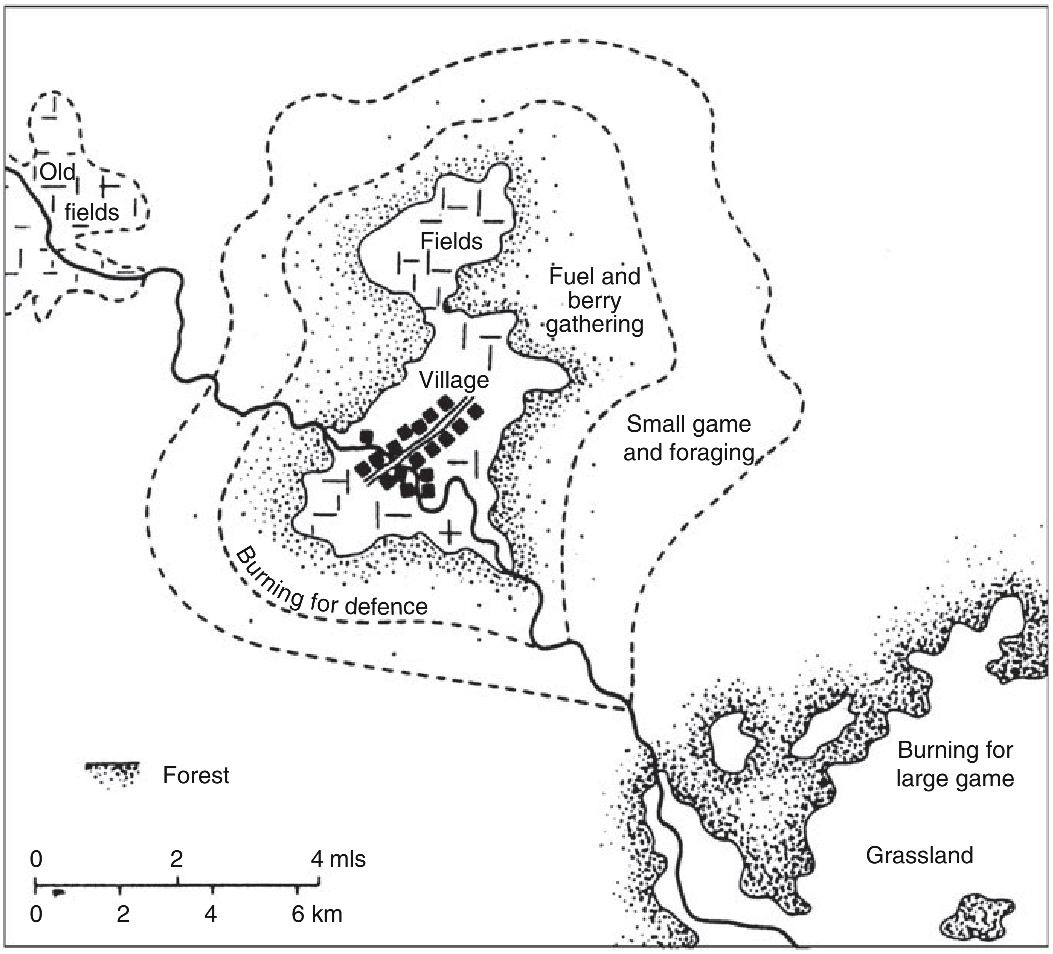

Fig. 12.2 Schematic of a Native American settlement and surrounding managed landscape (From Williams 1989)

Estimates of the Native American population ca. 1500 AD in the eastern USA range between 0.5 and 2.6 million, based on archaeological and historical information (Milner and Chaplin 2010). Their settlements and agricultural fields were located in spatially discrete, irregularly distributed aggregates across productive land, primarily along coastlines or (in the CHR) river valleys (Fig. 12.3) (Milner and Chaplin 2010). Nearly all Native Americans lived in villages of 50–1,000 people surrounded by fields (e.g., Fig. 12.2; Williams 1989). Some settlements were quite large; tens of thousands of people lived along a 100 km stretch along the Mississippi River and into the surrounding uplands in Cahokia, near east St. Louis (Ozark Highlands ecoregion), during the Mississippian period (800–1500 AD) (Denevan

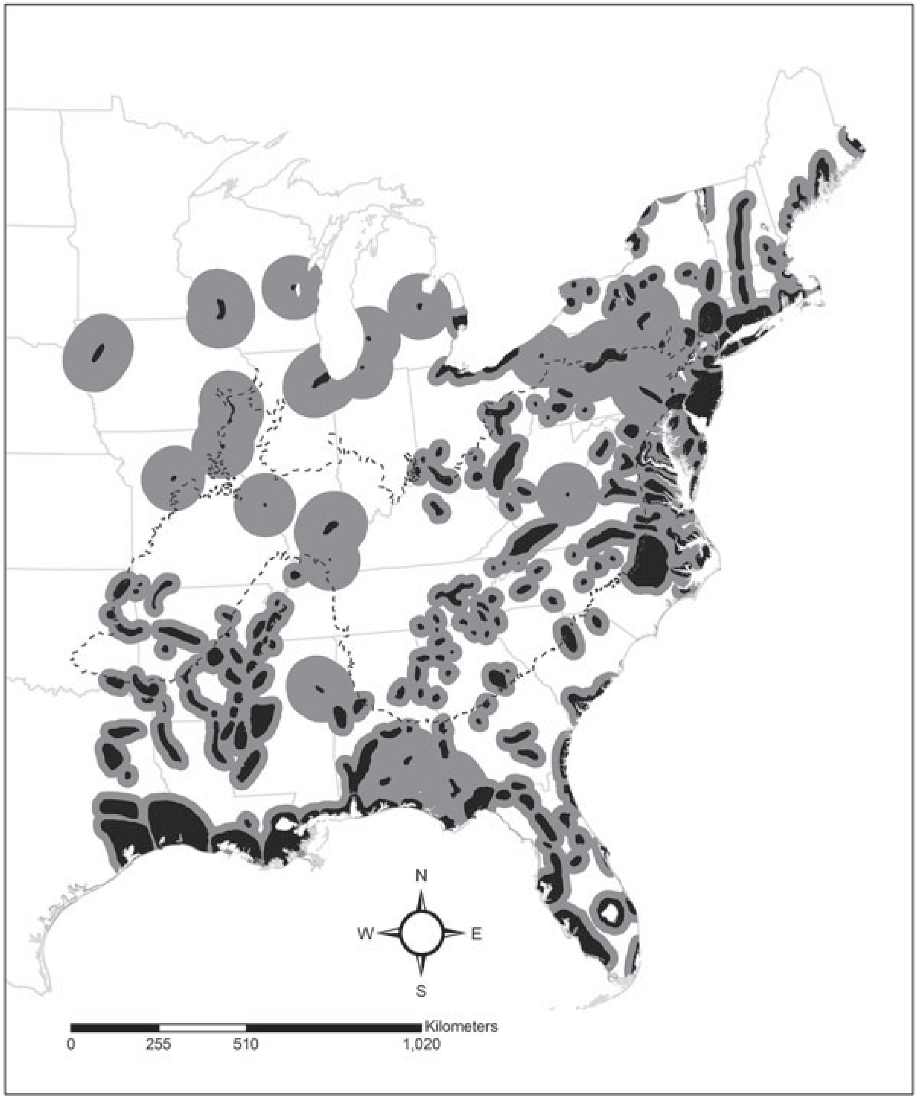

Fig. 12.3 Known population polygons of Native American settlements around 1500 AD based on archaeological and historical evidence (*black*), with buffers (*gray*) encompassing the potential zone of human influence, such as frequent fire, surrounding settlements (Adapted from Milner and Chaplin 2010)

1992; Milner and Chaplin 2010). Both population levels and the locations of settlements were dynamic over time. For example, a major depopulation occurred in the Midwest sometime between 1300 and 1500 AD, prior to European contact. Settlements sometimes relocated, likely as soil and fuel resource were depleted (Williams 1989).

Milner and Chaplin (2010) calculated the area of known Native American settlements ca. 1500 AD, and used nearest-neighbor statistics to calculate buffers surrounding them that incorporate the area of probable environmental impact. Based on their modeling, Native Americans impacted at least 7.1 % (settlements only), and up to 42.6 % (including buffers) of the landscape within the CHR ca. 1500 AD, prior to settlement by Europeans (Fig. 12.3). Landscapes heavily impacted by Native Americans likely expanded, contracted, and shifted with their populations and movements. Large tracts of mature or old-growth forest subjected primarily to non-anthropogenic natural disturbances likely created a matrix between populated areas and surrounding areas of environmental impact (Fritz 2000; Delcourt and Delcourt 2004). During this prehistoric moment, in a temporally and spatially dynamic landscape, suitable habitat was likely widely available for breeding bird species associated with mature- and young forests created by natural disturbances, as well as for species requiring different variants of land uses and early successional habitats that were created primarily by Native Americans.

12.6.2 *Descriptions of Native American Land Use and Historic Landscapes by Early European Explorers*

Accounts of pre-settlement landscapes by early naturalists and explorers are scant, and potentially biased, as most likely took routes most easily traversed and likely near or between Native American population centers. Nonetheless, several descriptions provide insight into landscape condition – thus the availability of different early successional wildlife habitats – at specific times and places, in different central hardwood ecoregions prior to or with minimal settlement by people of European descent.

In 1540, writings from Hernando DeSoto’s expedition described the landscape of the Blue Ridge Mountains ecoregion inhabited by the Lamar and Qualla cultures as “including palisaded towns and large expanses of cultivated fields” … “Ridges were well-wooded, and outside the cultivated valleys, the land was all forest” (as cited in Yarnell 1998). In Virginia, the Shenandoah Valley between the Blue Ridge Mountains and the Alleghenies was described in the mid-1700s as a vast grass prairie covering more than 2,590 km^2, which was burned annually by Native Americans (Van Lear and Waldrop 1989). In 1670 German explorer John Lederer described the Roanoke Valley along the Virginia-North Carolina border and along the border with West Virginia as forested, but “where it was inhabited by Indians, it lay in open in spacious plains,” and “by the industry of these Indians as… very open and clear of wood” (John Lederer as cited in Williams 1989).

Prairie-like openings throughout the Piedmont ecoregion, some up to 40 km across, were described by several early explorers and traders (see Barden 1997). In 1540 Spanish and Portuguese narratives described "many fine fields… the forest was more open and there were very good fields along streams… They traveled a full league [5 km] through a garden-like land of fruit-bearing trees, among which a horse could be ridden without any trouble" near Camden, South Carolina. Further north along the Catawba River they describe several plains and "many fine fields of tilled lands" (Rostlund 1957 as cited in Barden 1997). In 1567 Spanish explorer Juan Pardo describes "very large and good plains… clear land… beautiful plains" including one near Charlotte North Carolina (Rostlund 1957 as cited in Barden 1997) during his travels through the Piedmont ecoregion. Other travelers (e.g., John Lederer in 1670; John Speed in 1676; John Lawson 1701; Catesby in 1720s (as cited in Barden 1997)) describe large savanna and prairie throughout the Piedmont ecoregion maintained by frequent burning. In winter 1701, John Lawson noted "the woods being newly burnt and on fire in many places," and in the 1720s Mark Catesby observed many fires started by Native Americans, observing that "in February and March the inhabitants have a custom of burning the woods, which causes such a continual smoke, that not knowing the cause, it might be imagined to proceed from the fog… an annual custom of the Indians in their huntings, of setting the woods on fire many miles in extent" (as cited in Barden 1997).

The Coosa chiefdom, including an area from the confluence of the French Broad and Tennessee Rivers to around Talladega Alabama in the Southwestern Appalachians, Ridge and Valley, and Blue Ridge Mountains ecoregions, was described by the DeSoto expedition (1540) as "thickly settled in numerous towns with fields between, extending from one to another" (US Congress as cited in Williams 1989). Bartram (Van Doren 1928) describes endless savannas along the Tennessee River to the west of the Appalachians in the Interior Plateau ecoregion in his 1775 travels.

The first white settlers in western Kentucky encountered the Big Barrens (Interior River Valleys and Hills, and Interior Plateau ecoregions), encompassing an estimated 12,950–15,540 km^2. They described it as vast grassland with only occasional stunted trees unsuitable for building material, fences, and fuel (Owen 1856 and Hussey 1876 as cited in McInteer 1946). Early writers thought that the open prairie vegetation of the Big Barrens was created and maintained through frequent burning by Native Americans to attract game, and later by the first European settlers to maintain pasturage for cattle (Michaux 1805; McInteer 1946). The prairie vegetation of the Big Barrens may be partly explained by its unique limestone geology, but a rapid shift to forest vegetation as well as cultivated fields and pasture by the early 1800s – soon after white settlement – indicates that frequent fire was instrumental in maintaining these open, prairie conditions (see McInteer 1946; Baskin et al. 1994).

Historic accounts of the Ouachita Mountains ecoregion indicate that forests were more open, with lower tree density and basal area and more shortleaf pine than today; extensive prairies occurred in the western Ouachita Mountains (Foti and Glenn 1990). Le Page du Pratz of Natchez wrote of his travels from the Natchez to the St. Francis in the late 1720s "during the summer, the grass is too high for travelling;

whereas in the month of September the meadows, the grass of which is then dry, are set on fire and the ground becomes smooth, and easy to walk on: and hence it is, that at this time, clouds of smoke are seen for several days together to extend over a long track [sic] of country; sometimes to the extent of between 20 [100 km] and 30 [150 km] leagues in length, by two or three leagues in breadth, more or less…" and after rains "the game spread themselves all over the meadows and delight to feed on the new grass…" (du Pratz 1774 as cited in Foti and Glenn 1990). He writes further "The lands we find in going up the Black [Ouachita] River… in general may be considered as one very extensive meadow, diversified with little groves, and cut only by the Black River and little brooks, bordered with wood up to their sources" (du Pratz 1774 as cited in Foti and Glenn 1990). Dunbar and Hunter described the hills near the Ouachita River in 1804 and 1805 as being sometimes barren, with oak-dominated and pine woods variously in the area (Rowland 1930 as cited in Foti and Glenn 1990). In 1819–1820, botanist Edwin James described the Ouachita Mountains as covered with small and scattered trees or nearly treeless with some denser forests along the bases of mountains east of Hot Springs (James 1823 as cited in Foti and Glenn 1990). In 1844, Featherstonhaugh wrote that Indian fires thinned the forests but did not destroy them and "now that Indians have abandoned the country, the undergrowth is rapidly occupying the ground again" (Featherstonhaugh 1844 as cited in Foti and Glenn 1990).

During their 1818–1819 travels through the Ozark Highlands ecoregion, Henry Schoolcraft and Levi Pettibone noted valley bottoms of dense, pristine deciduous forest, valley walls covered with oak, hickory and pine forests, and uplands covered by a mosaic of prairie, oak savanna, oak woods with open undergrowth, and open grassy glades or barrens. These were probably enlarged and maintained by the Osage Indians who set fire to prairies to drive game into the wooded areas where the animals could be more easily killed (Rafferty 1996). Brackenridge wrote of his voyage up the Missouri River in 1811 that "… notwithstanding the ravages of fire, the marks of which are everywhere to be seen, the woods, principally hickory, ash, and walnut formed a forest tolerably close" (Brackenridge 1816 as cited in Spetich et al. 2011). Between the early nineteenth and late twentieth century, tree density in the Boston Mountains ecoregion tripled, increasing from 133 to 378 trees per ha, and from 123 to 287 per ha in the Ozark Highlands ecoregion, likely due to changes in the cultural practice of intentional burning (Foti 2004).

Clearly, Native Americans throughout the CHR created abundant open conditions in and surrounding their settlements by clearing for settlements and cropland, and by their frequent, widespread use of fire to manage fields, woodlands, and grasslands. Through their land management activities, Native Americans functioned as a keystone species by creating specific variants of early successional habitats required by different disturbance-dependent species. Without human-created habitats, species strongly associated with grasslands, savannas or prairies (e.g., elk, bison, bobwhite quail (*Colinus virginianus*), eastern meadowlark (*Sturnella magna*), field sparrow (*Spizella pucilla*), grasshopper sparrow (*Ammodramus savannarum*)), abandoned fields (e.g., yellow-breasted chat (*Icteria virens*), blue grosbeak (*Passerina caerulea*), or gardens and suburbs (e.g., song sparrow (*Melospiza melodia*), northern mockingbird (*Mimus polyglotus*), or chipping sparrow (*Spizella passerina*)) would likely have been uncommon or highly restricted in their distribution (e.g., beaver meadows) in the CHR (Table 12.1).

12.6.3 European Settlement

DeSoto's explorations in 1540 mark the first Native American contact with Europeans, and the start of Native American depopulation from newly introduced diseases and warfare (Yarnell 1998). European settlement of the CHR began in the mid- to late 1700s (Williams 1989). By the early 1800s most Native American populations had been severely reduced and secondary forests began to overtake their abandoned fields and farmlands (Yarnell 1998).

European settlers in the CHR continued the Native American practice of burning, and perhaps increased the area and frequency. Human habitation was concentrated in the river valleys and lowlands, where agriculture and burning made their greatest mark on the landscape and surrounding slopes. As the post-Civil War population of settlers increased in the CHR, so did populations of free-ranging cattle, pigs, and other domestic animals – even at higher elevations of the southern Appalachian ecoregion. The frequency – often annual – of burning large landscapes also increased to expand the area of woodlands and grasslands as pasturage (Ashe and Ayers 1901; Yarnell 1998). In 1885, ornithologist William Brewster (1886) wrote of the Blue Ridge Mountains ecoregion "Much of the low country, especially those portions bordering or near the larger streams, is under cultivation… Extensive areas, however, are everywhere still clothed in forest, either of vigorous second-growth or fine old timber." Brewster (1886) also wrote "in many places… trees are scattered about in groups or singly at intervals of one or more hundred feet, with grassy openings in between, giving the country a park-like appearance." Yellow pine forests, open woodlands, and grasslands remained abundantly available surrounding settled areas during this period due to the land management activities of European settlers (Ashe and Ayers 1901; Mattoon 1915; Ashe 1922; Balch 1928).

12.7 Recent Changes in Land Use and Condition: The Past 120 Years

Many variants of early successional or heavily disturbed habitats were likely at their historical high for several decades in the early 1900s for several reasons: (1) much of the CHR was systematically and progressively logged, resulting in large areas of young forest, with new areas cut as others grew up and matured; (2) large wildfires were common, ignited both intentionally and by sparks from trains using railroads built to extract timber, fueled by recently cutover, dry forestland; (3) family-run farming practices commonly left weedy fencerows, fallow fields, and untilled patches; (4) the demise of American chestnut (*C. dentata*) created forests with large numbers of standing dead trees, followed by heavily perforated canopies lasting for many years as the 'mighty giants' fell and before their replacement in the canopy by oak and other forest tree species.

Conversely, both young forest and other early successional habitats may be at an historical low today because: (1) family-run farming operations have diminished since the 1960s, replaced by industrialized farming practices using equipment and herbicides that eliminate weed and brush cover; (2) forests on public lands have been allowed to mature for the past century, with dramatic reductions in regeneration harvest levels in recent decades (Shifley and Thompson 2011); (3) human population growth, land ownership patterns, urban sprawl, and second homes have fragmented forests and removed large areas from the wildland base.

Additionally, in the past century, humans have had substantial indirect impact on forest structure and tree species dominance by introducing non-native forest pests and pathogens that have effectively wiped out (or soon will) entire tree species within the CHR (Hicks 1998). In the early 1900s introduction of the non-native chestnut blight (*Cryphonectria parasitica*) gradually killed all mature American chestnut trees, then a dominant species throughout most of the CHR that composed up to 50 % of forest trees in some locations. Since then, gypsy moth (*Lymantria dispar*), balsam wooly adelgid (*Adelges piceae*), hemlock wooly adelgid (*Adelges tsugae*) and others have (or soon will) dramatically altered CHR by killing important tree species that are dominant in several forest types. Introductions of non-native wildlife species such as starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*), and increases in domestic and feral predators such as dogs (*Canis lupus familiaris*) and cats (*Felis catus*) also negatively affect wildlife populations and communities.

12.7.1 Reduced Fire Frequency: Suppression… or Changes in Cultural Burning Practices?

Many of the open woodlands, yellow pine forests, prairies, and other fire-maintained conditions in the CHR began to transition to closed canopy hardwood forests between the 1920s and 1940s, after the federal government began a campaign to curtail the use of fire across the landscape (Spetich et al. 2011). Fire suppression policies followed on the heels of several notable fires that burned vast areas of coniferous forest and killed people in the western USA or in northern states (e.g., upstate New York and Minnesota) (Spetich et al. 2011). Catastrophic crown fires are integral to the ecology of some coniferous ecosystems such as lodgepole pine (*P. contorta*) forests in the western USA, boreal forests in northern states (Schoennagel et al. 2004), and sand pine (*P. clausa*) scrub in Florida (Greenberg et al. 1995); in these ecosystems, mortality of mature pine trees is rapidly followed by release of their seed onto the bare, fire-'prepared' seedbed, with regenerating forests developing directly back to the original pine forest type. In contrast, crown fires are nearly unheard of in hardwood forests of the CHR. Wildfires in the CHR are typically surface fires that generally do not kill mature trees, and result in few long-term changes to either fuels or forest structure as shrubs rapidly resprout, and leaf litter is replenished as deciduous leaves drop the following autumn (Stottlemyer et al. 2006; Waldrop et al. 2007, 2010).

Historically, continuous, grassy fuels likely carried fire across frequently burned prairies, savannas and open woodlands that were locally interspersed with closed canopy forests throughout the CHR (Flatley et al. 2013) (e.g., Fig. 12.1). However, the relatively low frequency of lightning-ignited fire (e.g., Tuttle et al. Chap. 10; Greenberg et al. Chap. 1, Table 1.6), and the high fire frequency required to create and maintain a grassy ground cover, suggests that these habitats would have been rare in the absence of frequent, intentional burning by Native Americans (and subsequently by European settlers) (Lorimer 2001; Delcourt and Delcourt 2004; Guyette et al. 2006a; see Sect. 12.4.2). A hypothetical historical CHR landscape without forest management by Native Americans may have been dominated by primarily mature or old growth forest, interspersed with beaver-engineered wetlands and meadows along waterways, and subject to sporadic and varying natural disturbances (see Chaps. 1, 2, 3, 4, 5, 6, 7, 8, and 9, this volume) including occasional low-severity (e.g., low tree mortality) lightning-ignited fire; high-severity (e.g., heavy tree mortality) lightning-ignited fires were likely mainly limited to specific topographic positions and (or) under infrequent severe drought conditions. The decline of open, fire-maintained habitats in the CHR resulted from (1) eliminating the accepted cultural practice of frequently and repeatedly burning forests by Native American and (later) European settlers; and (2) suppressing wildfires that were predominantly ignited by humans, either intentionally or accidentally (e.g., Tuttle et al. Chap. 10; Greenberg et al. Chap. 1, Table 1.6 and Sect. 12.4.2), rather than suppression of natural (lightning-ignited) wildfires, or fire suppression policies per se.

12.8 Habitat Requirements of Disturbance-Dependent Wildlife: Were Natural Disturbances Enough?

Breeding bird species in the CHR differ in their associations with specific structural features (MacArthur and MacArthur 1961; Askins 2001), and across the gradient of conditions created by different natural and anthropogenic disturbances (Table 12.1). Many forest interior species, such as the wood thrush (*Hylocichla mustelina*) and ovenbird (*Seiurus aurocapillus*), are primarily associated with relatively large tracts of undisturbed closed-canopy forests but often use young, productive forests with abundant fruit and insect foods (Greenberg et al. 2011b) to forage during the post-fledgling period (Lanham and Whitehead 2011; Stoleson 2013). Others, such as the northern cardinal (*Cardinalis cardinalis*), eastern titmouse (*Baeolophus bicolor*), Carolina chickadee (*Poecile carolinensis*), Carolina wren (*Thyrothorus ludovicianus*), eastern towhee (*Pipilo erythrophthalmus*), and American robin (*Turdus migratorius*) are generalists, able to thrive across a wide range of forest conditions and land uses.

Disturbance-dependent species are associated with open habitats created by disturbances, but may differ in their specific requirements. Some, such as indigo buntings, can thrive in most open habitats with adequate perch and nest sites, including small to extensive patches of young forest created by natural disturbances such as hurricane-related winds (Greenberg and Lanham 2001), tornadoes (Newbold 1996), or high-severity fire (e.g., Greenberg et al. 2013), or by anthropogenic disturbances such as recently harvested forest (e.g., Greenberg et al. 2014), shrubby pasturelands, or even utility rights-of-way (Lanham and Whitehead 2011). In contrast, requirements of many other CHR disturbance-dependent species are relatively specialized, and often associated with early successional habitats that are and historically were created primarily by humans (Table 12.1). On a hypothetical historical (Holocene) CHR landscape without humans, most of these more specialized species would likely have had lower population levels and narrower distributions. This suggests that many such species either co-evolved with Native American forest management, or were able to expand their ranges in response to land uses by Native Americans in the CHR.

12.8.1 Breeding Bird Response to Natural Disturbances

Our literature search indicates a paucity of studies on wildlife response to natural disturbances in the CHR. Studies of breeding birds in upland hardwood forests of the Ozark Mountains ecoregion of Arkansas (Prather and Smith 2003) and in the Ridge and Valley ecoregion of Tennessee (Newbold 1996) reported that the number and abundance of early successional species increased, and densities of most mature forest species remained high in tornado-damaged sites compared to mature forest. In the Blue Ridge Mountains ecoregion Greenberg and Lanham (2001) also reported higher species richness and relative abundance of breeding birds – including closed canopy-, edge-, and gap-associated species – in large (0.1–1.2 ha), 'incomplete' canopy gaps created by hurricane-related downbursts of wind that downed many, but not all trees. These studies of natural disturbances, together with studies of anthropogenically-disturbed (recently harvested) young forests in several different ecoregions indicate that the presence of a residual, partial canopy and dense shrubs or stump sprouts from damaged trees provide suitable habitat for forest canopy-, shrub-, and some disturbance-dependent species, resulting in higher species richness and density of breeding birds compared to mature forest (see Greenberg et al. 2014). However, many other disturbance-dependent breeding bird species of the CHR do not commonly occur in young forest, instead requiring more open ground, grass cover, or old field conditions (Table 12.1) that historically were created primarily by humans.

12.8.2 Breeding Bird Response to Anthropogenic Disturbances

Several breeding bird species in the CHR are uniquely associated with specific human-modified environments (Table 12.1). For example, eastern meadowlarks require open fields with tall, continuous grass cover. Bobwhite quail require continuous, tall grass and shrub cover with open- or no forest canopy. Golden-winged warblers (*Vermivora chrysoptera*) require open, grassy areas with some shrub and sapling cover in a forested matrix, at elevations greater than 850 m in the Blue Ridge Mountains ecoregion or lower elevations at higher latitudes (Rosenberg et al. in press). Chipping sparrows require open, mowed areas. Eastern bluebirds (*Sialia sialis*) require wide open fields where nest boxes are provided (or high-severity burns with standing snags (Greenberg et al. 2013), which are rare in the CHR). Field sparrows, yellow-breasted chats, and blue grosbeaks require abandoned pastures and old fields with mosaics of grass, shrubs, and saplings. Song sparrows and northern mockingbirds occur almost exclusively in garden habitats or suburban residential areas (Table 12.1).

By creating required habitat conditions for species that would otherwise be rare or limited in distribution, humans – first Native Americans and later European settlers – have functioned as a keystone species for thousands of years. Native Americans created and maintained savannas, prairies, and open woodlands by frequent, intentional burning; these habitats were used by elk and bison that helped to maintain them by grazing. Villages and agricultural fields were created by clearing and burning, and abandoned to revert to old fields, yellow pine forests, or other successional conditions. Historically, these anthropogenically-created habitats allowed many disturbance-dependent breeding bird species with specific requirements for differing variants of early successional habitats to occur and thrive within the CHR.

12.9 Historic Abundance and Shifting Distributions of Breeding Birds

Habitat availability affects both local and regional distributions of mobile species such as disturbance-dependent breeding birds that can opportunistically exploit ephemeral habitats. Historically, populations of breeding bird species dependent on anthropogenically-created habitats such as gardens, old fields, and grasslands likely tracked spatially and temporally dynamic Native American populations, settlement patterns, and increasing reliance on agricultural crops. Over the past several decades changes in land use and management practices have reduced the quantity and suitability of anthropogenically-disturbed habitats for many disturbance-dependent breeding bird species, with direct and indirect effects on their populations. The greater prairie chicken (*Tympanuchus cupido*), a grassland associate once common in the Big Barrens region of south-central Kentucky were extirpated largely due to the disappearance of vast, fire-maintained prairies within the region (Hunter et al. 2001). More than 70 % of eastern grassland-associated breeding bird species such as grasshopper sparrow, savannah sparrow (*Passerculus sandwichensis*), Henslow's sparrow (*Ammodramus henslowii*), Vesper sparrow (*Pooecetes gramineus*), bobolink (*Dolichonyx oryzivorus*), and eastern meadowlark have significantly declined over the past several decades (Askins 1993, 2000, 2001; Knopf 1994; Sauer et al. 2000) due to intensive management of pasture and haylands and loss or fragmentation of agricultural grasslands to development.

Similarly, nearly half of shrub-early successional breeding birds have significantly declined over the past several decades (Sauer et al. 2000). The disappearance of family farms, where low-intensity livestock grazing created and maintained a mosaic of grass, shrubs, and saplings, has resulted in the steep decline in golden-winged warbler populations in the Blue Ridge Mountains ecoregion where they were once common (Rosenberg et al. in press). Other bird species that depend on scrub/shrub or other early successional habitats, such as blue-winged warbler (*Vermivora pinus*), prairie warbler (*Setophaga discolor*), yellow-breasted chat, common yellowthroat (*Geothlypis trichas*), chestnut-sided warbler (*Setophaga pensylvanica*), American woodcock (*Scolopax minor*), field sparrow, indigo bunting, brown thrasher (*Toxostoma rufum*), and eastern towhee, have declined from 10 to 60 % in the eastern USA over the past 40 years (Partners in Flight 2013). Declines in ruffed grouse (*Bonasa umbellus*) populations are associated with a dearth of dense, sapling stage forest that develops 8–15 years after regeneration harvests (Thompson and Dessecker 1997). This is partly due to changes in federal land management policies that have greatly reduced timber harvests on National Forests. These strong correlations between land use change and populations of bird species associated with specific land uses or conditions suggests that their populations, and those of other wildlife species with similar habitat requirements, also likely increased or decreased historically with the shifting availability of suitable habitats created by weather-related natural disturbances, pests and pathogens, keystone wildlife species, and humans.

Historical shifts in the geographic distribution of some breeding bird species are documented, and are associated with changes in habitat availability corresponding with a dynamic climate and changing land uses or conditions. For example, red-cockaded woodpeckers (*Picoides borealis*) occurred until only a few decades ago at the northern extent of their range in isolated stands of shortleaf or Virginia pine or pine-oak in the Southwestern Appalachians and Blue Ridge Mountains ecoregions of Tennessee and Kentucky (Nicholson 1977). These small populations have disappeared as their fire-maintained yellow pine forest habitats declined due to southern pine beetle outbreaks (Nicholson 1977; see Nowak et al. Chap. 4), elimination of the cultural practice of intentional burning, and fire suppression. Historically, red-cockaded woodpeckers and other yellow pine forest associates such as brown-headed nuthatches (*Sitta pusila*) and pine warblers (*Setophaga pinus*) may have been more widely distributed in the CHR in yellow pine forests that commonly established on farmlands and old fields abandoned first by Native Americans and later by European settlers through the mid-twentieth century.

Similarly, the breeding distribution of golden-winged warblers has expanded and contracted within some CHR ecoregions over the past 150 years in response to regional changes in land use or condition, hence habitat availability (Rosenberg et al. in press). During the late nineteenth and early twentieth century widespread timber cutting and later abandonment of agricultural lands provided abundant early successional habitat for golden-winged warblers (Rosenberg et al. in press). In his visits to the Blue Ridge Mountains ecoregion Brewster (1886) wrote "Common in Jackson and Macon Counties, ranging 2,000–4,100 feet [610–1,250 meters], and haunting open oak woodlands, and second growth on hillsides. In many such tracts it seemed to be the most abundant and characteristic species…" Just a century later, golden-winged warblers only occur in isolated, higher elevation locations where habitat exists (Rosenberg et al. in press).

Brewster (1886) went on to describe abundant populations of other disturbance-dependent breeding bird species that today are relatively rare in the Blue Ridge Mountains ecoregion. Bobwhite quail were "Abundant everywhere, in grain fields in the valleys, oak woodland over the mountain sides, and throughout the balsam forests that cover the higher peaks and ridges..."; golden eagles [*Aquila chrysaetos*] were "frequently seen… said to breed on inaccessible cliffs and ledges of the higher mountains, whence they often descend into the valleys to prey on young geese, lambs, etc." Bartram noted many species associated with early successional habitats such as blue linnet (indigo bunting), yellow-breasted chats, and golden-winged warblers (Van Doren 1928).

Just as some disturbance-dependent species have declined or even disappeared from large areas of the CHR, they may persist in patches of suitable habitat, or colonize or recolonize areas if suitable habitats become available. For example, Henslow's sparrows were recorded on the Cumberland Plateau in Tennessee (Southwestern Appalachians ecoregion) for the first time after a large, local farm was left unmanaged for a few years, allowing suitable grassland conditions to develop (Lance 2014). American kestrels (*Falco sparverius*) and bobwhite quail are common in and near the large, open, grassy meadows at the Sandy Mush Game Lands in Buncombe County, but rare throughout most of western North Carolina. Prairie warblers (Greenberg et al. 2013) and red-headed woodpeckers (*Melanerpes erythrocephalus*) (Greenberg et al. unpubl. data) recently colonized tracts of upland hardwood forest in the Blue Ridge Mountains ecoregion, within several years after experimental high-severity burns killed most trees. Bobolinks, rare in the CHR, recently colonized hayfields managed with low-intensity mowing in Watauga County, North Carolina (K. Weeks, pers. obs.). These examples illustrate how 'if you build it they will come,' and suggest that managing for specific variants of early successional habitats could increase populations and distributions of targeted disturbance-dependent species.

12.10 Wildlife Conservation and Management within the Historic Range of Variation

Historically, humans were a keystone species, having a profound influence on the abundance, distribution, and diversity of disturbance dependent breeding birds and other wildlife species. Land management activities and land uses by Native

Americans such as clearing for settlements and agriculture, farmland abandonment, and frequent burning to create and maintain open grasslands and woodlands provided variants of early and later successional habitats for specialized species that would otherwise have been rare or absent in the CHR. On a hypothetical historical landscape without humans, mobile disturbance-dependent species that require edge and young forest conditions would likely have been transient in their distributions as natural disturbances created suitable conditions lasting only several years before canopy closure. However, except for those that could use once-common beaver meadows, breeding bird species requiring grassland, old field, garden-'suburb,' open woodland, and even yellow pine forest habitats (with some exceptions) would have been uncommon or absent within the CHR.

Forest management within the historic range of variation of natural disturbances first requires a subjective decision regarding whether prehistoric land management activities by humans should be regarded as a natural disturbance. If not, it becomes challenging to envision an historic CHR that approaches accuracy, because humans have occupied the CHR for more than 13,000 years; prior to human occupation, much of the CHR was in tundra-boreal forest with megafauna as primary agents of disturbance. Further, under that paradigm forest management is irrelevant; a laissez faire approach will allow non-anthropogenic disturbances to occur regardless, and any management would, by definition, be outside the historic range of variation. Both a 'no management' and a 'manage for a landscape as it might have been without humans' approach are confounded by a current forest condition that has been modified by humans for millennia and likely alters and influences the effects of natural disturbances. If so, then what moment in time should be selected to reference 'historic conditions' in a long and dynamic history of human population levels, settlement patterns, and land management practices – both Native American and European – on the landscape? Reference conditions including specific quantities, patch sizes, compositions, and structures simulating the gradient of conditions created by both anthropogenic and non-anthropogenic disturbances must be specifically defined.

Alternatively, forest and land use planning for diverse wildlife conservation might more logically start with clear objectives, and proceed with management activities targeted toward attaining them. Rather than debating an unknowable and dynamic historical condition, or what should or should not be considered a natural disturbance, a more pertinent question might be (1) do we want to maintain viable populations of diverse disturbance-dependent species? If yes, then (2) where, how much, and what methods should be used to attain targeted forest composition and structural conditions, and different variants of early successional habitats required by those species?

Clear conservation objectives and targeted management activities are confounded by the 'real world' of conservation planning, land management, and current forest condition (Foster and Aber 2004; Warburton et al. 2011; Zenner Chap. 14). The majority (90 %) of land within the CHR is in private ownership (see Greenberg et al. Chap. 1); its use and management is the decision of landowners, and may or may not be compatible with a landscape level conservation vision or strategy. Much of the land base that was historically mature or disturbed forest, or variants of early successional habitats managed by Native Americans is now urban, suburban, plantation, even-aged forest, or industrialized agriculture; tracts of land that were once continuous wildlands are now fragmented by development. On public lands, where large tracts provide the greatest opportunity for wildlife and wildlands conservation, policy, public opinion, and human values other than biodiversity must also be considered including (among others) aesthetics, recreation, endangered species, and forest products. Conservation management on a landscape scale will require a multi-pronged strategy by citizens, local, state, and tribal governments, non-governmental organizations, and the federal government to address deficiencies in the conservation of natural resources that Americans value. An important, currently deficient component of conservation delivery is management for disturbance-dependent wildlife and their habitats.

Acknowledgements We thank George R. Milner and George Chaplin for fruitful insights, and for allowing us to use their figure. Gary Wein provided GIS support. We thank Scott Stoleson, Robert Askins, and William (Billy) Minser for reviewing an earlier version of this chapter and helping to improve it. E. Daniel Moss and Craig Harper also provided useful information and insights.

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Chapter 2
Gap-Scale Disturbances in Central Hardwood Forests with Implications for Management

Justin L. Hart

Abstract All forest ecosystems are subject to canopy disturbance events that influence species composition and stand structure, and drive patterns of succession and stand development. Disturbances may be categorized by a variety of characteristics, but they are most often classified along a gradient according to their spatial extent, magnitude, and frequency. This gradient spans from broad-scale, stand-replacing events where most of the overstory is removed to fine-scale events which result from the removal of a single canopy individual or a small cluster of trees. The disturbance regimes of most stands in the Central Hardwood Region are characterized by fine-scale events. At the stand scale, these localized and asynchronous events can create a patchwork mosaic of microsites comprised of different tree species, ages, diameters, heights, crown spreads, and growth rates. Through the modification of fine-scale biophysical conditions, these localized canopy disturbances promote heterogeneity and biodiversity in forest ecosystems. Forest management based on natural disturbance processes should consider elements of the gap-scale disturbance regime, such as frequency, size, shape, and closure mechanisms, and the historical range of variation associated with these characteristics. Silvicultural prescriptions are available for gap-based management designed to promote oak regeneration and mimic natural disturbance processes.

Keywords Canopy gap • Disturbance • Silviculture • Succession • Stand development

2.1 Introduction

All forests are subject to disturbance events which influence forest composition and structure and thus, drive successional and developmental pathways. Forest disturbances may be categorized by a variety of characteristics, but are most often

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C.H. Greenberg, B.S. Collins (eds.), *Natural Disturbances and Historic Range of Variation*, Managing Forest Ecosystems 32,
DOI 10.1007/978-3-319-21527-3_2

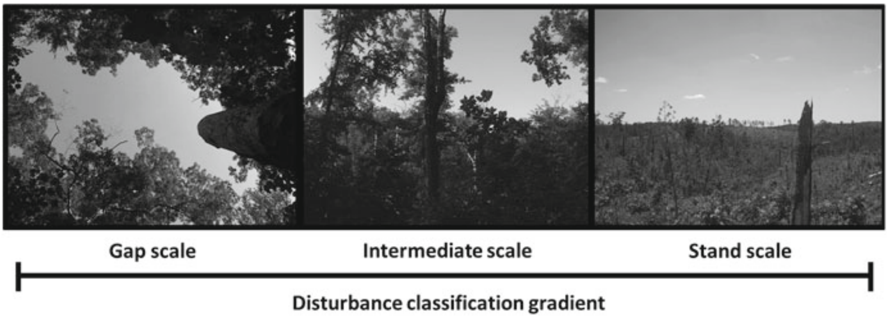

Fig. 2.1 Disturbance classification gradient based on spatial extent and magnitude of a discrete disturbance event (Photographs by author)

classified according to spatial extent, magnitude, and frequency, and occur along a gradient that spans from fine-scale events that result from the loss of a single canopy tree or a small cluster of individuals to broad-scale, stand-replacing events when most of the overstory is removed (Fig. 2.1; Oliver and Larson 1996). The disturbance regimes of most hardwood stands in the Central Hardwood Region (CHR) (Greenberg et al. Chap. 1, Fig. 1.1) are characterized by fine-scale events (Lorimer 1980; Barden 1981; Runkle 1981, 1982, 1996, 2000; Cho and Boerner 1991). At the stand-scale, these localized canopy disturbances create a patchwork mosaic of microsites which may be comprised of different tree species, ages, diameters, heights, and crown spreads (Runkle 1981, 1985; Canham and Marks 1985; Phillips and Shure 1990). By modifying fine-scale biophysical conditions, these gap-scale canopy disturbances may increase heterogeneity and biodiversity in forest ecosystems (Putz 1983; Abe et al. 1995).

Canopy gaps are typically defined as visible void spaces in the main forest canopy within which gap stems are shorter than a specified threshold (e.g., 20 m) or shorter than a percentage of the canopy trees surrounding the void (e.g., <75 % canopy height), and a gapmaker tree or trees are present (Yamamoto 2000; Richards and Hart 2011). The area directly beneath the canopy void is typically considered to be the canopy gap (sometimes called the true gap, light gap, or observed gap). However, because this void area changes with time since gap formation, and insolation and other abiotic variables are not limited to the area directly underneath the canopy void, canopy gaps can also be described as the total terrestrial area below the gap and extending to the bases of the canopy trees surrounding the gap. This is termed the expanded or extended gap (Fig. 2.2; Runkle 1981). Canopy gaps may be characterized by a range of different physical parameters, but the metrics most commonly measured are canopy gap formation mechanisms, gap formation frequency, gap size and shape distributions, fraction of land in gaps, gap closure mechanisms, and advanced reproduction within gaps. In this chapter, I attempted to synthesize information on these characteristics from studies conducted throughout the CHR and provide recommendations for management based on natural gap-scale disturbance processes.

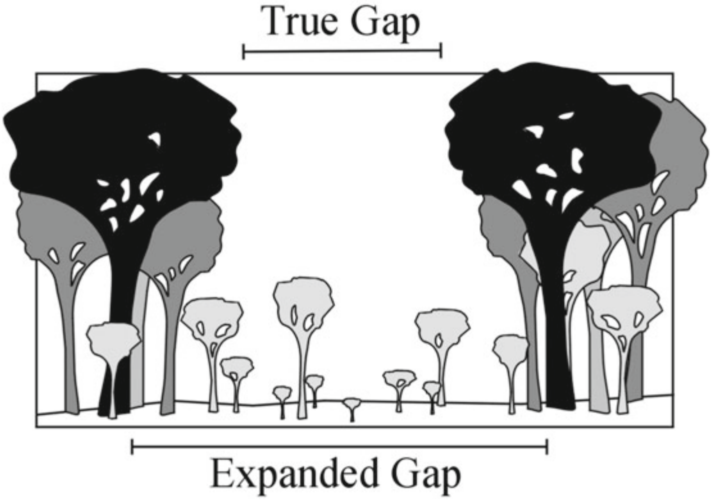

Fig. 2.2 The true gap (also called observed or light gap) and expanded gap (also called extended gap) environments. The *black* trees represent canopy dominants along the periphery of the gap

2.2 Gap Formation Mechanisms

Canopy gaps occur on sites where partial or total death of one or a small cluster of canopy individuals has occurred (Watt 1947; Runkle 1981, 1985). As such, canopy gaps may be caused by a variety of disturbance agents such as strong winds and insect outbreaks. Individual canopy gaps are formed by trees that have been uprooted (root network uplifted), stems that have been snapped (bole broken below the crown), or snags (standing dead trees with crowns mostly intact; Putz 1983; Clinton et al. 1993; Yamamoto 2000; Richards and Hart 2011).

Tree uprooting typically results from strong winds and may be related to soil depth where trees are not firmly anchored (Schaetzl et al. 1989), soil saturation which reduces soil cohesion and shear strength (Beatty and Stone 1986; Schaetzl et al. 1989), or biotic factors such as infection by the fungus *Armillaria mellea*, which weakens root systems (Williams et al. 1986). Uprooting may also be caused by crown asymmetry, which occurs as gap neighbors benefit from adjacent canopy gaps and undergo lateral branch growth to fill the void from the side, unequal crown growth of trees at different elevations on steep slopes, and/or twig loss and abrasion from wind (Young and Hubbell 1991; Rentch et al. 2010; Peterson et al. Chap. 5). In mesic hardwood stands of the CHR, wind-induced mortality is the predominant gap formation mechanism (Barden 1979; Runkle 1981, 1982, 1996). Snapped stem-formed gaps may be caused by strong wind events when the stem fails above ground level (Quine and Gardiner 2007) or by trees that first formed as snags that subsequently snapped. Snag-formed gaps are common in upland stands of the CHR (Clinton et al. 1993, 1994; Richards and Hart 2011). In this region, snag-formed gaps are most typically found on xeric sites where water can be limiting and are hypothesized to often result directly or indirectly from water stress (McComb and Muller 1983; Hart and Kupfer 2011; Hart et al. 2012). Standing dead trees are often removed by mild to severe wind events and this process complicates formation-specific gap investigations because the category likely represents a combination of gaps that formed directly by stem snapping and those that first formed as snags. Snags that are eventually snapped likely create distinct microenvironmental conditions and the response of residual trees may differ between these gaps and those that are formed rapidly (Krasney and Whitmore 1992; Clinton et al. 1994).

Biophysical gap characteristics may be influenced by the formation mechanism and thus, gap environments and gap-phase processes may differ according to mode of tree mortality (Krasney and Whitmore 1992; Clinton et al. 1994; Himes and Rentch 2013). Gaps caused by uprooting may be larger in size and more elliptical in shape relative to snag-formed gaps that are often comparatively small and circular (Hart and Grissino-Mayer 2009). Gaps formed by uprooting are also more likely to involve two or more canopy trees compared to snag-formed gaps as the fall of an uprooted gapmaker has a greater probability of removing neighboring individuals (Yamamoto and Nishimura 1999). Snag gaps are typically smaller in size and they release growing space more gradually as they shed limbs rather than instantaneously. I note however, that once the snag is barren of leaves the majority of the growing space has been released as woody material restricts a relatively small proportion of insolation. Additionally, composition of gaps created by uprooting events may differ significantly from that in gaps created by snags or snapped stems (Hart and Kupfer 2011). Such patterns may be attributed to the physical alteration of the gap environment by the uprooting process as intra-gap heterogeneity caused by uprooting canopy trees (e.g., pit and mound topography) has been shown to be an important determinant of species composition in gaps (Hutnik 1952; Putz 1983; Runkle 1985). However, gap formation is coupled with other factors. For example, soils, slope aspect, and steepness influence the gap formation mechanism and the gap formation mechanism in turn influences gap size. Hart and Kupfer (2011) found that snag-formed gaps were most common on south-facing slopes on soils with low moisture holding capacity on the Cumberland Plateau in Tennessee. Species composition of these gaps differed from that of gaps caused by tree uprooting; however, tree uprooting was largely restricted to north-facing slopes on soils with higher moisture holding capacities. Thus, although forest community response to a disturbance event is constrained by the physical environment, the disturbance regime itself may also be strongly influenced by the physical setting.

2.3 Gap Formation Frequency

Disturbance regimes and forest response to discrete events vary by forest developmental stage attributed largely to differences in species composition, stand structure, and tree age distributions (Table 2.1). Exogenous disturbance events are stochastic

Table 2.1 Typical canopy gap characteristics in relatively young and old central hardwood forest stands

Characteristic	Young	Old
Gap frequency	High	Low
Gap size	Small	Large
Gap duration	Short	Long
Gap fraction	–	–
Gap closure	Lateral crown expansion	Sub-canopy height growth

and not related to stand age, but responses of residual trees to these discrete events may differ (e.g., some old trees may be less likely to respond to increased resources and growing space compared to younger, more vigorous individuals).

Although gap formation frequency varies through time (because of the stochastic nature of exogenous disturbance) and by stage of development (because of the factors listed above), estimates on the rate of canopy gap formation have been developed. For hardwood stands in the CHR, the canopy gap formation rate is typically 0.5–2 % per year (Runkle 1982, 1985). Based on these values, the average time between natural canopy disturbances for a given site is 50–200 years (Runkle 1985). However, some recent research indicates that exogenous canopy gap formation rates may have declined over the past 400 years in white oak (*Quercus alba*) stands of the eastern USA (Buchanan and Hart 2012). The authors speculated this pattern may have been attributed to changes in drought frequency and intensity, changes is anthropogenic land-use patterns, and the extinction of Passenger Pigeon (*Ectopistes migratorious*) (Greenberg et al. Chap. 12). Thus, the estimated gap formation rate (i.e., background mortality) of 0.5–2 % per year may be slightly lower than that of centuries prior because of changes in the frequency of exogenous disturbance events. I stress that this pattern has not been found in all canopy disturbance reconstruction studies in the region. For example, Rentch et al. (2003) did not find differences in canopy gap formation frequency in five old-growth oak stands across the 1700s, 1800s, or 1900s. More research on potential changes in canopy gap formation in central hardwood forests is warranted.

The proportion of stands in the eastern USA in the complex stage of development at European settlement was estimated to be much higher than at present (Whitney 1994; Lorimer 2001). In complex stage stands canopy tree heights and crown volumes are more highly variable, which creates more complex canopy topography (Oliver and Larson 1996). Stands with old trees and with more complex canopy topography are more likely to experience damage (i.e., localized tree mortality) from strong wind events (Runkle 1985; Foster 1988; Quine and Gardiner 2007). Thus, a single storm event may influence stands differently across stages of development, with stands in the complex stage being the most sensitive to wind-induced damage. Although the frequency and intensity of severe wind events in the eastern USA may not have changed over the past few centuries, the conversion of stands throughout the CHR to more simple structures may have reduced the frequency of localized canopy disturbances in these systems, which may in turn have influenced regeneration patterns.

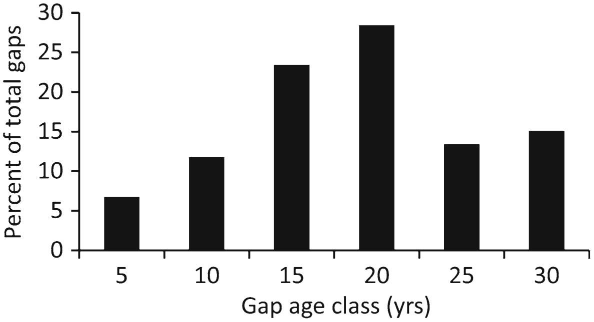

Fig. 2.3 Distribution of 60 canopy gaps by five-year age class bins in upland hardwood stands on the Bankhead National Forest, Alabama (Adapted from Richards and Hart 2011)

If the gap closure rate approximates the gap formation rate in a stand, gap fraction is considered to be in dynamic equilibrium (Himes and Rentch 2013). If gap formation and gap closure are in equilibrium, the gap age distribution should reveal a high frequency of young gaps and the number of gaps should decline with increased age. However, superimposed over the natural background mortality rate are exogenous disturbances; events which may create a high frequency of localized, gap-scale disturbances throughout a stand. These punctuated events may cause the gap age distribution to become irregular (Fig. 2.3).

The most commonly used disturbance classification terminology is based on spatial extent and magnitude of damage caused by a discrete event (Oliver and Larson 1996). However, for some events it may be the timing of formation that dictates the disturbance classification (e.g., gap-scale v. intermediate-scale disturbances). For example, strong wind events may remove trees singularly or in small groups (i.e., create localized canopy disturbances) throughout a stand. The size of individual canopy disturbances may be of the scale that constitutes a gap, but if the gaps were created across a broad area of the stand the disturbance may in fact have removed enough basal area to be considered of the intermediate scale. In such instances it would be gap formation rate that determines the disturbance classification. Disturbance history reconstructions using tree-ring records and forest inventory data have been conducted in some hardwood stands of the CHR. The common convention in these studies is to classify gap-scale disturbances that removed trees from at least 25 % of the stand as stand-wide events. The return interval of these stand-wide events was typically 20–40 years (Nowacki and Abrams 1997; Ruffner and Abrams 1998; Hart and Grissino-Mayer 2008; Hart et al. 2012). At the stand scale, these disturbance events may have removed enough basal area to be considered intermediate-scale disturbances, but the mortality was localized (i.e., gap scale) throughout the stands.

2.4 Canopy Gap Sizes and Shapes

Canopy gap size is highly variable and is influenced by factors such as the number of trees removed, the height and crown volume of removed trees, and the gap formation mechanism. The range of gap sizes reported from hardwood stands in the CHR ranges from 5 m^2, in gaps that are just about to close, to greater than 4,000 m^2 (Barden 1980; Clinton and Baker 2000; Hart and Grissino-Mayer 2009). Some authors have suggested that canopy disturbances exceed the size of canopy gaps (i.e., they are not gap scale, but intermediate- or stand-scale events) if the canopy void space exceeds 1,000 m^2 (Yamamoto 2000). Nonetheless, gap-scale disturbance studies from the central hardwood forests have typically found true canopy gaps to range from 30–140 m^2 and expanded canopy gaps to typically range from 200–500 m^2 (Barden 1980, 1981; Runkle 1981, 1982, 1990; Runkle and Yetter 1987; Clinton et al. 1993, 1994; Hart and Grissino-Mayer 2009; Richards and Hart 2011; Himes and Rentch 2013). Gap size may also be expressed in relation to adjacent canopy tree height by comparing gap diameter to mean canopy height (D:H). Such comparisons in central hardwood forests have found that the D:H of most gaps is <1.0 (Runkle 1985; Richards and Hart 2011).

Canopy gap shapes typically range from circular to elliptical, but gap shape varies and the patterns can be blocky rather than elliptical (Lima 2005). However, the majority of gap-based research in central hardwood forests has noted elliptical shapes (Runkle 1982, 1992; Clinton et al. 1993; Hart and Grissino-Mayer 2009, Richards and Hart 2011). Gap shapes may be quantified by calculating the gap length (longest axis of the gap) to gap width (longest distance perpendicular to length) and analyzing the length-to-width ratio (L:W; Hart and Grissino-Mayer 2009; Rentch et al. 2010; Richards and Hart 2011). The gap formation mechanism may be a strong determinant of gap shape. Snag-formed gaps tend be more circular in shape and have L:W of about 1.0. In contrast, gaps formed by uprooted and snapped stems tend to be more ellipsoidal with L:W of >2.0 (Hart and Grissino-Mayer 2009).

2.5 Canopy Gap Fraction

Canopy gap fraction is the percent of a stand that is within a true or expanded canopy gap. Gap fraction in central hardwood forests for true gaps typically ranges from 3–25 % and for expanded gaps often ranges from 8–30 % (Romme and Martin 1982; Runkle 1982; Runkle 1985; Keller and Hix 1999; Busing 2005; Hart and Grissino-Mayer 2009; Himes and Rentch 2013; Weber 2014). Although gap frequency and size vary by stage of stand development, gap fraction may be rather similar. Hart and Grissino-Mayer (2009) found gap fraction in upland oak stands on the Cumberland Plateau at age 80 years approximated the values reported from much older stands throughout the region. Thus, the percentage of land area in gap environments in relatively young and old stands was similar, but the distribution of the gap area was quite different (Table 2.1). Young stands are characterized by a high frequency of small gaps and older stands are characterized by a relatively small number of large gaps.

2.6 Gap Closure and Structural Development

Hardwood stands during the stem exclusion and understory reinitiation phases of development are characterized by high densities of relatively small individuals of similar age (Oliver and Larson, 1996). Intense competition for resources and self-thinning in developing stands result in a high frequency of localized canopy disturbances (Clebsch and Busing 1989; Hart and Grissino-Mayer, 2009). In such systems, when a canopy individual dies residual neighboring stems are able to quickly capture the released growing space and close the canopy void via lateral crown extension, thereby altering tree size, tree architecture, and stand structure (Hart and Grissino-Mayer 2008). Conversely, during the complex stage of development stands contain fewer individuals and have reduced competition and mortality rates resulting in a reduced frequency of endogenous canopy disturbance events (Zeide 2005). Most canopy trees in complex stage hardwood stands have comparatively large crowns and when one of these individuals is removed from the canopy, a relatively large void is created and peripheral trees are often incapable of closing the gaps through lateral crown extension (Tyrell and Crow 1994; Yamamoto 2000). These larger gaps should require relatively long periods to close because of their size, which increases the probability of a new individual recruiting to a dominant or codominant position through subcanopy ascension (Runkle 1985; Rentch et al. 2003; Webster and Lorimer 2005; Zeide 2010). These comparatively large gaps in old stands may also allow for the establishment of new individuals and may therefore promote multi-aged stands. In the absence of exogenous disturbance events, structural changes with maturity are driven by these localized canopy disturbances (Johnson et al. 2009). Indeed, it is gap-scale disturbance processes that create the complexity that defines old-growth structure in hardwood systems (Oliver and Larson 1996; Frelich 2002; Richards and Hart 2011).

2.7 Gap-Phase Succession

Forest community responses to gap-scale disturbances are influenced by a range of gap characteristics such as size (Runkle and Yetter 1987), age (Brokaw 1985), formation frequency (Canham 1989), formation mechanism (Putz 1983; Clinton et al. 1993), distance from edge (Kupfer et al. 1997), topographic position (Clinton et al. 1994; Abe et al. 1995) and orientation (Poulson and Platt 1988) among others. Throughout the CHR, light is commonly the most limiting factor (Oliver and Larson 1996) and gap characteristics are important because of their direct influence on understory light regimes (Canham et al. 1990). Gap-scale disturbances influence all forest strata, but the biophysical changes caused by local canopy removal are typically most evident in the regeneration layer (Brokaw and Busing 2000; Yamamoto 2000). Responses in this stratum are important because saplings represent the pool of species likely to recruit to larger size classes, so sapling composition in gaps is often an important determinant of future canopy composition in stands with disturbance regimes dominated by gap-scale processes (Wilder et al. 1999; Taylor and Lorimer 2003).

Gaps are stochastic and favor species in the understory or midstory of the gap environment. Without competition from shade-tolerant mesophytes, oaks have the physiological capability for long-term survival beneath an oak-dominated canopy, and may be considered a gap-phase genus (Orwig and Abrams 1995; Abrams 1996; Rentch et al. 2003) as these trees are able to persist in low light conditions and maintain the ability to respond to increased resources associated with canopy disturbance in their vicinity. During the twentieth century, the understory strata of oak-dominated stands across a variety of site types came to support a high density of shade-tolerant individuals, principally red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) (i.e., the oak-to-maple transition; McEwan et al. 2011). The driver of this widespread understory composition shift may vary according to site, but was likely a function of climate change, herbivore population density fluctuation, loss of American chestnut (*Castanea dentata*) and Passenger Pigeon (*Ectopistes migratorious*) (Greenberg et al. Chap. 12), changes in land-use patterns, and modification of the fire regime (Lorimer 1993; Abrams 2003; Nowacki and Abrams 2008; McEwan et al. 2011; Grissino-Mayer Chap. 6). When a canopy gap forms in a stand exhibiting the oak-to-maple transition, the probability of a shade-tolerant individual being in the gap environment is greater than the likelihood of a shade-intolerant or moderately-tolerant species being in the gap. Furthermore, small canopy gaps typically close quickly by lateral crown expansion and may not permit enough time for even fast growing shade-intolerant species to colonize the gap environment and then ascend to the canopy prior to gap closure. For these reasons, gap-scale disturbances typically favor shade-tolerant species. As canopy oaks die in oak-dominated stands, the gaps formed provide a mechanism for shade-tolerant stems that are abundant in the understory to recruit to larger size classes and to ascend to canopy positions. This gap-scale process is driving the observed successional replacement of oak by maple throughout central hardwood forests.

2.8 Gap-Based Management

In recent decades, there has been a fundamental philosophical change in the management of forest resources. Increasingly, managers are utilizing approaches that emulate natural ecological processes including natural disturbance regimes (Franklin and Johnson 2012; Hanson et al. 2012; Zenner Chap. 14). This approach emphasizes creating structures and community assemblages through silviculture that are similar to those that were historically produced by natural disturbance processes (Seymour and Hunter 1999). Wind is the most common and arguably the most influential canopy disturbance agent in hardwood forests of the eastern USA (Runkle 1996). The goal of natural disturbance-based management is not to mimic the actual disturbance event (i.e., trees are not typically felled by winching to emulate the effects of strong winds), but rather to use the effects of such events (e.g., the altered light regime) as models for individual and cumulative silvicultural treatments with the goal of minimizing the structural, compositional, and functional disparities between managed and unmanaged stands. The rationale for such an approach is that emulation of natural events restores and/or maintains resilience to a range of environmental challenges, critical ecosystem functions, and native forest biodiversity (Long 2009). The success of this management approach requires clear and tangible guidelines that are based on quantitative data from stands that are situated in similar biophysical settings and are therefore appropriate analogues (Seymour et al. 2002; Franklin et al. 2007).

Uneven-aged management approaches have commonly relied upon single tree and group selection systems (Nyland 2002). Removing trees singly or in small groups will certainly emulate the sizes of naturally formed canopy gaps. However, through much of the CHR, markets have historically not supported such an approach. As a consequence, operators are often not experienced with single tree and group selection harvests. In addition, single tree and small group selections typically promote shade-tolerant species, and with few exceptions, this approach has not worked to maintain strong components of moderately-tolerant taxa such as oak and hickory (*Carya* spp.) in the CHR (Nyland 2002; Johnson et al. 2009).

A gap-based silvicultural approach that utilizes even-aged treatments applied in groups rather than evenly throughout an entire stand may be sufficient to maintain dominance of moderately-tolerant taxa such as oak and hickory, be economically viable throughout central hardwood forests, and fall within the historical range of variation of the disturbance regime. Oak stands in this region are most often managed with an even-aged approach; by modifying the size and spatial arrangement of even-aged treatments, managers may be able to fulfill multiple management objectives: commodity production, oak maintenance, and entries that fall within the historical range of variation.

I emphasize that there is no specific gap size that is guaranteed to promote oak recruitment (Lhotka 2013). Rather, gap size should be viewed based largely on the D:H. Oak reproduction will usually grow well if stems receive 20–50 % of full sunlight, which is typically met in gaps with a D:H of about 1.0 (Marquis 1965). Gaps of this size may be slightly larger than most naturally formed single tree fall gaps of central hardwood forests (Runkle 1985), but may still fall within the historical range of variation and may approximate the size of natural multi-tree fall events. In addition, such approaches should be placed strategically around existing oak advanced reproduction. The return interval of stand-wide, canopy disturbance events reported from hardwood stands through the CHR is 20–40 years. This return interval may be used to help guide the timing between entries in a single stand. Subsequent entries could create new group selection openings or could expand the size of the gaps created prior (i.e., femelschlag; Lhotka and Stringer 2013). I also note that the canopy gap formation rate of 0.5–2 % per year reported from the region may be somewhat low compared to centuries prior (Buchanan and Hart 2012) although more data are needed to verify this claim. Nonetheless, larger or more frequent harvest-created gaps may not be outside the historical range of variation in the disturbance regime.

For those who wish to adopt a management approach that emulates natural disturbance processes, it is important to recognize that many of the contemporary oak-dominated stands that occur throughout the CHR of the eastern USA were not the result of natural disturbance events (Cowell 1998, Foster et al. 2002). Managers that wish to maintain oak dominance and adhere to a natural disturbance-based management approach will likely need to make a compromise between a silvicultural system designed to emulate natural disturbances and one designed to maintain desired species assemblages. Oak regeneration failure has been reported widely across all but the most xeric site conditions throughout the CHR (Abrams 1992, Lorimer 1993, Nowacki and Abrams 2008, McEwan et al. 2011). Although variability exists at the species-level, oak are generally considered only moderately tolerant of shade, and canopy disturbance events that increase insolation in the understory are required for regeneration (Dey 2002). These canopy disturbances must be sufficiently large to provide adequate light levels for small oak, but not so large that they allow for the establishment of shade-intolerant species that can outcompete oak in high light environments (Runkle 1985, Grayson et al. 2012). Thus, gap opening size and the density and size of oak and its competition are critical factors to be considered in developing a silvicultural prescription to maintain oak dominance. In stands with a significant component of shade-tolerant mesophytes in the understory and where the management objective is to maintain oak, entries designed to release advanced oak reproduction should be implemented in conjunction with competition reduction measures such as fire or herbicide application (Loftis 1990, Schweitzer and Dey 2011, Hutchinson et al. 2012, Brose et al. 2013). Oak seedlings are often abundant in successional stands with abundant shade tolerant stems in the understory, but most of these oak seedlings will not recruit to sapling or small tree size classes and may be considered ephemeral (i.e., the oak bottleneck). Without competition reduction measures, advanced oak reproduction will be sparse, and oak reproduction should be in place before overstory trees are removed (Johnson et al. 2009). Although competition removal may fall outside the historical range of variation, these actions may be essential to maintain oak dominance in stands with strong maple or other shade tolerant components. Competition reduction is not without its problems. For example, many managers have found that prescribed fire is not an effective control measure for a prolific sprouting species like red maple and herbicide can be cost prohibitive.

Acknowledgments I would like to thank Merrit Cowden, Lauren Cox, Tom Weber, James Rentch, Beverly Collins, and Cathryn Greenberg for their many helpful comments on earlier drafts.

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LANDSLIDES AND CLEARCUTS:

What Does The Science Really Say?

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The table below summarizes 26 separate data sets from 22 scientific studies which inventoried the relative number and volume of landslides in forested areas compared to harvested areas and roadways in the Pacific northwest. The table shows that clearcuts and forest roads are associated with dramatic increases in both the number of slides and the volume of slides relative to natural forest conditions.

Slide Risk for Clearcuts vs. Forested Areas

In terms of the number of slides per unit area, several of the studies indicate that clearcuts exhibit landslide rates up to 20 times higher than the background landslide rate observed in forested areas. (The average among all the data sets was 13x)

In terms of total slide volume per unit area, several of the studies showed that clearcuts exhibit soil transfer rates up to 8 times higher than forested areas. (The average among all the data sets was 7x) Slide Risk for Roadways vs. Forested Areas

In terms of the number of slides per unit area, several of the studies indicate that road rights-of-way exhibit landslide rates as much as 300 times higher than forested areas. (The average among all the data sets was 210x).

In terms of total slide volume per unit area, several of the studies showed that road rights-of-way exhibit soil transfer rates up to 200 times higher than forested areas. (The average among all the data sets was 103x)

Causal Mechanisms: How Clearcutting and Roadbuilding Increase Landslide Risk

The mechanisms whereby logging causes an increase in landslide risk include:

Large living trees have strong roots that often penetrate fractured bedrock (providing vertical soil cohesion) and make lateral connections with the roots of nearby trees and shrubs (providing horizontal soil cohesion). When the trees are harvested, the roots of the stumps decay and begin to lose their strength so the soil loses its vertical and horizontal cohesion. (Root strength is directly proportional to root size, so full recovery of soil cohesion is not realized for decades after harvest);

Unlike living trees, each of which might have a full acre of leaf surface area available to draw water out of the ground and transpire it to the air, stumps lack living leaves and are unable to transpire water out of the soil. This leads to increases in soil saturation, subsurface flow and surface run-off. (The natural hydrologic function of a forest does not recover for 100 years or more);

The removal of the forest canopy eliminates a partial "umbrella" that intercepts some rain and disperses the effects of intense storm events;

Dragging logs across steep slopes and using heavy machinery damages the soil surface and the roots that help hold the soil. Log yarding can also disrupt natural pathways for water drainage and can create new pathways as well. Logging, yarding and heavy equipment also damages "toe slopes" that act as retaining walls and help hold the soil on steep slopes;

Logging "slash" (debris left over after timber harvest) can accumulate in small stream gullies forming water blockages that can trigger slides;

Logging removes trees and damages root columns that buttress soil masses on the hill above them. The soil above and between two tree root columns can also form a structural "arch" that helps hold the soil on the slope above the arch;

Harvest sites are often burned after logging to prepare the site for replanting. Intense burning adversely affects soil cohesiveness so that the top layers of soil just dissolve and disappear with the first big rain. Fire can also kill residual vegetation initiate the decay of residual roots in shrubs, ferns, and grasses that may have survived the logging operation; and

Herbicide spraying is often done to reduce competition between unwanted plants and the small tree seedlings in a plantation. Such chemical spraying kills residual vegetation and initiates the decay and loss of strength in the roots of plants that survived the logging operation.
In addition to removing all trees, stumps, and other vegetation, road building has a few of its own causal mechanisms:
Roadbuilding completely disrupts the natural soil profile.

Heavy equipment creates large amounts of unconsolidated soil that is often "sidecast" along miles and miles of roadway. This sidecast material can overload and "oversteepen" already steep slopes.

Road building disrupts subsurface drainage, turning subsurface flow into surface flow, and often creates dangerous areas of water concentration;

Road culverts often dump large amounts of water on unconsolidated fill material;

Are the Current Forest Practice Rules Good Enough?

Some people say that the slides are caused by past practices, especially old road-building techniques that (according to some) are no longer practiced. Unfortunately, the backbone of Oregon's forest transportation system is the older roads built with the old practices. Private landowners are also much slower to adopt modern techniques than the federal forest managers. These old high risk roads should be modified or their impacts mitigated.

While it's true that roadways experience a period of relatively higher risk of sliding within a few years after they are built, these old roads remain at high risk relative to forested areas for decades after construction. Also, many of our older roads follow streams for miles often being within flood plains where rivers and streams continually shift and can erode their fill slopes which tends to increase slide risk.

Furthermore, there's not much that can be done to mitigate for a clearcut. All things being equal, most slides are initiated where clearcutting is still practiced the old-fashioned way-- either along intermittent stream courses or on midslope areas-- where current forest practice rules provide very little protection. Experts also often point out that while roads have a higher relative risk of sliding than clearcuts, they occupy a much smaller portion of the land base. In many of our private land areas, clearcutting rates are so high that up to 50 percent of the land area is in age classes less than 20 years which puts them at higher risk of landslides.

Potential Mitigation: What Can We Do To Minimize The Risks?

It might be possible to mitigate the increase in landslide risk caused by timber harvest, but that will require significant modifications to our forest practices rules:

1) Leaving some large areas uncut because they are simply too risky in terms of human life, potential property damage or critical water quality impacts (e.g., community water supply and salmon habitat);

2) Leaving uncut "leave areas" in high risk areas (with significant buffers, so that wind storms don't play havoc with small leave areas and actually increase the slide risk as has been observed in some studies);

3) Leaving significantly wider stream buffers, and adding protection for intermittent streams and incipient channels where there is virtually no protection in the state forest practice rules today; and

4) Leaving large firmly-rooted trees well-distributed across every acre of potentially unstable ground. (No one has shown that such thinning actually works. The influence of wind on the remaining trees in the thinned stand might actually cause more slides than if more or less trees were left, but it's worthy of some research.)

Explanation and Discussion of the Table (see below)

The column entitled "Study Period" shows the length of time during which slides occurred and were inventoried. This ranges from many decades to one winter or even one storm. In general, longer study periods would have larger sample sizes and statistically more reliable results, but longer study periods sometimes introduce difficulties of inventorying slides that occurred in the past that are now partially grown over with vegetation.

Another problem with study periods is that some of the investigators used different time periods for different land uses. That is, they inventoried slides in forested areas that occurred over many decades, while they inventoried slides in harvested areas over a more recent and shorter time period during which the area was affected by timber harvest. Some investigators used the "cumulative area total" method to account for this difference others did not. In general, use of longer study periods for forested areas than for harvested areas and failure to account for the cumulative time that the area was forested or harvested or roaded would tend to bias the results toward under-estimating the risk of slides in clearcuts and roadways.

The column titled "Study Area" shows the area of land inventoried in square kilometers. In general, larger study areas would have larger sample sizes and more reliable statistics but larger study areas also increase the difficulty of completing comprehensive surveys. Most of the largest studies were done using aerial survey techniques which probably increases the likelihood that the inventory missed some slides. Aerial techniques probably miss slides in all three land use categories-- forested areas, clearcuts, and roadways-- but there will likely be a slight bias towards under-estimating the risk of slides in forested area. Any of the studies that have results in the column titled "Relative Soil Transfer Rates" presumably involved ground-based measurement of slide volumes. This ground-based activity may have led to the identification of additional slides that were not found during aerial surveys which might partially correct the bias.

The column titled "Relative Rate of Slide Initiation for Forest/Clearcut/Road" represents the relative number of slides per unit area. The number of slides per unit area of clearcut and road right-of-way were represented as multiples of the background rate of slides in forested areas.

The column titled "Relative Soil Transfer Rate for Forest/Clearcut/Road" represents the relative volume of slide material per unit area. The soil transfer rate for clearcut areas and road rights-of-way were represented as multiples of the background soil transfer rate in forested areas.

The bottom of this page set forth the full citations of the studies presented in the table.

Table of Pacific Northwest Landslide Surveys

Author(s) and date(s) of publication	Study Location	Study Period	Study Area (km2)	Relative Rate of Slide Initiation for Forest/Clearcut/Road	Relative Soil Transfer Rate for Forest/Clearcut/Road	Survey Method: Aerial or Ground
Bishop et al 1964	Southeast Alaska Maybeso Creek Neets Bay	1948-1962 ~14 years.	na	1x | 93x | na1	na	Both
Dyrness 1967	Oregon Cascades H.J.Andrews Forest	1964-1965 1 winter	61	1x | 10x | 309x	1x | 8x | 60x	Ground
O'Laughlin 1972, Swanston et al 1976	Southwest British Columbia Coastal Mountains	1939-1972 ~33 years	640	1x | 5x | 20x	1x | 2x | 25x	Aerial
Fiksdal 1974	Washington Stequaleho Creek	1887-1971 ~84 years	24.5	1x | na | 1600x	1x | na | 224x	Both
Swanson et al 1975	Oregon Cascades HJ Andrews Forest	1946-1972 ~26 years	64	1x | 3x | 33x	1x | 3x | 30x	Both
Morrison 1975	Oregon Cascades Alder Creek	1946-1975 ~29 years	174	1x | 12x | 366x	1x | 2.6x | 343x	Both
Gresswell et al 1976	Oregon Coast Range Mapleton RD	1975 1 winter	760	1x | 24x | 73x	na	Aerial
Swanson et al 1977	Oregon Coast Range Mapleton RD	1957-1977 ~20 years	64	1x | 1x | 7x	1x | 2x | 45x	Both
Swanson et al 1977	Cedar Creek Oregon	?	?	1x | 5x | 40x	na	?

	Mapleton RD					
Ketcheson 1977, Ketcheson et al 1978	Oregon Coast Range Mapleton RD	1963-1978 ~15 years	7.28	1x | 2x | na	1x | 3.4x | na	Ground
Hughes 1978	Umpqua NF Granite Ck, Oregon	1971-1978 ~7 years	0.8	na	1x | 10x | 27x	Ground
Marion 1981	Oregon Cascades Blue River	1946-1981 ~34 years	61.66	1x | 10x | 106x	1x | 9x | 44x	Both
Lyons 1981	Oregon Cascades Middle Fork Willamette River	1959-1967 ~8 years	668	1x | 23x | 29x	na	Aerial
Lyons 1981	Oregon Cascades Middle Fork Willamette River	1967-1972 5 years	657.7	1x | 7x | 10x	na	Aerial
Hicks 1982	Oregon Cascades Middle Santiam R.	1955-1981 ~26 years	60	1x | 3x | 74x	1x | 3.4x | 95x	Aerial
Chesney 1982	Oregon Cascades Willamette NF	1949-1959 ~11 years	5262	1x | 4x | 33x	na	Aerial
"	Oregon Cascades Willamette NF	1959-1967 ~9 years	5240	1x | 13x | 208x	na	Aerial
"	Oregon Cascades Willamette NF	1967-1972 ~6 years	5240	1x | 22x | 705x	na	Aerial

"	Oregon Cascades Willamette NF	1972-1979 ~8 years	5240	1x | 5x | 254x	na	Aerial
Swanson et al 1982	Willamette NF (moderately stable areas)	~30 years	6700?	1x | 3x | 47x	1x | 2.5x | 37x	Both
"	Willamette NF (unstable areas)	~30 years	6700?	1x | 7x | 336x	1x | 5.5x | 250x	Both
Schwab 1983	British Columbia Rennel Sound	1978 1 winter	160	1x | 17x | 28x	1x | 41x | 46x	Both
McCashion et al 1983, Amaranthus et al 1985	Northwest California	na	na	1x | na | 9x	na	Both
Schroeder 1984	Oregon Coast Range Palouse Creek	1981-1982 1 winter	11.35	1x | 10x | na	na	Aerial
"	Oregon Coast Range Larson Creek	1981-1982 1 winter	9.72	1x | 6x | na	na	Aerial
Amaranthus et al 1985	Siskiyou NF Klamath Mountains, Oregon	1956-1976 ~20 years	556	1x | 19x | 138x	1x | 7x | 112x	Aerial

1. In Bishop et al 1964 the 93x slide risk factor probably represents the combined effect of clearcutting and roads.

Pacific Northwest Landslide Surveys Listed in Table

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Meeting GHG reduction targets requires accounting for all forest sector emissions

To cite this article: Tara W Hudiburg *et al* 2019 *Environ. Res. Lett.* **14** 095005

IOP Publishing *Environ. Res. Lett.* **14** (2019) 095005 https://doi.org/10.1088/1748-9326/ab28bb

Environmental Research Letters

OPEN ACCESS

RECEIVED
20 February 2019

REVISED
3 June 2019

ACCEPTED FOR PUBLICATION
11 June 2019

PUBLISHED
23 August 2019

LETTER

Meeting GHG reduction targets requires accounting for all forest sector emissions

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Keywords: carbon, forests, wood products, climate mitigation, GHG mandates

Supplementary material for this article is available online

Abstract

Atmospheric greenhouse gases (GHGs) must be reduced to avoid an unsustainable climate. Because carbon dioxide is removed from the atmosphere and sequestered in forests and wood products, mitigation strategies to sustain and increase forest carbon sequestration are being developed. These strategies require full accounting of forest sector GHG budgets. Here, we describe a rigorous approach using over one million observations from forest inventory data and a regionally calibrated life-cycle assessment for calculating cradle-to-grave forest sector emissions and sequestration. We find that Western US forests are net sinks because there is a positive net balance of forest carbon uptake exceeding losses due to harvesting, wood product use, and combustion by wildfire. However, over 100 years of wood product usage is reducing the potential annual sink by an average of 21%, suggesting forest carbon storage can become more effective in climate mitigation through reduction in harvest, longer rotations, or more efficient wood product usage. Of the ∼10 700 million metric tonnes of carbon dioxide equivalents removed from west coast forests since 1900, 81% of it has been returned to the atmosphere or deposited in landfills. Moreover, state and federal reporting have erroneously excluded some product-related emissions, resulting in 25%–55% underestimation of state total CO_2 emissions. For states seeking to reach GHG reduction mandates by 2030, it is important that state CO_2 budgets are effectively determined or claimed reductions will be insufficient to mitigate climate change.

Introduction

Heat trapping greenhouse gases (GHGs) are being added to the atmosphere at an accelerating rate by fossil fuel combustion and land use change. Climate change consequences were recently described by the Intergovernmental Panel on Climate Change (IPCC) and the United States National Climate Assessment (USGCRP 2018). The IPCC Special Report (IPCC 2018), Global Warming of 1.5 °C, concludes that to keep global average temperature below 1.5 °C by 2100, it is essential to reduce fossil fuel emissions by 45% by 2030, while substantially increasing the removal of atmospheric CO_2. Both reports emphasize the need to increase atmospheric CO_2 removal strategies by forests in addition to sustaining current forest carbon uptake (Houghton and Nassikas 2018). Some states in the US have set targets for reducing GHGs that include forest climate mitigation options (Anderson *et al* 2017, Law *et al* 2018), yet consistent, rigorous accounting methods are required for evaluating options. Challenges include determining the extent that forests, harvest operations, and wood products affect GHG budgets and emissions accountability.

The most recent global carbon budget estimate indicates that land-based sinks remove 29% of anthropogenic emissions (including land use change) with a significant contribution from forests (Le Quéré *et al* 2018). However, none of the agreements or policies (IPCC 2006, NRCS 2010, Brown *et al* 2014, Doe 2017, EPA 2017, Duncan 2017) provides clear and consistent procedures for quantitatively assessing the extent forests and forest products are increasing or reducing carbon dioxide concentrations in the atmosphere. Assessments are challenging because they involve components that require multiple types of expertise and accounting methods (i.e. forest ecosystem processes, wood products, and inherently uncertain substitution credits). Methods are often in disagreement over the wood product Life Cycle Assessment (LCA) assumption of *a priori* carbon neutrality, where biogenic emissions from the combustion and decomposition of wood is ignored because the carbon released from wood is assumed to be replaced by subsequent tree growth in the following decades (EPA 2016). Despite a multitude of analyses that recognize that the assumption is fundamentally flawed (Harmon *et al* 1996, Gunn *et al* 2011, Haberl *et al* 2012, Schulze *et al* 2012, Buchholz *et al* 2016, Booth 2018), it continues to be used in mitigation analyses, particularly for wood bioenergy.

Forests are sustainable *net* sinks as long as forest carbon uptake from the atmosphere exceeds emissions from harvesting, wood product use and decomposition, and wildfire. Wood products ultimately release CO_2 to the atmosphere as they are manufactured, disposed of, and decompose or are burned. However, because of concerns about double-counting, significant emissions associated with harvest and wood product use have not been counted for any sector (EPA 2018). These emissions are often not included in state CO_2 budget estimates (Brown *et al* 2014, Oregon Global Warming Commission 2017), even when they are included in national budgets (EPA 2017) (table S1 is available online at stacks.iop.org/ERL/14/095005/mmedia). If US states intend to use forests for mitigation strategies, they must account for all contributing sources and sinks of forests and forest-derived products (Stockmann *et al* 2012, IPCC 2014).

By focusing on a region with sufficient information to conduct a meaningful LCA, we demonstrate how a quantitative assessment of forests, management practices and wood products can assess the actual role played by forests and forestry practices in managing atmospheric CO_2. We calculate the regional forest carbon balance (from 2001 to 2016) using observations from over 24 000 forest inventory plots in Washington, Oregon, and California (states with GHG reduction mandates). Net forest sector carbon balance is quantified using an improved LCA including harvest, transportation, manufacturing, wood product pool storage and decay, emissions associated with fire, and substitution for both building construction and energy production. We specifically consider global warming potential associated with carbon dioxide and do not include additional GHGs such as nitrous oxide and methane. Our aim is to provide an accurate cradle-to-grave, transparent and transferable accounting method of all forest-derived carbon for other states and countries with GHG reduction mandates (figure 1; box 1; figure S1; tables S2–S6).

Results

Western US forest ecosystem CO_2 balance (2001–2016)

Forest carbon uptake and release (net ecosystem production (NEP); figure 1(a)) controlled by ecosystem biological processes is calculated as the balance between forest carbon uptake (net primary production (NPP)) and forest carbon release through the decomposition of dead organic matter (heterotrophic respiration; R_h). In this study, a negative number indicates a net carbon sink (removal from the atmosphere) and a positive number indicates a net carbon source (addition to the atmosphere). The coastal Western US states together are a strong forest carbon sink with NEP of −292 ± 36 million metric tonnes (MMT) CO_2e per year (−857 g CO_2e m^{-2} yr^{-1}) (table 1; table S1), and account for approximately 60% of total Western US forest NEP (coastal, southwestern, and intermountain regions).

In addition to NEP, disturbances from harvest and wildfire influence estimates of net ecosystem carbon balance (NECB = NEP minus losses Chapin *et al* 2006; figure 1(a)). In the Western US states, the significant carbon losses from the forest are primarily from removals of wood through harvest, decomposition or burning of aboveground and belowground harvest residues, and wildfire (Law and Waring 2015). Significant harvest has been occurring in the western US since the early 20th century (figure S2). Up to 40% of the harvested wood does not become a product and the products themselves decay over time, resulting in product accumulation much smaller than the total amount harvested (figure 2(a); solid line) (Harmon *et al* 1996, Dymond 2012, Williams *et al* 2016, EPA 2017). Emissions include combustion of wood that does not become a product, combustion for energy, decomposition and/or combustion at end-of-life (table 1; rows 5, 6, 9, and 10). When these carbon losses are accounted for, these forests remain significant carbon sinks at −187 ± 33 MMT CO_2e per year (−551 g CO_2e m^{-2} yr^{-1}), with the largest sink in California (40%) followed by Oregon (33%) and Washington (27%). Despite California having twice the fire emissions of the other states (~10 versus ~5 MMT CO_2e yr^{-1} per state) the ranking is due to much lower harvest removals in California (~12 MMT CO_2e yr^{-1}) compared to almost double in

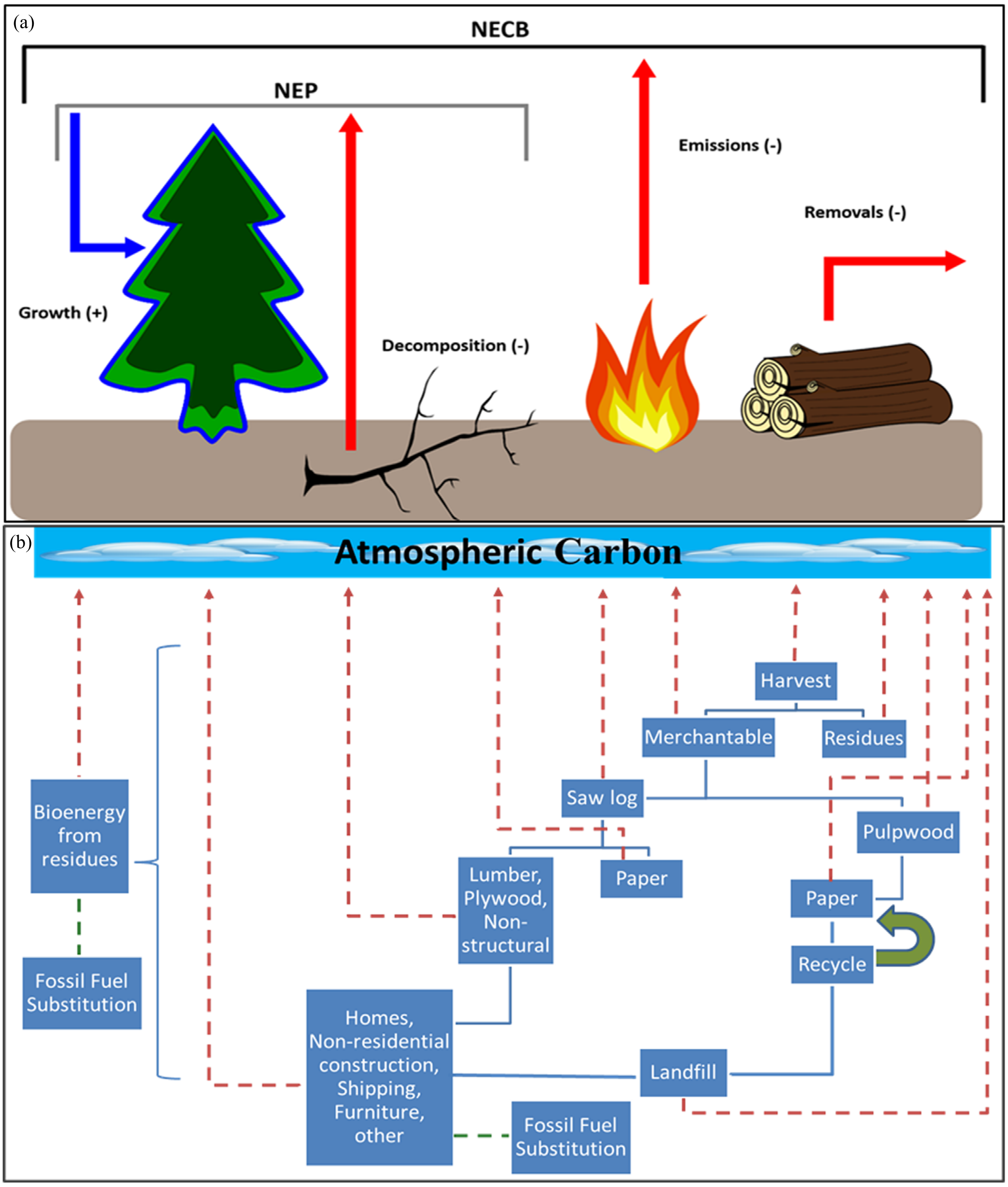

Figure 1. Conceptual diagram of Forest-GHG (a) describes the natural, land-based forest carbon sink where the net of growth and decomposition is net ecosystem production (NEP), and after accounting for removals from fire and harvest, the balance is net ecosystem carbon balance (NECB), (b) describes the cascade of wood products until eventual deposition in landfills or the atmosphere and shows the pathway of emissions.

Washington (~20 MMT $CO_2e\ yr^{-1}$) and triple in Oregon (~31 MMT $CO_2e\ yr^{-1}$). Fire emissions are a third of harvest removals region-wide.

Building on our earlier work (Harmon *et al* 1996, Hudiburg *et al* 2011, Law *et al* 2018), we developed a modified cradle-to-grave model (Forest-GHG) for combining the balance of carbon captured in forest ecosystems, wood product use, lifetime emissions, and eventual return to the atmosphere or long-term storage in landfills. Forest-GHG tracks emissions associated with harvest of wood and manufacturing, transport and use of wood products. Harvest removals result in immediate (combustion of residues on-site or as mill residues with and without energy recapture), fast (short-lived products such as paper), decadal (long-lived products such as wood) and centuries-long (older buildings and land-filled) timeframes before emissions are released back to the atmosphere (figures 1(b) and S1). Our model includes seven product pools and temporally dynamic recycling and landfill rates. Most importantly, we now include a more mechanistic representation of longer-term structural wood in buildings, by moving beyond a simple half-life with exponential decay (figure 3 and SI methods and SI tables 2–6). Our new building cohort-component method tracks decay of short- and

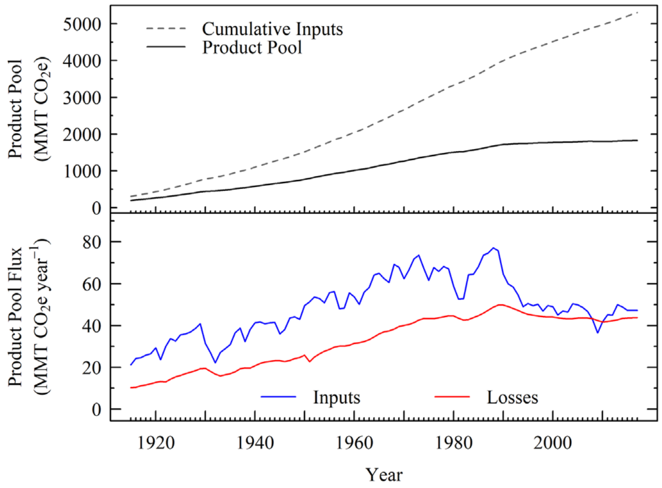

Figure 2. Wood product inputs and outputs from 1900 to 2016 for Washington, Oregon, and California. (A) Cumulative production in MMT CO_2e per year assuming no losses over time (dotted grey line) versus the realized in-use wood product pool over time after accounting for decay (losses). (B) Yearly product inputs over time (blue line) that represents the fraction of harvest (removed wood) that becomes a product versus the decay emissions from the pool over time (red line).

Table 1. Average annual total fluxes by state and region from 2001 to 2016. All units are in million MT CO_2e. Negative numbers indicate a carbon sink (CO_2 is being removed from the atmosphere). The more negative the number, the stronger the sink. Grey shading is used to indicate net values that represent carbon sink strength both before and after removals are accounted for.

Ecosystem	Washington	Oregon	California	Total
1. Forested area (million hectares)	9.7	12.4	11.9	34.0
2. Net ecosystem production (NEP)	**−89.9**	**−102.0**	**−99.8**	**−291.6**
3. Fire emissions	5.1	5.3	10.3	20.7
4. Harvest removals	18.5	30.5	11.5	60.5
Net ecosystem carbon balance (NECB) (sum of rows 1 through 4)	**− 66.4**	**−66.2**	**−78.0**	**−210.5**

Forest industry	Washington	Oregon	California	Total
5. Harvest residue combustion (onsite)	3.9	6.5	2.5	12.9
6. Harvest, transportation, manufacturing (FFE emissions)	2.8	4.6	1.6	9.0
7. Wood product pool annual inputs	−18.5	−30.5	−11.5	−60.5
8. Landfill annual inputs (from products)	−6.8	−11.9	−4.2	−22.9
9. Wood manufacturing losses	3.9	6.5	3.9	14.3
10. Wood product and landfill decomposition	21.4	36.2	13.3	71.0
Net forest sector carbon balance (NECB + sum of rows 5 through 10)	**−59.5**	**−54.7**	**−72.4**	**−186.6**
11. Wood product substitution (wood)	−3.0	−4.9	−1.6	−9.4
12. Wood product substitution (energy)	−1.8	−3.0	−1.8	−6.6
Net forest sector carbon balance (with credits; NECB + sum of rows 5 through 12)	**−64.3**	**−62.6**	**−75.8**	**−202.7**

long-lived building components annually, and the lag time associated with these losses (figure S3). Our wood bioenergy substitution credits (Sathre and O'Connor 2010) include wood waste from harvest, mill residues, and wood products displacement of more fossil fuel intensive materials.

Using our component tracking LCA, we found that of the $\sim$10 700 MMT CO_2e of wood harvested in all three states since 1900 (figure 2), only 2028 MMT CO_2e are currently stored in wood products with half stored in Oregon (1043 MMT CO_2e). In just over 100 years, Oregon has removed the equivalent of all live trees in the state's Coast Range forests (Law *et al* 2018), and returned 65% to the atmosphere and transferred 16% to landfills. Even though these are some of the most productive and carbon dense forests in the world (Hudiburg *et al* 2009), the carbon accumulated in much of the removed biomass took up to 800 years to accumulate—and cannot be recovered if current management practices continue.

Forest harvest-related emissions have averaged 107 MMT CO_2e annually from 2001 to 2016 (table 1; row 5, 6, 9, and 10). Emissions are highest from decay of the wood product pool that has been accumulating for over 100 years (table 1 row 10; figures 3 and S3). This is after accounting for recycling and semi-permanent storage in landfills. Structural wood product decay for long- and short-term components (wood in buildings; figure 3) account for about 30%–35% of wood product and landfill decomposition while paper and non-building wood products account for about 65%–70%. Under this complete accounting, the

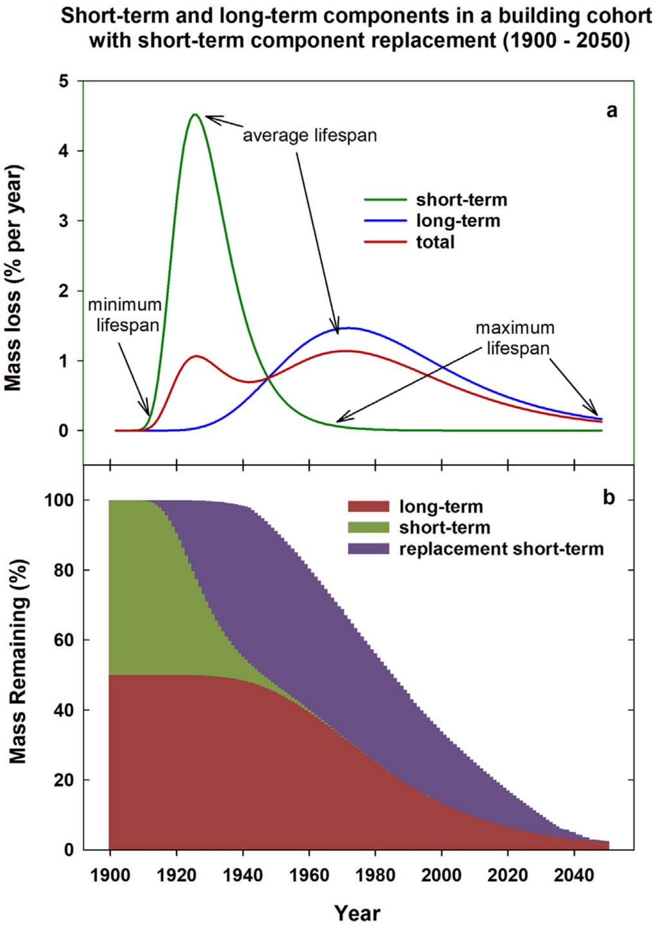

Figure 3. Conceptual models of the Forest-GHG cohort-component method for: (a) mass loss in a cohort of buildings with a 75 year average life span that accounts for the short and long-term portions of buildings and (b) mass remaining in a single building cohort over time (with replacement). Data presented is based on the 1900 cohort of single-family homes built in Oregon.

lowest contribution to overall emissions is from fossil fuel usage during harvest, transportation, and manufacturing, i.e. less than 10% of total wood product-related emissions in the three states.

We found that wood-related substitution for construction materials (0.54 fossil fuel carbon emissions avoided per unit carbon of wood; table 1 row 11) and energy (0.68 fossil fuel carbon emissions avoided; table 1 row 12) may offset 18% of forest industry emissions. This assumes 50% of wood-derived construction products are substituted for a non-wood product and that 75% of mill residues are substituted for fossil fuel energy (Berg *et al* 2016).

We varied the maximum average life spans of the wood products used in construction (e.g. buildings) to examine its effect on emissions estimates. Emissions are minimally reduced by 2%–4% in each state when a longer average maximum lifespan is used (100 years) for the long-term building components and minimally increased by 2%–3% when a shorter average maximum lifespan is used (50 years, which is the mean lifetime of buildings in the US EPA 2013).

Combined, the US west coast state forest sector (cradle-to-grave) is a net carbon sink, removing ~187 MMT CO_2e annually from the atmosphere and potentially reducing fossil fuel emissions by up to another 20 MMT CO_2e through product and energy substitution. Harvest-related emissions reduce the natural sink (NEP—Fire) by 34, 46, and 27% for Washington, Oregon, and California, respectively. When substitution credits are included, this changes to reductions of 27%, 37%, and 23%. Harvest rates have been highest in Oregon (table 1), contributing to increasing wood product emissions and the largest reductions to forest sink capacity.

Discussion

NECB is a good estimate of ecosystem carbon uptake, e.g. for carbon offsets programs (Anderson *et al* 2017), and can be compared spatially with changing environmental conditions or disturbances, but is an incomplete calculation of the entire forest sector emissions. It does not include emissions from wood products caused by machinery, transport, manufacturing and losses—emissions that can equal up to 85% of the total versus 15% from fire, insects, and land use change (Williams *et al* 2016). Nor does it account for the storage and subsequent release of carbon in varying end uses with varied product lifetimes. Given that not all harvested wood is an immediate source to the atmosphere and very little harvested wood is stored in perpetuity, it is essential to track associated emissions over time. For state- or region-level carbon budgets, a cradle-to-grave carbon LCA should be combined with the ecosystem carbon balance (NEP and NECB) to account for how much the forestry sector is contributing to or offsetting total carbon emissions.

If wood buildings are replaced by wood buildings, substitution is not occurring, and because wood is preferred for construction of single-family housing in North America, some of our substitution values are overestimated (Sathre and O'Connor 2010). Wood products store carbon temporarily, and a larger wood product pool increases decomposition emissions over time (figure 3). This emphasizes that increasing the wood product carbon sink will require shifts in product allocation from short-term to long-term pools such as reclaimed (re-used) wood products from demolition of buildings, and reduction of product manufacturing losses (EPA 2016). Clearly, there is potential for climate mitigation by using forests to sequester carbon in biomass and reduce losses associated with the wood product chain (Law *et al* 2018).

It is argued that there may be reductions in fossil carbon emissions when wood is substituted for more fossil fuel intensive building materials (e.g. steel or concrete) or used as an alternative energy source (Butarbutar *et al* 2016). Substitution is a one-time credit in the year of the input. Studies have reported a range of substitution displacement factors (from negative to positive displacement; Sathre and O'Connor 2010, Smyth *et al* 2017), but we found no study that has tracked the actual amount of construction product substitution that is occurring or has occurred in the past in the United States. This makes substitution one of the most uncertain parts of this carbon budget. It may be more easily tracked in the fossil fuel sector through a decrease in emissions because of reduction in product supply, in which case it would be double counting to then include it as a credit for the forest sector. We show results with and without the substitution credit (a decrease in forest sector emissions) because it cannot be verified. We show the potential impact it has on the overall forest sector carbon sink, even though the displacement factor may be unrealistically high (Smyth *et al* 2017, Dugan *et al* 2018). For forest sector emissions assessments, the uncertainty suggests exclusion of the credit.

Currently, state's GHG accounting budgets are incorrect because they are not full cradle-to-grave estimates of all CO_2 emissions associated with forest natural processes and human influences. For accurate GHG accounting, these emissions should be included in the forestry sector as they are not accounted for by state's energy and transportation sectors (IPCC 2006) (table S1). The US EPA reported average fossil fuel CO_2 emissions of 491 MMT CO_2e yr^{-1} for the three states combined (2013–2016). Forest industry harvest, transportation, and manufacturing fossil fuel emissions are included in this total. However, it is unclear to what extent wood product decay and combustion emissions are also counted in state budgets. In Oregon, they are not included at all, resulting in state CO_2 emissions that have been underestimated by up to 55% (Oregon Global Warming Commission 2017, Law *et al* 2018). Washington includes combustion emissions from the current year's harvest (table 1; Manufacturing losses; row 9), but not from wood product decay, resulting in up to a 25% underestimation of state CO_2 emissions. Because California's emissions from other sectors are so high (76% of regional total), and harvest rates have been historically lower than in Oregon and Washington, the impact of not including these emissions is very small as a proportion of the total. Although fire in California has received much attention, it only accounts for 3% of the state's total fossil fuel CO_2 emissions.

These underestimates are especially alarming for Oregon where GHG reduction targets are to be 10% below 1990 levels by 2020 and at least 75% below 1990 levels by 2050 (Pietz and Gregor 2014). California and Washington emissions are to be reduced to 1990 levels by 2020 (Nunez 2006), and 80% and 50% below 1990 levels by 2050 (Washington State 2008), respectively.

In contrast, the US EPA reports emissions from wood product decay and landfills (EPA 2017) per the IPCC guidelines (IPCC 2006) (table S1). However, combustion emissions from logging and mill residues are not reported (EPA 2017). Moreover, ecosystem carbon losses are indirectly estimated through changes in biomass pools with measurement uncertainty that can be greater than the change (Ferster *et al* 2015). So even at the national level, emissions (as a fraction of fossil fuel emissions) would be underestimated by 10% and 24% in Washington and Oregon, respectively. Undoubtedly, there are implications for reduction mandates when the magnitude of emissions themselves are incorrect.

Conclusions

The goal for all societies and governments as stated in Article 2 of the *United Nations Framework Convention on Climate* Change (Oppenheimer and Petsonk 2005) should be '…stabilization of GHG concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system.' The Paris Climate Agreement (UNFCCC 2015) aims to keep global average temperature from rising by no more than 2 °C above preindustrial levels, and if possible no more than 1.5 °C. Forests are identified as part of the strategy (UNFCCC 2015).

Although some US states have attempted to quantify a portion of forest-related emissions, improved estimates are essential to track emissions to meet reduction goals. We identified the main components that should be part of the forest sector state estimates. We found that emissions have been underestimated by up to 55% in Oregon and 25% in Washington, and that at present, these emissions are not reported in state GHG reporting guidelines. The accuracy of forest sector emissions estimates can be improved with sub-regional data on residential and commercial building lifespans, recycling, verifiable substitution benefits and accurate monitoring of growth rates of forests. However, verifiable substitution of one material for another may be more readily quantified in the fossil fuel sector.

The 2006 IPCC GHG guidelines provide three different approaches for calculating emissions from harvested wood products (IPCC 2006) (including reporting 'zero') and reporting of this component is not required by UNFCCC. To complicate accounting further, several studies have shown that using the different recommended approaches results in emissions that differ by over 100% (Green *et al* 2006, Dias *et al* 2007). Moreover, according to IPCC and UNFCCC, emissions of CO_2 from forest bioenergy are to be counted under land use change and not counted in the energy sector to avoid double counting. However, this provides a 'loophole' leading to their not being counted at all.

The United States government currently requires all federal agencies to count forest bioenergy as carbon neutral because the EPA assumes replacement by future regrowth of forests somewhere that may take several decades or longer (EPA 2018). While it is theoretically possible that a replacement forest will grow and absorb a like amount of CO_2 to that emitted decades or a century before, there is no guarantee that this will happen, and the enforcement is transferred to future generations. In any rational economic analysis, a benefit in the distant future must be discounted against the immediate damage associated with emissions during combustion. Furthermore, the goal for climate protection is not climate neutrality, but rather reduction of net GHGs emissions to the atmosphere to avoid dangerous interference with the climate system. Allowing forests to reach their biological potential for growth and sequestration, maintaining large trees (Lutz *et al* 2018), reforesting recently cut lands, and afforestation of suitable areas will remove additional CO_2 from the atmosphere. Global vegetation stores of carbon are 50% of their potential including western forests because of harvest activities (Erb *et al* 2017). Clearly, western forests could do more to address climate change through carbon sequestration if allowed to grow longer.

Since it is now clear that both CO_2 emissions and removal rates are essential to meet temperature limitation goals and prevent irreversible climate change, each should be counted and reported. We recommend that international agreements and states utilize a consistent and transparent carbon LCA that explicitly accounts for all forest and wood product storage and emissions to determine compliance with goals to lower atmospheric GHGs. Only by using a full accounting of GHGs can the world manage its emissions of heat trapping gases to achieve concentrations in the atmosphere that will support a stable climate.

Materials and methods

We calculated the 2001 to 2016 average net forestry sector emissions from cradle-to-grave, accounting for all carbon captured in biomass and released through decomposition by forest ecosystems and wood products industry in Washington, Oregon, and California. Building on our previous work (Harmon *et al* 1996, Hudiburg *et al* 2011, Law *et al* 2013, Law *et al* 2018), we developed a modified and expanded LCA method to combine with our ecosystem carbon balance, now called Forest-GHG (version 1.0; figure 1 and box 1). We accounted for all carbon removed from forests through fire and harvest. All harvested carbon was tracked until it either was returned to the atmosphere through wood product decomposition/combustion or decomposition in landfills, minus the amount semi-permanently stored in landfills (buried). This required calculating the carbon removed by harvest operations starting in 1900 to present day because a portion of the wood removed in the past century is still in-use or decomposing. In addition to carbon in biomass, we also accounted for all carbon emissions associated with harvest (equipment fuel, transportation, manufacturing inputs). Moreover, our wood product life-cycle assessment includes pathways for recycling and deposition in landfills. Finally, we give substitution credits for not using more fossil fuel intensive materials than wood used in construction of buildings and energy production.

Observed carbon stocks and fluxes (ecosystem carbon balance)

Carbon stock and flux estimates were calculated from over 30 000 forest inventory plots (FIA) containing over 1 million tree records in the region following methods developed in previous studies (Law *et al* 2018) (SI Methods). Flux calculations include NPP (Clark *et al* 2001) NEP, and NECB. The NECB represents the net rate of carbon accumulation in or loss from ecosystems.

Off-site emissions associated with harvest (LCA)

Decomposition of wood through the product cycle was computed using a LCA (Harmon and Marks 2002, Law *et al* 2018). A 117 year wood products pool (1900–2016) was simulated using reported harvest rates from 1900 to 2016 for Oregon and Washington (Harmon *et al* 1996, DNR 2017, Oregon Department of Forestry 2017) and from the California State Board of Equalization (CA 2018). Harvest was converted to

Box 1. Terminology and Flux Definitions for table 1

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1. Forest Area = sum of all forest area in each state derived from US Forest Service forest area map (30 m resolution). Includes all ownerships.

1. NEP = Net Primary Production—heterotrophic respiration; microbial respiration as they decompose dead organic matter in an ecosystem.

1. Fire emissions = the emissions associated with *combustion* of organic matter at the time of the fire. Most of what burns is fine surface fuels, averaging 5% of aboveground biomass in mixed severity fires of Oregon and Northern California.

1. Harvest removals = Wood actually removed from the forest (not the total aboveground biomass killed). Removals are not equal to emissions but are the removed carbon from the forests at the time of harvest. This is subtracted from NEP along with fire emissions to calculate the net forest carbon balance from the viewpoint of the forest ecosystem.

NECB = NEP + Fire Emissions + Harvest Removals. The term is the simplest expression of forest carbon balance without tracking wood through the product life cycle. Although not all of the harvest removals will result in instant or near-term emissions, NECB still captures the impact of the removed carbon on the forest ecosystem carbon balance, and is consistent with international agreements (REDD+, conservation).

1. Harvest Residue Combustion = the emissions associated with combustion of slash piles; the branches, foliage, and non-merchantable wood left after harvest operations (remains in the forest) and burned onsite (assumed to be 50% of slash).

1. Harvest, Transportation, Manufacturing (FFE emissions) = the fossil fuel emissions associated with harvest (skidding, sawing, etc), transportation of logs to mills, manufacturing of wood and paper products, and transportation of products to stores (see table S5 for coefficients).

1. Wood Product Pool Annual Inputs = Harvest removals

1. Landfill Annual Inputs (from products) = The amount of wood and paper that is sent to landfills at end of life. In Forest-GHG, this occurs incrementally from 1950 to 1960 and then in 1961 is assumed to be constant at the current rate.

1. Wood Manufacturing Losses = fraction of wood that is lost at the mill (sawdust, etc) and is assumed to be returned to the atmosphere within one year through combustion (with 75% energy recapture) or decomposition.

1. Wood Product and Landfill Decomposition = fraction of the total wood product and non-permanent landfill carbon pools that is returned to the atmosphere annually.

Net Forest Sector Carbon Balance = sum of NECB and rows 5 through 10. Emission sources are rows 5, 6, 9, and 10. Sinks are rows 7 and 8.

1. Wood product substitution (Wood) = carbon credits that account for the displaced fossil fuel emissions when wood is substituted for a fossil fuel derived product in buildings (e.g. concrete or steel). We assume 0.54 g C fossil fuel emissions avoided per g of C of wood biomass used.

Box 1. (Continued.)

1. Wood product substitution (Energy) = carbon credits that account for the displaced fossil fuel emissions when wood is substituted for energy. In the Oregon, Washington, and California this primarily a mix of natural gas and coal. We include the biogenic emissions from combustion of forest-derived woody biomass and include an energy substitution credit if it is combusted with energy recapture.

Net Forest Sector Carbon Balance (with substitution credit) = sum of NECB and rows 5 through 12.

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total aboveground biomass using methods from (Law *et al* 2018). The carbon emissions to the atmosphere from harvest were calculated annually over the timeframe of the analysis (1900–2016).

The coefficients and sources for the Forest-GHG LCA (figures 1(b) and S1) are included in table S1 through S6 with all units expressed as a function of the wood biomass being cut, transported, manufactured, burned, etc. We accounted for the fossil fuel emissions that occur during harvest (fuel for equipment) and the fossil fuel emissions associated with transport of wood to mills. Then, we accounted for the fossil fuel emissions associated with manufacturing of products followed by a second transportation emission for delivery of products to stores and warehouses. Wood that is not made into a wood or paper product (e.g. waste) is assumed to be combusted onsite at the mill (with 50% energy recapture as combined heat and power) or used in a product that will return the carbon to the atmosphere within one year (table 1 and box 1; Wood Manufacturing Losses).

Wood products are divided into varying product pools and are then tracked through the wood product cascade until end of life (figure 1(b)). Wood products are split into seven product pools: single-family homes, multi-family homes, mobile homes, non-residential construction, furniture and manufacturing, shipping, and other wood. We simulated wood product storage and emissions to 2050 for display purposes in the figures assuming a constant harvest rate after 2016.

We estimate the carbon pools and fluxes associated with buildings by separating buildings into components with different life spans (figures 3 and S3). This allows components and buildings to have a lag time before significant losses occur, and recognizes the difference between building life span and the residence time of carbon in a building. This also allows capacity for Forest-GHG to have component and building life spans evolve over time as construction practices and the environment (including biophysical, economic, and social drivers) change.

In Forest-GHG, a fraction of each year's new harvest is allocated to residential (single-family, multi-family, and mobile homes) and non-residential construction (Smith *et al* 2006). This fraction is further divided into the short-term (23%) and long-term (77%) components. The resulting pools are tracked independently, quantifying losses through decay and demolition from the year they start until then end of the simulation.

All the components created in a given year are considered a building cohort that is also tracked separately each year. All components are summed to give the total amount of building carbon remaining in a cohort at a given time (figure S3). For each year, the amount lost to the atmosphere or to the landfills through demolition, is simply the current year's total wood product carbon pool plus the current years inputs and minus last year's total wood product carbon pool.

Substitution

We calculated wood product substitution for fossil fuel derived products (concrete, steel and energy). The displacement value for product substitution was assumed to be 0.54 Mg fossil C/Mg C (Smyth *et al* 2017, Dugan *et al* 2018) wood use in long-term structures (Sathre and O'Connor 2010). Although the displacement value likely fluctuates over time, we assumed it was constant for the simulation period. We accounted for losses in product substitution associated with building replacement (Harmon *et al* 2009), but ignored the leakage effect related to fossil C use by other sectors. We assumed 75% of 'waste wood' was used for fuelwood in homes or at mills (wood manufacturing losses in table 1). We accounted for displacement of fossil fuel energy sources using a displacement factor of 0.68 assuming a mix of coal and natural gas replacement (Smyth *et al* 2017, Dugan *et al* 2018).

Uncertainty estimates and sensitivity analysis

We calculate a combined uncertainty estimate for NEP and NECB using the uncertainty in the observations and input datasets (climate, land cover, harvest amounts). For the biomass and NPP observations, we performed Monte Carlo simulations of the mean and standard deviations for NPP (Hudiburg *et al* 2011) derived for each plot using three alternative sets of allometric equations. Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest removals (7%), and land cover estimates (10%) using the propagation of error approach. Sensitivity analysis was only used for the long-term wood product pool by varying the average life spans of buildings by ±25 years in our new cohort component method. Our estimates varied by 7%. This was combined with the uncertainty in NECB to calculate total uncertainty on the net forest sector carbon balance.

Acknowledgments

This research was supported by the Agriculture and Food Research Initiative of the US National Institute of Food and Agriculture Grant 2013-67003-20652 and the National Science Foundation award number DEB-1553049.

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ENVIRONMENTAL RESEARCH
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To cite this article: Tara W Hudiburg *et al* 2019 *Environ. Res. Lett.* **14** 095005

IOP Publishing Environ. Res. Lett. 14 (2019) 095005 https://doi.org/10.1088/1748-9326/ab28bb

Environmental Research Letters

OPEN ACCESS

RECEIVED
20 February 2019

REVISED
3 June 2019

ACCEPTED FOR PUBLICATION
11 June 2019

PUBLISHED
23 August 2019

LETTER

Meeting GHG reduction targets requires accounting for all forest sector emissions

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Keywords: carbon, forests, wood products, climate mitigation, GHG mandates

Supplementary material for this article is available online

Abstract

Atmospheric greenhouse gases (GHGs) must be reduced to avoid an unsustainable climate. Because carbon dioxide is removed from the atmosphere and sequestered in forests and wood products, mitigation strategies to sustain and increase forest carbon sequestration are being developed. These strategies require full accounting of forest sector GHG budgets. Here, we describe a rigorous approach using over one million observations from forest inventory data and a regionally calibrated life-cycle assessment for calculating cradle-to-grave forest sector emissions and sequestration. We find that Western US forests are net sinks because there is a positive net balance of forest carbon uptake exceeding losses due to harvesting, wood product use, and combustion by wildfire. However, over 100 years of wood product usage is reducing the potential annual sink by an average of 21%, suggesting forest carbon storage can become more effective in climate mitigation through reduction in harvest, longer rotations, or more efficient wood product usage. Of the ~10 700 million metric tonnes of carbon dioxide equivalents removed from west coast forests since 1900, 81% of it has been returned to the atmosphere or deposited in landfills. Moreover, state and federal reporting have erroneously excluded some product-related emissions, resulting in 25%–55% underestimation of state total CO_2 emissions. For states seeking to reach GHG reduction mandates by 2030, it is important that state CO_2 budgets are effectively determined or claimed reductions will be insufficient to mitigate climate change.

Introduction

Heat trapping greenhouse gases (GHGs) are being added to the atmosphere at an accelerating rate by fossil fuel combustion and land use change. Climate change consequences were recently described by the Intergovernmental Panel on Climate Change (IPCC) and the United States National Climate Assessment (USGCRP 2018). The IPCC Special Report (IPCC 2018), Global Warming of 1.5 °C, concludes that to keep global average temperature below 1.5 °C by 2100, it is essential to reduce fossil fuel emissions by 45% by 2030, while substantially increasing the removal of atmospheric CO_2. Both reports emphasize the need to increase atmospheric CO_2 removal strategies by forests in addition to sustaining current forest carbon uptake (Houghton and Nassikas 2018). Some states in the US have set targets for reducing GHGs that include forest climate mitigation options (Anderson *et al* 2017, Law *et al* 2018), yet consistent, rigorous accounting methods are required for evaluating options. Challenges include determining the extent that forests, harvest operations, and wood products affect GHG budgets and emissions accountability.

The most recent global carbon budget estimate indicates that land-based sinks remove 29% of anthropogenic emissions (including land use change) with a significant contribution from forests (Le Quéré *et al* 2018). However, none of the agreements or policies (IPCC 2006, NRCS 2010, Brown *et al* 2014, Doe 2017, EPA 2017, Duncan 2017) provides clear and consistent procedures for quantitatively assessing the extent forests and forest products are increasing or reducing carbon dioxide concentrations in the atmosphere. Assessments are challenging because they involve components that require multiple types of expertise and accounting methods (i.e. forest ecosystem processes, wood products, and inherently uncertain substitution credits). Methods are often in disagreement over the wood product Life Cycle Assessment (LCA) assumption of *a priori* carbon neutrality, where biogenic emissions from the combustion and decomposition of wood is ignored because the carbon released from wood is assumed to be replaced by subsequent tree growth in the following decades (EPA 2016). Despite a multitude of analyses that recognize that the assumption is fundamentally flawed (Harmon *et al* 1996, Gunn *et al* 2011, Haberl *et al* 2012, Schulze *et al* 2012, Buchholz *et al* 2016, Booth 2018), it continues to be used in mitigation analyses, particularly for wood bioenergy.

Forests are sustainable *net* sinks as long as forest carbon uptake from the atmosphere exceeds emissions from harvesting, wood product use and decomposition, and wildfire. Wood products ultimately release CO_2 to the atmosphere as they are manufactured, disposed of, and decompose or are burned. However, because of concerns about double-counting, significant emissions associated with harvest and wood product use have not been counted for any sector (EPA 2018). These emissions are often not included in state CO_2 budget estimates (Brown *et al* 2014, Oregon Global Warming Commission 2017), even when they are included in national budgets (EPA 2017) (table S1 is available online at stacks.iop.org/ERL/14/095005/mmedia). If US states intend to use forests for mitigation strategies, they must account for all contributing sources and sinks of forests and forest-derived products (Stockmann *et al* 2012, IPCC 2014).

By focusing on a region with sufficient information to conduct a meaningful LCA, we demonstrate how a quantitative assessment of forests, management practices and wood products can assess the actual role played by forests and forestry practices in managing atmospheric CO_2. We calculate the regional forest carbon balance (from 2001 to 2016) using observations from over 24 000 forest inventory plots in Washington, Oregon, and California (states with GHG reduction mandates). Net forest sector carbon balance is quantified using an improved LCA including harvest, transportation, manufacturing, wood product pool storage and decay, emissions associated with fire, and substitution for both building construction and energy production. We specifically consider global warming potential associated with carbon dioxide and do not include additional GHGs such as nitrous oxide and methane. Our aim is to provide an accurate cradle-to-grave, transparent and transferable accounting method of all forest-derived carbon for other states and countries with GHG reduction mandates (figure 1; box 1; figure S1; tables S2–S6).

Results

Western US forest ecosystem CO_2 balance (2001–2016)

Forest carbon uptake and release (net ecosystem production (NEP); figure 1(a)) controlled by ecosystem biological processes is calculated as the balance between forest carbon uptake (net primary production (NPP)) and forest carbon release through the decomposition of dead organic matter (heterotrophic respiration; R_h). In this study, a negative number indicates a net carbon sink (removal from the atmosphere) and a positive number indicates a net carbon source (addition to the atmosphere). The coastal Western US states together are a strong forest carbon sink with NEP of -292 ± 36 million metric tonnes (MMT) CO_2e per year (-857 g CO_2e m^{-2} yr^{-1}) (table 1; table S1), and account for approximately 60% of total Western US forest NEP (coastal, southwestern, and intermountain regions).

In addition to NEP, disturbances from harvest and wildfire influence estimates of net ecosystem carbon balance (NECB = NEP minus losses Chapin *et al* 2006; figure 1(a)). In the Western US states, the significant carbon losses from the forest are primarily from removals of wood through harvest, decomposition or burning of aboveground and belowground harvest residues, and wildfire (Law and Waring 2015). Significant harvest has been occurring in the western US since the early 20th century (figure S2). Up to 40% of the harvested wood does not become a product and the products themselves decay over time, resulting in product accumulation much smaller than the total amount harvested (figure 2(a); solid line) (Harmon *et al* 1996, Dymond 2012, Williams *et al* 2016, EPA 2017). Emissions include combustion of wood that does not become a product, combustion for energy, decomposition and/or combustion at end-of-life (table 1; rows 5, 6, 9, and 10). When these carbon losses are accounted for, these forests remain significant carbon sinks at -187 ± 33 MMT CO_2e per year (-551 g CO_2e m^{-2} yr^{-1}), with the largest sink in California (40%) followed by Oregon (33%) and Washington (27%). Despite California having twice the fire emissions of the other states (~10 versus ~5 MMT CO_2e yr^{-1} per state) the ranking is due to much lower harvest removals in California (~12 MMT CO_2e yr^{-1}) compared to almost double in

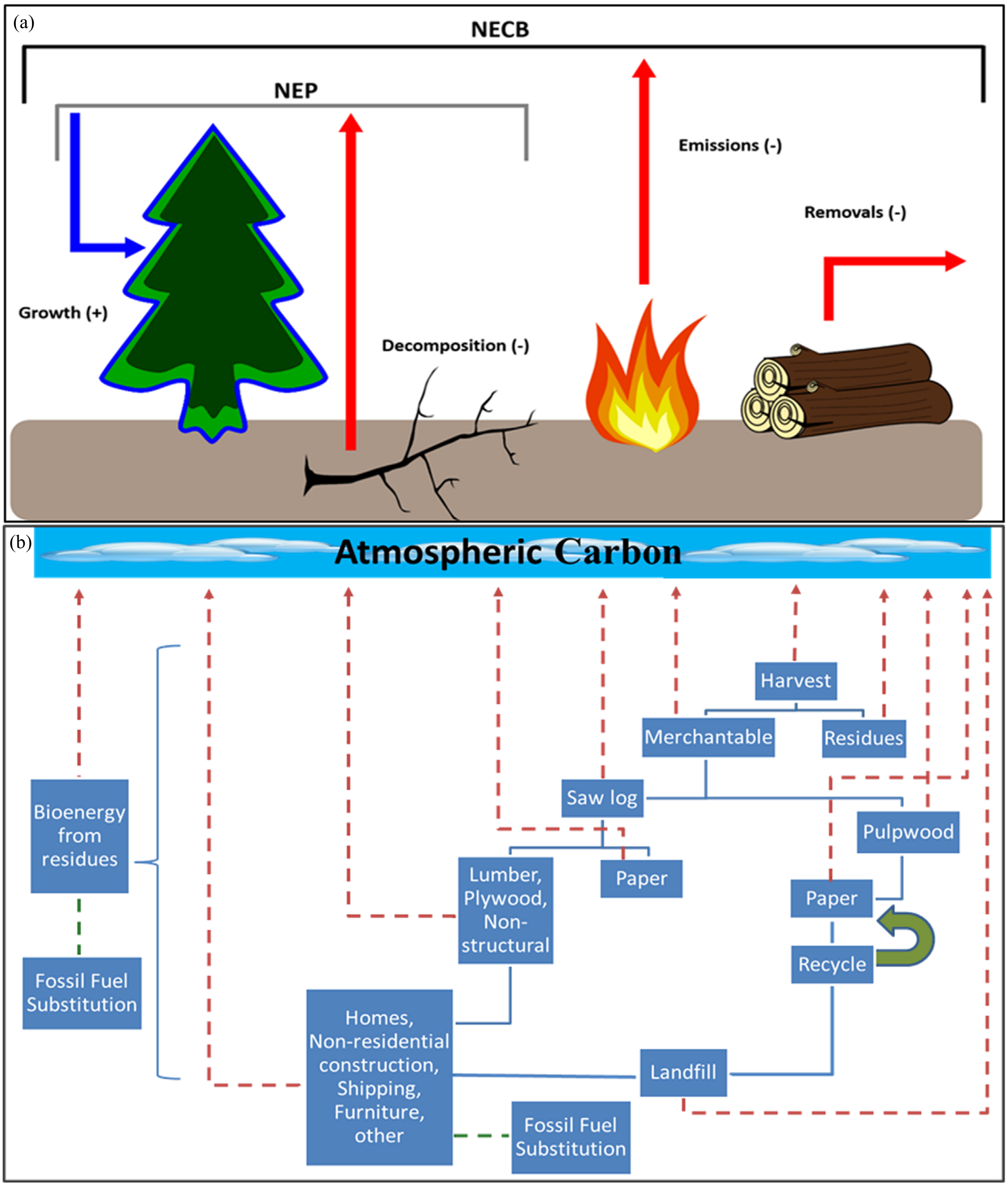

Figure 1. Conceptual diagram of Forest-GHG (a) describes the natural, land-based forest carbon sink where the net of growth and decomposition is net ecosystem production (NEP), and after accounting for removals from fire and harvest, the balance is net ecosystem carbon balance (NECB), (b) describes the cascade of wood products until eventual deposition in landfills or the atmosphere and shows the pathway of emissions.

Washington (~20 MMT CO_2e yr^{-1}) and triple in Oregon (~31 MMT CO_2e yr^{-1}). Fire emissions are a third of harvest removals region-wide.

Building on our earlier work (Harmon *et al* 1996, Hudiburg *et al* 2011, Law *et al* 2018), we developed a modified cradle-to-grave model (Forest-GHG) for combining the balance of carbon captured in forest ecosystems, wood product use, lifetime emissions, and eventual return to the atmosphere or long-term storage in landfills. Forest-GHG tracks emissions associated with harvest of wood and manufacturing, transport and use of wood products. Harvest removals result in immediate (combustion of residues on-site or as mill residues with and without energy recapture), fast (short-lived products such as paper), decadal (long-lived products such as wood) and centuries-long (older buildings and land-filled) timeframes before emissions are released back to the atmosphere (figures 1(b) and S1). Our model includes seven product pools and temporally dynamic recycling and landfill rates. Most importantly, we now include a more mechanistic representation of longer-term structural wood in buildings, by moving beyond a simple half-life with exponential decay (figure 3 and SI methods and SI tables 2–6). Our new building cohort-component method tracks decay of short- and

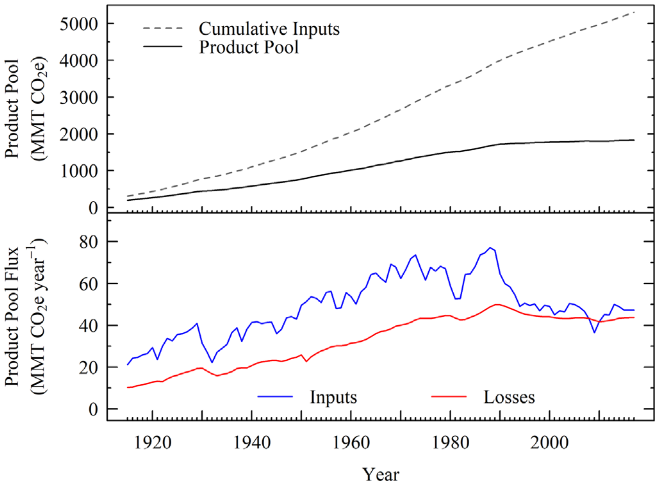

Figure 2. Wood product inputs and outputs from 1900 to 2016 for Washington, Oregon, and California. (A) Cumulative production in MMT CO_2e per year assuming no losses over time (dotted grey line) versus the realized in-use wood product pool over time after accounting for decay (losses). (B) Yearly product inputs over time (blue line) that represents the fraction of harvest (removed wood) that becomes a product versus the decay emissions from the pool over time (red line).

Table 1. Average annual total fluxes by state and region from 2001 to 2016. All units are in million MT CO_2e. Negative numbers indicate a carbon sink (CO_2 is being removed from the atmosphere). The more negative the number, the stronger the sink. Grey shading is used to indicate net values that represent carbon sink strength both before and after removals are accounted for.

Ecosystem	Washington	Oregon	California	Total
1. Forested area (million hectares)	9.7	12.4	11.9	34.0
2. Net ecosystem production (NEP)	**−89.9**	**−102.0**	**−99.8**	**−291.6**
3. Fire emissions	5.1	5.3	10.3	20.7
4. Harvest removals	18.5	30.5	11.5	60.5
Net ecosystem carbon balance (NECB) (sum of rows 1 through 4)	**− 66.4**	**−66.2**	**−78.0**	**−210.5**
Forest industry	Washington	Oregon	California	Total
5. Harvest residue combustion (onsite)	3.9	6.5	2.5	12.9
6. Harvest, transportation, manufacturing (FFE emissions)	2.8	4.6	1.6	9.0
7. Wood product pool annual inputs	−18.5	−30.5	−11.5	−60.5
8. Landfill annual inputs (from products)	−6.8	−11.9	−4.2	−22.9
9. Wood manufacturing losses	3.9	6.5	3.9	14.3
10. Wood product and landfill decomposition	21.4	36.2	13.3	71.0
Net forest sector carbon balance (NECB + sum of rows 5 through 10)	**−59.5**	**−54.7**	**−72.4**	**−186.6**
11. Wood product substitution (wood)	−3.0	−4.9	−1.6	−9.4
12. Wood product substitution (energy)	−1.8	−3.0	−1.8	−6.6
Net forest sector carbon balance (with credits; NECB + sum of rows 5 through 12)	**−64.3**	**−62.6**	**−75.8**	**−202.7**

long-lived building components annually, and the lag time associated with these losses (figure S3). Our wood bioenergy substitution credits (Sathre and O'Connor 2010) include wood waste from harvest, mill residues, and wood products displacement of more fossil fuel intensive materials.

Using our component tracking LCA, we found that of the ~10 700 MMT CO_2e of wood harvested in all three states since 1900 (figure 2), only 2028 MMT CO_2e are currently stored in wood products with half stored in Oregon (1043 MMT CO_2e). In just over 100 years, Oregon has removed the equivalent of all live trees in the state's Coast Range forests (Law *et al* 2018), and returned 65% to the atmosphere and transferred 16% to landfills. Even though these are some of the most productive and carbon dense forests in the world (Hudiburg *et al* 2009), the carbon accumulated in much of the removed biomass took up to 800 years to accumulate—and cannot be recovered if current management practices continue.

Forest harvest-related emissions have averaged 107 MMT CO_2e annually from 2001 to 2016 (table 1; row 5, 6, 9, and 10). Emissions are highest from decay of the wood product pool that has been accumulating for over 100 years (table 1 row 10; figures 3 and S3). This is after accounting for recycling and semi-permanent storage in landfills. Structural wood product decay for long- and short-term components (wood in buildings; figure 3) account for about 30%–35% of wood product and landfill decomposition while paper and non-building wood products account for about 65%–70%. Under this complete accounting, the

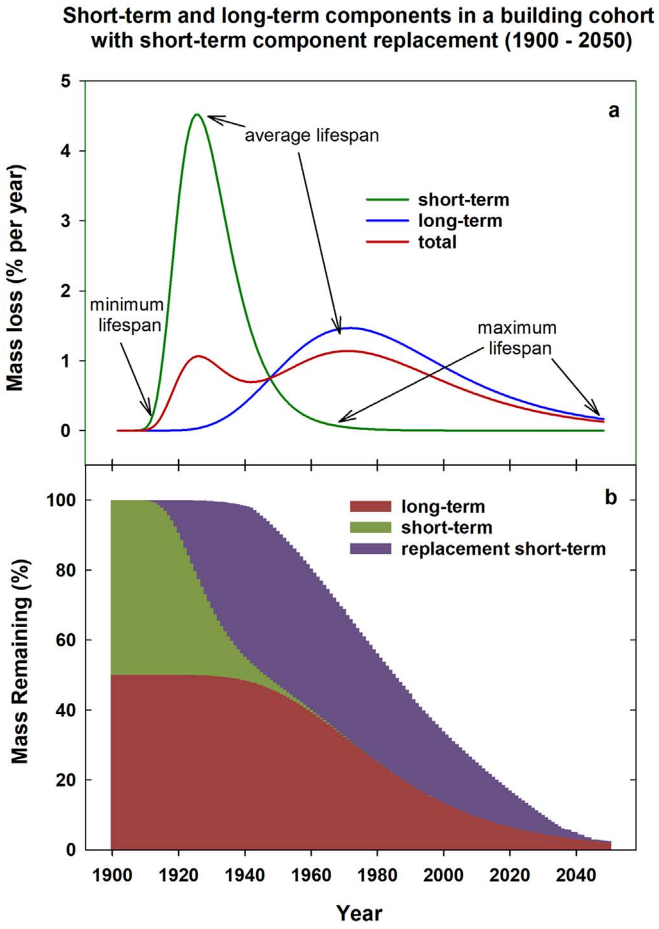

Figure 3. Conceptual models of the Forest-GHG cohort-component method for: (a) mass loss in a cohort of buildings with a 75 year average life span that accounts for the short and long-term portions of buildings and (b) mass remaining in a single building cohort over time (with replacement). Data presented is based on the 1900 cohort of single-family homes built in Oregon.

lowest contribution to overall emissions is from fossil fuel usage during harvest, transportation, and manufacturing, i.e. less than 10% of total wood product-related emissions in the three states.

We found that wood-related substitution for construction materials (0.54 fossil fuel carbon emissions avoided per unit carbon of wood; table 1 row 11) and energy (0.68 fossil fuel carbon emissions avoided; table 1 row 12) may offset 18% of forest industry emissions. This assumes 50% of wood-derived construction products are substituted for a non-wood product and that 75% of mill residues are substituted for fossil fuel energy (Berg *et al* 2016).

We varied the maximum average life spans of the wood products used in construction (e.g. buildings) to examine its effect on emissions estimates. Emissions are minimally reduced by 2%–4% in each state when a longer average maximum lifespan is used (100 years) for the long-term building components and minimally increased by 2%–3% when a shorter average maximum lifespan is used (50 years, which is the mean lifetime of buildings in the US EPA 2013).

Combined, the US west coast state forest sector (cradle-to-grave) is a net carbon sink, removing ~187 MMT CO_2e annually from the atmosphere and potentially reducing fossil fuel emissions by up to another 20 MMT CO_2e through product and energy substitution. Harvest-related emissions reduce the natural sink (NEP—Fire) by 34, 46, and 27% for Washington, Oregon, and California, respectively. When substitution credits are included, this changes to reductions of 27%, 37%, and 23%. Harvest rates have been highest in Oregon (table 1), contributing to increasing wood product emissions and the largest reductions to forest sink capacity.

Discussion

NECB is a good estimate of ecosystem carbon uptake, e.g. for carbon offsets programs (Anderson *et al* 2017), and can be compared spatially with changing environmental conditions or disturbances, but is an incomplete calculation of the entire forest sector emissions. It does not include emissions from wood products caused by machinery, transport, manufacturing and losses—emissions that can equal up to 85% of the total versus 15% from fire, insects, and land use change (Williams *et al* 2016). Nor does it account for the storage and subsequent release of carbon in varying end uses with varied product lifetimes. Given that not all harvested wood is an immediate source to the atmosphere and very little harvested wood is stored in perpetuity, it is essential to track associated emissions over time. For state- or region-level carbon budgets, a cradle-to-grave carbon LCA should be combined with the ecosystem carbon balance (NEP and NECB) to account for how much the forestry sector is contributing to or offsetting total carbon emissions.

If wood buildings are replaced by wood buildings, substitution is not occurring, and because wood is preferred for construction of single-family housing in North America, some of our substitution values are overestimated (Sathre and O'Connor 2010). Wood products store carbon temporarily, and a larger wood product pool increases decomposition emissions over time (figure 3). This emphasizes that increasing the wood product carbon sink will require shifts in product allocation from short-term to long-term pools such as reclaimed (re-used) wood products from demolition of buildings, and reduction of product manufacturing losses (EPA 2016). Clearly, there is potential for climate mitigation by using forests to sequester carbon in biomass and reduce losses associated with the wood product chain (Law *et al* 2018).

It is argued that there may be reductions in fossil carbon emissions when wood is substituted for more fossil fuel intensive building materials (e.g. steel or concrete) or used as an alternative energy source (Butarbutar *et al* 2016). Substitution is a one-time credit in the year of the input. Studies have reported a range of substitution displacement factors (from negative to positive displacement; Sathre and O'Connor 2010, Smyth *et al* 2017), but we found no study that has tracked the actual amount of construction product substitution that is occurring or has occurred in the past in the United States. This makes substitution one of the most uncertain parts of this carbon budget. It may be more easily tracked in the fossil fuel sector through a decrease in emissions because of reduction in product supply, in which case it would be double counting to then include it as a credit for the forest sector. We show results with and without the substitution credit (a decrease in forest sector emissions) because it cannot be verified. We show the potential impact it has on the overall forest sector carbon sink, even though the displacement factor may be unrealistically high (Smyth *et al* 2017, Dugan *et al* 2018). For forest sector emissions assessments, the uncertainty suggests exclusion of the credit.

Currently, state's GHG accounting budgets are incorrect because they are not full cradle-to-grave estimates of all CO_2 emissions associated with forest natural processes and human influences. For accurate GHG accounting, these emissions should be included in the forestry sector as they are not accounted for by state's energy and transportation sectors (IPCC 2006) (table S1). The US EPA reported average fossil fuel CO_2 emissions of 491 MMT CO_2e yr^{-1} for the three states combined (2013–2016). Forest industry harvest, transportation, and manufacturing fossil fuel emissions are included in this total. However, it is unclear to what extent wood product decay and combustion emissions are also counted in state budgets. In Oregon, they are not included at all, resulting in state CO_2 emissions that have been underestimated by up to 55% (Oregon Global Warming Commission 2017, Law *et al* 2018). Washington includes combustion emissions from the current year's harvest (table 1; Manufacturing losses; row 9), but not from wood product decay, resulting in up to a 25% underestimation of state CO_2 emissions. Because California's emissions from other sectors are so high (76% of regional total), and harvest rates have been historically lower than in Oregon and Washington, the impact of not including these emissions is very small as a proportion of the total. Although fire in California has received much attention, it only accounts for 3% of the state's total fossil fuel CO_2 emissions.

These underestimates are especially alarming for Oregon where GHG reduction targets are to be 10% below 1990 levels by 2020 and at least 75% below 1990 levels by 2050 (Pietz and Gregor 2014). California and Washington emissions are to be reduced to 1990 levels by 2020 (Nunez 2006), and 80% and 50% below 1990 levels by 2050 (Washington State 2008), respectively.

In contrast, the US EPA reports emissions from wood product decay and landfills (EPA 2017) per the IPCC guidelines (IPCC 2006) (table S1). However, combustion emissions from logging and mill residues are not reported (EPA 2017). Moreover, ecosystem carbon losses are indirectly estimated through changes in biomass pools with measurement uncertainty that can be greater than the change (Ferster *et al* 2015). So even at the national level, emissions (as a fraction of fossil fuel emissions) would be underestimated by 10% and 24% in Washington and Oregon, respectively. Undoubtedly, there are implications for reduction mandates when the magnitude of emissions themselves are incorrect.

Conclusions

The goal for all societies and governments as stated in Article 2 of the *United Nations Framework Convention on Climate* Change (Oppenheimer and Petsonk 2005) should be '…stabilization of GHG concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system.' The Paris Climate Agreement (UNFCCC 2015) aims to keep global average temperature from rising by no more than 2 °C above preindustrial levels, and if possible no more than 1.5 °C. Forests are identified as part of the strategy (UNFCCC 2015).

Although some US states have attempted to quantify a portion of forest-related emissions, improved estimates are essential to track emissions to meet reduction goals. We identified the main components that should be part of the forest sector state estimates. We found that emissions have been underestimated by up to 55% in Oregon and 25% in Washington, and that at present, these emissions are not reported in state GHG reporting guidelines. The accuracy of forest sector emissions estimates can be improved with subregional data on residential and commercial building lifespans, recycling, verifiable substitution benefits and accurate monitoring of growth rates of forests. However, verifiable substitution of one material for another may be more readily quantified in the fossil fuel sector.

The 2006 IPCC GHG guidelines provide three different approaches for calculating emissions from harvested wood products (IPCC 2006) (including reporting ‘zero’) and reporting of this component is not required by UNFCCC. To complicate accounting further, several studies have shown that using the different recommended approaches results in emissions that differ by over 100% (Green *et al* 2006, Dias *et al* 2007). Moreover, according to IPCC and UNFCCC, emissions of CO_2 from forest bioenergy are to be counted under land use change and not counted in the energy sector to avoid double counting. However, this provides a ‘loophole’ leading to their not being counted at all.

The United States government currently requires all federal agencies to count forest bioenergy as carbon neutral because the EPA assumes replacement by future regrowth of forests somewhere that may take several decades or longer (EPA 2018). While it is theoretically possible that a replacement forest will grow and absorb a like amount of CO_2 to that emitted decades or a century before, there is no guarantee that this will happen, and the enforcement is transferred to future generations. In any rational economic analysis, a benefit in the distant future must be discounted against the immediate damage associated with emissions during combustion. Furthermore, the goal for climate protection is not climate neutrality, but rather reduction of net GHGs emissions to the atmosphere to avoid dangerous interference with the climate system. Allowing forests to reach their biological potential for growth and sequestration, maintaining large trees (Lutz *et al* 2018), reforesting recently cut lands, and afforestation of suitable areas will remove additional CO_2 from the atmosphere. Global vegetation stores of carbon are 50% of their potential including western forests because of harvest activities (Erb *et al* 2017). Clearly, western forests could do more to address climate change through carbon sequestration if allowed to grow longer.

Since it is now clear that both CO_2 emissions and removal rates are essential to meet temperature limitation goals and prevent irreversible climate change, each should be counted and reported. We recommend that international agreements and states utilize a consistent and transparent carbon LCA that explicitly accounts for all forest and wood product storage and emissions to determine compliance with goals to lower atmospheric GHGs. Only by using a full accounting of GHGs can the world manage its emissions of heat trapping gases to achieve concentrations in the atmosphere that will support a stable climate.

Materials and methods

We calculated the 2001 to 2016 average net forestry sector emissions from cradle-to-grave, accounting for all carbon captured in biomass and released through decomposition by forest ecosystems and wood products industry in Washington, Oregon, and California. Building on our previous work (Harmon *et al* 1996, Hudiburg *et al* 2011, Law *et al* 2013, Law *et al* 2018), we developed a modified and expanded LCA method to combine with our ecosystem carbon balance, now called Forest-GHG (version 1.0; figure 1 and box 1). We accounted for all carbon removed from forests through fire and harvest. All harvested carbon was tracked until it either was returned to the atmosphere through wood product decomposition/combustion or decomposition in landfills, minus the amount semi-permanently stored in landfills (buried). This required calculating the carbon removed by harvest operations starting in 1900 to present day because a portion of the wood removed in the past century is still in-use or decomposing. In addition to carbon in biomass, we also accounted for all carbon emissions associated with harvest (equipment fuel, transportation, manufacturing inputs). Moreover, our wood product life-cycle assessment includes pathways for recycling and deposition in landfills. Finally, we give substitution credits for not using more fossil fuel intensive materials than wood used in construction of buildings and energy production.

Observed carbon stocks and fluxes (ecosystem carbon balance)

Carbon stock and flux estimates were calculated from over 30 000 forest inventory plots (FIA) containing over 1 million tree records in the region following methods developed in previous studies (Law *et al* 2018) (SI Methods). Flux calculations include NPP (Clark *et al* 2001) NEP, and NECB. The NECB represents the net rate of carbon accumulation in or loss from ecosystems.

Off-site emissions associated with harvest (LCA)

Decomposition of wood through the product cycle was computed using a LCA (Harmon and Marks 2002, Law *et al* 2018). A 117 year wood products pool (1900–2016) was simulated using reported harvest rates from 1900 to 2016 for Oregon and Washington (Harmon *et al* 1996, DNR 2017, Oregon Department of Forestry 2017) and from the California State Board of Equalization (CA 2018). Harvest was converted to

Box 1. Terminology and Flux Definitions for table 1

1. Forest Area = sum of all forest area in each state derived from US Forest Service forest area map (30 m resolution). Includes all ownerships.

1. NEP = Net Primary Production—heterotrophic respiration; microbial respiration as they decompose dead organic matter in an ecosystem.

1. Fire emissions = the emissions associated with *combustion* of organic matter at the time of the fire. Most of what burns is fine surface fuels, averaging 5% of aboveground biomass in mixed severity fires of Oregon and Northern California.

1. Harvest removals = Wood actually removed from the forest (not the total aboveground biomass killed). Removals are not equal to emissions but are the removed carbon from the forests at the time of harvest. This is subtracted from NEP along with fire emissions to calculate the net forest carbon balance from the viewpoint of the forest ecosystem.

NECB = NEP + Fire Emissions + Harvest Removals. The term is the simplest expression of forest carbon balance without tracking wood through the product life cycle. Although not all of the harvest removals will result in instant or near-term emissions, NECB still captures the impact of the removed carbon on the forest ecosystem carbon balance, and is consistent with international agreements (REDD+, conservation).

1. Harvest Residue Combustion = the emissions associated with combustion of slash piles; the branches, foliage, and non-merchantable wood left after harvest operations (remains in the forest) and burned onsite (assumed to be 50% of slash).

1. Harvest, Transportation, Manufacturing (FFE emissions) = the fossil fuel emissions associated with harvest (skidding, sawing, etc), transportation of logs to mills, manufacturing of wood and paper products, and transportation of products to stores (see table S5 for coefficients).

1. Wood Product Pool Annual Inputs = Harvest removals

1. Landfill Annual Inputs (from products) = The amount of wood and paper that is sent to landfills at end of life. In Forest-GHG, this occurs incrementally from 1950 to 1960 and then in 1961 is assumed to be constant at the current rate.

1. Wood Manufacturing Losses = fraction of wood that is lost at the mill (sawdust, etc) and is assumed to be returned to the atmosphere within one year through combustion (with 75% energy recapture) or decomposition.

1. Wood Product and Landfill Decomposition = fraction of the total wood product and non-permanent landfill carbon pools that is returned to the atmosphere annually.

Net Forest Sector Carbon Balance = sum of NECB and rows 5 through 10. Emission sources are rows 5, 6, 9, and 10. Sinks are rows 7 and 8.

1. Wood product substitution (Wood) = carbon credits that account for the displaced fossil fuel emissions when wood is substituted for a fossil fuel derived product in buildings (e.g. concrete or steel). We assume 0.54 g C fossil fuel emissions avoided per g of C of wood biomass used.

Box 1. (Continued.)

1. Wood product substitution (Energy) = carbon credits that account for the displaced fossil fuel emissions when wood is substituted for energy. In the Oregon, Washington, and California this primarily a mix of natural gas and coal. We include the biogenic emissions from combustion of forest-derived woody biomass and include an energy substitution credit if it is combusted with energy recapture.

Net Forest Sector Carbon Balance (with substitution credit) = sum of NECB and rows 5 through 12.

total aboveground biomass using methods from (Law *et al* 2018). The carbon emissions to the atmosphere from harvest were calculated annually over the time-frame of the analysis (1900–2016).

The coefficients and sources for the Forest-GHG LCA (figures 1(b) and S1) are included in table S1 through S6 with all units expressed as a function of the wood biomass being cut, transported, manufactured, burned, etc. We accounted for the fossil fuel emissions that occur during harvest (fuel for equipment) and the fossil fuel emissions associated with transport of wood to mills. Then, we accounted for the fossil fuel emissions associated with manufacturing of products followed by a second transportation emission for delivery of products to stores and warehouses. Wood that is not made into a wood or paper product (e.g. waste) is assumed to be combusted onsite at the mill (with 50% energy recapture as combined heat and power) or used in a product that will return the carbon to the atmosphere within one year (table 1 and box 1; Wood Manufacturing Losses).

Wood products are divided into varying product pools and are then tracked through the wood product cascade until end of life (figure 1(b)). Wood products are split into seven product pools: single-family homes, multi-family homes, mobile homes, non-residential construction, furniture and manufacturing, shipping, and other wood. We simulated wood product storage and emissions to 2050 for display purposes in the figures assuming a constant harvest rate after 2016.

We estimate the carbon pools and fluxes associated with buildings by separating buildings into components with different life spans (figures 3 and S3). This allows components and buildings to have a lag time before significant losses occur, and recognizes the difference between building life span and the residence time of carbon in a building. This also allows capacity for Forest-GHG to have component and building life spans evolve over time as construction practices and the environment (including biophysical, economic, and social drivers) change.

In Forest-GHG, a fraction of each year's new harvest is allocated to residential (single-family, multi-family, and mobile homes) and non-residential construction (Smith *et al* 2006). This fraction is further divided into the short-term (23%) and long-term (77%) components. The resulting pools are tracked independently, quantifying losses through decay and demolition from the year they start until then end of the simulation.

All the components created in a given year are considered a building cohort that is also tracked separately each year. All components are summed to give the total amount of building carbon remaining in a cohort at a given time (figure S3). For each year, the amount lost to the atmosphere or to the landfills through demolition, is simply the current year's total wood product carbon pool plus the current years inputs and minus last year's total wood product carbon pool.

Substitution

We calculated wood product substitution for fossil fuel derived products (concrete, steel and energy). The displacement value for product substitution was assumed to be 0.54 Mg fossil C/Mg C (Smyth *et al* 2017, Dugan *et al* 2018) wood use in long-term structures (Sathre and O'Connor 2010). Although the displacement value likely fluctuates over time, we assumed it was constant for the simulation period. We accounted for losses in product substitution associated with building replacement (Harmon *et al* 2009), but ignored the leakage effect related to fossil C use by other sectors. We assumed 75% of 'waste wood' was used for fuelwood in homes or at mills (wood manufacturing losses in table 1). We accounted for displacement of fossil fuel energy sources using a displacement factor of 0.68 assuming a mix of coal and natural gas replacement (Smyth *et al* 2017, Dugan *et al* 2018).

Uncertainty estimates and sensitivity analysis

We calculate a combined uncertainty estimate for NEP and NECB using the uncertainty in the observations and input datasets (climate, land cover, harvest amounts). For the biomass and NPP observations, we performed Monte Carlo simulations of the mean and standard deviations for NPP (Hudiburg *et al* 2011) derived for each plot using three alternative sets of allometric equations. Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest removals (7%), and land cover estimates (10%) using the propagation of error approach. Sensitivity analysis was only used for the long-term wood product pool by varying the average life spans of buildings by ±25 years in our new cohort component method. Our estimates varied by 7%. This was combined with the uncertainty in NECB to calculate total uncertainty on the net forest sector carbon balance.

Acknowledgments

This research was supported by the Agriculture and Food Research Initiative of the US National Institute of Food and Agriculture Grant 2013-67003-20652 and the National Science Foundation award number DEB-1553049.

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Land use strategies to mitigate climate change in carbon dense temperate forests

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Edited by William H. Schlesinger, Duke University, Durham, NC, and approved January 22, 2018 (received for review November 16, 2017)

Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but ecosystem process-based integration of climate change, enhanced CO_2, disturbance from fire, and management actions at regional scales are extremely limited. Here, we examine the relative merits of afforestation, reforestation, management changes, and harvest residue bioenergy use in the Pacific Northwest. This region represents some of the highest carbon density forests in the world, which can store carbon in trees for 800 y or more. Oregon's net ecosystem carbon balance (NECB) was equivalent to 72% of total emissions in 2011–2015. By 2100, simulations show increased net carbon uptake with little change in wildfires. Reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increase NECB 56% by 2100, with the latter two actions contributing the most. Resultant cobenefits included water availability and biodiversity, primarily from increased forest area, age, and species diversity. Converting 127,000 ha of irrigated grass crops to native forests could decrease irrigation demand by 233 billion $m^3 \cdot y^{-1}$. Utilizing harvest residues for bioenergy production instead of leaving them in forests to decompose increased emissions in the short-term (50 y), reducing mitigation effectiveness. Increasing forest carbon on public lands reduced emissions compared with storage in wood products because the residence time is more than twice that of wood products. Hence, temperate forests with high carbon densities and lower vulnerability to mortality have substantial potential for reducing forest sector emissions. Our analysis framework provides a template for assessments in other temperate regions.

forests | carbon balance | greenhouse gas emissions | climate mitigation

Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but regional assessments to determine feasibility, timeliness, and effectiveness are limited and rarely account for the interactive effects of future climate, atmospheric CO_2 enrichment, nitrogen deposition, disturbance from wildfires, and management actions on forest processes. We examine the net effect of all of these factors and a suite of mitigation strategies at fine resolution (4-km grid). Proven strategies immediately available to mitigate carbon emissions from forest activities include the following: (*i*) reforestation (growing forests where they recently existed), (*ii*) afforestation (growing forests where they did not recently exist), (*iii*) increasing carbon density of existing forests, and (*iv*) reducing emissions from deforestation and degradation (1). Other proposed strategies include wood bioenergy production (2–4), bioenergy combined with carbon capture and storage (BECCS), and increasing wood product use in buildings. However, examples of commercial-scale BECCS are still scarce, and sustainability of wood sources remains controversial because of forgone ecosystem carbon storage and low environmental cobenefits (5, 6). Carbon stored in buildings generally outlives its usefulness or is replaced within decades (7) rather than the centuries possible in forests, and the factors influencing product substitution have yet to be fully explored (8). Our analysis of mitigation strategies focuses on the first four strategies, as well as bioenergy production, utilizing harvest residues only and without carbon capture and storage.

The appropriateness and effectiveness of mitigation strategies within regions vary depending on the current forest sink, competition with land-use and watershed protection, and environmental conditions affecting forest sustainability and resilience. Few process-based regional studies have quantified strategies that could actually be implemented, are low-risk, and do not depend on developing technologies. Our previous studies focused on regional modeling of the effects of forest thinning on net ecosystem carbon balance (NECB) and net emissions, as well as improving modeled drought sensitivity (9, 10), while this study focuses mainly on strategies to enhance forest carbon.

Our study region is Oregon in the Pacific Northwest, where coastal and montane forests have high biomass and carbon sequestration potential. They represent coastal forests from northern California to southeast Alaska, where trees live 800 y or more and biomass can exceed that of tropical forests (11) (Fig. S1). The semiarid ecoregions consist of woodlands that experience frequent fires (12). Land-use history is a major determinant of forest carbon balance. Harvest was the dominant cause of tree mortality (2003–2012) and accounted for fivefold as much mortality as that from fire and beetles combined (13). Forest land ownership is predominantly public (64%), and 76% of the biomass harvested is on private lands.

Significance

Regional quantification of feasibility and effectiveness of forest strategies to mitigate climate change should integrate observations and mechanistic ecosystem process models with future climate, CO_2, disturbances from fire, and management. Here, we demonstrate this approach in a high biomass region, and found that reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increased net ecosystem carbon balance by 56% by 2100, with the latter two actions contributing the most. Forest sector emissions tracked with our life cycle assessment model decreased by 17%, partially meeting emissions reduction goals. Harvest residue bioenergy use did not reduce short-term emissions. Cobenefits include increased water availability and biodiversity of forest species. Our improved analysis framework can be used in other temperate regions.

Author contributions: B.E.L. and T.W.H. designed research; B.E.L., T.W.H., and P.C.B. performed research; M.E.H. contributed new reagents/analytic tools; B.E.L., L.T.B., J.J.K., and P.C.B. analyzed data; B.E.L., T.W.H., L.T.B., and M.E.H. wrote the paper; and M.E.H. contributed the substitution model.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: The CLM4.5 model data are available at Oregon State University (terraweb.forestry.oregonstate.edu/FMEC). Data from the >200 intensive plots on forest carbon are available at Oak Ridge National Laboratory (https://daac.ornl.gov/NACP/guides/NACP_TERRA-PNW.html), and FIA data are available at the USDA Forest Service (https://www.fia.fs.fed.us/tools-data/).

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1720064115/-/DCSupplemental.

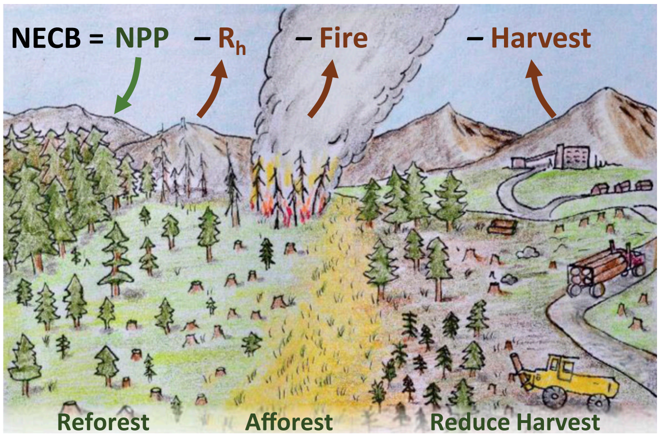

Fig. 1. Approach to assessing effects of mitigation strategies on forest carbon and forest sector emissions. NECB is productivity (NPP) minus Rh and losses from fire and harvest (red arrows). Harvest emissions include those associated with wood products and bioenergy.

Many US states, including Oregon (14), plan to reduce their greenhouse gas (GHG) emissions in accordance with the Paris Agreement. We evaluated strategies to address this question: How much carbon can the region's forests realistically remove from the atmosphere in the future, and which forest carbon strategies can reduce regional emissions by 2025, 2050, and 2100? We propose an integrated approach that combines observations with models and a life cycle assessment (LCA) to evaluate current and future effects of mitigation actions on forest carbon and forest sector emissions in temperate regions (Fig. 1). We estimated the recent carbon budget of Oregon's forests, and simulated the potential to increase the forest sink and decrease forest sector emissions under current and future climate conditions. We provide recommendations for regional assessments of mitigation strategies.

Results

Carbon stocks and fluxes are summarized for the observation cycles of 2001–2005, 2006–2010, and 2011–2015 (Table 1 and Tables S1 and S2). In 2011–2015, state-level forest carbon stocks totaled 3,036 Tg C (3 billion metric tons), with the coastal and montane ecoregions accounting for 57% of the live tree carbon (Tables S1 and S2). Net ecosystem production [NEP; net primary production (NPP) minus heterotrophic respiration (Rh)] averaged 28 teragrams carbon per year (Tg C y^{-1}) over all three periods. Fire emissions were unusually high at 8.69 million metric tons carbon dioxide equivalent (tCO$_2$e y^{-1}, i.e., 2.37 Tg C y^{-1}) in 2001–2005 due to the historic Biscuit Fire, but decreased to 3.56 million tCO$_2$e y^{-1} (0.97 Tg C y^{-1}) in 2011–2015 (Table S4). Note that 1 million tCO$_2$e equals 3.667 Tg C.

Our LCA showed that in 2001–2005, Oregon's net wood product emissions were 32.61 million tCO$_2$e (Table S3), and 3.7-fold wildfire emissions in the period that included the record fire year (15) (Fig. 2). In 2011–2015, net wood product emissions were 34.45 million tCO$_2$e and almost 10-fold fire emissions, mostly due to lower fire emissions. The net wood product emissions are higher than fire emissions despite carbon benefits of storage in wood products and substitution for more fossil fuel-intensive products. Hence, combining fire and net wood product emissions, the forest sector emissions averaged 40 million tCO$_2$e y^{-1} and accounted for about 39% of total emissions across all sectors (Fig. 2 and Table S4). NECB was calculated from NEP minus losses from fire emissions and harvest (Fig. 1). State NECB was equivalent to 60% and 70% of total emissions for 2001–2005 and 2011–2015, respectively (Fig. 2, Table 1, and Table S4). Fire emissions were only between 4% and 8% of total emissions from all sources (2011–2015 and 2001–2004, respectively). Oregon's forests play a larger role in meeting its GHG targets than US forests have in meeting the nation's targets (16, 17).

Historical disturbance regimes were simulated using stand age and disturbance history from remote sensing products. Comparisons of Community Land Model (CLM4.5) output with Forest Inventory and Analysis (FIA) aboveground tree biomass (>6,000 plots) were within 1 SD of the ecoregion means (Fig. S2). CLM4.5 estimates of cumulative burn area and emissions from 1990 to 2014 were 14% and 25% less than observed, respectively. The discrepancy was mostly due to the model missing an anomalously large fire in 2002 (Fig. S3*A*). When excluded, modeled versus observed fire emissions were in good agreement ($r^2 = 0.62$; Fig. S3*B*). A sensitivity test of a 14% underestimate of burn area did not affect our final results because predicted emissions would increase almost equally for business as usual (BAU) management and our scenarios, resulting in no proportional change in NECB. However, the ratio of harvest to fire emissions would be lower.

Projections show that under future climate, atmospheric carbon dioxide, and BAU management, an increase in net carbon uptake due to CO$_2$ fertilization and climate in the mesic ecoregions far outweighs losses from fire and drought in the semiarid ecoregions. There was not an increasing trend in fire. Carbon stocks increased by 2% and 7% and NEP increased by 12% and 40% by 2050 and 2100, respectively.

We evaluated emission reduction strategies in the forest sector: protecting existing forest carbon, lengthening harvest cycles, reforestation, afforestation, and bioenergy production with product substitution. The largest potential increase in forest carbon is in the mesic Coast Range and West Cascade ecoregions. These forests are buffered by the ocean, have high soil water-holding capacity, low risk of wildfire [fire intervals average 260–400 y (18)], long carbon residence time, and potential for high carbon density. They can attain biomass up to 520 Mg C ha^{-1} (12). Although Oregon has several protected areas, they account for only 9–15% of the total forest area, so we expect it may be feasible to add carbon-protected lands with cobenefits of water protection and biodiversity.

Reforestation of recently forested areas include those areas impacted by fire and beetles. Our simulations to 2100 assume regrowth of the same species and incorporate future fire responses to climate and cyclical beetle outbreaks [70–80 y (13)]. Reforestation has the potential to increase stocks by 315 Tg C by 2100, reducing forest sector net emissions by 5% by 2100 relative to BAU management (Fig. 3). The East and West Cascades ecoregions had the highest reforestation potential, accounting for 90% of the increase (Table S5).

Afforestation of old fields within forest boundaries and nonfood/nonforage grass crops, hereafter referred to as "grass crops," had to meet minimum conditions for tree growth, and crop grid cells had to be partially forested (*SI Methods* and Table S6). These crops are not grazed or used for animal feed. Competing land uses may decrease the actual amount of area that can be afforested. We calculated the amount of irrigated grass crops (127,000 ha) that could be converted to forest, assuming success of carbon offset programs (19). By 2100, afforestation increased stocks by

Table 1. Forest carbon budget components used to compute NECB

Flux, Tg C·y^{-1}	2001–2005		2006–2010		2011–2015		2001–2015
NPP	73.64	7.59	73.57	7.58	73.57	7.58	73.60
Rh	45.67	5.11	45.38	5.07	45.19	5.05	45.41
NEP	27.97	9.15	28.19	9.12	28.39	9.11	28.18
Harvest removals	8.58	0.60	7.77	0.54	8.61	0.6	8.32
Fire emissions	2.37	0.27	1.79	0.2	0.97	0.11	1.71
NECB	17.02	9.17	18.63	9.14	18.81	9.13	18.15

Average annual values for each period, including uncertainty (95% confidence interval) in Tg C y^{-1} (multiply by 3.667 to get million tCO$_2$e).

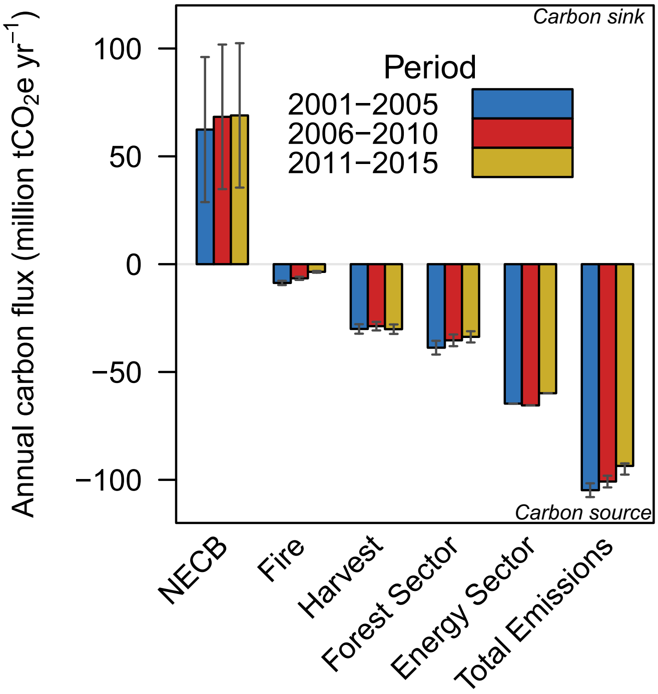

Fig. 2. Oregon's forest carbon sink and emissions from forest and energy sectors. Harvest emissions are computed by LCA. Fire and harvest emissions sum to forest sector emissions. Energy sector emissions are from the Oregon Global Warming Commission (14), minus forest-related emissions. Error bars are 95% confidence intervals (Monte Carlo analysis).

94 Tg C and cumulative NECB by 14 Tg C, and afforestation reduced forest sector GHG emissions by 1.3–1.4% in 2025, 2050, and 2100 (Fig. 3).

We quantified cobenefits of afforestation of irrigated grass crops on water availability based on data from hydrology and agricultural simulations of future grass crop area and related irrigation demand (20). Afforestation of 127,000 ha of grass cropland with Douglas fir could decrease irrigation demand by 222 and 233 billion m^3·y^{-1} by 2050 and 2100, respectively. An independent estimate from measured precipitation and evapotranspiration (ET) at our mature Douglas fir and grass crop flux sites in the Willamette Valley shows the ET/precipitation fraction averaged 33% and 52%, respectively, and water balance (precipitation minus ET) averaged 910 mm·y^{-1} and 516 mm·y^{-1}. Under current climate conditions, the observations suggest an increase in annual water availability of 260 billion m^3· y^{-1} if 127,000 ha of the irrigated grass crops were converted to forest.

Harvest cycles in the mesic and montane forests have declined from over 120 y to 45 y despite the fact that these trees can live 500–1,000 y and net primary productivity peaks at 80–125 y (21). If harvest cycles were lengthened to 80 y on private lands and harvested area was reduced 50% on public lands, state-level stocks would increase by 17% to a total of ∼3,600 Tg C and NECB would increase 2–3 Tg C y^{-1} by 2100. The lengthened harvest cycles reduced harvest by 2 Tg C y^{-1}, which contributed to higher NECB. Leakage (more harvest elsewhere) is difficult to quantify and could counter these carbon gains. However, because harvest on federal lands was reduced significantly since 1992 (NW Forest Plan), leakage has probably already occurred.

The four strategies together increased NECB by 64%, 82%, and 56% by 2025, 2050, and 2100, respectively. This reduced forest sector net emissions by 11%, 10%, and 17% over the same periods (Fig. 3). By 2050, potential increases in NECB were largest in the Coast Range (Table S5), East Cascades, and Klamath Mountains, accounting for 19%, 25%, and 42% of the total increase, whereas by 2100, they were most evident in the West Cascades, East Cascades, and Klamath Mountains.

We examined the potential for using existing harvest residue for electricity generation, where burning the harvest residue for energy emits carbon immediately (3) versus the BAU practice of leaving residues in forests to slowly decompose. Assuming half of forest residues from harvest practices could be used to replace natural gas or coal in distributed facilities across the state, they would provide an average supply of 0.75–1 Tg C y^{-1} to the year 2100 in the reduced harvest and BAU scenarios, respectively. Compared with BAU harvest practices, where residues are left to decompose, proposed bioenergy production would increase cumulative net emissions by up to 45 Tg C by 2100. Even at 50% use, residue collection and transport are not likely to be economically viable, given the distances (>200 km) to Oregon's facilities.

Discussion

Earth system models have the potential to bring terrestrial observations related to climate, vulnerability, impacts, adaptation,

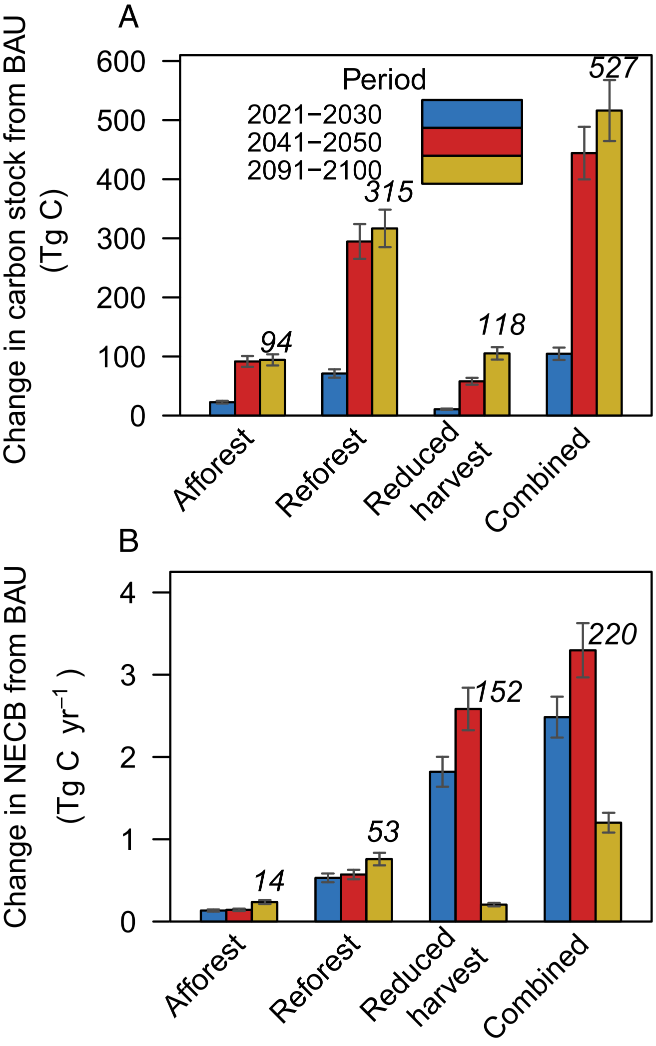

Fig. 3. Future change in carbon stocks and NECB with mitigation strategies relative to BAU management. The decadal average change in forest carbon stocks (*A*) and NECB relative to BAU (*B*) are shown. Italicized numbers over bars indicate mean forest carbon stocks in 2091–2100 (*A*) and cumulative change in NECB for 2015–2100 (*B*). Error bars are ±10%.

and mitigation into a common framework, melding biophysical with social components (22). We developed a framework to examine a suite of mitigation actions to increase forest carbon sequestration and reduce forest sector emissions under current and future environmental conditions.

Harvest-related emissions had a large impact on recent forest NECB, reducing it by an average of 34% from 2001 to 2015. By comparison, fire emissions were relatively small and reduced NECB by 12% in the Biscuit Fire year, but only reduced NECB 5–9% from 2006 to 2015. Thus, altered forest management has the potential to enhance the forest carbon balance and reduce emissions.

Future NEP increased because enhancement from atmospheric carbon dioxide outweighed the losses from fire. Lengthened harvest cycles on private lands to 80 y and restricting harvest to 50% of current rates on public lands increased NECB the most by 2100, accounting for 90% of total emissions reduction (Fig. 3 and Tables S5 and S6). Reduced harvest led to NECB increasing earlier than the other strategies (by 2050), suggesting this could be a priority for implementation.

Our afforestation estimates may be too conservative by limiting them to nonforest areas within current forest boundaries and 127,000 ha of irrigated grass cropland. There was a net loss of 367,000 ha of forest area in Oregon and Washington combined from 2001 to 2006 (23), and less than 1% of native habitat remains in the Willamette Valley due to urbanization and agriculture (24). Perhaps more of this area could be afforested.

The spatial variation in the potential for each mitigation option to improve carbon stocks and fluxes shows that the reforestation potential is highest in the Cascade Mountains, where fire and insects occur (Fig. 4). The potential to reduce harvest on public land is highest in the Cascade Mountains, and that to lengthen harvest cycles on private lands is highest in the Coast Range.

Although western Oregon is mesic with little expected change in precipitation, the afforestation cobenefits of increased water availability will be important. Urban demand for water is projected to increase, but agricultural irrigation will continue to consume much more water than urban use (25). Converting 127,000 ha of irrigated grass crops to native forests appears to be a win–win strategy, returning some of the area to forest land, providing habitat and connectivity for forest species, and easing irrigation demand. Because the afforested grass crop represents only 11% of the available grass cropland (1.18 million ha), it is not likely to result in leakage or indirect land use change. The two forest strategies combined are likely to be important contributors to water security.

Cobenefits with biodiversity were not assessed in our study. However, a recent study showed that in the mesic forests, cobenefits with biodiversity of forest species are largest on lands with harvest cycles longer than 80 y, and thus would be most pronounced on private lands (26). We selected 80 y for the harvest cycle mitigation strategy because productivity peaks at 80–125 y in this region, which coincides with the point at which cobenefits with wildlife habitat are substantial.

Habitat loss and climate change are the two greatest threats to biodiversity. Afforestation of areas that are currently grass crops would likely improve the habitat of forest species (27), as about 90% of the forests in these areas were replaced by agriculture. About 45 mammal species are at risk because of range contraction (28). Forests are more efficient at dissipating heat than grass and crop lands, and forest cover gains lead to net surface cooling in all regions south of about 45° latitude in North American and Europe (29). The cooler conditions can buffer climate-sensitive bird populations from approaching their thermal limits and provide more food and nest sites (30). Thus, the mitigation strategies of afforestation, protecting forests on public lands and lengthening harvest cycles to 80–125 y, would likely benefit forest-dependent species.

Oregon has a legislated mandate to reduce emissions, and is considering an offsets program that limits use of offsets to 8% of the total emissions reduction to ensure that regulated entities substantially reduce their own emissions, similar to California's program (19). An offset becomes a net emissions reduction by increasing the forest carbon sink (NECB). If only 8% of the GHG reduction is allowed for forest offsets, the limits for forest offsets would be 2.1 and 8.4 million metric tCO_2e of total emissions by 2025 and 2050, respectively (Table S6). The combination of afforestation, reforestation, and reduced harvest would provide 13 million metric tCO_2e emissions reductions, and any one of the strategies or a portion of each could be applied. Thus, additionality beyond what would happen without the program is possible.

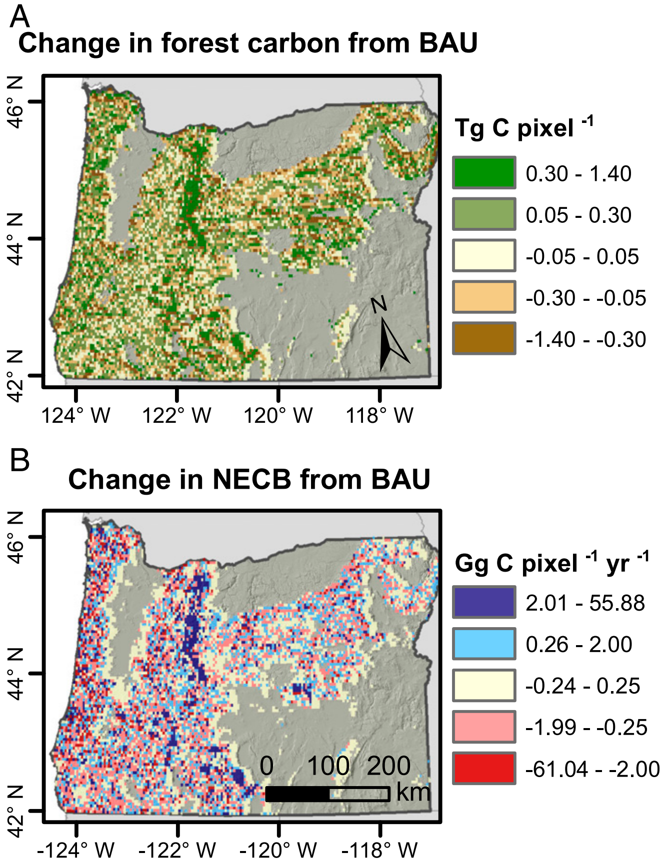

Fig. 4. Spatial patterns of forest carbon stocks and NECB by 2091–2100. The decadal average changes in forest carbon stocks (*A*) and NECB (*B*) due to afforestation, reforestation, protected areas, and lengthened harvest cycles relative to continued BAU forest management (red is increase in NECB) are shown.

State-level reporting of GHG emissions includes the agriculture sector, but does not appear to include forest sector emissions, except for industrial fuel (i.e., utility fuel in Table S3) and, potentially, fire emissions. Harvest-related emissions should be quantified, as they are much larger than fire emissions in the western United States. Full accounting of forest sector emissions is necessary to meet climate mitigation goals.

Increased long-term storage in buildings and via product substitution has been suggested as a potential climate mitigation option. Pacific temperate forests can store carbon for many hundreds of years, which is much longer than is expected for buildings that are generally assumed to outlive their usefulness or be replaced within several decades (7). By 2035, about 75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends (31, 32). Recent analysis suggests substitution benefits of using wood versus more fossil fuel-intensive materials have been overestimated by at least an order of magnitude (33). Our LCA accounts for losses in product substitution stores (PSSs) associated with building life span, and thus are considerably lower than when no losses are assumed (4, 34). While product substitution reduces the overall forest sector emissions, it cannot offset the losses incurred by frequent harvest and losses associated with product transportation, manufacturing, use, disposal, and decay. Methods for calculating substitution benefits should be improved in other regional assessments.

Wood bioenergy production is interpreted as being carbon-neutral by assuming that trees regrow to replace those that burned. However, this does not account for reduced forest carbon stocks that took decades to centuries to sequester, degraded productive capacity, emissions from transportation and the production process, and biogenic/direct emissions at the facility (35). Increased harvest through proposed thinning practices in the region has been shown to elevate emissions for decades to centuries regardless of product end use (36). It is therefore unlikely that increased wood bioenergy production in this region would decrease overall forest sector emissions.

Conclusions

GHG reduction must happen quickly to avoid surpassing a 2 °C increase in temperature since preindustrial times. Alterations in forest management can contribute to increasing the land sink and decreasing emissions by keeping carbon in high biomass forests, extending harvest cycles, reforestation, and afforestation. Forests are carbon-ready and do not require new technologies or infrastructure for immediate mitigation of climate change. Growing forests for bioenergy production competes with forest carbon sequestration and does not reduce emissions in the next decades (10). BECCS requires new technology, and few locations have sufficient geological storage for CO_2 at power facilities with high-productivity forests nearby. Accurate accounting of forest carbon in trees and soils, NECB, and historic harvest rates, combined with transparent quantification of emissions from the wood product process, can ensure realistic reductions in forest sector emissions.

As states and regions take a larger role in implementing climate mitigation steps, robust forest sector assessments are urgently needed. Our integrated approach of combining observations, an LCA, and high-resolution process modeling (4-km grid vs. typical 200-km grid) of a suite of potential mitigation actions and their effects on forest carbon sequestration and emissions under changing climate and CO_2 provides an analysis framework that can be applied in other temperate regions.

Materials and Methods

Current Stocks and Fluxes. We quantified recent forest carbon stocks and fluxes using a combination of observations from FIA; Landsat products on forest type, land cover, and fire risk; 200 intensive plots in Oregon (37); and a wood decomposition database. Tree biomass was calculated from species-specific allometric equations and ecoregion-specific wood density. We estimated ecosystem carbon stocks, NEP (photosynthesis minus respiration), and NECB (NEP minus losses due to fire or harvest) using a mass-balance approach (36, 38) (Table 1 and *SI Materials and Methods*). Fire emissions were computed from the Monitoring Trends in Burn Severity database, biomass data, and region-specific combustion factors (15, 39) (*SI Materials and Methods*).

Future Projections and Model Description. Carbon stocks and NEP were quantified to the years 2025, 2050, and 2100 using CLM4.5 with physiological parameters for 10 major forest species, initial forest biomass (36), and future climate and atmospheric carbon dioxide as input (Institut Pierre Simon Laplace climate system model downscaled to 4 km × 4 km, representative concentration pathway 8.5). CLM4.5 uses 3-h climate data, ecophysiological characteristics, site physical characteristics, and site history to estimate the daily fluxes of carbon, nitrogen, and water between the atmosphere, plant state variables, and litter and soil state variables. Model components are biogeophysics, hydrological cycle, and biogeochemistry. This model version does not include a dynamic vegetation model to simulate resilience and establishment following disturbance. However, the effect of regeneration lags on forest carbon is not particularly strong for the long disturbance intervals in this study (40). Our plant functional type (PFT) parameterization for 10 major forest species rather than one significantly improves carbon modeling in the region (41).

Forest Management and Land Use Change Scenarios. Harvest cycles, reforestation, and afforestation were simulated to the year 2100. Carbon stocks and NEP were predicted for the current harvest cycle of 45 y compared with simulations extending it to 80 y. Reforestation potential was simulated over areas that recently suffered mortality from harvest, fire, and 12 species of beetles (13). We assumed the same vegetation regrew to the maximum potential, which is expected with the combination of natural regeneration and planting that commonly occurs after these events. Future BAU harvest files were constructed using current harvest rates, where county-specific average harvest and the actual amounts per ownership were used to guide grid cell selection. This resulted in the majority of harvest occurring on private land (70%) and in the mesic ecoregions. Beetle outbreaks were implemented using a modified mortality rate of the lodgepole pine PFT with 0.1% y^{-1} biomass mortality by 2100.

For afforestation potential, we identified areas that are within forest boundaries that are not currently forest and areas that are currently grass crops. We assumed no competition with conversion of irrigated grass crops to urban growth, given Oregon's land use laws for developing within urban growth boundaries. A separate study suggested that, on average, about 17% of all irrigated agricultural crops in the Willamette Valley could be converted to urban area under future climate; however, because 20% of total cropland is grass seed, it suggests little competition with urban growth (25).

Landsat observations (12,500 scenes) were processed to map changes in land cover from 1984 to 2012. Land cover types were separated with an unsupervised K-means clustering approach. Land cover classes were assigned to an existing forest type map (42). The CropScape Cropland Data Layer (CDL 2015, https://nassgeodata.gmu.edu/CropScape/) was used to distinguish nonforage grass crops from other grasses. For afforestation, we selected grass cropland with a minimum soil water-holding capacity of 150 mm and minimum precipitation of 500 mm that can support trees (43).

Afforestation Cobenefits. Modeled irrigation demand of grass seed crops under future climate conditions was previously conducted with hydrology and agricultural models, where ET is a function of climate, crop type, crop growth state, and soil-holding capacity (20) (Table S7). The simulations produced total land area, ET, and irrigation demand for each cover type. Current grass seed crop irrigation in the Willamette Valley is 413 billion $m^3 \cdot y^{-1}$ for 238,679 ha and is projected to be 412 and 405 billion m^3 in 2050 and 2100 (20) (Table S7). We used annual output from the simulations to estimate irrigation demand per unit area of grass seed crops (1.73, 1.75, and 1.84 million $m^3 \cdot ha^{-1}$ in 2015, 2050, and 2100, respectively), and applied it to the mapped irrigated crop area that met conditions necessary to support forests (Table S7).

LCA. Decomposition of wood through the product cycle was computed using an LCA (8, 10). Carbon emissions to the atmosphere from harvest were calculated annually over the time frame of the analysis (2001–2015). The net carbon emissions equal NECB plus total harvest minus wood lost during manufacturing and wood decomposed over time from product use. Wood industry fossil fuel emissions were computed for harvest, transportation, and manufacturing processes. Carbon credit was calculated for wood product storage, substitution, and internal mill recycling of wood losses for bioenergy.

Products were divided into sawtimber, pulpwood, and wood and paper products using published coefficients (44). Long-term and short-term products were assumed to decay at 2% and 10% per year, respectively (45). For product substitution, we focused on manufacturing for long-term structures (building life span >30 y). Because it is not clear when product substitution started in the Pacific Northwest, we evaluated it starting in 1970 since use of concrete and steel for housing was uncommon before 1965. The displacement value for product substitution was assumed to be 2.1 Mg fossil C/Mg C wood use in long-term structures (46), and although it likely fluctuates over time, we assumed it was constant. We accounted for losses in product substitution associated with building replacement (33) using a loss rate of 2% per year (33), but ignored leakage related to fossil C use by other sectors, which may result in more substitution benefit than will actually occur.

The general assumption for modern buildings, including cross-laminate timber, is they will outlive their usefulness and be replaced in about 30 y (7). By 2035, ∼75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends, resulting in threefold as many buildings as there are now [2005 baseline (31, 32)]. The loss of

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SUSTAINABILITY SCIENCE

the PSS is therefore PSS multiplied by the proportion of buildings lost per year (2% per year).

To compare the NECB equivalence to emissions, we calculated forest sector and energy sector emissions separately. Energy sector emissions ["in-boundary" state-quantified emissions by the Oregon Global Warming Commission (14)] include those from transportation, residential and commercial buildings, industry, and agriculture. The forest sector emissions are cradle-to-grave annual carbon emissions from harvest and product emissions, transportation, and utility fuels (Table S3). Forest sector utility fuels were subtracted from energy sector emissions to avoid double counting.

Uncertainty Estimates. For the observation-based analysis, Monte Carlo simulations were used to conduct an uncertainty analysis with the mean and SDs for NPP and Rh calculated using several approaches (36) (*SI Materials and Methods*). Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest emissions (7%), and land cover estimates (10%) using the propagation of error approach. Uncertainty in CLM4.5 model simulations and LCA were quantified by combining the uncertainty in the observations used to evaluate the model, the uncertainty in input datasets (e.g., remote sensing), and the uncertainty in the LCA coefficients (41).

Model input data for physiological parameters and model evaluation data on stocks and fluxes are available online (37).

ACKNOWLEDGMENTS. We thank Dr. Thomas Hilker (deceased) for producing the grass data layer, and Carley Lowe for Fig. 1. This research was supported by the US Department of Energy (Grant DE-SC0012194) and Agriculture and Food Research Initiative of the US Department of Agriculture National Institute of Food and Agriculture (Grants 2013-67003-20652, 2014-67003-22065, and 2014-35100-22066) for our North American Carbon Program studies, "Carbon cycle dynamics within Oregon's urban-suburban-forested-agricultural landscapes," and "Forest die-off, climate change, and human intervention in western North America."

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Land use strategies to mitigate climate change in carbon dense temperate forests

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Edited by William H. Schlesinger, Duke University, Durham, NC, and approved January 22, 2018 (received for review November 16, 2017)

Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but ecosystem process-based integration of climate change, enhanced CO_2, disturbance from fire, and management actions at regional scales are extremely limited. Here, we examine the relative merits of afforestation, reforestation, management changes, and harvest residue bioenergy use in the Pacific Northwest. This region represents some of the highest carbon density forests in the world, which can store carbon in trees for 800 y or more. Oregon's net ecosystem carbon balance (NECB) was equivalent to 72% of total emissions in 2011–2015. By 2100, simulations show increased net carbon uptake with little change in wildfires. Reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increase NECB 56% by 2100, with the latter two actions contributing the most. Resultant cobenefits included water availability and biodiversity, primarily from increased forest area, age, and species diversity. Converting 127,000 ha of irrigated grass crops to native forests could decrease irrigation demand by 233 billion $m^3 \cdot y^{-1}$. Utilizing harvest residues for bioenergy production instead of leaving them in forests to decompose increased emissions in the short-term (50 y), reducing mitigation effectiveness. Increasing forest carbon on public lands reduced emissions compared with storage in wood products because the residence time is more than twice that of wood products. Hence, temperate forests with high carbon densities and lower vulnerability to mortality have substantial potential for reducing forest sector emissions. Our analysis framework provides a template for assessments in other temperate regions.

forests | carbon balance | greenhouse gas emissions | climate mitigation

Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but regional assessments to determine feasibility, timeliness, and effectiveness are limited and rarely account for the interactive effects of future climate, atmospheric CO_2 enrichment, nitrogen deposition, disturbance from wildfires, and management actions on forest processes. We examine the net effect of all of these factors and a suite of mitigation strategies at fine resolution (4-km grid). Proven strategies immediately available to mitigate carbon emissions from forest activities include the following: (*i*) reforestation (growing forests where they recently existed), (*ii*) afforestation (growing forests where they did not recently exist), (*iii*) increasing carbon density of existing forests, and (*iv*) reducing emissions from deforestation and degradation (1). Other proposed strategies include wood bioenergy production (2–4), bioenergy combined with carbon capture and storage (BECCS), and increasing wood product use in buildings. However, examples of commercial-scale BECCS are still scarce, and sustainability of wood sources remains controversial because of forgone ecosystem carbon storage and low environmental cobenefits (5, 6). Carbon stored in buildings generally outlives its usefulness or is replaced within decades (7) rather than the centuries possible in forests, and the factors influencing product substitution have yet to be fully explored (8). Our analysis of mitigation strategies focuses on the first four strategies, as well as bioenergy production, utilizing harvest residues only and without carbon capture and storage.

The appropriateness and effectiveness of mitigation strategies within regions vary depending on the current forest sink, competition with land-use and watershed protection, and environmental conditions affecting forest sustainability and resilience. Few process-based regional studies have quantified strategies that could actually be implemented, are low-risk, and do not depend on developing technologies. Our previous studies focused on regional modeling of the effects of forest thinning on net ecosystem carbon balance (NECB) and net emissions, as well as improving modeled drought sensitivity (9, 10), while this study focuses mainly on strategies to enhance forest carbon.

Our study region is Oregon in the Pacific Northwest, where coastal and montane forests have high biomass and carbon sequestration potential. They represent coastal forests from northern California to southeast Alaska, where trees live 800 y or more and biomass can exceed that of tropical forests (11) (Fig. S1). The semiarid ecoregions consist of woodlands that experience frequent fires (12). Land-use history is a major determinant of forest carbon balance. Harvest was the dominant cause of tree mortality (2003–2012) and accounted for fivefold as much mortality as that from fire and beetles combined (13). Forest land ownership is predominantly public (64%), and 76% of the biomass harvested is on private lands.

Significance

Regional quantification of feasibility and effectiveness of forest strategies to mitigate climate change should integrate observations and mechanistic ecosystem process models with future climate, CO_2, disturbances from fire, and management. Here, we demonstrate this approach in a high biomass region, and found that reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increased net ecosystem carbon balance by 56% by 2100, with the latter two actions contributing the most. Forest sector emissions tracked with our life cycle assessment model decreased by 17%, partially meeting emissions reduction goals. Harvest residue bioenergy use did not reduce short-term emissions. Cobenefits include increased water availability and biodiversity of forest species. Our improved analysis framework can be used in other temperate regions.

Author contributions: B.E.L. and T.W.H. designed research; B.E.L., T.W.H., and P.C.B. performed research; M.E.H. contributed new reagents/analytic tools; B.E.L., L.T.B., J.J.K., and P.C.B. analyzed data; B.E.L., T.W.H., L.T.B., and M.E.H. wrote the paper; and M.E.H. contributed the substitution model.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: The CLM4.5 model data are available at Oregon State University (terraweb.forestry.oregonstate.edu/FMEC). Data from the >200 intensive plots on forest carbon are available at Oak Ridge National Laboratory (https://daac.ornl.gov/NACP/guides/NACP_TERRA-PNW.html), and FIA data are available at the USDA Forest Service (https://www.fia.fs.fed.us/tools-data/).

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1720064115/-/DCSupplemental.

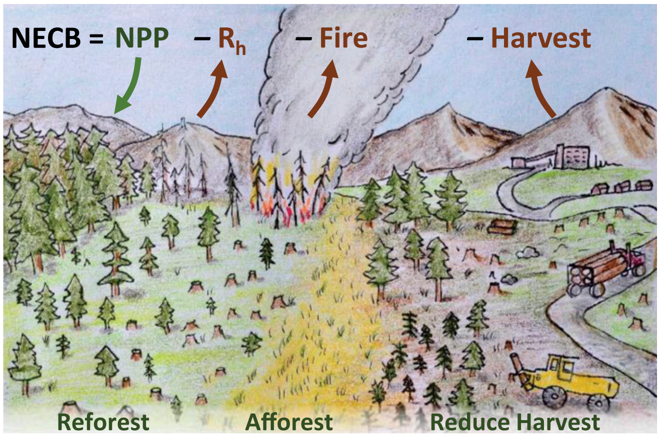

Fig. 1. Approach to assessing effects of mitigation strategies on forest carbon and forest sector emissions. NECB is productivity (NPP) minus Rh and losses from fire and harvest (red arrows). Harvest emissions include those associated with wood products and bioenergy.

Many US states, including Oregon (14), plan to reduce their greenhouse gas (GHG) emissions in accordance with the Paris Agreement. We evaluated strategies to address this question: How much carbon can the region's forests realistically remove from the atmosphere in the future, and which forest carbon strategies can reduce regional emissions by 2025, 2050, and 2100? We propose an integrated approach that combines observations with models and a life cycle assessment (LCA) to evaluate current and future effects of mitigation actions on forest carbon and forest sector emissions in temperate regions (Fig. 1). We estimated the recent carbon budget of Oregon's forests, and simulated the potential to increase the forest sink and decrease forest sector emissions under current and future climate conditions. We provide recommendations for regional assessments of mitigation strategies.

Results

Carbon stocks and fluxes are summarized for the observation cycles of 2001–2005, 2006–2010, and 2011–2015 (Table 1 and Tables S1 and S2). In 2011–2015, state-level forest carbon stocks totaled 3,036 Tg C (3 billion metric tons), with the coastal and montane ecoregions accounting for 57% of the live tree carbon (Tables S1 and S2). Net ecosystem production [NEP; net primary production (NPP) minus heterotrophic respiration (Rh)] averaged 28 teragrams carbon per year (Tg C y^{-1}) over all three periods. Fire emissions were unusually high at 8.69 million metric tons carbon dioxide equivalent (tCO_2e y^{-1}, i.e., 2.37 Tg C y^{-1}) in 2001–2005 due to the historic Biscuit Fire, but decreased to 3.56 million tCO_2e y^{-1} (0.97 Tg C y^{-1}) in 2011–2015 (Table S4). Note that 1 million tCO_2e equals 3.667 Tg C.

Our LCA showed that in 2001–2005, Oregon's net wood product emissions were 32.61 million tCO_2e (Table S3), and 3.7-fold wildfire emissions in the period that included the record fire year (15) (Fig. 2). In 2011–2015, net wood product emissions were 34.45 million tCO_2e and almost 10-fold fire emissions, mostly due to lower fire emissions. The net wood product emissions are higher than fire emissions despite carbon benefits of storage in wood products and substitution for more fossil fuel-intensive products. Hence, combining fire and net wood product emissions, the forest sector emissions averaged 40 million tCO_2e y^{-1} and accounted for about 39% of total emissions across all sectors (Fig. 2 and Table S4). NECB was calculated from NEP minus losses from fire emissions and harvest (Fig. 1). State NECB was equivalent to 60% and 70% of total emissions for 2001–2005 and 2011–2015, respectively (Fig. 2, Table 1, and Table S4). Fire emissions were only between 4% and 8% of total emissions from all sources (2011–2015 and 2001–2004, respectively). Oregon's forests play a larger role in meeting its GHG targets than US forests have in meeting the nation's targets (16, 17).

Historical disturbance regimes were simulated using stand age and disturbance history from remote sensing products. Comparisons of Community Land Model (CLM4.5) output with Forest Inventory and Analysis (FIA) aboveground tree biomass (>6,000 plots) were within 1 SD of the ecoregion means (Fig. S2). CLM4.5 estimates of cumulative burn area and emissions from 1990 to 2014 were 14% and 25% less than observed, respectively. The discrepancy was mostly due to the model missing an anomalously large fire in 2002 (Fig. S3*A*). When excluded, modeled versus observed fire emissions were in good agreement ($r^2 = 0.62$; Fig. S3*B*). A sensitivity test of a 14% underestimate of burn area did not affect our final results because predicted emissions would increase almost equally for business as usual (BAU) management and our scenarios, resulting in no proportional change in NECB. However, the ratio of harvest to fire emissions would be lower.

Projections show that under future climate, atmospheric carbon dioxide, and BAU management, an increase in net carbon uptake due to CO_2 fertilization and climate in the mesic ecoregions far outweighs losses from fire and drought in the semiarid ecoregions. There was not an increasing trend in fire. Carbon stocks increased by 2% and 7% and NEP increased by 12% and 40% by 2050 and 2100, respectively.

We evaluated emission reduction strategies in the forest sector: protecting existing forest carbon, lengthening harvest cycles, reforestation, afforestation, and bioenergy production with product substitution. The largest potential increase in forest carbon is in the mesic Coast Range and West Cascade ecoregions. These forests are buffered by the ocean, have high soil water-holding capacity, low risk of wildfire [fire intervals average 260–400 y (18)], long carbon residence time, and potential for high carbon density. They can attain biomass up to 520 Mg C ha^{-1} (12). Although Oregon has several protected areas, they account for only 9–15% of the total forest area, so we expect it may be feasible to add carbon-protected lands with cobenefits of water protection and biodiversity.

Reforestation of recently forested areas include those areas impacted by fire and beetles. Our simulations to 2100 assume regrowth of the same species and incorporate future fire responses to climate and cyclical beetle outbreaks [70–80 y (13)]. Reforestation has the potential to increase stocks by 315 Tg C by 2100, reducing forest sector net emissions by 5% by 2100 relative to BAU management (Fig. 3). The East and West Cascades ecoregions had the highest reforestation potential, accounting for 90% of the increase (Table S5).

Afforestation of old fields within forest boundaries and nonfood/nonforage grass crops, hereafter referred to as "grass crops," had to meet minimum conditions for tree growth, and crop grid cells had to be partially forested (*SI Methods* and Table S6). These crops are not grazed or used for animal feed. Competing land uses may decrease the actual amount of area that can be afforested. We calculated the amount of irrigated grass crops (127,000 ha) that could be converted to forest, assuming success of carbon offset programs (19). By 2100, afforestation increased stocks by

Table 1. Forest carbon budget components used to compute NECB

Flux, Tg C·y^{-1}	2001–2005		2006–2010		2011–2015		2001–2015
NPP	73.64	7.59	73.57	7.58	73.57	7.58	73.60
Rh	45.67	5.11	45.38	5.07	45.19	5.05	45.41
NEP	27.97	9.15	28.19	9.12	28.39	9.11	28.18
Harvest removals	8.58	0.60	7.77	0.54	8.61	0.6	8.32
Fire emissions	2.37	0.27	1.79	0.2	0.97	0.11	1.71
NECB	17.02	9.17	18.63	9.14	18.81	9.13	18.15

Average annual values for each period, including uncertainty (95% confidence interval) in Tg C y^{-1} (multiply by 3.667 to get million tCO_2e).

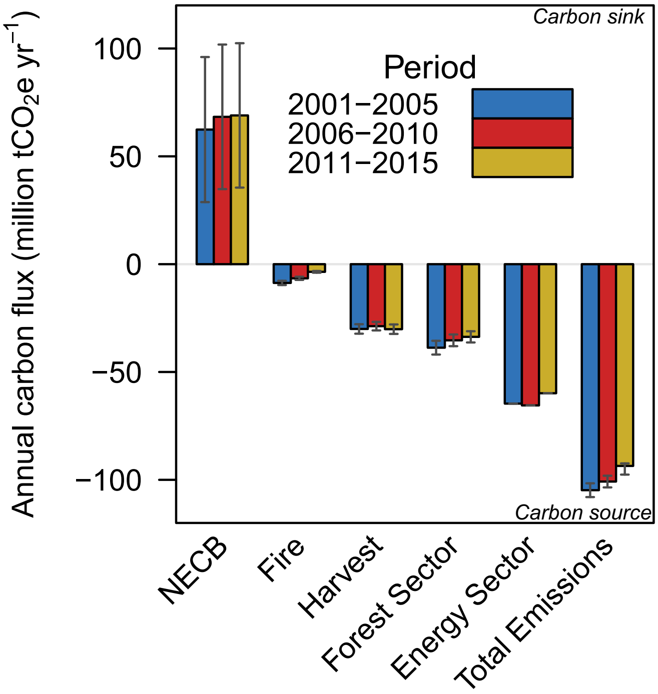

Fig. 2. Oregon's forest carbon sink and emissions from forest and energy sectors. Harvest emissions are computed by LCA. Fire and harvest emissions sum to forest sector emissions. Energy sector emissions are from the Oregon Global Warming Commission (14), minus forest-related emissions. Error bars are 95% confidence intervals (Monte Carlo analysis).

94 Tg C and cumulative NECB by 14 Tg C, and afforestation reduced forest sector GHG emissions by 1.3–1.4% in 2025, 2050, and 2100 (Fig. 3).

We quantified cobenefits of afforestation of irrigated grass crops on water availability based on data from hydrology and agricultural simulations of future grass crop area and related irrigation demand (20). Afforestation of 127,000 ha of grass cropland with Douglas fir could decrease irrigation demand by 222 and 233 billion m^3·y^{-1} by 2050 and 2100, respectively. An independent estimate from measured precipitation and evapotranspiration (ET) at our mature Douglas fir and grass crop flux sites in the Willamette Valley shows the ET/precipitation fraction averaged 33% and 52%, respectively, and water balance (precipitation minus ET) averaged 910 mm·y^{-1} and 516 mm·y^{-1}. Under current climate conditions, the observations suggest an increase in annual water availability of 260 billion m^3· y^{-1} if 127,000 ha of the irrigated grass crops were converted to forest.

Harvest cycles in the mesic and montane forests have declined from over 120 y to 45 y despite the fact that these trees can live 500–1,000 y and net primary productivity peaks at 80–125 y (21). If harvest cycles were lengthened to 80 y on private lands and harvested area was reduced 50% on public lands, state-level stocks would increase by 17% to a total of ∼3,600 Tg C and NECB would increase 2–3 Tg C y^{-1} by 2100. The lengthened harvest cycles reduced harvest by 2 Tg C y^{-1}, which contributed to higher NECB. Leakage (more harvest elsewhere) is difficult to quantify and could counter these carbon gains. However, because harvest on federal lands was reduced significantly since 1992 (NW Forest Plan), leakage has probably already occurred.

The four strategies together increased NECB by 64%, 82%, and 56% by 2025, 2050, and 2100, respectively. This reduced forest sector net emissions by 11%, 10%, and 17% over the same periods (Fig. 3). By 2050, potential increases in NECB were largest in the Coast Range (Table S5), East Cascades, and Klamath Mountains, accounting for 19%, 25%, and 42% of the total increase, whereas by 2100, they were most evident in the West Cascades, East Cascades, and Klamath Mountains.

We examined the potential for using existing harvest residue for electricity generation, where burning the harvest residue for energy emits carbon immediately (3) versus the BAU practice of leaving residues in forests to slowly decompose. Assuming half of forest residues from harvest practices could be used to replace natural gas or coal in distributed facilities across the state, they would provide an average supply of 0.75–1 Tg C y^{-1} to the year 2100 in the reduced harvest and BAU scenarios, respectively. Compared with BAU harvest practices, where residues are left to decompose, proposed bioenergy production would increase cumulative net emissions by up to 45 Tg C by 2100. Even at 50% use, residue collection and transport are not likely to be economically viable, given the distances (>200 km) to Oregon's facilities.

Discussion

Earth system models have the potential to bring terrestrial observations related to climate, vulnerability, impacts, adaptation,

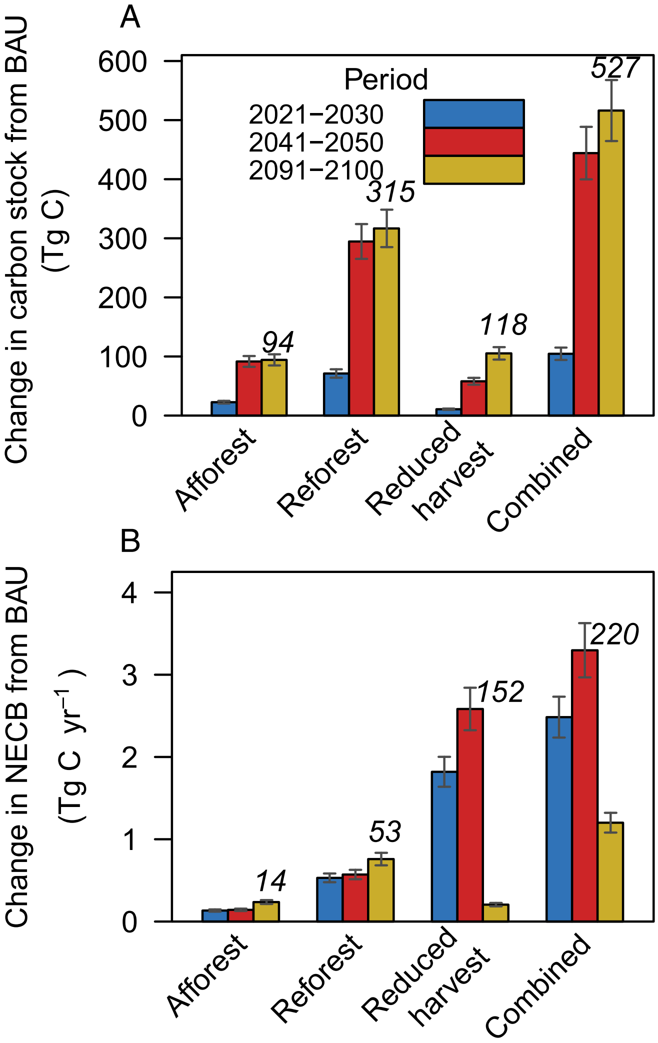

Fig. 3. Future change in carbon stocks and NECB with mitigation strategies relative to BAU management. The decadal average change in forest carbon stocks (*A*) and NECB relative to BAU (*B*) are shown. Italicized numbers over bars indicate mean forest carbon stocks in 2091–2100 (*A*) and cumulative change in NECB for 2015–2100 (*B*). Error bars are ±10%.

and mitigation into a common framework, melding biophysical with social components (22). We developed a framework to examine a suite of mitigation actions to increase forest carbon sequestration and reduce forest sector emissions under current and future environmental conditions.

Harvest-related emissions had a large impact on recent forest NECB, reducing it by an average of 34% from 2001 to 2015. By comparison, fire emissions were relatively small and reduced NECB by 12% in the Biscuit Fire year, but only reduced NECB 5–9% from 2006 to 2015. Thus, altered forest management has the potential to enhance the forest carbon balance and reduce emissions.

Future NEP increased because enhancement from atmospheric carbon dioxide outweighed the losses from fire. Lengthened harvest cycles on private lands to 80 y and restricting harvest to 50% of current rates on public lands increased NECB the most by 2100, accounting for 90% of total emissions reduction (Fig. 3 and Tables S5 and S6). Reduced harvest led to NECB increasing earlier than the other strategies (by 2050), suggesting this could be a priority for implementation.

Our afforestation estimates may be too conservative by limiting them to nonforest areas within current forest boundaries and 127,000 ha of irrigated grass cropland. There was a net loss of 367,000 ha of forest area in Oregon and Washington combined from 2001 to 2006 (23), and less than 1% of native habitat remains in the Willamette Valley due to urbanization and agriculture (24). Perhaps more of this area could be afforested.

The spatial variation in the potential for each mitigation option to improve carbon stocks and fluxes shows that the reforestation potential is highest in the Cascade Mountains, where fire and insects occur (Fig. 4). The potential to reduce harvest on public land is highest in the Cascade Mountains, and that to lengthen harvest cycles on private lands is highest in the Coast Range.

Although western Oregon is mesic with little expected change in precipitation, the afforestation cobenefits of increased water availability will be important. Urban demand for water is projected to increase, but agricultural irrigation will continue to consume much more water than urban use (25). Converting 127,000 ha of irrigated grass crops to native forests appears to be a win–win strategy, returning some of the area to forest land, providing habitat and connectivity for forest species, and easing irrigation demand. Because the afforested grass crop represents only 11% of the available grass cropland (1.18 million ha), it is not likely to result in leakage or indirect land use change. The two forest strategies combined are likely to be important contributors to water security.

Cobenefits with biodiversity were not assessed in our study. However, a recent study showed that in the mesic forests, cobenefits with biodiversity of forest species are largest on lands with harvest cycles longer than 80 y, and thus would be most pronounced on private lands (26). We selected 80 y for the harvest cycle mitigation strategy because productivity peaks at 80–125 y in this region, which coincides with the point at which cobenefits with wildlife habitat are substantial.

Habitat loss and climate change are the two greatest threats to biodiversity. Afforestation of areas that are currently grass crops would likely improve the habitat of forest species (27), as about 90% of the forests in these areas were replaced by agriculture. About 45 mammal species are at risk because of range contraction (28). Forests are more efficient at dissipating heat than grass and crop lands, and forest cover gains lead to net surface cooling in all regions south of about 45° latitude in North American and Europe (29). The cooler conditions can buffer climate-sensitive bird populations from approaching their thermal limits and provide more food and nest sites (30). Thus, the mitigation strategies of afforestation, protecting forests on public lands and lengthening harvest cycles to 80–125 y, would likely benefit forest-dependent species.

Oregon has a legislated mandate to reduce emissions, and is considering an offsets program that limits use of offsets to 8% of the total emissions reduction to ensure that regulated entities substantially reduce their own emissions, similar to California's program (19). An offset becomes a net emissions reduction by increasing the forest carbon sink (NECB). If only 8% of the GHG reduction is allowed for forest offsets, the limits for forest offsets would be 2.1 and 8.4 million metric tCO_2e of total emissions by 2025 and 2050, respectively (Table S6). The combination of afforestation, reforestation, and reduced harvest would provide 13 million metric tCO_2e emissions reductions, and any one of the strategies or a portion of each could be applied. Thus, additionality beyond what would happen without the program is possible.

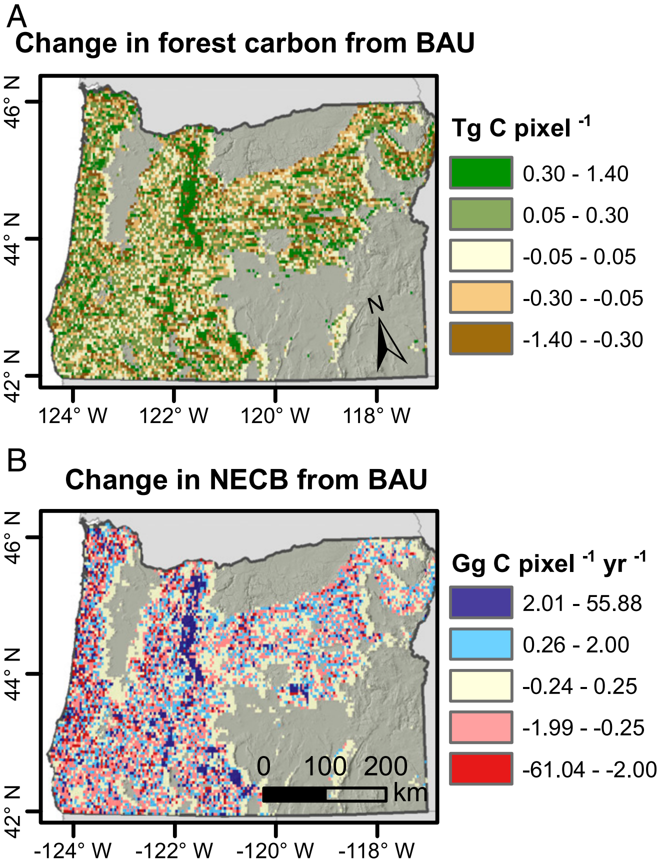

Fig. 4. Spatial patterns of forest carbon stocks and NECB by 2091–2100. The decadal average changes in forest carbon stocks (*A*) and NECB (*B*) due to afforestation, reforestation, protected areas, and lengthened harvest cycles relative to continued BAU forest management (red is increase in NECB) are shown.

State-level reporting of GHG emissions includes the agriculture sector, but does not appear to include forest sector emissions, except for industrial fuel (i.e., utility fuel in Table S3) and, potentially, fire emissions. Harvest-related emissions should be quantified, as they are much larger than fire emissions in the western United States. Full accounting of forest sector emissions is necessary to meet climate mitigation goals.

Increased long-term storage in buildings and via product substitution has been suggested as a potential climate mitigation option. Pacific temperate forests can store carbon for many hundreds of years, which is much longer than is expected for buildings that are generally assumed to outlive their usefulness or be replaced within several decades (7). By 2035, about 75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends (31, 32). Recent analysis suggests substitution benefits of using wood versus more fossil fuel-intensive materials have been overestimated by at least an order of magnitude (33). Our LCA accounts for losses in product substitution stores (PSSs) associated with building life span, and thus are considerably lower than when no losses are assumed (4, 34). While product substitution reduces the overall forest sector emissions, it cannot offset the losses incurred by frequent harvest and losses associated with product transportation, manufacturing, use, disposal, and decay. Methods for calculating substitution benefits should be improved in other regional assessments.

Wood bioenergy production is interpreted as being carbon-neutral by assuming that trees regrow to replace those that burned. However, this does not account for reduced forest carbon stocks that took decades to centuries to sequester, degraded productive capacity, emissions from transportation and the production process, and biogenic/direct emissions at the facility (35). Increased harvest through proposed thinning practices in the region has been shown to elevate emissions for decades to centuries regardless of product end use (36). It is therefore unlikely that increased wood bioenergy production in this region would decrease overall forest sector emissions.

Conclusions

GHG reduction must happen quickly to avoid surpassing a 2 °C increase in temperature since preindustrial times. Alterations in forest management can contribute to increasing the land sink and decreasing emissions by keeping carbon in high biomass forests, extending harvest cycles, reforestation, and afforestation. Forests are carbon-ready and do not require new technologies or infrastructure for immediate mitigation of climate change. Growing forests for bioenergy production competes with forest carbon sequestration and does not reduce emissions in the next decades (10). BECCS requires new technology, and few locations have sufficient geological storage for CO_2 at power facilities with high-productivity forests nearby. Accurate accounting of forest carbon in trees and soils, NECB, and historic harvest rates, combined with transparent quantification of emissions from the wood product process, can ensure realistic reductions in forest sector emissions.

As states and regions take a larger role in implementing climate mitigation steps, robust forest sector assessments are urgently needed. Our integrated approach of combining observations, an LCA, and high-resolution process modeling (4-km grid vs. typical 200-km grid) of a suite of potential mitigation actions and their effects on forest carbon sequestration and emissions under changing climate and CO_2 provides an analysis framework that can be applied in other temperate regions.

Materials and Methods

Current Stocks and Fluxes. We quantified recent forest carbon stocks and fluxes using a combination of observations from FIA; Landsat products on forest type, land cover, and fire risk; 200 intensive plots in Oregon (37); and a wood decomposition database. Tree biomass was calculated from species-specific allometric equations and ecoregion-specific wood density. We estimated ecosystem carbon stocks, NEP (photosynthesis minus respiration), and NECB (NEP minus losses due to fire or harvest) using a mass-balance approach (36, 38) (Table 1 and *SI Materials and Methods*). Fire emissions were computed from the Monitoring Trends in Burn Severity database, biomass data, and region-specific combustion factors (15, 39) (*SI Materials and Methods*).

Future Projections and Model Description. Carbon stocks and NEP were quantified to the years 2025, 2050, and 2100 using CLM4.5 with physiological parameters for 10 major forest species, initial forest biomass (36), and future climate and atmospheric carbon dioxide as input (Institut Pierre Simon Laplace climate system model downscaled to 4 km × 4 km, representative concentration pathway 8.5). CLM4.5 uses 3-h climate data, ecophysiological characteristics, site physical characteristics, and site history to estimate the daily fluxes of carbon, nitrogen, and water between the atmosphere, plant state variables, and litter and soil state variables. Model components are biogeophysics, hydrological cycle, and biogeochemistry. This model version does not include a dynamic vegetation model to simulate resilience and establishment following disturbance. However, the effect of regeneration lags on forest carbon is not particularly strong for the long disturbance intervals in this study (40). Our plant functional type (PFT) parameterization for 10 major forest species rather than one significantly improves carbon modeling in the region (41).

Forest Management and Land Use Change Scenarios. Harvest cycles, reforestation, and afforestation were simulated to the year 2100. Carbon stocks and NEP were predicted for the current harvest cycle of 45 y compared with simulations extending it to 80 y. Reforestation potential was simulated over areas that recently suffered mortality from harvest, fire, and 12 species of beetles (13). We assumed the same vegetation regrew to the maximum potential, which is expected with the combination of natural regeneration and planting that commonly occurs after these events. Future BAU harvest files were constructed using current harvest rates, where county-specific average harvest and the actual amounts per ownership were used to guide grid cell selection. This resulted in the majority of harvest occurring on private land (70%) and in the mesic ecoregions. Beetle outbreaks were implemented using a modified mortality rate of the lodgepole pine PFT with 0.1% y^{-1} biomass mortality by 2100.

For afforestation potential, we identified areas that are within forest boundaries that are not currently forest and areas that are currently grass crops. We assumed no competition with conversion of irrigated grass crops to urban growth, given Oregon's land use laws for developing within urban growth boundaries. A separate study suggested that, on average, about 17% of all irrigated agricultural crops in the Willamette Valley could be converted to urban area under future climate; however, because 20% of total cropland is grass seed, it suggests little competition with urban growth (25).

Landsat observations (12,500 scenes) were processed to map changes in land cover from 1984 to 2012. Land cover types were separated with an unsupervised K-means clustering approach. Land cover classes were assigned to an existing forest type map (42). The CropScape Cropland Data Layer (CDL 2015, https://nassgeodata.gmu.edu/CropScape/) was used to distinguish nonforage grass crops from other grasses. For afforestation, we selected grass cropland with a minimum soil water-holding capacity of 150 mm and minimum precipitation of 500 mm that can support trees (43).

Afforestation Cobenefits. Modeled irrigation demand of grass seed crops under future climate conditions was previously conducted with hydrology and agricultural models, where ET is a function of climate, crop type, crop growth state, and soil-holding capacity (20) (Table S7). The simulations produced total land area, ET, and irrigation demand for each cover type. Current grass seed crop irrigation in the Willamette Valley is 413 billion $m^3 \cdot y^{-1}$ for 238,679 ha and is projected to be 412 and 405 billion m^3 in 2050 and 2100 (20) (Table S7). We used annual output from the simulations to estimate irrigation demand per unit area of grass seed crops (1.73, 1.75, and 1.84 million $m^3 \cdot ha^{-1}$ in 2015, 2050, and 2100, respectively), and applied it to the mapped irrigated crop area that met conditions necessary to support forests (Table S7).

LCA. Decomposition of wood through the product cycle was computed using an LCA (8, 10). Carbon emissions to the atmosphere from harvest were calculated annually over the time frame of the analysis (2001–2015). The net carbon emissions equal NECB plus total harvest minus wood lost during manufacturing and wood decomposed over time from product use. Wood industry fossil fuel emissions were computed for harvest, transportation, and manufacturing processes. Carbon credit was calculated for wood product storage, substitution, and internal mill recycling of wood losses for bioenergy.

Products were divided into sawtimber, pulpwood, and wood and paper products using published coefficients (44). Long-term and short-term products were assumed to decay at 2% and 10% per year, respectively (45). For product substitution, we focused on manufacturing for long-term structures (building life span >30 y). Because it is not clear when product substitution started in the Pacific Northwest, we evaluated it starting in 1970 since use of concrete and steel for housing was uncommon before 1965. The displacement value for product substitution was assumed to be 2.1 Mg fossil C/Mg C wood use in long-term structures (46), and although it likely fluctuates over time, we assumed it was constant. We accounted for losses in product substitution associated with building replacement (33) using a loss rate of 2% per year (33), but ignored leakage related to fossil C use by other sectors, which may result in more substitution benefit than will actually occur.

The general assumption for modern buildings, including cross-laminate timber, is they will outlive their usefulness and be replaced in about 30 y (7). By 2035, ∼75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends, resulting in threefold as many buildings as there are now [2005 baseline (31, 32)]. The loss of the PSS is therefore PSS multiplied by the proportion of buildings lost per year (2% per year).

To compare the NECB equivalence to emissions, we calculated forest sector and energy sector emissions separately. Energy sector emissions ["in-boundary" state-quantified emissions by the Oregon Global Warming Commission (14)] include those from transportation, residential and commercial buildings, industry, and agriculture. The forest sector emissions are cradle-to-grave annual carbon emissions from harvest and product emissions, transportation, and utility fuels (Table S3). Forest sector utility fuels were subtracted from energy sector emissions to avoid double counting.

Uncertainty Estimates. For the observation-based analysis, Monte Carlo simulations were used to conduct an uncertainty analysis with the mean and SDs for NPP and Rh calculated using several approaches (36) (*SI Materials and Methods*). Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest emissions (7%), and land cover estimates (10%) using the propagation of error approach. Uncertainty in CLM4.5 model simulations and LCA were quantified by combining the uncertainty in the observations used to evaluate the model, the uncertainty in input datasets (e.g., remote sensing), and the uncertainty in the LCA coefficients (41).

Model input data for physiological parameters and model evaluation data on stocks and fluxes are available online (37).

ACKNOWLEDGMENTS. We thank Dr. Thomas Hilker (deceased) for producing the grass data layer, and Carley Lowe for Fig. 1. This research was supported by the US Department of Energy (Grant DE-SC0012194) and Agriculture and Food Research Initiative of the US Department of Agriculture National Institute of Food and Agriculture (Grants 2013-67003-20652, 2014-67003-22065, and 2014-35100-22066) for our North American Carbon Program studies, "Carbon cycle dynamics within Oregon's urban-suburban-forested-agricultural landscapes," and "Forest die-off, climate change, and human intervention in western North America."

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Formulating an Expanding-Gap Regeneration System for *Quercus* Dominated Stands

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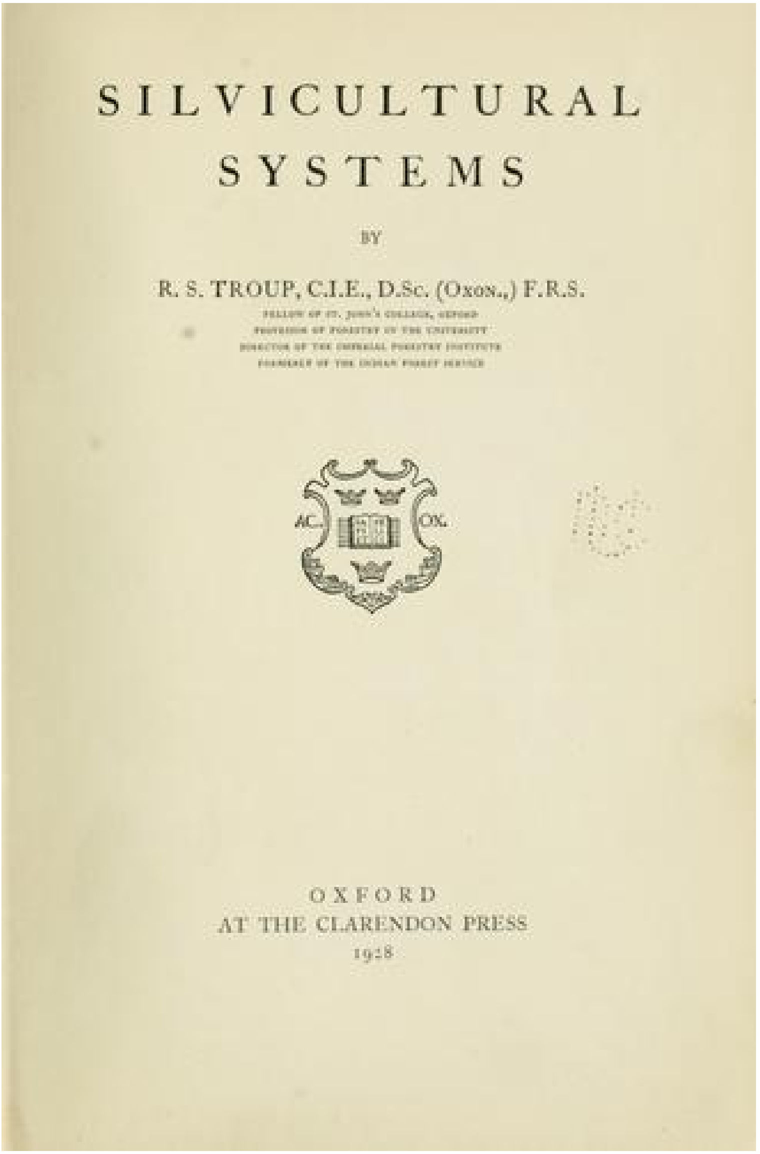
Presentation Outline

- What is an irregular shelterwood system?
- Rational for applying an irregular shelterwood system in *Quercus* stands
- “Proof of concept” study and future exploration

Historical Context



SILVICULTURAL
SYSTEMS

BY

R. S. TROUP, C.I.E., D.Sc. (Oxon.,) F.R.S.

OXFORD
AT THE CLARENDON PRESS
1928

Historical Context

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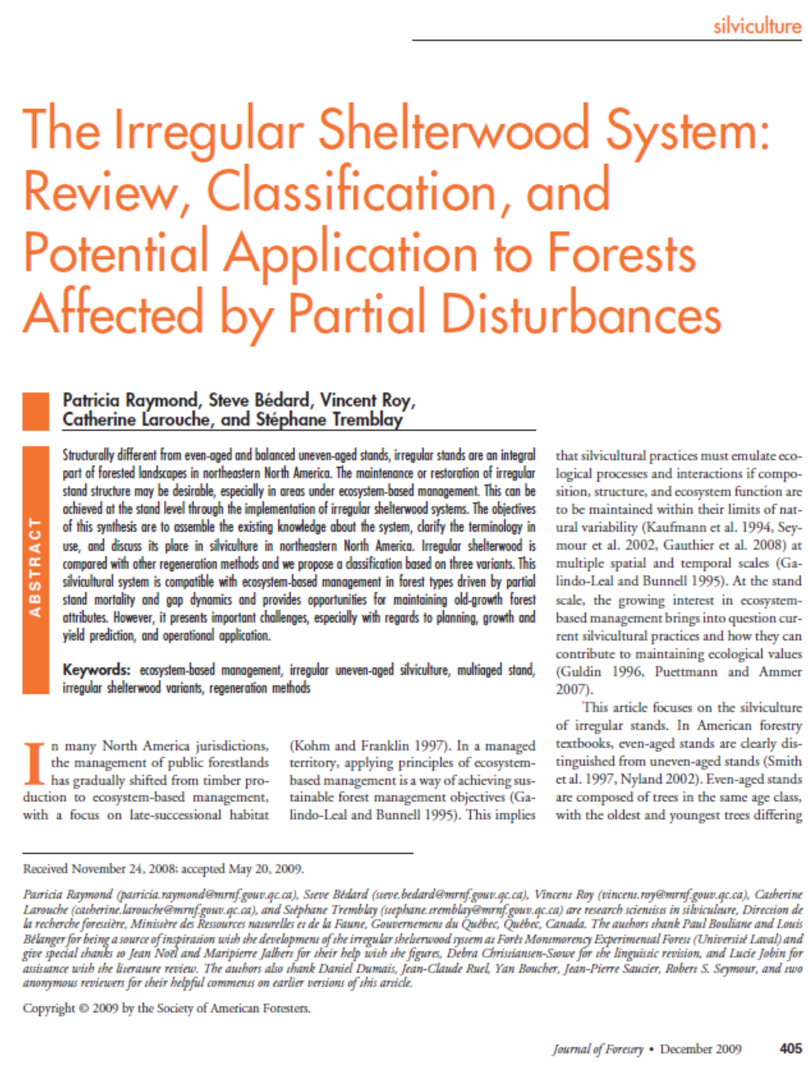

silviculture

The Irregular Shelterwood System: Review, Classification, and Potential Application to Forests Affected by Partial Disturbances

Patricia Raymond, Steve Bédard, Vincent Roy, Catherine Larouche, and Stéphane Tremblay

ABSTRACT

Structurally different from even-aged and balanced uneven-aged stands, irregular stands are an integral part of forested landscapes in northeastern North America. The maintenance or restoration of irregular stand structure may be desirable, especially in areas under ecosystem-based management. This can be achieved at the stand level through the implementation of irregular shelterwood systems. The objectives of this synthesis are to assemble the existing knowledge about the system, clarify the terminology in use, and discuss its place in silviculture in northeastern North America. Irregular shelterwood is compared with other regeneration methods and we propose a classification based on three variants. This silvicultural system is compatible with ecosystem-based management in forest types driven by partial stand mortality and gap dynamics and provides opportunities for maintaining old-growth forest attributes. However, it presents important challenges, especially with regards to planning, growth and yield prediction, and operational application.

Keywords: ecosystem-based management, irregular uneven-aged silviculture, multiaged stand, irregular shelterwood variants, regeneration methods

In many North America jurisdictions, the management of public forestlands has gradually shifted from timber production to ecosystem-based management, with a focus on late-successional habitat (Kohm and Franklin 1997). In a managed territory, applying principles of ecosystem-based management is a way of achieving sustainable forest management objectives (Galindo-Leal and Bunnell 1995). This implies that silvicultural practices must emulate ecological processes and interactions if composition, structure, and ecosystem function are to be maintained within their limits of natural variability (Kaufmann et al. 1994, Seymour et al. 2002, Gauthier et al. 2008) at multiple spatial and temporal scales (Galindo-Leal and Bunnell 1995). At the stand scale, the growing interest in ecosystem-based management brings into question current silvicultural practices and how they can contribute to maintaining ecological values (Guldin 1996, Puettmann and Ammer 2007).

This article focuses on the silviculture of irregular stands. In American forestry textbooks, even-aged stands are clearly distinguished from uneven-aged stands (Smith et al. 1997, Nyland 2002). Even-aged stands are composed of trees in the same age class, with the oldest and youngest trees differing

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Received November 24, 2008; accepted May 20, 2009.

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Irregular Shelterwood System Defined

Three general classifications:

- Expanding-gap irregular shelterwood
- Continuous cover irregular shelterwood
- Extended irregular shelterwood

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107(8):405-413.

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Irregular Shelterwood System Defined

Expanding-gap irregular shelterwood -

“Aims to regenerate new cohorts in groups that are gradually enlarged until the stand is totally removed”

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107(8):405-413.

Irregular Shelterwood System Defined

Continuous cover irregular shelterwood –

“Sequence of cuttings is applied more freely in space and time, which permits maintenance of a multicohort structure and a continuous forest cover ”

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107(8):405-413.

Irregular Shelterwood System Defined

Extended Irregular Shelterwood –

“Aims to regenerate the whole stand while … two cohorts are maintained for at least 20% of the rotation length”

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107(8):405-413.

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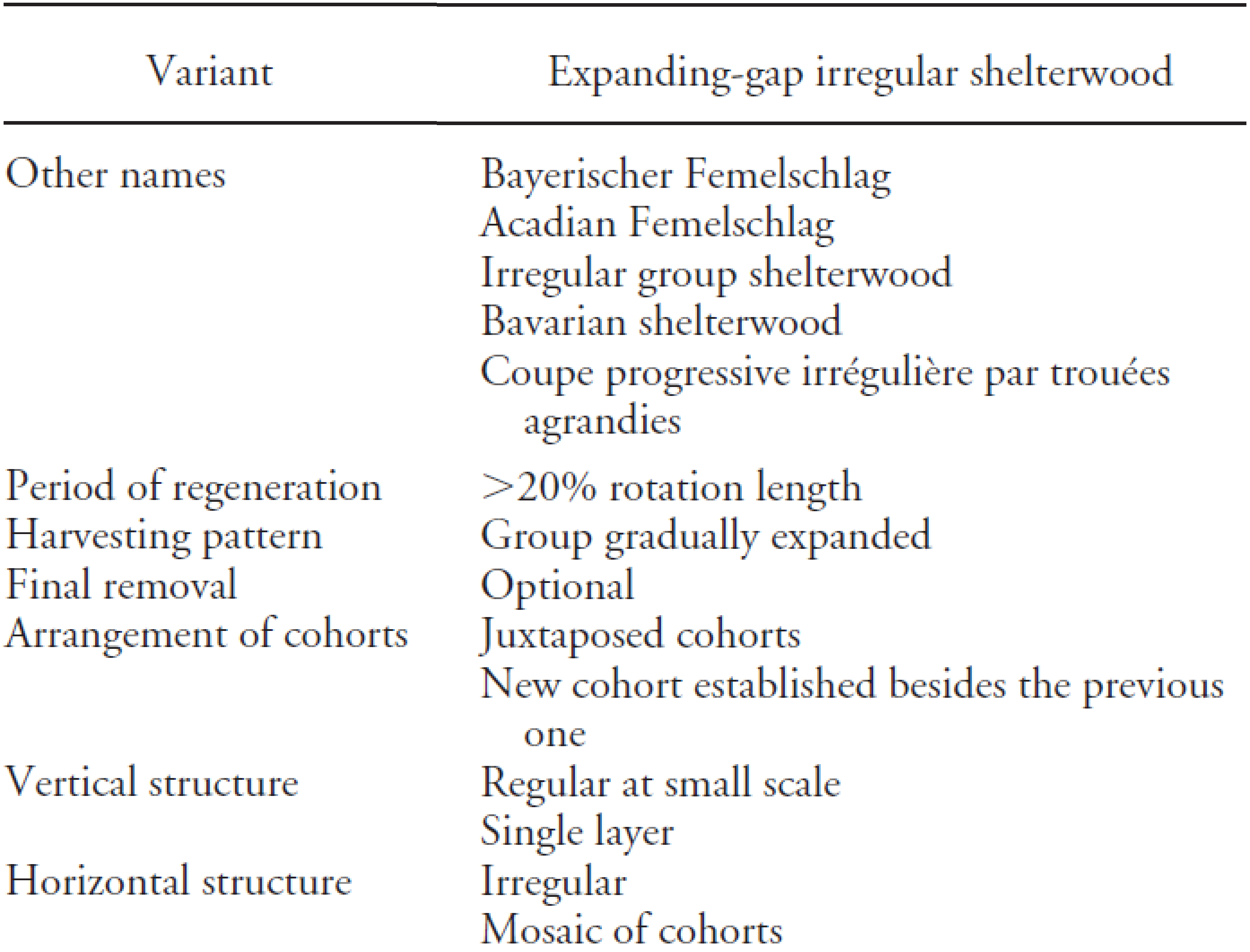
Expanding-gap irregular shelterwood



Variant	Expanding-gap irregular shelterwood
Other names	Bayerischer Femelschlag Acadian Femelschlag Irregular group shelterwood Bavarian shelterwood Coupe progressive irrégulière par trouées agrandies
Period of regeneration	>20% rotation length
Harvesting pattern	Group gradually expanded
Final removal	Optional
Arrangement of cohorts	Juxtaposed cohorts New cohort established besides the previous one
Vertical structure	Regular at small scale Single layer
Horizontal structure	Irregular Mosaic of cohorts

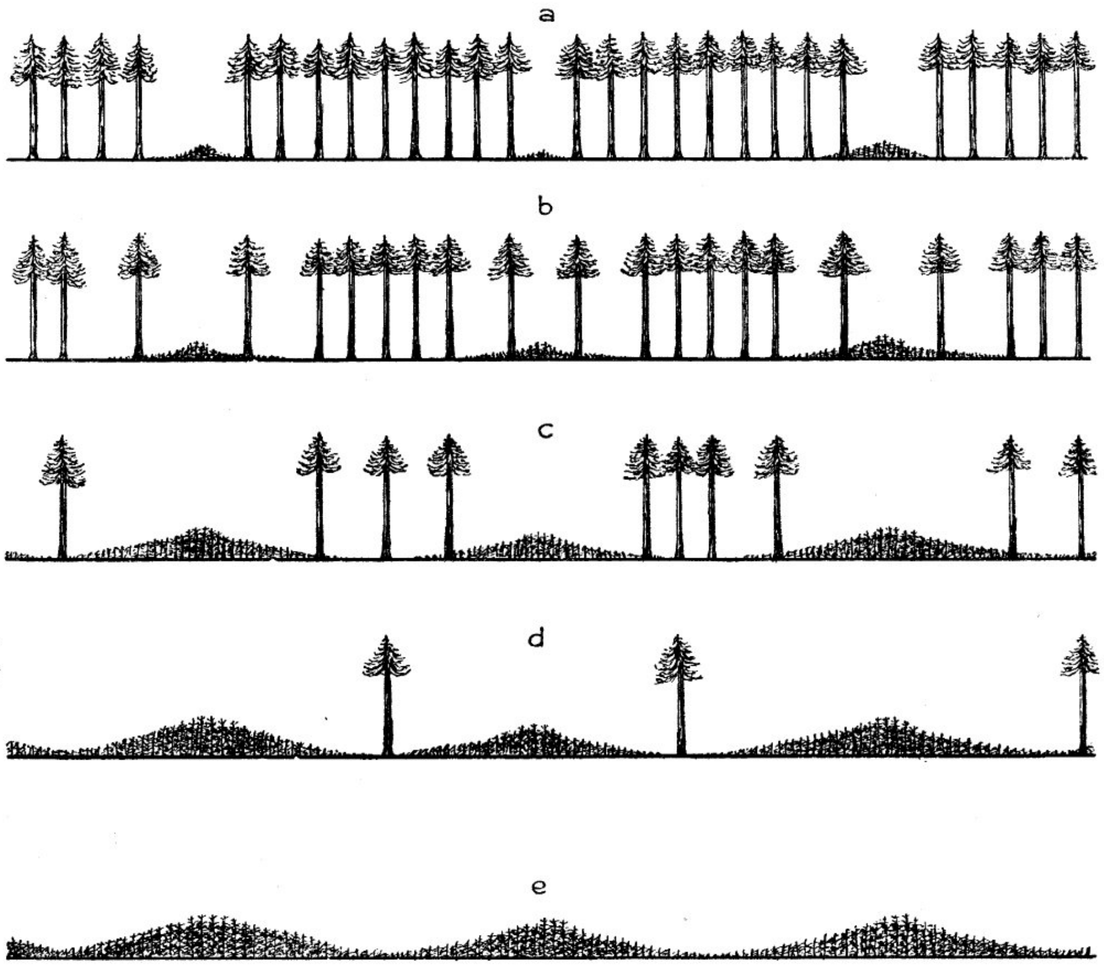
Irregular Shelterwoods and *Quercus* Forests

- *Femelschlag* systems are used throughout Europe
- While interest is gaining, no examples of expanding-gap irregular shelterwoods exist in North American oak forests
- Potential benefits of expanding-gap systems include:
  1. Structural complexity and continuous forest cover
  2. Multiple income flows over rotation
  3. Regeneration of diverse species groups, from shade intolerants in gap centers to intermediates and shade tolerants along gap edges

Research Goal

Our long-term goal is to develop an expanding-gap based silvicultural practices that address the oak regeneration problem present within the Central Hardwood Forest Region (CHFR)

Research Needed for System Development



Source: Troup 1928

Research Needed for System Development

Developing a expanding-gap regeneration system requires understanding of how the following factors influence spatial variation in resource gradients and regeneration dynamics:

- Gap size
- Edge effects
- Canopy structure in the forest matrix

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- Gap size
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- Canopy structure in the forest matrix

This presentation integrates results from complementary research studies that together support the basis for applying expanding-gap regeneration systems in oak dominated stands

Research Studies

Gap Size

Lhotka (In Press) tested the effect of three gap sizes on oak recruitment 48 years following treatment

Edge Effects

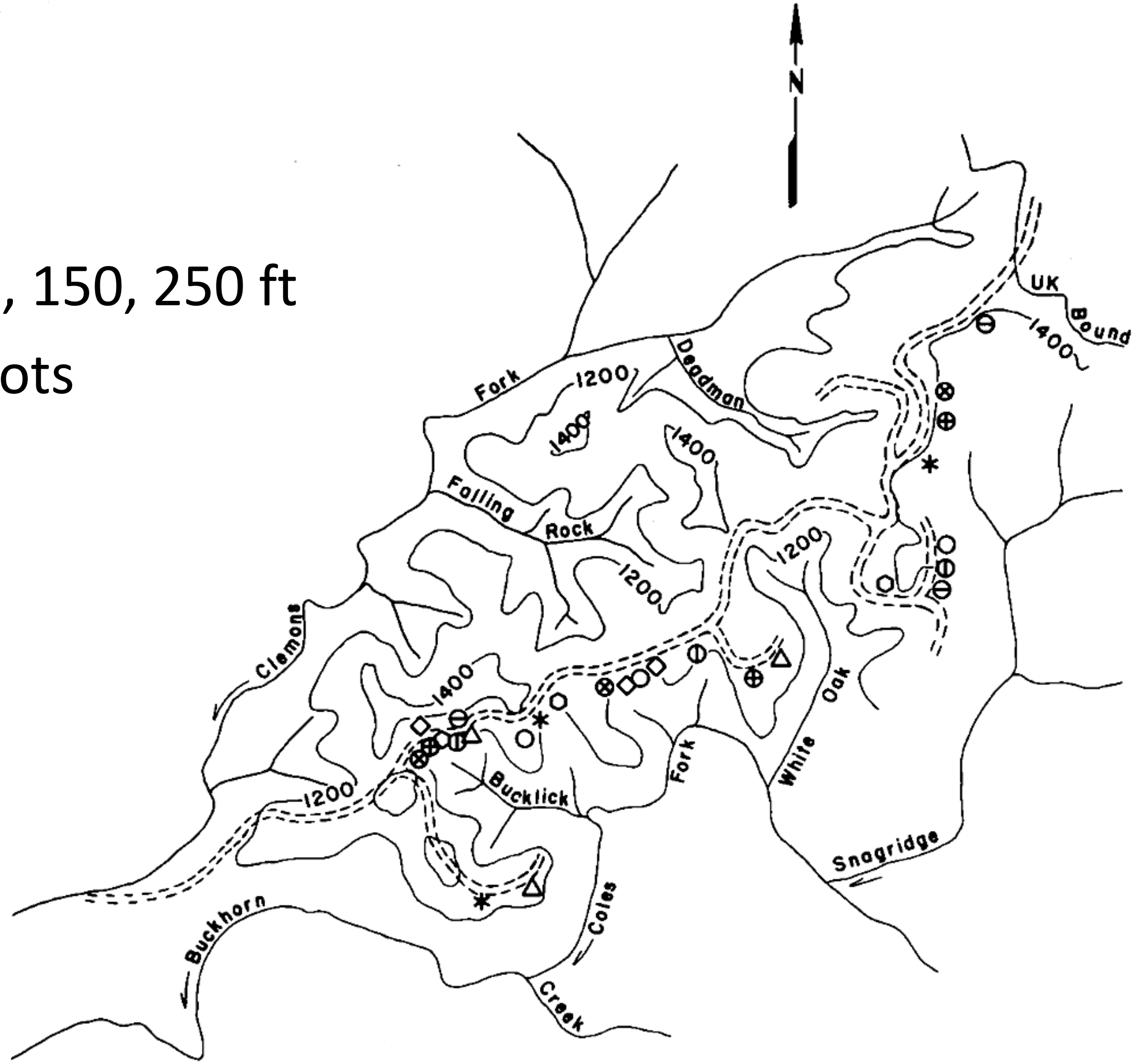
Lhotka and Stringer (In Review) characterized the relationship between distance from anthropogenically created edge and the height and density of oak reproduction

Midstory Removal

Parrott et al. (In Press) evaluated the effect of midstory removal on understory light availability and oak seedling survival and growth after 7 growing seasons

Robinson Forest Gap Size Study

- Established 1960
- Three gap sizes: 50, 150, 250 ft
- 27 experimental plots



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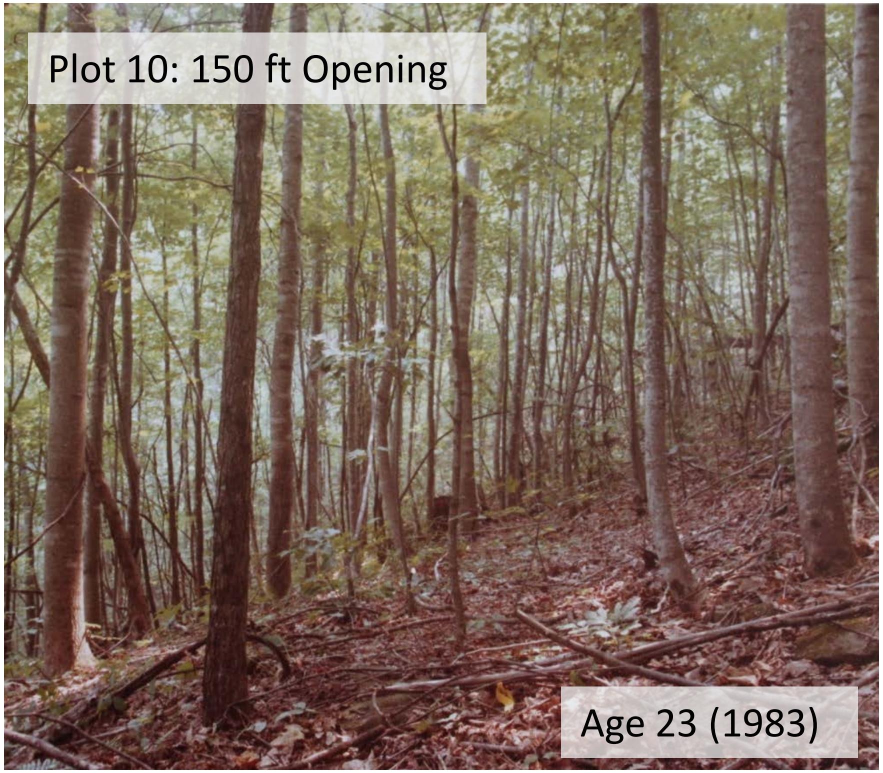
Robinson Forest Gap Size Study

Hill and Muller (UK): 1981, 1985, 1987
USDA Forest Service: 1991

Lhotka: 2008
*Thanks to Matt Strong



Plot 10: 150 ft Opening

Age 23 (1983)

Plot 10: 150 ft Opening

Age 48 (2008)

Robinson Forest Gap Size Study - Results

Stand Structure after 48 Years

Opening Size	BA (m^2 ha^{-1})	Trees (ha^{-1})	QMD (cm)	Top Height (m)
50	12.2^{a*}	1008.2^{a}	12.2^{a}	19.8^{a}
150	21.1^{b}	953.7^{a}	17.0^{b}	26.6^{b}
250	21.6^{b}	719.1^{a}	19.7^{c}	28.6^{b}

*Means with similar letters are not statistically different ($\alpha = 0.05$)

Robinson Forest Gap Size Study - Results

Overstory Trees ha^{-1} by Treatment following 48 Years

Species Group	Opening Size		
	50 ft	150 ft	250 ft
Oak	27.4^{a*}	89.3^{b}	49.5^{b}
Maple	82.2^{a}	51.4^{a}	52.4^{a}
Yellow-poplar	0^{a}	39.3^{b}	50.4^{b}
Hickory	12.1^{a}	4.7^{a}	2.9^{a}
Other Commercial	6.1^{a}	2.7^{a}	4.9^{a}
Other	9.1^{a}	5.4^{a}	3.4^{a}

*Means within a species group that have similar letters are not statistically different ($\alpha = 0.05$)

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Robinson Forest Gap Size Study - Results

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*Means within a species group that have similar letters are not statistically different ($\alpha = 0.05$)

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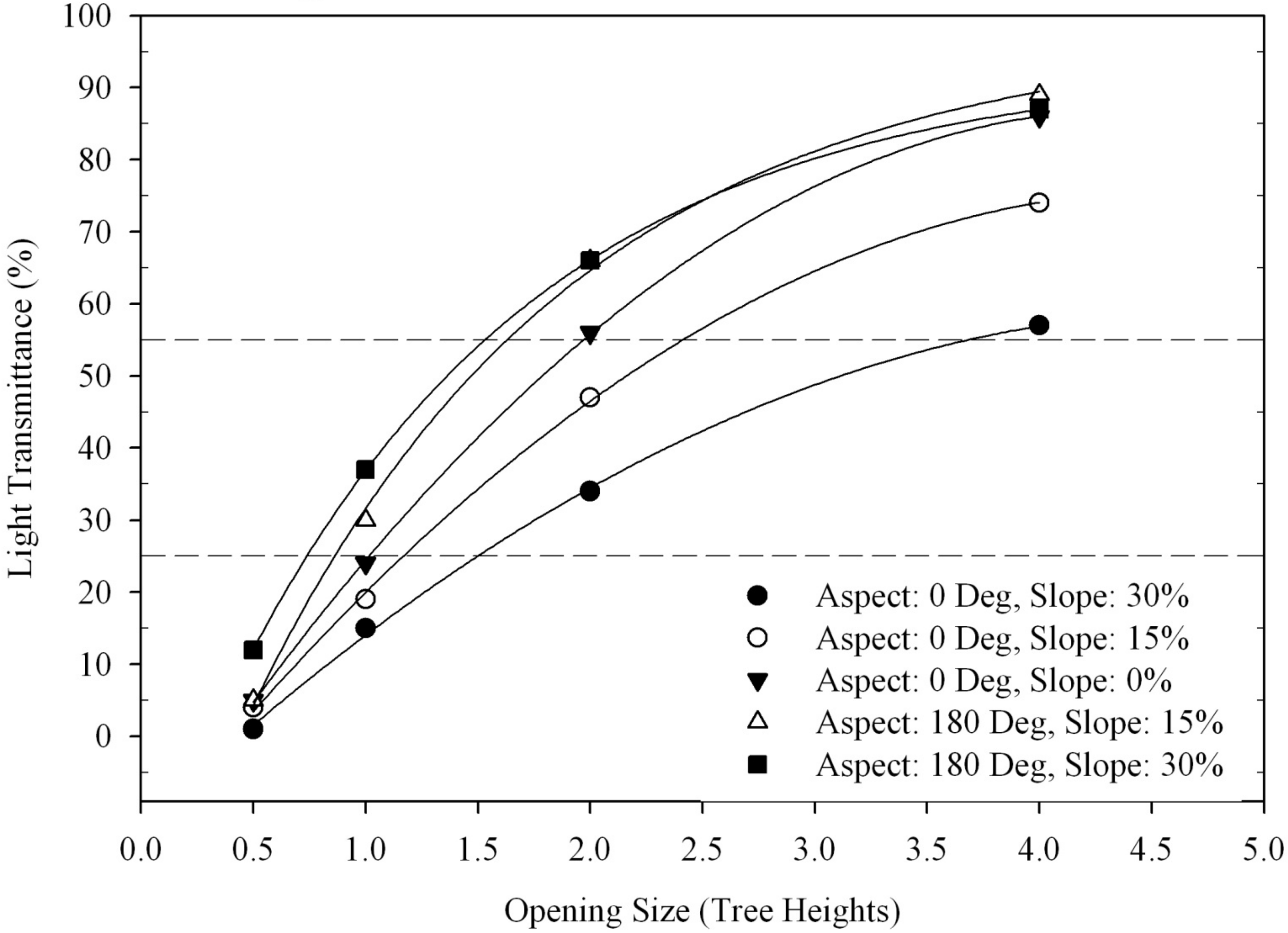
Robinson Forest Gap Size Study - Summary

Size of opening influenced structure and composition and apparent trends suggest:

- 50 ft opening favored maple
- Dominant and codominant oak density was “maximized” in 150 ft opening
- Yellow-poplar increased with larger opening sizes

Gap Size Study : Role of Light in Species Trends

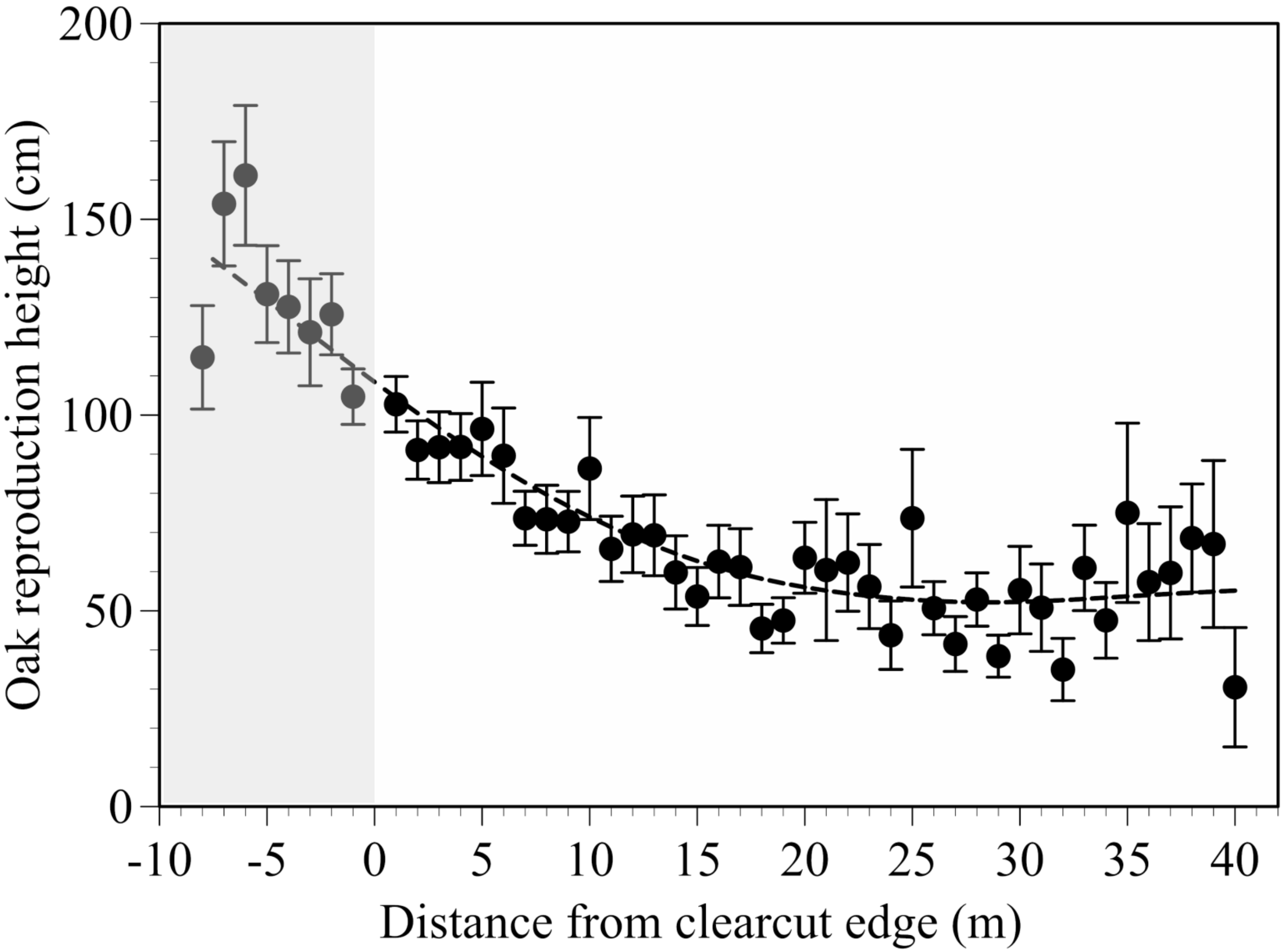
From: Fischer, B.C. 1981. Designing Forest Openings of the Group Selection Method. SO-GTR-34. pp 274-277.



Berea Forest Edge Effects Study

- Initiated by Lhotka and Stringer in 2011
- Goal was to further understanding of how forest edge influences the development of advance reproduction along the gradient extending from a regeneration opening into adjacent, intact forest areas
- 48 m transects surround to 9-year-old clearcuts on Berea College Forest

Berea Forest Edge Effects Study – Seedling Heights



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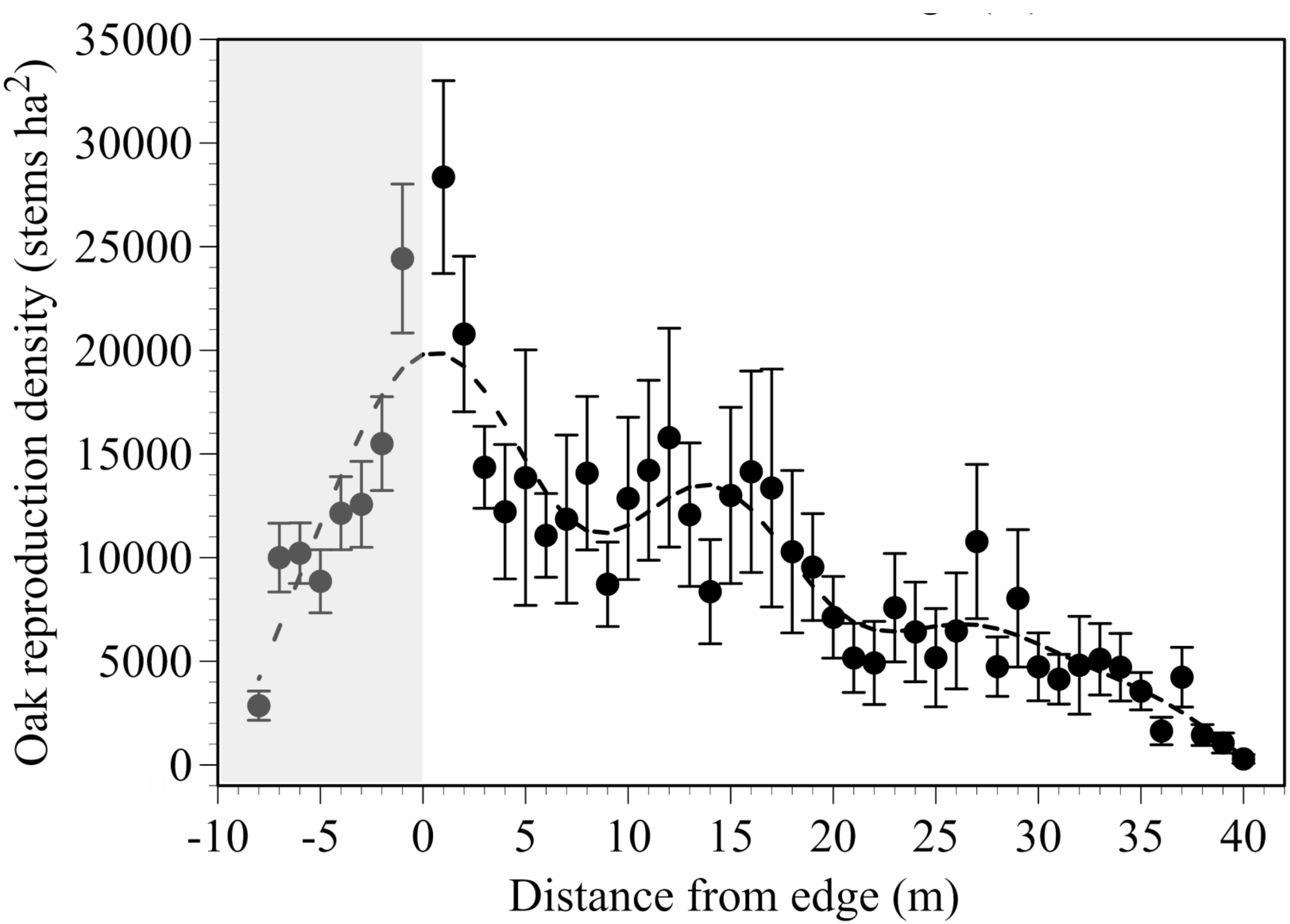
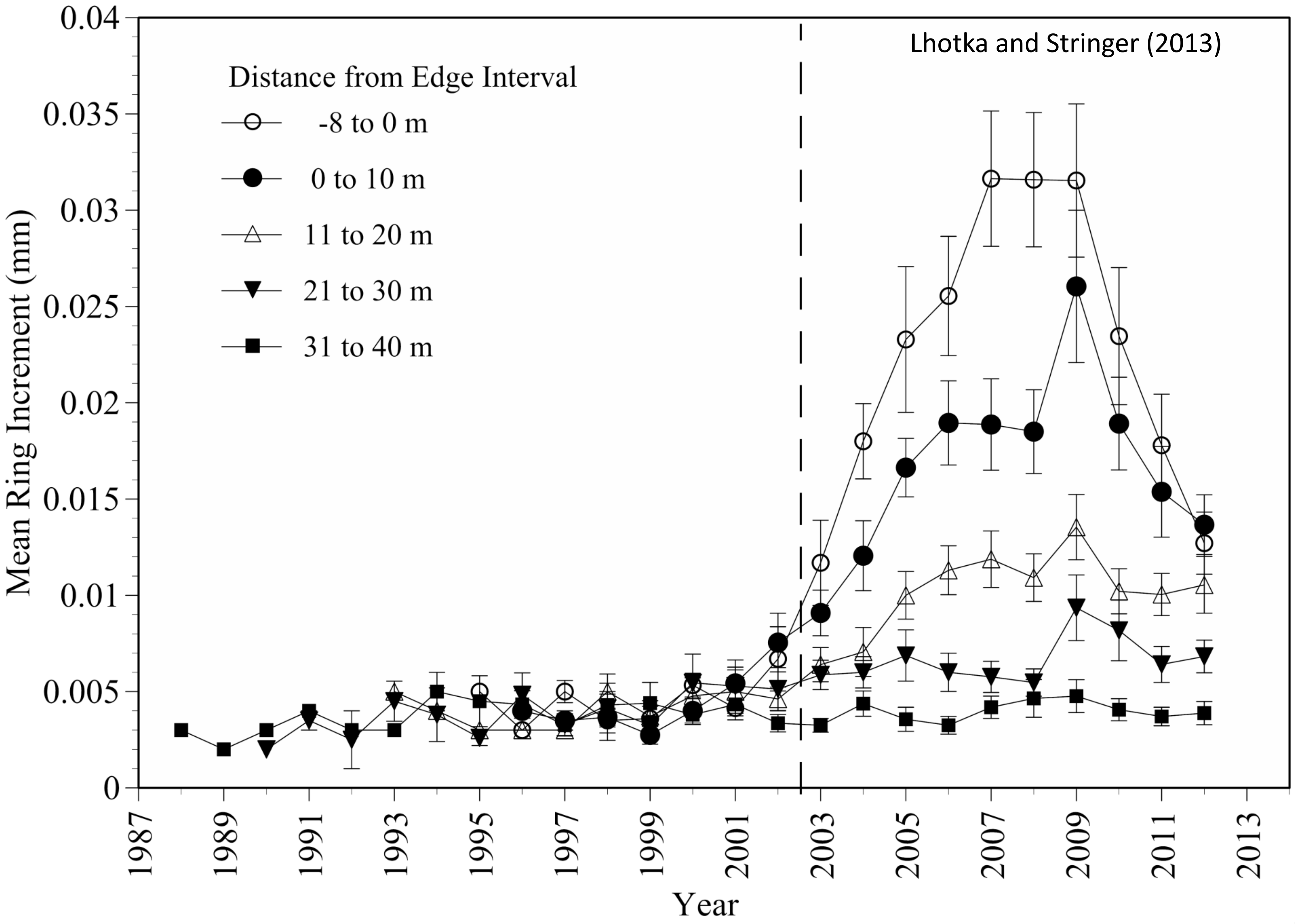
Berea Forest Edge Effects Study – Seedling Density



Edge Environment: Seedling Radial Growth



Berea Forest Edge Effects Study - Summary

Data indicate that environments associated with forest edges can increase the size and density of oak reproduction and that the edge influence may extend up to 20 m

Berea Midstory Removal Study

- Initiated by Dillaway and Stinger (2004)
- 4 sites, Berea College Forest
- Midstory removal treatment (20% basal area reduction)
- Natural advance reproduction and underplanted seedlings
- Monitored 7 years
- Understory microclimate characterized

Berea Midstory Removal Study - Results

- Midstory removal increased understory light availability
  - Removal 10.3% full sunlight
  - Control 1.5% full sunlight

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Berea Midstory Removal Study – Results

Seven-year natural and underplanted seedling responses to midstory removal (Parrott et al. In Press)

	Natural Reproduction			Underplanted	
	Black Oak	White Oak	Red Maple	Black Oak	White Oak
Survival (%)					
Control	---	70.4*	80.6*	15.7*	46.0*
Midstory Treatment	---	85.9*	87.9*	45.8*	78.3*
Mean height (cm)					
Control	52.3	28.9 *	41.6 *	37.4	31.0 *
Midstory removal	77.1	45.3 *	69.8 *	51.4	46.3 *
Mean GLD (mm)					
Control	8.5	4.7 *	6.5 *	7.0 *	7.4 *
Midstory removal	13.0	7.8 *	10.1 *	9.9 *	9.1 *

Developing a expanding-gap regeneration system

Understanding factors that influence spatial variation in resource gradients and regeneration dynamics:

- Gap size
- Edge effects
- Canopy structure in the forest matrix

An Expanding-Gap Approach for Oak

What about gap size?

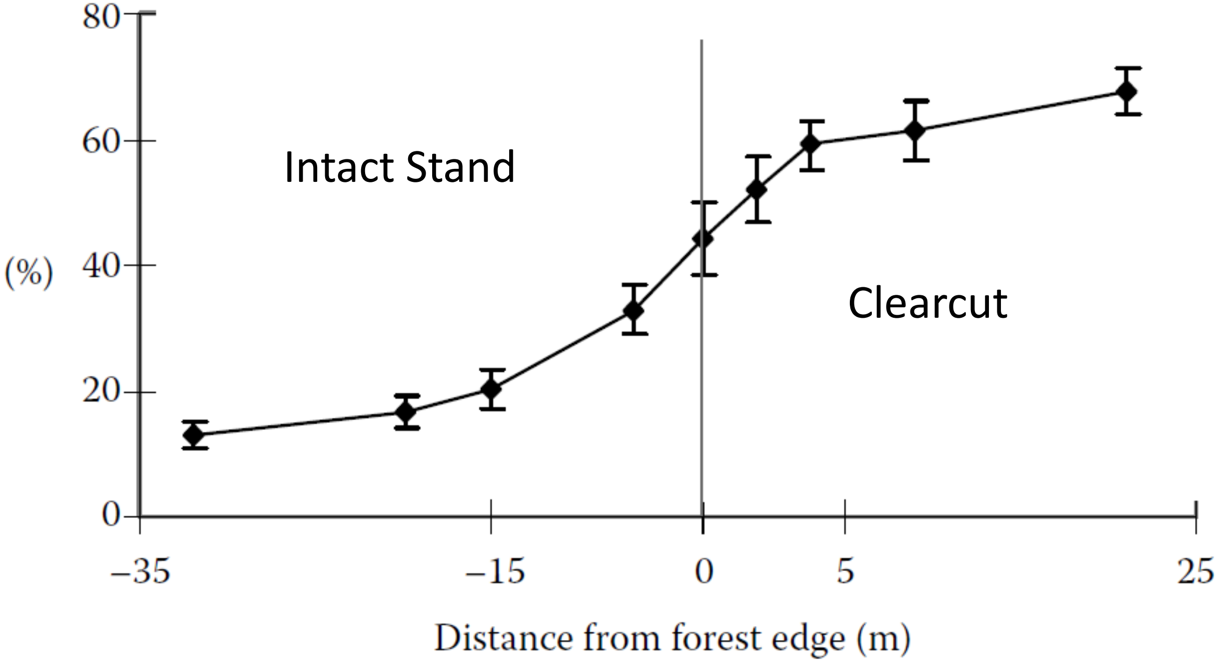
An Expanding-Gap Approach for Oak

What about gap size?

Research indicates that silvicultural gaps 1.5 to 2.5 times the dominant tree height can:

1. Improve oak recruitment within gaps
2. Create edge environments that may increase density and height of oak reproduction in the adjacent forest matrix

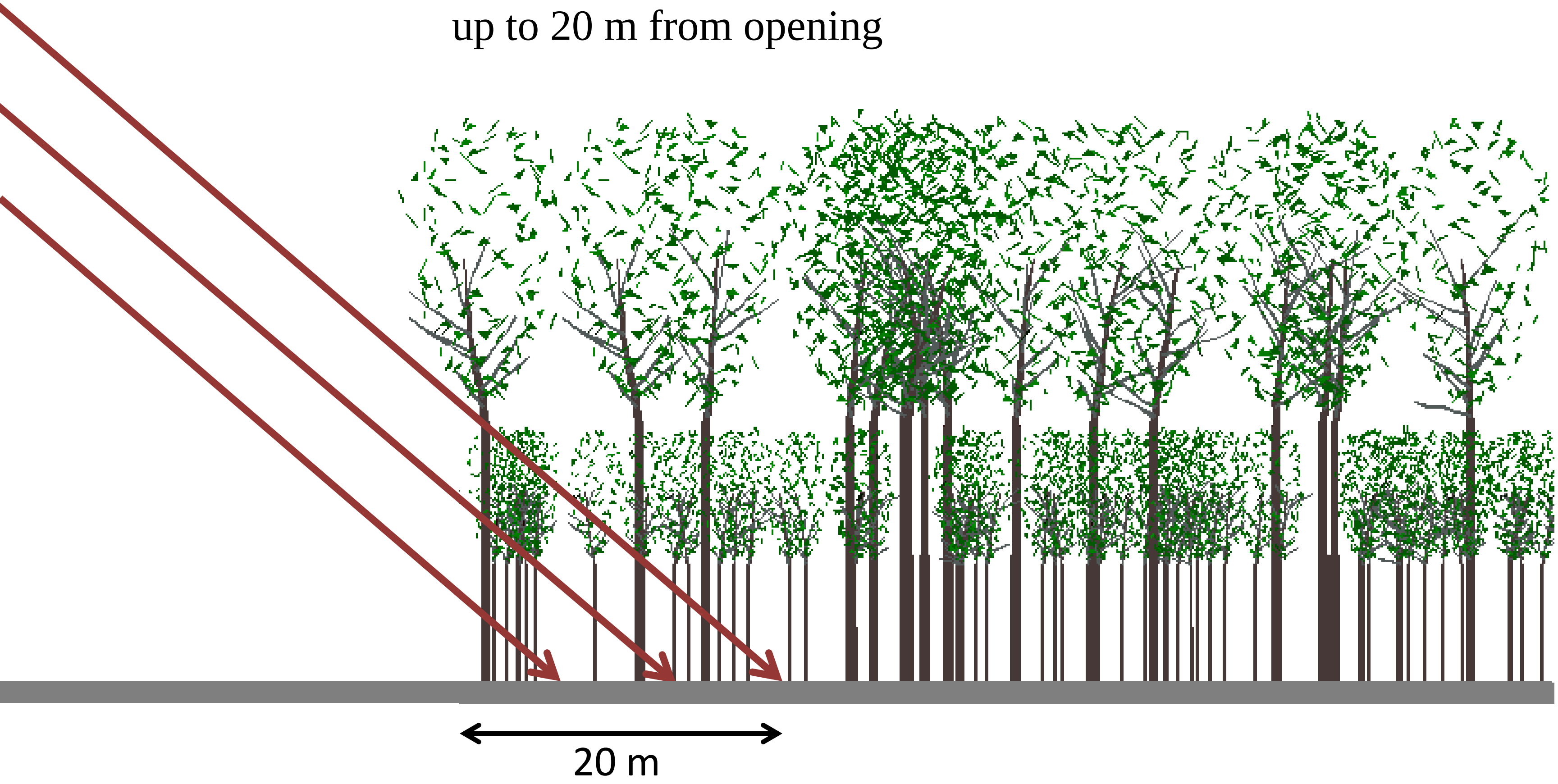
What about edge effects and forest structure in matrix?



Schmid, I., K. Klumpp, and M. Kazda. 2005. Light distribution within forest edges in relation to forest regeneration. Journal of Forest Science 51(1):1-5.

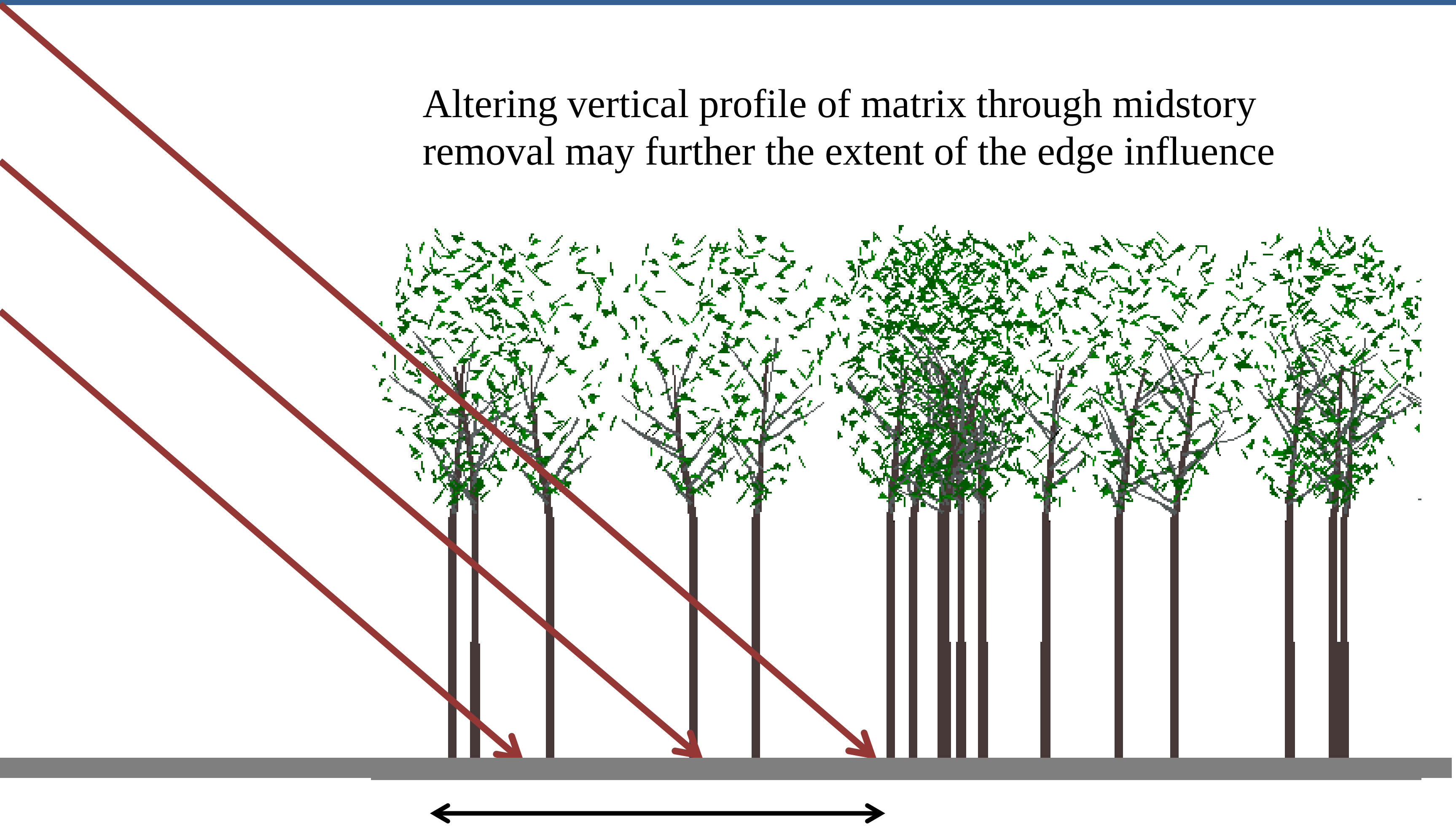
What about edge effects and forest structure in matrix?

Environmental effects of forest edges on oak may extend up to 20 m from opening



What about edge effects and forest structure in matrix?

Altering vertical profile of matrix through midstory removal may further the extent of the edge influence



Estimated to be 30 m

An Expanding-Gap Approach for Oak

What about edge effects and forest structure in matrix?

Removal of midstory canopies around silvicultural gaps may:

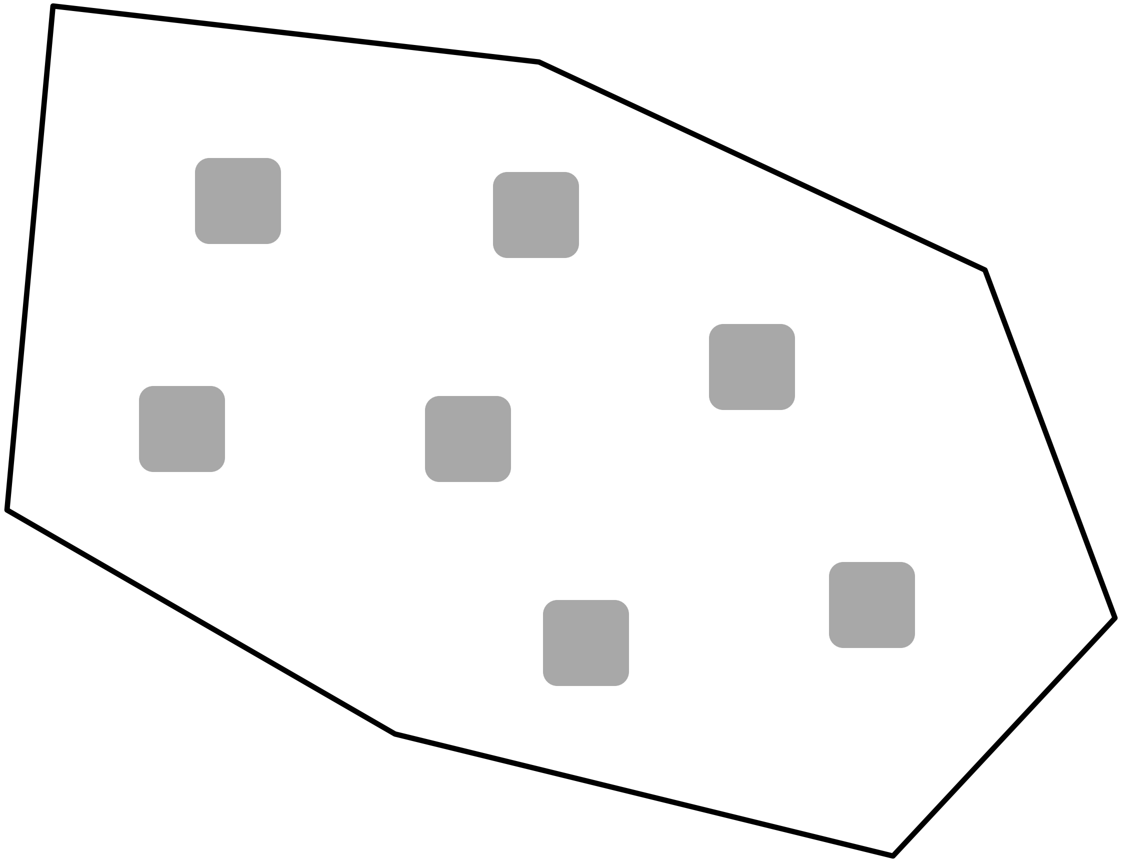
1. Improve oak survival and growth in areas to be released during subsequent gap expansions
2. Extend the enhancement effect of the edge environment on oak reproduction further in the forest matrix

An Expanding-Gap Approach for Oak

An expanding-gap irregular shelterwood that uses intermediate gap sizes and midstory removal as a preparatory treatment around gaps may represent a novel silvicultural practice for increasing oak regeneration potential within the CHFR

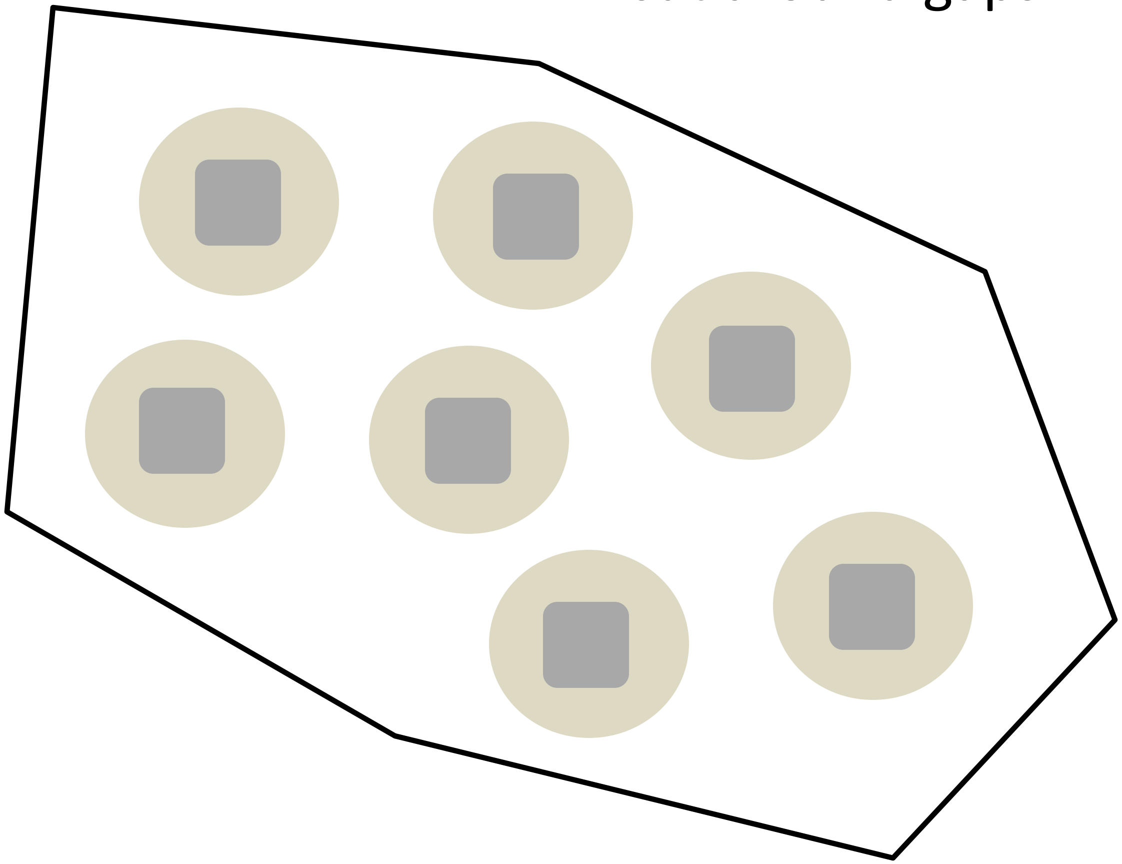
Expanding-Gap Irregular Shelterwood for Oak

Initial Gaps: 1.5 to 2.5 tree heights

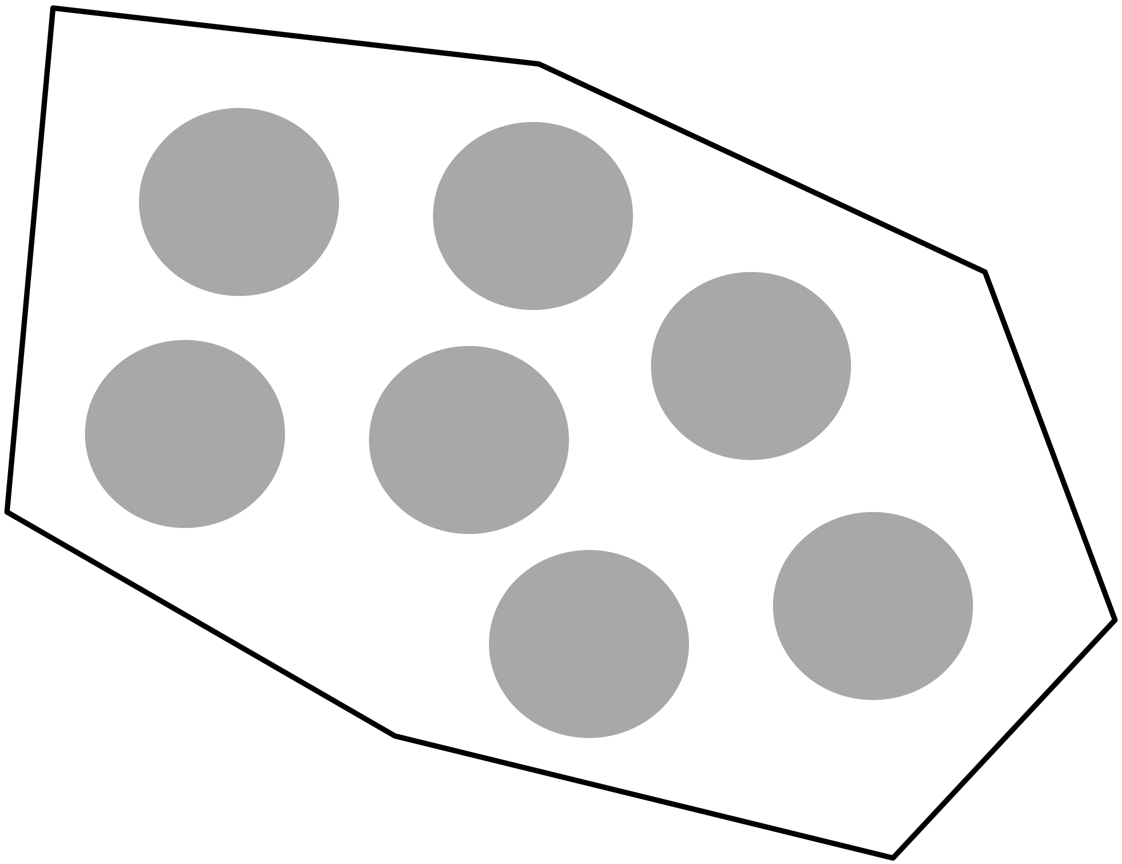


Expanding-Gap Irregular Shelterwood for Oak

Midstory removal as preparatory cut around gaps



Expanding-Gap Irregular Shelterwood for Oak



Subsequent gap expansion into midstory removal areas based upon oak reproduction development

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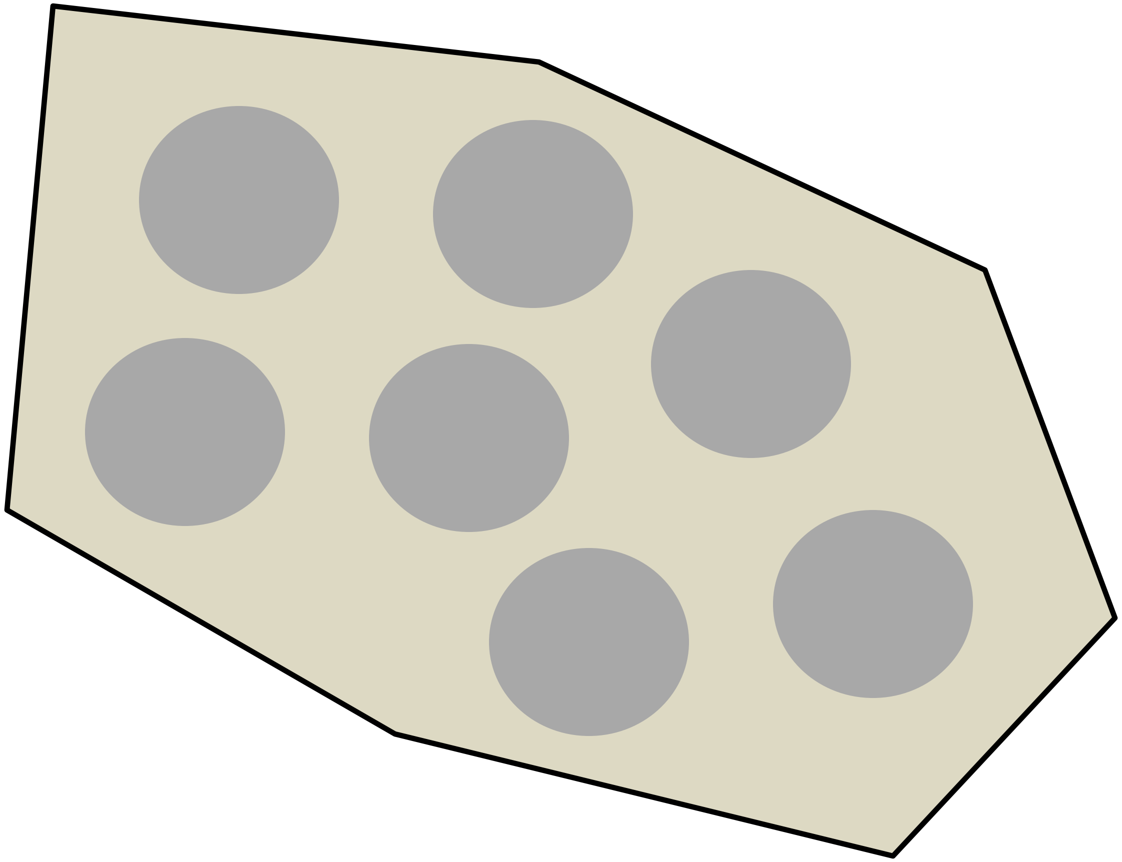
Expanding-Gap Irregular Shelterwood for Oak



Midstory removal following gap expansions

Berea Forest - Proof of Concept Study

- Expanding-gap Study
  - Lhotka, Stringer, Patterson
  - 12 replicated gaps
  - Two treatments
- Research foci:
  - Establishment and growth dynamics
  - Light transmittance modeling

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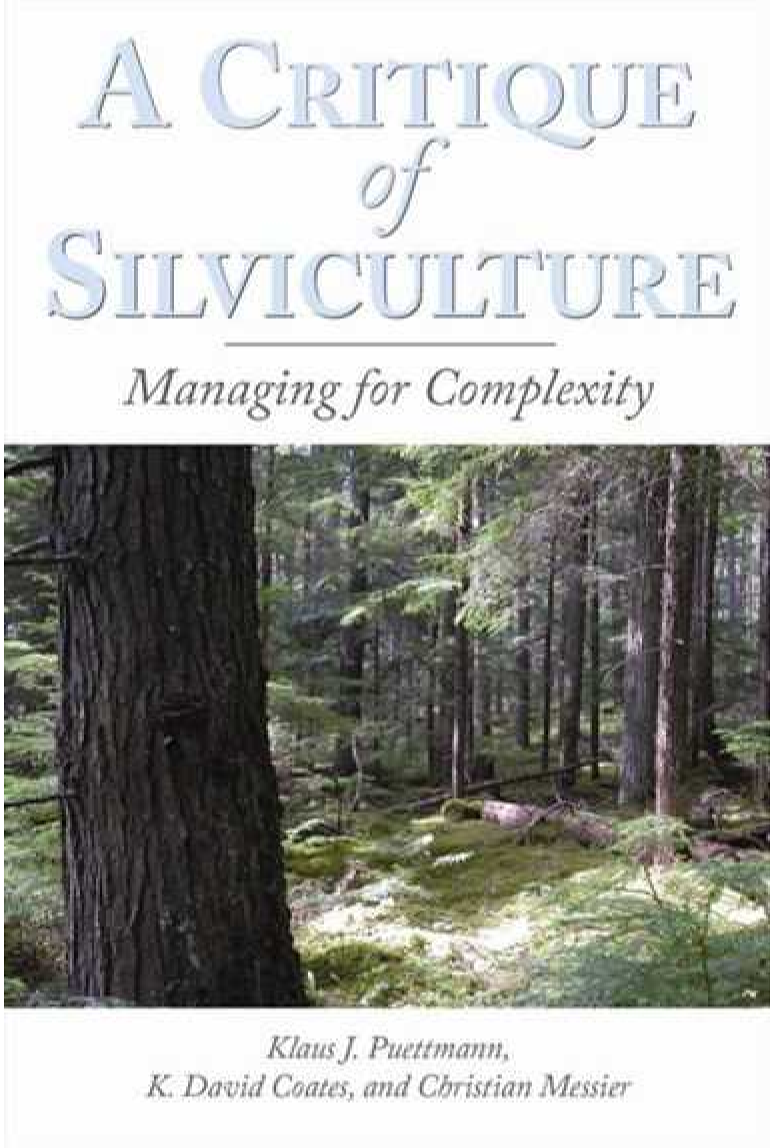
College of Agriculture

Future Extensions



A CRITIQUE of SILVICULTURE

Managing for Complexity

Klaus J. Puettmann,
K. David Coates, and Christian Messier

Applied Vegetation Science **17** (2014) 312–322

Fire and gap dynamics over 300 years in an old-growth temperate forest

Ryan W. McEwan, Neil Pederson, Adrienne Cooper, Josh Taylor, Robert Watts & Amy Hruska

Keywords
Canopy gap; Fire scar; Oak; Release detection; Tree-ring; Wildfire

Nomenclature
Jones (2005)

Received 10 April 2013
Accepted 16 July 2013
Co-ordinating Editor: Jörg Ewald

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Abstract

Questions: What are the long-term patterns of wildfire occurrence and gap dynamics in an old-growth deciduous forest? Are there temporal patterns in fire and gap dynamics over the last ca. 300 yrs? How is drought related to fire occurrence? Are there temporal interactions between gap dynamics and fire?

Location: Lilley Cornett Woods Appalachian Research Station, Southeastern Kentucky, USA. LCW; 37°05′ N, 83°00′ W.

Methods: We cross-dated and analysed annually-resolved tree-ring data from 35 tree cross-sections in an old-growth deciduous forest to reconstruct historical fire and canopy disturbance and explore connections among these processes. Canopy disturbance patterns as indicated by tree growth release within this collection [fire history collection: (FHC)] were compared to cores from 26 trees collected in 1983 for the purposes of climate reconstruction [climate collection: (CC)].

Results: Initiation dates in the FHC ranged from ca. 1670 to 1925. Thirty-three fire scars were identified from 1678 to 1956. The mean interval between fire events was 9.3 yrs, and there were many more fires after 1800 than before that date. Gap dynamics, as reconstructed through growth release detection, were relatively constant through the FHC record and were supported by a similar result in the CC. The mean number of years between detected release events was 5.2 yrs. Many individual trees, and the mean growth chronology for the FHC, indicate that many oak trees exhibit growth release after long periods of suppression and, after a final release, exhibit a step-change in growth rate suggesting canopy accession.

Conclusions: Fire and gap dynamics occurred through much of the last ca. 350 yrs in this old-growth forest. There was not evidence to support that these two processes were temporally linked – gap dynamics were ostensibly independent of fire occurrence. Even so, we posit that these two processes may have a synergistic effect on long-term dynamics, wherein fire ‘filters’ the seedling pool and gap openings provide canopy accession opportunities. We also note several instances where release events are associated with stand-wide growth increases suggesting large-scale canopy accession. These events could influence the overstorey composition of the forest for centuries.

Introduction

An early, but sophisticated, conception of the relationship between forest dynamics and historical disturbance was delivered by A.S. Watt (1947; pp 13–14) who noted that:

> … there are exceptional factors of rare or sporadic occurrence, such as storms, fire, drought, epidemics, which create…an age class of abnormal area…. In other words, the relative areas under the age classes…need bear no relation to current meteorological factors but be explicable in terms of some past event which happened, it may be, 200 or 300 years ago.

This idea has gained much support, and many studies have shown that forest structure and composition can be mediated by disturbance and successional processes that can unfold over centuries (e.g. White 1979; Sprugel 1991; Turner et al. 1998; Jackson et al. 2009; McEwan et al. 2011). For instance, variability in drought conditions and

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fire regimes can drive long-term patterns in tree recruitment, and those trees can then dominate stands for centuries (Swetnam & Betancourt 1998; Brown & Wu 2005; Brown 2006). Establishing historical baselines for disturbance processes is important for both theory and management, and is increasingly pressing in an era of 'compounded perturbations' (*sensu* Paine et al. 1998), including pulses of tree mortality due to exotic pests and pathogens, and climate change (Rizzo & Garbelotto 2003; van Mantgem et al. 2009; Knight et al. 2013).

The fire and oak hypothesis is an important disturbance ecology paradigm for the Eastern Deciduous Forest (EDF) in North America. Fire is postulated to have been a relatively constant disturbance process historically and has been associated with ignitions from Native Americans and Euro-American settlers (e.g. Abrams 1992; Brose et al. 2001; Nowacki & Abrams 2008). Fire suppression (and other factors) have caused the virtual elimination of fire in the EDF, and this change is thought to have benefited 'mesophytic' species (especially maples: *Acer rubrum, Acer saccharum*) and hindered oak regeneration (Abrams 1992; Brose et al. 2001; Nowacki & Abrams 2008). The oak-to-maple dynamic has important ecological and economic ramifications, and impeding 'oak loss' is an important consideration in oak forest management (Nodvin & Waldrop 1991; Yaussy 2000; Albrecht & McCarthy 2006; Chiang et al. 2008; Alexander & Arthur 2010; Hutchinson et al. 2012). There are well-replicated and verified fire scar data from forests of the western margin of the EDF that support the idea that fire was an important and dynamic factor over the last 400 yrs (e.g. Cutter & Guyette 1994; Guyette et al. 2002; Guyette & Spetich 2003). In other regions of the EDF, there are plentiful fire scar data from the last ca. 100 yrs (e.g. McEwan et al. 2007; Hutchinson et al. 2008); however, tree-ring data that could provide a pre-European baseline for fire are relatively scarce (Aldrich et al. 2010; Hessl et al. 2011).

The quasi-random process of individual tree death and canopy gap formation is another important deciduous forest disturbance paradigm. Long-term forest development is thought to proceed through a directional, multi-phased process culminating in old-growth forests in which gap dynamics are prevalent (e.g. Braun 1950; Bormann & Likens 1979; Runkle 1982; Oliver & Larson 1996). As trees die due to age, pathogens, wind or other factors, a gap is created in the forest canopy (Franklin et al. 1987). The gap is captured by individuals 'recruiting' into the canopy from the mid-storey or sapling layer, and by lateral branch extension from trees adjacent to the gap. Canopy gaps effectively 'release' suppressed understorey individuals by providing a high light patch in an otherwise densely shaded environment. Gap dynamics are an essential part of most forest development models and a distinguishing feature of mature deciduous forests (Bormann & Likens 1979; Runkle & Yetter 1987; Sprugel 1991; Oliver & Larson 1996; Rentch et al. 2003; Buchanan & Hart 2012).

We used dendroecology to reconstruct ca. 330 yrs of fire and gap dynamics in an old-growth temperate deciduous forest in the central Appalachians of North America. This system offered a unique opportunity due to (1) the depth of the available chronology; (2) the fact that the system is deciduous (instead of pine-dominated); and (3) the species compliment in the site is representative of forests across much of the EDF. Our overall goal was to describe tree establishment and growth, and the activity of fire and gap dynamics over the course of the available chronology. We hypothesized that (H_1) both fire and gap dynamics would be relatively constant through time except for the last several decades where fire suppression should eliminate fire while gap dynamics continue unabated. Fire is often associated with the occurrence of drought, and we hypothesized that (H_2) fire scars would coincide with periods of drought, as indicated in the chronology. This study relied on analysis of tree cross-sections from upper slopes in the watershed; however, we also had access to data from increment cores collected in an adjacent old-growth area as part of an earlier climatological study. We compared tree-ring measurements in this climate collection (CC) with cross-section data from the fire history collection (FHC) to confirm the occurrence and timing of gap dynamics, and also to test for differences between the collection types.

Methods

Study area description

This study was conducted in Big Everidge Hollow (BEH), a 52-ha watershed within the Lilley Cornett Woods Appalachian Research Station (LCW; 37°05′ N, 83°00′ W) on the Cumberland Plateau in southeastern Kentucky, USA (Martin 1975). The climate at the study site was temperate humid continental with warm summers, cool winters and no distinct dry season (Trewartha 1968). Mean annual precipitation and temperature were 113 cm and 13 °C, respectively (Hill 1976). Elevation in the study site ranged from 320 to 600 m a.s.l. with a mean slope of 55% (Muller 1982). There was no evidence of commercial timber cutting or significant damage from ice glaze or severe winds in BEH (R. Watts, pers. obs.).

This project represents an extension of a long-term ecological analysis of the site (e.g. Muller 1982; McEwan & Muller 2011; Chapman & McEwan 2012). Decadal woody species inventories have been ongoing since 1975 (Martin 1975; Muller 1982), and coarse woody debris, vegetation–site relationships of woody species and patterns of overstorey dynamics have been previously described (e.g. Muller 2003; McEwan et al. 2005; McEwan & Muller 2006).

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Upper slopes, and mid-slopes on south-facing aspects, have been shown to be sites of oak dominance, where species such as *Quercus alba, Quercus montana* and *Quercus velutina* intermingle with hickories (e.g. *Carya ovata, Carya tomentosa*) and a mix of other species (McEwan & Muller 2006). Mid-slopes are dominated by 'mixed mesophytic' vegetation (Braun 1950) while lower slopes are dominated by *Tsuga canadensis* and *Fagus grandifolia* (McEwan & Muller 2006). On the oak-dominated upper slopes, maples (*A. rubrum* and *A. saccharum*) have been shown to have substantially higher densities than oaks in sub-canopy strata (Chapman & McEwan 2012). Invasive species were present at exceedingly low densities at the time of this sampling and had not impacted dynamics in the system (Chapman et al. 2012). Taxonomic nomenclature follows Jones (2005).

Sample collection, lab methods and sample dating procedure

During the summer of 2009, samples of large downed trees were opportunistically collected within BEH on oak-dominated upper slopes. Live tree sampling was not allowed due to the quality and uniqueness of the old-growth forest. Fire history samples were collected from 41 trees through ca. 25 ha across the upper slopes of the watershed including north-, south- and east- facing slopes in elevations ranging from ca. 450 to 600 m a.s.l. The most frequent species in the sample collection were *Q. montana* (n = 12) and *Q. alba* (n = 10), and an additional six samples were sound enough for data collection but could not be classified below the white oak subgroup Leucobalanus (n = 6). Samples were also collected from *Q. velutina* (n = 3), and two stems were classified into the red oak subgroup Erythrobalanus without being identified to species (n = 2). Additional samples were collected from two hickory (*Carya* sp.; n = 2) stems not identified to species. In total, six stems were collected but were unusable for data collection (e.g. too extensively decayed for data collection; n = 6) and were discarded, leaving a total of 35 stems in the fire history analysis. One *Q. velutina* and one *Q. montana* sample were datable and were used in the fire history analysis, but ring measurements were not made because of distortions and decay, leaving 33 samples for disturbance analyses. In general, because we collected cross-sections near the tree base, and we did not collect samples that were badly decayed; the inner ring dates presented in this paper are from actual pith dates.

All samples were processed following typical dendrochronology methods (Stokes & Smiley 1968). Each ring was dated using the 'list' method (Yamaguchi 1991). Annual increments were then measured to the nearest 0.001 mm using a VELMEX unislide stage (VELMEX Inc., Bloomfield, NY, USA) with at least two radii measured within each cross-section when possible. Occasionally four radii were measured. Increasing the number of radii sampled per tree can improve reconstructions of disturbance history (Copenheaver et al. 2009). The accuracy of assigned dates was then verified, first by comparing radii within each tree, and then within each species using the program COFECHA (Holmes 1983). Flagged segments were examined under the microscope to ensure dating accuracy. Finally, dating was checked vs existing tree-ring data for Lilley Cornett Woods (see below) and in-house data including series of old-growth *Q. alba* and *Q. montana* from nearby Blanton Forest (Pederson et al. 2012). Inter-series correlation of the 67 measured series within the fire history collection was 0.505 ($P < 0.001$). Inter-series correlations ranged from 0.427 for the combined series from the *Quercus* subgroup Erythrobalanus to 0.511 for the unidentifiable trees falling into the *Quercus* subgroup Leucobalanus. Composite master series of each group (*Q. alba*, *Q. montana*, *Quercus* subgroup Erythrobalanus, *Quercus* subgroup Leucobalanus and *Carya* sp.) were correlated against pre-existing species-appropriate residual chronologies in or near LCW. All series presented here are significantly correlated with one another and prior collections from old-growth forests, except for the *Carya* sp. collection (of two trees) vs the two Blanton Forest (Kentucky) chronologies (Table S1). Dating in each group prior ca. 1700 was constrained by the heavy suppression experienced by sampled trees from that era and low replication.

Determination of fire history

All wound events were dated and seasonality of wounding was noted. Wound data were entered into the fire scar analysis software FHX2 (Grissino-Mayer 2001); a fire history diagram was generated and summary statistics were calculated. The mean number of years between fires is presented excluding the years after 1954 due to fact that recent decades are during the fire suppression era.

Reconstruction of canopy disturbance history

Tree-ring methods were used for canopy disturbance reconstruction (Lorimer 1980, 1985; Lorimer & Frelich 1989). In particular, we used ring-width intervals of 15 yrs and thresholds of growth increases of at least 50% to infer canopy disturbance events (McEwan & McCarthy 2008). These thresholds, which are generally more conservative than the method developed by Lorimer & Frelich (1989), were used to reduce the number of potential false-positive growth release detections. The threshold for a 'minor release' was a growth release of 50–99.99% over a 15-yr period vs the prior 15-yr period. The major release thresh-

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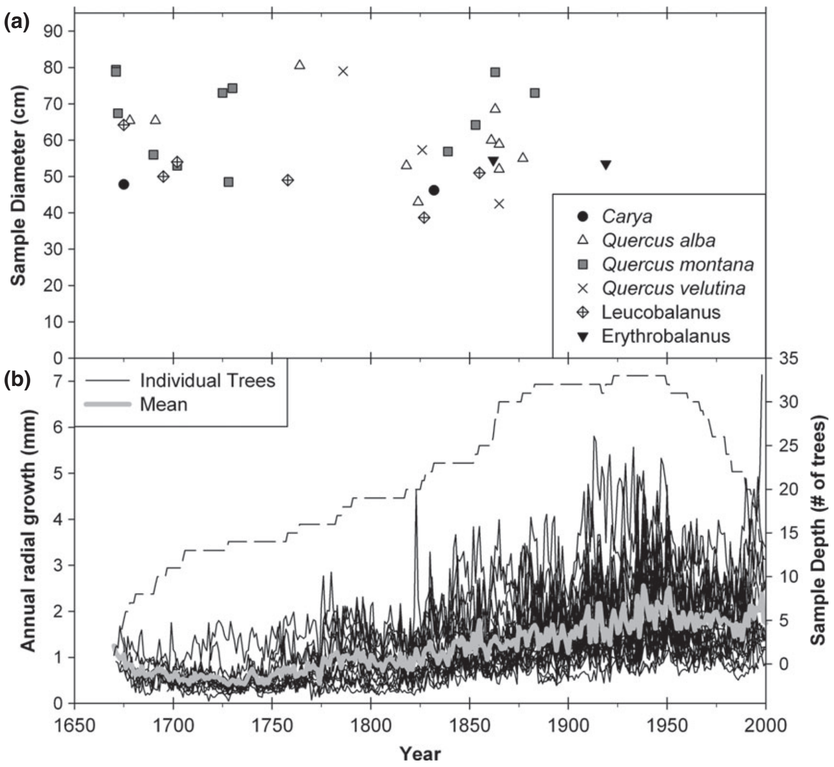

Fig. 1. Diameter and initiation dates **(a)** and annual growth **(b)** of tree cross-sections collected in an old-growth temperate deciduous forest, central Appalachian Mountains, USA.

old, likely to be canopy accession events (Lorimer & Frelich 1989), was set at ≥100%. Following Fraver & White (2005), mathematically determined releases at low radial growth, intervals when radial increment was <0.5 mm·yr^{-1}, were not counted as a release to reduce the risk of potential false-positive growth release events. Detected events are presented at the annual time step as all series were cross-dated and the lag between disturbance and growth response is often 2 yrs or less (Rentch et al. 2002). To verify patterns of canopy disturbance in BEH, a collection of *Q. alba* ring widths from 26 trees in Lilley Cornett Woods was downloaded from the International Tree-ring Databank (ITRDB; Cook 1982). Similar to the fire history collection, this collection targeted large, downed trees from old-growth forest. The main differences between the two collections are that the tree samples collected by E. Cook and P. Sheppard in 1983 were cored for characteristics of great age in another part of Lilley Cornett Woods for an investigation of regional drought (hereafter CC for 'Climate Collection').

Test for drought association

We assessed the relationship between drought, as estimated by a reconstruction of the Palmer Drought Severity Index (PDSI; Palmer 1965), and both fire and canopy release. Data were extracted from a 0.5°× 0.5 version (2a) of the North American Drought Atlas (Cook et al. 1999, 2004; Cook 2008). For this study, 16 grid points within a 2° square box (36.00°–38.00° N, 81.50°–83.50° W) were averaged to create a single time series of reconstructed drought for the LCW region. The relationship between fire and drought was assessed using Superposed Epoch Analysis comparing fire years and reconstructed drought (see below).

Results

The earliest tree-ring date for the FHC was 1669, and 16 of the samples initiated before 1800 (Fig. 1a). The median inner ring date in this collection was 1782. Only three of the samples initiated after 1870, and the most recent inner ring date is 1918 (Fig. 1a). Sample diameters ranged from ca. 40–80 cm. There was no statistically discernible relationship between sample diameter (tree size) and initiation date (tree age) in these samples (Fig. 1a; line not shown: $P = 0.17$, $r^2 = 0.054$). Considering all stems, and all years, tree-ring width ranged from ca. <1 to 5 mm, and mean tree growth for all samples ranged generally between 1 to 2 mm (Fig. 1b). There was some indication that ring widths increased consistently over the life span of the trees sampled here (grey line, Fig. 1b). Individual series exhibited long-term growth patterns characterized by suppression and growth pulses. For example, the oldest tree in the FHC was a *Quercus montana* (top panel, Fig. 2) that exhibited ca. 100 yrs of suppression followed by a growth release that resulted in a step change increase in growth rate. The overall pattern, as evidenced by individual series (Fig. 2) and the mean for all samples (Fig. 1b), suggests that maximum growth rates for these trees were being achieved near the end of the chronology, after the trees were ca. 200 yrs old.

A total of 33 fire scars representing 29 fire years were identified from 21 samples (60%) while 14 samples did not contain fire scars (top panel, Fig. 3). Years with fire scars on more than one tree were 1948 (*n* = 2), 1880 (*n* = 3) and 1820 (*n* = 2). Across all dates, the mean number of years between a detected fire was 9.3 (SD of the mean: 10.9). The composite fire record suggests that the study site experienced relatively infrequent fires in the pre-settlement period followed by an increase in burn frequency ca. 1870–1950 (Fig. 3). Only four fires were detected in the ca. 100 yrs from the beginning of the chronology to 1775 (Fig. 3).

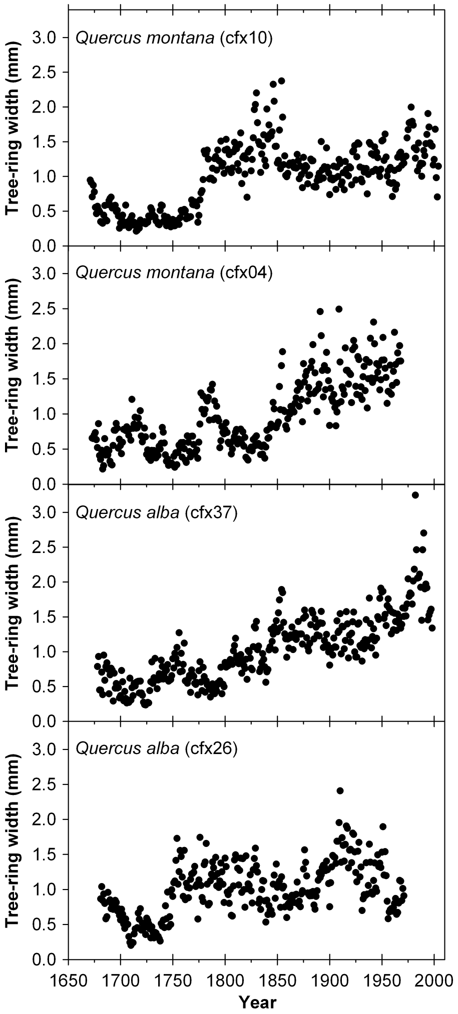

Fig. 2. Long-term growth patterns of the four oldest trees sampled as part of a fire history collection made in an old-growth temperate deciduous forest, central Appalachian Mountains, USA.

In the FHC, a total of 70 growth releases were found in 58 different years, and 31 of the 33 trees (94%) exhibited at least one growth release (bottom panel, Fig. 3). The mean number of years between detected release events was 5.2 yrs (SD: 4.7 yrs). Median release per tree was two with a maximum of five growth releases in a single tree. Growth releases were relatively evenly distributed throughout the chronology (bottom panel, Fig. 3). One important feature of the FHC release event record is that over the last 100 yrs of the chronology, the number of detected releases in the oldest trees is far fewer than those in younger trees (bottom panel, Fig. 3). Of the 19 releases during the 1900s, 14 come from trees <200 yrs and only five are found in the trees >200 yrs (Fig. 3).

In the CC, a total of 42 growth releases were found in 37 different years, and 20 of the 21 trees (95%) exhibited at least one growth release. Similar to the fire collection, median release per tree was two with a maximum of four growth releases in a single tree. The earliest first date of major growth release was similar in both collections (1718 in the fire collection vs 1719 in the dendroclimatic collection). The collections were similar in years between the inner ring and (1) the first major growth release; (2) the last major growth release; and (3) last growth release (Table S2).

Evidence of a temporal link between fire and growth release was circumstantial and weak. We found growth releases in the late 1700s and early 1800s during long periods where we did not detect fires, and also growth releases after 1954 when there were no fires (Fig. 3). To compare these two disturbance processes more specifically we trimmed both chronologies to exclude the 15 yrs prior to 1686, during which time it would be mathematically impossible to detect release due to our methodology, and after 1954, as this time period is during the era of fire suppression. During the intervening 271 yrs, there were 28 yrs in which a fire was detected and 51 yrs during which a growth release was detected, yielding 75 total 'event years'. During this time period, there were only 4 yrs (5.3%) when there was both a fire and release event detected. To examine the possibility that fire could create a release after a time lag, we sought instances of release in the 3 yrs following each fire. We detected 17 (out of 51 possible) release years in the 3 yrs following a fire, suggesting that only 33% of releases in our record have some possibility of a temporal link with fire occurrence.

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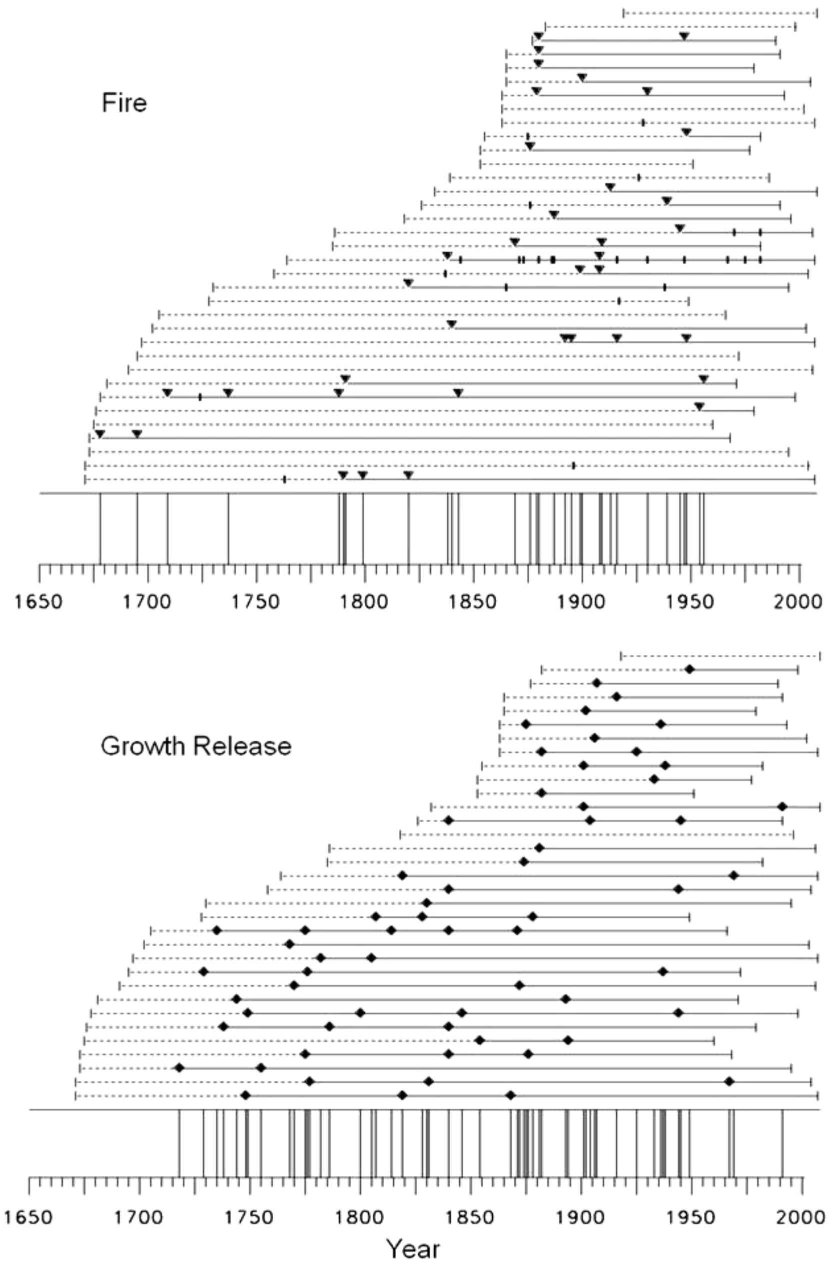

Fig. 3. Fire history and growth release from trees in an old-growth temperate deciduous forest, central Appalachian Mountains, USA. Horizontal lines represent the individual tree chronologies. In top panel, triangles indicate fire scars and dashes represent non-fire wound events. In bottom panel, diamonds represent release events (both major and minor releases). Lines are dotted prior to the occurrence of an event and solid afterward. A horizontal line below the individual tree lines represents a composite for the site and lines connecting these to the chronology (at the bottom of the panel) indicate the year of an event (either fire or release).

We did not find an overall statistically significant relationship linking fire and drought (Fig. 4). The long-term mean (±SE) reconstructed PDSI value for years without fire (-0.014 ± 0.07) was not statistically different from that of fire years (-0.13 ± 0.25). Superposed Epoch Analysis did not reveal a significant association between fire and drought the year of the fire ($P = 0.76$), the prior year ($P = 0.11$) or any of the preceding 10 yrs ($P > 0.1$ for all years). There were instances of apparent association between fire and drought. In particular, the years 1820 and 1880, which were years of multiple scars, were also 1 yr after a major drought (Fig. 4).

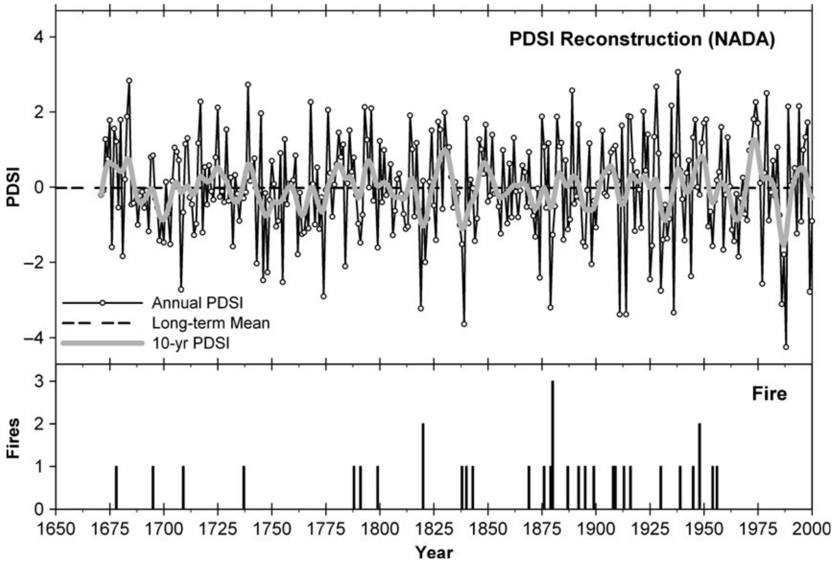

Fig. 4. Climate and fire in an old-growth temperate deciduous forest, central Appalachian Mountains, USA. Palmer Drought Severity Index (PDSI) indicates moisture levels on the landscape where negative values are dry years. Fire histograms (bottom panel) represent the number of trees recording a fire event.

Discussion

Development of temporally deep fire histories for deciduous forests in eastern North America provides an important context for management and a baseline for understanding long-term vegetation dynamics. Long and extensive fire histories have been developed in the Ozark and Ouachita Mountains and along the broader prairie–forest boundary in central North America (e.g. Cutter & Guyette 1994; Guyette et al. 2002; Guyette & Spetich 2003). In the central Appalachian region, some dendroecological work has connected fire and forest dynamics, especially in pine stands (Mann et al. 1994; Aldrich et al. 2010), and post-settlement fire history is well-developed in some areas (Lafon et al. 2005; McEwan et al. 2007; Hessl et al. 2011). Temporally deep fire history has been derived from charcoal in pollen and soil cores that clearly demonstrates fire was present in these systems for thousands of years (Davis 1969; Clark & Royall 1996; Parshall & Foster 2003; Hart et al. 2008; Fesenmyer & Christensen 2010). Despite this progress, annually resolved fire histories from deciduous forests in the centuries just prior to Euro-American settlement are relatively rare.

In our old-growth study site, fire was detected over most of the 350-yr chronology. This finding supports the idea of fire as an important disturbance process in Appalachian oak forests (e.g. Abrams 1992; Brose et al. 2001; Nowacki & Abrams 2008). We hypothesized (H_1) that fire would be a relatively constant factor in this forest except for recent decades where fire suppression was in force. The disappearance of fire near the end of our timeline (1950–Present) was obvious and has been generally detected in forests of eastern North America (McEwan et al. 2007). We detected many fewer fires in the 1700s and early 1800s than in the period from 1875 to 1950. Studies conducted in deciduous forests that have access to fire scars from prior to 1850 largely support these findings. For instance, working in southern Indiana, Guyette et al. (2003) found an absence of fire in the landscape from ca. 1675 to 1800, which was followed by a period of frequent fires, particularly from 1880 to 1930. Working in the Boston Mountains of Arkansas, Guyette et al. (2006) found a longer return interval (34.7 yrs) from ca. 1605 to 1810, followed by a much shorter return interval (around 2 yrs) from 1810 up through 1920. Hessl et al. (2011) studied fire scars from three species in West Virginia with trees dating to ca. 1780 and reported an absence of fire on the landscape until 1868. An increase in the frequency of fire as a landscape process has been attributed to settlement activities by Euro-Americans (Guyette et al. 2002). Drought and fire occurrence (H_2) were not statistically linked in our data set. This lack of coherence between fire and drought was also found by McEwan et al. (2007) who posited that the fire regime post-1850 is related to settlement and land development activity, such that ignition pressures overwhelm the climatic pattern.

There are at least two important, and countervailing, caveats associated with our data set. The first is that trees are imperfect recorders of fire history. McEwan et al. (2007) found that oak trees were excellent recorders of fire if there were several years between fires, but noted a ‘blind spot’ relative to fires that occur in concurrent years. All dendrochronological records suffer from the 'fading record' phenomenon, in which the record becomes increasingly less reliable from the present into the past. For instance, older fires may not have been recorded because (1) not all trees are scarred by any given fire; and (2) fires may have passed through the stand scarring trees that have since fallen and decayed and are, thus, unavailable for sampling. In fact, the fading record phenomenon could help explain why relatively few fires were detected early in our chronology. For these reasons, the fire history presented here could be considered a baseline minimum of fire occurrence.

The second caveat in our fire history reconstruction is that, for oak trees, wounds that are caused by fire scars are difficult to distinguish from wounds caused by other sources of injury (falling branches, animal activity, etc.; McEwan et al. 2007). In this study, we only include wounds that have the characteristics of fire scars as indicated in McEwan et al. (2007); however, because fire-related wounds on oak trees are most often caused by heating of the cambium, but not combustion of the bark, these wounds did not include charcoal and are technically impossible to differentiate from other kinds of wounds. In fact, McEwan et al. (2007) suggest that fire history reconstruction from scars that do not contain charcoal should require a minimum of two wounds in a given year to identify a fire year. If we had applied the two scar per year 'filtering' to our data set we would have only identified three fires in the stand over the nearly 350 yrs represented in our chronology – with fire absent from the forest until Euro-Americans were already involved in settlement activity in the region (1820). For these reasons, the fire history presented here could be considered a vast overestimation of the actual occurrence of fire in the stand. This uncertainty is an unavoidable feature of this kind of reconstruction. The more conservative approach of requiring two scars/year has not been generally adopted in the field, thus we defaulted to standard data presentation and interpretation.

Release events occurred throughout the chronology, consistent with gap-phase-dominated forests, and some instances of stand-wide changes in growth were associated with release events. One important pattern we found in the release chronology was an apparent decrease in release detection in older trees. The FHC collection included a range of tree ages, and we note that, particularly over the last 100 yrs, the releases detected in our chronology were generally in younger trees (Fig. 3). Canopy trees, by definition, have achieved a full-light condition for at least a substantial portion of their leaf mass and are less sensitive to reductions in competition; thus these trees are less likely to respond to, and record, a disturbance (Nowacki & Abrams 1997; Rentch et al. 2002). This is an important finding for studies that focus on canopy disturbance using targeted tree collections like those from the International Tree-ring Data Bank. Due to the lack of sensitivity in disturbance detection in canopy trees, using targeted collections of samples from trees that have long-since attained canopy status could be subject to false-negative bias.

Individual tree mortality and the subsequent formation of canopy gaps are thought to be fundamental to the ecology of old-growth forests (Romme & Martin 1982; Runkle 1982; Runkle & Yetter 1987; Wright et al. 2003; Buchanan & Hart 2012). Our data suggest that gap creation and capture were relatively even throughout the 300+ yr time span of this study. We also found instances of synchronicity in gap occurrence. For instance, four of the five times when average ring width abruptly increases across the landscape, ca. 1730s–early 1740s, late 1770s, late 1820s, 1840s and ca. 1910, we also detected release events. Interestingly, we found that many individual trees, and also the population as a whole, exhibit patterns wherein tree growth increases markedly and then remains elevated for centuries (examples shown in Fig. 2). The 1770s event, most notably, is a period of intense canopy disturbance and inferred canopy accession which matches findings from other regional forests (Lorimer 1980).

In this study we have simultaneously assessed gap dynamics and fire over a long period (ca. 350 yrs) using annually resolved data in a deciduous forest. Although impossible for us to experimentally verify, it is highly probable that these processes interact, and synergies between the two may be a key feature of long-term forest dynamics. Fires in oak forests are generally low intensity with very little mortality of overstorey trees associated with any particular fire and little change to the understorey light environment (Chiang et al. 2008). Even so, fires could play a critical role in selectively filtering understorey seedlings, which then access the forest canopy via the patches of high light levels associated with canopy gaps generated by natural disturbance (e.g. windthrow, disease, insects, etc.). Experimental work of Hutchinson et al. (2012) demonstrates this kind of interaction. They show that multiple prescribed fires result in an altered tree regeneration layer, where oaks (*Quercus* spp.), hickories (*Carya* spp.) and sassafras (*Sassafras albidum* L.) are promoted and are then able to respond to canopy gaps caused by tree mortality (Hutchinson et al. 2012). This interaction of disturbance processes provides an opportunity for management application and is likely a key component of the long-term ecology of deciduous forests. A long-term fire regime, such as is suggested by our data, coupled with gap formation and capture, could synergistically drive long-term dominance in oak forests. One important advance suggested by our data is the idea of temporal clustering of gaps, and simultaneous canopy accession, occurring in our site over a time frame that matches findings in other forests (Lorimer 1980). We propose that historical interactions between gap formation and fire occurrence could drive landscape-scale canopy accession of fire-tolerant species which then maintain dominance for centuries (McEwan et al. 2011) – a process that would support Watt's formulation (1947) and could provide new opportunities for understanding long-term dynamics in deciduous forests.

Acknowledgements

We would like to express our thanks to the Division of Natural Areas at Eastern Kentucky University for allowing access to the research site, and student support that allowed for collection of the fire history samples. Thanks to Justin Price for assistance with sample collection and processing, and Julia Chapman for assistance with data analysis. Comments on the manuscript were provided by members of the McEwan lab group at the University of Dayton, including Julia Chapman, Jessica Davis, Charlie Jackson, Ellen Comes and Rachel McNeish. The manuscript was also greatly improved by editorial comments from Hugo Asselin, Christian Messier, Christian Zang and one anonymous reviewer. This is contribution number # 40 from the Lilley Cornett Woods Appalachian Ecological Research Station, Eastern Kentucky University.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Correlation matrix of residual chronologies from new fire collections by species or subgenus versus residual chronologies from local and nearby old-growth forest chronologies.

Table S2. Comparison of growth-release structure between fire ($n = 33$) and dendroclimatological ($n = 21$) collections at LCW.

Doi: 10.1111/avsc.12060

Supplemental Table 1.

Correlation matrix of residual chronologies from new fire collections by species or subgenus versus residual chronologies from local and nearby old-growth forest chronologies. Significant correlations at 99% confidence level r ≥ 0.328 are italicized. Only the *Carya* collection, composed of only two trees, is not consistently and significantly correlated to other chronologies. Results indicate, however, these trees are correct as dated. The Erythrobalanus collection was compared to D. Stahle and M. Therrell's *Quercus velutina* record from Lynn Hollow, TN (available from the International Tree-ring Databank; ITRDB). The two series are significantly correlated (r = 0.400). Blan = Blanton Forest Kentucky; Cook = *Q. alba* chronology from Lilley Cornett Woods collected by E. Cook (1982), from the ITRDB. QUAL = *Q. alba*; QUMO = *Q. montana*; Eury = *Q.* subgenus Erythrobalanus; Leuco = *Q.* subgenus Leucobalanus.

	Blan QUAL	Blan QUMO	Cook QUAL	Lilley QUAL	Lilley QUMO	Lilley Eury	Lilley Leuco	Lilley Carya
Blan QUAL	-							
Blan QUMO	*0.651*	-						
Cook QUAL	*0.529*	*0.445*	-					
Lilley QUAL	*0.484*	*0.439*	*0.587*	-				
Lilley QUMO	*0.436*	*0.457*	*0.557*	*0.643*	-			
Lilley Eury	*0.417*	*0.486*	*0.606*	*0.595*	*0.595*	-		
Lilley Leuco	*0.369*	*0.426*	*0.588*	*0.592*	*0.553*	*0.569*	-	
Lilley Carya	0.258	0.300	*0.385*	*0.329*	*0.376*	*0.458*	*0.361*	-

Supplemental Table 2.

Comparison of growth-release structure between fire (*n* = 33) and dendroclimatological (*n* = 21) collections at LCW.

	FHC	CC	FHC	CC	FHC	CC
	Median		Min		Max	
Inner Ring Date	1782	1689	1669	1659	1919	1734
Date of 1st Accession Event	1782	1776	1718	1719	1933	1909
Date of Last Accession Event	1840	1776	1718	1719	1992	1909
Last Growth Release	1914	1817	1755	1737	1992	1909
Years Between Inner Ring Date and 1st Accession Event	69	86	32	15	137	186
Years Between Inner Ring Date and Last Accession Event	82	86	32	29	298	186
Years After Inner Ring Date and Last Event	111	111	32	29	298	230

Alteration of North American Streams by Beaver
Author(s): Robert J. Naiman, Carol A. Johnston, James C. Kelley
Source: *BioScience*, Vol. 38, No. 11, How Animals Shape Their Ecosystems, (Dec., 1988), pp. 753-762
Published by: American Institute of Biological Sciences
Stable URL: http://www.jstor.org/stable/1310784

Alteration of North American Streams by Beaver

The structure and dynamics of streams are changing as beaver recolonize their historic habitat

Robert J. Naiman, Carol A. Johnston, and James C. Kelley

Beaver (*Castor canadensis*) provide a striking example of how animals influence ecosystem structure and dynamics in a hierarchical fashion. Initially beaver modify stream morphology and hydrology by cutting wood and building dams. These activities retain sediment and organic matter in the channel, create and maintain wetlands, modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and animal community composition and diversity (Naiman and Melillo 1984, Naiman et al. 1986). In addition to their importance at the ecosystem level, these effects have a significant impact on the landscape and must be interpreted over broad spatial and temporal scales as beaver population dynamics shift in response to disturbance, food supply, disease, and predation.

Although once more prevalent than they are today, beaver-induced alterations to drainage networks are not localized or unusual. Where beaver remain largely free of management or trapping, their activities may influence a large proportion of streams in a drainage network; and these alterations may remain as part of the landscape for centuries (Ives 1942, Johnston and Naiman 1987, Rudemann and Schoonmaker 1938).

We see a complex pattern that may involve formation of marshes, bogs, and forested wetlands

The objectives of this article are to briefly summarize the history of beaver in North America, then describe some of the ecosystem-level responses of streams to beaver-induced alterations and, finally, to describe beaver-induced changes in the landscape that take place over broad spatial and temporal scales. Our research has been conducted in Quebec, Minnesota, Montana, and Alaska, and it should be representative of northern regions.

History of beaver in North America

Before the arrival of Europeans in North America, the beaver population was estimated to be 60–400 million individuals (Seton 1929), with a geographic range of about 15 million km^2 (Jenkins and Busher 1979). Beaver were found in nearly all aquatic habitats from the arctic tundra to the deserts of northern Mexico. Historical records provide a chronology of their demise in New England, where nearly every body of water was occupied by beaver prior to European settlement (Rudemann and Schoonmaker 1938). In the early 17th century extensive removal began in North America with more than 10,000 beaver per year taken for the fur trade in Connecticut and Massachusetts between 1620 and 1630 (Moloney 1967). From 1630 to 1640, approximately 80,000 per year were taken from the Hudson River and western New York (Hays 1871). As the eastern beaver population declined, expeditions to the West (1800–1850) often were made solely for the purpose of discovering new trapping areas (Cline 1974). By 1900, continued exploitation left beaver almost extinct in North America (Jenkins and Busher 1979, Johnson and Chance 1974). Concomitantly, since 1834, approximately 195,000–260,000 km^2 of US wetlands have been converted to dry land (Shaw and Fredine 1971). Undoubtedly, a large proportion of these wetlands was beaver habitat.

Today, with a relative absence of predators, laws regulating trapping, and an abundance of forage and habitat, the beaver population is increasing rapidly. The current population is thought to be between 6 and 12 million individuals. Yet, for most of North America, the present population represents only a small fraction of earlier numbers. Many attributes of stream ecosystems were changed by beaver removal long before mod-

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By building dams, beaver appear to moderate stream discharge regimes.

ern limnological research began. Therefore, much of our understanding of stream ecosystems is derived from sites that lack the influence of this previously abundant and ecologically important herbivore.

Stream channel alterations

Beaver primarily alter the stream channel by impounding water. Their ability to build dams and expand the wetted area increases the amount of beaver habitat available, often increases their food supply, and offers protection from predators (primarily wolf, *Canis lupus*). This ability comes, in part, from their unique habit of cutting mature trees for food and building material. Although several tree species may be used in construction, beaver prefer aspen (*Populus*) for food.[1]

Dam-building changes the annual stream discharge regime, decreases current velocity, gives the channel gradient a stair-step profile, expands the area of flooded soils, and increases the retention of sediment and organic matter (Figure 1). Most dams occur on first- through fourth-order streams, because dams in larger streams are often removed by freshets.

The frequency of dams in first- to fourth-order streams may be substantial, especially if the topography and the beaver food supply are adequate. In Quebec, along the North Shore of the Gulf of St. Lawrence, the dam frequency ranges from 8.6 to 16.0 dams/km and averages 10.6 dams/km (Naiman et al. 1986). On the 294-square-kilometer Kabetogama Peninsula in northern Minnesota the frequency ranges from 2.0 to 3.9 dams/km, with an average of 2.5 dams/km. This frequency of dams is reasonable when one considers that the population density may reach 3 colonies/km^2, with typical values in favorable habitat ranging between 0.4 and 0.8 colonies/km^2 (Aleksiuk 1968, Bergerud and Miller 1977, Voigt et al. 1976). Each colony contains, on average, four to eight beaver (Jenkins and Busher 1979).

Every dam has the potential to retain a substantial amount of sediment depending upon its size and geomorphic position in the channel. We have measured several instances where a small dam with 4–18 m^3 of wood was able to retain 2000–6500 m^3 of sediment (Naiman et al. 1986). We refer to accumulations of water and sediment in the stream channel as patch bodies (Johnston and Naiman 1987); that is, volumetric landscape units that have surficial boundaries with upper and lower strata, and lateral boundaries with adjacent patches within the same stratum (Figure 2). These expanded patch bodies produced by beaver are important because they provide the large reserve of carbon and nutrients needed for ecosystem stability.

Patch bodies created by beaver impoundments include the beaver pond, the aerobic soil beneath the pond, and the underlying anaerobic soil. These patch bodies contain some of the same basic physical structures and processes as patch bodies in the orig-

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[1] C. A. Johnston and R. J. Naiman, 1988, manuscript submitted.

Figure 1. Beaver build primary dams in locations that will pond a maximum amount of water to insure an abundant food supply. This dam in Voyageurs National Park, Minnesota, is about 80 m long and 2 m high, hydrologically influencing about 1 km^2.

inal stream channel, but the relative size and, thus, the relative importance of specific processes are different. This can, for instance, be seen in invertebrate community structure, in carbon budgets, and in ecosystem-level efficiencies calculated for streams and ponds in Quebec (McDowell and Naiman 1986, Naiman et al. 1986).

Beaver activities influence invertebrate community structure by replacing running-water taxa by pond taxa (primarily a response to finer sediments and a decrease in current speed). Beaver activities also influence community function by increasing the absolute importance of collectors and predators, while decreasing the relative importance of shredders and scrapers in impounded sites (McDowell and Naiman 1986). Running-water communities that are normally dominated by blackflies, Tanytarsini midges, scraping mayflies, and net spinning caddisflies are replaced in impoundments by Tanypodinae and Chironomini midges, predaceous dragonflies, tubificid worms, and filtering clams. Total density and biomass in ponds may be two to five times greater than those of riffle sites, ranging from 11,000 to 73,000 organisms/m^2 and from 1 to 11 g/m^2, depending upon the season.

Despite these differences, the total number of species in beaver ponds appear to be similar to those in the natural stream channel. Invertebrate communities in beaver impoundments, however, resemble those in slow-water habitats of larger order streams (e.g., the alcoves and pools).[2] Therefore, invertebrate communities in the beaver impoundments may not be unique within the drainage network but likely represent unparalleled assemblages in small streams (McDowell and Naiman 1986).

Beaver-induced stream channel alterations also change the way materials flow through streams. Beaver activities substantially change the absolute amounts of carbon inputs, standing stock, and outputs (Table 1). In Beaver Creek, Quebec, riffles received a total carbon input of 220 g $C \cdot m^{-2} \cdot yr^{-1}$ as compared to 65 g $C \cdot m^{-2} \cdot yr^{-1}$ for the beaver pond. Yet, the standing stock (4400 g C/m^2 versus 12,000 g C/m^2) and total carbon output (51 versus 121 g $C \cdot m^{-2} \cdot yr^{-1}$ were much less in the riffle than in the beaver pond. Since, in this case, beaver transformed a one-meter-wide stream into an impoundment averaging 7 m in width, the impact of beaver on the total carbon budget per unit of channel length would be seven times the values given per unit area in Table 1. Thus, total carbon inputs per unit

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[2] S. R. Reice and R. J. Naiman, 1988, unpublished data.

length of channel were 48% of those in the pond, the standing stock of carbon in the riffle was only 5% of that in the pond, and the total outputs in the riffle were only 6% of those measured in the pond.

Alterations to the carbon budget are also manifested in ecosystem-level efficiency for the retention and processing of organic carbon (Table 2). This efficiency is reflected in the turnover time for carbon, with the standing stock of carbon in the riffle being replaced every 24 years as compared with 161 years for the pond. The stream metabolism index (SMI), a measure of ecosystem efficiency for the utilization or storage of organic inputs, also demonstrates the pond to be more retentive (SMI of 1.63 as compared with 0.30 for the riffle.) Values of more than 1.00 suggest that organic inputs are being accrued or processed; little material, relative to the amount received, is being transported downstream. These increases in retention and processing are caused by the 80–90% decrease in turnover length and rate of downstream movement of organic carbon in the pond compared with the riffle (Table 2). Together, these data on community composition, carbon cycling, and ecosystem processing efficiency indicate that beaver, by changing the hydrologic regime, substantially alter the character of stream channels when compared with unmodified reaches.

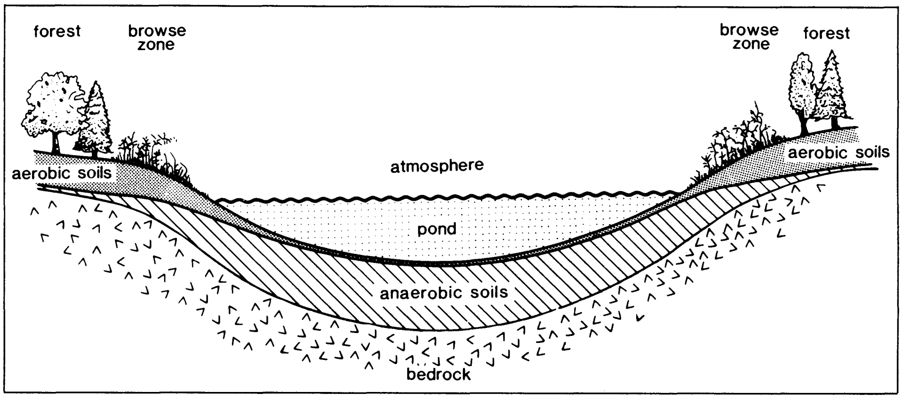

Figure 2. Patch bodies associated with beaver ponds (from Johnston and Naiman 1987). Patch bodies shown are the pond water volume and the volumes of aerobic soils and anaerobic sediments.

Riparian zone alterations

Beaver also have a substantial impact on the structure and productivity of the riparian zone, primarily by cutting trees and shrubs (Jenkins 1980). Beaver are central place foragers (Orians and Pearson 1979) in that they continuously return to their lodge or winter food cache after feeding. In northern regions they annually cut at least a metric ton of wood within approximately 100 m of their pond (Howard 1982, Johnston and Naiman 1987, McGinley and Whitham 1985). Riparian zones dominated by deciduous species preferred by beaver, such as trembling aspen (*Populus tremuloides*), may be virtually clear-cut. The riparian zone initially becomes more open as shrubs (e.g., alder, *Alnus*, and hazel, *Corylus*) and root suckers of aspen become the dominant growth form. Eventually, nonbrowsed species in the understory, such as black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*), may overtop the shrubs and become the dominant streamside vegetation. Occasionally, selective cutting of the aspen releases understory fir and spruce, and no shrub stage occurs.

Table 1. Comparison of mean annual standing stocks and annual fluxes of carbon in a riffle and pond in Beaver Creek, Quebec. Data are from Naiman et al. 1986.

Component	Carbon		Ratio
	Riffle	Pond	Riffle:Pond
INPUT ($g \cdot m^{-2} \cdot yr^{-1}$)			
Precipitation and throughfall	16.9	6.9	2.45
Direct allochthonous	123.1	52.6	2.36
Lateral allochthono	55.8	4.3	12.98
Periphyton production	24.7	1.7	14.53
Total input	220.5	65.1	3.39
STANDING STOCK (g/m^2)			
Water column	2.0	18.0	0.11
Coarse wood	3926.9	3129.2	1.25
CPOM	419.4	5152.0	0.08
FPOM	33.7	3738.8	0.01
Primary producers	0.5	0.1	5.00
Invertebrates	0.4	2.7	0.15
Total standing stock	4382.9	12040.8	0.36
OUTPUTS ($g \cdot m^{-2} \cdot yr^{-1}$)			
Detritus respiration	22.0	111.5	0.20
Autotrophic respiration	28.0	1.6	17.50
Methane evasion	0.5	7.4	0.07
Insect emergence	0.3	0.4	0.75
Total outputs	50.8	120.9	0.42

By initially reducing vegetation height and then altering biomass partitioning, beaver exert a substantial impact on the structure and function of adjacent terrestrial ecosystems and on terrestrial-aquatic interactions. These alterations influence the amount and character of inputs from the uplands to the stream channel, the amount of light reaching the channel, the development of riparian soils through changes in litter quality returned to the soil, and the availability of nutrients in groundwater moving through the riparian zone to the channel (Naiman et al. 1988, Pringle et al. 1988).

A spatial and temporal mosaic

Changes to the stream channel and the riparian zone become especially important when watersheds are considered. It is first necessary to recognize that the ontogeny of a beaver pond, from its formation to its eventual decay and return to an unaltered stream channel, may range from a year to many centuries, with the

Table 2. Processing efficiencies for carbon are compared for a riffle and adjacent beaver pond in Quebec. Calculations are from Naiman et al. 1986.

Parameter	Riffle	Pond	Riffle:Pond
Turnover time (yr)	**24.4**	**160.7**	0.15
Stream metabolism index	0.30	1.63	0.18
Turnover length (km)	8.0	1.2	6.67
Rate of downstream movement (m/d)	0.25	0.03	8.33

pond's physical and chemical characteristics shifting during the aging process. Beaver ponds are a shifting mosaic of environmental conditions, dependent upon pond age and size, successional status, substrate, hydrologic characteristics, and resource inputs.

This shifting mosaic has both spatial and temporal components. Since all ponds along a reach of stream are not identical habitat, the magnitudes or rates of specific ecosystem parameters do not remain spatially constant. The result is a situation where the relative magnitude of an ecosystem parameter varies along the channel (Figure 3a). For example, one pond may be predominantly a bog (due to local hydrology and topography) with one characteristic rate of primary production, another pond may be an emergent marsh with a different rate of primary production, while the connecting riffle has a production rate of the normal second-order stream. Further, since the beaver population will wax and wane (in response to predation, constraints imposed by the food supply, or disease) and ponds will pass through a natural ontogeny (or succession), there will be temporal shifts in the density and diversity of beaver-mediated habitats (Figure 3b). These changes are manifested by alterations to biogeochemical pathways and by alterations to the total watershed budget for specific parameters.

We are currently quantifying the response of a boreal forest landscape to this type of beaver activity on the Kabetogama Peninsula in northern Minnesota. We have been able to document beaver alterations to the hydrology and the vegetation over space and time using eight sets of aerial photographs taken during 46 years (1940–1986), a geographic information system, and information on the number of active colonies since 1958.

Extensive fires and logging after the turn of the century resulted in a large supply of aspen on the peninsula by 1940. In combination with a low density of predatory wolves and more than 300 km of stream channel available for colonization, beaver increased their habitat use from 71 dams in 1940 to 835 dams in 1986. Less than 1% of the peninsula was impounded by beaver in 1940, as compared with 13% in 1986 (Figure 4). Additionally, 12–15% of the uplands in the riparian zone were altered during the same period by beaver browsing.

As the number of beaver impoundments increased, their spatial distribution changed from scattered individual impoundments to a mosaic of contiguous impoundments along entire valleys. Beaver impoundments in 1940 were widely distributed in the landscape (Figure 5). By 1961, subsequent impoundments had been built in waterways connecting these initial foci. After completely impounding the connecting waterways, by 1986 beaver began building extensions on existing ponds. New beaver ponds created by 1961 were significantly larger than those created after 1961,[3] and beaver ponds impounded first tend to have the greatest longevity (Howard and Larson 1985). Altogether, this evidence implies that beaver are selecting optimal pond sites first, then flooding more marginal areas as their population increases and resources are depleted.

A beaver-impounded landscape is thus a mosaic of different vegetation types—due to the dynamic hydrology of beaver ponds, the diversity of preimpoundment vegetation, and the changes caused by beaver foraging in the riparian zone. Using US Fish and Wildlife Service designations (Cowardin et al. 1979), we mapped 32 different classes of wetland vegetation on the Kabetogama Peninsula. Even when generalized to eight different categories, the vegetative pattern is complex (Figure 5). The relative proportion of different vegetation types in beaver impoundments has changed as total impoundment area has increased over time. In 1940, when many of the impoundments appeared to be abandoned, two of the drier vegetation types predominated: bog

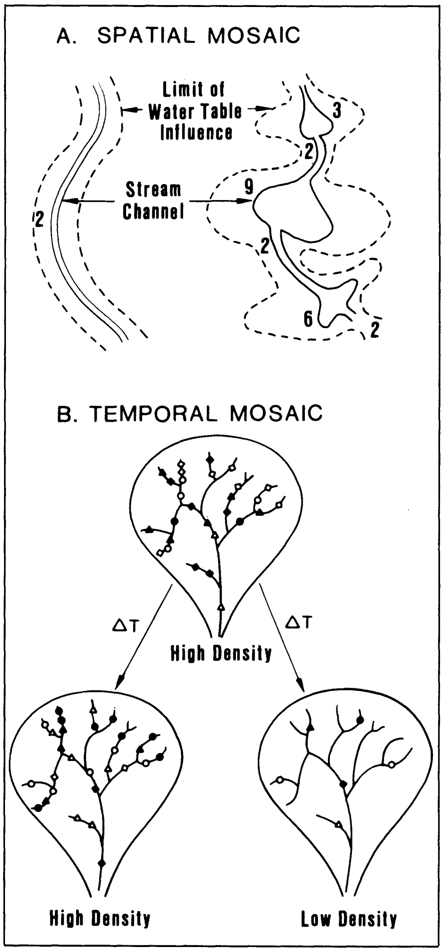

Figure 3. a. The spatial mosaic of beaver-altered habitat changes along stream channels in response to pond age, successional status, and the local environment. In this example, the type of primary production has been shifted from the normal second-order stream to a diversity of habitat types represented by different numbers. **b.** The spatial mosaic in **a** will also shift over time. Where beaver density has remained high (left), the number of ponds has remained the same, but the arrangement in the drainage network has changes as ponds undergo succession. Where the beaver population has decreased (right), both the spatial arrangement and the density of ponds in the drainage network have been affected. Symbols refer to beaver ponds in different successional stages.

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[3] C. A. Johnston and R. J. Naiman, 1988, unpublished data.

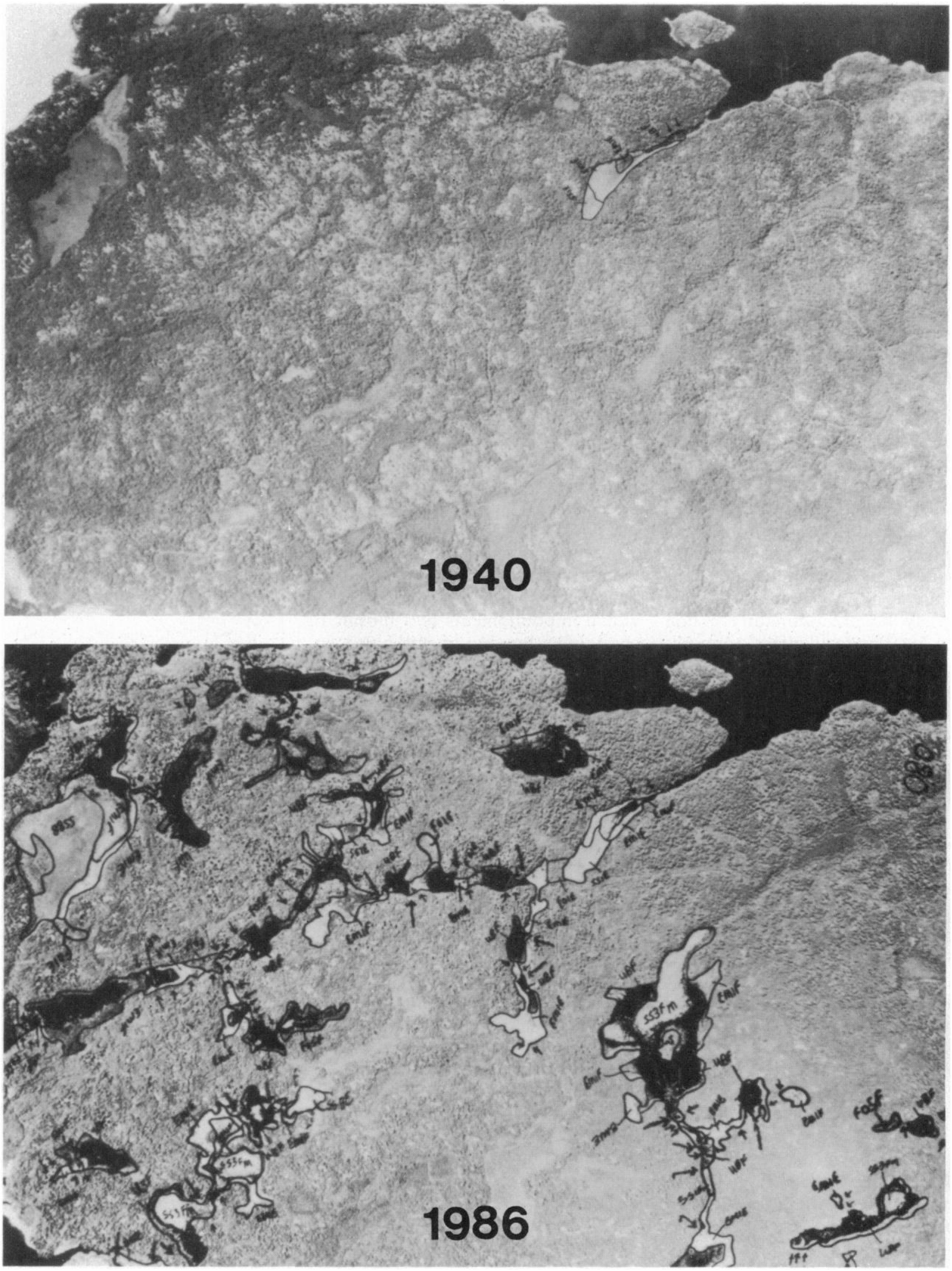

Figure 4. Beaver have had a substantial impact on the drainage network of the Kabetogama Peninsula, Minnesota, between 1940 and 1986. Shown is a representative area. The areas affected by beaver are enclosed by dark lines.

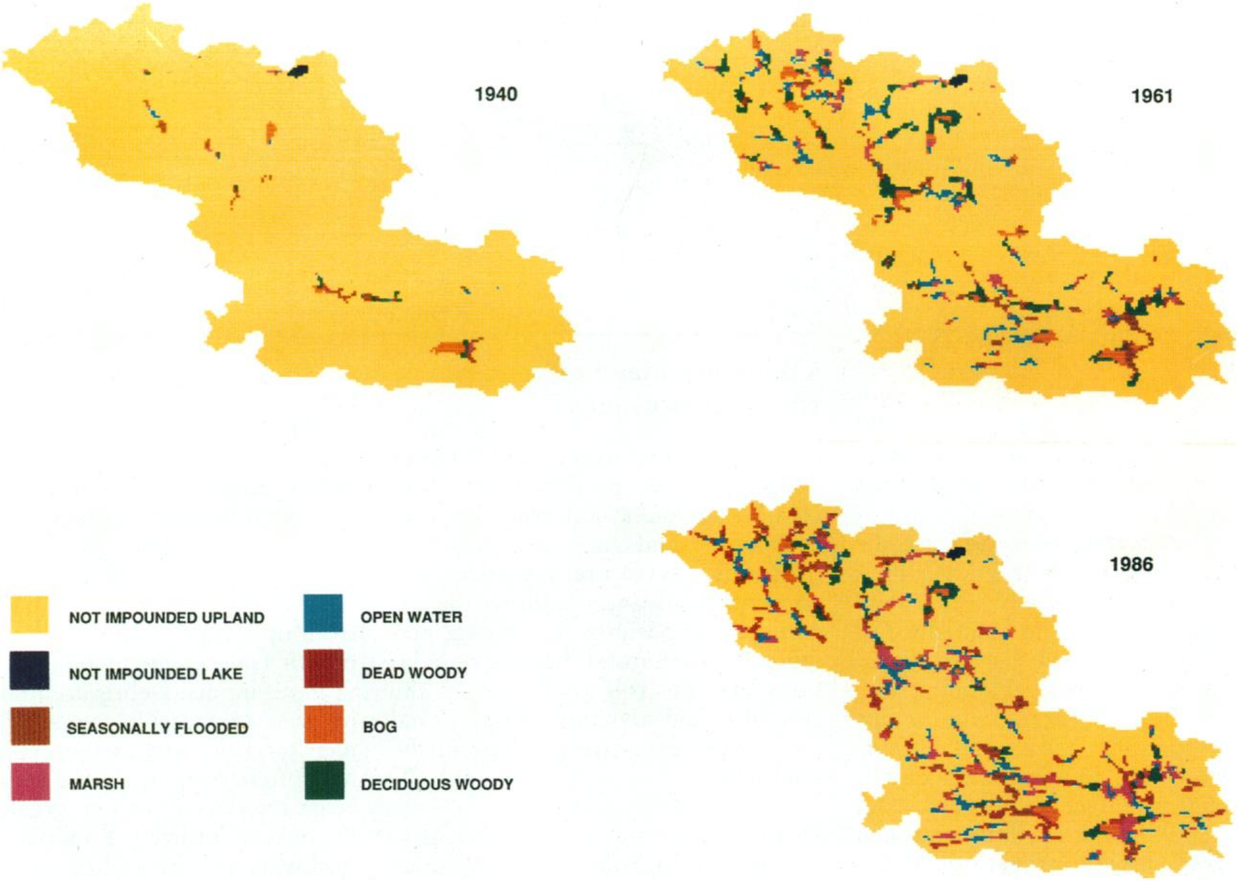

Figure 5. Vegetative change effected by beaver on a 45-square-kilometer watershed on the Kabetogama Peninsula. Colors of individual pixels represent different vegetative community types. Note the increase in dam density between 1940 and 1986, and the shift in vegetative community types over the same period.

and seasonally flooded meadow. By 1986, however, open water was the major impoundment type. The proportion of dead woody vegetation has also increased, because beaver are now flooding more forested areas than they were initially.

Some impoundment types are resistant to change, while others change rapidly as they are flooded and then abandoned by beaver. Bogs impounded by beaver change little over time because of the bog's ability to float up and down with beaver-induced water level changes, so the location and extent of beaver-impounded bog has remained relatively constant since 1961 (Figure 5). The most dynamic categories are open water, marsh, and seasonally flooded meadow, which replace each other in the cycle of beaver-pond abandonment.

The rate of conversion from one impoundment type to another has also changed as the beaver-impounded landscape has matured. In the 1940s, beaver were primarily creating new impoundments rather than altering existing ones. They converted uplands to wet woods, emergent marshes, or ponds (Figure 6). During the 1970s, new impoundments constituted only 9% of the changes, while 25% of the impoundments changed from one vegetation type at the onset of the decade to another by the end. The majority of the impoundments, however, remained in the same vegetative category over the ten-year period.

Accompanying these vegetative and hydrologic trends are changes in the manner and extent to which nitrogen is cycled. We know, for example, that gradients of soil redox potential (Eh) and pH exist along transects from flooded pond sediments to adjacent upland soils (Table 3). Along this

Table 3. Average redox potential (Eh) and acidity (pH) in 1986 for soil and sediment in the vegetative-hydrologic cover types on the Kabetogama Peninsula, Minnesota.

	Eh (mv)		pH	
Cover type	$\bar{x}$	$S\bar{x}$	$\bar{x}$	$S\bar{x}$
Forest	638	22.2	3.93	0.27
Moist	587	32.1	4.72	0.28
Wet	−19	38.1	5.80	0.07
Pond	−180	35.7	6.01	0.06

hydrologic gradient, soil Eh increases from reducing values in flooded soils (less than -175 mV) to oxidizing values (more than 500 mV) in well-drained soils. Along the same hydrologic gradient, pH decreases more than two units. These shifts in Eh and pH represent a shift from anaerobic to aerobic conditions and, together with oxygen availability, affect processes controlling the concentrations and cycling of nitrogen in soils and sediments.

Flooding of soil increases the amount of reduced nitrogen (NH_4-N) and available forms of nitrogen in soil solutions. Under flooded conditions oxidized nitrogen species (NO_3-N) are rapidly lost through denitrification if the pond periodically becomes anaerobic.

Two properties of ponds set the stage for anaerobic conditions: their tranquil flow regime, which results in poor aeration, and the abundance of organic matter with its associated high oxygen demand. Flooding creates conditions where accumulations of particulate nitrogen are likely, further increasing the nitrogen content of beaver pond sediments. Our data indicate that plant-available nitrogen (KCl-extractable nitrogen plus dissolved nitrogen in the soil solution) are up to 4.3 times greater under flooded and waterlogged conditions and that beaver activity thus enhances nitrogen availability on the landscape (Table 4).

The relationship between flooding and nitrogen availability, coupled with the dramatic increase in beaver activity on the Kabetogama Peninsula, demonstrates that beaver have had a profound effect on the amount and distribution of nitrogen. During the period from 1940 to 1986, as a result of wetland creation by beaver, we calculate that available forms of nitrogen in pond sediments and the riparian zone has more than doubled (Table 4).

This available nitrogen is strategically situated in or near the aquatic environment where it can undergo substantially different fates than terrestrial nitrogen. For example, decomposition of organic matter in spring and early summer may deplete dissolved oxygen, leading to denitrification in late summer at the aerobic-anaerobic boundary.

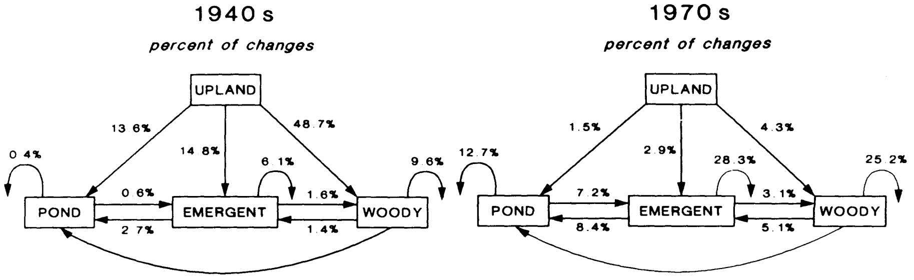

Figure 6. Impoundment conversions, by vegetative type. Expressed as percentage of total area impounded at the end of the decade. New impoundments are indicated by arrows emanating from the upland box. Conversion rates are compared for the 1940s and 1970s for the four-principal community types.

Changing image of stream ecosystems

Collectively, our studies and those of colleagues have produced two conceptual advances concerning stream ecosystems and raise a number of questions for future research. The conceptual advances address the organizational patterns of drainage networks with natural beaver populations and the role of beaver in the complex and dynamic successional pattern of vegetative patches on the landscape.

Drainage networks. Historically, streams throughout North America had different features than they do today (Bakeless 1950, Bartram 1791, Morgan 1868, Sedell and Froggett 1984). Where beaver were present in small streams (i.e., approximate orders 1–4) there were numerous reaches with open canopy, large accumulations of detritus and nutrients, expanded wetted areas (including riparian zones), and substantial shifts to anaerobic biogeochemical cycles (Ford and Naiman 1988, Naiman et al. 1986). In middle-order streams (i.e., orders 5–8), beaver-cut wood from upstream and the immediate riparian zone augmented local allochthonous inputs. Debris accumulations resulted in massive storage of sediment and detritus in the main channel, often forming small islands. In large rivers (i.e., orders greater than 9) beaver utilized floodplains and backwaters, where they constructed dams and canals and cut large amounts of wood. Although these activities diversified stream habitat in the short term, centuries of sediment deposition behind beaver dams may

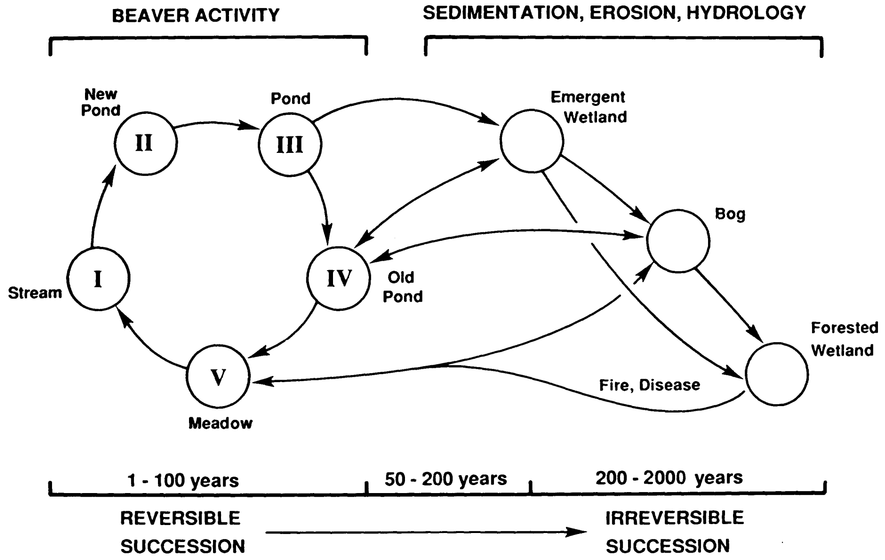

Figure 7. Beaver activity results in multisuccessional pathways, some of which can affect the landscape for centuries. Shown is our concept of how beaver may be affecting the boreal forest landscape of northern Minnesota.

Table 4. Comparison of vegetative-hydrologic cover types, available forms of soil/sediment nitrogen and total nitrogen for 1940 and 1986 on the Kabetogama Peninsula, Minnesota.

		Concentrations		Absolute amounts	
Cover type	Area (ha)	Total nitrogen (kg/ha)	Available nitrogen (kg/ha)	Total nitrogen (kg)	Available nitrogen (kg)
1940:					
Forest	3508	3050	6.8	5.34×10^6	11.92×10^3
Moist	215	3216	7.7	0.35×10^6	0.83×10^3
Wet	28	2912	16.2	0.04×10^6	0.23×10^3
Pond	16	3543	29.8	0.03×10^6	0.24×10^3
Total	3767			5.76×10^6	13.22×10^3
1986:					
Forest*	0	3050	6.8	0	0
Moist	1367	3216	7.7	2.20×10^6	5.26×10^3
Wet	1029	2912	16.2	1.50×10^6	8.33×10^3
Pond	1371	3543	29.8	2.43×10^6	20.41×10^3
Total	3767			6.12×10^6	34.01×10^3

*For 1986 we assume the area affected by beaver is a maximum. Thus, no additional forest area will be affected.

have reduced floodplain complexity (Rutten 1967). The effects of this activity, which can still be seen in the terrestrial vegetation of meadowlands centuries after the extirpation of beaver (Ives 1942, Rudemann and Schoonmaker 1938), is testimony to their widescale influence on the landscape of North America.

These alterations had a substantial effect on the ability of stream ecosystems to resist and recover from disturbance. It has been suggested that modern streams are easily disturbed but have a high resiliency, returning rapidly to a predisturbance condition (Reichle et al. 1975, Webster et al. 1975). A factor contributing to the low resistance is the absence of large stable pools of biomass and nutrients with slow turnover rates to buffer the system from disturbance (e.g., expanded patch bodies). We have suggested that patch bodies associated with beaver ponds function as large-mass, slow-turnover components in stream ecosystems, and that streams with beaver ponds probably have a high resistance to disturbance (Naiman et al. 1986). Beaver also assist in returning the stream to a predisturbance condition, as they rebuild dams that accumulate water and sediment. This concept has been used in Wyoming and Oregon to rehabilitate streams after a long history of abuse.[4]

Vegetative succession. Originally, we envisioned that beaver build dams on a stream and through time the ponds age, are abandoned, meadows form and mature, and eventually a stream is reformed as a new channel is cut and the riparian vegetation matures. In the boreal forests of northern Minnesota, Quebec, and Alaska, however, we see a complex pattern that may involve the formation of emergent marshes, bogs, and forested wetlands, which appear to persist in a somewhat stable condition for centuries (Figure 7). The multisuccessional pathways are complex. Factors responsible for individual successional pathways include existing vegetation, hydrology, topography, fire, disease, herbivory, and beaver. We are not yet sure how the specific beaver activities interact in this process, but they are an essential component given their ability to influence hydrology and vegetation patterns. Certainly the dynamics of the system would be quite different without beaver. We are currently investigating these complex interactions using the Kabetogama Peninsula as a model, and we hope to be able to provide additional insights in the next few years.

Acknowledgments

Research funds were provided by the National Science Foundation, the Woods Hole Oceanographic Institution, and the State of Minnesota. We thank Voyageurs National Park for support, and J. Pastor and T. Frost for constructive comments on the manuscript.

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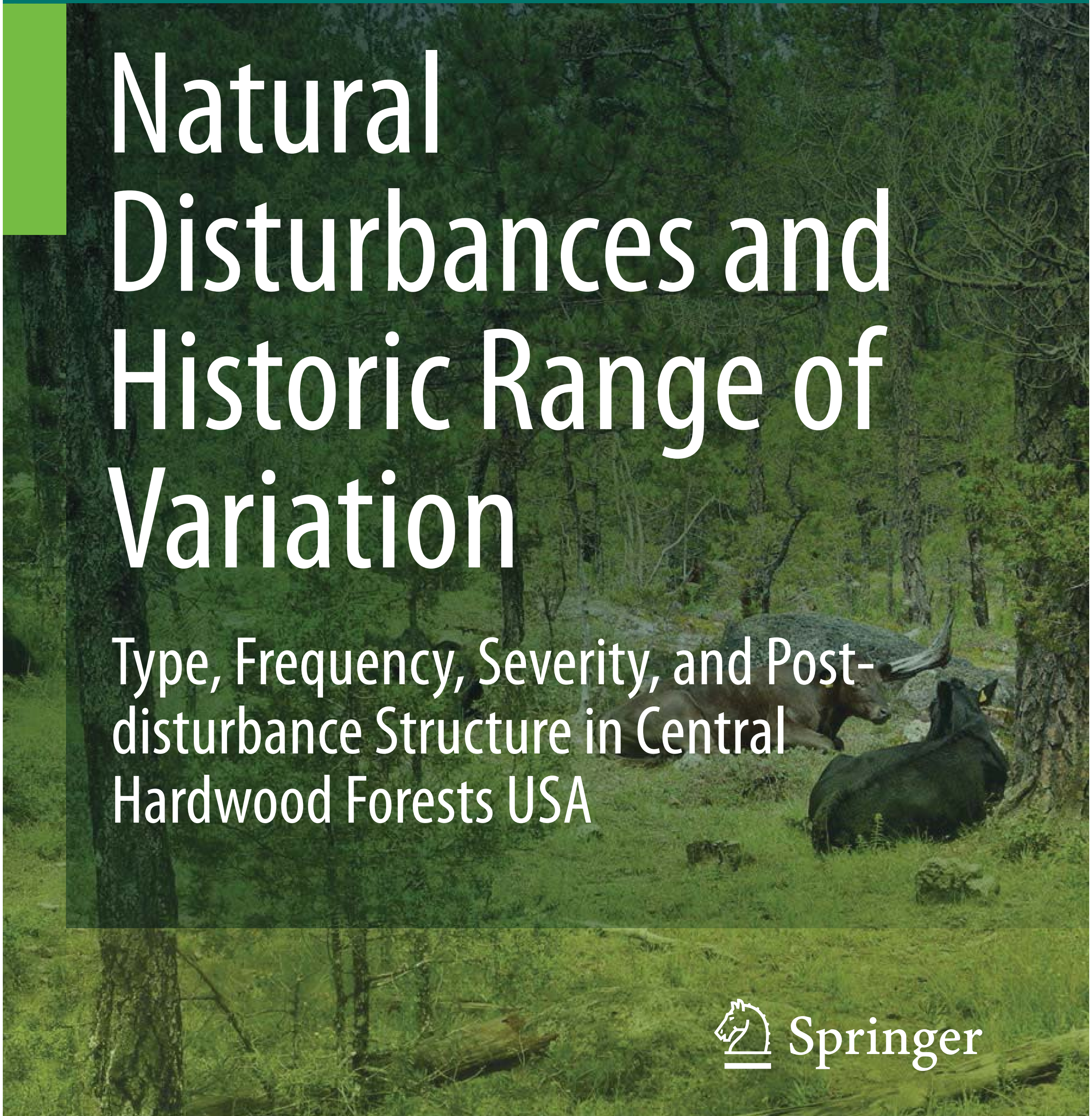
Managing Forest Ecosystems

Cathryn H. Greenberg
Beverly S. Collins *Editors*



Natural Disturbances and Historic Range of Variation

Type, Frequency, Severity, and Post-disturbance Structure in Central Hardwood Forests USA

Springer

Managing Forest Ecosystems

Volume 32

Aims & Scope

Well-managed forests and woodlands are a renewable resource, producing essential raw material with minimum waste and energy use. Rich in habitat and species diversity, forests may contribute to increased ecosystem stability. They can absorb the effects of unwanted deposition and other disturbances and protect neighbouring ecosystems by maintaining stable nutrient and energy cycles and by preventing soil degradation and erosion. They provide much-needed recreation and their continued existence contributes to stabilizing rural communities

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Cathryn H. Greenberg • Beverly S. Collins
Editors

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ISSN 1568-1319 ISSN 2352-3956 (electronic)
ISBN 978-3-319-21526-6 ISBN 978-3-319-21527-3 (eBook)
DOI 10.1007/978-3-319-21527-3

Library of Congress Control Number: 2015953434

Springer Cham Heidelberg New York Dordrecht London
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Preface

This edited volume addresses the historic range of variation (HRV) in types, frequencies, severities, and scales of natural disturbances, and how they create heterogeneous structure within upland hardwood forests of Central Hardwood Region (CHR). The idea for this book was partially in response to a new (2012) forest planning rule which requires national forests to be managed to sustain 'ecological integrity' and within the 'natural range of variation' of natural disturbances and vegetation structure. This new mandate has brought to the forefront discussions of HRV (e.g., what is it?) and whether natural disturbance regimes should be the primary guide to forest management on national forests and other public lands. Natural resource professionals often seek 'reference conditions,' based on HRV, for defining forest management and restoration objectives. A large body of literature addresses changes in forest structure after natural disturbance, but most studies are limited to a specific site, disturbance event, forest type, or geographic area. Several literature reviews address a single natural disturbance type within a limited geographic area (often not the CHR), but do not address others or how their importance may differ among ecoregions. Synthesizing information on HRV of natural disturbance types, and their impacts on forest structure, has been identified as a top synthesis need.

Historically, as they are today, natural (non-anthropogenic) disturbances were integral to shaping central hardwood forests and essential in maintaining diverse biotic communities. In addition to a 'background' of canopy gaps created by single tree mortality, wind, fire, ice, drought, insect pests, oak decline, floods, and landslides recurringly or episodically killed or damaged trees, at scales ranging from scattered, to small or large groups of trees, and across small to large areas. Additionally, some animals, such as beavers, elks, bisons, and perhaps passenger pigeons, functioned as keystone species by affecting forest structure and thus habitat availability for other wildlife species. Prehistoric anthropogenic disturbances – fire and clearing in particular – also influenced forest structure and composition throughout much of the CHR and therefore the distribution of disturbance-dependent wildlife species. The spatial extent, frequencies, and severities differed among these natural disturbance types and created mosaics and gradients of structural conditions and canopy openness within stands and across the landscape.

A full-day symposium, organized by the editors, at the 2014 Association of Southeastern Biologists conference in Spartanburg, South Carolina, was the basis for this book. Our goal was to present original scientific research and knowledge synthesis covering major natural disturbance types, with a focus on forest structure and implications for forest management. Chapters were written by respected experts on each topic with the goal of providing current, organized, and readily accessible information for the conservation community, land managers, scientists, students and educators, and others interested in how natural disturbances historically influenced the structure and composition of central hardwood forests and what that means for forest management today.

Chapters in this volume address questions sparked by debated and sometimes controversial goals and 'reference conditions' in forest management and restoration, such as the following: What was the historic distribution, scale, and frequency of different natural disturbances? What is the gradient of patch sizes or level of tree mortality conditions created by these disturbances? How do gradual disturbances such as oak decline, occurring over a long period of time and across a broad landscape, differ in effects from discrete disturbances such as tornadoes? How does topography influence disturbance regimes or impacts? How do native biotic (insects or fungi, keystone wildlife species) and abiotic (precipitation, drought, temperature, wind, and soil) agents interact to alter disturbance outcomes? What was the diversity of age classes and gradient of forest structure created by natural disturbances alone? How might disturbance-adapted plants and animals have fared in the hypothetical historic absence of anthropogenic disturbances? How might climate change alter disturbance regimes and structure of upland hardwood forests in the future? And finally, should, and how, can land managers manage these forests within the HRV of natural disturbance frequencies, spatial extents, and gradient of conditions they create?

We sincerely thank all those who encouraged and aided in the development of this book. Each chapter was peer-reviewed by at least two outside experts and both coeditors, and we thank these colleagues for their useful suggestions: Chris Asaro, Robert Askins, Francis Ashland, Bart Cattanach, Steven Croy, Kim Daehyun, Dianne DeSteven, Chris Fettig, Mark Harmon, Matthew Heller, Louis Iverson, John Kabrick, Tara Keyser, Scott Lecce, William MacDonald, Henry McNab, Manfred Mielke, Billy Minser, Scott Pearson, Duke Rankin, Jim Rentch, John Stanturf, Scott Stoleson, Ben Tanner, and Thomas Wentworth. We also thank the Association of Southeastern Biologists for allowing us to host a conference symposium on this important topic, and the National Forests of North Carolina for assistance with travel costs for speakers. We especially thank each author for contributing, and for timely chapter revisions, which made this book possible.

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Chapter 3
Oak Decline in Central Hardwood Forests: Frequency, Spatial Extent, and Scale

Steven W. Oak, Martin A. Spetich, and Randall S. Morin

Abstract Oak decline is a widely distributed disease that results from an interacting set of factors in the Central Hardwood Region. Episodes of decline have been reported since before the turn of the twentieth century and from every state in the region. It is a stress-mediated disease that results from the interactions of physiologically mature trees, abiotic and biotic stressors that alter carbohydrate physiology, and opportunistic fungal pathogens and inner bark-feeding insects. Symptoms include reduced radial growth and slow, progressive crown dieback. Decline occurs over several years or decades, ending in death of vulnerable trees. Patterns of oak decline vary from a few trees in stands with diverse species composition and age structure, to areas covering several thousand ha in landscapes with more uniform composition of susceptible, physiologically mature red oak group species. Prolonged periods of drought that occur in combination with repeated spring defoliations by leaf-feeding insects exacerbate decline. Past disturbances have shaped current forest species composition and age structure, favoring physiologically mature stands with a large oak component, and are thus inextricably linked to oak decline vulnerability. Noteworthy examples are the functional extirpation of the American chestnut by the non-indigenous chestnut blight pathogen, combined with changing disturbance patterns, including fire suppression and reduced harvesting, during the early twentieth century. Data from extensive regional surveys have been used to develop models predicting the probability and impacts of oak decline events as part of the Forest Vegetation Simulator.

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C.H. Greenberg, B.S. Collins (eds.), *Natural Disturbances and Historic Range of Variation*, Managing Forest Ecosystems 32,
DOI 10.1007/978-3-319-21527-3_3

Keywords Crown dieback • Oak mortality • Predisposing factors • Oak decline survey • Oak decline event monitor

3.1 Historical Context for Oaks in Central Hardwood Forests

Oak (*Quercus*) forest types currently dominate the Central Hardwood Region (CHR), and oak decline is a widely distributed change agent altering species composition and forest structure throughout the region. The disease has regulated oak populations since oak species and interacting antagonists first appeared in the CHR, and that role continues to the present. Impacts of oak decline would have varied through time, as oak composition has shifted over the past several millennia with changing climate, weather, and the extent, frequency, and intensity of fire (e.g., Delcourt and Delcourt 2004). Human interventions and preferences have intentionally or unintentionally shaped forest composition and structure, either favoring or disfavoring oak populations. The expression of these preferences began with the arrival of the first aboriginal people into the region, who undoubtedly used fire to create desirable forest structures around settlements and in hunting lands (see also Greenberg et al. Chap. 1). Although managing tree species composition may not have been a primary objective, the use of fire certainly favored species well-adapted to it such as oaks, American chestnut (*Castanea dentata*), and pines (*Pinus* spp.). The extent of such landscape management increased with the human population, and accelerated with the arrival of European migrants. The introduction of destructive non-indigenous pathogens and insects continues into present decades, stimulated by increased international movement of products and people. Even though the forces shaping CHR forests operated for millennia, the relevant historical context for oak decline as observed from the mid-twentieth to the present is relatively recent. It was triggered by biological, social, and political events in the early twentieth century which altered historic disturbance regimes.

Prior to the turn of the twentieth century, forests in many parts of the CHR were dominated in composition by American chestnut and subject to frequent disturbance by fire (sometimes by natural causes, but mostly by human ignitions; see Greenberg et al. Chap. 1, Table 1.6). In 1880, 98.6 % of fires in the CHR were human caused with the top three causes attributed to land clearing, hunters and locomotives (Spetich et al. 2011). Logging to supply fuel and building materials to a pre-, and later, emerging- industrial society also was an important and widespread disturbance factor in the late nineteenth and early twentieth centuries.

Two events then occurred that had far-reaching consequences on forest landscapes. First, the chestnut blight was discovered in New York City in 1904. The cause of the disease was a non-indigenous fungal pathogen, most likely introduced with Asian chestnut varieties imported by the nursery trade to many locations in the eastern USA as early as 1876. The native American chestnut had no inherent resistance to the pathogen, and within a few decades of the discovery of the disease in New York City, the species was functionally extirpated throughout its range. Since then, it has survived only as root sprouts before once again becoming blighted and killed in a cycle that is repeated to the present day.

The second event was the 1911 enactment of the Weeks Act authorizing acquisition of land for national forests to protect headwaters of navigable streams. It was drafted in part as a response to a disastrous fire season the previous year that included 'The Great Fire of 1910' that burned over 808,000 ha and resulted in the deaths of 87 people in northeast Washington, northern Idaho, and western Montana. Though it occurred in vastly different ecosystems than those in the CHR, this catastrophe crystallized national policy and prompted the USDA Forest Service to make fire suppression a primary mission everywhere (see also Zenner Chap. 14). Further, the Weeks Act incorporated provisions for the development of federal-state cooperative fire control programs.

Prior to the Weeks Act, oaks dominated the CHR due to traits that made them more resilient to fire. The species builds large, belowground reserves of carbohydrates in root systems protected from fire. When fire killed aboveground shoots of small trees, these belowground carbohydrate reserves allowed new shoots to resprout rapidly. Large oaks also have relatively thick bark that helps reduce damage from ground-level fires. Thus, oaks had a competitive advantage over other tree species less well adapted to fire. In 1924 the Clark-McNary Act was passed, expanding the Weeks Act. Among other provisions, this Act encouraged states to form their own forestry agencies and further advanced fire suppression programs. These agencies and the laws and practices they spawned, combined with rapidly increasing efficiencies in agricultural production in the early twentieth century, gradually began to transform forests of the CHR. Open woodland conditions that had been maintained by fire, grazing and harvesting for millennia gradually became more closed as cohorts of oaks already established in the understory grew into dominant and codominant crown positions in the absence of frequent fire and other disturbance (Abrams 1992). Concurrent with these ecological changes, the USA population was growing and society was shifting from agrarian and rural, with a resource utilization ethic, to industrial and urban, with an emerging conservation ethic. By the late twentieth century, oak cohorts 80–100 years old dominated the CHR, especially on publicly owned lands not subject to development and urbanization. Table 3.1 summarizes general social and forest dynamics attributes before and after the turn of the twentieth century that help explain oak density and oak decline patterns of the more recent past.

Oak density for contemporary forests of CHR ecoregions resulting from these historic influences was determined using plots in the USDA Forest Service Forest Inventory and Analysis (FIA) Eastwide data base (Hansen et al. 1992). Data collected during the 1980s and 1990s were extracted from 26,662 plots in 20 states (Table 3.2). Overall, one third of the basal area (BA) in the CHR was comprised of oak species, with the highest average oak density values occurring in the Ozark Highlands, Boston Mountains, Arkansas Valley, and Ridge and Valley ecoregions. The Ozark Highlands had, by far, the highest oak density of all ecoregions (63.5 %)

Table 3.1 Prevalent historic attributes of CHR forests

Attribute	Pre-twentieth century	Twentieth century to present
Social/cultural	Small agrarian population	Large urbanized population
	Resource utilization/exploitation perspective	Resource conservation/protection perspective
Disturbance	Frequent fire of mostly anthropogenic origin	Near-complete fire suppression
	Frequent logging/utilization	Limited logging
Forest composition	American chestnut regionally abundant	Mixed oak predominant
	Vigorously sprouting woody species favored (e.g. oaks)	More shade tolerant woody species favored (e.g. red maple)
Forest structure	Diverse herbaceous understory; woody understory persists as sprouts	Dense woody understory
	Widely spaced, large diameter overstory	Dense, smaller diameter overstory
	More complex age structure	Aging oak cohorts 80–100 years old

Table 3.2 Mean proportion of BA in oak species and number of FIA plots in each oak BA proportion category by CHR ecoregion

	Mean %	Percentage oak BA category				
Ecoregion	oak BA	0	1–25	26–50	51–75	>75
Arkansas Valley	44.0	53	103	102	110	102
Blue Ridge Mountains	31.8	305	351	418	345	182
Boston Mountains	48.3	24	59	111	130	136
Central Appalachians	28.6	475	716	477	375	253
Interior Plateau	25.3	597	755	551	415	346
Interior River Valleys and Hills	31.4	505	439	391	374	320
Northern Piedmont	33.4	113	102	75	62	72
Ouachita Mountains	31.6	192	230	243	134	78
Ozark Highlands	63.5	114	242	478	907	2,121
Piedmont	21.8	2,031	1,429	1,048	667	355
Ridge and Valley	37.1	463	630	617	604	618
Southwestern Appalachians	31.7	143	247	309	237	106
Western Allegheny Plateau	25.0	715	698	455	329	268
Entire Central Hardwood Region	33.2	5,730	6,001	5,275	4,689	4,957

and the highest proportion of plots in the densest category (55 % of all plots with >75 % oak BA). The ecoregion with the next highest oak density was the Boston Mountains – 48.3 % mean oak BA and 30 % of all plots with >75 % oak BA. The only ecoregion with mean percent oak density below 25 % was the Piedmont at 21.8 % (see Greenberg et al. Chap. 1, Fig. 1.1 for ecoregions map).

The geographic distribution of the proportion of oak BA on forested lands was mapped by interpolating plot values (Fig. 3.1). Plots in the >75 % oak BA category were particularly concentrated in the Ozark Highlands of Missouri. In addition, oak BA exceeded 50 % in parts of the Arkansas Valley, and Boston and Ouachita Mountains as well as the Western Highland Rim area of the Interior Plateau in Tennessee and the northern half of the Ridge and Valley in Virginia, West Virginia and western Maryland. Non-forest land was most noticeable in the Northern Piedmont and Interior River Valleys and Hills, though a few pockets of high oak BA forest were detected in the latter ecoregion. Details of the methodology employed to create the interpolated BA surface displayed in Fig. 3.1 are available in Morin et al. (2005).

There is no doubt that contemporary forest composition and structure are products of prevalent disturbances over at least the past two centuries. Choosing the reference condition upon which to base management practices compatible with the historic range of variation of natural disturbances presents a dilemma for land managers concerning the role of humans in forest ecosystems. The range of natural disturbance and the shape of forest composition and structure prior to human habitation of the CHR can only be generally inferred and ignores the reality of the past five to ten millennia (see Greenberg et al. Chap. 12). Alternatively, selecting a dis-

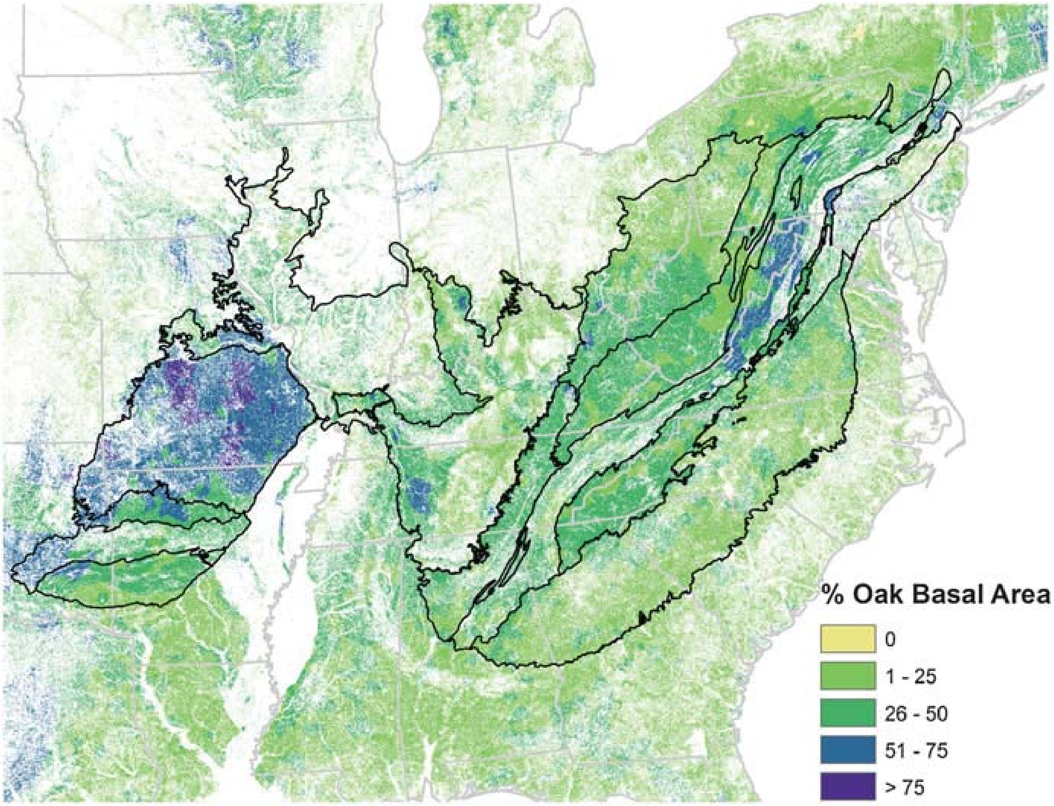

Fig. 3.1 The geographic distribution of the proportion (%) of oak basal area on forested lands in the eastern USA. The map was created by interpolating the values from 93,611 forest inventory plots in 37 states (Morin et al. 2005). The data were extracted from the USDA Forest Service Forest FIA Eastwide data base, which consists of data collected during the 1980s and 1990s (Hansen et al. 1992) (Map credit to Randall S. Morin)

turbance regime that includes human interventions along a spectrum from early aboriginal to contemporary times is a philosophical and arbitrary process. In any case, CHR forests cannot be termed ‘natural’ until the full suite of forest plants (including American chestnut) and animals present before the arrival of humans in the CHR are restored and functioning as part of ecosystems (see Zenner Chap. 14).

3.2 Oak Decline Etiology and Symptoms

Oak decline is a stress-mediated disease that results from the interactions of three groups of factors first described by Sinclair (1965), and later elaborated by Manion (1991). The individual factors in each group that combine to result in a specific oak decline episode can vary widely. The first group includes long-term predisposing factors that act to reduce the resilience of healthy trees to stress or attack by pathogens and insects. Among these are edaphic conditions such as soil depth and texture; topographic factors such as slope and aspect; and physiological maturity (distinguished from chronological age). Hyink and Zedaker (1987) characterized the concept of physiological age as having greater biological significance than chronological age. They described advanced physiological age (senescence) as the progression toward critical levels of physiological relationships such as water transport and translocation efficiencies, hormone balances, and the balance between photosynthesis and respiration. When critical levels are exceeded, internal resources are unavailable for effective tree response to stressors thereby predisposing them to decline. Oak et al. (1991) created an index of physiological age using site index (SI) and chronological age that was useful in oak decline risk rating (Oak et al. 1996).

The second group is comprised of inciting factors associated with the initiation of decline and the earliest, non-specific symptoms: depletion of stored food reserves, reduced growth, and dieback. Factors in this group include prolonged drought or spring defoliation caused by some insect species or late frost. The third group is comprised of contributing factors. These are biotic agents and often are implicated as the cause of mortality but in fact, are opportunists normally incapable of killing vigorous trees. However, they are well adapted to exploit predisposed trees that have been further weakened by the inciting factors. The most commonly cited fungal parasites involved in oak decline mortality are *Armillaria mellea* (though complex interactions with other *Armillaria* species have been described by Bruhn et al. 2000) and *Biscogniauxia atropunctata* (cause of hypoxylon canker of oaks). Both are widely distributed facultative parasites in natural ecosystems. *Armillaria mellea* is common in soil, decaying roots, and dead wood; *Biscogniauxia atropunctata* resides as an endophyte in stems and branches decaying sapwood. They become more aggressive pathogens when conditions are appropriate for pathogenesis and cause root disease and stem cankers. The most commonly cited insect pest is the two-lined chestnut borer (*Agrilus bilineatus*) which creates meandering galleries in the inner bark of weakened trees (Wargo et al. 1983).

The earliest visible aboveground symptom of oak decline is dieback of the live crowns of trees in upper canopy positions beginning with the outer twigs and branches. This can sometimes occur during the growing season, leaving dead foliage attached. More commonly it occurs during the dormant period with affected limbs failing to refoliate the following spring. Relatively slow, progressive dieback downward and inward, involving larger limbs occurs over years or even decades and is a distinctive symptom of oak decline. The death of branches in the crown results in the production of sprouts along the larger limbs and main stem. Eventually, severely declined trees die. Species in the red oak group (e.g., black oak (*Q. velutina*), scarlet (*Q. coccinea*), northern red oak (*Q. rubra*), southern red oak (*Q. falcata*), and blackjack oak (*Q. marilandica*)) are more susceptible to decline-induced mortality than are species in the white oak group including white oak (*Q. alba*), chestnut oak (*Q. montana*), and post oak (*Q. stellata*).

Crown dieback reflects root disease progression belowground where armillaria root disease is an important contributing factor. Carbohydrate chemistry is altered in roots of trees stressed by drought and defoliation and is accompanied by decreased levels of starch and increased levels of simple sugars (Parker 1970; Wargo 1972, 1977). Growth of *A. mellea* is stimulated by these changes and becomes more aggressive, attacking more of the stressed tree's root system. The crown must die back to accommodate the impaired root system. Long-term monitoring of symptomatic trees has shown that dieback (and presumably root disease) may abate 10 years after the return of good growing conditions so long as it has not progressed beyond about one-third of the live crown volume (Oak, unpubl. data). Moisture stress also is important in stimulating *Biscogniauxia atropunctata* to transform from a sapwood endophyte to a more aggressive cankering pathogen and sapwood rotter (Bassett and Fenn 1984).

3.3 Distribution

Millers et al. (1989) reviewed the literature of forest tree declines and reported 57 episodes in the eastern USA between 1856 and 1986 where oak mortality was higher than expected in areas covering at least 400 ha. Details of survey methodology and data collection often were not included, and authors of cited reports usually attributed the mortality to one or two causes without naming oak decline specifically. This was true even after the first elucidation of decline etiology and symptoms was published (Sinclair 1965). Despite this lack of specificity, the summarized causes included multiple interactions consistent with the published disease etiology. The first systematic regional surveys of oak decline using consistent data collection protocols were conducted mostly in the South in the mid-1980s using ground and aerial photo methodologies (Starkey et al. 1989, 2000; Oak et al. 1990), and continuous forest inventory plot networks (Oak et al. 1991, 2004). Combining these sources reveals that every state in the CHR has experienced oak decline damage and mortality in at least one decade dating back to earliest reports in the mid-nineteenth century (Table 3.3). Notable concentrations of oak decline episodes were evident in Appalachian and Ozark Mountain states (Arkansas, Georgia, Missouri, North

Table 3.3 Oak decline and mortality reports for states within the CHR by decade

	Pre-1900	1900s										2000s	
State[a]		00	10	20	30	40	50	60	70	80	90	00	10–13
AL									■	■			
AR							■		■	■	■	■	
DE							■			■			
GA	■		■	■			■	■	■	■	■		
IA									■	■			
IN									■				
IL									■	■			
KY									■	■			
MD							■			■			
MO									■	■		■	
NC	■		■	■		■	■	■	■	■	■		
NJ							■	■	■				
NY							■	■	■	■			
OH									■				
OK									■				
PA					■	■	■	■	■	■			
SC										■			
TN			■	■		■				■	■		
VA	■		■	■		■	■	■	■	■	■		
WV	■						■		■	■			

Adapted from Millers et al. (1989), Starkey et al. (1989, 2000), Oak et al. (2004)

[a] Most states are only partially within the CHR

Carolina, Pennsylvania, Tennessee, Virginia, and West Virginia) from the 1950s through the 1990s. Intensified survey activities may have contributed to part of the increase in reported oak decline distribution, incidence, and severity over this period. The USDA Forest Service formed the Division of Forest Pest Control in 1956 (later variously named Forest Insect and Disease Control, Forest Insect and Disease Management, Forest Pest Management, and Forest Health Protection) to survey and interpret forest health conditions on federal lands. State forest health programs servicing state and private forest landowners began in the 1960s under cost sharing agreements with the USDA Forest Service State and Private Forestry and have flourished in the decades since.

3.4 Oak Decline Patterns at Various Spatial Scales

Oak decline patterns have been described and analyzed across a range of spatial scales with varying methodologies tailored to survey objectives. Reports commonly included estimates of areal extent (patch size), incidence and severity of symptoms, and (less frequently) description of effects on growth, species composition, and forest structure. Patch size, incidence and severity, and effects will be detailed within this section.

Initial surveys were at a local scale and limited to the characterization of decline-affected stands (Millers et al. 1989; Starkey et al. 1989; Law and Gott 1987). Random surveys representing all health classes were conducted later and broadened the scope to establish disease incidence and impacts in a landscape context. These surveys used large format aerial photography (Oak et al. 1990) or aerial sketch mapping (Starkey et al. 2000) and were supported by ground sampling for validation. Description of stand and site features from the ground validation was used later for risk rating and effects modeling (Oak et al. 1996). Regional scale analyses were conducted using data collected from risk-based polygon sampling (Guldin et al. 2006) and by continuous forest inventory plot networks (Oak et al. 1991, 2004; Fan et al. 2012).

3.4.1 Patch Size

The pattern of oak decline on the landscape varies widely with tree species composition, age structure, and mortality incidence. Small patches consisting of scattered individuals or small groups of oaks occur in landscapes where age structure, tree species composition, and correlated site conditions are relatively diverse. In contrast, patches encompassing several thousand ha can occur where species composition and site conditions are relatively less diverse. Such large areas have developed on landscapes in the Blue Ridge Mountains and Ridge and Valley ecoregions of western Virginia, and more recently in the Ozark Highlands, Boston Mountains, and Ouachita Mountains ecoregions of Missouri, Arkansas, and Oklahoma. Landscapes in these provinces are dominated by cohorts of physiologically mature trees in species of the red oak subgenus growing on sites of average to lower productivity and are subject to periodic drought (Greenberg et al. Chap. 1, Fig. 1.8). Since the mid-1980s in the east, recurrent defoliation by the non-indigenous gypsy moth has also been an important inciting factor. During the 1990s in the west, unprecedented outbreaks of the indigenous red oak borer (*Enaphalodes rufulus*) contributed.

Aerial survey methods supplemented with ground truth assessments provide the perspective for estimating patch size that is lacking in ground-based surveys alone. Oak decline and mortality were evaluated on two national forests in the Ridge and Valley and Blue Ridge Mountains ecoregions of Virginia by Rauschenberger and Ciesla (1966) using aerial sketch mapping of about 70 % of the forest land inside the forest boundaries, supplemented with ground survey. Areas delineated with at least 5 % mortality totaled approximately 42,016 ha on the George Washington National Forest in northwestern Virginia. Patch size ranged from 61 to 2,424 ha. Mortality was less prevalent and patches were smaller overall on the Jefferson National Forest in southwestern Virginia (range 113–485 ha; mean = 297). This survey predated by 20 years the widespread infestation of Virginia forests by the gypsy moth (*Lymantria dispar*). Outbreaks of this insect usually are of longer duration, the intensity of defoliation greater and return interval shorter than for native defoliators. These dynamics often incite very severe decline episodes with catastrophic levels of mortality. While patch size estimates are lacking for post-gypsy moth decline episodes in Virginia, they are likely substantially larger.

Law and Gott (1987) interpreted large-scale color infrared aerial photos acquired over the Mark Twain National Forest, Missouri within the Ozark Highlands ecoregion and found mortality areas ranged from <0.5 to 28 ha (mean = 4 ha). The decline episode that prompted this assessment followed prolonged drought and several other predisposing and inciting conditions. However, about a decade later a much more severe and widespread episode occurred, accompanied by an unprecedented outbreak of the red oak borer. As was the case for gypsy moth-associated decline events in Virginia, the size of mortality patches were not measured, but probably increased significantly over earlier estimates.

3.4.2 Incidence and Severity

Starkey et al. (1989) surveyed 38 decline-affected stands from Virginia to Georgia and west to Arkansas and Missouri. All were on public lands with most located in National Forests. Oaks dominated the composition, with 50 % in red oak group species, 31 % in white oak group species, and 7 % hickory (*Carya*) species. Diagnosis of decline and decline mortality was confined to dominant and codominant trees with progressive dieback symptoms. Dieback and mortality among trees of all species in intermediate and suppressed crown positions was attributed to suppression and not to decline. Decline was observed in 80 % of dominant and codominant trees of all species. Hickories were the only non-oak species exhibiting appreciable symptom incidence. Advanced decline (>33 % live crown loss) was present in 20 % of all trees, and 17 % were dead with decline symptoms. Red oak group species were more prone to decline-associated mortality compared with white oak group species (24 % vs. 8 %, respectively). Among red oak group species, black oak was most vulnerable to oak decline mortality (34 %) followed by scarlet oak (23 %). The mortality incidence among hickory species was comparable to that recorded among white oak trees (12 %).

In addition to mortality impacts, Starkey et al. (1989) also analyzed the impact of oak decline on tree growth. Radial growth for 77 pairs of declined and healthy red oak trees was compared by in stands located in North Carolina, Tennessee, and Arkansas. Overall, declined trees grew 17 % more slowly than healthy trees for the last 45 years of the growth history, and 27 % more slowly for the last 20 years.

Tainter et al. (1990) further elaborated the predisposing effects of drought that were evident for several decades after the cessation of stress on oak populations of different physiological ages. They suggested that severe drought over several years in the early 1950s altered oak populations resulting in two health classes. One class had diminished resilience to subsequent droughts and eventually died while the other survived and recovered at least some of its former growth rate. Dwyer et al. (1995) observed similar drought dynamics in different age classes of black and scarlet oaks in Missouri dating back to stress events up to 45 years earlier.

Reports of increased oak mortality in the Ozark Highlands ecoregion on the Mark Twain National Forest, Missouri prompted surveys of declined areas on the Fristoe Unit in 1982 (Law and Gott 1987). Mortality areas were detected by interpretation of large-scale aerial photographs on 15.6 % of the 2,384 ha surveyed. Ground validation surveys confirmed that 53 % of the volume in scarlet oak was dead or dying, along with 35 % of black oak and 26 % of northern red oak. The 71–80 year age class was the most severely affected with 42 % of stand volume dead or dying.

Aerial sketch mapping followed by ground validation surveys were initiated in 1999 after concentrations of oak decline damage were reported on the Pleasant Hill Ranger District, Ozark National Forest, Arkansas in the Boston Mountains ecoregion. Moderate-to-severe damage was detected on approximately 17,372 ha (16 %) of the Ranger District. In the severe damage stratum, 24 % of the BA was declined or dead (Starkey et al. 2000).

Oak decline in a larger, landscape, context was evaluated in surveys of three national forest ranger districts: the Lee Ranger District on the George Washington National Forest in the Ridge and Valley ecoregion in Virginia; the Wayah Ranger District on the Nantahala National Forest in the Blue Ridge Mountains ecoregion in North Carolina; and the Buffalo Ranger District on the Ozark National Forest in the Boston Mountains ecoregion in Arkansas (Oak et al. 1990). These areas represented much of the diversity in climate, physiography, soils, and hardwood tree species composition where oak decline had been a recurring problem (Millers et al. 1989). A two-stage sampling design was used. Large-scale aerial photo samples were interpreted and stratified by tree size and damage class, with the results validated by ground plot sub-sampling. The survey yielded decline damage area and damage severity estimates. The Lee Ranger District had the highest incidence of decline (56 % of hardwood forest type). The Wayah Ranger District had intermediate incidence (35 % of hardwood forest type), whereas 28 % was affected on the Buffalo Ranger District. Within damaged strata, incidence of mortality plus advanced decline ranged from 10 % to 16 % of dominant and codominant trees compared with 1–3 % in undamaged strata.

Guldin et al. (2006) evaluated oak decline on 181 plots systematically distributed across the Interior Highlands of Arkansas, Oklahoma, and Missouri, and found about 12 % of the area in the most heavily damaged class (>6.67 m^2/ha of BA unhealthy, a category which included dead trees and those displaying at least 34 % crown dieback). Mean stem density over the entire surveyed area was 95.3 trees/ha, of which 12.9 trees/ha were unhealthy (13.4 %). The percentage of mean total BA in an unhealthy condition was slightly higher (14.5 %). This damage was concentrated in the red oak group. Thirty percent of the BA in species of this group was unhealthy compared with about 9 % of species in the white oak group.

Other regional oak decline assessments were possible using large-scale continuous forest inventory plot networks. A 1986 inventory in Virginia afforded the opportunity to evaluate oak decline in the northern Piedmont and western mountains survey units (Oak et al. 1991) that lie within the Northern Piedmont, Blue Ridge Mountains, and Ridge and Valley ecoregions. Virginia had experienced chronic and severe oak decline since the earliest reports of the disease (Millers et al. 1989) and was in the midst of a widely reported severe decline episode during the inventory year. Decline occurred on an estimated 444,400 ha of oak forest (16.4 %) with the northern mountain unit (Blue Ridge Mountains and Ridge and Valley ecoregions) sustaining the highest incidence (29.7 %). Estimated annual mortality was greatest for counties with concentrations of decline. Shenandoah County in the Ridge and Valley ecoregion sustained average losses of 1.74 m^3 per ha per year from 1977 to 1986 which represented the highest rate in the assessment area. Average annual mortality in decline-affected plots overall was 1.84 m^3 per ha compared with 1.03 m^3 per ha in unaffected plots.

Stand and site factors associated with oak decline incidence (vulnerability) and severity (risk, as measured by volume losses when decline did occur) were examined for potential use in predicting oak decline. Factors showing promise included tree species composition, site quality, stand age, SI to age ratio, physiography, and stand density. The relationships between individual factors and oak decline vulnerability and risk were complex. For example, less productive sites were more vulnerable to oak decline but 33 % of the total affected area and 36 % of the oak mortality still occurred on sites with higher productivity ($SI \geq 21$ m). Chestnut oak forest types were the most vulnerable to oak decline, but risk was highest in oak-hickory forest types.

Oak et al. (2004) used FIA inventory data collected by the USDA Forest Service Southern and Southeastern Forest Experiment Stations to conduct an analysis of geographic and temporal decline trends in 12 southern states over two survey periods, 1984–89 and 1990–97. Data were originally interpreted by state, but were partitioned by CHR ecoregions within the inventoried area for this discussion. The Northeastern Forest Experiment Station FIA unit used different damage coding methods during these periods which precluded analysis in the northern part of the CHR (Fig. 3.2).

Just under half of the total CHR area, 47 million ha, was included in the oak decline analyses (Table 3.4). Ecoregions poorly or not represented were the Interior River Valleys and Hills (0 % inventoried), Western Allegheny Plateau (0 %), Central Appalachians (11 %), Ozark Highlands (24 %), northern Piedmont (25 %) and Interior Plateau (40 %). Among these, the Central Appalachians and Western Allegheny Plateau have high relative oak density (Table 3.2; Fig. 3.1) and have experienced recurrent, and sometimes severe, oak decline episodes in historical accounts (Millers et al. 1989).

Inventories conducted during the 1980s detected forests vulnerable to oak decline on about 9.8 million ha in CHR ecoregions, of which about 10.3 % were affected

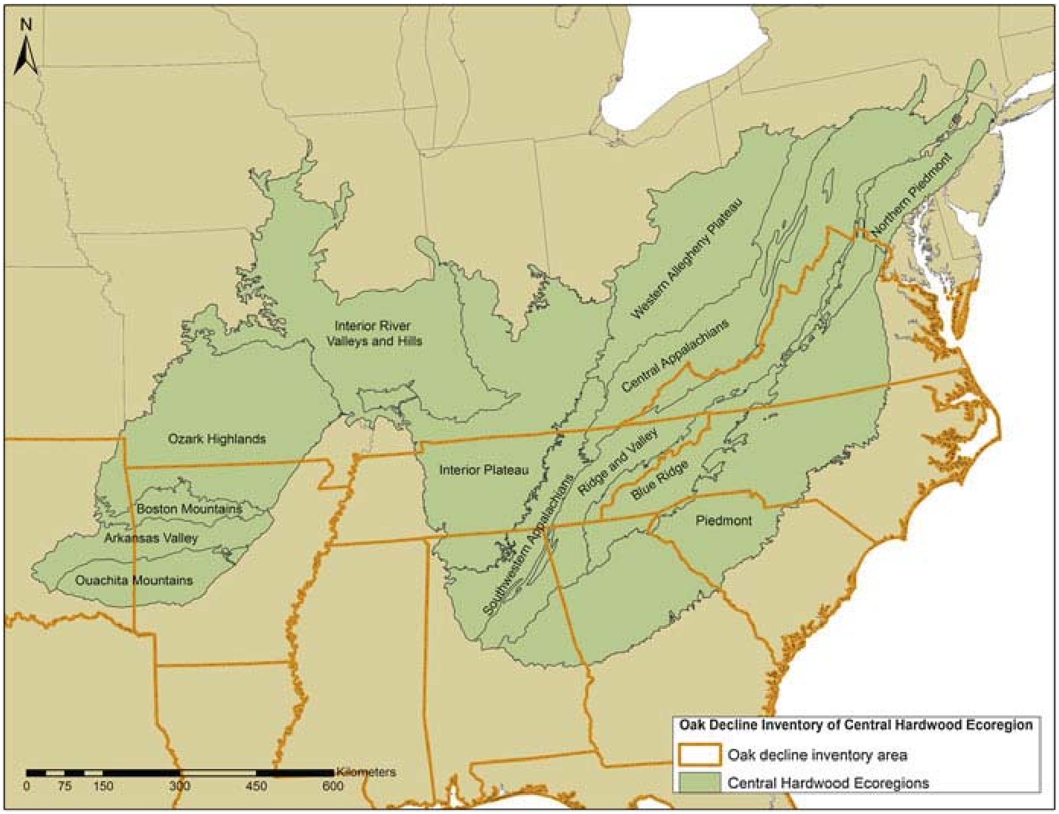

Fig. 3.2 CHR ecoregions and area included in USDA Forest Service FIA oak decline assessments conducted between 1984 and 1997 (Oak et al. 2004) (Map credit to Ida Evretjarn)

Table 3.4 Area of CHR ecoregions inventoried for oak decline by USDA Forest Service Southeastern and Southern Research Station FIA work units, 1984–1997

	Area (1000 ha)		
Ecoregion	Total	Inventoried	Percent
Arkansas Valley	2,842.1	2,842.1	100
Blue Ridge Mountains	4,659.5	4,506.5	96.7
Boston Mountains	1,417.8	1,417.8	100
Central Appalachians	6,205.0	674.6	10.9
Interior Plateau	12,352.3	4,951.8	40.1
Interior River Valleys and Hills	12,040.5	0	0.0
Northern Piedmont	3,045.9	748.0	24.6
Ouachita Mountains	2,689.6	2,689.6	100
Ozark Highlands	10,639.1	2,597.2	24.4
Piedmont	16,611.7	16,611.7	100
Ridge and Valley	11,548.3	6,511.3	56.4
Southwestern Appalachians	3,799.4	3,272.4	86.1
Western Allegheny Plateau	8,144.0	0	0.0
Total	95,995.2	46,823.1	48.8

Table 3.5 Oak decline vulnerable area, affected area, and affected incidence in CHR ecoregions in successive FIA inventory cycles 1984–1989 and 1990–1997

	1984–1989			1990–1997		
	Area (1000 ha)		Incidence (%)	Area (1000 ha)		Incidence (%)
Ecoregion	Vulnerable	Affected		Vulnerable	Affected	
Arkansas Valley	474.1	14.7	3.1	438.0	46.7	10.7
Blue Ridge Mountains	1,497.9	191.9	12.8	1,454.1	309.7	21.3
Boston Mountains	512.8	36.8	7.2	693.6	79.1	11.4
Central Appalachians	227.0	50.2	22.1	232.5	18.1	7.8
Interior Plateau	818.0	126.5	15.5	875.7	59.6	6.8
Northern Piedmont	135.0	32.6	24.1	131.1	33.0	25.2
Ouachita Mountains	621.3	17.6	2.8	670.0	44.2	6.6
Ozark Highlands	695.3	49.0	7.0	811.2	107.8	13.3
Piedmont	2,437.6	139.3	5.7	2,233.9	224.8	10.1
Ridge and Valley	1,588.9	319.1	20.1	1,629.1	299.3	18.4
Southwestern Appalachians	788.9	36.0	4.6	997.4	69.6	7.0
Total	9,797.0	1,013.6	10.3	10,166.6	1,291.9	12.7

Adapted from Oak et al. (2004)

(1.0 million ha; Table 3.5). Ecoregions with incidence greater than the overall mean included the Blue Ridge Mountains, Central Appalachians, Northern Piedmont, and Ridge and Valley. However, relatively small portions of the Central Appalachians and Northern Piedmont were inventoried, yielding small sample sizes (around 100 vulnerable plots each). Therefore, confidence in the oak decline incidence estimates for these ecoregions overall is low compared to incidence estimates for ecoregions receiving more intensive inventory. The Ridge and Valley ecoregion had over 20.1 % oak decline incidence based on about 1.6 million acres of vulnerable forest (806 plots). Western ecoregions of the CHR (Arkansas Valley, Boston Mountains, Ouachita Mountains, and Ozark Highlands) had among the lowest oak decline incidences (2.8–7.2 % individually; 5.1 % combined).

The geographic distribution of plots vulnerable to oak decline during the 1980s inventories (Fig. 3.3a) generally reflected oak density displayed in Fig. 3.1, with high oak concentrations throughout the Blue Ridge Mountains, Ridge and Valley, Ozark Highlands, Boston Mountains and Ouachita Mountains, and in portions of the Southwestern Appalachians and Interior Plateau. High density of plots vulnerable to oak decline did not, however, translate directly to high density of affected plots. Instead, these were concentrated in the northern Ridge and Valley in Virginia; the southern Blue Ridge Mountains in North Carolina; and on the Western Highland Rim area of the Interior Plateau in Tennessee (Fig. 3.3b).

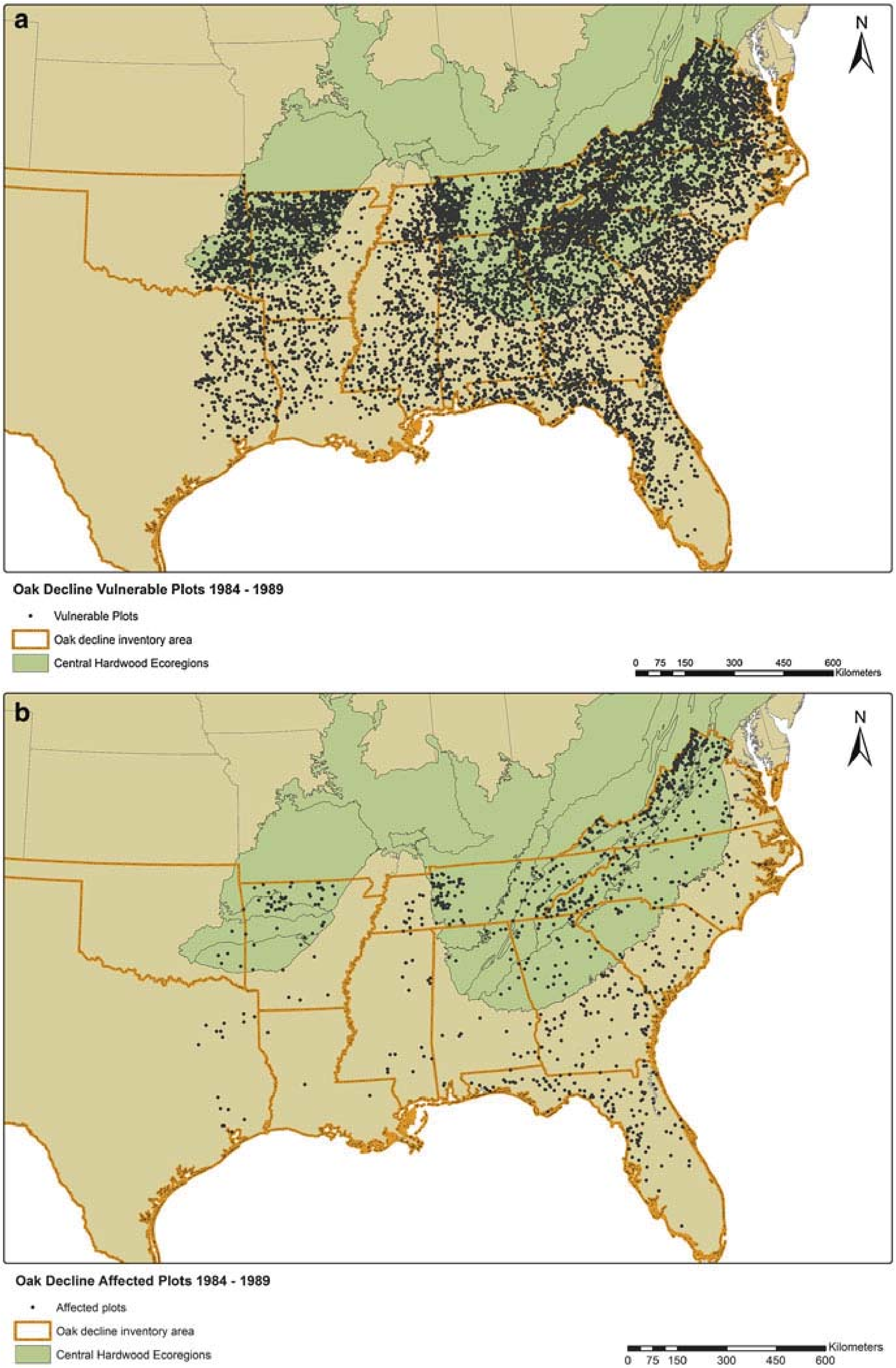

Fig. 3.3 Geographic distribution of USDA Forest Service FIA plots inventoried between 1984 and 1989 (**a**) vulnerable to and; (**b**) affected by oak decline within CHR ecoregions (Adapted from Oak et al. (2004); map credit to Ida Evretjarn)

The area vulnerable to oak decline increased in the 1990s over 1980s inventories by nearly 370,000 ha while affected area increased by 278,000 ha. A large increase in vulnerable area in the Southwestern Appalachians of more than 200,000 ha was offset by an equally large decrease in the Piedmont, with most of the net increase accounted for in the Boston Mountains and Ozark Highlands. Overall, incidence in inventoried CHR ecoregions increased to 12.7 % (Table 3.5). Incidence in the Ridge and Valley remained high while it increased markedly in the Blue Ridge Mountains (from 12.8 % incidence in the 1980s inventories to 21.3 % in the 1990s). Incidence nearly doubled in the westernmost ecoregions of the CHR (Ozark Highlands, Boston Mountains, Arkansas Valley, and Ouachita Mountains) from 5.1 % to 10.6 %, though the combined mean for these ecoregions was still slightly below the 1990s mean for the entire CHR. These inventories detected only the early stages of a very severe oak decline episode that would continue and intensify over the next decade (Starkey et al. 2000; Guldin et al. 2006; Fan et al. 2008, 2012). FIA inventories in Arkansas and Oklahoma which encompass the western ecoregions were conducted in 1995 and 1999, respectively (Hansen et al. 1992).

The increase in vulnerable area noted in Table 3.5 was barely detectable in the geographic distribution of vulnerable plots (Fig. 3.4a). However, increased density of affected plots was observed in the Blue Ridge Mountains ecoregion in western North Carolina and in the Ozark Highlands, Boston Mountains, Arkansas Valley, and Ouachita Mountains ecoregions of Arkansas and Oklahoma (Fig. 3.4b).

Fan et al. (2012) used 1999–2010 data from 6,997 FIA plots to examine spatial and temporal trends of oak decline across the Ozark Highlands of Arkansas and Missouri. This period marked the culmination of the oak decline episode first detected in the preceding inventory evaluated Oak et al. (2004). They found that mortality of red oak group species increased by 11 % of relative density and 15 % of relative BA while mortality among white oak group species remained comparable to non-oak species. Drought events were key inciting factors with unprecedented outbreaks of the red oak borer serving as contributing factors. The oak mortality response lasted up to 10 years after the cessation of inciting drought.

3.4.3 Oak Decline Effects on Forest Structure

An obvious and immediate change in oak abundance in overstory crown positions was noted following oak decline episodes due to mortality. Oak diversity was also reduced as a consequence of greater susceptibility of red oak group species relative to white oak group species. Long term changes in species composition are dependent upon canopy replacement of oak species by reproduction in competitive positions in the canopy gaps. Competitive advance oak reproduction (i.e., large seedlings and saplings) is lacking throughout CHR forests (Loftis 1983; Beck and Hooper 1986), as are disturbance regimes necessary for development and subsequent recruitment into the forest overstory (McEwan et al. 2011). As a result, oaks are

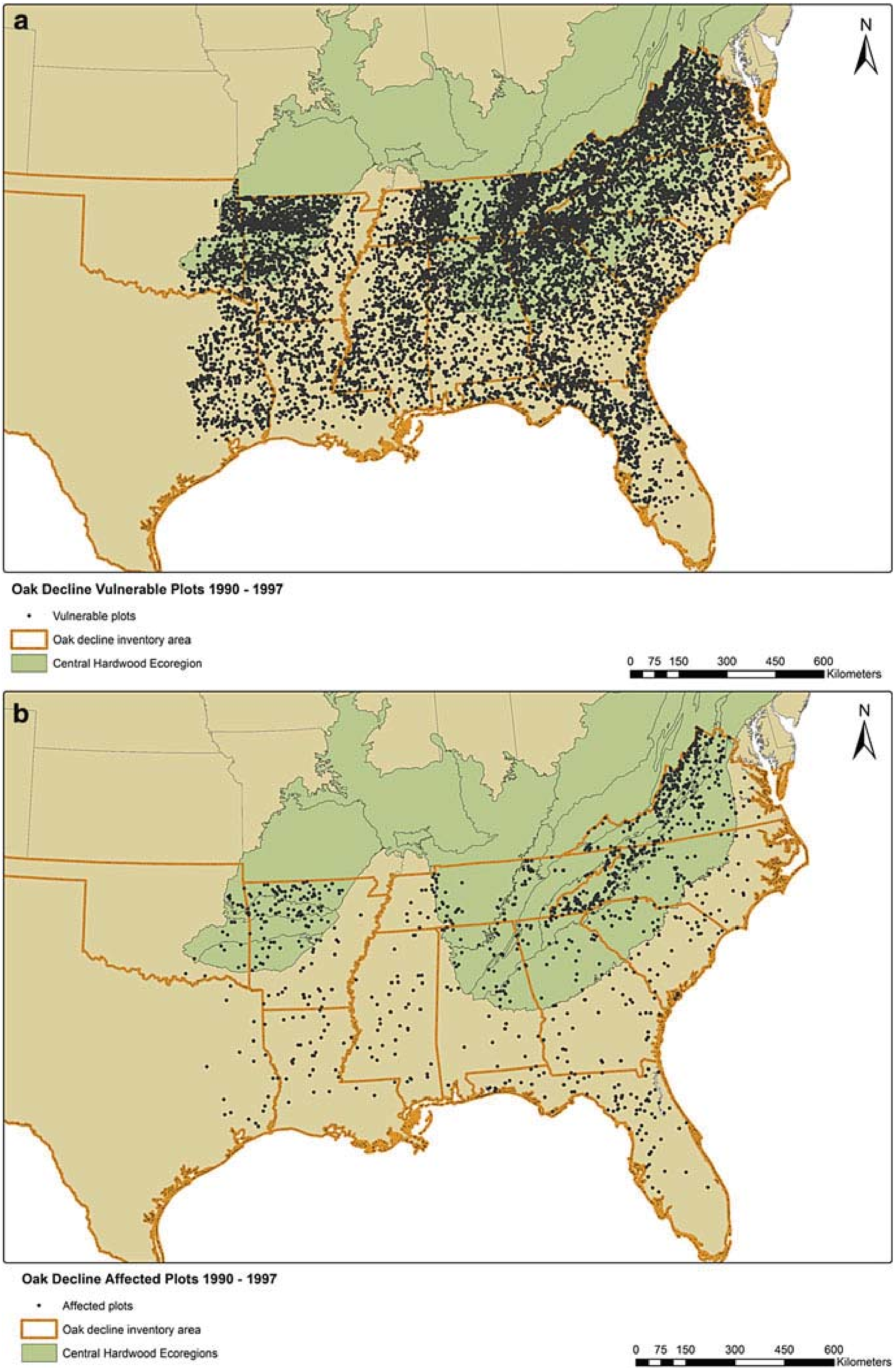

Fig. 3.4 Geographic distribution of USDA Forest Service FIA plots inventoried between 1990 and 1997 (**a**) vulnerable to and; (**b**) affected by oak decline within CHR ecoregions (Adapted from Oak et al. (2004); map credit to Ida Evretjarn)

already decreasing relative to other hardwood species (Abrams 1992; Aldrich et al. 2005; McGee and Hooper 1970; Loftis 1983; Beck and Hooper 1986). Oak recruitment into canopy positions after silvicultural disturbances is widely acknowledged to be problematic on more productive sites (McGee and Hooper 1970; Loftis 1983; Beck and Hooper 1986) but not on less productive sites (Roach and Gingrich 1968; Sander and Clark 1971). However, oak regeneration performance has been studied only in the context of silvicultural disturbances (e.g., clearcutting and shelterwood cutting, with or without treatment of competing vegetation). Whether these site productivity relationships and oak reproduction performance will hold following oak decline mortality, with or without silvicultural interventions, is unresolved. However, the relationship between the current importance values of oaks and maples and a regeneration index presented by McEwan et al. (2011) strongly suggests the oak composition will continue to decrease over a wide range of sites throughout the CHR under prevailing disturbance regimes.

3.5 Modeling and Managing Oak Decline Using the Forest Vegetation Simulator

The probability and severity of oak decline events in the CHR and effects on forest dynamics can be simulated using the Oak Decline Event Monitor (http://www.fs.fed.us/foresthealth/technology/od_rating.shtml), which was developed using data from extensive regional surveys of affected and healthy areas (Starkey et al. 1989; Oak et al. 1990; Oak and Croll 1995; Starkey et al. 2000). The Event Monitor runs within the structure of the Forest Vegetation Simulator (FVS), an individual-tree, distance-independent, growth and yield model (Dixon 2002). The probability of an oak decline event is computed from stand and site data (Oak et al. 1996), and mortality is scheduled according to the stand risk rating, with greater mortality scheduled for stands with elevated risk. Variants of FVS and the Event Monitor are available for the southern and central states sub-regions within the CHR. Table 3.6 displays output from simulation of a mixed oak stand in the Blue Ridge Mountains ecoregion of North Carolina using the Southern Variant of FVS. In this example, oak decline risk was high in the first simulation cycle and remained so through 7 cycles (35 years) Based on probability computed from stand and site factors, oak decline events were scheduled at the end of the second and seventh cycles (+10 and +35 years). Total stand BA was reduced by 8.3 m^2 per ha after the first event and by 6.4 m^2 per ha after the second. The effect on species composition was a depletion of the oak component from 84 % of stocking at the beginning of the simulation to 23 % after 10 cycles (50 years). The simulated changes in overall stand density and oak composition after the eighth cycle resulted in a reduction of decline risk to the low category.

FVS and the Oak Decline Event Monitor can be used to evaluate the potential of management actions for reducing oak decline risk and for mitigating changes

Table 3.6 Output selected from a 50-year simulation of a mixed oak stand in the Blue Ridge Mountains ecoregion, North Carolina. The probability of an oak decline event in a subject stand is calculated using a logistic regression (Oak et al. 1996) from stand and site factors collected during standard inventories. An oak decline event is scheduled (value of 1 in this table) when the calculated probability exceeds a generated random number between 0.00 and 1.00. The severity of the event is determined by oak decline risk classification (Oak and Croll 1995) and mortality is imposed based on expectations synthesized from numerous published local and regional oak decline assessments. Different mortality rates are imposed on red oak group species (highest mortality rate), white oak group species (intermediate mortality rate), and hickory species (lowest mortality rate). After imposition of mortality, stand growth is simulated using the appropriate regional FVS variant for the selected time interval (the Southern Variant at 5 year intervals for this case), and a new oak decline probability computed from the new stand attributes. Results were converted to metric units. In this simulation, oak decline events were scheduled at 10 and 35 years. The consequence of these events resulted in a reduction of oak BA from 18.86 m^2/ha (84 % of total stand BA) to 5.06 m^2/ha (23 % of total stand BA) after 10 simulation intervals (50 years). Oak decline risk was reduced to the low category after the +35 year oak decline event due a reduction of oak density resulting from cumulative mortality

			BA (m^2/ha)		
Time (years)	Risk	Decline event	Total	Oak	% Oak
+5	High	0	22.54	18.86	84
+10	High	1	23.91	19.78	83
+15	High	0	15.64	11.04	71
+20	High	0	17.02	11.50	68
+25	High	0	18.17	12.19	67
+30	High	0	20.01	12.88	64
+35	High	1	22.08	13.34	60
+40	Low	0	15.64	4.60	29
+45	Low	0	20.01	4.83	24
+50	Low	0	22.08	5.06	23

deemed detrimental for various desired future stand compositions and structures. Managers may choose to change outcomes by altering susceptibility (risk or probability of an oak decline event) or vulnerability (severity of damage should a decline event occur). Susceptibility is influenced by changing species composition while vulnerability is reduced by improving overall stand vigor through removal of trees likely to die in such a decline event. Fan et al. (2008) examined more than 4,000 randomly selected trees in the Ozark Highlands during an oak decline event from 2002 to 2006. They found that oak mortality was mainly related to crown width and amount of crown dieback and produced models useful for marking trees for thinning or harvest. Though intended for stands threatened by defoliation caused by gypsy moth, many prescriptions described by Gottschalk (1993) are useful for managing stands susceptible or vulnerable to oak decline. Spring defoliation is a major inciting factor in oak decline etiology, and the outbreak dynamics of this non-indigenous insect compared with native defoliators (outbreaks of longer duration, shorter return interval, and with more complete defoliation) have often resulted in catastrophic mortality from oak decline.

3.6 Summary

Oak decline has been recorded throughout the CHR since the 1800s. Affected contiguous areas may range from a few to thousands of hectares and severity also can be highly variable. Severe and recurrent damage has been reported in the Northern Piedmont, Blue Ridge Mountains, and Ridge and Valley ecoregions in the eastern CHR, and in the Ozark Highlands, Boston Mountains, and Ouachita Mountains ecoregions in the western CHR. Advanced physiologic age and drought are common interacting factors throughout, with catastrophic mortality occurring where gypsy moth defoliation has occurred in the eastern CHR, and more recently in concert with outbreaks of a contributing factor, red oak borer, in the western CHR.

Visible symptomology includes slow, progressive crown dieback from the top down and from the outside inward of trees in upper canopy positions followed by tree mortality and typically occurs over many years or decades. This crown dieback is an indicator of the progression of root disease belowground. These symptoms are the result of a complex of many interacting factors. Etiology includes issues that stress healthy trees and are classified into three general groups: predisposing, long-term factors that reduce tree resilience, inciting factors that add further stresses to trees invoking the decline event, and contributing factors that take advantage of stressed trees but by themselves do not invoke oak decline. There can be considerable variation in the combination of these factors from one decline event or area to another.

Composition and structure of CHR forests have been altered through the influence of human activity, forest management policies and introduced pathogens. Two influences are particularly notable. The loss of American chestnut by way of an introduced pathogen, and the reduced incidence of fire used as a cultural practice for millennia by people inhabiting the CHR have had far-reaching impacts on these forests. Changes include less complex age structure, more shade tolerant fire sensitive woody species, and a dense, relatively small-diameter overstory. Thus, what was once an ecosystem dominated by American chestnut and mediated by fire of mostly anthropogenic origin has been radically transformed. Land managers are presented with a dilemma concerning the role of humans in forest ecosystems when choosing the reference condition upon which to base management practices compatible with the 'historic range of variability' in natural disturbances, particularly concerning fire, non-indigenous plants, pathogens, and insects, and extirpation of native flora and fauna. The range of natural disturbance effects on the shape of forest composition and structure prior to human habitation of the CHR can only be generally inferred and ignores the reality of the past five to ten millennia (see Greenberg et al. Chap. 12). Alternatively, selecting a disturbance regime that includes human interventions along a spectrum from early aboriginal to contemporary times is a philosophical and arbitrary process. In any case, CHR forests cannot be termed 'natural' until the full suite of forest plants (including American chestnut) and animals (see Greenberg et al. Chap. 12) present before the arrival of humans in the CHR are restored and functioning as part of ecosystems.

Systematic surveys of oak decline began in the mid-1980s and were invaluable in elucidating its spatial and temporal context. In the southern half of the CHR, the oak decline-affected area was shown to encompass over a million hectares from 1984–1987 and 1.3 million hectares from 1990–1997. Survey methodologies were refined and standardized during this time, resulting in a more comprehensive understanding of decline events, revealing factors that may help in the prediction of future decline.

The most significant impact of oak decline is due to tree mortality resulting in major changes in forest structure and composition with red oak group species typically having much higher mortality rates than species of the white oak group. Drought has been a major inciting factor in oak decline across the CHR and the impact of the cumulative influence of drought on oak decline related mortality may last for decades.

Acknowledgments We recognize with gratitude the career contributions of Dale A. Starkey in helping to increase understanding of oak decline in the southeastern USA. The assistance of Anthony Elledge and Edwin Yockey in recovery of FIA oak decline assessment data is gratefully acknowledged. We thank Ida Evretjarn for GIS analysis of these data and production of map products.

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Vol 455 | 11 September 2008 | doi:10.1038/nature07276 nature

LETTERS

Old-growth forests as global carbon sinks

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Old-growth forests remove carbon dioxide from the atmosphere[1,2] at rates that vary with climate and nitrogen deposition[3]. The sequestered carbon dioxide is stored in live woody tissues and slowly decomposing organic matter in litter and soil[4]. Old-growth forests therefore serve as a global carbon dioxide sink, but they are not protected by international treaties, because it is generally thought that ageing forests cease to accumulate carbon[5,6]. Here we report a search of literature and databases for forest carbon-flux estimates. We find that in forests between 15 and 800 years of age, net ecosystem productivity (the net carbon balance of the forest including soils) is usually positive. Our results demonstrate that old-growth forests can continue to accumulate carbon, contrary to the longstanding view that they are carbon neutral. Over 30 per cent of the global forest area is unmanaged primary forest, and this area contains the remaining old-growth forests[7]. Half of the primary forests (6×10^8 hectares) are located in the boreal and temperate regions of the Northern Hemisphere. On the basis of our analysis, these forests alone sequester about 1.3 ± 0.5 gigatonnes of carbon per year. Thus, our findings suggest that 15 per cent of the global forest area, which is currently not considered when offsetting increasing atmospheric carbon dioxide concentrations, provides at least 10 per cent of the global net ecosystem productivity[8]. Old-growth forests accumulate carbon for centuries and contain large quantities of it. We expect, however, that much of this carbon, even soil carbon[9], will move back to the atmosphere if these forests are disturbed.

We conducted a literature search to test the hypothesis that old-growth forests continue to accumulate atmospheric carbon dioxide (CO_2). Site-level estimates of the annual sums of carbon-cycle components were compiled, including those of biometry-based net primary production (NPP), eddy-covariance or biometry-based net ecosystem production (NEP) and chamber-based heterotrophic respiration. The data set was completed with site information related to stand characteristics, standing biomass and stand age. Data were compiled from 519 plot studies that reported one or more components of the carbon cycle. The studies involved boreal (~30%) and temperate (~70%) forests and represented the full range of conditions of such forests, excluding those subjected to experimental treatments such as fertilization and irrigation (Supplementary Information, section 1.1). Tropical forests were excluded from the analysis because only 12 sites were found for which NEP and age estimates are available.

The NEP is the net carbon balance of the forest as a whole, and is the difference between CO_2 uptake by assimilation and losses through plant and soil respiration. On the basis of our global data set we find that in forests between 15 and 800 years old, the NEP is usually positive; that is, the forests are CO_2 sinks (Fig. 1a). The maximum probabilities of finding a single forest to be a source of carbon at 60, 180 and 300 years of age are 0.20, 0.25 and 0.35, respectively. However, the probability of finding an ensemble of ten old-growth forests that are carbon neutral is negligible (Supplementary Fig. 1). In the small number of case studies on the effect of age on the carbon balance of forests, several have demonstrated some age-related decline in NEP but very few have shown old forests to be sources[1,2,10–13]. Our NEP estimates suggest that forests 200 years old and above sequester on average $2.4 \pm 0.8\,\mathrm{tC\,ha^{-1}\,yr^{-1}}$ (tC, tonnes of carbon; Fig. 1a). In our model (Supplementary Information, section 1.3), we find that old-growth forests accumulate $0.4 \pm 0.1\,\mathrm{tC\,ha^{-1}\,yr^{-1}}$ in their stem biomass and $0.7 \pm 0.2\,\mathrm{tC\,ha^{-1}\,yr^{-1}}$ in coarse woody debris, which implies that about $1.3 \pm 0.8\,\mathrm{tC\,ha^{-1}\,yr^{-1}}$ of the sequestered carbon is contained in roots and soil organic matter.

The commonly accepted and long-standing view that old-growth forests are carbon neutral (that is, that photosynthesis is balanced by respiration) was advanced in ref. 6 and was originally based on ten years' worth of data from a single site[5]. It is supported by the observed decline of stand-level NPP with age in plantations[14,15], but is not apparent in some ecoregions[16]. Yet a decline in NPP is commonly assumed in ecosystem models (Supplementary Information, section 1.4). Moreover, it has led to the view that old-growth forests are redundant in the global carbon cycle.

If, however, the hypothesis of carbon neutrality[6] were correct, the expected probabilities of observing a sink or source would be equal and around one-half, the average sink strength for a random ensemble of forests 200 years old and above would be zero and the mean CO_2 release from heterotrophic respiration would equal the mean CO_2 sequestration through NPP (thus, the ratio of heterotrophic respiration to NPP would be approximately one). However, we observe this ratio to be well below one on average (Fig. 1b) and not to increase with age. Hence, all three quantitative tests fail to support the hypothesis of carbon neutrality. The currently available data consistently indicate that carbon accumulation continues in forests that are centuries old.

In fact, young forests rather than old-growth forests are very often conspicuous sources of CO_2 (Fig. 1a) because the creation of new forests (whether naturally or by humans) frequently follows disturbance to soil and the previous vegetation, resulting in a decomposition rate of coarse woody debris, litter and soil organic matter (measured as heterotrophic respiration) that exceeds the NPP of the regrowth[2,17–22] (Fig. 1b).

The scatter in the relationship between NPP and age is considerable, but given the climatic, edaphic and biological diversity of the observations in combination with differences in disturbance histories, this is to be expected. There is some degree of age-related decline in NPP beyond 80 years of age (Fig. 1c), and temperate and boreal forests both show a consistent pattern of declining NPP beyond an early maximum (Supplementary Fig. 2a) when analysed separately. The decline in NPP could be partly attributed to the presence or absence of management (Supplementary Fig. 2b). However, we expect that this decline is not strictly a management effect, but a

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reflection of differences in disturbance history between managed and unmanaged forests.

Consistent with earlier studies[2], biomass continues to increase for centuries irrespective of whether forests are boreal or temperate (Supplementary Fig. 3). In the course of succession, plants compete for resources and self-thinning[23] (or thinning by humans in the case of managed forests) occurs (Fig. 2), so the older stands contain a relatively small number of individuals, although of course these trees tend to be large. Obviously biomass cannot accumulate forever. Our data (Supplementary Fig. 3) suggest a possible upper limit somewhere between 500 and 700 tC ha^{-1} (equivalent to 1,400 to 1,800 cubic metres of wood per hectare); these high-biomass forests were located in the Pacific Northwest USA[16].

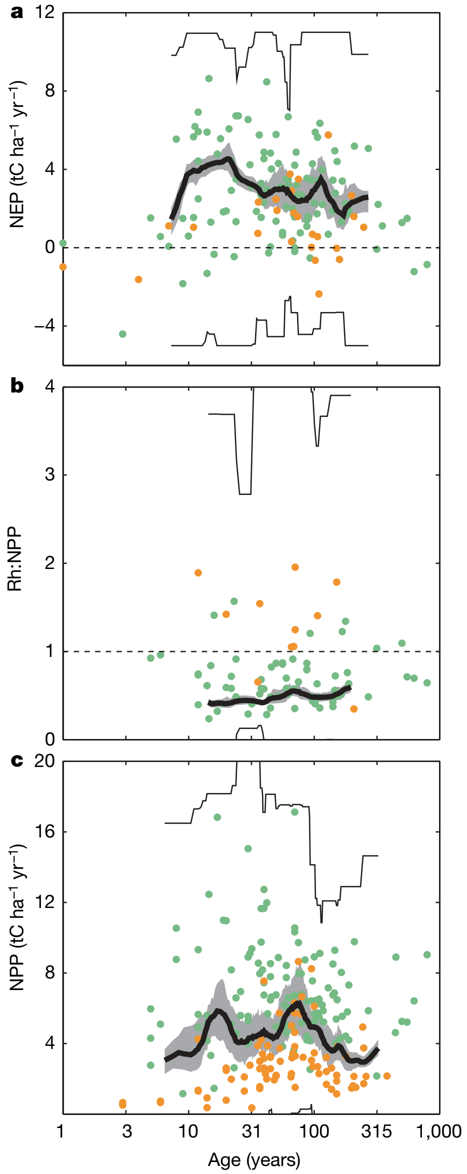

Figure 1 | Changes in carbon fluxes as a function of age. **a**, Observed NEP versus age; positive values indicate carbon sinks and negative values indicate carbon sources. **b**, Observed ratio of heterotrophic respiration (Rh) to NPP versus age; Rh:NPP < 1 indicates a carbon sink. **c**, Observed NPP versus age. It appears that temperate and boreal forests both show a pattern of declining NPP. Most probably, the late-successional increase in NPP is caused by the combination of data from different climate regions or the combination of disturbance regimes (Supplementary Fig. 2a, b). In each panel, the green dots show observations of temperate forests, the orange dots show observations of boreal forests, the thick black line shows the weighted mean within a moving window of 15 observations, the grey area around this line shows the 95% confidence interval of the weighted mean and the thin black lines delineate the 95% confidence interval (where visible) of the individual flux observations.

We speculate that when high above-ground biomass is reached, individual trees are lost because of lightning, insects, fungal attacks of the heartwood by wood-decomposers, or trees becoming unstable in strong wind because the roots can no longer anchor them. If old-growth forests reach high above-ground biomass and lose individuals owing to competition or small-scale disturbances, there is generally new recruitment or an abundant second canopy layer waiting in the shade of the upper canopy to take over and maintain productivity.

Although tree mortality is a relatively rapid event (instantaneous to several years long), decomposition of tree stems can take decades. Therefore, the CO_2 release from the decomposition of dead wood adds to the atmospheric carbon pool over decades, whereas natural regeneration or in-growth occurs on a much shorter timescale. Thus, old-growth forest stands with tree losses do not necessarily become carbon sources, as has been observed in even-aged plantations (that is, where trees are all of the same age). We recognize that self-thinning theory was originally developed and validated for even-aged single-species stands; however, it has been shown to hold for uneven-aged multi-species plant communities (Supplementary Information, section 1.3). In reasonable agreement with our observations (Fig. 1b), self-thinning theory predicts that the ratio between heterotrophic respiration and NPP is constant and around 0.65 ± 0.02 (indicating a carbon sink; Supplementary Fig. 4), as long as stand density is driven by small-scale, rather than stand-replacing, disturbances. Old stands, with sufficiently high densities (that is, through development of a multilayer canopy structure) are thus expected to maintain biomass accumulation for centuries. Hence, we postulate that biomass accumulation and decline are largely driven by stand structure.

A stand must be spared for centuries from stand-replacing disturbances (such as fires, insect outbreaks, wind-throw and avalanches) in order to accumulate sufficient aboveground biomass to become old growth. Because the cumulative probability of disturbances is higher in stands with high above-ground biomass, old stands are rarer than young stands, even in unmanaged landscapes. At the landscape level, we expect a mosaic of forests characterized by different times since the last stand-replacing disturbance[24]. Despite differences in age and density, these forests are, however, expected to follow the same relationship between biomass and density (Fig. 2).

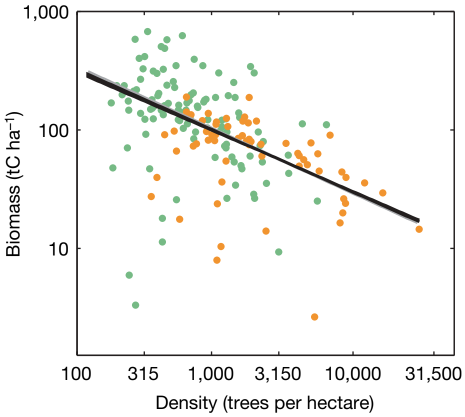

Figure 2 | Biomass accumulation as a function of stand density. Each data point represents a different forest, many of which have different growing conditions and tree species. Not all growing conditions and species compositions allow for the accumulation of the global maximum observed biomass. Self-thinning, the process of density-dependent mortality, is shown (solid line, of slope γ) as the relationship between the logarithm of above-ground biomass and the logarithm of stand density according to ref. 23 ($\gamma = -0.51 \pm 0.08$, $r^2 = 0.25$, $P < 0.01$). The green dots show observations of temperate forests, the orange dots show observations of boreal forests and the grey area (which is barely wider than the solid line) shows the 95% confidence interval of the median.

Under the Kyoto Protocol (http://unfccc.int/resource/docs/convkp/kpeng.pdf) only anthropogenic effects on ecosystems are considered (Article 2 of the Framework Convention on Climate Change (http://unfccc.int/resource/docs/convkp/conveng.pdf); Supplementary Fig. 5) and the accounting for changes in carbon stock by afforestation, reforestation and deforestations is mandatory (Article 3.3), operating from a base line of 1990. Leaving forests intact was not perceived as an anthropogenic activity. In addition, the potential consequences of excluding old-growth forests from national carbon budgets and from the Kyoto Protocol were downplayed in the carbon-neutrality hypothesis[6]. However, over 30% (1.3×10^9 ha) of the global forest area is classified[7] by the Food and Agriculture Organization of the United Nations as primary forest, and this area contains the world's remaining old-growth forests. Half (0.6×10^9 ha) of the primary forests are located in the boreal and temperate regions of the Northern Hemisphere. On the basis of our analysis, we expect that these forests alone sequester at least $1.3 \pm 0.5\,\mathrm{GtC\,yr^{-1}}$. Hence, 15% of the global forest surface, which is currently not being considered for offsetting increasing atmospheric CO_2 concentrations, is responsible for at least 10% of the global NEP[8]. Sporadic disturbances will interrupt carbon accumulation, implying that net biome productivity[25] will be lower, but it will remain positive as demonstrated by the accumulation of carbon in soils[4,26], coarse woody debris and charcoal[27,28].

The present paper shows that old-growth forests are usually carbon sinks. Because old-growth forests steadily accumulate carbon for centuries, they contain vast quantities of it. They will lose much of this carbon to the atmosphere if they are disturbed, so carbon-accounting rules for forests should give credit for leaving old-growth forest intact.

METHODS SUMMARY

We conducted a literature and database search to determine the fate of the carbon sequestered in forests. Observation-based estimates were compiled for carbon-cycle components, including biometry-based NPP, eddy-covariance or biometry-based NEP and chamber-based heterotrophic respiration[29]. The data set was extended with site information related to stand characteristics, standing biomass and stand age. In general, uncertainties in flux estimates were not reported in the literature. Therefore, we estimated the total uncertainty for every component flux contained in the data set using a consistent framework based on expert judgment (Supplementary Information, section 1.2). The uncertainty framework in our database was designed to account for differences in data quality between sites due to length of time series, methodology and conceptual difficulties (that is, gap filling and dark respiration). Also, an uncertainty of 20% was assigned to the biomass, age and density estimates. These uncertainties were propagated through the statistical analyses by means of random realizations based on Monte Carlo principles. Within each of the 1,000 random realizations, normally distributed random errors, based on the uncertainty framework of our database, were added to the observed fluxes. Therefore, all results that are based on flux data are reported as the weighted mean and the 95% confidence interval of the probability distribution.

Despite the climatic, edaphic and biological diversity of our observations, above-ground biomass was observed to be related to stand density in the way described by self-thinning theory[23]. Although, this theory was initially developed for even-aged single-species plant communities, we applied it to our data (Supplementary Information, section 1.3) to determine the components of the flux-computed NEP, specifically the above-ground biomass, woody debris and soil sequestration. Furthermore, self-thinning theory was used to calculate the theoretical ratio of heterotrophic respiration to NPP and compare it with the observed ratio in support of the hypothesis that biomass accumulation and decline are largely driven by stand structure.

Received 18 January; accepted 7 July 2008.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank all site investigators, their funding agencies and the various regional flux networks (Afriflux, AmeriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, ChinaFlux, Fluxnet-Canada, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia and USCCC), and the Fluxnet project, whose support was essential for obtaining our measurements. S.L. was supported by CoE ECO UA-Methusalem and the Research Foundation - Flanders (FWO-Vlaanderen) with a post-doctoral fellowship and a research grant. A.K. was supported by the European Union with a Marie Curie fellowship, and B.E.L. was supported by the regional North American Carbon Program project ORCA (US Department of Energy, Terrestrial Carbon Program, award number DE-FG02-04ER63917). E.-D.S. was supported by DFG-Exploratories. Additional funding for this study was received from CarboEuropeIP (project number GOCE-CT-2003-505572) and Ameriflux.

Author Contributions S.L., B.E.L., A.K. and P.C. compiled the data set. S.L., A.B. and D.H wrote code and analysed the data. S.L., E.-D.S., A.K., B.E.L., P.C. and J.G. designed the analyses and wrote the manuscript.

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1 Methods and materials

1.1 Data selection for this study

We compiled a comprehensive database (see §1.2) on carbon fluxes, ecosystem properties and stand characteristics of forest stands[29]. For this study, the database was queried for biometric-based NPP, chamber-based Rh, eddy-covariance or biometric-based NEP, their uncertainties and ecosystem attributes such as aboveground biomass, stand age, stand height and stand density. The quality of the data set used in this study was enhanced by excluding model-based flux estimates and flux estimates for fertilized and irrigated experimental treatments. Data from a total of 519 temperate and boreal forests that reported one or more of the variables were used in this study.

1.2 The database

A comprehensive relational database structure was designed to store information on carbon fluxes, ecosystem properties, and site information of forest stands. Data entries originated from peer-reviewed literature, established databases e.g.[30,31] and personal communications with research groups involved in regional networks (AmeriFlux, AsiaFlux, CarboEurope-IP, ChinaFlux, Fluxnet-Canada, NECC, TCOS-Siberia, USCCC), and the Fluxnet project[32]. The high quality of the database is ensured by several features: (i) referential integrity is ensured by the structure of the database, (ii) literature and databases are browsed without discrimination for sites, regions, biomes or climate zones; data selection is only based on strict methodological criteria, (ii) consistency of the NPP data is ensured by a hierarchical framework, (iv) uncertainty of the fluxes are estimated in a consistent manner accounting for the methodological approach and the length of the time series, (v) the uncertainty of aggregated fluxes is estimated, and (vi) a variety of observed and/or modelled meta-data is included in the database.

Structure of the database

The database is structured by site. A site is a forest or a stand with a known geographical location, biome (USA Department of Agriculture biome classification[33]), tree species composition and management regime. Hence, different treatments within an experimental forest or different aged stands that form a chronosequence were recorded as different sites. Each site in the database is linked to at least one carbon balance component and each component is further linked to the methodology that was used to estimate it. Due to its structure, the database can contain multiple estimates of the same flux for the same year (i.e. if these estimates were reported in different studies or estimated with different measurement techniques). Because data from different sources or references are stored as different entries, the structure of the database thus ensures referential integrity.

Selection criteria

NPP estimates were included in the database when they were based on direct measurements of the main components of NPP[34] if these achieved these criteria: the net annual production of leaves or needles was determined by collecting leaf/needle fall throughout the year; annual stem and branch increment were determined using species- and region-specific allometric equations relating aboveground woody biomass increment to the change in basal area of individual trees in the plot; and coarse-root production was determined through species- and region-specific allometric equations relating root mass to basal area and fine-root production was determined by repeated soil coring, isotopic estimates of fine-root turnover combined with biomass measurements, upscaled root-length production observed in minirhizotrons or the soil respiration and litterfall constraint formulated by Raich and Nadelhoffer (1989)[35]. Furthermore, to be included in the database, foliage, stem, branch, coarse and fine root biomass increment had to be corrected for the annual litterfall of these components.

Direct measurements of annual and multiple-year NEP were included in the database when based on continuous measurements with a tower-based eddy covariance system. NEP estimates were accepted when data gaps due to system failure, stable atmospheric conditions or data rejection were filled by means of standardized methods[36,37] to provide complete datasets. These data, however, do not include corrections for possible effects of advection, which may lead to a biased night time respiration even at high turbulence.

Biometric NEP estimates were included in our database when they were based on the difference between biomass production and heterotrophic respiration e.g. see[38] or repeated biomass inventories and soil respiration measurements e.g. see[39].

Estimates of heterotrophic respiration Rh were included in the database when based on subtracting chamber measurements from undisturbed plots from measured and up-scaled root respiration[40] or chamber measurements after trenching or girdling.

Consistency of the flux data

Although NPP data are more widely available than other carbon-flux estimates, there are considerable problems of consistency among NPP studies. Reported NPP values can range from the net primary production of a single component (e.g. foliage NPP) to the complete NPP of the ecosystem. In this study we accounted for these inconsistencies by combining 6 components and 4 aggregation levels of NPP in a hierarchical framework. For more details see Fig. 1 in[29]. At the lowest hierarchical level, stem and foliage NPP were used to calculate aboveground NPP ($ANPP_1$; foliage + stem NPP). The next hierarchical level included branch NPP. If branch NPP was measured, wood NPP (stem + branch NPP) and $ANPP_2$ (foliage + stem + branch NPP or foliage + wood NPP) were calculated. Coarse and fine root NPP were recorded as separate components and summed to obtain the below ground NPP ($BNPP_1$; coarse + fine roots NPP). If all required low level components were available, the total NPP ($TNPP_1$) was calculated as $ANPP_2$ + $BNPP_1$. The framework was considered hierarchical because a certain level of NPP was calculated only when all underlying components were measured.

Given this careful processing and quality evaluation of data for each site, the NPP data are consistent when a single level of NPP data is used. It should be noted that minor inconsistencies remain within an individual component (i.e. the use of different cut-off diameters between coarse and fine roots). However, the variation due to these inconsistencies is expected to disappear when NPP estimates of a higher level are used (i.e. the variation due to different cut-off diameters are expected to disappear when total belowground NPP ($BNPP_1$) is used).

Uncertainty of the measured CO_2-fluxes

Our flux data span multiple biomes and the data come from diverse sources. Different biomes have different sources of uncertainty[41,42]. Although recently efforts have been made to quantify the uncertainties of eddy covariance measurements[43-47], uncertainty of CO_2-flux estimates are only rarely reported in the literature and when reported it is often unclear whether the given value denotes instrumental, spatial, temporal and/or other sources of variability. Therefore, we did not use the reported uncertainty and instead estimated the total uncertainty for every component flux contained in the database. The uncertainty was estimated in a uniform way based on expert judgment[48]. We could not identify prior information that could constrain the absolute range of the estimated NEP. Without measurements or prior information, experts agreed that the NEP of a forest most likely ranges from -100 to 600 g C m^{-2} yr^{-1}. The absolute range of the NEP estimate is thus ± 350 g C m^{-2} yr^{-1} ([29]). However, all methodological approaches contained in the database used site-specific observations and are therefore expected to reduce the uncertainty surrounding the NEP estimates. Hence, the uncertainty was reduced with a method-specific factor. When NEP was determined by eddy covariance measurements the method-specific factor was set to 0.3 or 30% of 350 g C m^{-2} yr^{-1} to reproduce the uncertainty estimate of 105 g C m^{-2} yr^{-1} presented by[49-51]. The other method-specific reduction factors were then set between 0.2 and 1.0 and selected by expert judgment. The applied method-specific reduction factors (i.e. 30% for eddy covariance), are tabulated in[29]. When a flux was a multiple-year mean value, its value is less prone to inter-annual variability and therefore its uncertainty (s_{ij}) was further reduced by accounting for the length of the time series. Thus:

$$s_{ijl} = \left(p_i \times RF_j\right) \Big/ \sqrt{l_{ijl}} \qquad (1)$$

Where p_i is the initial uncertainty for site *i* in the absence of measurements (see Table 2 in[29]) and RF_j is the reduction factor for method *j* according to Luyssaert et al.[29] and l_{ij} is the length of the time series (in years) for site *i* for which the fluxes where estimated with method *j* in year *l*. Our uncertainty framework resulted in 95% confidence intervals (based on s_{ijl}) ranging between 105 and 350 g C m^{-2} yr^{-1} for NEP.

A similar approach was followed to estimate the uncertainty of NPP and Rh. However, for these fluxes the latitude of the site contained prior information regarding their absolute range (i.e. NPP at a boreal site is likely lower than the NPP at a temperate site [29]). Consequently, the absolute range for NPP in the absence of measurements depends on the latitude. For each site contained in the database the latitude was known and as such, the absolute range in the absence of measurements (p_i) could be estimated. This initial uncertainty was then reduced by the method-specific factor and further adjusted for the length of the time series. Our uncertainty framework resulted in 95% confidence intervals ranging between 110 and 545 g C m^{-2} yr^{-1} for NPP. This range compares to uncertainties reported for a single forest[34,52]. The 95% confidence intervals of Rh ranged between and 95 and 295 g C m^{-2} yr^{-1}.We are not aware of observation-based studies that report the uncertainty of Rh observations. Therefore, the spatial variability of Rh in the database (250 g C m^{-2} yr^{-1}) was used to validate the expert-based assessment.

Aggregated fluxes and their uncertainty

According to the analyses presented in this study the data had first to be aggregated by year and then by site. For a given site (i), a single weighted mean flux estimate (F) was produced for each available year l. When the flux component was determined with k different methods j in year l, the flux determined by method j for site i was then given as F_{ijl}. The average flux across methods (F_{il}) was calculated as the weighted mean:

$$F_{il} = \sum_{j=1}^{k} \left(w_{ijl} \times F_{ijl} \middle/ \sum_{j=1}^{k} w_{ijl} \right) \tag{2}$$

Where, $w_{ijl} = 1/s_{ijl}^2$. The uncertainty of the weighted mean was estimated by means of error propagation:

$$s_{il} = \sqrt{\sum_{j=1}^{k} s_{ijl}^4 \times w_{ijl}} \tag{3}$$

Following, the weighted mean flux component was calculated across years:

$$F_i = \sum_{l=1}^{m} \left(w_{il} \times F_{il} \middle/ \sum_{l=1}^{m} w_{il} \right) \tag{4}$$

Where, $w_{il} = 1/s_{il}^2$, m the number of years for which flux estimates are available for site i. The uncertainty of the weighted mean was estimated by means of error propagation:

$$s_i = \sqrt{\sum_{l=1}^{m} s_{il}^4 \times w_{il}} \tag{5}$$

Site description data

Additional site information related to stand characteristics, standing biomass, leaf area index and growing environment were added to the database as separate tables. Stand characteristics such as basal area, mean tree diameter, mean tree height, mean tree density and mean stand age are available for many sites. Also the observed standing biomass and its major components, the maximal observed leaf area index, and some methodological details of the leaf area measurement technique were available and stored in the database for many sites.

Availability of the database

The database its manual and appendices can be downloaded from ftp://ftp.bgc-jena.mpg.de/pub/outgoing/mjung/CfluxDB_Luyssaert/ and http://www.ua.ac.be/main.aspx?c=sebastiaan.luyssaert&n=35884

1.3 Self-thinning and data modeling

Self-thinning is the process of density-dependent mortality. For even-aged, single species stands Yoda *et al.*[23] proposed an empirical summary of this process:

$$W = c \cdot n^{\gamma - 1} \qquad (4)$$

where W is the mean biomass of an individual tree (g tree^{-1}), n the decreasing stand density (tree m^{-2}), and c a stand-specific constant (g m$^{2(\gamma-1)}$ tree$^{-\gamma}$) that dependents on species, light regime and nutrition status. The exponent γ (dimensionless) has been derived from tree geometry (i.e. height and ground area)[23]. The biomass per unit area (B; g m^{-2}) equals the product of W and n, therefore, the self thinning law for stands is derived by multiplying Eq. 4 by n:

$$B = c \cdot n^{\gamma} \tag{5}$$

Taking the logarithm of this equation yields a linear relationship:

$$\log(B) = \log(c) - \gamma \cdot \log(n) \tag{6}$$

For even-aged single-species stands γ was estimated at -0.5 ([23]) In Fig. 2 we used the functional relationship of Eq. 6 and estimated c and γ at the biome-level. During the life-time of a forest its density decreases from n_{start} to n_{end}, n_{end} -n_{start} individual trees will be lost. The biomass of each tree is given by Eq. 4 and the total loss of biomass (L) during the life-time of the forest is given by:

$$L = \sum_{nstart}^{nend} c \cdot n^{\gamma - 1} \tag{7}$$

At the same time the standing biomass increased according to Eq. 5:

$$G = c \cdot (n_{end} - n_{start})^{\gamma} \tag{8}$$

Self-thinning theory was originally developed and validated for even-aged single-species stands. Since it was first published, it has been shown to be equally valid for uneven-aged multi-species plant communities[53,54]. Applying Eqs. 4 to 8 to uneven-aged forests requires that the biomass of recruitment is negligible. In the old growth beech forest of Hainich[11] the upper canopy layer accounted for 91% of the biomass, the 2nd canopy for 9% and recruitment for less than 1%. Consequently, ignoring recruitment most likely will result in only small errors in G and L. There are no theoretical grounds for not being able to apply self-thinning estimates to multi-species plant communities because the primary driver of self-thinning is similarity in resource use[55]; the trade-off between density and size will be compensated among species[56]. Consistent with this, we observed that all boreal and temperate forests (Fig. 2), including the sub set of unmanaged boreal and temperate forests (not shown), followed the self-thinning theory with γ approaching -0.5. We interpreted this as a negligible effect of recruitment and species interactions on biomass and, therefore, used the observed relationship between biomass and density data to calculate a proxy for NPP and Rh components of flux-computed NEP. Nevertheless, these proxies were only used for interpretation of the primary results. Thus, all green and orange symbols (Figs 1, 2, S2, S3 and S4) are field-observations.

In this study, self-thinning theory was only applied to: (1) estimate the expected ratio between Rh and NPP across densities and (2) estimate the importance of woody biomass production in NEP of old forests. First, the gross biomass production (B_{gross}) (including branches, stem and coarse roots) is thus G+L. G, L and B_{gross} can be calculated for tree-by-tree changes in density from n_{start} to n_{end} (Fig. S5a). Following a change in density, the sequestered carbon is then given by the difference of B_{gross} before and just after tree mortality occurred. The carbon released through decomposition of woody debris is given by *L* (Fig. S5b). Assuming foliage and fine root NPP and their decomposition offset each other, allows us to apply $\Delta L{:}\Delta Bgross$ as a proxy for Rh:NPP (Fig. S5c). It should, however, be noted that legacy woody debris that existed prior to stand establishment is not included in our estimate of *L*. With a decomposition rate of 1 to 3% yr^{-1} [57], ΔL is likely to underestimate Rh for the first 30 to 100 years. Second, $\Delta Bgross$ (and ΔL) are expressed on a per tree basis (gC m^{-2} lost $tree^{-1}$) but need to be converted on a per year basis to obtain woody NPP (gC m^{-2} yr^{-1}). The observed maximum and minimum density for stands older than 200 years was used as n_{start} to n_{end} and the observed age range was used to determine the time required to realize this density decrease (lost tree yr^{-1}). $\Delta Bgross$, Δn and Δt were combined to estimate woody NPP (gC m^{-2} yr^{-1}) for forests of 200 years and older.

1.4 Odum's hypothesis as an implicit assumption in ecosystem models

The mathematical equation which governs NEP in models is $dM/dt = NPP - k \cdot M$ where, *M* is the carbon stock (g C m^{-2}), *k* is a decay rate describing the biomass mortality and soil carbon decomposition and *NPP* (g C m^{-2} yr^{-1}) is the net primary production. When the modeled leaf area index (LAI), atmospheric CO_2 concentration and climate are constant, NPP is also constant. During a spin-up, which is required to reach steady state, LAI, atmospheric CO_2 concentration and climate are constant. Hence, M approaches NPP/k and thus dM/dt (or NEP) is zero. In addition, modeled forests are usually mature but of unknown age. Consequently, in the absence of disturbances, ecosystem models predict that mature forests are carbon neutral and thus reflect Odum's hypothesis.

1.5 Data processing

The total uncertainty (s_i) for the flux contained in the data set were estimated using a framework based on expert judgment (See §1.2). The uncertainty framework was designed to account for differences in data quality between sites due to length of time series, methodology and conceptual difficulties (i.e. gap filling). The uncertainties were propagated throughout the analyses by means of random realizations based on Monte Carlo principles[58].

The 95% uncertainty interval for biomass, age and density was set to 20% of the observed values and the uncertainties for NPP, wNPP, Rh and NEP were extracted from the database. One thousand realizations of the dataset were simulated by adding a normally distributed uncertainty to the observed estimates for both the dependent and independent variable. The normally distributed uncertainties were calculated by multiplying the total uncertainty of the flux (s_i) by a normally distributed random number with a mean equal to zero and a variance equal to one. Following, each relationship or test between a dependent and independent variable was estimated a thousand times, once for each random realization.

For the relationships between age, NEP, Rh/NPP and NPP, the moving weighted mean was calculated for a moving window of 15 observations. For a given age we then plotted the mean value for all 1000 simulations (i.e. black line) and the 95% confidence interval of the mean value (i.e. gray area around the black line). For a given age, the confidence interval was estimated as the 2.5 and 97.5 percentile of the mean values of the 1000 simulations. Also for a given age, the 2.5 and 97.5 percentile of all 1000 random realizations for the individual sites within a window of 15 observations was used as the uncertainty to estimate the probability that an individual forest is a source rather than a sink.

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Supplementary figures

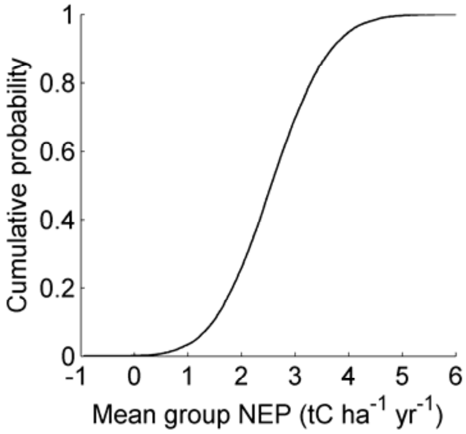
Figure S1. Cumulative probability of finding a given mean NEP for a group of 10 randomly selected forests older than 200 years. The minimal group NEP for forests older than 100 years was -0.5 tC ha^{-1} yr^{-1} with a probability of 0.0012 (negative value indicates a source), -1.1 tC ha^{-1} yr^{-1} for forests older than 200 years ($p = 0.0008$) and -0.9 tC ha^{-1} yr^{-1} for forests older than 300 years ($p = 0.0007$). Overlapping cumulative distribution functions (not shown) suggested that the results did not depend on the selected age threshold when set to 100, 200 or 300 years. The group probabilities were calculated by simulating 1000 possible realizations of the NEP data and their uncertainties.

Figure S2. Changes in net primary production (NPP) as a function of forest age (a) Relationships of observed NPP vs. age where green shows the temperate and orange the boreal forests. The thick black line shows the weighted mean within a moving window of 15 observations. The black lines above and below the weighted mean show the weighted mean NPP for temperate and boreal forests, respectively. The outer thin black line shows the 95% confidence interval of the individual flux observations. It appears that temperate and boreal forests each show a pattern of declining NPP. Only when the two data sets are combined is the late-successional increase apparent. This reflects the lack of data from boreal forests older than 300 years, considering that boreal NPP is usually lower than temperate NPP. The apparent increase in NPP is likely because the available estimates for the oldest forests are dominated by data from temperate regions that have higher average NPP; (b) Relationship between observed NPP and age where green shows the unmanaged and brown the managed forests. The thick black line shows the weighted mean within a moving window of 15 observations. The black lines above and below the weighted mean show the weighted mean NPP for managed and unmanaged forests, respectively. The outer thin black line shows the 95% confidence interval of the individual flux observations. NPP in unmanaged forests appears to be independent of age which could be due to differences in disturbance history.

Figure S3. Biomass accumulation as a function of stand age, shown as the relationship between aboveground biomass and the logarithm of stand age. The thick black line shows the weighted mean within a moving window of 15 observations. The grey area around this line shows the 95% confidence interval of the median. Each data point represents a forest stand (green is temperate, and orange is boreal), many of which have different growing conditions and species composition.

Figure S4. Productivity and productivity indexes derived from the self-thinning theory fitted to the observed biomass and density data. (a) Biomass losses (L; blue line), net biomass stock (B, red line) and gross biomass stock (B_{gross}, green line) as a function of stand density. (b) Changes in gross biomass and biomass losses expressed per tree lost as a function of stand density. (c) $\Delta L{:}\Delta Bgross$ (dotted line and dark confidence intervals) as a proxy of Rh:NPP. $\Delta L{:}\Delta Bgross$ which was obtained from the self-thinning plot (Fig. 2) is in reasonable agreement with the observed Rh:NPP (full line and light gray confidence intervals).

Figure S5. The reporting and accounting of carbon stocks under the UNFCCC is confined to national borders, because nations are the signing parties. Art. 2 of the UNFCCC calls for stabilization of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system[59]. Art. 4.2(a) clarifies that this should be achieved by national policies and taking corresponding measures on the mitigation of climate change, by limiting its anthropogenic emissions of greenhouse gases and protecting and enhancing its greenhouse gas sinks and reservoirs. However, unmanaged systems (red area) are traditionally considered to be carbon-neutral and therefore only managed ecosystems are considered within the Framework (cyan area). Nations have to report their carbon-stocks according to the rules set by the IPCC Good Practice Guidance which includes land-use types of Cropland, Grassland, Forest, Wetlands and Settlements (light and dark cyan area). Under the Kyoto Protocol the accounting of changes in carbon-stock by afforestation, reforestation and deforestation (ARD) is mandatory (Art. 3.3). In addition, Nations can select to account for changes of carbon-stocks in cropland, grassland, forest and revegetation projects (dark cyan area) or exclude certain regions (i.e. USA-Alaska). Most European countries have selected to include only forestry into their accounting system and thus not account for carbon-stock changes in agriculture. In addition, flexible mechanisms allow trading of carbon credits between countries. Nations can also receive credits from land-use projects funded in other industrial countries via the Joint Implementation (JI) mechanism. So far, the land-use sector is excluded from the European carbon trade. Also, afforestation projects funded in non-annex I countries may be added to the national carbon-balance via the Clean Development Mechanism (CDM), but this amount will be negligible until 2012.


Cumulative probability
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0.4
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Mean group NEP (tC ha^{-1} yr^{-1})

Figure S1

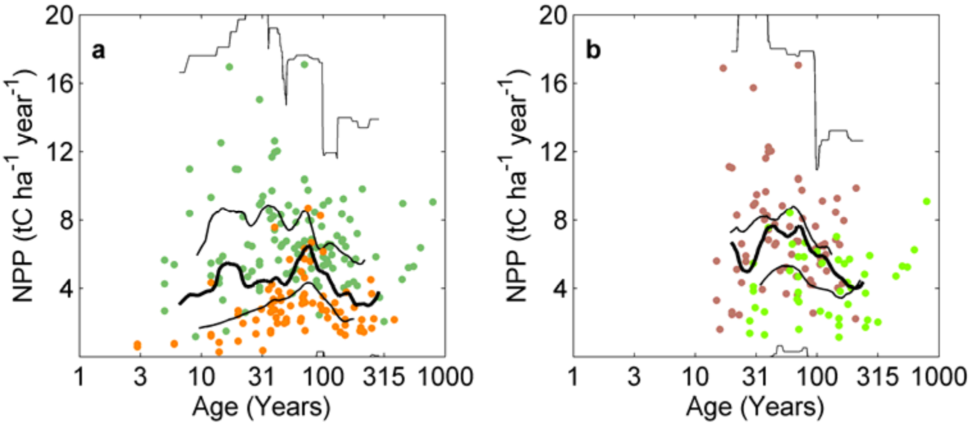
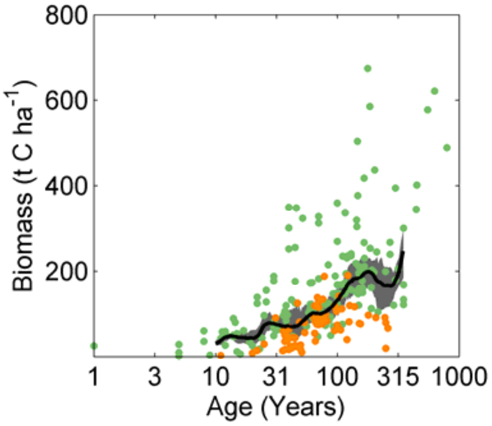


Figure S2



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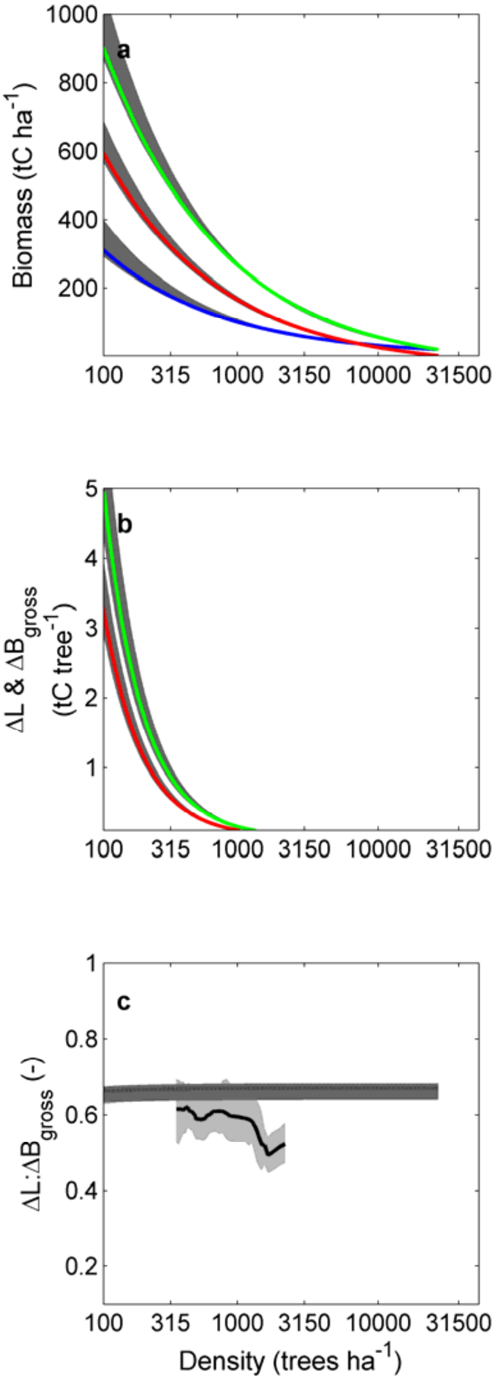
a
Biomass (tC ha^{-1})
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1000
3150
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b
ΔL & ΔB$_{gross}$ (tC tree^{-1})
5
4
3
2
1
100
315
1000
3150
10000
31500
c
ΔL:ΔB$_{gross}$ (-)
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0.6
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315
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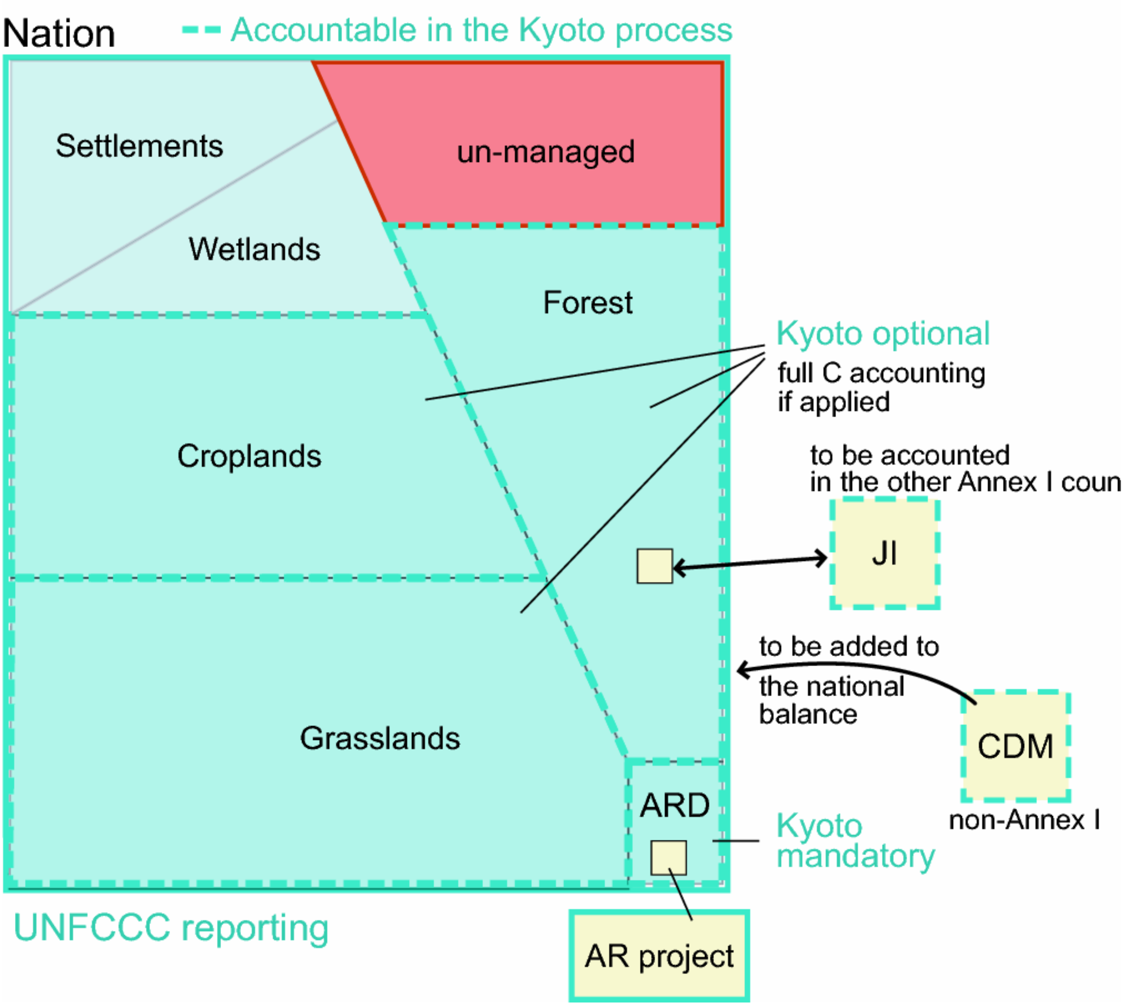
Density (trees ha^{-1})

Figure S4


Nation
Accountable in the Kyoto process
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Grasslands
to be added to
the national
balance
CDM
ARD
Kyoto
mandatory
non-Annex I
UNFCCC reporting
AR project

Figure S5

Oregon Forest Carbon Policy

Scientific and technical brief to guide legislative intervention

Center for
Sustainable
Economy
Analysis • Solutions • Advocacy

V1.0 12-11-17

I. Summary

- ✓ Timber harvesting is by far the largest source of greenhouse gas (GHG) emissions in Oregon. Since 2000, annual emissions associated with removal of stored carbon, sacrificed sequestration, and decay of logging residuals averaged 33 million metric tons carbon dioxide equivalent (mmt CO2-e). Nationwide, logging emits more carbon than the residential and commercial sectors combined.

- ✓ Yet in Oregon, across the US, and globally, timber harvest emissions are not reported or proposed for regulation because of a "carbon flux" accounting system developed by the timber industry that, in essence, grants an automatic offset for carbon sequestered by tree plantations managed in accordance with baseline legal requirements. No other sector is able to escape emissions reporting in this way.

- ✓ But sequestration by timber plantations and management in accordance with minimum requirements of Oregon's Forest Practices Act (OFPA) cannot meet two of the most basic tests for the validity of offsets: additionality and permanence.

- ✓ The additionality test cannot be met because where tree plantations have replaced natural forests all that has changed is a big increase in emissions with no corresponding increase in sequestration and storage capacity. Nothing has been added to nature's background rate of sequestration. Moreover, reforestation is the existing law, so there is nothing additional that it contributes. The permanence test cannot be met because tree plantations are simply emissions in waiting, released on increasingly short rotations. Because of this, timber harvest emissions should be reported and regulated on par with other sectors.

- ✓ Lack of ecological standards for state and private forestlands has resulted in a landscape dominated by short rotation timber plantations that store far less carbon than natural forests.

- ✓ These plantations also undermine climate resiliency because they are much more susceptible to drought, disease, wildfire, floods, landslides, low summertime streamflow, thermal pollution, fish kills, regeneration failures, exotic and invasive species and other climate change-induced impacts than natural forests.

- ✓ The lack of regulation has also resulted in a rapid increase in carbon sequestration "dead zones" – recently clearcut lands that emit more carbon than they absorb. Statewide, there has been a net loss of 1.7 million acres of forest cover since 2000 and much of this is due to a rapid rate of clearcutting.

- ✓ Cap and invest, forest carbon tax and reward, and an Oregon Forest Resiliency Act (OFRA) with a climate test for proposed logging operations are three workable legislative options to remedy this situation, incentivize climate smart forest practices, generate thousands of new jobs and vastly improve climate resilience.

Oregon Forest Carbon Policy

Scientific and technical brief to guide legislative intervention

Version 1.0: 12-11-17

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Content:

II. Key facts to guide legislative intervention

1. Timber harvesting is the single largest source of greenhouse gas emissions in Oregon taking into account (1) stored carbon removed from site and lost in the wood products manufacturing process and subsequent decay of final products; (2) the lost sequestration capacity of clearcut lands and logging roads, and; (3) emissions associated with decay of logging debris.

Timber harvest activities generate emissions associated with the loss of carbon stored on site, the foregone sequestration of clearcut lands, the decay and combustion of logging residuals (slash) left behind after harvest, application of chemical herbicides, pesticides and fertilizers, soil disturbance, transportation, and operation of equipment.

For this analysis, timber harvest emission calculations were limited to the first three sources since data on the amount, types, and frequency of chemical and fertilizer applications are lacking and since equipment and transportation emissions are generally assigned to other sectors (i.e. transportation and industrial processes) in existing greenhouse gas (GHG) inventory methods. Emissions from soil disturbance are also difficult to quantify at this time. So, for purposes of this analysis, timber harvest related emissions are calculated as follows:

ETH = (REM – STOR) + FS + DR, where

ETH = timber harvest related emissions (million metric tons CO2-e per year)
REM = CO2-e removed from site by timber harvest
STOR = CO2-e removed from site and stored in long-lived (100+ years) wood products
FS = Foregone sequestration from recently clearcut lands
DR = Decay and combustion of logging residuals

Timber harvest removals (REM)

The amount of forest carbon stored on site and removed by timber harvesting is reliably measured by multiple forest carbon monitoring platforms. The most ubiquitous is the Forest Inventory and Analysis (FIA) database managed by the USDA Forest Service. According to the most recent FIA data for Oregon, REM has averaged 34.75 mmt CO2-e per year between 2000 and 2015 (Appendix A).[1] An analysis by CSE, Oregon Wild, and Geos Institute generally corroborated the FIA data by combining forest carbon stock data from Woods Hole Research Center with forest cover loss (timber harvest related) satellite derived data from University of Maryland and World Resources Institute.[2] The CSE analysis found the value of REM on state and private lands in western Oregon to average 23.21 mmt CO2-e per year between 2000 and 2014, just slightly above the FIA estimates (23.16 mmt CO2-e) for that region (Appendix B).

Carbon stored in long-lived wood products (STOR)

Forest carbon removed from site during timber harvest has one of two ultimate fates over a 100-year period:[3] (1) through biomass combustion and decay of waste or wood products, it ends up in the atmosphere, or (2) a portion of it survives intact in long lived wood products like structural lumber or furniture or remains buried in landfills. STOR estimates the second. In a nationwide analysis, Ingerson (2009) estimated STOR to range from zero to 21% of REM depending upon assumptions about the disposition of harvested wood (Appendix C).[4] Forest Service data tables for the Pacific Northwest estimate that 40.9% of the embodied carbon in sawlogs is retained after 100 years in longer lived wood products and landfills and 7.6% of the

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[1] USDA Forest Service. 2016. Forest Inventory and Analysis (FIA) data for Oregon. Table 2A: Growth, removals, and mortality of CO2 equivalent, by ecoregion and owner class. Attached as Appendix A.

[2] Talberth, J., DellaSala, D., Fernandez, E. 2015. Clearcutting Our Carbon Accounts: How State and private forest practices are subverting Oregon's climate agenda. Lake Oswego, OR: Center or Sustainable Economy and Geos Institute. Page 56, attached as Appendix B.

[3] The 100-year framework is standard for GHG accounting in the US and for forest carbon offset projects. Generally, offset projects need to ensure that storage is guaranteed for at least this long. See, e.g. Ecotrust: A Landowner's Guide to Carbon Offsets (http://archive.ecotrust.org/forests/fco_intro.html).

[4] Ingerson, A., 2009 Wood Products and Carbon Storage: Can Increased Production Help Solve the Climate Crisis? Washington, DC: The Wilderness Society.

embodied carbon in pulpwood is retained 100 years after harvest in short lived wood products and landfills (Appendix D).[5]

A 2016 analysis found that about 52% of Oregon's timber harvest ends up as longer-lived wood products in the form of finished dry lumber, other sawn products, finished plywood or veneer, 41% to short-lived products and 7% to waste and shrinkage (Appendix E).[6] This suggests a weighted average value of STOR of (52% x 41%) + (41% x 7.6%) + (7% x 0%) =24.44%, largely corroborating Ingerson (2009). In its initial (2009) analysis of forest carbon issues, the Oregon Global Warming Commission assumed a value of 25% for STOR, which is adopted here as a placeholder pending more detailed review of the current disposition of Oregon's harvested timber (Appendix F).[7]

Foregone sequestration from clearcut units (FS)

When timber is harvested from a site, sequestration is reduced or eliminated until a new stand is established. All other factors held constant, the atmosphere will experience an increase in CO2 concentration merely because the carbon dioxide once removed from the atmosphere by forest carbon sequestration at the site of harvest no longer occurs. FS measures this indirect emission. Measuring FS is a standard technique for evaluating the carbon costs of land conversion, including conversion of natural forests to short rotation biofuel crops (Appendix G).[8] Consideration of foregone emissions and the loss of associated economic benefits is also consistent with federal guidelines for economic analysis, which require use of a "with and without" framework. In particular, for an analysis of a proposed federal action, including a federal logging project, the guidelines require consideration of the stream of sequestration benefits that would have occurred in its absence.[9]

Research has demonstrated that in western Oregon, where even-aged (clearcut) techniques prevail, sequestration capacity is eliminated for 13 years after harvest. In particular, net ecosystem productivity (NEP) – sequestration by young seedlings and brush minus emissions from decay and combustion of logging residuals – is negative for 13 years after clearcutting, meaning that these lands are not only carbon sequestration dead zones but net emissions

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[5] Smith, J.E., Heath, L.S., Skog, K.E., Birdsey, R.A., 2006. Methods for Calculating Forest Ecosystem and Harvested Carbon with Standard Estimates for Forest Types of the United States. Gen Tech. Rpt. NE-343. Morgantown, WV: USDA Forest Service, Northeastern Research Station.

[6] Simmons, E.A., Scudder, M.G., Morgan, T.A., Berg, E.C., Christensen, G.A. 2016. Oregon's Forest Products Industry and Timber Harvest 2013 With Trends Through 2014. Gen. Tech. Rpt. PNW-GTR-942. Portland, OR: USDA Forest Service Pacific Northwest Research Station.

[7] Kelly, P., 2009. A Greenhouse Gas Inventory of Oregon's Forests. Salem, OR: Oregon Global Warming Commission, Oregon Department of Energy.

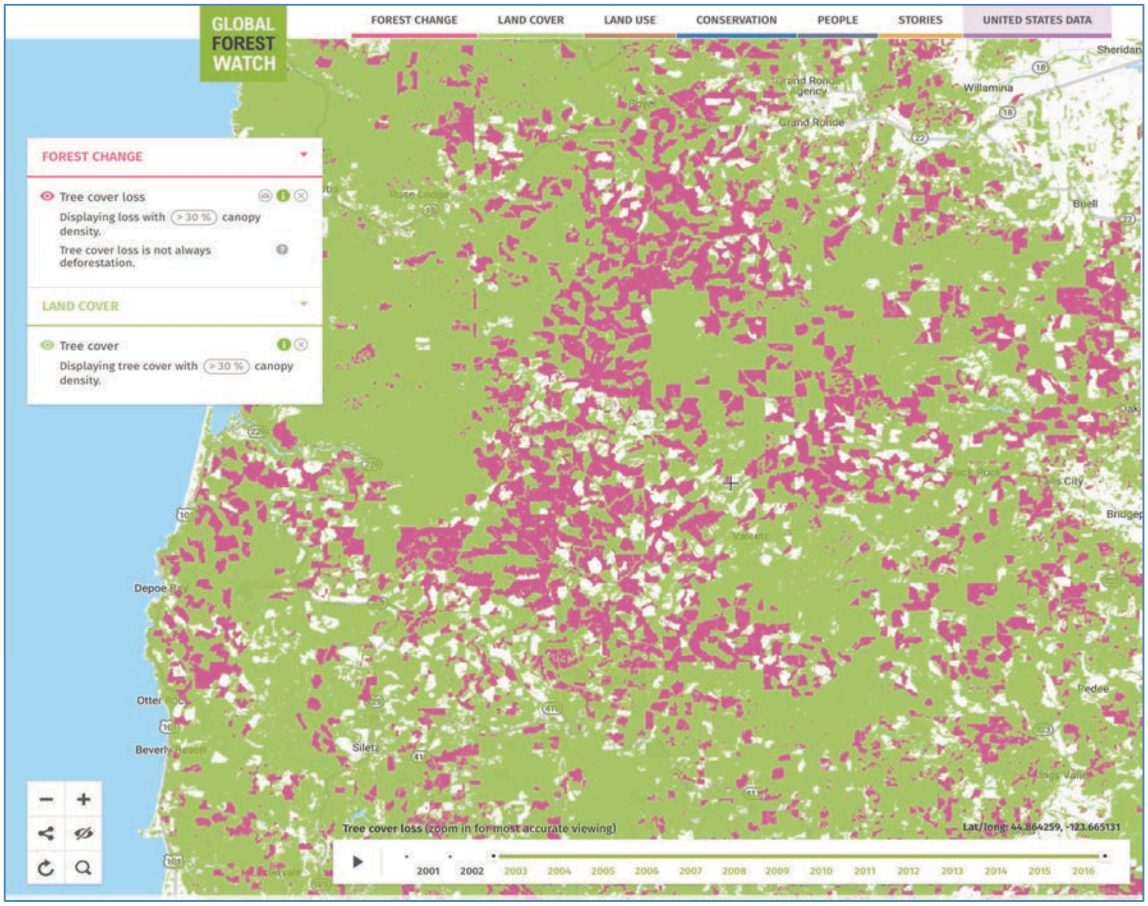
[8] Air Resources Board. 2014. Staff Report: Initial Statement of Reasons for Proposed Rulemaking. Appendix I, Detailed Analysis for Indirect Land Use Change. Sacramento, CA: California Environmental Protection Agency.

[9] Circular A-4 requires an analytical framework of with and without. Regulatory actions should be evaluated "by determining the net benefits of the proposed regulation with and without it." Circular A-4, Section E(3).

sources (Appendix H).[10] FS is simply the pre-harvest sequestration value multiplied by 13. Both the FIA data and the NEP data agree on a mean sequestration value for western Oregon state and private forestlands – 4.74 tCO2-e per acre per year. So total FS associated with a typical clearcut unit in western Oregon is 4.74 x 13 or, 61.62 tCO2-e per acre.

Satellite data can be used to estimate the amount of land clearcut each year and the amount of land in the 0-13 age class post harvesting. World Resources Institute's Global Forest Watch project (GFW) provides a convenient and easy to access tool to do this. It measures forest cover loss and gain annually and allows users to select the canopy closure thresholds particular to the forest type they are analyzing. Using GFW, the CSE/Geos analysis estimated an annual average rate of clearcutting of 91,529 acres on state and private lands in western Oregon alone after filtering out other sources of forest loss, such as wildfires and urban development. Multiplying this by the per acre forgone sequestration value implies an FS figure of at least 5.64 mmt CO2-e/yr from these lands.

Figure 1: Sequestration dead zones 2016, central Coast Range, Oregon
(*Areas in red were clearcut within the last 13 years and emit more carbon than they sequester*)



Displaying loss with (>30 %) canopy density.

Tree cover loss is not always deforestation.

Displaying tree cover with (>30 %) canopy density.

Tree cover loss (zoom in for most accurate viewing)

Lat/long: 44.864259, -123.665131

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[10] Turner, D.P., Guzy, M., Lefsky, M.A., Ritts, W.D., Van Tuyl, S., Law, B.E., 2004. Monitoring forest carbon sequestration with remote sensing and carbon cycle monitoring. *Environmental Management* 33(4): 457-466.

At the end of the analysis period (2000-2014), acreage in the 0-13 post-harvest age class was estimated to be roughly 1.2 million acres. And this figure is growing. An increase in the areal extent of carbon sequestration dead zones occurs when forest cover loss outpaces forest cover gain. CSE and Oregon Wild documented a net loss of over 520,000 acres in western Oregon alone since 2000.[11] Due to this effect, large portions of the Coast Range are now dominated by these sequestration dead zones (Figure 1). Statewide, since 2000, net forest cover loss (forest cover loss minus forest cover gain) is estimated to be 1.7 million acres – meaning that, as seen from the air, Oregon has 1.7 million acres less forest cover than it did in 2000 (Appendix I). As such, carbon sequestration capacity is decreasing at a fairly rapid rate.

Decay and combustion of logging residuals (DR)

As indicated in Appendix H, newly clearcut lands are net emissions sources, not sinks, for 13 years after harvest, largely as a result of the decay of logging residuals – slash, stumps, wasted logs and dead roots – as well as their combustion when burned. The NEP data can be used to calculate these emissions. An average value for western Oregon (combining data for the Coast Range and West Cascades) is 1.1 tCO2-e per acre per year. The CSE/Geos analysis estimates that, presently, there are about 1.2 million acres on state and private lands in western Oregon alone in the 0-13 age class post-clearcut harvest. This implies a current annual DR value of at least 1.32 mmt CO2-e.

Total emissions related to timber harvest (ETH)

Combining emissions associated with timber harvest removals (REM), storage in long-lived wood products (STOR), foregone sequestration (FS), and decay and combustion of logging residuals (DR) suggests that emissions associated with timber harvest (ETH) averaged 33.03 mmt CO2-e per year between 2000 and 2015 (Figure 2). This is a minimum figure since it includes an optimistic figure (25% for RES) and only assigns forgone sequestration to a portion of the landscape affected by clearcutting. Putting this figure into perspective, it represents by far the largest source of emissions statewide (Figure 3). Across the US, and just counting REM minus STOR, timber harvest emissions are larger than emissions from the residential and commercial sectors combined.[12]

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[11] Talberth, J., Fernandez, E., 2015. Deforestation, Oregon Style. Lake Oswego, OR: Center for Sustainable Economy.

[12] Moomaw, B., Smith, D., 2017. The Great American Stand. US Forests and the Climate Emergency. Asheville, NC: The Dogwood Alliance.

Figure 2: Components of timber harvest related emissions in Oregon (2000-2015 average)

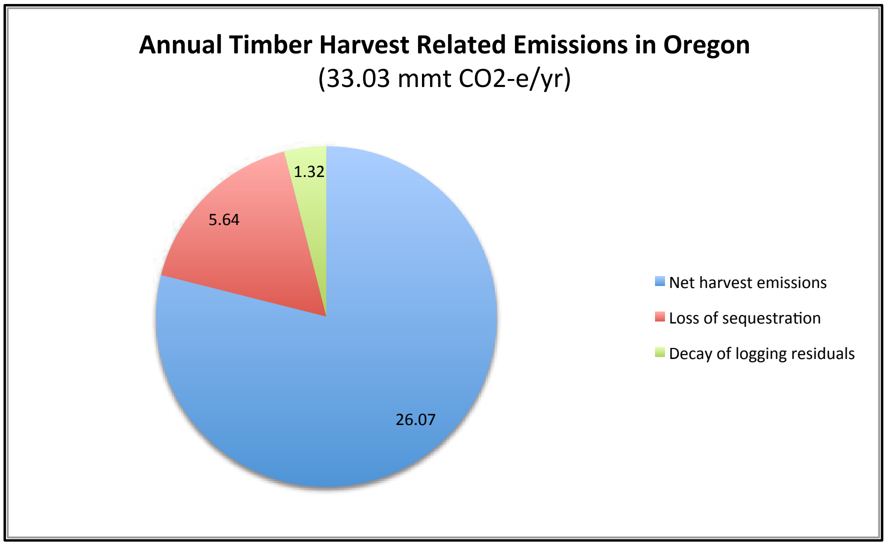
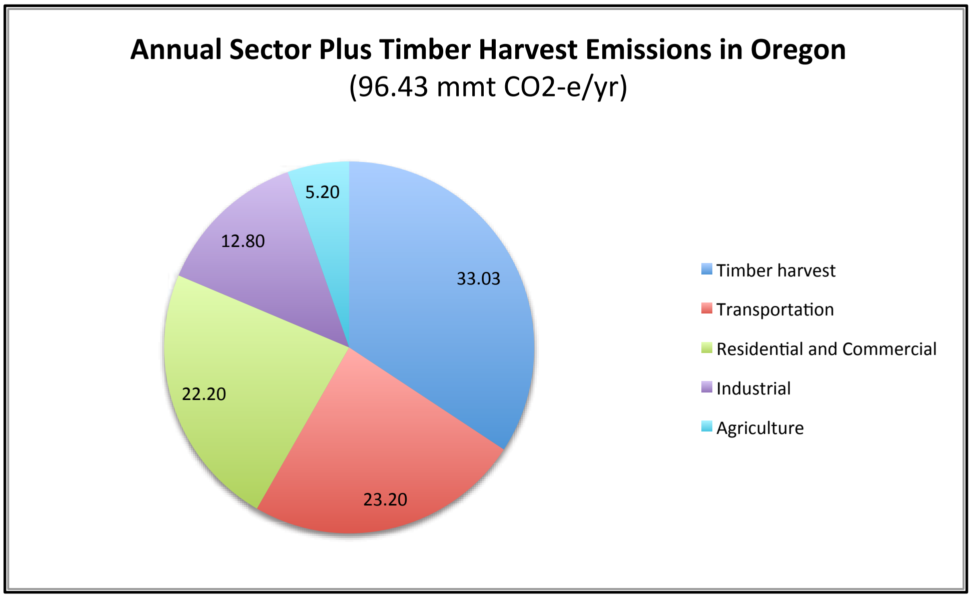


Figure 3: Timber harvest is by far the largest source of GHG emissions in Oregon each year



2. The timber industry has evaded responsibility for these emissions by developing a forest carbon accounting system that grants 100% offsets for carbon captured by short rotation timber plantations despite the lack of additionality or permanence associated with their management.

Given the complexities of forest carbon accounting international agencies allowed the timber industry to write its own rules. They were adopted as a subset of the GHG inventory rules for the broad Land Use, Land Use Change, and Forestry (LULUCF) sector adopted by the UN at COP 7 in Marrakesh in 2001. As noted by several NGOs who closely monitored the situation "[t]he rules agreed on LULUCF at COP7 in Marrakesh were designed largely by the forest industry and driven by Annex 1 Parties seeking to evade accounting for emissions in the agriculture, forestry and land use (AFOLU) sector and to reach their emissions targets more easily" (Appendix J).[13]

In the accounting rules, this is accomplished by a focus on carbon flux – the wrong policy metric – and by ignoring the potential to capture and store vastly more carbon on the land through improved practices. Carbon flux merely measures the ins and outs of carbon on the landscape year to year rather than what is being permanently stored relative to capacity. A Christmas tree farm or even a suburban lawn can be managed in a way to balance the ins and outs each year. In this way, the often-heard phrase "our forests capture more carbon than they emit" becomes a meaningless statement. However, the timber industry has been successful at making the argument that so long as ins and outs are balanced there are no net emissions to report and the sector need not be regulated.

And decision makers have fallen for that logic. The EPA has duly noted that "[i]n the United States overall, since 1990 land use, land-use change, and forestry activities have resulted in more removal of CO2 from the atmosphere than emissions. Because of this, the Land Use, Land-Use Change, and Forestry (LULUCF) sector in the United States is considered a net sink, rather than a source, of CO2 over this period."[14] The Oregon Global Warming Commission followed suit, with even more optimistic language in its Forestry Roadmap for 2020. It noted "Oregon's forests are a carbon sink, capturing more carbon than they release. As such, Oregon's forests and its forest sector have and will continue to contribute to the goal of achieving reductions in greenhouse gas emissions by remaining a robust and sustainable sector in Oregon."[15] As a metric to guide policy, the carbon flux approach is problematic for a number of reasons:

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[13] Global Witness, Wetlands International, Rainforest Action Network, The Wilderness Society. 2003. De-Constructing LULUCF and its Perversities. Published online at: www.ecosystemsclimate.org.

[14] US EPA. Sources of Greenhouse Gas Emissions. Land Use, Land Use Change, and Forestry Sector Emissions. Available online at: https://www.epa.gov/ghgemissions/sources-greenhouse-gas-emissions#land-use-and-forestry.

[15] Oregon Global Warming Commission (OGWC). 2010. Interim Roadmap to 2020. Salem, OR: OGWC.

- Storage is more important. Forest carbon storage (carbon density) relative to natural capacity is a far more important and policy relevant metric. This metric tells us how much more carbon can be removed from the atmosphere and permanently stored in service of leveling out and then reducing global CO2 concentrations back to the 350 parts per million (ppm) safe zone.[16] A zero carbon flux policy objective (making sure that on average, over time, emissions are balanced by sequestration) supports business as usual "catch and release" forest practices while one that sets targets for storage supports climate smart "catch and store" practices that are vital on the path to 350 ppm.

- No additionality. The timber industry has done nothing to deserve an effective 100% offset for carbon captured by its short rotation timber plantations. Reforestation is the law. So is management by the crude standards of the Oregon Forest Practices Act. If that's all that's being done, then there is no additionality. As defined by Senate Bill 557 (2017), additionality means that offsets "[m]ust result in greenhouse gas emissions reductions or removals that are in addition to greenhouse gas emissions reductions or removals otherwise required by law..".[17] Additionality is also an illusion because long before the timber industry came along, forests blanketing the state were already sequestering carbon. Nothing has been added to nature's background rate of sequestration.

- Nor is there permanence. A key aspect of valid offsets is that they must store carbon for at least 100 years. Rotations are approaching 35 years or less. Whatever carbon is being sequestered in these tree plantations is merely being stockpiled for release relatively soon.

- Bad actors are hidden from view. Good actors and bad actors are lumped together in one big "forest sector" that allows bad actors to evade detection and be credited with sequestration that occurs on lands they do not own. In particular, bad actors with high emissions from clearcutting are able to mask their emissions behind the sequestration accomplished on national forests and other relatively well protected lands – lands, ironically, that they have fought hard against protecting. Regardless of whether or not the forest sector as a whole sequesters more carbon on balance that it releases, the reality is that within this sector there are high carbon emitters that need to be regulated and phased out in order to widen the gap between sequestration and emissions and thereby quicken the accumulation of carbon stored permanently on the land.

No other sector now regulated or proposed for regulation enjoys the advantages conferred by this carbon flux approach. Other sectors must adhere to a strict process for qualifying anything

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[16] Rockstrom, J., Steffen, W., Noone, K., et al., 2009. A safe operating space for humanity: identifying and quantifying planetary boundaries that must not be transgressed could help prevent human activities from causing unacceptable environmental change. *Nature* 461, 24 September 2009, available online at: https://www.nature.com/articles/461472a.

[17] SB 557, 2017 Oregon Legislative Assembly § Section 9(3)b(B).

they do as offsets against their emissions. Rules for other sectors do not permit major emission sources (bad actors) to invoke emissions reductions by others (good actors) as an excuse for ignoring the former. The other major sector that both emits and sequesters carbon – agriculture – is not governed by a carbon flux approach. Instead, agriculture emissions are reported as just that – emissions, without invoking any of the sequestration that may be associated with crops, riparian zones, idled farmland, cover crops or other best management practices. And while agricultural emissions are reported alongside other sectors in the OGWC's biennial reports, the timber industry's emissions are conspicuously absent.

3. If allowed to mature, Pacific Northwest forests can capture and store more carbon per acre than any other major forest type on the planet. Old growth forests in western Oregon can store over 1,000 tons CO2-e per acre.

The Intergovernmental Panel and Climate Change (IPCC) has produced carbon storage metrics for 13 forest biomes within four global forest types: tropical, subtropical, temperate, and boreal. Pacific Northwest forests are part of the cool temperate moist biome, which is the most carbon rich biome on Earth with mean storage of 233 tons carbon per hectare (tC/ha).[18] This biome "default" value, however, includes both cutover and old growth lands and various forest types. Old growth forests in the Pacific Northwest store far more. Forest carbon density in Oregon's ancient forests has been found to top 1,000 tC/ha. For example, throughout the H.J. Andrews Experimental Forests, Seidel et al. (2012) found mean carbon storage in old growth to be 724.5 tC/ha, with maximum values over 1,200 tC/ha. The mean value is equivalent to 1,076 tCO2-e per acre (Appendix N).[19]

4. Vast improvements in carbon storage can be achieved on all forestlands in Oregon. A modest increase of 25% to 66% depending on ownership class could increase storage by over 3 billion metric tons CO2-e, equivalent to 50 years of Oregon's fossil fuel-related emissions.

Current carbon stocks are just a fraction of what existed in ancient forests that once dominated the landscape, and modest storage improvements can have globally significant benefits. Appendix M presents data from the most recent FIA estimates of carbon density on Oregon forestlands prepared for the Oregon Global Warming Commission.[20] In western Oregon, carbon density across ownerships is closely related to how intensively these lands are managed from a timber supply standpoint. Simple mean densities for two sub-regions – the Coast Range and Western Cascades – is at its lowest (108 tC/ac) for private industrial lands and highest (157

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[18] Keith, H., MacKey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biome carbon stocks and lessons from the world's most carbon-dense forests. PNAS 106(28): 11635-11640).

[19] Seidl, R., Spies, T.A., Rammer, W., Steel, E.A., Pabst, R.J., Olsen, K., 2012. Multi-scale drivers of spatial variation in old-growth forest carbon density disentangled with Lidar and an Individual-Based Landscape Model. Ecosystems 15: 1321-1335.

[20] OGWC, 2016. Table 5. Estimates of carbon stocks in Oregon by pool type, from FIA data 2001-2010 (soil C modeled), by ecoregion section and owner group.

tC/ac) for national forest lands. This range is 34% to 49% of an old growth reference value of 320 tC/ac.

Modest improvements in carbon density through implementation of climate smart practices can have a globally significant impact. There has been no systematic evaluation of what can be attained at this time. However, a hypothetical scenario that improves carbon storage by 25% on private industrial lands, 33% for non-industrial lands, 50% on state lands, and 66% on national forest lands could capture and permanently store over 3 gigatons (3 GtCO2-e). This is equivalent to about 50 years of currently reported emissions associated with fossil fuel combustion in Oregon.

5. Carbon emissions and low carbon storage are not the only climate concerns. Landscapes dominated by industrial tree plantations also undermine climate resiliency by accelerating the extinction of species that need real forests to survive and migrate, by increasing water temperatures, by decreasing summertime water flow, decreasing long term site productivity and by increasing the incidence and severity of wildfires, insect outbreaks, disease, and landslides.

Large swaths of the forested landscape in western Oregon are dominated by tree plantations.[21] Plantations also exist east of the Cascades, but represent a smaller share. The extent of these plantations is not monitored because state law and state forest inventory data do not distinguish between these plantations and natural forests. However, about 13.4 million acres in western Oregon are not legally restricted from timber harvest and on the vast majority of this land base natural forests have long been replaced by replanted stands.[22] The most intensively managed plantations are found on the 4.2 million acres of industrial (corporate) forestland in western Oregon.

From a climate policy standpoint, failure to address the extent and spread of timber plantations is a major gap because these plantations pose a grave risk to native ecosystems and forest dependent communities as climate change unfolds. This is because these plantations are far more vulnerable to drought, disease, wildfire, floods, landslides, low dry season streamflow, thermal pollution, fish kills, regeneration failures, exotic and invasive species and other climate change-induced impacts than natural late successional forests and riparian vegetation. For example:

- Depleted water supplies. Dry season stream flows are today dramatically depleted on a widespread basis across western Oregon and the Pacific Northwest as a consequence

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[21] Franklin, J., Johnson, K., 2012. A restoration framework for federal forests in the Pacific Northwest. *Journal of Forestry* 110(8): 429-439.

[22] Bansal, S., Brodie, L., Stanton, S., Waddell, K., Palmer, M., Christensen, G., Kuegler, O., 2017. Oregon's Forest Resources, 2001-2010: Ten Year Forest Inventory and Analysis Report. Gen. Tech. Rpt. PNW-GTR-958. Portland, OR: USDA Forest Service Pacific Northwest Research Station.

of extensive logging and vegetative regrowth in plantations following logging (Perry and Jones, 2016).[23] Long-term paired watershed experiments indicate that the conversion of mature and old growth conifer forests to plantations of native Douglas fir produced persistent summer streamflow deficit of 50 percent relative to reference basins, in plantations aged 25 to 45 years (BLM, 2017).[24] Climate change will make matters worse by further reducing dry season flows thereby straining "the ability of existing infrastructure and operations to meet the many and varied water needs of Oregonians."[25]

- **Water pollution**. As the climate warms and dries in the summer, Oregon's waterways will also warm. This thermal pollution is made worse by plantation forestry. Department of Forestry modeling concludes that a typical clearcut compliant with the OFPA on average, boosts water temperatures by 2.6 degrees Fahrenheit over and above any background increase due to climate change.[26] According to multiple federal agencies, "the evidence is . . . overwhelming that forest practices on private lands in Oregon contribute to widespread stream temperature problems."[27] Warmer water, in turn, will cause "harmful algal blooms to occur more often, in more waterbodies and to be more intense."[28]

- **Fish kills**. Salmon, steelhead, and trout are among Oregon's coldwater dependent fish that are already harmed by higher water temperatures, sedimentation, and hydrological changes caused by industrial tree plantations. Climate change will accelerate the loss of fish habitat on these lands by increasing the frequency and severity of storms that deliver high sediment loads to streams and periods when high water temperatures become lethal.[29] In 2015, over a quarter million salmon were killed by warm water as they returned to the Columbia River and its tributaries.[30]

- **Greater wildfire risk**. Timber plantations burn hotter and faster than natural forests. This is because they lack the moisture content and structural complexity needed to keep

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[23] Perry, T. D., Jones, J.A., 2016. Summer streamflow deficits from regenerating Douglas-fir forest in the Pacific Northwest, USA. *Ecohydrology.* 1-13.

[24] Bureau of Land Management, 2017. Environmental Assessment and Draft Finding of No Significant Impact for the Pickett West Forest Management Project. Grants Pass, OR: USDI Bureau of Land Management Grants Pass Field Office.

[25] Dalton, M.M., K.D. Dello, L. Hawkins, P.W. Mote, and D.E. Rupp, 2017 *The Third Oregon Climate Assessment Report*, Oregon Climate Change Research Institute, College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, OR, page 18.

[26] Oregon Department of Forestry (ODF), 2015. Detailed analysis: predicted temperature change results. Agenda Item 7, Attachment 3 to the meeting packet prepared for the Board of Forestry, June 3rd, 2015. Salem, OR: ODF.

[27] EPA-FWS-NMFS, 2/28/01 Stream Temperature Sufficiency Analysis Letter to ODF and ODEQ.

[28] US Environmental Protection Agency, "Climate change and harmful algae blooms," available online at: https://www.epa.gov/nutrientpollution/climate-change-and-harmful-algal-blooms.

[29] Dalton et al., 2017, op. cit. note 23, page 25.

[30] Ridler, K., 2015. "Hot water kills half of Columbia River sockeye salmon." Associated Press, published online on Oregon Live at: http://www.oregonlive.com/environment/index.ssf/2015/07/hot_water_killing_half_of_colu.html.

wildfires in check. Decades of monitoring by firefighters and researchers have shown that fires that burn in complex natural forests create a mosaic of intensely burned and relatively untouched areas. Conversely, fires that burn in homogenous tree plantations are more likely to be uniformly severe.[31]

- Landslides and flash floods. The vast network of clearcuts and logging roads that permeate industrial timber plantations present a big risk for landslides, especially during extreme precipitation events such as the 1996 floods. Under almost all climate change scenarios for Oregon, the frequency of these events will increase. Maintenance of strong root systems is an important factor in stabilizing soils during these events. Clearcutting reduces the strength of these root systems dramatically, and thus is a major factor in increased landslide risk.[32] Logging roads channel water runoff and result in debris torrents that can travel many miles downstream, pick up momentum, and cause widespread destruction.[33] Studies indicate that clearcuts exhibit landslide rates up to 20 times higher than the background rate. Near logging roads, landslide rates are up to 300 times higher than forested areas.[34]

- Invasive species. Invasive species find few barriers in monoculture tree plantations since key natural processes that keep these species in check have been removed. As succinctly stated by Norse (1990) "in monocultures, without barriers to dispersal, insects and pathogens find unlimited resources in all directions."[35] As Oregon's climate changes, a wide variety of non-native plants, insects, and disease-causing organisms, such as viruses, bacteria, prions, fungi, protozoans, and internal (roundworms, tapeworms) and external (lice, ticks) parasites will spread, and adversely affect the health of humans, livestock, and pets in addition to fish and wildlife. For example, a recent Forest Service assessment concluded "[e]vidence suggests that future climate change will further increase the likelihood of invasion of forests and rangelands by nonnative plant species that do not normally occur there (invasive plants), and that the consequences of those invasions may be magnified."[36]

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[31] See, e.g. Stone, C., Hudak, A., Morgan, P., 2008. Forest harvest can increase subsequent forest fire severity. In Proceedings of the Second International Symposium on Fire Economics, Planning and Policy: A Global View. Armando González-Cabán, ed. Riverside, CA: USDA Forest Service, Pacific Southwest Research Station.

[32] Schmidt, K.M, J. J. Roering, J.D. Stock, W.E. Dietrich, D.R. Montgomery, Schaub, T. 2001. The variability of root cohesion as an influence on shallow landslide susceptibility in the Oregon Coast Range. *Can. Geotech. J* (38): 995-1024.

[33] Swanson, F. J., J. L. Clayton, W. F. Megahan, Bush, G., 1989. Erosional processes and long-term site productivity, pp. 67-81 in *Maintaining the Long-Term Productivity of Pacific Northwest Forest Ecosystems*. D. A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C.R. Perry, R. F. Powers, eds. Portland, Oregon: Timber Press.

[34] Heiken, D., 2007. Landslides and Clearcuts: What Does the Science Really Say? Eugene, OR: Oregon Wild.

[35] Norse, E., 1990. Ancient Forests of the Pacific Northwest. Washington, DC: The Wilderness Society.

[36] Kerns, B., Guo, Q., 2012. Climate Change and Invasive Plants in Forests and Rangelands. U.S. Department of Agriculture, Forest Service, Climate Change Resource Center. Available online at: https://www.fs.usda.gov/ccrc/topics/climate-change-and-invasive-plants-forests-and-rangelands.

In addition to these risks, as climate change unfolds, the 1,100 or so species associated with late successional and old growth forests (LSOG) west of the Cascades need room to migrate – otherwise they are bottled up on federal lands where LSOG stands continue to be lost to logging and are threatened by climate change. To prevent these species from spiraling into extinction, timber harvest techniques need to change to halt and reverse the spread of biologically impoverished tree plantations and accelerate the development of LSOG conditions that could provide refugia for species displaced by adverse changes on federal lands.

6. Climate smart forest practices can significantly reduce emissions, enhance sequestration, build permanent storage, and increase climate resilience. These include forest carbon reserves, restoration of damaged and degraded land, alternatives to clearcutting, alternatives to chemicals and fertilizers, longer rotations, and various silvicultural practices that enhance sequestration of natural stands while building old growth characteristics.

The adverse effects of industrial forest practices on Oregon's climate agenda can be dramatically reduced by transforming these practices into climate smart alternatives. While the term 'climate smart' is a concept in need of further refinement it nonetheless is a useful one that can be applied to a number of specific practices that simultaneously reduce timber harvest emissions, increase permanent carbon storage on the land, and improve resiliency of the forested landscape. Rebuilding permanent carbon storage is key since it represents one of the few realistic pathways to reducing CO2 concentrations in the atmosphere back to the 350 ppm scientific safe zone. There are several general categories of climate smart practices that can accomplish these goals.

Forest carbon reserves

One obvious climate smart practice is setting aside all existing high-density forest carbon stocks as permanent reserves so that these stocks remain intact on the landscape rather than being released into the atmosphere through timber harvesting. Such high-density stocks – found mostly in late successional and old growth forests (LSOG) – make up a small fraction of the forested landscape in the Pacific Northwest. Within the range of the northern spotted owl, roughly 7% of the landscape exists in old growth forest condition, down from an historic distribution of between 30% and 70% at any one time.[37]

Most of the remaining endowment of LSOG forests on federal lands is administratively protected under existing management plans, however, loopholes in that protection coupled with increased pressure to reduce the extent of reserves by the Trump Administration is jeopardizing their status. On state and private lands, LSOG forests continue to be logged

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[37] Rapp, V., 2003. Science Update: New Findings About Old-Growth Forests. Portland, OR: USDA Forest Service, Pacific Northwest Research Station.

because there is very little protection under the Oregon Forest Practices Act or state forest practices laws in California or Washington. As a result, between 1994 and 2007, logging removed about 13% (491,000 acres) of what remains.[38]

Any climate policy designed to maintain and rebuild high density carbon stocks must halt any further loss and protect all remaining late successional and old growth forests from logging and other forms of anthropogenic disturbance. Forest carbon reserves should also include younger, highly productive forests that are likely to capture and store carbon rapidly while evolving into LSOG stands. Including forest carbon reserves in the portfolio of climate smart practices promoted under the state's climate agenda will help accomplish this goal.

Thinning dense tree plantations and other younger forests

Since carbon storage and resiliency to fires, drought, floods, and pathogens is maximized in LSOG forests, anything that can be done to put existing timber plantations and other younger forests on a trajectory to eventually develop LSOG conditions is smart climate policy. Importantly, this does not mean excluding timber harvest. To the contrary, in existing plantations and other younger forests it may require thinning in multiple entries over several decades to accomplish and thus provide a sustainable timber supply while rebuilding carbon stocks, improving climate resiliency, and enhancing other ecosystem services like water filtration and provision of fish, game, and non-timber forest products.

Over the past two decades, climate smart practices that accelerate the development of LSOG conditions from plantations have been field tested and verified, mostly on federal lands. For example, research in the Siuslaw National Forest has shown that thinning 30- to 35-year-old plantations to low densities and planting a mix of conifer seedlings can speed up development of old-growth characteristics in Douglas-fir forests.[39] There have been dozens of similar studies. Kerr (2012) provides a useful science synthesis on ecological restoration thinning techniques to accelerate the growth of large trees, create multiple canopy layers, increase understory plant diversity, and maintain deep crowns (branches growing well down the trunk). In moist forest plantations, he notes that "[t]he best available science concludes that [variable density thinning] VDT (leaving skips and gaps and using variable tree spacing, unlike an industrial thinning regime) can accelerate the onset of some characteristics of late-successional (mature and old growth) forests.[40]

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[38] Moeur,M., Ohmann J.L., Kennedy, R.E., Cohen, W.B., Gregory, M.J., Yang, Z., Roberts, H.M, Spies, T.A., Fiorella, M., 2011. Northwest Forest Plan, the First 15 Years (1994-2008). Status and Trends of Late-Successional and Old Growth Forests. Gen. Tech. Rpt. PNW-GTR-853. Portland, OR: USDA Forest Service Pacific Northwest Research Station.

[39] Chan, S.S., Larson, D.J., Maas-Hebner, K.G., Emmingham, W.H., Johnston, S.R., Mikowski, D.A., 2006. Overstory and understory development in thinned and underplanted Oregon Coast Range Douglas-fir stands. Can. J. For. Res. 36: 2696-2711.

[40] Kerr, A. 2012. Ecologically Appropriate Restoration Thinning in the Northwest Forest Plan Area. A Policy and Technical Analysis. Conservation Northwest, Geos Institute, Klamath-Siskiyou Wildlands Center, and Oregon Wild.

While thinning itself produces GHG emissions and reduces carbon stocks temporarily, it also accelerates the growth of trees left behind so over the long run carbon stocks accumulate not only in large, older trees, but in snags and downed logs that recycle stored carbon into the soil. In this way timber harvest and increased carbon storage are compatible. As noted by Busing and Garman (2002), "[t]hinning from below can expedite the development of large live and dead trees, and canopy height diversity without greatly diminishing wood quantity or quality."[41]

Alternatives to clearcutting, chemicals and fertilizers

As referenced earlier, clearcuts are carbon sequestration dead zones for roughly 13 years after harvest because emissions from the decay and combustion of logging residuals and losses of soil carbon outweigh any sequestration by seedlings and new growth (Appendix H). Moreover, the application of chemical herbicides and fertilizers used to suppress competing vegetation and enhance seedling growth in clearcuts generates additional carbon emissions above and beyond the emissions associated with timber harvest because they contain embodied carbon that is released into the atmosphere in a short period of time.[42] In addition, nitrogen-based fertilizers (urea being the most common) applied to forestlands increases atmospheric nitrous oxide, the third most harmful greenhouse gas behind methane and CO2.

Profitable, climate smart techniques that leave forest cover intact and obviate the need for use of chemical herbicides and fertilizers are routinely practiced by small scale, sustainable forestry operations Zena Forest, Hyla Woods and Shady Creek Forest Resources. Techniques include individual and group tree selection, small patch cuts, thinning, and management for a diverse mix of both hardwoods and softwoods.[43] Wood is removed but a forest is left behind. The practicality and ecological benefits of alternatives to conventional clearcutting have been extremely well documented.[44] The relative climate benefits of such practices are fourfold – (a) the areal extent of carbon sequestration dead zones is minimized or eliminated; (b) emissions associated with timber harvesting, chemicals, and fertilizers are reduced or eliminated; (c) the structural diversity and climate resiliency of stands improve, and (d) permanent carbon storage on the land is significantly higher.

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[41] Busing, R.T., Garman, S.L., 2002. "Promoting old-growth characteristics and long-term wood production in Douglas-fir forests." *Forest Ecology and Management* 160 (2002): 161-175.

[42] See, e.g. Lal, R., 2004. "Carbon emissions from farm operations." Environment International 30 (2004): 981-990.

[43] For a profile of these foresters and their techniques, see Segerstrom, C., 2017. Slow Wood: Reimagining the value and values of timber. *Eugeneweekly.com*, August 3rd, 2017. Available online at: http://www.eugeneweekly.com/20170803/lead-story/slow-wood.

[44] See, e.g. Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. "Alternative silvicultural approaches to timber harvesting: variable retention harvest systems." Chapter 7 in Kohm, K.A., Franklin, J.F., eds. Creating a Forestry for the 21st Century. Washington, DC: Island Press.

Long rotations

Even if conventional clearcutting and even aged practices are used, significantly extending rotation lengths (time between harvests) can mitigate many of the adverse impacts and flip high emissions landscapes back into those that accumulate and store high densities of carbon.

The ecological and economic benefits of long rotations have been extremely well researched and established. Curtis (1997) summarized a number of key benefits, including reduced land area in recent clearcut condition, larger trees and higher quality wood, less need for herbicides, higher quality wildlife habitat, more stable hydrological regimes (lower peak flows and higher dry season flows), enhanced long-term site productivity and improved carbon storage.[45] Economically, long rotations vastly improve the standing asset value of a forest. In an analysis of the effects of extended rotations on timber supply and three asset value categories – carbon, conservation, and standing timber – Talberth (2015) found that by extending rotation age from 40 to 240 years Oregon can boost the permanent value of state forestland in the northern Coast Range from roughly $3.9 billion to over $21 billion (Appendix L).[46] Modeled carbon stocks in a 240-year rotation regime were 3.5 times greater than the 40-year rotation baseline.

Extending rotation lengths is also critical for transforming bad actors into good ones from a carbon emissions standpoint. The key is the amount of land area in recent clearcut condition at one time – i.e. carbon sequestration dead zones. From a net ecosystem productivity (NEP) perspective, such lands are not only sequestration dead zones, but also significant net emissions sources due to the decay of logging residuals (Appendix H). Short rotations mean a greater areal extent of these carbon emitting dead zones since more land is clearcut each year relative to longer rotation lengths.

Appendix K and Figure 4 illustrate the effects of extended rotations on annual emissions using the timber harvest emissions approach summarized in Section 1. The bad actor scenario depicted here is modeled as an industrial forestland owner using conventional clearcutting practices on a 35-year rotation across its 10,000-acre ownership. The good actor scenario depicted extends that rotation length to 120 years. The analysis takes into account the area of land in recent clearcut condition (0-13 age class) at any one time, the foregone sequestration associated with those lands, the emissions on those lands from decay of logging residuals, timber harvest emissions, and sequestration by lands not affected by timber harvest in any one year. Appendix K provides details on all the key numerical assumptions. One key metric is the extent of carbon sequestration dead zones under each scenario. Under the bad actor scenario,

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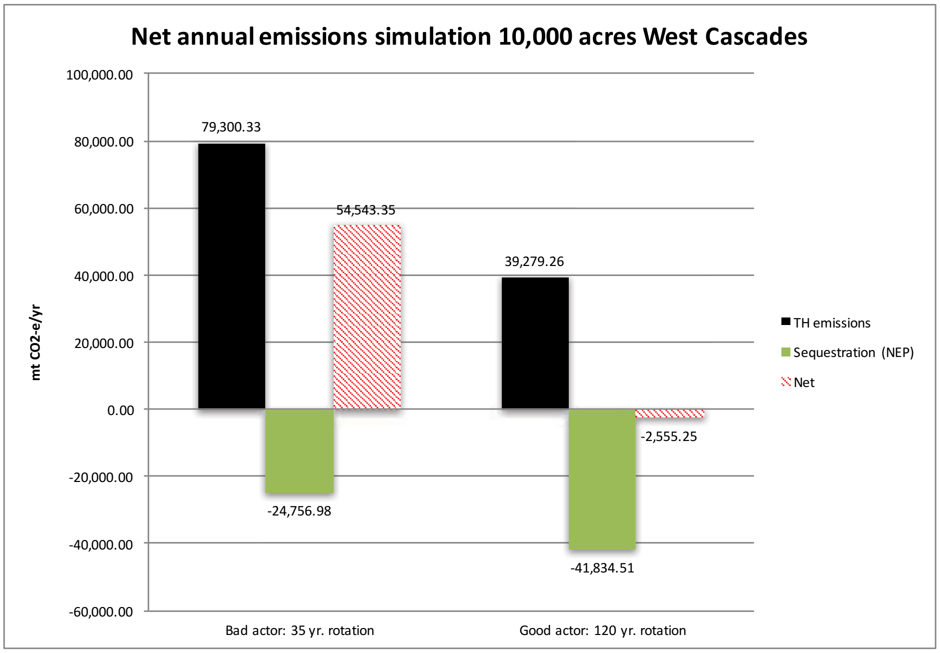
[45] Curtis, R.O., 1997. "The role of extended rotations." Chapter 10 in Kohm, K.A., Franklin, J.F., eds. Creating a Forestry for the 21st Century. Washington, DC: Island Press.

[46] Talberth, J., 2015. Testimony of Dr. John Talberth before the Oregon Board of Forestry. Subcommittee on alternative forest management plans for northwest state forests. October 19th, 2015. Lake Oswego, OR: Center for Sustainable Economy.

acres falling into the 0-13 age class are maintained at 4,000 acres per year, while under the good actor scenario this figure is 1,667 acres.

The analysis is preliminary, and since use of NEP is a significant departure from using conventional measures such as net primary productivity (NPP) as a basis for sequestration, will need to be validated through other methods and reconciled with mass balance requirements since the short rotation scenario implies a steady reduction in carbon density over time.[47] Nonetheless it suggests that moving from a 35 to a 120-year rotation has the potential to transform intensively managed ownerships from significant net sources of carbon emissions (>54,000 mtCO2-e/yr) to ones that sequester more CO2 than they emit (<-2,555 mt CO2-e/yr) and thereby build carbon density over time.

Figure 4: The effects of extended rotations on net annual carbon emissions of a typical managed landscape in the Oregon Cascades



Afforestation

Afforestation is the process of establishing forests where they do not presently exist because the land has been converted to other uses or because forests were not established there by natural processes. There has been no assessment of afforestation potential in Oregon, however, one way to consider the potential is to retrace how much forestland has been

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[47] The mass balance requirement is simply the law of conservation of matter and energy. If short rotation plantations deplete carbon storage over time then it is important to understand what carbon pools are being drawn down (i.e. soils and live trees) and what pools are increasing (atmosphere) and how these balance over time.

converted to agricultural land since it can theoretically be reverted back to forest and ecologically sustained.

In the Willamette Valley, for example, historic records show that 59% of the land base was occupied by forests, woodlands, and pine-oak savannas.[48] Today, forests and woodlands account for just 34%.[49] The native pine-oak savanna has been reduced to just tiny fraction of its original extent. So the afforestation potential is there. But a good portion of this land is now in high-value agricultural uses that will be costly to convert back to forests. The afforestation potential is greater, however, on marginal, frequently idled, and non-food producing farmlands such as grass seed and Christmas tree farms since the opportunity costs are much less. Additional afforestation opportunities may be found on residential lands in rural and suburban areas, since many of these properties include large, undeveloped open spaces that are not presently sustaining any intensive land uses.

7. The timber industry argues that if wood products consumption falls, it will be replaced by more carbon intensive substitutes. But there are many less carbon intensive alternatives to Oregon's wood products including solar and wind instead of biomass for energy, conservation, efficiency, bamboo and other alternative fibers for paper products, and recycled and reused materials.

The timber industry often makes the claim that reducing its harvests to protect environmental values will have the unintended consequence of increasing consumption of substitutes that have a higher carbon footprint. Using wood in buildings rather than concrete or steel, or using biomass for energy rather than fossil fuels are the most often cited examples.[50]

In buildings, there is ample documentation to show that life-cycle emissions associated with wood relative to concrete and steel are lower. But these analyses lack data on forest practices at the source. For example, wood derived from deforestation or the conversion of old growth forests to tree plantations carries with it a high carbon footprint that lasts generations and overshadows any beneficial substitution effect. Moreover, most studies fail to account for the fact that storage in wood products is only temporary, requiring replacement down the road with a renewed cycle of timber harvest emissions and reduced sequestration capacity.

For biomass to energy, many studies show that it is just as bad or even worse than burning coal. In a recent report issued by Chatham House, researchers found that "[o]verall, while some instances of biomass energy use may result in lower life-cycle emissions than fossil fuels, in

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[48] Christy, J.A., Alverson, E.R., 2011. "Historical vegetation of the Willamette Valley, Oregon, circa 1850. Northwest Science 85(2): 93-107.

[49] Wilson, T.S., Sorenson, D.G. Willamette Valley Ecoregion Summary. USGS Land Cover Trends Project, available online at: https://landcovertrends.usgs.gov/west/eco3Report.html.

[50] See, e.g. Wilson, J., 2006. Using wood products to reduce global warming. Chapter 7 in Forests, Carbon and Climate Change. A Synthesis of Science Findings. Oregon Forest Resources Institute, OSU College of Forestry and the Oregon Department of Forestry.

most circumstances, comparing technologies of similar ages, the use of woody biomass for energy will release higher levels of emissions than coal and considerably higher levels than gas."[51] The notion that biomass is somehow a clean fuel has been widely discredited.

For these and other reasons, several studies have come to the conclusion that taking land out of timber production and putting it into conservation status has a net climate mitigation benefit, even after taking these substitution effects into account.[52]

Moreover, for most wood product end uses, there are many less carbon intensive substitutes available, including solar and wind instead of biomass for energy, bamboo and other alternative fibers for paper products, and recycled and reused materials. Relative to wood, the climate benefits of these alternative fibers have been well established. For example, fast growing bamboo plantations grown on agricultural lands have been shown to be carbon neutral or even carbon negative thereby reducing pressure on forests so they can be left to accumulate carbon.[53] Industrial, non-cannabis hemp has a wide diversity of end uses that can displace wood derived paper and building materials and result in substantial carbon savings.[54] The assumption that all wood substitutes are more carbon intensive is unfounded.

The bottom line is that logging to produce wood products of any kind generates significant carbon emissions and reduces carbon sequestration capacity with certainty while the climate mitigation benefits of substituting wood for other materials is speculative and extremely case dependent. As a result, the practice of promoting wood products as a climate solution regardless of how they were sourced and regardless of the end use has no scientific validity.

III. Legislative options

8. Legislative interventions consistent with global climate change mitigation goals should simultaneously reduce timber harvest related emissions, enhance sequestration, increase permanent carbon storage, and improve climate resiliency.

Legislative interventions are needed to enroll the timber industry into Oregon's climate agenda because the Oregon Forest Practices Act does not include any relevant statutory provisions.

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[51] Brack, D., 2017. Woody Biomass for Power and Heat: Impacts on the Global Climate. London, UK: The Royal Institute of International Affairs, Chatham House.

[52] See, e.g. Keith, H., Lindenmayer, D., Macintosh, A., Mackey, B. 2015. Under what circumstances do wood products from native forests benefit climate change mitigation? PLoS ONE 10(10): e0139640., doi:10.1371/journal.pone.0139640

[53] Vogtlander, J.G., Van der Lugt, P., 2015. The Environmental Impact of Industrial Bamboo Products: Life-cycle Assessment and Carbon Sequestration. INBAR Technical Report No. 35. The Netherlands: MOSO Research and Development Center and the Delft University of Technology.

[54] Johnston, S., 2016. The Environmental Benefits of Industrial Hemp. Nellysford, VA: Virginia Industrial Hemp Coalition.

Nor can voluntary agreements or incentives like carbon offsets have much of an impact because they are at present and likely to remain very limited in scope, and effectiveness.

During the 2018 legislative session, there are three legislative approaches that have been suggested by CSE and its partners to simultaneously advance four essential forest carbon goals as swiftly as possible (1) reducing emissions from logging; (2) enhancing sequestration capacity; (3) increasing permanent carbon storage back towards natural capacity, and (4) expediting the restoration of industrial tree plantations into climate resilient forests. The approaches, explored in more detail below, include cap-and-invest, forest carbon tax and reward, and an Oregon Forest Resiliency Act.

9. Legislative option 1: Enrolling forestland owners who are major greenhouse gas emitters into emerging cap-and-invest legislation (SB 1070).

The cap and invest approach has been drafted into legislation in the form of SB 1070, at the time of this writing.[55] The approach is synonymous with cap and trade, and is built around a system of declining allowances for CO2 emissions from major sources, auctions of excess allowances, investment of auction revenues into various funds that advance climate mitigation and adaptation goals, use of offsets where compliance is prohibitively expensive and penalties for noncompliance. Major sources include those that generate 25,000 mt CO2-e per year from their use of electricity, fossil fuels and industrial processes. It has been estimated that 100 facilities and businesses would be regulated under this standard.[56] Emissions from farms or logging operations are excluded. The current targets for emissions reductions achieved through this approach include:

a) A statewide greenhouse gas emissions goal for the year 2025 to limit greenhouse gas emissions to levels that are at least 20 percent below 1990 levels;
b) A statewide greenhouse gas emissions limit for the year 2035 that limits greenhouse gas emissions to levels that are at least 45 percent below 1990 levels; and
c) A statewide greenhouse gas emissions limit for the year 2050 that limits greenhouse gas emissions to levels that are at least 80 percent below 1990 levels.

Modifying SB 1070 to address emissions from industrial logging and threats to climate resiliency is relatively straightforward. The Sustainable Energy and Economy Network (SEEN) has submitted proposed amendments that are relatively minor in length and complexity but will have a significant impact by helping to incentivize climate smart practices and phase out harmful ones and enroll big emitters (forestland owners whose practices emit 25k+ CO2 each

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[55] The Legislature has posted a useful overview of SB 1070 here: https://www.oregonlegislature.gov/helm/workgroup_materials/Overview%20of%20SB%201070%20(2017).pdf

[56] Oregon Department of Environmental Quality. 2017. Considerations for Designing a Cap-and-Trade Program in Oregon. Salem, OR: DEQ. Available online at: http://www.oregon.gov/deq/FilterDocs/ghgmarketstudy.pdf.

year) as covered entities regulated by the cap-and-invest market on par with other sources (Appendix Q).[57] The amendments would achieve the following:

1) Expands the list of covered entities to include forestland owners whose logging practices generate 25,000 metric tons CO2-e or more on an annual basis. This is about the level of emissions generated by a single, 120 acre clearcut in western Oregon.
2) Directs the Environmental Quality Commission to adopt a method for calculating timber harvest related emissions that takes into account loss of carbon storage, loss of sequestration capacity, emissions associated with decay of logging residuals, and emissions associated with chemical pesticides and fertilizers.
3) Reduces emissions associated with clearcutting and conventional logging practices on the same timetable as other covered entities (20% by 2025; 45% by 2035; 80% by 2050).
4) Establishes the date of enactment as the baseline year.
5) Exempts timber harvest emissions associated with climate-smart practices from the cap.
6) Refines existing Oregon Global Warming Commission duties to track and evaluate climate smart practices that increase carbon storage back to historic levels and reduce emissions associated with logging.
7) Requires registration and reporting of timber harvest-related emissions.
8) Ensures accountability of offset projects through public review mechanisms.

Calculation methods for emissions have already been worked out, so the EQC process will not be that complex. Reporting infrastructure is already in place. Private timberland owners are already required to notify the State Forester and Department of Revenue and Taxation before commencing of logging operations with all the information needed to keep track of associated emissions.[58] The Forest Service and BLM have separate notification systems that are just as easy to access. And, as discussed earlier, a typology of climate smart practices has already been well researched. So it appears the task of including industrial forestland owners into the SB 1070 framework is doable without any significant increase in reporting by covered entities.

10. Legislative option 2: Forest carbon tax and reward is a feasible market-based approach for dramatically scaling up climate smart practices and creating thousands of new jobs in the woods.

In the run-up to the 2017 Legislative Assembly outgoing Representative Peter Buckley and incoming Representative Pamela Marsh facilitated the drafting of model forest carbon tax and reward legislation (FCTR) with CSE (Appendix O).[59] The overall goal would be to tax high-

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[57] A copy of SEEN's submission can be accessed here: https://www.oregonlegislature.gov/helm/workgroup_materials/WG%201%20-%20Public%20Comments%20from%20Sustainable%20Energy%20Economy%20Network.pdf.

[58] An overview of Oregon's e-notification system can be accessed here: http://www.oregon.gov/ODF/Working/Pages/ENotification.aspx.

[59] A full text version of the draft legislation can be accessed here:

emissions (bad actor) practices and use proceeds to provide cost-share assistance to forestland owners implementing climate smart forest practices (good actors). The legislation would add a carbon emissions component to current timber harvest taxes collected each year. The tax would be would be levied on all volume harvested in excess of growth by natural (non-plantation) forests across the owner's property at a rate pegged to the federal social cost of carbon (SCC), which stands at about $42/tCO2-e.

After accounting for emissions associated with timber removals, foregone sequestration, decay of logging residuals, and forest chemicals, the initial gross SCC-based charge would be roughly $210 per thousand board feet (mbf) harvested for a typical landowner in western Oregon. The State Forester, working with the Oregon Global Warming Commission, would meet annually to adjust this rate taking the best scientific information available into account.

Forestland owners would receive up to a 50% credit against the gross levy for the proportion of lands managed under third-party certified long-term carbon storage agreements. In addition, all volume extracted from such lands would be exempted. So the net tax would be computed in the following manner:

TAX = (VTH – VNG – VCS) x $210 x (1-CR), where

TAX = Net tax paid by forest landowner
VTH = Volume of annual timber harvest
VNG = Volume of natural forest growth
VCS = Volume removed from climate smart forest practices
CR= Proportion of land managed under certified storage agreement (50% max)

Tax revenues would be deposited into a Forest Carbon Incentive Fund (FCIF), jointly managed by the Department of Forestry (ODF) and the Oregon Global Warming Commission (OGWC). Payments from the fund would be made to qualified landowners to offset costs associated with climate smart forest practices. ODF and OGWC would develop, maintain, and update a list of approved climate smart practices and information about their efficacy and cost. Funds would also be used to offset all ODF and OGWC expenses associated with administering the FCIF and also support research and monitoring activities.

A FCTR program in Oregon can be expected to have the following climate and economic benefits:

- Hundreds of millions of dollars could be available each year to invest in climate smart forest practices. A hypothetical analysis of potential tax revenues from western Oregon industrial forestlands, albeit with a somewhat different methodology than what is set forth in LC 2875, suggests that gross revenues (before credits and exemptions) could top $500 million per year (Appendix P). Net revenues could easily top $100 million per year.

- Many new jobs would be created. An investment of $100 million each year in climate smart forest practices could support between 3,000 and 4,000 new jobs according to standard multipliers applied to forest restoration work.[60]

- Emissions from timber harvest will fall. Timber harvest related emissions will fall due to (a) less timber harvesting from conventionally managed forests; (b) a reduction in emissions associated with foregone sequestration on clearcut lands, and (c) a reduction in emissions associated with decay of logging residuals.

- Sequestration will increase. Sequestration will not be eliminated after timber harvest on lands managed in accordance with climate smart standards. Instead, sequestration will increase as stands are thinned to maximize the growth of residual trees and as current carbon sequestration dead zones revert back into healthy forests.

- Longer-lived wood products would be incentivized. The tax rate would be adjusted to account for the share of timber harvests allocated to long-lived vs. short-lived wood products, with the tax rate lower for the former.

- The amount of forestland managed with climate smart practices that result in continuous increases in carbon storage (capture and store) will dramatically increase.

- The landscape will begin a transformation away from short rotation timber plantations and towards more climate resilient natural forests.

11. Legislative option 3: An Oregon Forest Resiliency Act will help jumpstart the restoration of industrial tree plantations into climate resilient forests and include a climate test for proposed logging operations.

A third approach more directly focused on the climate risks of industrial tree plantations is a proposed Oregon Forest Resiliency Act developed by CSE as a legislative concept note (Appendix R). The proposed legislation would amend and revise the Oregon Forest Practices Act to require implementation of climate smart practices to enhance the resiliency of private forestlands to drought, disease, wildfire, floods, landslides, low summertime streamflow, thermal pollution, fish kills, regeneration failures and other threats associated with climate change. It would accomplish this through six key mechanisms:

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[60] See, e.g. Moseley, C., Nielsen-Pincus, M., 2009. Economic Impact and Job Creation from Forest and Watershed Restoration: A Preliminary Assessment. Eugene, OR: University of Oregon Ecosystem Workforce Program; BenDor, T.K., Lester, T.W., Livengood, A., 2014. Exploring and Understanding the Restoration Economy. Chapel Hill, NC: University of North Carolina.

a) Climate resiliency plans (CRPs). Requires large forestland owners (>5,000 acres) to prepare and adhere to climate resiliency plans that describe existing conditions, climate threats, and climate smart practices that will be undertaken to comply with requirements of this Act. CRPs also must include hard targets for rebuilding carbon density, one of the key policy recommendations from the Oregon Global Warming Commission.[61] CRPs would be based on the best available science and subject to multi-agency review and approval. CRPs would serve as a comprehensive permit and require public participation, multi-agency review and approval.

b) A climate test for timber harvest plans (THPs). Requires large forestland owners (>5,000 acres) proposing clearcut harvest methods to file a THP for approval by the State Forester describing harvest, regeneration and resource protection measures needed to ensure the climate resiliency of future stands. THPs must also include a consistency determination with CRPs. This provision would, in essence, provide a "climate test" applicable to timber harvesting. To pass the test and receive authorization, a proposed timber harvest would have to ensure that it helps achieve both carbon density and climate resiliency goals set forth in the CRP.

c) Protection and restoration of native riparian vegetation and drinking watersheds. To protect and restore native riparian vegetation and drinking water supplies, establishes water resource management areas (WRMAs) along all rivers, streams, lakes, wetlands and shorelines consistent with the best available science and the state's non-degradation policy. Designates all surface drinking water assessment areas as WRMAs. Prohibits clearcutting and chemical sprays in WRMAs. Directs the State Forester, in consultation with the Department of Environmental Quality and Department of Fish and Wildlife to develop a list of acceptable timber harvest methods within WRMAs that ensure the resiliency of water supplies and native fish and wildlife populations to climate change and enhance the role of riparian zones in mitigating wildfire threat.

d) Protection and restoration of climate resilient forests. Prohibits the conversion of any remaining natural, late successional or old growth forests into tree plantations. For entities required to prepare CRPs, requires allocation of a portion of forestlands to protect or promote the establishment of climate resilient stands of late successional and old growth forest (LSOG) through appropriate silvicultural and restoration techniques. Establishes criteria for selection of LSOG management areas. Requires delineation of such lands on maps and Department of Fish and Wildlife approval.

e) Alternatives to clearcutting and timber plantations. Provides exemptions from reforestation requirements for climate smart practices that rely on natural regeneration

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[61] Oregon Global Warming Commission. 2017. Forest Carbon Policy Choices, Powerpoint slide deck prepared for the July 28th meeting. Available online at: http://www.keeporegoncool.org/meeting/oregon-global-warming-commission-meeting-july-2017.

and leave sufficient amounts of biological legacy to maintain forest cover, protect soil and watershed conditions, and enhance long term site productivity.

IV. Future iterations of this report

CSE has prepared this report as a convenient source of scientific and technical information relevant to forest carbon policy in Oregon as well as a repository for legislative concepts being fielded to address the twin threats associated with logging related emissions and loss of climate resiliency. For most policy makers, the learning curve is steep, and so we have attempted to make all of the data presented as transparent and easy to understand as possible with all of the key sources extensively documented in footnotes, hyperlinks, and the appendices. It will be maintained as a living, open source document where researchers will be invited to share alternative data sources as needed to replace ones that are either outdated or superseded by more precise studies. Alternative views and competing conclusions drawn from the data will be noted and incorporated into the next iterations where appropriate.

V. Acknowledgements

CSE would like to extend our warmest thanks to the many people who reviewed earlier drafts of this document and help us improve both the accuracy of the information presented as well as the conclusions drawn. Special thanks to Ernie Niemi and Doug Heiken for their constructive edits and suggestions. We would also like to thank the Laird Norton Family Foundation and the Alex C. Walker Foundation for their generous financial support of this work.

Appendix A

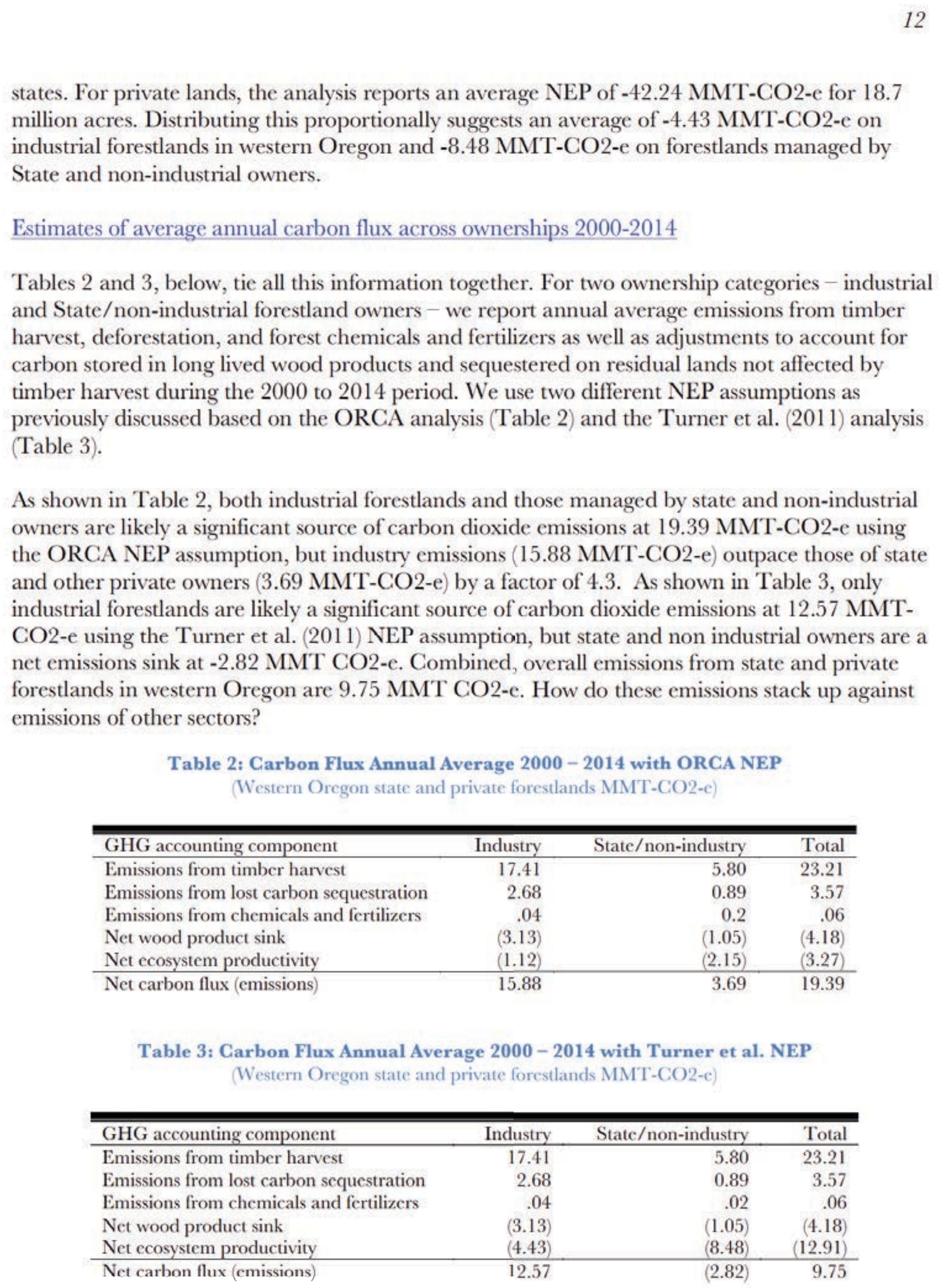
Table 2A. Growth, Removals and Mortality of CO2 equivalent, by ecoregion

All Oregon

Source: FIA (2001-2005; 2011-2015)

	Public										**Private**					
	NFS		**BLM**		**NPS**		**State**		**Other Public**		**Private Industry**		**Private Non-industrial**		**Total**	
	Total	**SE**	**Total**	**SE**	**Total**	**SE**	**Total**	**SE**	**Total**	**SE**	**Total**	**SE**	**Total**	**SE**	**Total**	**SE**
	thousand metric tons per year															
Time 1	1,776,928	27,917	434,725	22,653	22,672	7,389	153,243	12,212	15,077	5,741	610,831	26,036	204,422	17,048	3,217,898	44,066
Gross Ingrowth																
Ingrowth	2,711	87	950	163	13	5	249	59	88	41	6,127	490	1,175	181	11,313	549
Reversion	266	60	20	11	--	--	82	57	13	13	15	10	258	127	654	152
Total	2,977	103	969	164	13	5	331	85	101	43	6,142	490	1,433	220	11,966	566
Accretion	29,998	410	11,206	528	321	107	4,512	331	458	157	22,427	1,001	6,836	584	75,758	1,181
Gross Growth	32,975	425	12,175	564	334	111	4,843	368	559	174	28,569	1,152	8,269	661	87,724	1,322
Mortality	15,847	765	1,872	248	265	120	938	231	63	36	3,385	393	890	121	23,260	933
Removals																
Cut Trees	2,996	343	760	256	--	--	2,741	742	299	216	24,013	2,345	3,890	867	34,698	2,569
Diversion	38	15	10	11	--	--	--	--	--	--	--	--	7	5	55	19
Total	3,035	343	771	256	--	--	2,741	742	299	216	24,013	2,345	3,896	867	34,754	2,569
Net Growth	17,129	870	10,303	606	70	80	3,905	405	496	157	25,183	1,146	7,379	625	64,465	1,586
Net Change	14,094	933	9,532	635	70	80	1,165	856	197	212	1,171	2,682	3,483	953	29,711	3,178
Time 2	1,917,834	29,052	529,110	24,300	23,354	7,555	164,942	13,929	16,936	6,153	622,608	29,434	238,728	19,396	3,513,511	48,602

Appendix B



states. For private lands, the analysis reports an average NEP of -42.24 MMT-CO2-e for 18.7 million acres. Distributing this proportionally suggests an average of -4.43 MMT-CO2-e on industrial forestlands in western Oregon and -8.48 MMT-CO2-e on forestlands managed by State and non-industrial owners.

Estimates of average annual carbon flux across ownerships 2000-2014

Tables 2 and 3, below, tie all this information together. For two ownership categories – industrial and State/non-industrial forestland owners – we report annual average emissions from timber harvest, deforestation, and forest chemicals and fertilizers as well as adjustments to account for carbon stored in long lived wood products and sequestered on residual lands not affected by timber harvest during the 2000 to 2014 period. We use two different NEP assumptions as previously discussed based on the ORCA analysis (Table 2) and the Turner et al. (2011) analysis (Table 3).

As shown in Table 2, both industrial forestlands and those managed by state and non-industrial owners are likely a significant source of carbon dioxide emissions at 19.39 MMT-CO2-e using the ORCA NEP assumption, but industry emissions (15.88 MMT-CO2-e) outpace those of state and other private owners (3.69 MMT-CO2-e) by a factor of 4.3. As shown in Table 3, only industrial forestlands are likely a significant source of carbon dioxide emissions at 12.57 MMT-CO2-e using the Turner et al. (2011) NEP assumption, but state and non industrial owners are a net emissions sink at -2.82 MMT CO2-e. Combined, overall emissions from state and private forestlands in western Oregon are 9.75 MMT CO2-e. How do these emissions stack up against emissions of other sectors?

Table 2: Carbon Flux Annual Average 2000 – 2014 with ORCA NEP
(Western Oregon state and private forestlands MMT-CO2-e)

GHG accounting component	Industry	State/non-industry	Total
Emissions from timber harvest	17.41	5.80	23.21
Emissions from lost carbon sequestration	2.68	0.89	3.57
Emissions from chemicals and fertilizers	.04	0.2	.06
Net wood product sink	(3.13)	(1.05)	(4.18)
Net ecosystem productivity	(1.12)	(2.15)	(3.27)
Net carbon flux (emissions)	15.88	3.69	19.39

Table 3: Carbon Flux Annual Average 2000 – 2014 with Turner et al. NEP
(Western Oregon state and private forestlands MMT-CO2-e)

GHG accounting component	Industry	State/non-industry	Total
Emissions from timber harvest	17.41	5.80	23.21
Emissions from lost carbon sequestration	2.68	0.89	3.57
Emissions from chemicals and fertilizers	.04	.02	.06
Net wood product sink	(3.13)	(1.05)	(4.18)
Net ecosystem productivity	(4.43)	(8.48)	(12.91)
Net carbon flux (emissions)	12.57	(2.82)	9.75

Appendix C

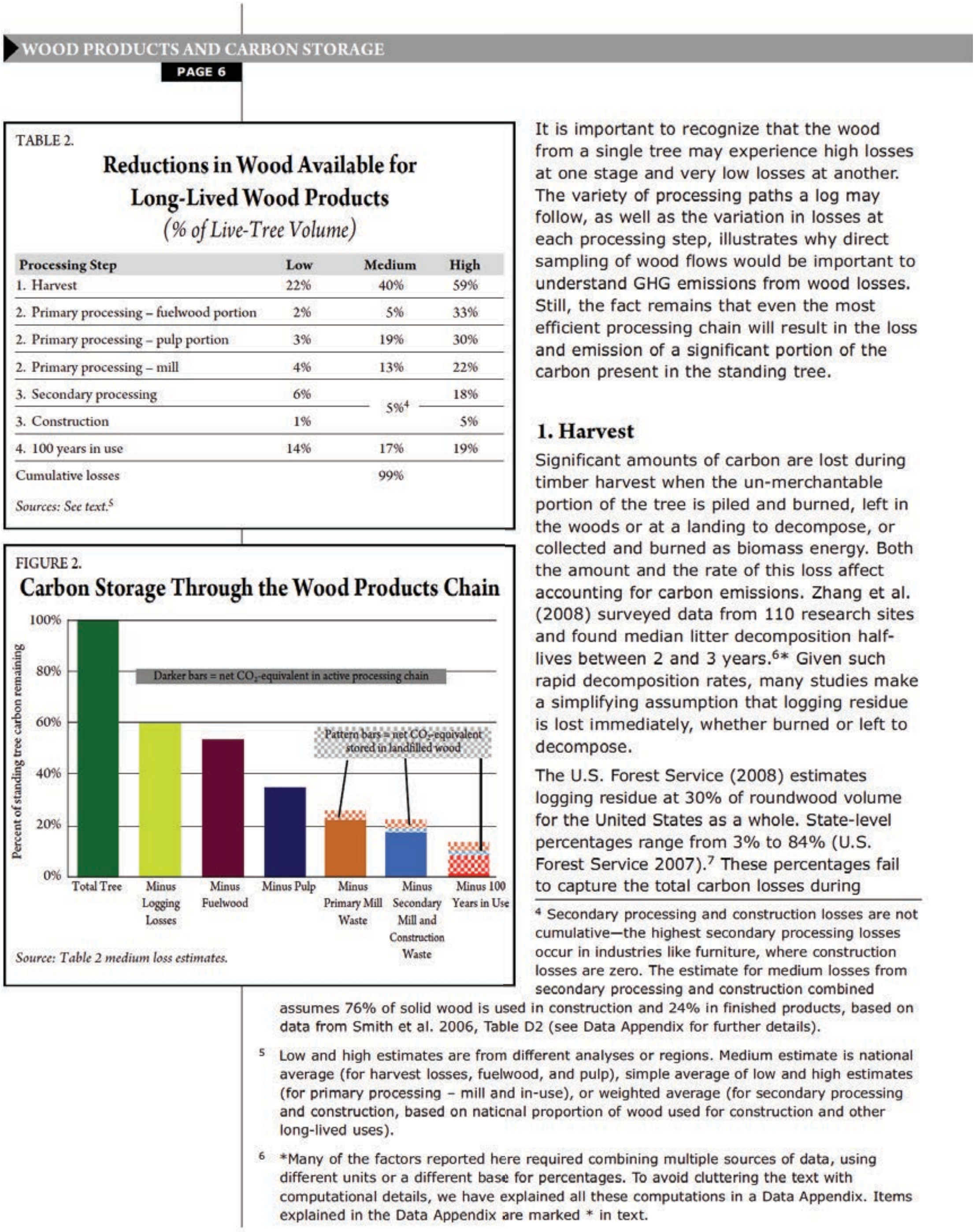


TABLE 2.

Reductions in Wood Available for Long-Lived Wood Products

(% of Live-Tree Volume)

Processing Step	Low	Medium	High
1. Harvest	22%	40%	59%
2. Primary processing – fuelwood portion	2%	5%	33%
2. Primary processing – pulp portion	3%	19%	30%
2. Primary processing – mill	4%	13%	22%
3. Secondary processing	6%	5%[4]	18%
3. Construction	1%		5%
4. 100 years in use	14%	17%	19%
Cumulative losses		99%	

Sources: See text.[5]

FIGURE 2.

Carbon Storage Through the Wood Products Chain

Source: Table 2 medium loss estimates.

It is important to recognize that the wood from a single tree may experience high losses at one stage and very low losses at another. The variety of processing paths a log may follow, as well as the variation in losses at each processing step, illustrates why direct sampling of wood flows would be important to understand GHG emissions from wood losses. Still, the fact remains that even the most efficient processing chain will result in the loss and emission of a significant portion of the carbon present in the standing tree.

1. Harvest

Significant amounts of carbon are lost during timber harvest when the un-merchantable portion of the tree is piled and burned, left in the woods or at a landing to decompose, or collected and burned as biomass energy. Both the amount and the rate of this loss affect accounting for carbon emissions. Zhang et al. (2008) surveyed data from 110 research sites and found median litter decomposition half-lives between 2 and 3 years.[6]* Given such rapid decomposition rates, many studies make a simplifying assumption that logging residue is lost immediately, whether burned or left to decompose.

The U.S. Forest Service (2008) estimates logging residue at 30% of roundwood volume for the United States as a whole. State-level percentages range from 3% to 84% (U.S. Forest Service 2007).[7] These percentages fail to capture the total carbon losses during

---

[4] Secondary processing and construction losses are not cumulative—the highest secondary processing losses occur in industries like furniture, where construction losses are zero. The estimate for medium losses from secondary processing and construction combined assumes 76% of solid wood is used in construction and 24% in finished products, based on data from Smith et al. 2006, Table D2 (see Data Appendix for further details).

[5] Low and high estimates are from different analyses or regions. Medium estimate is national average (for harvest losses, fuelwood, and pulp), simple average of low and high estimates (for primary processing – mill and in-use), or weighted average (for secondary processing and construction, based on naticnal proportion of wood used for construction and other long-lived uses).

[6] *Many of the factors reported here required combining multiple sources of data, using different units or a different base for percentages. To avoid cluttering the text with computational details, we have explained all these computations in a Data Appendix. Items explained in the Data Appendix are marked * in text.

Appendix D

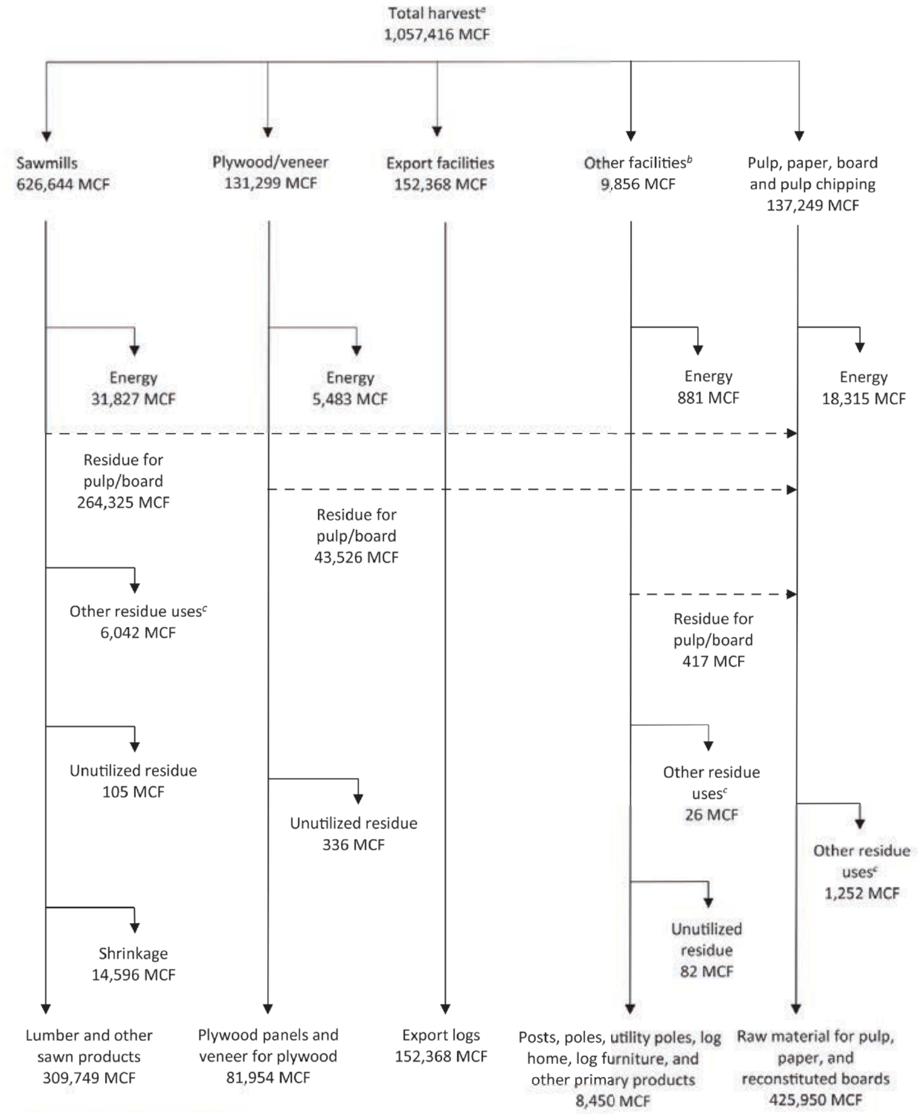
Table 6.—continued

Year after production	Pacific Northwest, West, Softwoods							
	Saw log				Pulpwood			
	In use	Landfill	Energy	Emitted without energy	In use	Landfill	Energy	Emitted without energy
0	0.740	0.000	0.125	0.135	0.500	0.000	0.352	0.148
1	0.703	0.018	0.134	0.144	0.422	0.026	0.382	0.170
2	0.670	0.035	0.141	0.153	0.357	0.047	0.409	0.187
3	0.640	0.050	0.148	0.161	0.301	0.064	0.433	0.202
4	0.613	0.064	0.154	0.169	0.254	0.078	0.453	0.215
5	0.589	0.076	0.160	0.176	0.215	0.089	0.471	0.226
6	0.566	0.088	0.165	0.182	0.180	0.098	0.486	0.236
7	0.545	0.098	0.169	0.188	0.150	0.106	0.499	0.245
8	0.525	0.108	0.174	0.194	0.121	0.112	0.512	0.254
9	0.506	0.117	0.178	0.199	0.096	0.118	0.523	0.262
10	0.489	0.125	0.182	0.204	0.075	0.122	0.533	0.270
15	0.423	0.157	0.196	0.224	0.020	0.127	0.559	0.295
20	0.376	0.179	0.206	0.239	0.004	0.119	0.567	0.309
25	0.340	0.195	0.213	0.252	0.001	0.110	0.569	0.319
30	0.310	0.208	0.219	0.263	0.000	0.103	0.569	0.327
35	0.284	0.218	0.224	0.273	0.000	0.097	0.569	0.334
40	0.263	0.227	0.228	0.282	0.000	0.092	0.569	0.339
45	0.244	0.234	0.232	0.290	0.000	0.088	0.569	0.342
50	0.228	0.240	0.234	0.298	0.000	0.085	0.569	0.345
55	0.213	0.246	0.237	0.305	0.000	0.083	0.569	0.348
60	0.200	0.251	0.238	0.311	0.000	0.081	0.569	0.349
65	0.188	0.255	0.240	0.317	0.000	0.080	0.569	0.351
70	0.178	0.259	0.240	0.322	0.000	0.079	0.569	0.352
75	0.168	0.263	0.241	0.328	0.000	0.078	0.569	0.353
80	0.159	0.267	0.242	0.332	0.000	0.077	0.569	0.353
85	0.151	0.270	0.242	0.337	0.000	0.077	0.569	0.354
90	0.143	0.273	0.242	0.341	0.000	0.076	0.569	0.354
95	0.136	0.276	0.242	0.345	0.000	0.076	0.569	0.355
100	0.130	0.279	0.242	0.349	0.000	0.076	0.569	0.355

Continued

Appendix E

GENERAL TECHNICAL REPORT PNW-GTR-942



[a] Harvest volume does not include bark.
[b] Other facilities include producers of posts, poles, utility poles, log homes, log furniture, energy, energy products, and other products.
[c] Other uses include landscape, mulch, and animal bedding.

Figure 8—Oregon's timber harvest and products flow, 2013. MCF = thousand cubic feet.

Appendix F

of crown-cover is burned, thus omitting areas that are partially burned or only have understory fires. They assume 100% of foliar, fine root, and litter carbon is emitted, and that 7% of aboveground wood is emitted (Turner et al., 2007 p. 601). Though a variety of methods exist for estimating fire emissions, it was decided to use the estimates from ORCA since data on NBP is also coming from the same source.

Timber Harvest

Timber harvest data are also from ORCA, who received them from the Oregon Department of Forestry. Data include harvest from both public and private lands. Unlike other data within the inventory, data on timber harvest prior to 1990 and after 2002 are available. They indicate that timber harvest significantly declined around 1990, and have been stable in recent years. Note that Timber Harvest does not account for the carbon stored in long-lived forest product or in landfills, which is accounted for in the category "Net Product Sink" and is estimated at 25% of the annual Timber Harvest.

Table 3: Carbon (expressed as MMT CO_2) removed by timber harvest removal, 1980-2005

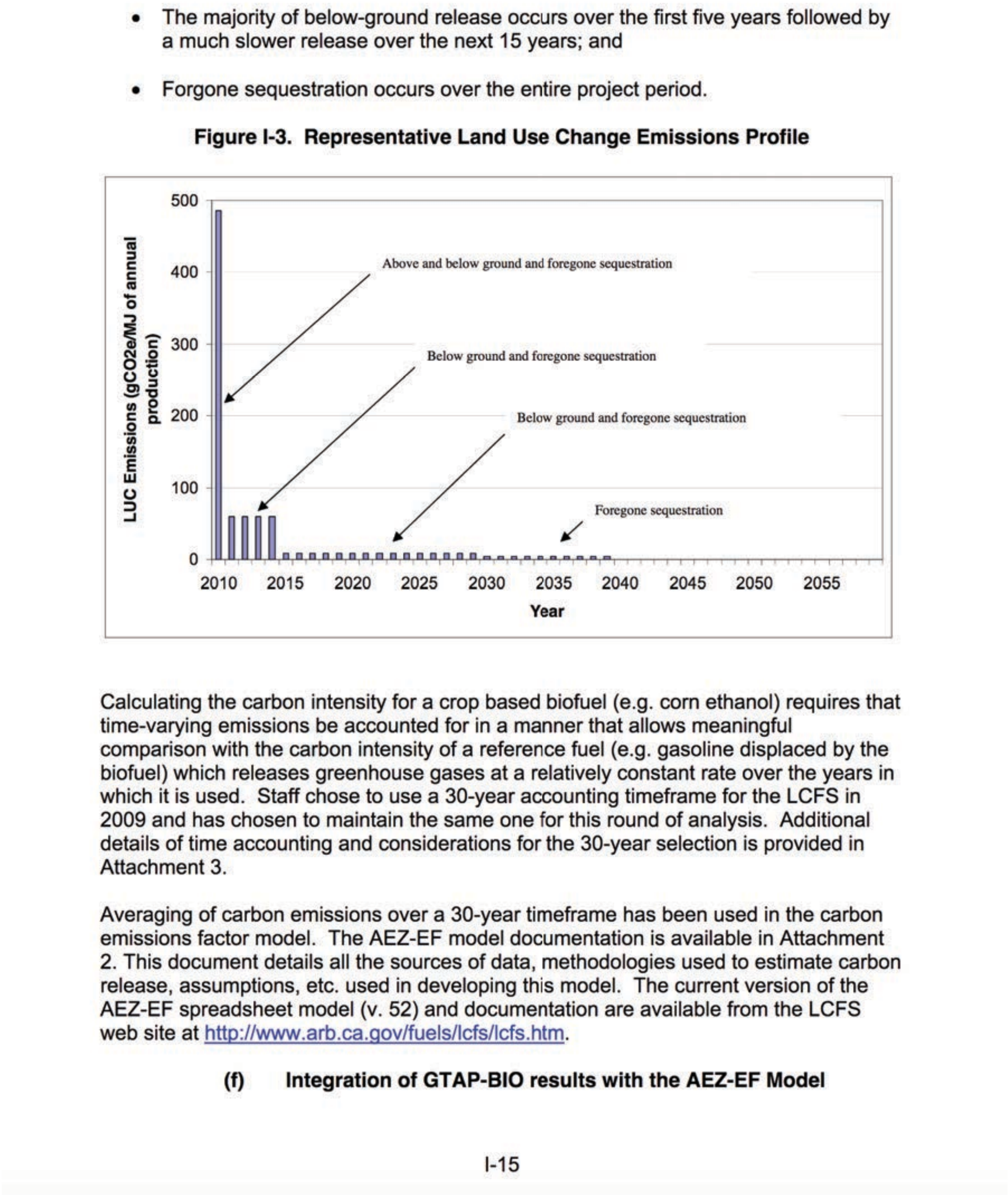
	Harvest Removal (in MMT CO_2)
1980	38.91
1981	33.37
1982	33.74
1983	43.74
1984	44.24
1985	47.63
1986	51.23
1987	48.14
1988	50.48
1989	49.34
1990	36.44
1991	35.63
1992	33.65
1993	31.02
1994	24.42
1995	25.22
1996	22.98
1997	23.92
1998	20.70
1999	22.03
2000	22.58
2001	20.16
2002	22.98
2003	23.45
2004	26.08
2005	25.52

Note that some of this carbon stays sequestered in the form of harvested wood product, as described in Net Product Sink below.

Net Product Sink

Researchers estimate that there is"disequilibrium between harvest emissions from all previous harvests and total current harvests".[22] That leads to the estimate that between 20-25% of a year's harvested forest

Appendix G



- The majority of below-ground release occurs over the first five years followed by a much slower release over the next 15 years; and
- Forgone sequestration occurs over the entire project period.

Figure I-3. Representative Land Use Change Emissions Profile

Calculating the carbon intensity for a crop based biofuel (e.g. corn ethanol) requires that time-varying emissions be accounted for in a manner that allows meaningful comparison with the carbon intensity of a reference fuel (e.g. gasoline displaced by the biofuel) which releases greenhouse gases at a relatively constant rate over the years in which it is used. Staff chose to use a 30-year accounting timeframe for the LCFS in 2009 and has chosen to maintain the same one for this round of analysis. Additional details of time accounting and considerations for the 30-year selection is provided in Attachment 3.

Averaging of carbon emissions over a 30-year timeframe has been used in the carbon emissions factor model. The AEZ-EF model documentation is available in Attachment 2. This document details all the sources of data, methodologies used to estimate carbon release, assumptions, etc. used in developing this model. The current version of the AEZ-EF spreadsheet model (v. 52) and documentation are available from the LCFS web site at http://www.arb.ca.gov/fuels/lcfs/lcfs.htm.

(f) Integration of GTAP-BIO results with the AEZ-EF Model

Appendix H

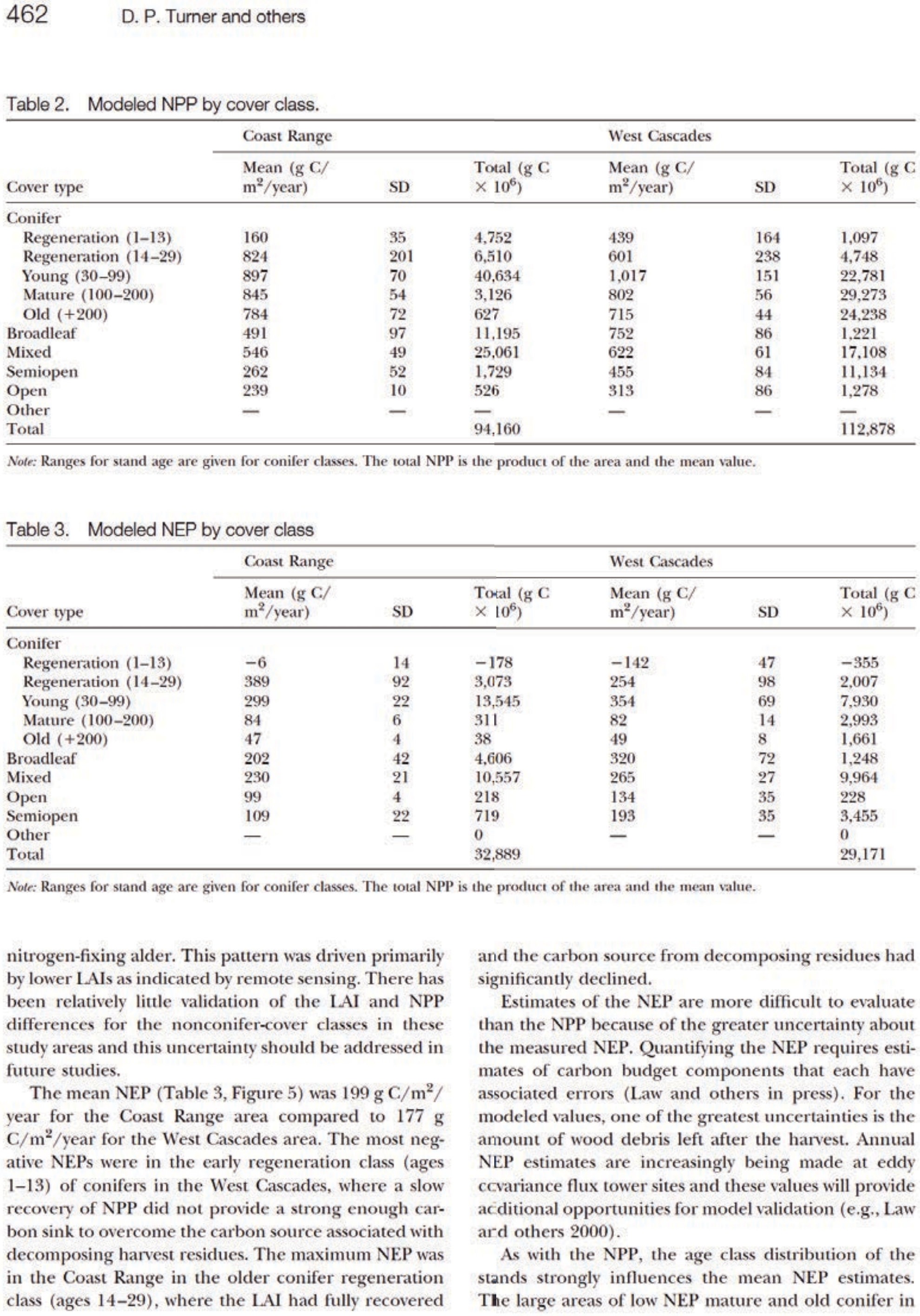


Table 2. Modeled NPP by cover class.

	Coast Range			West Cascades		
Cover type	Mean (g C/ m^2/year)	SD	Total (g C × 10^6)	Mean (g C/ m^2/year)	SD	Total (g C × 10^6)
Conifer						
Regeneration (1–13)	160	35	4,752	439	164	1,097
Regeneration (14–29)	824	201	6,510	601	238	4,748
Young (30–99)	897	70	40,634	1,017	151	22,781
Mature (100–200)	845	54	3,126	802	56	29,273
Old (+200)	784	72	627	715	44	24,238
Broadleaf	491	97	11,195	752	86	1,221
Mixed	546	49	25,061	622	61	17,108
Semiopen	262	52	1,729	455	84	11,134
Open	239	10	526	313	86	1,278
Other	—	—	—	—	—	—
Total			94,160			112,878

Note: Ranges for stand age are given for conifer classes. The total NPP is the product of the area and the mean value.

Table 3. Modeled NEP by cover class

	Coast Range			West Cascades		
Cover type	Mean (g C/ m^2/year)	SD	Total (g C × 10^6)	Mean (g C/ m^2/year)	SD	Total (g C × 10^6)
Conifer						
Regeneration (1–13)	−6	14	−178	−142	47	−355
Regeneration (14–29)	389	92	3,073	254	98	2,007
Young (30–99)	299	22	13,545	354	69	7,930
Mature (100–200)	84	6	311	82	14	2,993
Old (+200)	47	4	38	49	8	1,661
Broadleaf	202	42	4,606	320	72	1,248
Mixed	230	21	10,557	265	27	9,964
Open	99	4	218	134	35	228
Semiopen	109	22	719	193	35	3,455
Other	—	—	0	—	—	0
Total			32,889			29,171

Note: Ranges for stand age are given for conifer classes. The total NPP is the product of the area and the mean value.

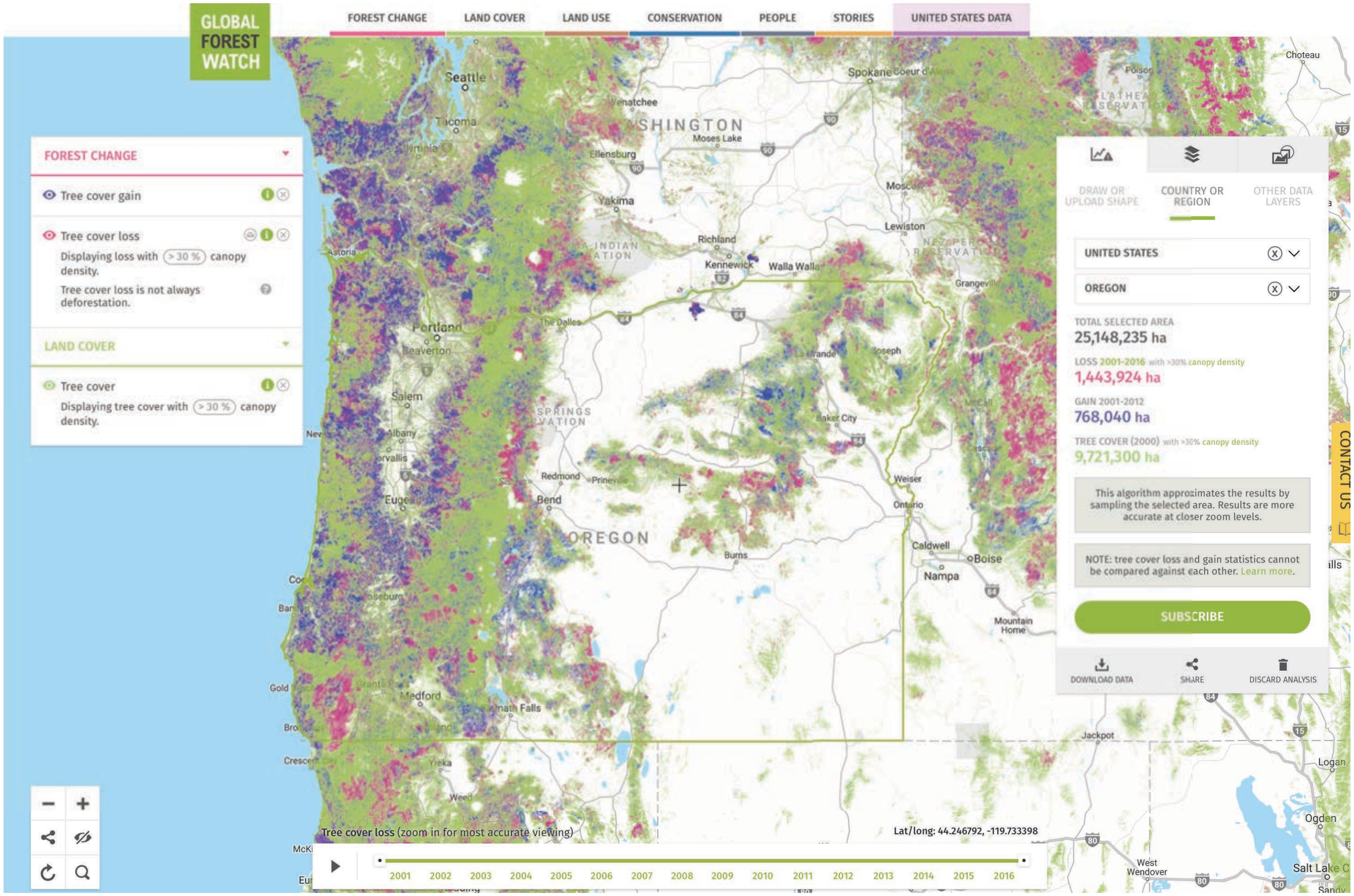
nitrogen-fixing alder. This pattern was driven primarily by lower LAIs as indicated by remote sensing. There has been relatively little validation of the LAI and NPP differences for the nonconifer-cover classes in these study areas and this uncertainty should be addressed in future studies.

The mean NEP (Table 3, Figure 5) was 199 g C/m^2/year for the Coast Range area compared to 177 g C/m^2/year for the West Cascades area. The most negative NEPs were in the early regeneration class (ages 1–13) of conifers in the West Cascades, where a slow recovery of NPP did not provide a strong enough carbon sink to overcome the carbon source associated with decomposing harvest residues. The maximum NEP was in the Coast Range in the older conifer regeneration class (ages 14–29), where the LAI had fully recovered and the carbon source from decomposing residues had significantly declined.

Estimates of the NEP are more difficult to evaluate than the NPP because of the greater uncertainty about the measured NEP. Quantifying the NEP requires estimates of carbon budget components that each have associated errors (Law and others in press). For the modeled values, one of the greatest uncertainties is the amount of wood debris left after the harvest. Annual NEP estimates are increasingly being made at eddy covariance flux tower sites and these values will provide additional opportunities for model validation (e.g., Law and others 2000).

As with the NPP, the age class distribution of the stands strongly influences the mean NEP estimates. The large areas of low NEP mature and old conifer in

Appendix I



FOREST CHANGE

- Tree cover gain
- Tree cover loss
  Displaying loss with >30 % canopy density.
  Tree cover loss is not always deforestation.

LAND COVER

- Tree cover
  Displaying tree cover with >30 % canopy density.

UNITED STATES

OREGON

TOTAL SELECTED AREA
25,148,235 ha

LOSS 2001-2016 with >30% canopy density
1,443,924 ha

GAIN 2001-2012
768,040 ha

TREE COVER (2000) with >30% canopy density
9,721,300 ha

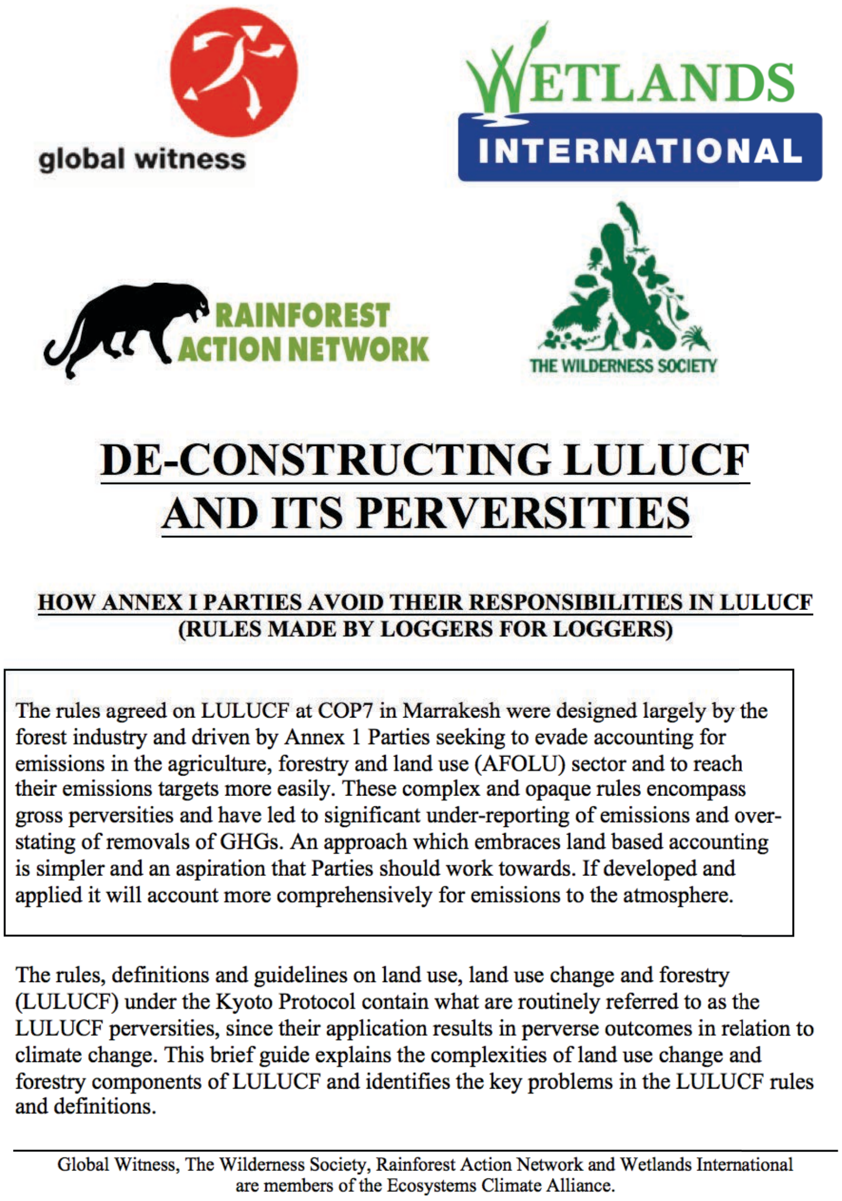
This algorithm approximates the results by sampling the selected area. Results are more accurate at closer zoom levels.

NOTE: tree cover loss and gain statistics cannot be compared against each other. Learn more.

Tree cover loss (zoom in for most accurate viewing)

Lat/long: 44.246792, -119.733398

Appendix J



DE-CONSTRUCTING LULUCF AND ITS PERVERSITIES

HOW ANNEX I PARTIES AVOID THEIR RESPONSIBILITIES IN LULUCF (RULES MADE BY LOGGERS FOR LOGGERS)

The rules agreed on LULUCF at COP7 in Marrakesh were designed largely by the forest industry and driven by Annex 1 Parties seeking to evade accounting for emissions in the agriculture, forestry and land use (AFOLU) sector and to reach their emissions targets more easily. These complex and opaque rules encompass gross perversities and have led to significant under-reporting of emissions and over-stating of removals of GHGs. An approach which embraces land based accounting is simpler and an aspiration that Parties should work towards. If developed and applied it will account more comprehensively for emissions to the atmosphere.

The rules, definitions and guidelines on land use, land use change and forestry (LULUCF) under the Kyoto Protocol contain what are routinely referred to as the LULUCF perversities, since their application results in perverse outcomes in relation to climate change. This brief guide explains the complexities of land use change and forestry components of LULUCF and identifies the key problems in the LULUCF rules and definitions.

Global Witness, The Wilderness Society, Rainforest Action Network and Wetlands International are members of the Ecosystems Climate Alliance.

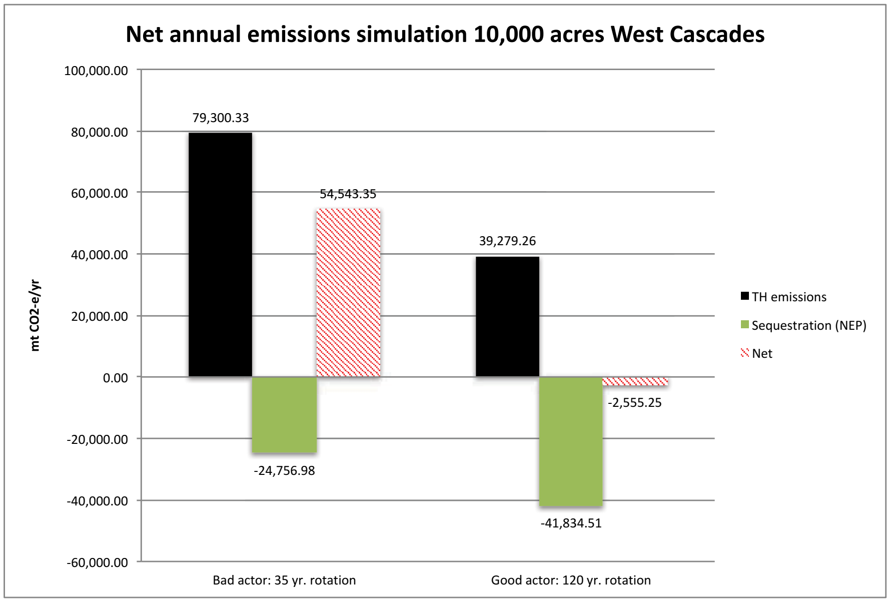
Appendix K

Good actor bad actor bar chart - West Cascades

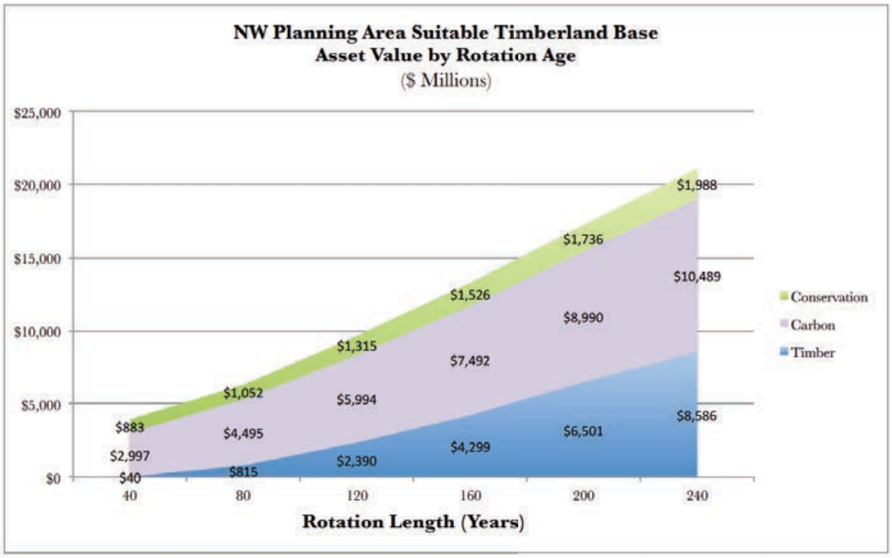
	TH emissions	Sequestration (NEP)	Net
Bad actor: 35 yr. rotation	79,300.33	-24,756.98	54,543.35
Good actor: 120 yr. rotation	39,279.26	-41,834.51	-2,555.25

	Bad actor	Good actor
Ownership size	10,000.00	10,000.00
Rotation	35.00	120.00
Embodied emissions/mbf	6.46	6.46
Mean mbf/acre	40.00	80.00
Annual acres cut	285.71	83.33
TH emissions	55,371.43	32,300.00
Acres in 0-13 at one time	4,000.00	1,166.67
FS charge	19,528.90	5,695.93
DR charge	4,400.00	1,283.33
Total annual emissions	79,300.33	39,279.26
Acres 14-29 at one time	4,571.43	1,333.33
Acres 30-99 at one time	1,428.57	7,000.00
Total annual sequestration	-24,756.98	-41,834.51
Net	54,543.35	-2,555.25

West Cascades NEP	
0-13 gC/m2/yr	-142
0-13 tCO2-e/ac/yr	-2.11
14-29 gC/m2/yr	254
14-29 tCO2-e/ac/yr	3.77
30-99 gC/m2/yr	354
30-99 tCO2-e/ac/yr	5.26



Appendix L

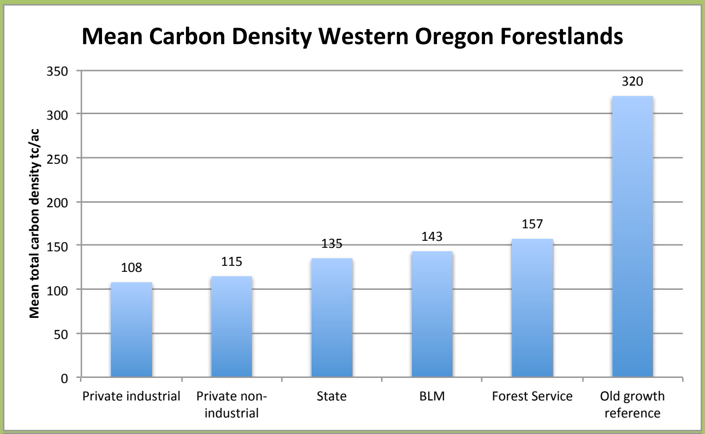


Key assumptions:

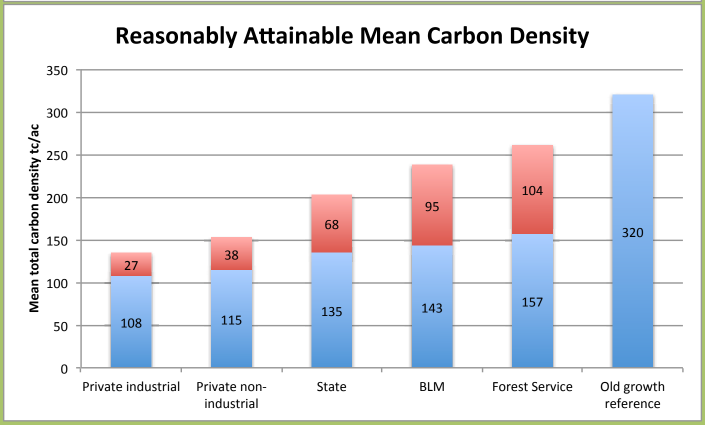
- Conservation values from historical land purchase agreements. Values represent roughly 10 times ODR's 2015 bare land specially assessed forestland values and range from $2,830 per acre for young stands to $10,410 for late successional/old growth forest.
- Carbon density in metric tons carbon per acre increases from 60 to 360 based on data from Woods Hole Institute and the USDA Forest Inventory and Analysis. Following BLM, stock is valued at the current $40/mt CO2-e social cost of carbon dioxide emissions.
- Stumpage values per million board feet increase across five product types: poles and pulpwood, small sawtimber, median sawtimber, large sawtimber, and prime veneer logs. Stumpage range of $300-$378 per MBF taken from Forest Service research and ODF bid sheets.
- Mean annual increment (MAI) figures taken from Wigg (1989). MAI by age group is as follows: 0-39 (21.1 bf/acre), 40-79 (254), 80-119 (424.1), 120-159 (459.4), 160-199 (489.1), 200-239 (453.9).

Appendix M

Scaling Up Forest Carbon Storage



Mean Carbon Density Western Oregon Forestlands



Reasonably Attainable Mean Carbon Density

One hypothetical scenario and its effects:

- ✓ Increase mean carbon density by 25% on private industrial lands, 33% on non-industrial lands, 50% on state lands, and 66% on federal lands.
- ✓ The resulting increase in storage would top 3 billion metric tons CO2-e.
- ✓ This is equivalent to 50 years of Oregon's currently reported emissions.
- ✓ This is equivalent to the annual emissions from 871 coal fired plants

Appendix N

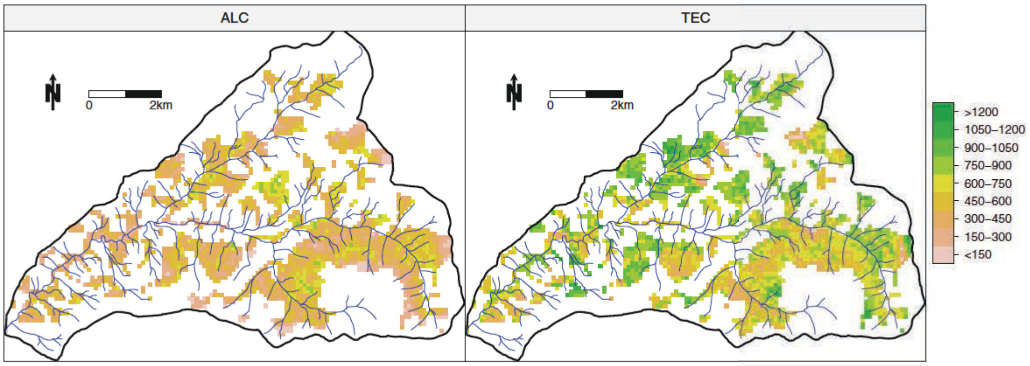


Figure 3. Aboveground live carbon (ALC, derived from Lidar) and total ecosystem carbon (TEC, simulated with iLand) in old-growth forests at the HJ Andrews Experimental Forest (Mg C ha^{-1}). (Color figure online)

Table 3. Carbon Storage in Old-Growth Forests of the HJ Andrews Experimental Forest

		ALC (Lidar)	ALC (iLand)	TEC (iLand)
Central tendency	Mean (Mg C ha^{-1})	435.1	396.5	724.5
Variation (Spatially non-explicit)	R^1_{90} (Mg C ha^{-1})	496.7	428.2	583.5
	CV^2 (%)	34.3	34.9	26.2
Variation (Spatially explicit)[3]	Patch density[4] (100 ha^{-1})	22.1	18.1	26.5
	Division index[5] (dim.)	0.995	0.981	0.995

ALC = aboveground live carbon; TEC = total ecosystem carbon.

[1] *90th percentile range (that is, the range between the 5th and 95th percentile of landscape C density).*

[2] *Coefficient of variation.*

[3] *Results were grouped into 150 Mg C ha^{-1} classes to identify homogeneous patches (see Figure 3).*

[4] *Number of patches per 100 ha (McGarigal and others 2002).*

[5] *The probability that two randomly chosen places in the landscape are not situated in the same undissected patch (Jaeger 2000); the minimum division index from separate calculations for all C classes is reported here.*

Drivers of Spatial Variation in C Density

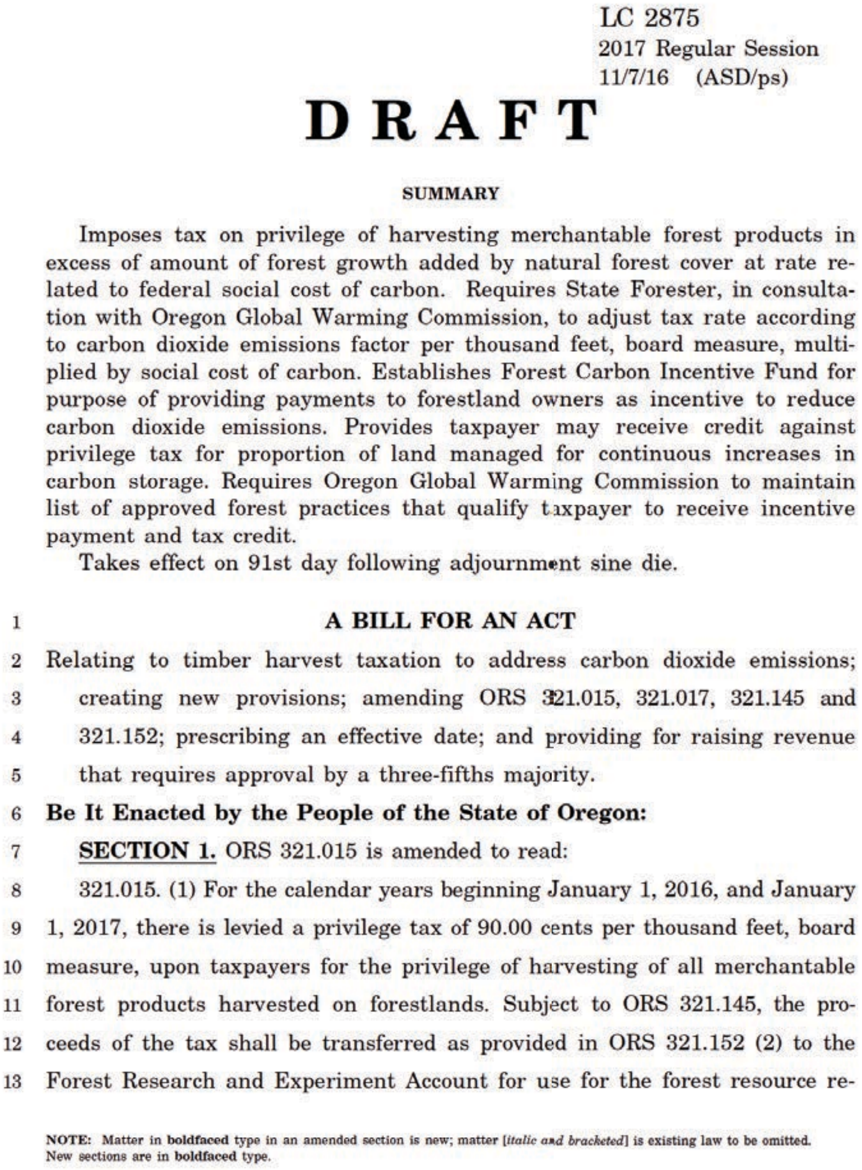
Lidar-based ALC densities were only weakly correlated with individual environmental drivers, with radiation and effective soil rooting depth being the most prominent factors (Figure 4). A stronger relationship was found with individual indicators of stand structure, with Lidar-based ALC moderately correlated to vertical and horizontal heterogeneity (that is, rumple index and SD_{dbh}) as well as size and stocking level (N_{100} and BA). However, because of the hierarchical nature of influence (coincident effect of environment on both stand dynamics and ecosystem productivity) and the multicollinearity between individual factors these correlations allow only limited insight into the processes driving variation in C density of old-growth forests at HJA.

We thus conducted a full factorial simulation experiment with a process-based model to disentangle environmental effects from the influence of stand dynamics on C density. We found that variation in environmental drivers was responsible for 55.3% of the spatial variation in TEC density (53.8% for ALC). Radiation was identified as the most important environmental driver (Figure 5A). According to our analysis, solar energy thus had a stronger influence on C storage than climatic factors limiting plant metabolism (for example, temperature) in the mountainous terrain of HJA. Furthermore, soil physical properties (that is, the local ability to store water) were found more influential on variation in C than the overall amount of precipitation. Precipitation is generally high throughout the landscape (see Figure 1B) but is unevenly distributed over the year, with a distinct dry season in summer, which makes the ability to store precipitation and runoff from snow-melt a crucial parameter for plant growth in (solar energy-rich) early summer.

In a subsequent step, we analyzed how much of the C variation not explained by environmental

Appendix O

For the full text of this proposed legislation, please visit: http://sustainable-economy.org/wp-content/uploads/2017/02/LC2875_DRAFT_2017_Regular_Session.pdf



LC 2875
2017 Regular Session
11/7/16 (ASD/ps)

DRAFT

SUMMARY

Imposes tax on privilege of harvesting merchantable forest products in excess of amount of forest growth added by natural forest cover at rate related to federal social cost of carbon. Requires State Forester, in consultation with Oregon Global Warming Commission, to adjust tax rate according to carbon dioxide emissions factor per thousand feet, board measure, multiplied by social cost of carbon. Establishes Forest Carbon Incentive Fund for purpose of providing payments to forestland owners as incentive to reduce carbon dioxide emissions. Provides taxpayer may receive credit against privilege tax for proportion of land managed for continuous increases in carbon storage. Requires Oregon Global Warming Commission to maintain list of approved forest practices that qualify taxpayer to receive incentive payment and tax credit.

Takes effect on 91st day following adjournment sine die.

A BILL FOR AN ACT

Relating to timber harvest taxation to address carbon dioxide emissions; creating new provisions; amending ORS 321.015, 321.017, 321.145 and 321.152; prescribing an effective date; and providing for raising revenue that requires approval by a three-fifths majority.

Be It Enacted by the People of the State of Oregon:

SECTION 1. ORS 321.015 is amended to read:

321.015. (1) For the calendar years beginning January 1, 2016, and January 1, 2017, there is levied a privilege tax of 90.00 cents per thousand feet, board measure, upon taxpayers for the privilege of harvesting of all merchantable forest products harvested on forestlands. Subject to ORS 321.145, the proceeds of the tax shall be transferred as provided in ORS 321.152 (2) to the Forest Research and Experiment Account for use for the forest resource re-

NOTE: Matter in **boldfaced** type in an amended section is new; matter *[italic and bracketed]* is existing law to be omitted. New sections are in **boldfaced** type.

Appendix P

Oregon Forest Carbon Taxable Emissions Worksheet

All values = annual averages 2000-2014

Emissions	⬛
Store/sequest	🟥

Region:	Western
Ownsership:	Pvt Industry

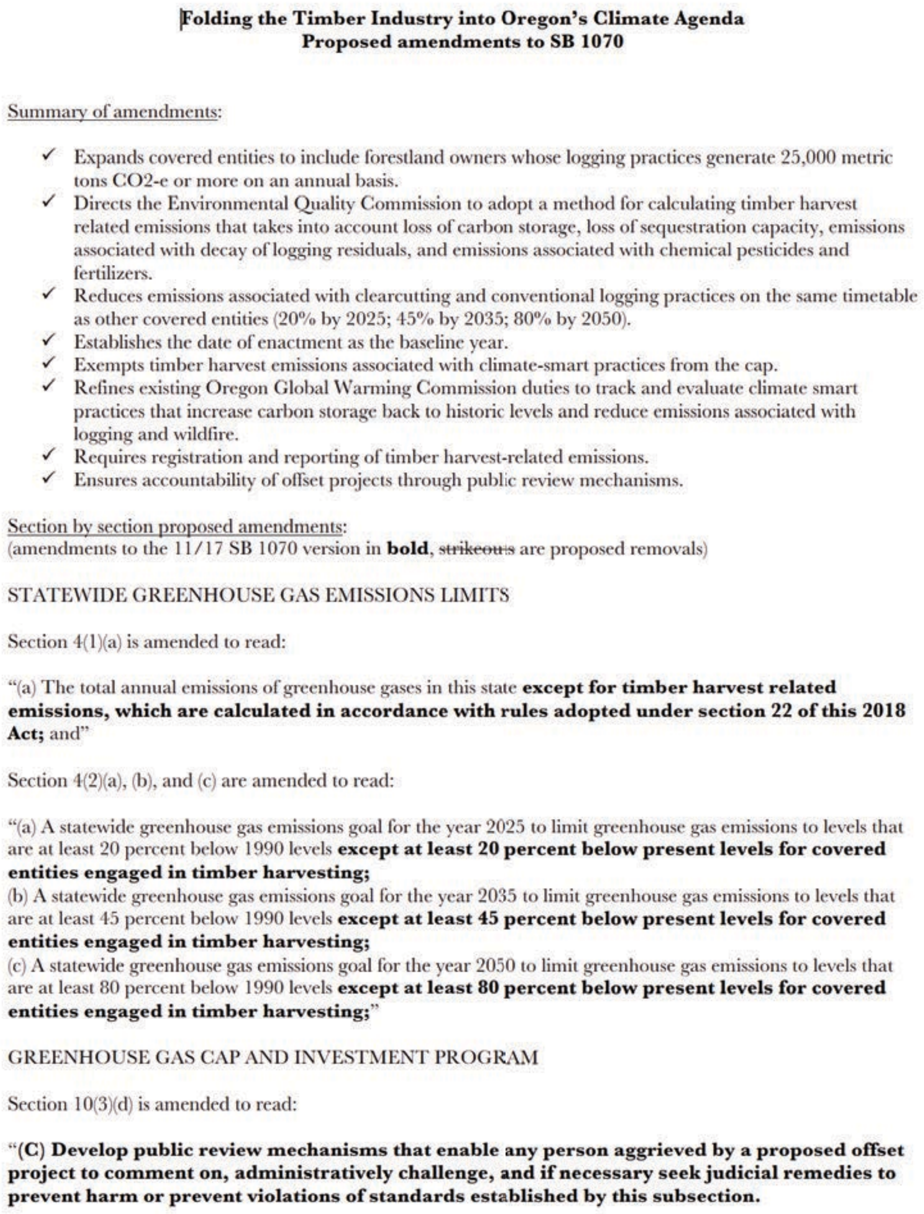
Emissions		
Volume timber harvest (mbf)	*2,696,467*	
Embodied CO2 factor (co2-e/mbf)	*6.46*	
Gross timber harvest emissions (MMtco2-e)		**17.41**
Share of volume to short-lived wood products	0.75	
Share of volume to long-lived wood products	0.25	
Storage in long-lived wood products (tco2-e/yr)		**4.35**
Forest cover loss	91,548	
Sacrificed sequestration factor (tco2-e/acre/yr)	4.74	
Years of loss	13	
Indirect emissions from sacrificed sequestration		**5.64**
Acreage in 0-13 age class	1,190,127	
Emissions factor 0-13 age class (NEP basis) tco2-e/ac/yr	1.11	
Direct emissions from logging residue decay		**1.32**
Pesticide and herbicide applications (kg)	9,092,570	
Pesticide and hericide emissions factor (kgCo2-e/kg)	16.43	
Fertilizer applications (kg)	6,461,538	
Fertilizer emissions factor (kgCo2-e/kg)	4.771	
Emissions from chemical and fertilizer applications		**0.18**
Total emissions (tco2-e/yr)		**20.20**

Sequestration		
Forestland acres	5,800,000	
Foresetland acres in 0-13 age class	1,190,127	
Does not meet additionality and permanence test	2,765,924	
Area occcupied by roads and infrastructure	150,000	
Natural sequestration lands	1,693,949	
Average sequestration rate (tco2-e/ac/yr)	4.74	
Sequestration on natural forestlands (tco2-e/yr)		**8.03**

		Current SCC
Taxable emissions	**12.17**	$42.42
Gross revenue ($millions) @ current SCC ($42.34/t)	**$516.28**	

Appendix Q

For the full text of these proposed amendments, please visit: https://www.oregonlegislature.gov/helm/workgroup_materials/WG%201%20-%20Public%20Comments%20from%20Sustainable%20Energy%20Economy%20Network.pdf.



Folding the Timber Industry into Oregon's Climate Agenda
Proposed amendments to SB 1070

Summary of amendments:

- ✓ Expands covered entities to include forestland owners whose logging practices generate 25,000 metric tons CO2-e or more on an annual basis.
- ✓ Directs the Environmental Quality Commission to adopt a method for calculating timber harvest related emissions that takes into account loss of carbon storage, loss of sequestration capacity, emissions associated with decay of logging residuals, and emissions associated with chemical pesticides and fertilizers.
- ✓ Reduces emissions associated with clearcutting and conventional logging practices on the same timetable as other covered entities (20% by 2025; 45% by 2035; 80% by 2050).
- ✓ Establishes the date of enactment as the baseline year.
- ✓ Exempts timber harvest emissions associated with climate-smart practices from the cap.
- ✓ Refines existing Oregon Global Warming Commission duties to track and evaluate climate smart practices that increase carbon storage back to historic levels and reduce emissions associated with logging and wildfire.
- ✓ Requires registration and reporting of timber harvest-related emissions.
- ✓ Ensures accountability of offset projects through public review mechanisms.

Section by section proposed amendments:
(amendments to the 11/17 SB 1070 version in **bold**, ~~strikeouts~~ are proposed removals)

STATEWIDE GREENHOUSE GAS EMISSIONS LIMITS

Section 4(1)(a) is amended to read:

"(a) The total annual emissions of greenhouse gases in this state **except for timber harvest related emissions, which are calculated in accordance with rules adopted under section 22 of this 2018 Act;** and"

Section 4(2)(a), (b), and (c) are amended to read:

"(a) A statewide greenhouse gas emissions goal for the year 2025 to limit greenhouse gas emissions to levels that are at least 20 percent below 1990 levels **except at least 20 percent below present levels for covered entities engaged in timber harvesting;**
(b) A statewide greenhouse gas emissions goal for the year 2035 to limit greenhouse gas emissions to levels that are at least 45 percent below 1990 levels **except at least 45 percent below present levels for covered entities engaged in timber harvesting;**
(c) A statewide greenhouse gas emissions goal for the year 2050 to limit greenhouse gas emissions to levels that are at least 80 percent below 1990 levels **except at least 80 percent below present levels for covered entities engaged in timber harvesting;**"

GREENHOUSE GAS CAP AND INVESTMENT PROGRAM

Section 10(3)(d) is amended to read:

"**(C) Develop public review mechanisms that enable any person aggrieved by a proposed offset project to comment on, administratively challenge, and if necessary seek judicial remedies to prevent harm or prevent violations of standards established by this subsection.**

Appendix R

Legislative Concept Note – 2018

Working title: Oregon Forest Resiliency Act

Purpose: Amends and revises the Oregon Forest Practices Act to require implementation of climate smart practices to enhance the resiliency of private forestlands to drought, disease, wildfire, floods, landslides, low summertime streamflow, thermal pollution, fish kills, regeneration failures and other threats associated with climate change.

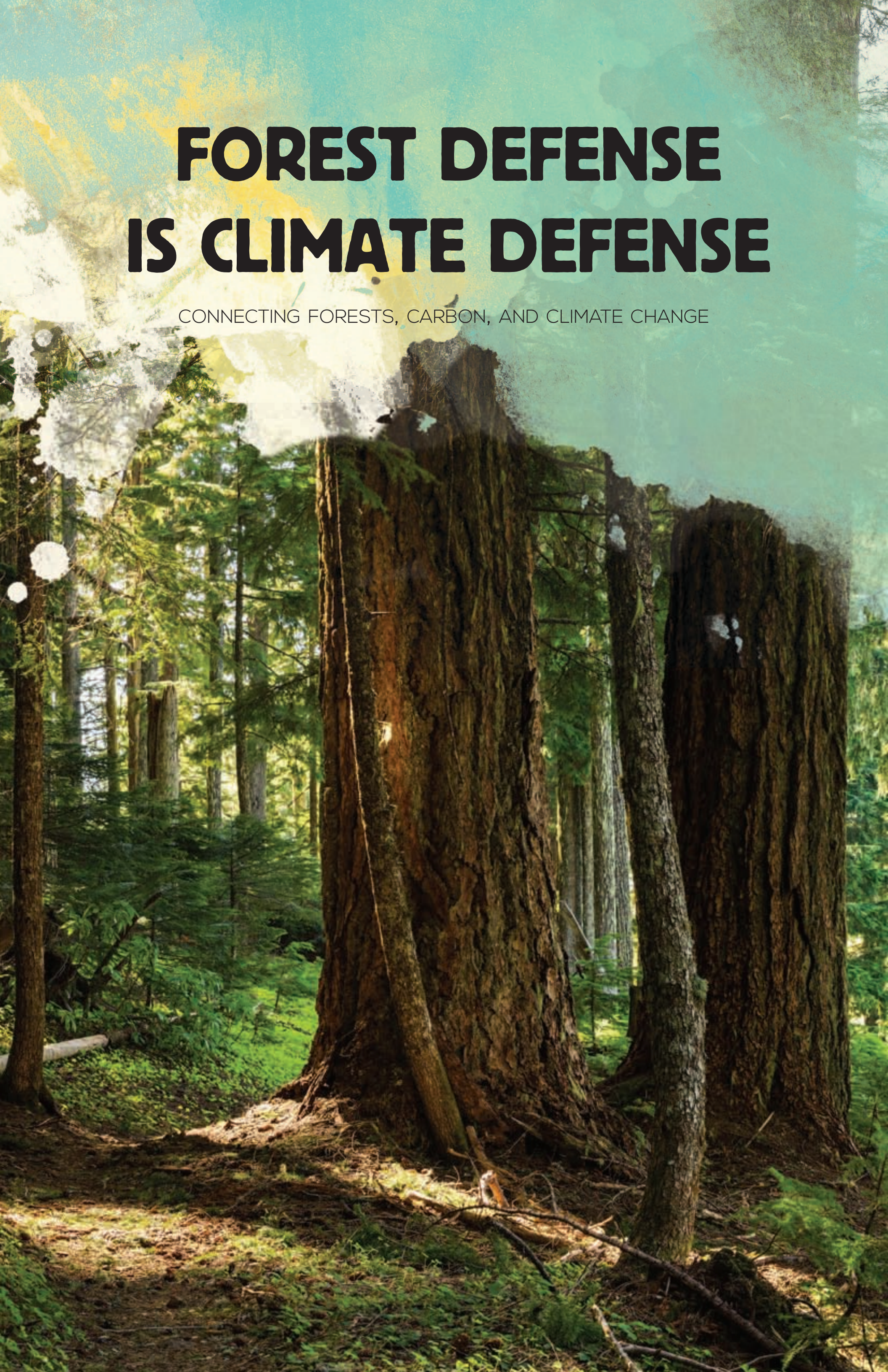
Statement of the problem: Oregon's forestlands are threatened by climate change in a number of ways, all of which have the potential to be costly for forestland owners, nearby communities, for counties and the State. Even-aged industrial tree plantations managed on short rotations are at the heart of the problem because they are far more vulnerable to drought, disease, wildfire, floods, landslides, low summertime streamflow, thermal pollution, fish kills, regeneration failures and other climate change-induced impacts than natural late successional forests and riparian vegetation. The lack of native riparian vegetation along most streams also undermines climate resiliency by removing "nature's fire breaks," thereby exacerbating wildfire risk. As such, restoration of industrial tree plantations back into climate resilient landscapes in ways that maintain timber supply should be a central feature of Oregon's climate agenda.

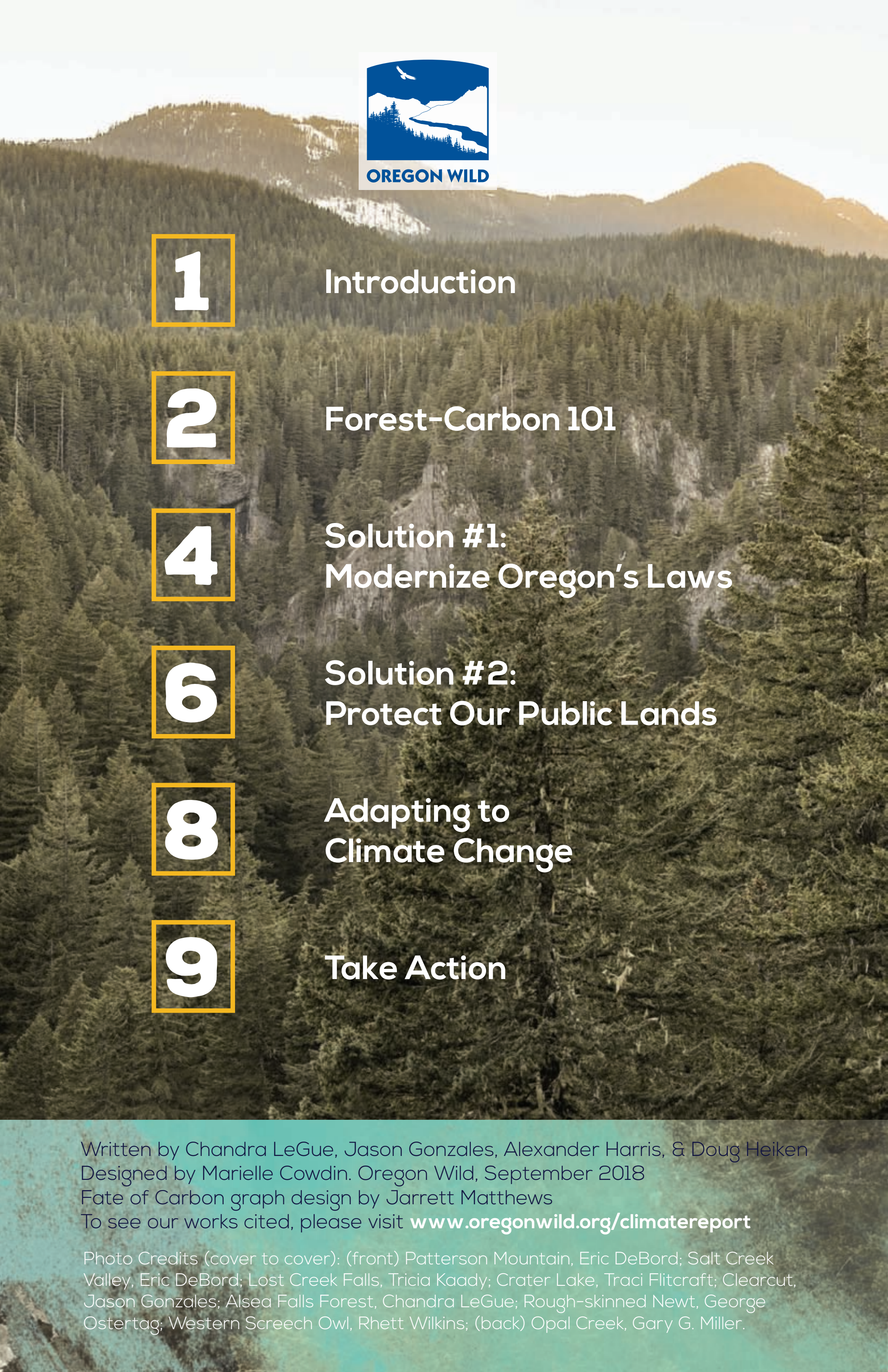
What the bill would do:

1. Climate resiliency plans (CRPs): Requires large forestland owners (>5,000 acres) to prepare and adhere to climate resiliency plans that describe existing conditions, climate threats, and climate smart practices that will be undertaken to comply with requirements of this Act. CRPs shall be based on the best available science and subject to multi-agency review and approval. CRPs will serve as a comprehensive permit and require public participation, multi-agency review and approval.
2. Timber harvest plans (THPs). Requires large forestland owners (>5,000 acres) proposing clearcut harvest methods to file a THP for approval by the State Forester describing harvest, regeneration and resource protection measures needed to ensure the climate resiliency of future stands. THPs must also include a consistency determination with CRPs.
3. Protection and restoration of native riparian vegetation and drinking watersheds: To protect and restore native riparian vegetation and drinking water supplies, establishes water resource management areas (WRMAs) along all rivers, streams, lakes, wetlands and shorelines consistent with the best available science and the state's non-degradation policy. Designates all surface drinking water assessment areas as WRMAs. Prohibits clearcutting and chemical sprays in WRMAs. Directs the State Forester, in consultation with the Department of Environmental Quality and Department of Fish and Wildlife to develop a list of acceptable timber harvest methods within WRMAs that ensure the resiliency of water supplies and native fish and wildlife populations to climate change and enhance the role of riparian zones in mitigating wildfire threat.
4. Protection and restoration of climate resilient forests: Prohibits the conversion of any remaining natural, late successional or old growth forests into tree plantations. For entities required to prepare CRPs, requires allocation of a portion of forestlands to protect or promote the establishment of climate resilient stands of late successional and old growth forest (LSOG) through appropriate silvicultural and restoration techniques. Establishes criteria for selection of LSOG management areas. Requires delineation of such lands on maps and Department of Fish and Wildlife approval.
5. Alternatives to clearcutting and timber plantations: Provides exemptions from reforestation requirements for climate smart practices that rely on natural regeneration and leave sufficient amounts of biological legacy to maintain forest cover, protect soil and watershed conditions, and enhance long term site productivity.

FOREST DEFENSE IS CLIMATE DEFENSE

CONNECTING FORESTS, CARBON, AND CLIMATE CHANGE





Written by Chandra LeGue, Jason Gonzales, Alexander Harris, & Doug Heiken
Designed by Marielle Cowdin. Oregon Wild, September 2018
Fate of Carbon graph design by Jarrett Matthews
To see our works cited, please visit **www.oregonwild.org/climatereport**

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INTRODUCTION

Global climate change presents perhaps the most profound and complex challenge the human species has ever faced. Climate change is already having a measurable impact on Oregon's forests, watersheds, and treasured wild places, and as the planet continues to warm at an unprecedented pace, we will continue to see significant impacts to Oregon's economy, communities, ecosystems, and our way of life.

In recent years, Oregonians have been talking more about ways to reduce the carbon emissions from our energy and transportation sectors; however, notably absent from these conversations is Oregon's largest source of carbon emissions: logging. Recent research, including a groundbreaking study from Oregon State University, shows that Oregon's logging industry emits more carbon into our atmosphere than any other sector.

The single biggest step Oregon can take to combat climate change is to modernize our forest management laws. If we do this, and protect our public lands, the sprawling forestlands that blanket half of our state could become an invaluable asset in mitigating and adapting to climate change. This report highlights two main ways that our state can reduce carbon emissions from logging and increase our forests' natural capacity to capture and store carbon:

1. Modernize Oregon's outdated logging laws to reduce clearcutting and encourage climate-smart practices

2. Permanently protect our remaining old-growth forests and encourage forest restoration on our public lands.

By taking these steps, Oregon can dramatically reduce its carbon emissions, create a stronger and more sustainable economy, and serve as a leader to other forested parts of the world.

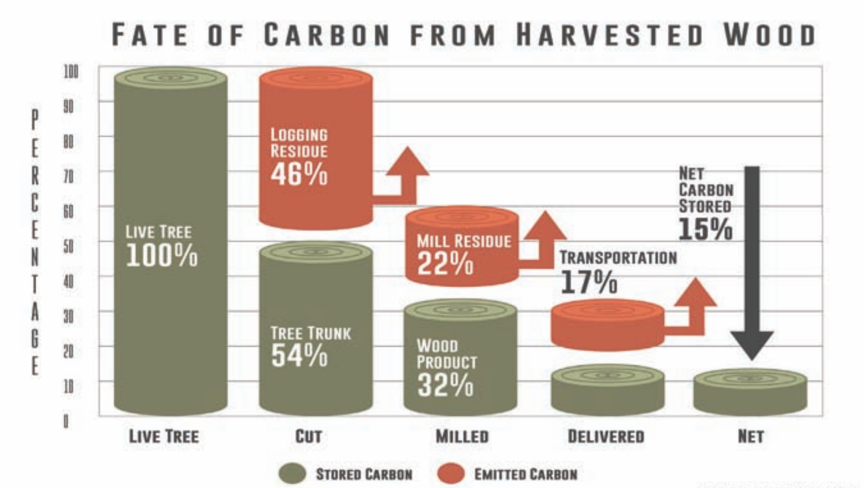
FOREST-CARBON 101

Forests are among the largest stores of living carbon on the planet, and it turns out that the forests of western Oregon have a higher carbon density than almost any other forest type in the world. Unfortunately, the destruction and mismanagement of these forests over the past century has transferred massive amounts of stored carbon to the atmosphere, which has contributed significantly to the warming of the planet. We can't change the past, but the policy choices we make today will either continue to make forests a part of the climate problem, or ensure that they are part of the solution.

HOW DO TREES STORE CARBON?

Carbon is one of the building blocks of life. As forests grow, trees intake carbon from the atmosphere to build living structures and store it in their trunks, bark, branches, and extensive root networks. This natural process, known as "carbon sequestration," converts carbon dioxide from its gaseous state into a solid that remains safely stored for long periods of time.

Oregon's oldest forests are particularly good at capturing and storing carbon, and they continue to absorb carbon even after tree growth appears to have slowed. The logging industry has falsely claimed that fast-growing young forests are better at absorbing carbon; however, research shows that old forests store far more carbon. Logging older trees and replacing them with younger ones emits tremendous amounts of CO2 and creates a "carbon debt" that takes many decades or centuries to repay.



◆ DATA FROM SMITH ET AL. 2006 AND GOWER ET AL. 2006

LOGGING: OREGON'S BIGGEST CLIMATE POLLUTER

Unfortunately, a century of industrial logging practices has eliminated most of Oregon's original old-growth forests and disrupted this natural carbon cycle. Logging kills trees, stops them from growing, and accelerates the transfer of carbon from the forest to the atmosphere. Our carbon-intensive logging practices make the timber industry Oregon's largest source of global warming emissions.

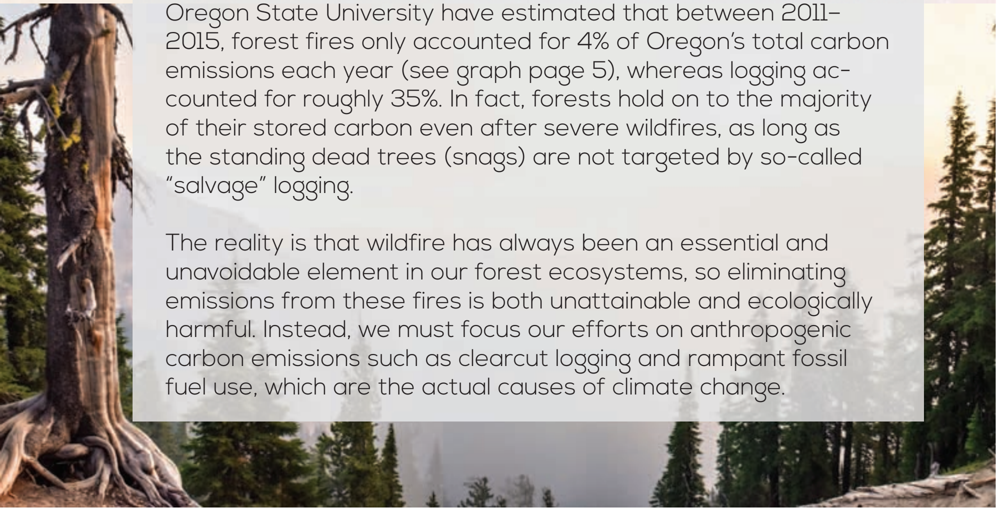
To understand where all this carbon comes from, you need to look at the entire lifecycle of wood products. When a forest is clearcut, the branches, tree tops, and other logging residue left behind is usually burned or left to decompose. This process quickly releases large amounts of carbon that would have otherwise remained stored in the forest for many more years. There are also significant carbon emissions from the fossil fuels burned by logging equipment and log trucks. Once logs reach a mill, even more carbon is lost as the wood is processed and cut into two by fours and lumber. By the time wood products reach their end destination, only a fraction of the original carbon from the forest remains.

On top of all these emissions, logging destroys the living machinery that removes carbon from the atmosphere. The forest eventually regrows, but there is a significant pause in the forest's natural capacity to capture and store carbon, which further exacerbates climate change.

HOW SIGNIFICANT ARE EMISSIONS FROM WILDFIRE?

Despite their impressive smoke plumes, Oregon's wildfires are not major sources of carbon emissions. Researchers with Oregon State University have estimated that between 2011–2015, forest fires only accounted for 4% of Oregon's total carbon emissions each year (see graph page 5), whereas logging accounted for roughly 35%. In fact, forests hold on to the majority of their stored carbon even after severe wildfires, as long as the standing dead trees (snags) are not targeted by so-called "salvage" logging.

The reality is that wildfire has always been an essential and unavoidable element in our forest ecosystems, so eliminating emissions from these fires is both unattainable and ecologically harmful. Instead, we must focus our efforts on anthropogenic carbon emissions such as clearcut logging and rampant fossil fuel use, which are the actual causes of climate change.



SOLUTION #1

MODERNIZE OREGON'S LOGGING LAWS

In Oregon, about 40% of forestland is owned by logging corporations, family foresters, the State of Oregon, counties, and tribes. Those lands are governed by the Oregon Forest Practices Act, or OFPA, first passed in 1972. Although Oregon was one of the earliest states to adopt a Forest Practices Act, researchers have learned a lot about how logging impacts wildlife, water quality, streamflow, carbon storage, and forest health in recent decades. While the OFPA has had minor updates over the years, it has been slow to adapt forest practices to adequately conform to science.

> OREGON HAS THE WEAKEST LOGGING RULES IN THE REGION.

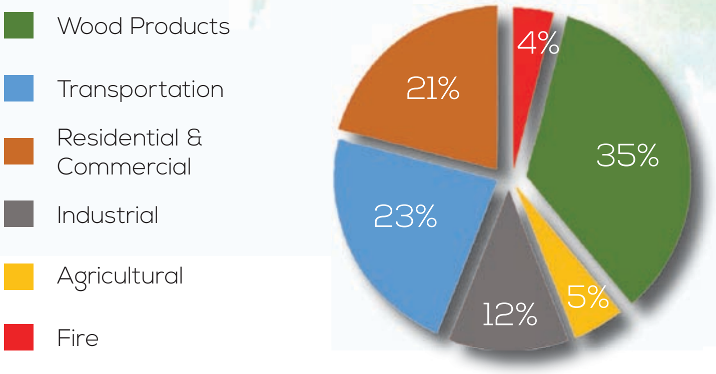
Today, Oregon has the weakest logging rules in the region. The neighboring states of Washington, California, and Idaho all do more to protect streams and communities from the impacts of logging practices like clearcutting and the aerial spraying of herbicides. In fact, logging corporations seem to be headed in the opposite direction of the best available science and what is needed for Oregon to have resilient forests that store carbon.

PROTECTING FORESTS PROTECTS OUR CLIMATE

Oregon’s logging laws present an enormous opportunity for the state to not only prioritize resilient forests over corporate profits, but also become a leader in applying the best available science to combat climate change. Researchers and forward-thinking foresters have already laid the groundwork. Recommendations to modernize Oregon’s logging laws include:

- **LET FORESTS GROW LONGER BETWEEN HARVESTS.** Growing forests for 80-100 years instead of 30-40 years before harvest will allow them to accumulate and store more carbon on the landscape and reduce the many other adverse effects of clearcutting.
- **LEAVE MORE LIVE AND DEAD TREES IN THE FOREST AFTER LOGGING.** Green trees, snags and down wood will help store carbon and mitigate the effects of logging (and climate change) on wildlife.
- **PROTECT STREAMS AND RIVERS.** Larger buffers of intact forests on the sides of streams and on steep slopes will help forests store carbon and protect waterways from the effects of climate change, safeguarding both salmon and clean water.
- **ENCOURAGE BIODIVERSITY.** Currently, clearcut logging relies heavily on toxic chemicals to kill competing vegetation in tree plantations, killing native plants, harming wildlife, and endangering human health. Practices such as selective harvest, more restrictive herbicide use, and encouragement of diverse plant life can not only enhance biodiversity, but also lead to a forest more capable of storing carbon and more resilient to climate change.

OREGON’S ANNUAL CARBON EMISSIONS (2011-2015)



SOLUTION #2

PROTECT OUR PUBLIC LANDS

OLD-GROWTH FORESTS, OUR CLIMATE DEFENDERS

If we want to avoid the worst effects of climate change we need to both reduce carbon emissions as well as capture and store more carbon pollution from our atmosphere. It's becoming increasingly clear that the single biggest step Oregon can take to do this is by better protecting our forests, especially our public lands.

Oregon's old-growth forests are powerful carbon sinks that can help stabilize the climate through the uptake and storage of carbon for long periods of time. These forests also provide clean, cold water, support healthy soil, and provide essential habitat for wildlife. Unfortunately, after a century of aggressive industrial logging only a small fraction of original old-growth forests remain today.

OREGON NEEDS MORE PROTECTED FORESTS!

Oregon's remaining mature and old-growth forests are almost entirely found in our National Forests and Bureau of Land Management (BLM) public lands. These lands, which belong to all Americans, include some of the state's most treasured landscapes, such as Mount Hood and the Cascade-Siskiyou National Monument. Oregon's protected forests play a huge role in storing carbon and provide a natural refuge for plants and animals as the climate changes.

Here are some important ways we can ensure our public forests are part of the solution to climate change:

THE SINGLE BIGGEST STEP OREGON CAN TAKE ON CLIMATE IS TO BETTER PROTECT OUR FORESTS.

- **CUT LOGGING ON PUBLIC LANDS IN HALF.** In recent years, there have been numerous attempts to dramatically increase logging in our National Forests and other public lands; however, if we are to curb emissions from Oregon's most polluting sector we need to log our public forests less aggressively. A recent study by Oregon State University found that halving the amount of logging in our public forests would take a huge bite from Oregon's carbon emissions.

- **DESIGNATE MORE WILDERNESS.** Wilderness designation permanently protects public lands from logging and development, while preserving the public's ability to use the land for hiking, camping, hunting, fishing, and other activities. Oregon lags far behind its neighbor in protecting public lands. For example, only 4% of the state has been designated as protected Wilderness, compared to 10% in Washington and 15% in California. Congress should act to safeguard the additional four million acres of eligible wilderness in Oregon that remains unprotected.

- **DEFEND THE LANDS WE'VE ALREADY PROTECTED.** Logging corporations and their political allies frequently launch attacks on our National Parks and Monuments, Wilderness and roadless areas, and on the environmental laws that help protect our public lands. Defending the protected areas we already have, and laws like the Endangered Species Act, is vital to combating climate change.

- **RESTORE OUR FORESTS THROUGH ECOLOGICAL FOREST MANAGEMENT.** By utilizing the best available science and traditional ecological knowledge, we can restore the complexity and diversity of Oregon's forest ecosystems that have been severely damaged by past logging and fire suppression. Oregon's forests thrived for thousands of years while still providing valuable resources to the humans who lived in them. Restoring these forests will not only lead to greater carbon storage, but also make these stands more resilient to the impacts of climate change.

ADAPTING TO CLIMATE CHANGE

Climate change is already having a measurable impact on our forests. Expanding protections for our public lands and reforming our outdated forest management practices would not only help us reduce excess carbon emissions, but would also help make Oregon's forest ecosystems more resilient to the impacts of a changing climate.

WATER

By protecting and restoring our forests, we can bolster the ***resilience of our watersheds***. As the climate warms, Oregon will continue to see more precipitation falling as rain instead of snow, more floods and landslides, and more frequent and prolonged droughts. Healthy watersheds with low road density, mature trees, and intact stream buffers provide a natural system for slowing run-off, storing and filtering water, and reducing the risk of landslides. Mature and intact forests also provide shade that keeps streams cool and oxygenated for salmon and trout.

PLANTS AND ANIMALS

One of the best ways we can ***help plants and animals adapt to climate change*** is by expanding protections for public lands and creating habitat connectivity corridors. Large, intact wild areas, such as Wilderness, Monuments, and roadless areas, facilitate the migration of species to higher latitudes and elevations where they can find cooler areas or more suitable habitat. For example, the Cascade-Siskiyou National Monument in Southern Oregon links together several ecoregions and mountain ranges, and spans a wide elevation range, all vital in a changing climate.

FOREST FIRES

Fires are a natural part of Oregon's forests, but as the planet warms we are seeing hotter, drier summers and longer fire seasons. Studies show that old-growth forests are much ***more resilient to forest fires*** compared to young, dense tree plantations. Protecting these older forests, and using controlled burns to reduce the risk of unnaturally severe fires can help restore more natural forest structure and enhance their resilience to a changing climate.

TAKE ACTION

Oregon's forests offer a tremendous opportunity for storing carbon and mitigating climate change, but only if we modernize our logging laws and protect more of our public forests. Your elected officials need to hear from you about how we need to act on climate by improving the management of our forests!

1. CALL OREGON'S GOVERNOR TO HELP REFORM OREGON'S OUTDATED LOGGING LAWS

Oregon's timber industry adds more carbon pollution into the atmosphere every year than any other sector. Oregon's state and private forest lands can only reach their potential to combat climate change if state logging laws are reformed and incentives are created to encourage climate-friendly practices.

Call the Governor today! 503-378-4582

Find out about other ways to take action at **www.clearcutoregon.com**

2. URGE YOUR REPS IN CONGRESS TO PROTECT PUBLIC LANDS

Over the past few years, there have been numerous efforts to sell off our public lands and increase the scope and scale of logging in our public forests. One of the best ways to ensure that our forests continue to capture and store carbon is to reduce the rate of logging and permanently protect our forests as Wilderness.

Call your Senators and Congressional Representative today!

OREGON SENATORS

Sen. Wyden: **(202) 224-5244**
Sen. Merkley: **(202) 224-3753**

OREGON REPRESENTATIVES

Rep. Blumenauer: **(202) 225-4811**
Rep. Schrader: **(202) 225-5711**
Rep. Bonamici: **(202) 225-0855**
Rep. Defazio: **(202) 225-6416**
Rep. Walden: **(202) 225-6730**

OREGON WILD

Oregon Wild works to protect and restore Oregon's wildlands, wildlife, and waters as an enduring legacy for future generations.

Guidance for Conserving and Restoring Old-Growth Forest Communities on National Forests in the Southern Region

Report of the Region 8 Old-Growth Team

June 1997

CONTENTS

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ACKNOWLEDGMENTS

The effort to provide working definitions and guidance for management of old-growth forest communities in the South has been ongoing since 1989. Much of this effort has involved USDA Forest Service research station scientists. Their work to describe eastern old-growth communities has been difficult. Even though their work is not complete, the scientists were gracious in sharing their information with our team. We would like to recognize the following researchers for providing drafts of their descriptions of old-growth forests to the team and also for providing reviews of the report:

William B. Batista, Louisiana State University
William Boyer, Auburn University
Margaret Devall, Southern Research Station
David Graney, Southern Research Station
Cathryn Greenberg, Southern Research Station
William Harms, Southern Research Station
Harvey Kennedy, Southern Research Station
Larry Landers (deceased), J.W. Jones Ecological Research Center
Tom Lloyd, Southern Research Station
David Loftis, Southern Research Station
James Meadows, Southern Research Station
Paul Murphy, Southern Research Station
Greg Nowacki, Forest Service, Region 10
William Platt, Louisiana State University
Shear, Ted North Carolina State University
Lucy Tyrrell, North Central Research Station
David White, Southern Research Station

We received excellent comments and ideas from Forest Service employees throughout the region. This input significantly improved the content of this publication.

During the development of the regional guidance, the team interacted with many individuals interested in this process. We would like to thanks those who took the time to attend our public meetings and briefings. The team would like to especially thank Susan Andrews, Deborah Baker, Matt Bennett, Paul Carlson, Jim Crouch, Tom Foti, Chris Haney, Kit Hart, Steve Henson, Hugh Irwin, Norma Ivey, Jim Loesel, Lamar Marshall, Rob Messick, Gene Sirmon, Arthur Smith, Ron Wieland, and Douglas Zollner for their perspectives and involvement. Susan Smith and Bob Wilhelm provided expertise for the analysis of the many comments from reviewers. Carol Lowe and Dale McDaniel edited the final manuscript. Finally, we would like to thank Renee Baker and Diane Dennis for providing word processing and data entry support.

The Region 8 Old-Growth Team

LIST OF TABLES

INTRODUCTION

The U.S. Department of Agriculture, Forest Service, Southern Region, recognizes old-growth forests as a valuable natural resource worthy of protection, restoration, and management. Old-growth forests provide a variety of values, such as biological diversity, wildlife habitat, recreation, esthetics, soil productivity, water quality, aquatic habitat, cultural values, and high-value timber products. Old-growth communities are rare or largely absent in the southeastern forests of the United States. Existing old-growth communities may represent around 0.5 percent (approximately 676,000 acres) of the total forest acreage (approximately 108,400,000 acres) in the Southeast (Davis 1996). For these reasons the national forests are making efforts to address the restoration of this missing portion of the southern forest ecosystems. The future decisions made regarding old growth on national forests during forest plan revisions will be based on sound ecological principles and on consideration of the many social values throughout the region. These guidelines do not render any programmatic or site-specific decisions related to old-growth forests, but rather aim to build a framework to be used by the southern national forests in making decisions about the protection, restoration, and management of old-growth forest communities.

Background

The current Federal laws and regulations associated with the management of national forests do not specifically mandate old-growth management. These various laws do, however, provide direction to the Forest Service in such areas as the management of multiple natural resources and values, the protection and recovery of federally listed threatened and endangered species and their habitats, providing habitats to sustain viable populations of vertebrate species, and maintaining and enhancing the diversity of plant and animal communities that would be expected in a natural forest. These considerations have been at the heart of old-growth planning in the Pacific Northwest (Hardt and Newman 1995).

In 1989, the Forest Service chief Dale Robertson at that time, issued a national position statement on old-growth forests (USDA FS 1989). He provided a generic definition stating, "Old-growth forests are ecosystems distinguished by old trees and related structural attributes. Old growth encompasses the later stages of stand development that typically differ from earlier stages in a variety of characteristics which may include tree size, accumulation of large wood material, number of canopy layers, species composition, and ecosystem function.

The age at which old growth develops and the specific structural attributes that characterize old growth will vary widely according to forest type, climate, site conditions, and disturbance regime. Old growth in fire-dependent forest types may not differ from younger forests in the number of canopy layers or accumulation of down woody material. However, old growth is typically distinguished from younger growth by several of the following attributes:

1. Large trees for the species and site.
2. Wide variation in tree sizes and spacing.
3. Accumulations of large-sized dead standing and fallen trees that are high relative to earlier stages.
4. Decadence in the form of broken or deformed tops or boles and root decay.
5. Multiple canopy layers.
6. Canopy gaps and understory patchiness."

In response to this position statement, efforts began in 1990 among the National Forest System in Regions 8 and 9; the Forest Service research arm (Southern Research Station, North Central Experiment Station, and Northeastern Experiment Station); and The Nature Conservancy to develop old-growth definitions by forest community type (USDA FS 1992). The definitions developed for each forest community type included a description, a listing of representative old-growth stands, the geographic distribution, and old-growth attributes as described in the national position statement. These scientific definitions are currently in various stages of development.

In the absence of the definitions, the Southern Region has relied on age criteria, site productivity, and administrative land classifications to initially identify possible old-growth forests (USDA FS 1993a). Current land management decisions regarding old growth have been implemented on the Ouachita National Forest (USDA FS 1994b), the Nantahala-Pisgah National Forests (USDA FS 1994c), and the George Washington National Forest (USDA FS 1993b).

In December, 1995, the regional forester chartered the Region 8 Old-Growth Team "to finalize the old growth effort and make the [draft] definitions operational and useful." This report is the culmination of the team's effort over the past year and a half.

Team Goals and Objectives

The management of old-growth forests in the Southeast is a challenging issue. Today, old-growth forests are limited in area and distribution on the southern landscape due to past natural events and human disturbances. For this reason, strategies addressing old-growth forest communities will primarily address the restoration of existing second-growth forests to develop old-growth attributes over time. Also of importance are identifying existing old-growth forest communities and developing directions for these representative sites.

Due to the finite number of representative old-growth sites, the available scientific information is somewhat limited for defining old-growth conditions and attributes. Martin (1992) in discussing the difficulty of defining "old growth" stated: "Old growth should reflect the evolutionary history of a forest, but it is difficult for us to understand it. The long-term history of a forest is like a motion picture representing thousands and millions of years. Unfortunately, we will only see one or two frames in our lifetime. From these frames we are supposed to interpret the past, predict the future, and manage accordingly." Adding to the difficulty of defining "old growth" in the South is the wide range of ecological conditions and diversity of forest communities. But regardless of this difficulty and the inherent information gaps when dealing with this natural resource issue, there is an immediate need to provide regional old-growth guidance (Hardt and Newman 1995). The following are the Region 8 Old-Growth Team's goals and objectives.

Team Goals

The goals of the Region 8 Old-Growth Team as stated in the charter are to:

1. Review the definitions (drafted from the research) and other related information to develop guidance for useful operational applications across the Region

2. Develop consistency in this information for use in forest and project-level planning

3. Include internal as well as external reviews as part of this process

4. Coordinate this effort with other agencies and regions as appropriate.

Team Objectives

The objectives of the Southern Region's old-growth strategy are to:

1. Finalize operational definitions for 16 old-growth communities that are found on southern national forests utilizing scientific descriptions being developed by researchers and augmenting these descriptions with additional current information

2. Provide guidelines to inventory all possible old-growth communities during forest land management planning using consistent criteria

3. Provide considerations for determining minimum amounts and spatial distribution of old-growth communities at the subregional, forest, and local levels

4. Develop procedures and rules for identifying existing and future old growth during the implementation of the forest plan through field inventories, which will be based on the operational definitions and

5. Provide regional standards for maintaining data about old-growth forests.

Team Process

After first considering a total of 24 old-growth forest community types, the team determined that 19 had the potential to occur on national forests in the Southern United States. The team then decided that the sand pine forests and woodlands (type 34), cedar woodlands (type 37), and bay forests (type 41) would be addressed better in the context of rare natural communities than as old-growth community types. Furthermore, none of the tropical old-growth (primary) forest community types in the Caribbean National Forest are included in these guidelines. The recent revision of the Caribbean National Forest land management plan addressed these tropical primary forests. These decisions resulted in a total of 16 old-growth forest community types with the potential of occurring on national forests in the Southern United States.

Researchers have been working on the scientific definitions for these 16 old-growth forest community types following the national protocol as provided by Chief Robertson (USDA FS 1989). Because the old-growth definitions are in various stages of completion the team requested that each of the principal scientists working on the definitions provide summaries of their work for developing operational definitions.

All of the researchers provided this information, including narrative descriptions of the old-growth forest community types, a discussion of the geographic distribution, a listing of representative stands for each type, and the measurements of various attributes as described in the national generic definition (USDA FS 1989). Originally, the team intended for the information provided by the researchers to serve both as summaries of the scientific definitions and as operational definitions. However, after reviewing the scientific information received from Forest Service personnel, researchers, and outside interests, the operational definitions and the summaries of the scientific definitions were treated separately.

The purpose of operational definitions is to provide a simplified set of criteria for making decisions in the field regarding a forest stand’s status as old growth. The summaries of the scientific definitions serve as descriptions of the old-growth forest community types and help to formulate forest plans regarding the desired future conditions of old-growth stands, management prescriptions, and monitoring to determine if the desired conditions are met.

With the operational definitions and the summaries of scientific definitions completed, the team developed guidance for addressing old growth in forest and project-level planning and monitoring.

INCORPORATING OLD GROWTH INTO FOREST PLAN REVISIONS

Overview

National forests will have the opportunity to develop management strategies for old-growth forest communities when forest plans are revised. The successful restoration of old-growth stands will require broad-scale information and coordination among national forest managers whose forests share similar ecological and social settings. Old-growth management will be accomplished in the context of ecosystem management principles that include both biological and social considerations. Due to the current scarcity of old-growth communities, most of the efforts on southern national forests will involve identifying areas for old-growth restoration. The guidance, which will be implemented through the individual forest plans, include:

- developing a preliminary inventory of old-growth communities
- evaluating the old-growth values and developing issues
- developing land allocation strategies during alternative development
- providing management direction for old-growth allocations and individual stands of old-growth forest communities.

Terminology

Various terms are used to describe old growth such as: primary forest; virgin forest; potential old growth; designated old growth; type A, B, or C old growth; ancient forest; or old forest. To minimize confusion, these guidelines use three terms to be used by national forests when describing old growth:

> **Existing Old Growth.** Forest stands or patches that meet the age, disturbance, basal area, and tree size criteria described in the operational definitions for the 16 forest community types. A stand or patch must meet all four criteria in order to be classified as existing old growth.
>
> **Future Old Growth.** Forest stands or patches allocated to old growth through land management decisions, but which do not meet one or more of the old-growth criteria in the operational definitions.
>
> **Possible Old Growth.** Forest stands identified during the preliminary inventory of old growth because they meet one or more of the preliminary inventory criteria. The areas of possible old growth will be used to help identify areas to consider for old-growth allocation during forest plan alternative development and to establish priorities for areas of old-growth field inventories during project-level planning. The identification of a

stand as possible old growth infers no land management decision regarding the stand's status as existing or future old growth.

Preliminary Inventory of Possible Old-Growth Forests

In preparing to revise forest plans and prior to alternative development, a preliminary inventory of possible old growth will be conducted on the national forests to analyze the distribution and representation of possible old-growth communities. This process will need to be coordinated among national forests sharing common ecological boundaries, the public, and other State and Federal agencies.

The preliminary inventory will not, in itself, identify areas of old-growth for protection, restoration, or management. However, it does provide information for alternative development and for making planning decisions. Some national forests have already conducted this inventory using previous criteria (USDA FS 1994a). For the Southern Appalachians Assessment (SAA), an "initial old-growth inventory" was used. This SAA inventory will be updated as part of the forest plan revisions. The following criteria for the preliminary inventory replace all previous criteria and should be followed by national forests in the revising or amending their forest plans. The national forests within the SAA will notify the public when the shift from the SAA initial inventory to the preliminary inventory based on these regional guidelines is made.

This preliminary inventory will be developed based on information the national forests currently have available from internal as well as external sources. The preliminary inventory process and screening criteria include:

1. Refine the relationship between the Continuous Inventory of Stand Condition (CISC) forest types and the 16 old-growth forest community types as shown in this report.

2. Include stands identified by national forests as old growth through past inventories or land management decisions.

3. Include all areas allocated to old-growth management through past land management decisions.

4. Identify additional areas (not already identified in number 2 or 3 above) as possible old growth. Criteria for identifying these additional areas of possible old growth are needed because current forest cover information for national forests is incomplete regarding old-growth conditions. Since a final inventory of those forests containing old-growth characteristics will not be available for many years, an inventory of additional areas of possible old growth will be required as part of the current forest-planning process using the following criteria:

- Query CISC, based on the relationship between the old-growth forest community types and CISC forest type codes, to supply a list of stands/areas with ages equal to or greater than the minimum ages shown in table 1 for each old-growth forest community type. This list will include stands currently classified as suitable and unsuitable for timber production.

- Include all lands, whether CISC data about them exist or not, that are congressionally or administratively precluded from timber production such as wildernesses, wild and scenic rivers, and research natural areas.

- Due to the limitations associated with CISC stand ages, supplement the CISC query with information from additional areas that may also contain old-growth forest communities. Utilize people who know of possible areas that might be included such as:

    - Forested and relatively undisturbed riparian areas of stand size

    - Late successional forest areas, in which relatively little human disturbance has occurred over the past five decades

    - Late successional areas which are inaccessible from roads;

    - Stands of low site productivity that have had little or no human disturbance (productivity class 7; i.e., less than 20 ft^3/acre/year growth capability) and

    - Consult other inventories concerning possible old growth on national forest lands as appropriate (including information from other agencies and the public).

5. Display the preliminary inventory information in both spatial and tabular format for all stands identified in the inventory by individual national forest and by ecological section. Make the inventory available for public review prior to the development of alternatives in the forest plan. Display the information from criteria 2, 3, and 4 according to:

-total acres of possible old growth stratified by old-growth forest community types, including uninventoried acres not assigned to a community type. The CISC stand description data may or may not exist for unsuitable forest land. Where possible,

Table 1. - *The minimum stand age by old-growth forest community type for use during the preliminary inventory of possible old growth on southern national forests.*

Old-Growth Community Type	**Minimum Stand Age**
	Years
Northern hardwood forest	100
Conifer-northern hardwood forest	140
Mixed mesophytic and western mesophytic forests	140*
Coastal plain upland mesic hardwood forest	120*
Hardwood wetland forest	120*
River floodplain hardwood forest	100
Cypress-tupelo swamp forest	Pondcypress - 120 Baldcypress - 200
Dry-mesic oak forest	130*
Dry and xeric oak forest, woodland, and savanna	Widespread subtype - 110* Southern subtype - 90*
Xeric pine and pine-oak forest and woodland	Shortleaf - 100* Other pine and mixed - 100
Dry and dry-mesic oak-pine forest	120*
Upland longleaf and south Florida slash pine forest, woodland, and savanna	Longleaf - 110 Slash - 80
Seasonally wet oak-hardwood woodland	100*
Eastern riverfront forest	100*
Southern wet pine forest, woodland, and savanna	Longleaf - 110 Slash - 80 Pond - 80
Montane and allied spruce and spruce-fir forest	120*

*Based on half life (typical mortality) of dominant tree species (Loehle 1988).

augment this information gap with available satellite imagery or aerial photography to come up with estimates of acres of each old-growth forest community type for these areas

-acres of possible old growth stratified by the selection criteria (i.e.,
wildernesses, research natural areas, minimum ages, past allocations)

-acres of possible old-growth forest community types stratified according to lands suitable and unsuitable for timber production (as identified in the existing forest plan).

A purpose for the preliminary inventory is to ensure that management options related to possible old growth on national forests are identified, so the areas can be fully considered during forest plan revisions. Once these possible old-growth areas are identified in the preliminary inventory and until the revised forest plan is approved, the environmental analysis for project-level activities proposed within these areas will consider the effects the proposed action has on the area's old-growth forest characteristics (USDA FS 1994a).

First, it should be determined if the stand meets the criteria for existing old growth based on the operational definitions (table 2) through field inventory. If the stand is existing old growth, then the effects of a proposed project on the stand's old-growth characteristics will be fully disclosed and considered through the National Environmental Protection Act (NEPA) process. The district should consult with the forest-planning team regarding draft forest plan options under consideration for the old-growth forest community type in question, as well as for the entire project area.

Second, if the stand in question is determined not to be existing old growth, a project-level analysis should consider if the area is being included as part of an old-growth allocation in the revised forest plan alternatives. The analysis should consider the effects of the proposed actions to the old-growth allocation area. If the area does not meet the old-growth operational definition and is not being considered as part of an old-growth allocation area, then there is no old-growth issue related to the area.

Determining Forest-wide Old-Growth Issues

Public Scoping

The protection, restoration, and management of old-growth forests through an ecological approach is an important issue to many public interests and is a major concern to national forest managers. National forests should actively seek public input and participation while addressing this issue. During this involvement, national forest managers should begin to understand the public's perception of old-growth forests and their values. Other Federal agencies, State agencies, non-governmental organizations, and academia must be included when developing issues and strategies for old-growth forests. After the public scoping process and following the issuance of the notice of intent (NOI) to revise forest plans, the national forests will clarify and define the old-growth issues for each forest plan. The clarification should include land allocation concerns, biological values and requirements, and social values. Public involvement will be important in determining the areas to be allocated to old growth in the forest plan alternatives and in developing the desired future conditions and objectives.

Determining Biological and Social Values of Old-Growth Forests

An important step in addressing the old-growth issue is to determine the relationship of old-growth communities to biological resources, as well as recreational, scientific, and cultural values. Building these relationships will be important in determining areas to be allocated to old growth and in providing a credible analysis of effects to these various values for different alternatives. Old growth should be considered in the context of a wide array of possible vegetative/habitat conditions, resource objectives, scientific values, and social/cultural values.

Wildlife and Botanical Resources. -- Habitat relationships among special plant and animal species identified using the screening process (SAMAB 1996, USDA FS 1996) to meet forest-planning regulations (36 CFR 219.) should include old-growth habitats. These special species will include federally listed species, Forest Service sensitive species, game species, species with high-management and public interest, species with demanding habitat requirements, and species considered keystone species. The habitat relationships for these species should be determined for all forest cover types and successional classes, rare communities, and special habitat variables. Old-growth communities should be included in developing these habitat relationships. Based on the documented habitat relationships, the contribution of old growth to wildlife and botanical species' habitats can be assessed. This analysis should be quantified according to acres of suitable habitat for the appropriate group of species.

To date no species or species group has been identified as being obligate to old-growth forest communities. However, old-growth forest communities may serve as optimal habitat for some species associates (i.e., red-cockaded woodpecker and landbird late successional habitat associates). Much is still unknown about many species (especially non-vascular plants and invertebrates) associated with old growth. To account for these unknowns, the argument to provide representative old-growth forest communities goes back to Aldo Leopold's conservative approach of "keeping all of the pieces" (Leopold 1949). This "coarse filter" approach of providing a representation of the different old-growth forest communities will help to address overall biological diversity goals and to provide a “biological safety net.”

Recreational Values. -- The contributions of old growth to forest recreational use should be considered. These contributions include nature watching, hunting, camping, hiking, and photography. While these activities may not necessarily be dependent upon old-growth forest communities, the relationship of recreation activities to old-growth forest communities should be estimated.

Research and Scientific Values. -- Old-growth areas can provide opportunities to further understand the ecological processes associated with these communities and to further test the principles of forest dynamics and development. Martin (1992) stated that old-growth forests “are invaluable because they provide the controls against which to best test hypotheses about younger, successional forests and forests actively managed for specific products or purposes. These baseline sites can be systematically compared and contrasted with old growth of different forest types to promote a more integrated understanding of structure and function of all forests. . . . They can and should serve as monitoring sites to follow natural processes through periods of time that extend beyond funding cycles and the lifetimes of decision-makers, scientists, and resource managers.”

The best data for investigating the changes that occur in a forest over time come from permanent plots that have been frequently measured. However, many forests are unstudied or have been examined only briefly, and such data are often not available. In the absence of long-term studies, dendrochronology can be useful in providing information on the history of old-growth forests. Tree growth rings provide a permanent record of the effects of climate on tree growth as well as a record of disturbances caused by fire, insects, or pollution. Tree rings are available whether or not the forest has been studied in the past (Stahle and others 1988).

Educational Values. -- Old-growth areas provide opportunities for outdoor classrooms to teach old-growth processes and to furnish examples of natural history.

Cultural and Spiritual Values. -- The values associated with people’s cultural and spiritual attitudes toward old-growth forests are complex and difficult to describe. Many times these attitudes do not easily conform to scientific definitions of old growth, but people can obtain religious experiences or rejuvenation that come with solitude in nature. Some cultures may have traditional ties to old-growth areas (Standing Women and Comer 1996). These complex values should be considered when defining old-growth issues.

Due to the longevity and low disturbance of some old-growth areas, they may have historical values or archeological sites related to past historical events.

Existence Values. -- Many people may value southern old-growth forest communities, but never visit them. These existence values related to people "just knowing" that old-growth forests exist should be included in any consideration of old-growth values.

Potential High-Value Timber Products. -- The management of forests to achieve old growth has the potential to produce high-value sawtimber products. The forest plans will need to determine which of these areas will be part of the "suitable" timber base (with planned scheduled harvests) and which areas will be part of the "unsuited" timber base.

Realistically, many areas allocated to old-growth management will probably be classified as unsuitable for timber production. While these areas may contain valuable wood products, the products would most likely not be available for regulated harvesting. In addition, depending on the decisions made when revising upcoming forest plans, the potential exists for old-growth allocations to reduce the acreage of national forest lands suitable for timber production.

Values Associated with Other Land Uses.-- The relationship of old growth to other land uses associated with economic and utilitarian values should also be considered. These relationships could be either positive or negative. Examples include current or planned needs for utility rights-of-way, mining, roads, recreational development, and recreational uses (i.e., off-road vehicles and hunting).

Developing Directions for Old Growth in Forest Plans

National forest managers will consider a range of possible areas to be allocated to old growth through the forest plan alternatives and the NEPA process. The amount of land allocated will be based upon the issues developed during public scoping, the goals and objectives within each alternative, and ecological capabilities of the planning area. The ecological classification system (ECS) will be used to provide information to help in the allocation of old growth by community types and to incorporate old growth into the overall management of the forest. Since very little old growth currently exists, managers will emphasize areas for developing or restoring old growth. This planning guidance includes developing a network of old-growth areas of varying sizes to provide for the distribution, linkages, and representation of all old-growth forest community types on national forest lands. The level of representation of the individual old-growth forest community types will depend on the range of resource and social issues at both the subregional and national forest levels. This process will require considerable coordination among national forests and will be open to the public.

Forest plans will provide directions for old growth through forest-wide and management area goals and objectives, management area allocations, and management standards and guidelines. These plans will require close coordination between national forests in close proximity to each other (e.g., national forests in the southern Appalachians). These plans will include goals and objectives needed to address the issues and demands for old growth and to identify the forests' contribution to regional old-growth conservation. In addition, managers will identify the methods by which these goals, objectives, standards and guidelines relating to old growth will be monitored. The monitoring program will address the ways that new information and research will be incorporated.

National Forest Goals and Objectives

The desired future condition (DFC) of the national forest and management areas will include descriptions of old-growth forest management, when appropriate. The DFC description, objectives, and standards will be quantified in terms of measurable parameters (i.e., acres or proportion of an area). Maps will be included showing areas allocated to old-growth management. The old-growth forest community types targeted in an area will be also be identified. The forest plans will use the summaries of the scientific definitions of old-growth forest community types contained within this guidance to help formulate the DFC statements related to old-growth areas.

When the DFC, goals, and objectives of the forest plan for an old-growth area is compatible with timber production, this area will be classified as suitable. When these goals and objectives are not compatible with timber production, the lands will be classified as unsuitable.

Old-Growth Management Strategy

National forests managers will develop a network of old-growth areas of various sizes and will develop management prescriptions for these areas.

Developing a Network of Old-Growth Areas. -- A centerpiece of the regional guidance for conserving old-growth communities is a network of old-growth areas. Many of the concepts regarding this network of old-growth areas come from landscape ecology theories (Harris 1984, Hunter 1990, Vankat and others 1991). These theories relate to the effective patch size, the distribution of patches across the landscape, the relationship of the patches to the adjacent forest matrix, and the relationship or connectivity of the patches. These guidelines attempt to incorporate these theories by providing a network of old-growth areas of different sizes, which in the future will provide the ecological integrity of old-growth communities, the representatives of the 16 identified old-growth forest community types, and an adequate distribution of these community types. While there is a need for a consistent regional approach, individual national forests also need flexibility to address old-growth allocation based on local conditions and public issues. For instance, guidelines that work for national forests in the mountains may not work for national forests on the Coastal Plain. For this reason, this guidance is broadly written and distinguishes between areas within the region.

Old-Growth Patches of Different Sizes. National forest lands in the Southeastern United States will contain a mix of large-, medium-, and small-sized old-growth areas. The national forests in the Ozark/Ouachita Highlands and the SAA area will contain a mix of all three sizes. National forests within these subregions are in close proximity to each other, with fairly consolidated land ownership.

National forests in the Coastal Plains, Northern and Southern Cumberland Plateau, Southern Appalachian Piedmont, and Mississippi Alluvial Valley will, at a minimum, provide management direction for establishing a network of medium- and small-sized old-growth restoration areas during forest plan revisions. The national forests within these ecological units typically are distant from each other and contain broken ownership patterns. While the identification of large-sized patches is warranted for these areas, in reality the land ownership patterns and natural resource management considerations may make the identification of large-sized old-growth areas impractical. However, nothing in the guidance precludes national forests in these subregions from including large old-growth patches within their network.

Large-sized Areas. The large-sized areas are designed to ensure the integrity of ecological functions and the distribution of old-growth conditions at the subregional scale. A first step for national forests within the Ozark/Ouachita Highlands and the SAA area is to identify large old-growth areas when developing alternatives for forest plans. Planning for these large areas should be accomplished at the ecological section level and across forest administrative boundaries.

Determining the biological needs and minimum areas necessary to maintain the integrity of ecological functions requires consensus building. For example, the Nantahala-Pisgah National Forests identified large-sized old-growth patches as areas greater than 2,500 acres (USDA FS 1994c). The Nantahala-Pisgah National Forests used this size criteria primarily to address public issues pertaining to area size requirements and interior breeding habitats for some landbird species. The Ouachita National Forest identified areas for shortleaf old-growth restoration which ranged in size from 600 to 6,000 acres (USDA FS 1994b).

National forests sharing ecologically similar areas should use a consistent minimum patch size during forest planning when describing large-sized patches. The Nantahala-Pisgah National Forests documented the rationale for their minimum size criteria in a recent amendment to their forest plan (USDA FS 1994c), and the public comments related to the regional old-growth guidance supported their decisions related to size criteria for large patches. <u>To facilitate regional consistency and in the absence of other</u>

criteria indicating a different minimum, old-growth areas larger than 2,500 acres should be considered as large-sized patches. This minimum size criteria does not represent any specific biological requirements of species or groups of species associated with a specific forested habitat.

Medium-sized Areas. Next, the national forests in Ozark/Ouachita Highlands and the SAA area should identify medium-sized areas to fill in gaps in old-growth forest community type representation or to improve the spatial distribution between the large-sized areas.

A first step for national forests in the Coastal Plains, the Northern and Southern Cumberland Plateau, the Southern Appalachian Piedmont, and the Mississippi Alluvial Valley is to identify medium-sized old-growth areas during forest planning alternative development. For these national forests, the medium-sized areas should be designed to ensure the integrity of ecological functions, provide for the distribution of old-growth conditions at the forest level, and a representation of old-growth forest community types. An option for these forests is to use state-level information to put forest planning for old growth into the context of the larger landscape.

In the absence of other criteria, old-growth areas between 100 and 2,499 acres should be considered as medium-sized patches.

Small-sized Areas. The forest plans will provide for small-sized old-growth areas through the management prescription(s) for a particular management area and will be implemented through project-level decisions. The management prescriptions will define the procedures for determining the number and priority of the small-sized areas. The emphasis will be to identify stands which:

- meet the operational definitions (table 2) for existing old growth. The forest plan will then provide direction regarding the management of small-sized, existing old-growth stands when found.

- the forest plan has identified as a priority for future old growth, because they are an underrepresented old-growth forest community type and/or normally occur in small, isolated patches (e.g., montane spruce-fir forests and cypress-tupelo forests).

<u>In the absence of other criteria, it is recommended that old-growth areas between 1 and 99 acres should be considered as small-sized patches.</u>

Representation of Old-Growth Forest Community Types. Sixteen old-growth forest community types have the potential of occurring on southern national forest lands. National forests, in establishing a network of old-growth areas, will need to consider a representation of all potential old-growth forest community types. The level of representation of each community type will be based on the issues raised in the forest plans, as well as on the ecological capabilities of a particular national forest.

Distribution of Old-Growth Patches. The network of old-growth areas will be designed to provide a distribution of old-growth conditions representing various ecological sections for all national forests in the Southeast. The allocation of different size patches of old growth can be used to fill voids in their present distribution. The density of the old-growth areas (i.e., the number of areas per ecological section) will depend on the level of old-growth acreage needed to address the significant issues of each forest planning alternative. For example, an alternative with 15 percent of an ecological section allocated to old growth may have a higher density of old-growth areas than an alternative with 5 percent of an ecological section allocated to old growth.

Linkage of Old-Growth Patches. In most cases on national forests, the basic assumption is that management will lead to a forest matrix which includes a full array of forest conditions, but which is dominated primarily by mid- and late-successional forests (SAMAB 1996). Harris (1984) states: “a patch of old growth that is surrounded by mature timber is less distinct than a patch surrounded by regeneration areas.” For this reason, when old-growth areas are included within this type of forest matrix, there will not be a need to physically interconnect old-growth areas by the use of old-growth corridors. The forest conditions normally found on southern national forests should provide the necessary linkages for old-growth areas. As an additional safeguard, the guidance provides for identifying small-sized areas to improve the distribution of a particular forest community type and to provide a “stepping stone” effect between large-sized and medium-sized patches.

<u>Old-Growth Allocations and Management Prescriptions</u>. -- Based on the issues developed during public scoping and the preliminary inventory of possible old growth, national forests should develop alternatives containing different amounts of old-growth allocations. The old-growth areas will consist of a network of patches of varying sizes. The percentage of the total forest acres within an ecological section or an individual forest allocated to old growth will vary by alternative, based on the biological and social issues involved.

The purpose of the following guidance is to better clarify the relationships among the preliminary inventory, public comments regarding old growth, old-growth allocations, the probable range of management prescriptions for these allocations, and the relationship of the old-growth allocations to lands suitable or unsuitable for timber production. The national forests in the SAA area and the Ozark/Ouachita Highlands will be discussed separately from national forests in other areas of the Southeast.

The SAA area and the Ozark/Ouachita Highlands. National forests in these areas should, at a minimum, allocate a network of large- and medium-sized old-growth areas during forest plan revisions. In addition, the forest plans should provide directions regarding existing and future old growth which occurs in small patches. The Nantahala-Pisgah National Forests (USDA FS 1994c) and the Ouachita National Forest (USDA FS 1994b) Forest Plans provide excellent working examples of this process (see appendix A).

Public involvement may generate a range of options from "use only lands currently excluded from timber production to meet old-growth objectives" to "allocate additional lands for old-growth management to protect all existing old growth and for the purpose of managing the majority of national forest lands for future old growth."

Development of Allocations. To consider the range of alternatives for addressing public comments, national forest managers should consider the following screening process:

Screen for large-sized patches. Based on the preliminary inventory, national forests should first include all congressionally and administratively designated lands not available for timber production (e.g., wildernesses, wild and scenic rivers, research natural areas) and lands currently classified as unsuitable for timber production within an ecological section. To complete these large-sized areas, some additional stands classified as suitable for timber production may need to be included. When including these additional stands, consider the oldest available stands and the old-growth forest community types that may be underrepresented. National forest managers should determine which old-growth forest community types are represented within these large-sized areas (if data are available) and which ones are not. The amount, the number, and distribution of the large-sized old-growth areas should then be determined.

Next, national forests should identify additional large-sized old-growth areas which include primarily lands classified as suitable for timber, in order to address other public comments. The preliminary inventory should help to identify these areas. To complete these large-sized areas, some additional stands classified as unsuitable for timber production may need to be included. The emphasis of this step is to increase the proportion of national forests within an ecological section allocated to old growth, as well as the distribution of large-sized areas.

Screen for medium- and small-sized patches. After determining the locations of the large-sized old-growth areas, determine if some old-growth forest community types are not represented or if additional areas should be identified because the distance between the large-sized areas are too great. The representatives and amount of old-growth forest community types included in the large-sized areas should be analyzed.

If needed, medium-sized areas should be identified primarily from lands unsuitable for timber production, for the purpose of including old-growth community types which are absent or underrepresented in the large-sized areas. In addition, the identification of medium-sized areas can be used to improve the distribution of old-growth areas, when there is a great distance between the large-sized areas.

Next, if needed to address other public comments, national forests should identify additional medium-sized areas primarily from lands suitable for timber production.

Specific management direction will be provided to address the management of small-sized patches of old growth at the project-level, as discussed on page 26.

Management Prescriptions. The management prescriptions will specify the type of strategies for the areas allocated to old growth. Guidelines 1 through 3 should be used when determining the level of activities or intervention and the suitability for timber production for large-, medium-, and small-sized patches of old growth. Additionally, guidelines 4 and 5 should be used for only large-sized and medium-sized patches.

1. No management activities or intervention allowed for the entire area. The area would be classified as unsuitable for timber production.

2. Management activities for restoration, protection, or maintenance of old-growth conditions are prescribed.

The area would be classified as unsuitable for timber production.

3. A mix of no management and intensive restoration activities are prescribed, due to the mixture of old-growth forest community types within an area. The area would be classified as unsuitable for timber production.

4. The identification of small, core, old-growth areas, surrounded by extended forest rotations (even-aged or two-aged management), designed to sustain a flow of replacement old-growth stands over time. A certain proportion of the area would meet the old-growth operational definitions at any given time. The core old-growth area would be classified as unsuitable for timber production, and the portion under long forest rotations would be classified as suitable for timber production.

5. Small, core, old-growth areas, surrounded by uneven-aged forest management, would be designed to sustain a flow of old-growth conditions across most of the area over time. Much of the area would meet the old-growth operational definitions at any given time. The core old-growth area would be classified as unsuitable for timber production, and the portion under uneven-aged management would be classified as suitable for timber production.

National Forests in the Coastal Plains, Northern and Southern Cumberland Plateau, Southern Appalachian Piedmont, and Mississippi Alluvial Valley. National forests in these areas should, at a minimum, allocate medium-sized old-growth areas during forest plan revisions. In addition, the forest plans should provide directions regarding existing and future old growth which occurs in small patches to address remaining gaps in old-growth forest community representation, distribution of old-growth areas, or linkages between these areas.

Development of Allocations. The guidance for identifying areas of old-growth and for addressing issues raised by the public are similar to the guidance provided for the SAA and Ozark/Ouachita Highlands. The difference is that medium-sized areas will be the beginning point for national forests in the Coastal Plains, the Northern and Southern Cumberland Plateau, the Southern Appalachian Piedmont, and the Mississippi Alluvial Valley.

> **Management Prescriptions.** See guidelines 1 through 5 for medium-sized patches and guidelines 1 through 3 for small-sized patches, listed previously for the SAA area and the Ozark/Ouchita Highlands.

Effects Analysis

In describing the effects of the different forest plan alternatives, the following items should be addressed: (1) identify how old growth relates to other resources, and to social and economic issues; (2) for each alternative, identify those areas that, because of land allocations and prescriptions, will move toward an old-growth condition in the future (include such areas as Wildernesses, research natural areas, and special areas); and (3) disclose the effects on the old-growth component and the old-growth restoration areas of each alternative. These effects should be quantified using acres as the unit of measurement.

Forest Plan Monitoring

A long-term, old-growth monitoring program should include the monitoring of management activities associated with old growth to determine if directions in the forest plan are being implemented as stated.

In addition, field inventories will be conducted over time for old-growth areas, to track the effectiveness of the forest plan in moving these areas toward the old-growth DFC. These inventories determine if the stand contained existing old growth and would follow the protocol as discussed under the field inventory section.

Additional validation monitoring should include verifying the old-growth scientific definitions and management assumptions regarding the 16 old-growth forest community types. Additional data collection on structural and compositional attributes of existing old-growth stands would be required (see appendix B).

The implementation of this monitoring program will be challenging considering national forest budgets and workloads. Determining the status of existing old growth will take many years. National forests are encouraged to develop partnerships with researchers, other agencies, and public interests to implement the monitoring programs.

IMPLEMENTING DIRECTIONS IN FOREST PLANS

These project-level guidelines and operational definitions focus on identifying existing old growth in field inventories for project-level decision-making and monitoring. In addition, guidance is provided for tiering to the forest plan to identify small-sized old-growth areas.

Field Inventory of Old-Growth Forests

The guidance for field inventory to identify existing old-growth conditions is provided in this section. The team originally considered utilizing eight structural and demographic attributes for use in defining old growth during field inventory. However, this number of attributes caused concerns about consistent field applications, increased inventory work load, and the collection of unnecessary data for making decisions on existing old growth. Due to this, the team determined a simpler set of criteria would be used to make decisions regarding old growth in the field.

Operational Old-Growth Definitions

The information from the summaries of the scientific descriptions of the 16 old-growth communities were used to develop these operational definitions. The operational definitions are designed for field applications in determining the old-growth status of forest stands.. The determination of a stand's status as existing old growth will be based on age, past disturbance, basal area, and tree size. Table 2 provides the attributes for determining the old-growth status of forest stands on southern national forests. If during field inventory, a stand meets all four criteria, it will be considered existing old growth.

Project-Level Old-Growth Field Inventory

The field inventory for old growth will mostly follow the protocol used during Forest Service Silvicultural Examinations (USDA FS 2409.26d). The exception is that the age of the stands should be determined based on the oldest age class as opposed to the "representative stand age." The information collected or verified by Forest Service natural resource professionals will be used to make project-level decisions concerning old growth, to implement the forest plan, and to monitor and report forest-wide old growth.

Table 2. ***The operational definitions* to determine old-growth forest community types during the field inventory and monitoring on southern national forests.***

Old-growth forest community type	**Minimum age of the oldest existing age class**	**Minimum basal area**	**D.b.h. of largest trees**
	Years	Ft^2/acre	Inches
Northern hardwood forest	100	40	≥ 14
Conifer-northern hardwood forest	140	40	≥ 20
Mixed mesophytic and western mesophytic forest	140**	40	≥ 30
Coastal plain upland mesic hardwood forest	120**	40	≥ 24
Hardwood wetland forest	120**	40	≥ 20
River floodplain hardwood forest	100	40	≥ 16
Cypress-tupelo swamp forest	Pondcypress -120 Baldcypress - 200	40	≥ 8 ≥ 30
Dry-mesic oak forest	130**	40	≥ 20
Dry and xeric oak forest, woodland, and savanna	"Widespread" Subtype - 110** "Southern" Subtype - 90**	10 10	≥ 16 ≥ 8
Xeric pine and pine-oak forest and woodland	Shortleaf - 100** Pine & mixed - 100	30 20	≥ 20 ≥ 10
Dry and dry-mesic oak-pine forest	120**	40	≥ 19
Upland longleaf and south Florida slash pine forest, woodland, and savanna	Longleaf - 110	10	≥ 16
Seasonally wet oak-hardwood woodland	100**	40	≥ 20
Eastern riverfront forest	100**	40	≥ 25
Southern wet pine forest, woodland, and savanna	Longleaf - 110 Slash - 80 Pond Pine - 80	10 10 10	≥ 20 ≥ 21 ≥ 9
Montane and allied spruce and spruce-fir forest	120**	40	≥ 20

*The disturbance criteria is discussed in the narrative section.

**Based on half life (typical mortality) of dominant tree species (Loehle 1988)

Minimum Age of the Oldest Age Class. --Table 2 provides the minimum age for the oldest age class for each old-growth forest community type. In most cases, the scientific definitions do not contain information regarding the number of trees per acre in this age class. Some estimates were provided for the following forest community types: mixed mesophytic and western mesophytic forest (type 5); xeric pine and pine-oak forest and woodland (type 24); dry and dry-mesic oak-pine forest (type 25); eastern riverfront forest (type 28); and southern wet pine forest, woodland, and savanna (type 29). <u>Based on that information and as a conservative rule of thumb, the age criteria (table 2) is applicable when at least 8 to 10 trees per acre for pine forest community types (possibly fewer trees per acre for savanna conditions) or when at least 30 trees per acre for some deciduous community types are present</u>. There is a need for flexibility in applying this guidance during the field inventory, because these estimates are not absolutes. This criterion would be applicable to both even- and uneven-aged stands.

Disturbance Criteria. -- To many people interested in old-growth issues, past human disturbance is important in determining an area's status as existing old growth. However, the acceptable level of past human disturbance can prove difficult to quantify. For this reason, a "coarse, non-quantified, and common sense" approach will be used when considering past human disturbance. <u>For a stand to be considered as existing old growth, no obvious evidence of past human disturbance which conflicts with the old-growth characteristics of the area should be present</u>. Recent vegetative management activities which maintain characteristics consistent with old growth probably would not disqualify an area as existing old growth. Examples of these activities may include commercial thinnings, mid-story treatments, prescribed fire, or interpretive trails.

Minimum Basal Area. -- The minimum basal area for each old-growth forest community type in table 2 is a conservative estimate to ensure that stands are not excluded due to the variety of ecological conditions which exist in the Southeast. This minimum is provided as a measurement of stand density and reflects the variability among old-growth forest community types ranging from forests to savannas. Tree sizes for inclusion in the estimate of stand basal area will follow the Forest Service silvicultural stand examination protocols for pine and hardwood species.

Diameter at Breast Height (d.b.h.) of the Largest Trees. -- The presence of large trees is a key old-growth attribute. Again, the scientific definitions do not contain information regarding the number of trees per acre in the size categories shown in table 2. Some estimates for numbers of large trees per acre were provided for the following forest community types: mixed mesophytic and western mesophytic forest (type 5); xeric pine and pine-oak forest and woodland (type 24); dry and dry-mesic oak-pine forest (type 25); eastern riverfront forest (type 28); and southern wet pine forest, woodland, and savanna (type 29). <u>Based on that information and as a conservative rule of thumb, the criteria for the d.b.h.'s of the largest trees are applicable when at least 6 to 10 trees per acre for</u>

all old-growth forest community types (possibly fewer trees per acre for savanna conditions) are present. There is a need for flexibility in applying this guidance during the field inventory because there are situations in which the number of large trees per acre could be fewer.

Field Inventory Monitoring

Field inventories should be part of the long-term monitoring program to determine if forests in the old-growth allocations are moving toward the DFC. Because only small annual monetary commitments to this monitoring program are likely due to lack of funding, the use of challenge-cost share agreements should be considered. In addition, the information obtained during normal compartment prescription process should be included in the monitoring program.

Considerations for Old-Growth Forests During Project-Level Planning

During project-level planning, a first step is to review any stands identified in the preliminary inventory as possible old growth. These stands should be visited in the field in order to determine their status as existing old growth. As previously stated, a stand must meet all four criteria in the operational definitions (table 2) to be existing old growth. A second step is to determine the old-growth status of other stands in the project area. For those stands which meet the operational definitions for old growth, the directions in the forest plan will provide management options. For those stands that do not meet the operational definitions for old growth and if they are not a part of any old-growth allocation or management direction identified in the forest plan, then there is no old-growth issue associated with the project.

Project-level planning will be tiered to the forest plan direction for old growth when developing the project's purpose and needs, and proposed actions. When addressing areas allocated to old growth in the forest plan, the district managers should examine the current conditions and compare them to the DFC for the area in question. Based on this examination and public issues raised during public scoping, the district can implement natural resource management activities not restricted by the forest plan.

When addressing areas with old-growth direction, but containing no forest plan land allocations, the district will have the added responsibility of designating small-sized old-growth areas. The forest plan should provide directions regarding the portion of an area to be allocated to old growth, the distribution of these patches, and the old-growth forest community types involved. The district should use the information from the preliminary inventory and the field examination to help in designating these areas to old growth. The forest plan directions for the area, the current conditions, and public issues will determine the appropriate management activities.

When developing overall management strategies for an area, care should be taken not to isolate the medium- and small-sized old-growth patches from the mid- and late- successional forests. The districts should follow the forest plan directions for small, isolated, old-growth stands, identified as existing old growth during the field inventory, but which are located in areas not having old-growth objectives.

Monitoring Old-Growth Forests

National forest managers will gather information, utilizing data collected during field examinations within old-growth allocation areas and through compartment prescriptions, to track the development of old growth for the long-term (effectiveness monitoring). Inventory protocols are the same as those described for project-level planning. Managers should ensure that the management prescriptions are being implemented properly. In addition, priorities should be established for appropriate research to validate assumptions regarding the old-growth scientific definitions and associated silvicultural treatments. This more detailed validation monitoring will collect information on numerous old-growth variables to validate the scientific definitions and provide new information for modifying the definitions over time (see appendix B).

Information Management

The information for old-growth forests will be maintained in the National Forest Continuous Inventory of Stand Conditions (CISC) and related geographic information system (GIS) forest cover layers.

Old-Growth Land Classes

Stands allocated to old-growth management will be assigned the appropriate land class code based on the management prescriptions in the forest plan. The land class code may refer to the area allocated as old growth or be associated with another resource description (e.g.,. red-cockaded woodpecker [RCW] cluster or RCW foraging stand). The relationship between management prescriptions and timber suitability are discussed in the forest planning section of this guidance.

Old-growth areas identified as <u>suitable for timber production</u> and which do not have a compatible old-growth <u>special</u> land class or a <u>suitable</u> land class description (e.g., RCW foraging) will be assigned the following land class code:

- 699 - Old-Growth Area (even- or uneven-aged)

Old-growth areas identified as suitable for timber production and which already have a compatible old-growth <u>standard or special</u> land class description, will most likely maintain their current land class codes (e.g., RCW active cluster). Where possible, the stand will be coded with a 9 in the third digit for these land classes to denote old growth. If it is determined that old-growth management is the priority for a stand, then a special old-growth land class code (discussed in the previous paragraph) can be assigned.

Old-growth areas identified as unsuitable for timber production and which do not have a current reserved, deferred, lack of technology, not appropriate for timber production, or unproductive land class descriptions, will be assigned the following land class code:

- 819 - Old-Growth Area

Old-growth areas identified as unsuitable for timber production and which already have a current reserved, deferred, lack of technology, not appropriate for timber production, or unproductive land class description will most likely maintain their current land class codes (e.g., wilderness). Where possible, the stand/area will be coded with a 9 in the third digit of these land classes to denote old growth. If it is determined that old-growth management is the priority for a stand, then the old-growth land class code (discussed in previous paragraph) can be assigned.

Old-Growth Status and Forest Community Type

In addition, two local use columns in the CISC database will be used to specifically track information regarding old-growth stands. One column will be used to identify whether a stand is existing or future old growth as follows:

- Existing Old Growth - 01
- Future Old Growth - 02

Stands identified during the preliminary inventory as possible old growth should be made available to the districts to assist in making project-level decisions. If a forest chooses, these stands can be coded 03 in the same local use old-growth status column.

Stands coded as old growth will have an old-growth forest community type code in the other local use column as follows:

Northern hardwood forest	01
Conifer-northern hardwood forest	02
Mixed mesophytic and western mesophytic forest	05
Coastal plain upland mesic hardwood forest	06
Hardwood wetland forest	10
River floodplain hardwood forest	13
Cypress-tupelo swamp forest	14
Dry-mesic oak forest	21

THE OLD-GROWTH FOREST COMMUNITY TYPES OF THE SOUTHERN REGION

Overview

Sixteen old-growth forest community types occur on national forest lands in the Southeast based on information provided by research scientists developing definitions of the old-growth forest communities. The summary of scientific definitions provided in the following guidance are designed to help national forest managers describe the desired future condition (DFC) of old growth in forest plans. This information was also used to formulate the operational definitions previously described.

Each scientific summary contains a community description, a disturbance regime, and representative old-growth areas. As part of the definitions, tables are provided showing the relationship the old-growth forest community types have to current vegetation classifications, their relationship to ecological units and national forests, and various old-growth attributes.

Northern Hardwood Forest
Old-Growth Forest Community Type 1

Community Description

Northern hardwood forests occur exclusively in the northern tier of States in the East, except for a southern extension along the Appalachian Mountains (table 3). In the middle and southern Appalachians, this forest type is restricted to higher elevations that possess cool, mesic conditions. These conditions are most prevalent on northern- and eastern-facing slopes where direct radiation and evapotranspiration rates are reduced. These forests are poorly developed in certain parts of the Northern Ridge and Valley section, where elevation is relatively low (Tyrrell and others, in preparation).

Table 3. *The potential distribution of the northern hardwood old-growth forest community type.*

Ecological Province	**Ecological Section**	**National Forest**
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington - Jefferson
	Blue Ridge Mountains	Nantahala - Pisgah Chattahoochee (Brasstown and Tallulah RD*only) Sumter (Andrew Pickens RD*) Cherokee George Washington - Jefferson (Pedlar, Glenwood RD*, Mount Rogers NRA**)

*RD = Ranger district
**NRA = National recreation area

Sugar maple (Acer saccharum), American beech (Fagus grandifolia), and yellow birch (Betula alleghaniensis) are the dominant northern hardwood species (table 4.). Other deciduous associates include American basswood (Tilia americana), white ash (Fraxinus americana), red maple (A. rubrum), black cherry (Prunus serotina), northern red oak (Quercus rubra), and yellow poplar (Liriodendron tulipifera). Evergreen associates include eastern hemlock (Tsuga canadensis), eastern white pine (Pinus strobus), and red spruce (Picea rubens). The combined overstory coverage of these evergreen species is less than 25 percent in this old-growth forest community type (Nowacki 1993; Tyrrell and others, in preparation).

This old-growth forest community type can be distinguished from mixed mesophytic forests (old-growth forest community type 5) in that (1) northern hardwoods occur only at high elevations, (2) northern hardwoods have a lower level of tree species richness and diversity, and (3) the presence of northern plant species, such as yellow birch and red spruce (Nowacki 1993; Tyrrell and others, in preparation). Table 5 contains old-growth attributes for the northern hardwood forest community type.

Disturbance

Fires occur infrequently and are usually limited to small surface burns due to the moist conditions associated with this type. Ice and wind storms occur periodically and vary in intensity, ranging from complete destruction of a forest to removal of less than 10 percent of the canopy. Species composition is usually not significantly altered by these events.

Table 4. *The relationship of the northern hardwood old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	Code	Forest Type
National Forest CISC* cover type	81	Sugar maple - beech - yellow birch
Society of American Foresters forest type codes	25	Sugar maple-beech-yellow birch
	27	Sugar maple
	28	Black cherry-maple
	60	Beech-sugar maple
The Nature Conservancy International Classification of Ecological Communities **	I.B.2.N.b.010	Yellow birch
	I.B.2.N.b.020	Yellow birch-American beech-yellow buckeye-(sugar maple)
	I.B.2.N.b.040	American beech montane
	I.B.2.N.b.080	Red oak montane

*CISC = Continuous inventory of stand conditions
**Ecological communities = Forest alliances

Representative Northern Hardwood Old-Growth Stands

Black Mountain Research Natural Area, Yancey County, North Carolina
Cherry Cove, near the Blue Ridge Parkway, North Carolina
Walker Cove Research Natural Area, near Asheville, North Carolina
Wayah Bald Area, Nantahala National Forest, North Carolina

Table 5. *Attributes of the northern hardwood old-growth forest community type (Tyrrell and others, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Mean age of large trees	Sugar maple - 113 -136 yrs Beech - 104 - 173 yrs Unspecified - 59 - 238 yrs	Maine Critical Areas Program 1983
2. D.b.h. of largest trees	Sugar maple - 14 - 38 inches Beech - 6 - 28 inches Yellow birch - 13 - 37 inches	
3. Stand density	D.b.h. ≥4 - 153 - 235*	Carbonneau 1986, Leak 1973
	≥20 - 19 - 25*	Leak 1973, Tubbs 1977
	≥28 - 2 - 10*	Leak 1973, Milfred 1967
4. Stand basal area	D.b.h. ≥4 - 112 - 217**	Bourdo 1956, Carbonneau 1986, Pregitzer and Barnes 1984
	≥20 - 43**	Bourdo 1956
	≥28 - 8 **	Bourdo 1956
5. Number of standing snags per acre	13 - 350	Carbonneau 1986, Leopold and others 1988, Lutz 1930
6. Volume of downed logs per acre	3,244 - 6,874 ft^3	Carbonneau 1986
7. Number of canopy layers	1 to 3	Carbonneau 1986, Leopold et al. 1988, Lutz 1930,
8. Percentage of the canopy in gaps	3.2 to 25	Maine Critical Areas Program, 1983

*Trees per acre

**Ft^2 per acre

Conifer-Northern Hardwood Forest
Old-Growth Forest Community Type 2

Community Description

The distribution of conifer-northern hardwood forests is similar to that of northern hardwood forests (old-growth forest community type 1). Conifer-northern hardwood forests are found in the northern tier of States from Minnesota to Maine southward along the Appalachian Mountains to north Georgia (table 6).

Table 6. *The potential distribution of the conifer-northern hardwood old-growth forest community type.*

Ecological Provinces	**Ecological Sections**	**National Forest**
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington - Jefferson
	Blue Ridge Mountains	Nantahala - Pisgah Chattahoochee Sumter (Andrew Pickens RD*) Cherokee George Washington - Jefferson (Pedlar, Glenwood RD*, Mount Rogers NRA**)
Eastern Broadleaf Forest	Northern Cumberland Plateau	Daniel Boone

*RD = Ranger district
**NRA = National recreation area

In the southern Appalachians, this forest type occurs on cooler sites found primarily on north- and east-facing slopes. At least 25 percent of the overstory canopy contains either coniferous or deciduous trees (table 7). Three subtypes are recognized within this broad community type. Table 8 contains old-growth attributes for the conifer-northern hardwood forest community type.

Hemlock-Northern Hardwood Forest (Subtype 2a). - - Eastern hemlock (Tsuga canadensis) is considered a wet-mesic species, developing best on cool, moderately wet to somewhat poorly drained sites. Main associates are yellow birch (Betula alleghaniensis), sugar maple (Acer saccharum), American beech (Fagus grandifolia), red maple (A. rubrum), and eastern white pine (Pinus strobus). Soil surfaces consist mostly of needles and twigs. Hemlocks greatly limit the amount of light reaching the forest floor, which in turn results in sparse understory vegetation. The exception is in canopy gaps, where abundant understory vegetation exists.

Table 7. *The relationship of the conifer-northern hardwood old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	3	Eastern white pine
	4	Eastern white pine-hemlock
	5	Eastern hemlock
	8	Hemlock-hardwoods
	17	Red spruce-northern hardwoods
Society of American Foresters forest type code	20	White pine-northern red oak-red maple
	21	Eastern white pine (in part)
	22	White pine-hemlock
	23	Eastern hemlock
	24	Hemlock-yellow birch
	30	Red spruce-yellow birch
	31	Red spruce-sugar maple-beech
	32	Paper birch-red spruce-balsam fir (in part)
The Nature Conservancy International Classification of Ecological Communities*	I.B.8.N.b.140	Eastern white pine
	I.B.8.N.b.150	Eastern white pine-hemlock
	I.C.2.N.a.260	Eastern hemlock-tuliptree upland
	I.C.3.N.a.045	Red spruce-yellow birch
	I.A.2.N.c.070	Eastern hemlock upland

*CISC = Continuous inventory of stand conditions
**Ecological communities = Forest alliance

White Pine-Northern Hardwood Forest (Subtype 2b). -- The distribution of this type is closely related to historical fire patterns, largely occupying the drier end of the conifer-northern hardwood complex. Common associates include red maple and northern red oak (Quercus rubra) on dry sites and sugar maple, beech, white ash (Fraxinus americana), and hemlock on moist sites.

Red Spruce-Northern Hardwood Forest (Subtype 2c). -- This subgroup is found on cool microsites and occurs only in the Northern Ridge and Valley Section and Southern Blue Ridge Section. It is found at progressively higher elevations when moving south occurring only on mountaintops in the southern Appalachians. Common species associates include yellow birch, sugar maple, beech, and red maple.

Disturbance

For hemlock-northern hardwood forest (subgroup 2a), windthrow is particularly common on many sites due to high water tables, which limit the downward expansion of roots. This type of disturbance allows for frequent gap-phase regeneration. Pit-and-mound microtopography is characteristic of subtype 2. Currently, the hemlock woolly adelgid, an exotic insect, is causing widespread mortality among eastern hemlocks and will affect efforts to maintain or restore this old-growth forest community subtype. Fire has historically had little impact to this subtype. In contrast, fire plays a central role in maintaining eastern white pine in subtype 2b. Insect outbreaks, wind and ice storms, and fire are common disturbances in red spruce-northern hardwood forests (subgroup 2c).

Representative Conifer-Northern Hardwood Old-Growth Stands

Lilly Cornett Woods, Letcher County, Kentucky
Flagpole Knob, George Washington National Forest, Virginia
Hunting Creek, Bedford County, Virginia
The Skidmore Special Mgt. Area, George Washington National Forest, Virginia
Bottom Creek Gorge, Virginia
Roaring Branch, north of Big Stone Gap, Virginia

Table 8. *Attributes of the conifer-northern hardwood old-growth forest community type (Tyrrell and others, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Mean age of large trees	Eastern hemlock - 147 to 264 yrs. White pine - 153 to 272 yrs. Red spruce - 97 to 129 yrs. Sugar maple - 114 yrs	N/A
2. DBH of largest trees	Eastern hemlock - 15 to 51 inches White pine - 28 to 50 inches Red spruce - 6 to 28 inches Sugar maple - 38 inches	N/A
3. Stand density	D.b.h. ≥ 4 - 91 to 475* ≥ 20 - 3 to 33* ≥ 28 - 0 to 10*	N/A
4. Stand basal area	D.b.h. ≥ 4 - 107 - 279** ≥ 20 - 7 - 107** ≥ 28 - 0 - 59**	N/A
5. Number of standing snags per acre	6 to 73	N/A
6. Volume of downed logs per acre	157 to 5,374 ft^3	N/A
7. Number of canopy layers	N/A	N/A
8. Percentage of the canopy in gaps	2 to 17	N/A

*Trees per acre

**Ft^2 per acre

Mixed Mesophytic and Western Mesophytic Forest
Old-Growth Forest Community Type 5

Community Description

Western mesophytic forests are found in provinces in western portions of the Southeast and the mixed mesophytic forests can be found primarily in the southern Appalachians (table 9). Western mesophytic forests occur on a wide range of topographic positions, including drier sites than mixed mesophytic forests, which occur on lower north- and east-facing slopes and mesic coves up to an elevation of about 5,000 feet. In less mountainous terrain, they may cover the entire landscape where conditions are suitable.

Western mesophytic forests are typically dominated by oaks, but also include many of the species of the mixed mesophytic forests, which are among the most biologically diverse ecosystems of the United States. Species dominance patterns vary with geographic location and site condition, such as topographic features, moisture, and fertility.

Of 25 to 30 characteristic species the following are the most common: sugar maple (Acer saccharum), beech (Fagus grandifolia), hemlock (Tsuga canadensis), silverbell (Halesia carolina), yellow poplar (Liriodendron tulipfera), red maple (A. rubrum), white oak (Quercus alba), northern red oak (Q. rubra), yellow birch (Betula alleghaniensis), yellow buckeye (Aesculus flava), and basswood (Tilia americana) (table 10). Yellow buckeye and basswood are indicator species for the mixed mesophytic forests, but yellow buckeye is absent from western mesophytic forests. The age structure of the old growth is broadly uneven aged or all aged. Irregular distributions are common and reflect severe natural disturbances or irregularities in seed production (Greenberg and others, in preparation). Table 11 contains old-growth attributes for the mixed mesophytic and western mesophytic forest types.

Table 9. *The potential distribution of the mixed mesophytic and western mesophytic old-growth forest community type.*

Ecological Provinces	**Ecological Sections**	**National Forest**
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington - Jefferson
	Blue Ridge Mountains	Nantahala - Pisgah Chattahoochee Sumter (Andrew Pickens RD*) Cherokee George Washington - Jefferson (Pedlar, Glenwood RD*, Mount Rogers NRA**)
Southeastern Mixed Forest	Southern Ridge and Valley Section	Talladega (Talladega Division) Chattahoochee (Armuchee RD*)
	Southern Cumberland Plateau	Bankhead
	Southern Appalachian Piedmont	Sumter
Ouachita Mixed Forest	Ouachita Mountains	Ouachita
Lower Mississippi Riverine Forest	Mississippi Alluvial Basin	St. Francis
Eastern Broadleaf Forest	Ozark Highlands	Ozark NF
	Northern Cumberland Plateau	Daniel Boone

*RD = Ranger district
**NRA = National recreation area

Table 10. *The relationship of the mixed mesophytic and western mesophytic old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	41	Cove hardwoods-white pine-hemlock
	50	Yellow poplar
	56	Yellow poplar-white oak-northern red oak
	81	Sugar maple-beech-yellow birch (in part)
Society of American Foresters forest type code	25	Sugar maple-beech-yellow birch (in part)
	27	Sugar maple
	52	White oak-black oak-northern red oak
	57	Yellow poplar-eastern hemlock
	59	Yellow poplar-white oak-red oak
The Nature Conservancy International Classification of Ecological Communities**	I.B.2.N.a.235	Tuliptree-Appalachian basswood-yellow buckeye-sugar maple
	I.B.2.N.b.140	American beech lowland
	I.B.2.N.b.150	American beech-sugar maple-(tuliptree)
	I.B.2.N.a.070	Sugar maple-red oak-bitternut hickory
	I.B.2.N.a.235	Tuliptree-American basswood-yellow buckeye-sugar maple
	I.C.3.N.a.260	Eastern hemlock-tuliptree upland

*CISC=Continuous inventory of stand conditions

**Ecological communities=Forest alliance

Disturbance

The creation of relatively small canopy gaps from the death of a group of trees is the driving “background” disturbance and accounts for a relatively constant turnover of trees and species in old-growth mixed mesophytic forests.

Estimates of canopy turnover rates vary from less than 0.4 to 1.0 percent annually. Less frequent, large-scale disturbances such as severe windstorms, ice storms, floods, landslides, fire, damage by native or non-native insects, or fungal infections may also create openings. The shade tolerance of different species (as well as the initial composition of species and their regeneration strategies) influence tree regeneration in relation to the size and age of the gap.

Table 11. *Attributes of the mixed mesophytic and western mesophytic old-growth forest community type (Greenberg and others, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Maximum age of large trees	Yellow poplar - 226 yrs.	Runkle 1982
	Basswood - 198 yrs.	Runkle 1982
	Sugar maple - 372 yrs.	Tubbs 1977
	Yellow buckeye - 431 yrs.	Runkle 1982
	Beech - 412 yrs.	Morey 1936
	Eastern hemlock - 607 yrs.	Morey 1936
2. Maximum d.b.h. of largest trees	Yellow poplar - 65 inches Basswood - 77 inches Sugar maple - 46 inches Yellow buckeye - 41 inches Beech - 43 inches Eastern hemlock - 45 inches	McLeod, unpublished
3. Stand density	D.b.h. ≥ 4 - 68 to 184*	Bryant 1987, Muller 1982, Palmer 1987, McLeod, unpublished
4. Stand basal area	D.b.h. ≥ 4 - 113 to 296**	Bryant 1987, Muller 1982; Palmer 1987, McLeod, unpublished
5. Number of standing snags per acre	4 to 28	Muller 1982, McComb and Muller 1983, McLeod unpublished
6. Volume of downed logs per acre	944 to 5,862 ft^3	Muller and Liu 1991 McLeod, unpublished
7. Number of 4 inch size classes (trees ≥ 4” d.b.h.)	10 to 19	McLeod, unpublished
8. Percentage of the canopy in gaps	3 to 24	Runkle 1982

*Trees per acre

**Ft^2 per acre

Coastal Plain Upland Mesic Hardwood Forest
Old-Growth Forest Community Type 6

Community Description

These mixed evergreen-deciduous forests occur on the Coastal Plain at latitudes where evergreen species are not killed by cold winter temperatures. This old-growth forest community type most often occurs along mid-to-lower slopes on well drained, but moist, fine-textured soils protected from frequent fires (table 12).

These forests are multilayered, containing species of overstory trees that reach 60 to 110 feet in height and understory species that usually are less than 50 feet in height. Major overstory hardwood species commonly include American beech, (Fagus grandifolia), southern magnolia (Magnolia grandiflora), sweet gum (Liquidambar stryaciflua), several oak species (Quercus michauxii, Q. nigra, Q. alba, Q. shumardii), hickories (Carya glabra, C. cordiformis), and tulip poplar (Liriodendron tulipifera). In these forests, pines (particularly Pinus glabra and P. taeda) also may be among the most abundant overstory species. Composition shifts towards more evergreen species along the southern edge of the Coastal Plain. In Florida and Louisiana, these forests may be primarily live oaks (Q. virginiana) and palms (Sabal palmetto and S. minor) (table 13). Table 14 contains old-growth attributes for the Coastal Plain upland hardwood forest community type.

Dominant understory species commonly include hophornbeam (Ostrya virginiana), blue beech (Carpinus caroliniana), American holly (Ilex opaca), yaupon (I. vomitoria), flowering dogwood (Cornus florida), sourwood (Oxydendron arboreum), red maple (Acer rubrum), and horse sugar (Symplocos tincture). Many rarer species also are likely to be present in the understory, resulting in 40 or more woody species in these forests. Lianas are commonly present, such as grapes (Vitus rotundifolia), poison ivy (Rhus toxicodendron), Virginia creeper (Parthenocissus guinquefolia), and cross vine (Bignonia capreolata). Few herbaceous species occur beneath the multilayered canopy (Batista and Platte, in preparation).

Disturbance

Disturbances in this forest community type are characterized by frequent, small-scale gaps of one to a few overstory trees and periodic (every few decades) larger scale disturbances in the form of hurricanes. Even moderate intensity hurricanes may cause major damage of more than 25 percent of the overstory; mortality of these overstory trees may be as much as 10 percent several years after the hurricane. The proportion of shade-tolerant species, such as American beech and southern magnolia, relative to the proportion of light-demanding species, such as oaks, hickories, and pines, appears to reflect the frequency of large-scale disturbances such as hurricanes. Commonly, gaps are captured by understory species, and so large portions of the canopy (as much as 60 percent immediately after hurricanes and as much as 30 percent after several decades) contain no overstory trees. A large amount of coarse woody debris may be present after hurricanes, but this decays rapidly and does not last much beyond 10 years. Reductions in the frequency at which fires burn down slopes, especially under drought conditions, have resulted in the spread of mesic hardwood forests up slopes into longleaf pine stands. The role of fire in Coastal Plain upland mesic hardwood forests is unknown (Batista and Platte, in preparation).

Representative Coastal Plain Upland Mesic Hardwood Old-Growth Stands

Woodyard Hammock, Tall Timbers Research Station, Leon Co., Florida
Titi Hammock, Thomas Co., Georgia
San Felasco Hammock, Alachua Co., Florida
Highlands Hammock, Highlands Co., Florida
Raglan Hills, Forrest Co., Mississippi
Weir Woods, Hardin Co, Texas
Zemurray Forest, Tangipahoa Parish, Louisiana
Tunica Hills, West Feliciana Parish, Louisiana

Table 12. *The potential distribution of the Coastal Plain upland mesic hardwood old-growth forest community type.*

Ecological Provinces	**Ecological Sections**	**National Forest**
Outer Coastal Plain Mixed Forest	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Desoto Bienville Homochitto
	Atlantic Coastal Flatwoods	Osceola
	Florida Coastal Lowlands, Western Gulf Section	Apalachicola (in part)
	Coastal Plains and Flatwoods, Western Gulf Section	Kisatchie (all except Caney RD*) Davy Crockett Angelina Sabine (in part)
Southeastern Mixed Forest	Coastal Plain, Middle Section	Holly Springs Tombigbee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD* only) Sam Houston Sabine (in part) Ouachita (Tiak RD* only)

*RD=Ranger district

Table 13. *The relationship of the Coastal Plain upland mesic hardwood old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	13	Loblolly-pine hardwoods
	53	White oak-red oak-hickory
	69	Beech-magnolia
	77	Oak hammock
Society of American Foresters forest type code	82	Loblolly pine-hardwood
	89	Live oak (in part; mesic salt domes)
The Nature Conservancy International Classification of Ecological Communities**	I.C.3.N.a.170	Loblolly pine-(sweetgum, tuliptree) upland
	I.C.2.N.a.010	American beech-southern magnolia
	I.C.2.N.a.040	Live oak-sugarberry
	I.B.2.N.a.160	American beech-white oak
	I.B.2.N.a.250	White oak
	I.A.4.N.a.030	Live oak

*CISC=Continuous inventory of stand conditions

**Ecological communities=Forest alliance

Table 14. *Attributes of the Coastal Plain upland mesic hardwood old-growth forest community type (Batista and Platt, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Median age of large trees (from one site)	Southern magnolia - 214 yrs. American beech - 210 yrs. Sweetgum - 210 yrs. White oak - 170 yrs. Loblolly pine - 94 yrs.	Platt and Hermann 1986, Hirsh 1981, Platt and Schwartz 1990
2. Maximum d.b.h. of the largest trees	Southern magnolia - 28 - 50 inches American beech - 30 - 39 inches Sweetgum - 23 - 34 inches White oak - 19 - 32 inches Loblolly pine - 18 - 31 inches	Glitzenstein and others 1986; Harcombe and Marks 1978; Hirsh 1981; Platt 1985; Platt and Hermann 1986; Platt and Schwartz 1990; Quigley 1994; White 1987
3. Stand density	D.b.h. $\geq$ 4 inches - 139 - 186* $\geq$ 20 inches - 16 - 28*	Glitzenstein and others 1986; Harcombe and Marks 1978; Hirsh 1981; Platt 1985; Platt and Hermann 1986; Platt and Schwartz 1990; Quigley 1994; White 1987
4. Stand basal area	D.b.h. $\geq$ 4 inches - 118 - 165** $\geq$ 20 inches - 52 - 105**	Glitzenstein and others 1986; Harcombe and Marks 1978; Hirsh 1981; Platt 1985; Platt and Hermann 1986; Platt and Schwartz 1990; Quigley 1994; White 1987
5. Median number of standing snags per acre	4	Hirsh 1981; Platt and Hermann 1986; Platt and Schwartz 1990
6. Median volume of downed logs per acre	1,022 ft^3	Hirsh 1981; Platt and Hermann 1986; Platt and Schwartz 1990
7. Number of 4 inch size classes (trees $\geq$ 4" size class)	8-11	Glitzenstein and others 1986; Harcombe and Marks 1978; Hirsh 1981; Platt 1985; Platt and Hermann 1986; Platt and Schwartz 1990; Quigley 1994; White 1987

*Trees per acre

**Ft^2 per acre

Hardwood Wetland Forest
Old-Growth Forest Community Type 10

Community Description

Hardwood wetland forests occur mainly in nonriverine, topographically defined basins on uplands, small drainage's, and along the margins of Coastal Plain ponds and bays (Tyrrell and others, in preparation). High water tables are usually present, and most sites are moist to wet throughout most of the year (table 15).

Species include red maple (Acer rubrum), black ash (Fraxinus nigra), green ash (F. pennsylvanica), elms (Ulmus spp.), sweetgum (Liquidambar styraciflua), and black tupelo (Nyssa sylvatica). Other associates may include silver maple (A. saccharinum), swamp white oak (Quercus bicolor), bur oak (Q. macrocarpa), sycamore (Platanus occidentalis), and eastern cottonwood (Populus deltoides) (table 16). Highbush blueberry (Vaccinium corymbosum), black chokeberry (Aronia meloncarpa), and holly (Ilex spp.) are common shrubs (Tyrrell and others, in preparation). Table 17 contains old-growth attributes for the hardwood wetland old-growth forest community type.

Hardwood wetland forests are different from seasonally wet oak-hardwood woodlands (type 27) due to a lack of seasonal dryness, fewer oaks, and little to no disturbance from fire (Nowacki 1993).

Disturbance

Because high water tables restrict rooting and limit tree anchorage, trees may be prone to windthrow in some parts of these forests. This type of disturbance causes a prevalence of tip-up mounds, downed trees, and canopy gaps. Tree mortality is also caused by fluctuating water levels or flooding due to beaver activity (Nowacki 1993).

Representative Hardwood Wetland Forest Old-Growth Stands

Orange Black Gum Swamp, Franklin Co., Massachusetts
Brandon Swamp, Rutland Co., Vermont
Cornwall Swamp, Addison Co., Vermont

Table 15. *The potential distribution of the hardwood wetland old-growth forest community type.*

Ecological Province	Ecological Section	National Forest
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington-Jefferson
Southeastern Mixed Forest	Southern Appalachian Piedmont	Uwharrie Sumter Oconee
Outer Coastal Plain Mixed Forest	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Ocala Desoto Bienville Homochitto
	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Coastal Plains and Flatwoods Lower Section	Kisachie (All exept Caney RD*) Davy Crockett Angelina Sabine (in part)
Eastern Broadleaf Forest	Northern Cumberland Plateau	Daniel Boone

*RD = Ranger district

Table 16. *The relationship of the hardwood wetland old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	68	Sweet bay-swamp tupelo-red maple
	71	Black ash-American elm-red maple
Society of American Foresters forest type code	39	Black ash-American elm-red maple
	65	Pin oak-sweetgum (in part)
	104	Sweet bay-swamp tupelo-redbay
	108	Red maple
The Nature Conservancy International Classification of Ecological Communities**	I.B.2.N.d.200	Bur oak-swamp white oak-pignut hickory temporarily flooded
	I.B.2.N.e.020	Red maple-green ash seasonally flooded
	I.B.2.N.g.015	Red maple-blackgum saturated
	I.B.2.N.d.130	Blackgum temporarily flooded
	I.B.2.N.g.020	Swamp blackgum-Carolina red maple saturated

*CISC=Continuous inventory of stand conditions

**Ecological community = Forest alliance

Table 17. *Attributes of the hardwood wetland old-growth forest community type. (Tyrrell and others, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Maximum age of large trees (From one site)	Black gum - 400 yrs.	Vogelmann 1976
2. Maximum d.b.h. of the largest trees	Black gum - 23 inches Oak spp. - 39 inches	Boerner and Cho 1987; Vogelmann 1976
3. Stand density	All trees - 21 to 324*	Boerner & Kooser 1991; Lindsey et al. 1961
4. Stand basal area	All trees - 28 to 160**	Boerner & Kooser 1991; Lindsey and others 1961
5. Number of standing snags per acre	N/A	
6. Volume of downed logs per acre	N/A	
7. Number of 4 inch size classes (trees ≥ 4” size class)	N/A	

*Trees per acre

**Ft^2 per acre

N/A= Not available

River Floodplain Hardwood Forest
Old-Growth Forest Community Type 13

Community Description

River floodplain hardwood forests range from the Piedmont and the mountains, and into the Coastal Plain in the Southeast United States (table 18). These sites are some of the most productive in the South due to the deposit of sediments from periodic flooding. These river bottom (first bottom) soils are well-drained loam's and silt loam's. Tree species include red maple (Acer rubrum), river birch (Betula nigra), water hickory (Carya aquatica), water oak (Quercus nigra), green ash (Fraxinus pennsylvanica), sweetgum (Liquidambar styraciflua), sycamore (Platanus occidentalis), willow oak (Q. phellos), laurel oak (Q. laurifolia), overcup oak (Q. lyrata), and elms (Ulmus spp.) (table 19). Tree species on the adjacent higher elevation second bottoms where flooding is less frequent, include cherrybark oak (Q. falcata), swamp chestnut oak (Q. michauxii), hickories (Carya spp.), American beech (Fagus grandifolia), and tulip poplar (Liriodendron tulipifera) (Shear and others, in preparation). Table 20 contains old-growth attributes for the river floodplain hardwood forest community type.

Disturbance

The primary disturbances are flooding and natural tree mortality resulting in small gaps in the forest canopy. Infrequent fires could also play a role in this forest type during dry years. Because annual flooding cycles have been altered and fires have been suppressed, American beech and red maple may become more prominent in this community type (Shear and others, in preparation).

Meandering channels often isolate, then destroy significant areas of river floodplain hardwood forests along major rivers. Furthermore, tornado frequently occur in areas where this forest community predominates.

Representative River Floodplain Hardwood Forest Old-Growth Stands

Boiling Springs Natural Area, Sumter National Forest, South Carolina
Green Ash Research Natural Area, Delta National Forest, Mississippi
Red Gum Research Natural Area, Delta National Forest, Mississippi
Overcup Oak Research Natural Area, Delta National Forest, Mississippi
Mormon Branch Botanical Area, Coal National Forest, Florida
Congaree Swamp National Monument, Richland Co., South Carolina
Savannah River Site, near New Ellenton, South Carolina
Moro Creek Bottoms Preserve, south-central Arkansas

(Nowacki 1993; Shear and others, in preparation)

Table 18. *The potential distribution of the river floodplain hardwood old-growth-forest community type.*

Ecological Province	Ecological Section	National Forest
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington - Jefferson
Southeastern Mixed Forest	Southern Appalachian Piedmont	Uwharrie Sumter Oconee
Outer Coastal Plain Mixed Forest	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Ocala Desoto Bienville Homochitto
Southeastern Mixed Forest	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee Holly Springs Tombigbee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD* only) Sam Houston Sabine (in part) Ouachita (Tiak RD* only)
Lower Mississippi Riverine Forest	Mississippi Alluvial Basin	Delta St. Francis
Ouachita Mixed Forest	Ouachita Mountain	Ouachita
Eastern Broadleaf Forest	Ozark Highlands	Ozark
	Northern Cumberland Plateau	Daniel Boone

*RD=Ranger district

Table 19. *The relationship of the river floodplain hardwood old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	46	Bottomland hardwood- yellow pine
	71	Black ash-American elm-red maple
	58	Sweetgum-yellow poplar
	61	Swamp chestnut oak-cherrybark oak
	62	Sweetgum-nuttall oak-willow oak
	63	Sugarberry-American elm-green ash
	64	Laurel oak-willow oak
	65	Overcup oak-water hickory
	68	Sweet bay-swamp tupelo-red maple
	69	Beech-magnolia
	72	River birch-sycamore
	75	Sycamore-pecan-American elm
Society of American Foresters forest type code	65	Pin oak-sweetgum (in part)
	82	Loblolly pine-hardwood
	87	Sweetgum-yellow poplar
	88	Willow oak-water oak-laurel oak
	91	Swamp chestnut oak-cherrybark oak
	92	Sweetgum-willow oak
	93	Sugarberry-American elm-green ash
	94	Sycamore-sweetgum-American elm
	96	Overcup oak-water hickory
	108	Red maple (in part)

*CISC=Continuous inventory of stand conditions

Table 19 (continued). *The relationship of the river floodplain hardwood old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
The Nature Conservancy International Classification of Ecological Communities**	I.B.2.N.e.100	Overcup oak-(water hickory) seasonally flooded
	I.B.2.N.d.190	Laurel oak temporarily flooded
	I.B.2.N.e.020	Red maple-green ash seasonally flooded
	I.B.2.N.d.050	River birch-sycamore seasonally flooded
	I.B.2.N.d.250	(Willow oak, water oak, diamond leaf oak) temporarily flooded
	I.B.2.N.d.215	Water oak-cherrybark oak temporarily flooded
	I.B.2.N.d.110	Green ash-American elm-(northern hackberry, sugarberry) temporarily flooded

**Ecological communities=Forest alliance

Table 20. *Attributes of the river floodplain hardwood old-growth forest community type (Shear and others, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Age of oldest trees	≥ 100 yrs.	Shear and others, in preparation
2. D.b.h. of the largest trees	≥ 16 inches	Shear and others, in preparation
3. Stand density	≤ 162*	Shear and others, in preparation
4. Stand basal area	N/A	
5. Number of standing snags per acre	N/A	
6. Volume of downed logs per acre	N/A	
7. Number of 4 inch size classes (trees ≥ 4” size class	N/A	

*Trees per acre
N/A = Not available

Cypress-Tupelo Swamp Forest
Old-Growth Forest Community Type 14

Community Description

Cypress-tupelo forests occur mainly on the Coastal Plain from southern Delaware through south Florida to southeastern Texas and extend northward along the Mississippi River and its major tributaries to southern Illinois (table 21). Most of the cypress occurs within 100 feet of sea level. This forest community type is found almost exclusively in depressions that are prone to frequent flooding, such as swamps, deep sloughs, alluvial flats of major river floodplains, tidal estuaries, margins of coastal marshes, and isolated depressions of the Coastal Plain (Devall, in preparation).

Principal tree species include baldcypress (Taxodium distichum), pondcypress (T. ascendens), water tupelo (Nyssa. aquatica), and swamp tupelo (N.sylvatica var. biflora). These species occur either singly or in mixtures (table 22). Baldcypress grows larger and more rapidly than pondcypress and is usually associated with flowing water. Pondcypress ordinarily dominates shallow ponds, edges of strands, and other locations where water collects and stands for part of the year. Though these tree species are not considered shade tolerant, this forest community type as a whole is considered stable (climax) on most sites because prolonged periods of deep flooding curtail invasion by more shade-tolerant species. However, where sediment accumulates and/or the frequency of flooding diminishes, this forest type may be replaced by others (e.g., river floodplain hardwood forests) (Devall, in preparation). Table 23 contains attributes for the cypress-tupelo swamp old-growth forest community type.

Disturbance

Historically, low-intensity, small-scale disturbances were probably common in these forests, although their nearness to the coast ensured occasional large-scale disturbances, such as hurricanes. Due to hydric conditions, fire is unusual in these forests except during periods of drought. The principal tree species typically have long life spans; baldcypress, for instance, can live 1,600 years or longer.

Representative Cypress-Tupelo Swamp Forest Old-Growth Stands

Pondcypress Swamps, Apalachicola National Forest, Florida
Gum Swamp Research Natural Area, Osceola National Forest, Florida
Big Cypress, Bienville Parish, Louisiana
Congaree Swamp National Monument, Richland Co., South Carolina

Table 21. *The potential distribution of the cypress-tupelo swamp old-growth forest community type.*

Ecological Province	**Ecological Section**	**National Forest**
Outer Coastal Plain Mixed Forest	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Florida Coastal Lowlands, Western Gulf Section	Apalachicola (in part)
	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Ocala Desoto Bienville Homochitto
	Coastal Plains and Flatwoods, Western Gulf Section	Kisatchie (all except Caney RD*) Davy Crockett Angelina Sabine (in part)
Southeastern Mixed Forest	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee Holly Springs Tombigbee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD* only) Sam Houston Sabine (in part) Ouachita (Tiak RD* only)
Lower Mississippi Riverine Forest	Mississippi Alluvial Basin	Delta St. Francis

*RD=Ranger district

Table 22. The relationship of the cypress-tupelo swamp old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	23	Pondcypress
	24	Baldcypress
	67	Baldcypress-water tupelo
	68	Sweet bay-swamp tupelo-red maple
Society of American Foresters forest type code	100	Pondcypress
	101	Baldcypress
	102	Baldcypress-tupelo
	103	Water tupelo-swamp tupelo
The Nature Conservancy International Classification of Ecological Communities**	I.B.2.N.d.290	Pondcypress-sycamore temporarily flooded
	I.B.2.N.e.180	Pondcypress seasonally flooded
	I.B.2.N.e.190	Baldcypress-swamp tupelo seasonally flooded
	I.B.2.N.f.030	Water tupelo-(baldcypress) semipermanently flooded
	I.B.2.N..f.060	Baldcypress semipermanently flooded
	I.B.2.N.h.010	Swamp blackgum-(baldcypress) tidal
	I.B.2.N.g.050	Baldcypress-swamp blackgum

*CISC=Continuous inventory of stand conditions

**Ecological communities=Forest alliance

Table 23. *Attributes of the cypress-tupelo swamp old-growth forest community type (Devall, in preparation).*

Old-Growth Attribute	**Old-Growth Parameter**	**Data Sources**
1. Age of oldest tree	Baldcypress - 200 to 1200 yrs.	Ewel & Odom 1984; Hall and Penfound 1943; Lynch and others. 1991; Porcher 1981.
	Pondcypress - 120 to 900 yrs.	Schlesinger 1978
2. D.b.h. of largest trees	Baldcypress - 30 to 144 inches	Gresham 1995a; Gresham 1995b; Harlow and Ellwood 1969; Lindsey and others 1961; Lynch and others 1991
	Pondcypress - 8 to 27.5 inches (above swell)	Schlesinger 1978
3. Stand density	Baldcypress D.b.h. $\geq$ 1 inch - 36 to 52*	Hall and Penfound 1939a; Hall and Penfound 1939b
	Pondcypress D.b.h. $\geq$ 1 inch - 1447 to 7702*	Schlesinger 1978
4. Stand basal area	Baldcypress D.b.h. $\geq$ 1 inches - 203**	Hall and Penfound 1939a
	Pondcypress D.b.h. $\geq$ 1 inches - 202 to 443**	Schlesinger 1978
5. Number of standing snags per acre	3 to several	Martin and Smith 1991
6. Volume of downed logs per acre	3 to several	Martin and Smith 1991
7. Number of canopy layers	1	Hall and Penfound 1939a; Hall and Penfound 1943; Schlesinger 1978

*Trees per acre

**Ft^2 per acre

Dry-Mesic Oak Forest
Old-Growth Forest Community Type 21

Community Description

Dry-mesic oak forests occur throughout the South in all ecological provinces (table 24), most commonly in the mountains. They are usually found on dry, upland sites on southern and western aspects and ridgetops (Nowacki 1993).

The species composition of this forest type varies greatly due to its wide distribution. The major species include chestnut oak (Quercus montana), northern red oak (Q. rubra), black oak (Q. velutina), white oak (Q. alba), and scarlet oak (Q. coccinea). Additional associates include southern red oak (Q. falcata), post oak (Q. stellata), blackjack oak (Q. marilandica), pignut hickory (Carya glabra), mockernut hickory (C. tomentosa), and red maple (Acer rubrum) (table 25). Coniferous species such as shortleaf pine (Pinus echinata), eastern white pine (P. strobus), and table mountain pine (P. pungens) may occur as a mixture, with an overstory coverage of less than 25 percent. American chestnut (Castanea dentata) was a major species in this old-growth forest community type up until the 1930's (Nowacki 1993). Table 26 contains attributes for the dry-mesic oak old-growth forest community type.

The scarlet oak and chestnut oak stands (national forest [CISC] forest types 52, 59, and 60) associated with dry-xeric conditions are included in old-growth forest community type (22) to better separate old-growth forest community types 21 and 22.

Disturbance

The frequency of fire is important in the disturbance regime for this community type. The dry sites on which this community type occurs are conducive to recurring, low-intensity surface fires thought to have been quite common prior to European settlement. These fires helped maintain the oak component by eliminating fire-sensitive competitors and stimulating oak regeneration (Nowacki 1993). Furthermore, blowdowns of single or multiple trees result in gap phase regeneration, and infrequent tornadoes can destroy an entire stand. Other important disturbances for this community type include oak decline, infestations by gypsy moths, and ice storm damage.

Representative Dry-Mesic Oak Forest Old-Growth Stands

Joyce Kilmer Memorial Forest, Graham Co., North Carolina
Crabtree Creek, George Washington National Forest, Virginia
Dolly Anne Special Management Area, George Washington National Forest, Virginia
Little Walker Mountain, Jefferson National Forest, Virginia

The Skidmore Special Management Area, George Washington National Forest, Virginia
Linville Gorge, Pisgah National Forest, North Carolina
Mackey Mountain, Pisgah National Forest, North Carolina
Duncan Cove, Pisgah National Forest, North Carolina
Roaring Branch Research Natural Area, Ouachita National Forest, Arkansas

Table 24. *The potential distribution of the dry-mesic oak old-growth forest community type.*

Ecological Provinces	Ecological Sections	National Forest
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington - Jefferson
	Blue Ridge Mountains	Nantahala - Pisgah Chattahoochee Sumter (Andrew Pickens RD*) Cherokee George Washington-Jefferson (Pedlar, Glenwood RD*, Mount Rogers NRA**)
Southeastern Mixed Forest	Southern Ridge and Valley Section	Talladega (Talladega Division) Chattahoochee (Armuchee RD*)
	Southern Appalachian Piedmont	Uhwarrie Sumter Oconee
	Southern Cumberland Plateau	Bankhead
	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee Holly Springs Tombigbee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD* only) Sabine (in part) Sam Houston Ouachita (Tiak RD* only)

*RD=Ranger district

**NRA=National recreation area

Table 24 (continued). *The potential distribution of the dry-mesic oak old-growth forest community type.*

Ecological Provinces	**Ecological Sections**	**National Forest**
Outer Coastal Plain Mixed Forest	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Florida Coastal Lowlands, Western Gulf Section	Apalachicola (in part)
	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Ocala Desoto Bienville Homochitto
	Coastal Plains and Flatwoods, Western Gulf Section	Kisatchie (all except Caney RD*) Davy Crockett Angelina Sabine (in part)
Lower Mississippi Riverine Forest	Mississippi Alluvial Plain	St. Francis
Ouachita Mixed Forest	Ouachita Mountain	Ouachita
Eastern Broadleaf Forest	Ozark Highlands	Ozark
	Northern Cumberland Plateau	Daniel Boone

*RD=Ranger district

Table 25. *The relationship of the dry-mesic oak old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	Code	Forest Type
National Forest CISC* cover type	51	Post oak - black oak
	52	Chestnut oak (in part)
	53	White oak-red oak-hickory
	54	White oak
	55	Northern red oak
	59	Scarlet oak (in part)
	60	Chestnut oak-scarlet oak (in part)
Society of American Foresters forest type code	44	Chestnut oak
	52	White oak-black oak-Northern red oak
	53	White oak
	55	Northern red oak
	110	Black oak
The Nature Conservancy International Classification of Ecological Communities**	I.B.2.N.a.250	White oak
	I.B.2.N.a.260	White oak-(scarlet oak, red oak, black oak)
	I.B.2.N.a.270	White oak-red oak
	I.B.2.N.a.340	Rock chestnut oak-(white oak, southern red oak, red oak, black oak)
	I.B.2.N.a.360	Rock chestnut oak-red oak
	I.B.2.N.a.390	Black oak-white oak

*CISC=Continuous inventory of stand conditions

**Ecological community = Forest alliance

Table 26. *Attributes of the dry-mesic oak old-growth forest community type (Graney, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Age of large trees	Southern Appalachians White oak - 245 - 348 yrs.* Northern red oak - 240 - 270 yrs.* Black oak - 180 - 211 yrs.* Chestnut oak - 66 - 362 yrs.* Mockernut hickory - 335 yrs.* Pignut hickory - 327 yrs.*	Blozan 1994; Carlson 1995; White and Lloyd, in preparation
	Piedmont White oak/red oak/ black oak - 200 - 324 yrs.	Frei and Fairbrothers 1963; Monk 1961
	Interior Highlands White oak - 87-320 yrs. Northern red oak - 65-120 yrs. Post oak - 140-300 yrs. Chinkapin oak - 139-204 yrs. Shortleaf pine - 106-300 yrs.	Stahle and others 1985; Wuenscher 1967
2. D.b.h. of large trees	Southern Appalachians White oak - 14-27 inches Northern red oak - 22-26 inches Black oak - 18-26 inches Chestnut oak - 14-22 inches Mockernut and Pignut hickory - 14-26 inches	Blozan 1994; Carlson 1995; Delapp and Wentworth 1977
	Piedmont White oak - 20-40 inches Black oak - 20-40 inches Northern red oak and scarlet oak - 20-30 inches Red hickory - 15-25 inches	Monk 1961
	Interior Highlands White oak - 12-40 inches Northern red oak - 11-24 inches Post oak - 14-21 inches Chinkapin oak - 9-27 inches Shortleaf pine - 12-21 inches	Fountain and Sweeny 1985; Stahle and others, 1985; Wuenscher 1967
	Interior Low Plateau White oak - 20-32 inches Black oak - 20-32 inches Northern red oak - 15-20 inches Hickory spp. - 10-15 inches	Potzger and Friesner 1934

*Range includes ages reported as maximum ages

Table 26 (continued). *Attributes of the dry-mesic oak old-growth forest community type (Graney, in preparation)*

Old-Growth Attribute	Old-Growth Parameters	Data Sources
3. Stand density	Southern Appalachians	
	D.b.h. ≥ 4 inches 251-401**	Delapp and Wentworth 1977
	Piedmont	
	D.b.h. ≥ 1 inch 319-931**	Oosting 1942; Sulser 1971
	Interior Highlands	
	D.b.h. ≥ 4 inches 121-618**	Dale and Watts 1980
	Interior Low Plateau	
	D.b.h. ≥ 4 inches 153-174** (means)	Fralish and other, 1991; Potzger and Friesner 1934
4. Stand basal area	Southern Appalachians	
	D.b.h. ≥ 4 inches 73-115***	Delapp and Wentworth 1977
	Piedmont	
	D.b.h. ≥ 4 inches 87-191***	Oosting 1942; Sulser 1971
	Interior Highlands	
	D.b.h. ≥ 4 inches 53-139***	Dale and Watts 1980
	Interior Low Plateau	
	D.b.h. ≥ 4 inches 91-144*** (means)	Fralish and others, 1991; Potzger & Friesner 1934
5. Number of standing snags per acre	Southern Appalachians D.b.h. ≥ 4 inches 26-36 (means)	McComb and Muller 1983; Rosenburg and others 1988
	Piedmont	
	D.b.h. ≥ 6 inches 6 (mean)	Reiners and Reiners 1965
	Interior Highlands	
	D.b.h. ≥ 4 inches 0-53	N/A
6. Volume of downed logs per acre	Southern Appalachians D.b.h. ≥ 8 inches 403-1438 ft^3	Muller and Liu 1991
	Piedmont D.b.h. ≥ 4 inches 9.7 tons (mean)	Lang and Forman 1978
	Interior Highlands D.b.h. ≥ 4 inches 60-1831 ft^3	N/A
7. Percent canopy in gaps	1 to 13	Monk 1957; Monk 1961; Sulser 1971

**Trees per acre

***Ft^2 per acre

N/A = Not available

Dry and Xeric Oak Forest, Woodland, and Savanna
Old-Growth Forest Community Type 22

Community Description

Dry and xeric oak forests, woodlands, and savannas are found throughout the southeast in all ecological provinces. They usually occur on very dry and infertile uplands (table 27). They also occur on steep, south-facing slopes or rock outcrops. Soils are usually coarse textured, and dry soil conditions may prevail most of the year (Tyrrell and others, in preparation).

Two recognized subtypes occur in the South: the “widespread” subtype and the southern subtype. The southern subtype is associated primarily with longleaf (Pinus palustrus) or slash pine (P. elliottii) communities in the Coastal Plain and oak barrens located in the western portion of region. The southern subtype community is made up of small-statured trees that include turkey oak (Quercus laevis), bluejack oak (Q. incana), sand post oak (Q. margaretta), Mohr’s oak (Q. mohriana), and sand live oak (Q. geminata). Larger trees such as live oak (Q. virginiana) may also be present (table 28). Table 29 contains attributes for the dry and xeric oak forest, woodland, and savanna old-growth forest community type.

The “wide spread” subtype includes black oak (Quercus veltina), post oak (Q. stellata), blackjack oak (Q. marilandica), chestnut oak (Q. montana), scarlet oak (Q. coccinea), and white oak (Q. alba) as the major species (Nowacki 1993).

Disturbance

Periodic surface fires are important for maintaining the open condition of this old-growth forest community type. Fires are thought to have burned frequently enough to restrict tree density and promote the growth of shade intolerant grasses, forbs, and shrubs (Nowacki 1993).

Representative Dry and Xeric Oak Forest, Woodland, and Savanna Old-Growth Stands

Linville Gorge, Pisgah National Forest, North Carolina
Post Oak Stand, Long Cane Ranger District, South Carolina

Table 27. *The potential distribution of the dry and xeric oak forest, woodland, and savanna old-growth forest community type.*

Ecological Province	Ecological Section	National Forest
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington - Jefferson
	Blue Ridge Mountains	Nantahala - Pisgah Chattahoochee Sumter (Andrew Pickens RD*) Cherokee George Washington-Jefferson (Pedlar, Glenwood RD*, Mount Rogers NRA**)
Southeastern Mixed Forest	Southern Ridge and Valley Section	Talladega (Talladega Division) Chattahoochee (Armuchee RD*)
	Southern Appalachian Piedmont	Uhwarrie Sumter Oconee
	Southern Cumberland Plateau	Bankhead
	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee Holly Springs Tombigbee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD* only) Sam Houston Sabine (in part) Ouachita (Tiak RD* only)

*RD=Ranger district
**NRA=National recreation area

Table 27. (continued). *The potential distribution of the dry and xeric oak forest, woodland, and savanna old-growth forest community type.*

Ecological Provinces	Ecological Sections	National Forest
Outer Coastal Plain Mixed Forest	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Florida Coastal Lowlands, Western Gulf Section	Apalachicola (in part)
	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Ocala Desoto Bienville Homochitto
	Coastal Plains and Flatwoods, Western Gulf	Kisatchie (all except Caney RD *) Davy Crockett Angelina Sabine (in part)
Ouachita Mixed Forest	Ouachita Mountain	Ouachita
Lower Mississippi Riverine Forest	Mississippi Alluvial Basin	St. Francis
Eastern Broadleaf Forest	Ozark Highlands	Ozark
	Northern Cumberland Plateau	Daniel Boone

*RD=Ranger district

Table 28. *The relationship of the dry and xeric oak old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	52	Chestnut oak
	57	Scrub oak
	59	Scarlet oak
	60	Chestnut oak-scarlet oak
Society of American Foresters forest type code	40	Post oak-blackjack oak
	43	Bear oak (in part)
	44	Chestnut oak
	72	Southern scrub oak
	89	Live oak
	110	Black oak
The Nature Conservancy International Classification of Ecological Communities**	I.B.2.N.a.350	Rock chestnut oak - (scarlet oak-black oak) forest
	I.B.2.N.a.380	Post oak-blackjack oak forest
	II.B.2.N.a.050	Live oak-bluejack oak woodland
	II.B.2.N.a.060	Arkansas oak woodland
	II.B.2.N.a.080	Bluejack oak-Arkansas oak woodland
	II.B.2.N.a.100	Turkey oak woodland
	II.B.2.N.a.130	Rock chestnut oak-bluejack oak woodland
	II.B.2.N.a.140	Rock chestnut oak-blackjack oak woodland
	II.B.2.N.a.160	Post oak-blackjack oak woodland
	II.C.2.N.a.040	Live oak woodland
	II.C.2.N.a.050	Live oak-bluejack oak woodland
	II.A.2.N.a.060	Live oak-post oak woodland

*CISC=Continuous inventory of stand conditions

**Ecological communities = Forest and woodland alliance

Table 29. *Attributes of the dry and xeric oak forest, woodland, and savanna old-growth forest community type (Tyrrell and others, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Mean age of large trees	Oak sp. - 65 to 150 inches	N/A
2. D.b.h. of largest trees	Bur oak - 36 to 74 inches	Gleason 1913
	Black oak - 16 to 40 inches	N/A
	White oak - 36 to 61 inches	N/A
	Chestnut oak - 26 inches	Lindsey and others, 1961
3. Stand density	D.b.h. $\geq$ 4 inches 11 to 179*	McCarthy and others, 1987
4. Stand basal area	D.b.h. $\geq$ 4 inches 40 to 95**	McCarthy and others, 1987
5. Number of standing snags per acre	10	Johnson and Schnell 1985
6. Volume of downed logs per acre	N/A	
7. Number of canopy layers	N/A	
8. Percentage of the canopy in gaps	N/A	

*Trees per acre

**Ft^2 per acre

N/A = Not available

Xeric Pine and Pine-Oak Forest and Woodland
Old-Growth Forest Community Type 24

Community Description

Xeric pine and pine-oak forests and woodlands are found throughout most of the eastern United States, from southern Missouri and northeast Texas east to the Atlantic coastline from southern Maine to South Carolina (table 30). Because this old-growth forest community type covers a broad geographic range, there are distinctive differences between the communities separated by the Mississippi River. All principal species discussed below are found in the communities east of the river However, shortleaf pine (Pinus echinata) is the only pine species which occurs west of the river and chestnut oak is confined to the region east of the river. Xeric pine and pine-oak forests and woodlands typically occur on ridgetops and south-facing upper slopes in the mountains or on excessively-drained, sandy uplands in gentler terrain, such as in the Piedmont (Murphy and Nowacki, in preparation).

This old-growth forest community type normally exists on strong acidic soils with extreme moisture and nutrient deficiencies. Xeric site conditions may exist due to: (1) low precipitation, (2) limited moisture absorption/retention because of exposed bedrock, steep slopes, coarse-textured soils, rocky soils, or shallow soils, and/or (3) elevated evapotranspiration rates on southern-facing slopes. Principal overstory species of this community type include pitch pine (P. rigida), Virginia pine (P. virginiana), shortleaf pine, eastern white pine (P. strobus), table mountain pine (P. pungens), and chestnut oak (Quercus prinus) (table 31). Associated species include scarlet oak (Q. coccinea), black oak (Q. velutina), blackjack oak (Q. marilandica), post oak (Q. stellata), northern red oak (Q. rubra), southern red oak (Q. falcata), white oak (Q. alba), and pignut hickory (Carya glabra) (Murphy and Nowacki, in preparation). Table 32 contains attributes for the xeric pine and pine-oak forest community type.

Disturbance

Due to the prevailing xeric conditions and chemical content (volatile resins and pitch) of most plant species occurring in this community type, these forests and woodlands have historically experienced frequent fires. Most fires were probably low intensity, surface burns since they occurred frequently and did not allow significant amounts of fuel to build up, although occasional fires occurred in some areas that destroyed an entire stand. On sites where moisture and nutrients are not as limiting, periodic fires are required to maintain a dominance of yellow pines, because pine seedlings rarely become established in oak litter. Over many decades, increases in the amount of dead biomass can predispose these forests and woodlands to catastrophic fires, especially in older stands that have experienced mortality caused by southern pine beetles. In the absence of fire, successional changes on xeric sites are normally quite restricted.

On other sites, succession in the absence of fire leads to a dominance by oaks and/or white pine along with other shade tolerant and fire intolerant species (Murphy and Nowacki, in preparation).

Ice or glaze storms along with strong winds often cause extensive uprooting or blowdown of trees in these stands. These disturbances typically form large light gaps, and the downed biomass increases fuel loads which may lead to high-intensity fires.

Representative Xeric Pine and Pine-Oak Forest and Woodland Old-Growth Stands

Lake Winona Research Natural Area, Ouachita National Forest, Arkansas
Roaring Branch Research Natural Area, Polk Co., Arkansas
Marshall Forest Preserve, near Rome, Georgia
Linville Gorge, Pisgah National Forest, North Carolina
Torreya State Park, Liberty Co., Florida

Table 30. *The potential distribution of the xeric pine and pine-oak forest and woodland old-growth forest community type.*

Ecological Provinces	Ecological Sections	National Forest
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington - Jefferson
	Blue Ridge Mountains	Nantahala - Pisgah Chattahoochee Sumter (Andrew Pickens RD*) Cherokee George Washington - Jefferson (Pedlar, Glenwood RD*, Mount Rogers NRA**)
Southeastern Mixed Forest	Southern Ridge and Valley	Talladega (Talladega Division) Chattahoochee NF (Armuchee RD*)
	Southern Appalachian Piedmont	Uhwarrie Sumter Oconee
	Southern Cumberland Plateau	Bankhead
	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee Holly Springs Tombigbee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD* only) Sabine (in part) Sam Houston Ouachita (Tiak RD* only)
Outer Coastal Plain Mixed Forest	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Florida Coastal Lowlands, Western Gulf Section	Apalachicola (in part)
	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part)

*RD=Ranger district

**NRA=National recreation area

Table 30 (continued). *The potential distribution of the xeric pine and pine-oak forest and woodland old-growth forest community type.*

Ecological Provinces	Ecological Sections	National Forest
Ouachita Mixed Forest	Ouachita Mountain	Ouachita
Eastern Broadleaf Forest	Ozark Highlands	Ozark
	Northern Cumberland Plateau	Daniel Boone

Table 31. *The relationship of the xeric pine and pine-oak forest and woodland old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover types	32	Shortleaf pine
	33	Virginia pine
	38	Pitch pine
	39	Table mountain pine
	12	Shortleaf pine-oak
	15	Pitch pine-oak
	16	Virginia pine-oak
	20	Table mountain pine-hardwoods
Society of American Foresters forest type codes	43	Bear oak
	45	Pitch pine
	51	White pine-chestnut oak
	75	Shortleaf pine
	76	Shortleaf pine-oak
	78	Virginia pine-oak
	79	Virginia pine
The Nature Conservancy International Classification of Ecological Communities**	I.A.8.N.b.030	Shortleaf pine forest
	I.A.8.N.b.140	Eastern white pine forest
	I.A.8.N.b.190	Virginia pine forest
	I.A.8.N.b.070	Shortleaf pine-post oak-blackjack oak forest
	I.A.8.N.b.145	(Pitch pine, table mountain pine)-(rock chestnut oak, scarlet oak) forest
	I.A.8.N.b.220	Virginia pine-(white oak, post oak, southern red oak, black oak) forest
	I.A.8.N.b.230	Virginia pine-(scarlet oak, rock chestnut oak) forest
	I.C.3.N.a.060	Shortleaf pine-(scarlet oak, southern red oak, rock chestnut oak) forest
	I.C.3.N.a.160	Eastern white pine-(scarlet oak, rock chestnut oak) forest

*CISC=Continuous inventory of stand conditions

**Ecological community = Forest alliance

Table 32. *Attributes of the xeric pine and pine oak forest and woodland old-growth forest community type (Murphy and Nowacki, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Mean age of large trees	Shortleaf pine 200 yrs. Pitch pine 150 yrs. Tablemountain pine 200 yrs. Virginia pine 140 yrs.	Hepting 1971
2. D.b.h. of largest trees	Shortleaf pine 22 to 25 in. Pitch pine 12 to 15 in. Table mountain pine 10 to 15 in. Virginia pine 10 to 15 in.	Fountain and Sweeny 1985 Turner 1935
3. Stand density	Interior Highlands Shortleaf pine D.b.h. ≥ 4 in. 234 to 434* Hardwoods D.b.h. ≥ 4 in. 86 to 167*	Dale and Watts 1980; Fountain and Sweeny 1985; Johnson 1986
	Southern Appalachians Table mountain pine D.b.h. ≥ 4 in. 45*	Zobel 1969
4. Stand basal area	Interior Highlands Shortleaf pine D.b.h. ≥ 4 in. 37 to 77** Hardwoods D.b.h. ≥ 4 in. 18 to 22**	Dale and Watts 1980; Fountain and Sweeny 1985; Johnson 1986
	Southern Appalachians Table mountain pine D.b.h. ≥ 4 in. 24**	Zobel (1969)
5. Standing snags per acre	D.b.h. ≥ 3 in. 3.5 - 13.1 tons (range of means)	Johnson and Schnell 1985
6. Volume of downed logs per acre	0.1-4.2 tons (range of means)	Johnson and Schnell 1985
7. Number of 4” size classes	Shortleaf pine - 6 Hardwood - 4	Fountain and Sweeny 1985
8. Percentage of the canopy in gaps	N/A	

*Trees per acre

**Ft^2 per acre

Dry and Dry-Mesic Oak-Pine Forest

Old-Growth Forest Community Type 25

Community Description

Dry and dry-mesic oak-pine forests constitute a large part of the eastern deciduous forest, extending from southern Missouri and east Texas in the west to the Atlantic coast from New Jersey to north Florida (table 33). Most of these forests occur on coarse-textured soils on ridges and south-facing slopes in the mountains and droughty uplands in the Piedmont and Coastal Plain (White and Lloyd, in preparation). The oak-pine old-growth forest community type consists of least 20 percent of the basal area in pine and at least 20 percent in oak.

The dry and dry-mesic oak-pine (type 25) and dry-mesic oak (type 21) old-growth forest community types may develop on the same type of sites depending on type and intensity of disturbances. Across eastern old-growth sites, shortleaf pine (Pinus echinata) and white oak (Quercus alba) are the most common canopy species, whereas pitch pine (P. rigida), scarlet oak (Q. coccinea) and chestnut oak (Q. prinus) are more common in mountainous areas. Other common canopy species include Virginia pine (P. virginiana), table mountain pine (P. pungens), post oak (Q. stellata), blackjack oak (Q. marilandica) on dry sites and loblolly pine (P. taeda), southern red oak (Q. falcata), black oak (Q. velutina), mockernut hickory (Carya tomentosa), pignut hickory (C. glabra), and red maple (Acer rubrum) on dry-mesic sites (table 34). Ericaceous species, such as blueberry (Vaccinium spp.), huckleberry (Gaylusaccia spp.), and mountain laurel (Kalmia latifolia), typically dominate the shrub layer, while dogwood (Cornus florida), sourwood (Oxydendrum arboreum), sassafras (Sassafras albidum), and blackgum (Nyssa sylvatica) are common in the midstory. Common understory and vine species include sedges (Carex spp.), panicum grasses (Panicum spp.), broom sedge (Andropogon spp.) and other grasses, pipsessewa (Chimaphila maculata), begger’s ticks (Desmodium spp.), bracken fern (Pteridium spp.), greenbriar (Smilax spp.)., Virginia creeper (Parthenocissus quinquefolia), and grapes (Vitis spp.). Currently a lower frequency of fires is resulting in species composition changes. Table 35 contains attributes for the dry and dry-mesic oak-pine old-growth forest community type.

Disturbance

The dry and dry-mesic oak-pine old-growth forest community type is transitory on a given site. Historically, fire, aboriginal activities, windfall, natural mortality, and other disturbances maintained this forest community type. Disturbances vary across its range, with lightning fires prevalent in the Coastal Plain and Ozark Mountains, hurricanes in the Coastal Plain, and tornadoes in the Ouachita and Ozark Mountains. Fire is less frequent in the Appalachian Piedmont and Mountains. The frequency of natural fires is estimated at between 5 and 32 years throughout the Southeast (White and Lloyd, in preparation).

Beyond a certain gap size (0.1 acre in the Piedmont), fire (or other forest floor disturbance) is the limiting factor for maintaining this old-growth forest community type.

Representative Dry and Dry-Mesic Oak-Pine Forest Old-Growth Stands

John de la Howe Tract, near McCormick, South Carolina
Duke Forest, North Carolina
Roaring Branch Research Natural Area, Arkansas
Lake Winona Research Natural Area, Ouachita National Forest, Arkansas
Bob’s Creek Shortleaf Stand, Kisatchie National Forest, Louisiana
Old Shortleaf Slope Stand, Kisatchie National Forest, Louisiana

Table 33. *The potential distribution of the dry and dry-mesic oak-pine old-growth forest community type.*

Ecological Province	Ecological Section	National Forest
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington - Jefferson
	Blue Ridge Mountains	Nantahala - Pisgah Chattahoochee Sumter (Andrew Pickens RD*) Cherokee George Washington-Jefferson (Pedlar, Glenwood RD*, Mount Rogers NRA**)
Southeastern Mixed Forest	Southern Ridge and Valley	Talladega (Talladega Division) Chattahoochee (Armuchee RD*)
	Southern Appalachian Piedmont	Uhwarrie Sumter Oconee
	Southern Cumberland Plateau	Bankhead
	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee Holly Springs Tombigbee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD*) Sam Houston Sabine (in part) Ouachita (Tiak RD* only)

*RD = Ranger district
**NRA = National recreation area

Table 33 (continued). *The potential distribution of the dry and dry-mesic oak-pine old-growth forest community type.*

Ecological Provinces	**Ecological Sections**	**National Forest**
Outer Coastal Plain Mixed Forest	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Florida Coastal Lowlands, Western Gulf Section	Apalachicola (in part)
	Coastal Plains and Flatwoods Lower Section	Conecuh Apalachicola(in part) Ocala Desoto Bienville Homochitto
	Coastal Plains and Flatwoods Western Gulf	Kisatchie (all except Caney RD*) Davy Crockett Angelina Sabine (in part)
Lower Mississippi Riverine Forest	Mississippi Alluvial Basin	St. Francis
Ouachita Mixed Forest	Ouachita Mountain	Ouachita
Eastern Broadleaf Forest	Ozark Highlands	Ozark
	Northern Cumberland Plateau	Daniel Boone

*RD=Ranger district

Table 34. *The relationship of the dry and dry-mesic oak-pine old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	31	Loblolly pine
	32	Shortleaf pine (in part)
	33	Virginia pine (in part)
	10	White pine-upland hardwood
	12	Shortleaf pine-oak
	13	Loblolly pine-oak
	16	Virginia pine-hardwood
	44	Southern red oak-yellow pine
	45	Chestnut oak-scarlet oak-yellow pine
	47	White oak-black oak-yellow pine
	48	Northern red oak-hickory-yellow pine
Society of American Foresters forest type code	51	White pine-chestnut oak
	75	Shortleaf pine
	76	Shortleaf pine-oak
	78	Virginia pine-oak
	79	Virginia pine
	80	Loblolly pine-shortleaf pine
	81	Loblolly pine
	82	Loblolly pine-hardwood

*CISC=continuous inventory of stand conditions

Table 34 (continued). *The relationship of the dry and dry-mesic oak-pine old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
The Nature Conservancy International Classification of Ecological Communities**	I.C.3.N.a.050	Shortleaf pine-(white oak, southern red oak, post oak, black oak)
	I.C.3.N.a.060	Shortleaf pine-(scarlet oak, southern red oak, rock chestnut oak)
	I.C.3.N.a.070	Shortleaf pine-post oak-blackjack oak
	I.C.3.N.a.090	(Shortleaf pine, loblolly pine, Virginia pine) - (white oak, red oak) - tuliptree
	I.C.3.N.a.100	(Shortleaf pine, loblolly pine, Virginia pine) - (bluejack oak, sand post oak, laurel oak)
	I.C.3.N.a.110	(Shortleaf pine, Virginia pine) - tuliptree
	I.C.3.N.a.140	Longleaf pine-shortleaf pine-(loblolly pine) - (post oak, southern red oak)
	I.C.3.N.a.150	White pine - (white oak, red oak, black oak)
	I.C.3.N.a.230	Virginia pine - (scarlet oak, rock chestnut oak)
	I.C.3.N.a.220	Virginia pine - (white oak, post oak, southern red oak, black oak)
	I.C.3.N.a.190	Loblolly pine - (blackjack oak, southern red oak, post oak)
	I.C.3.N.a.160	Eastern white pine - (scarlet oak, rock chestnut oak)
	I.C.3.N.a.180	Loblolly pine - (white oak, southern red oak, post oak)

**Ecological community = Forest alliance

Table 35. *Attributes of the dry and dry-mesic oak-pine old-growth forest community type (White and Lloyd, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**		**Data Sources**
1. Age of large trees	Southern Appalachians		
	White oak	347 yrs.*	Blozan 1994; White and Lloyd, in preparation
	Black oak	180 yrs.*	
	Chestnut oak	66-347 yrs.*	
	Pignut hickory	327 yrs.*	
	Scarlet oak	72-165 yrs.*	
	Pitch pine	148 yrs.*	
	Piedmont		
	White oak	82-207 yrs.	White and Lloyd, in preparation
	Shortleaf pine	89-205 yrs.	
	Loblolly pine	79-189 yrs.	
	Hickory sp.	142-207 yrs.	
	Post oak	101-216 yrs.	
	Southern red oak	64-190 yrs.	
	Yellow poplar	94-194 yrs.	
	Interior Highlands		
	Shortleaf pine	108-314 yrs.	Stahle and others 1985
2. D.b.h. of large trees	Piedmont		
	White oak	12-33 inches	White and Lloyd, in preparation
	Post oak	8-19 inches	
	Shortleaf pine	11-32 inches	
	Loblolly pine	12-39 inches	
	Hickory sp.	10-23 inches	
	Interior Highlands		
	Shortleaf pine	14-26 inches	Stahle (1985)
3. Stand density	Southern Appalachians		
	D.b.h. ≥ 3 inches	312-328**	Delapp and Wentworth 1977;
	Piedmont		
	D.b.h. ≥ 4 inches	130-183**	White and Lloyd, unpublished data
	Interior Highlands		
	D.b.h. ≥ 4 inches	223-225**	Fountain and Sweeny 1985
	Gulf Coastal Plain		
	D.b.h. ≥ 5 inches	61-107**	Martin and Smith 1991

*Range includes ages reported as maximum ages

**Trees per acre

Table 35 (continued). *Attributes of the dry and dry-mesic oak-pine old-growth forest community type (White and Lloyd, in preparation)*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
4. Stand basal area	Southern Appalachians	
	D.b.h. ≥ 3 inches 90 to 110***	Delapp and Wentworth 1977
	Piedmont	
	D.b.h. ≥ 4 inches 64 to 150***	White and Lloyd, in preparation
	Interior Highlands	
	D.b.h. ≥ 4 inches 80 to 81***	Fountain and Sweeny 1985
	Gulf Coastal Plain	Martin and Smith 1991
	D.b.h. ≥ 5 inches 59 to 128***	
5. Number of standing snags per acre****	D.b.h. ≥ 4 inches 15 to 69 ≥ 20 inches 2 to 16	White & Lloyd (In Draft)
6. Volume of downed** logs per acre	747 to 2,528 ft^3 per acre	White & Lloyd (In Draft)
7. Number of canopy layers	2-3 (mean gap size - 0.002 to 0.5 ac.)	White & Lloyd (In Draft)
8. Percent canopy in gaps****	24 to 80 (37 mean)	White & Lloyd (In Draft)

***Ft^2 per acre

****The range of values given for these variables represent data collected from low to high mortality areas within a single stand which underwent significant insect-related pine mortality

Upland Longleaf and South Florida Slash Pine Forest, Woodland, and Savanna
Old-Growth Forest Community Type 26

Community Description

The upland longleaf pine forest, woodland, and savanna community type can be found from Virginia south through central Florida and west to east Texas, with extensions into the Appalachian Piedmont and Mountains of north Alabama and northwest Georgia (table 36). On the Coastal plains, this forest community is typically found on sandhills, although in central and south Florida, it occurs on slight rises in flatwoods. In the mountains, it is usually restricted to sites that are apt to burn, specifically ridge tops and middle and upper slopes with south and southwest exposures (Nowacki 1993).

In this old-growth forest community type the dominant canopy tree is longleaf pine (Pinus palustris), providing relatively dense to patchy and very open canopies. These old-growth communities have frequent transitions in ages, tree sizes, and tree density. Sometimes associated with this forest community type are clusters of deciduous scrub oaks, evergreen scrub oaks, and mesic hardwoods (table 37). The groundcover consists of hundreds of species of herbs and low shrubs sometimes dominated by wiregrass (Aristida stricta and A. beyrichiana) in the eastern portion of its range and by bluestem grasses (Schizachyrium tenerum and S. scoparium) in the western portion (Landers and Boyer, in preparation). Table 38 contains the attributes for the upland longleaf and south Florida slash pine old-growth forest community type.

The slash pine forest community forms large savannas in south Florida where it is considered an ecological equivalent of longleaf pine. This old-growth community has frequent transitions in ages, tree sizes, and tree density. Sometimes associated with this communities are clusters of deciduous scrub oaks, evergreen scrub oaks, and mesic hardwoods. In south Florida, the groundcover consists of hundreds of species of herbs and shrubs dominated by wiregrass. Slash pine communities outside south Florida typically contain large portions of evergreen shrubs such as Serenoa repens or Ilex glabra (Landers and Boyer, in preparation). No National Forest System land is within the range of south Florida slash pine.

Disturbance

Fires during the growing season are the major disturbances in the upland longleaf and south Florida slash pine old-growth communities. In most instances, the frequency of fires associated with maintaining longleaf pine is estimated to be every 2 to 4 years. In the Coastal Plain sandhills and transition areas, the frequency is estimated to be 3 to 10 years. In addition to normal fire regimes, other disturbances include lightening, wind events (e.g., tornadoes, tropical storms, and microbursts), and periodic droughts that result in conditions conducive to intense fires (Landers and Boyer, in preparation).

Representative Upland Longleaf and South Florida Slash Pine Forest, Woodland, and Savanna Old-Growth Stands

Boykins Springs Management Area, Angelina National Forest, Texas
Wade Tract Preserve, Thomas Co., Georgia
Moody Tract, Appling Co., Georgia
Big Woods, Greenwood Plantation, Thomas Co., Georgia
Big Cypress National Preserve, Collier Co., Florida
Patterson Natural Area, Eglin Air Force Base, Florida
Boyd Tract, Weymouth Woods Sandhills Nature Preserve,
    Moore Co., North Carolina
Havis Park, Flamaton Natural Area, Escambia Co., Alabama
Lostman’s Pines, Everglades National Park, Florida

Table 36. *The potential distribution of the upland longleaf and south Florida slash pine forest, woodland, and savanna old-growth forest community type.*

Ecological Provinces	Ecological Sections	National Forest
Southeastern Mixed Forest	Southern Ridge and Valley	Talladega (Talladega Division)
	Southern Appalachian Piedmont	Uhwarrie Sumter
	Southern Cumberland Plateau	Bankhead
	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD*) Sam Houston Sabine (in part) Ouachita (Tiak RD*)
Outer Coastal Plain Mixed Forest	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Florida Coastal Lowlands, Western Gulf Section	Apalachicola (in part)
	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Ocala Desoto Bienville Homochitto
	Coastal Plains and Flatwoods, Western Gulf	Kisatchie (all except Caney RD*) Davy Crockett Angelina Sabine (in part)

*RD=Ranger district

Table 37. *The relationship of the upland longleaf and south Florida slash pine forest, woodland, and savanna old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	21	Longleaf pine
Society of American Foresters forest type code	70	Longleaf pine
	71	Longleaf pine-scrub oak
	83	Longleaf pine-slash pine
The Nature Conservancy International Classification of Ecological Communities**	I.A.8.N.b.070	Longleaf pine-slash pine temporate forest
	I.A.4.N.a.130	Longleaf pine-oak species woodland
	I.A.4.N.a.120	Longleaf pine woodland
	I.A.4.N.f.060	Longleaf pine-pond pine-saturated woodland
	I.A.4.N.f.050	Longleaf pine-slash pine saturated woodland
	I.A.4.N.f.040	Longleaf pine saturated woodland

*CISC=Continuous inventory of stand conditions

**Ecological community = Forest and woodland alliance

Table 38. *Attributes of the upland longleaf and south Florida slash pine forest, woodland, and savanna old-growth forest community type (Landers and Boyer, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Minimum age	112 years	Schopmeyer (1974)
2. D.b.h. of oldest trees at minimum age	7 to 24 inches	Chapman 1909; Schwarz 1907
3. Stand density	D.b.h. ≥ 2 inches 52 to 167*	Schwarz 1907;
	≥ 1 inch 70*	Platt and others, 1988;
	≥ 1 inch 0.2-3.9**	Bartrum 1765-66
4. Stand basal area	N/A	
5. Number of standing snags per acre	0 to 12	Schwarz 1907
6. Volume of downed logs	N/A	
7. Percent canopy in gaps	N/A	

*Trees per acre

**Savanna condition

N/A = Not available

Seasonally Wet Oak-Hardwood Woodland
Old-Growth Forest Community Type 27

Community Description

Seasonally wet oak-hardwood woodlands are commonly known as oak glades or flatwoods and with relatively open understories. They occur from the Midwest to eastern Oklahoma and Texas and east to Virginia (table 39). This old-growth forest community type is most completely developed within the Ohio, Arkansas, and southern Mississippi River Valleys and occurs principally within river bottomlands and isolated depressions that are seasonally flooded for short periods (Kennedy and Nowacki, in preparation).

The principal species are pin oak (Quercus palustris), willow oak (Q. phellos), white oak (Q. alba), water oak (Q. nigra), laurel oak (Q. laurifolia), and nuttall oak (Q. nuttallii). Common associates include overcup oak (Q. lyrata), red maple (Acer rubra), sweetgum (Liquidambar styraciflua), water hickory (Carya aquatica), and waterlocust (Gleditsia aquatica) (Kennedy and Nowacki, in preparation). Table 40 contains the relationships between the seasonally wet oak-hardwood woodland old-growth community type and other forest classification systems, and table 41 contains its old-growth attributes.

Disturbance

Prior to European settlement, low-intensity fires may have occurred when dry surface conditions developed during the summer. Although such burns would probably have been confined to the litter layer, they would have helped to maintain open conditions in these woodlands. Current fire regimes have caused most of these communities to shift from woodlands to forests. Canopy tree deaths and gap phase regeneration are common in these old-growth stands resulting in a multiple-aged stand (Kennedy and Nowacki, in preparation).

Representative Seasonally Wet Oak-Hardwood Woodland Old-Growth Stands

Delta Experimental Forest, Washington County, Mississippi
Delta National Forest, Sharkey Co., Mississippi

Table 39. *The potential distribution of the seasonally wet oak hardwood woodland old-growth forest community type.*

Ecological Province	Ecological Section	National Forest
Outer Coastal Plain Mixed Forest	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Ocala Desoto Bienville Homochitto
Southeastern Mixed Forest	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee Holly Springs Tombigbee
	Southern Cumberland Plateau	Bankhead
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD*) Sam Houston Sabine (in part) Ouachita (Tiak RD*)
Ouachita Mixed Forest	Ouachita Mountain	Ouachita
Eastern Broadleaf Forest	Ozark Highlands	Ozark
	Northern Cumberland Plateau	Daniel Boone
Lower Mississippi Riverine Forest	Mississippi Alluvial Basin	Delta St. Francis

*RD=Ranger district

Table 40. *The relationship of the seasonally wet oak hardwood woodland old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC*		
cover type	54	White oak (in part)
	62	Sweetgum-nuttall oak-willow
	64	Laurel oak-willow oak
Society of American Foresters		
forest type code	53	White oak (in part)
	65	Pin oak-sweetgum
	68	Willow oak-water oak-laurel oak
The Nature Conservancy		
International Classification of Ecological Communities	N/A	N/A

*CISC=Continuous inventory of stand conditions
N/A = Not available

Table 41. *Attributes of the seasonally wet oak-hardwood woodland old-growth forest community type (Kennedy and Nowacki, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Age of large trees	80 to 150 yrs.	Frye 1980; Meadows 1992; Putman and Bull 1932
2. D.b.h. of largest tree	45 inches	Frye 1980; Meadows 1992
3. Stand density	D.b.h. $\geq$ 4 inches - 40 - 215*	Frye 1980; Meadows 1992; Putman and Bull
4. Stand basal area	D.b.h. $\geq$ 4 inches -44 - 214**	Frye 1980; Meadows 1992; Putman and Bull 1932
5. Number of standing snags per acre	D.b.h. $\geq$ 4 inches - 0 - 75	Frye 1980; Meadows 1992
6. Volume of downed logs	N/A	
7. Number of 4” dbh classes	9	Frye 1980

*Trees per acre
**Ft^2 per acre
N/A = Not available

Eastern Riverfront Forest
Old-Growth Forest Community Type 28

Community Description

Eastern riverfront forests occur over a large portion of the Eastern United States, from the forest-prairie margin eastward to the Atlantic coastline. These communities have the potential to occur on all national forests in the South. As the name implies, this forest community type is predominant on sites immediately adjacent to major rivers and streams (i.e., river banks and first bottoms, natural levees, sandbars, and islands).

The principal species in the eastern riverfront forest community type include river birch (Betula nigra), sycamore (Platanus occidentalis), silver maple (Acer saccharinum), American elm (Ulmus americana), eastern cottonwood (Populus deltoides), swamp cottonwood (P. heterophylla), sweetgum (Liquidambar styraciflua), black willow (Salix nigra), and live oak (Quercus virginiana) (table 42). Common associates are red maple (A. rubra), boxelder (A. negundo), hackberry (Celtis occidentalis), slippery elm (U. rubra), pin oak (Q. palustris), swamp white oak (Q. bicolor), green ash (Fraxinus pennsylvanica), sugarberry (C. laevigata), water oak (Q. nigra), and pecan (Carya illinoensis) (Meadows and Nowacki 1996). Table 43 contains old-growth attributes for the eastern riverfront forest community type.

Disturbance

This forest community type is restricted to riparian zones where intense flooding, such as ice and water scouring, routinely occur. These floods expose mineral soils, reduce competing undergrowth, and increase surface light levels. The locations of these forests will shift as the river courses change. In the absence of floods, these forests are susceptible to encroachment by shade tolerant species (Meadows and Nowacki 1996).

Representative Eastern Riverfront Forest Old-Growth Stands

Green Ash Natural Area, Delta National Forest, Mississippi
River Birch Bottom, Kisatchie National Forest, Louisiana

Table 42. *The relationship of the eastern riverfront old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	**Code**	**Forest Type**
National Forest CISC* cover type	72	River birch-sycamore
	73	Cottonwood
	74	Willow
	75	Sycamore-pecan-American elm
	76	Silver maple-American elm
	82	Black walnut
Society of American Foresters forest type code	61	River birch-sycamore
	62	Silver maple-American elm
	63	Cottonwood
	89	Live oak
	94	Sycamore-sweetgum-American elm
	95	Black willow
The Nature Conservancy International Classification of Ecological Communities**	I.B.2.N.d.280	Black willow temporarily flooded
	I.B.2.N.d.070	Pecan-(sugarberry) temporarily flooded
	I.B.2.N.d.160	Cottonwood temporarily flooded
	I.B.2.N.d.030	Silver maple temporarily flooded
	I.B.2.N.d.270	Carolina willow temporarily flooded
	I.B.2.N.d.050	River birch-(sycamore) temporarily flooded
	I.B.2.N.d.140	Sycamore-(green ash, sugarberry, silver maple) temporarily flooded
	I.B.2.N.d.210	(Swamp chestnut oak, cherrybark oak, shumard oak) - sweetgum temporarily flooded
	I.B.2.N.d.100	American beech temporarily flooded

*CISC=Continuous inventory of stand conditions

**Ecological community = Forest alliance

Table 43. *Attributes of the eastern riverfront old-growth forest community type (Meadows and Nowacki 1996.*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Age of large trees	All species - 58 to 120 yrs.	Hardin and others 1989; Lamb 1915; Martin and Smith 1991; Putman and Bull 1932; Williamson 1913
2. DBH of largest tree	All species - 25 to 72 inches	Lamb 1915; Martin and Smith 1991; Putman and Bull 1932; Williamson 1913
3. Stand density	D.b.h. ≥ 4 inches - 32 to 179*	Martin and Smith 1991; Williamson 1913
4. Stand basal area	D.b.h.≥4 inches - 160 to 220**	Robertson and others 1978; Wiseman 1982
5. Number of standing snags per acre	Several	Martin and Smith 1991
6. Volume of downed logs	High	Martin and Smith 1991
7. Number of canopy layers	≥ 3	Martin and Smith 1991; Putman and Bull 1932; Wiseman 1982
8. Number of 4” dbh classes	6 to 10	Martin and Smith 1991; Winters and others 1938; Wiseman 1982

*Trees per acre

**Ft^2 per acre

Southern Wet Pine Forest, Woodland, and Savanna
Old-Growth Forest Community Type 29

Community Description

Southern wet pine forests, woodlands, and savannas are part of the pine flatwoods forests of the Atlantic and Gulf Coastal Plain (table 44). Representative sites include boggy non-riverine flatlands, coastal flatlands, swamps, and lowlands adjacent to ponds, streams, and other wet areas.

Species composition differs widely among stands and is largely dependent on degree of flooding. On mineral soils where flooding is limited, longleaf pine (Pinus palustris) and/or slash pine (P. caribea) is predominant (table 45). Fire usually restricts hardwood species. Longleaf and slash pine are replaced by pond pine (Pinus serotina) on organic soils subject to prolonged flooding. Associates of the pond pine community are swamp tupelo (Nyssa sylvatica), water oak (Quercus nigra), baldcypress (Taxodium distichum), pondcypress (T. ascendens), sweetbay (Magnolia virginiana) and red bay (Persea borbonia) (Harms 1996, Nowacki 1993). Table 46 contains old-growth attributes for the southern wetland pine forest, woodland, and savanna forest community type.

Disturbance

This old-growth forest community type is fire dependent and in the absence of fire, pines are eventually replaced by hardwoods (Harms 1996).

Representative Southern Wet Pine Forest, Woodland, and Savanna Old-Growth Stands

Beehead Ranch Pine Flatwoods, Tosohatchee State Preserve, Florida
Big Cypress National Preserve, Collier Co., Florida
Slash Pine Tract, Bradwell Bay Wilderness, Apalachicola National Forest, Florida

Table 44. *The potential distribution of the southern wet pine forests, woodland, and savannas old-growth forest community type.*

Ecological Province	**Ecological Section**	**National Forest**
Outer Coastal Plain Mixed Forest	Atlantic Coastal Flatwoods	Francis Marion Croatan Osceola
	Florida Coastal Lowlands, Western Gulf Section	Apalachicola(in part)
	Coastal Plains and Flatwoods, Lower Section	Conecuh Apalachicola (in part) Ocala Desoto Bienville Homochitto
	Coastal Plains and Flatwoods, Western Gulf	Kisatchie (all except Caney RD*) Davy Crockett Angelina Sabine (in part)
Southeastern Mixed Forest	Coastal Plain, Middle Section	Talladega (Oakmulgee Division) Tuskegee
	Middle Coastal Plain, Western Section	Kisatchie (Caney RD*) Sabine (in part) Sam Houston Ouachita (Tiak RD*)

*RD=Ranger district

Table 45. *The relationship of the southern wet pine forest, woodland, and savanna old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	Code	Forest Type
National Forest CISC* cover type	21	Longleaf pine
	22	Slash pine
	14	Slash pine-hardwood
	36	Pond pine
	18	Pond pine-hardwood
Society of American Foresters forest type code	70	Longleaf pine
	83	Longleaf pine-slash pine
	84	Slash pine
	85	Slash pine-hardwood
	98	Pond pine
The Nature Conservancy International Classification of Ecological Communities**	I.A.8.N.g.070	Longleaf pine saturated forest
	I.A.8.N.g.060	Slash pine-pond pine saturated forest
	I.A.8.N.g.085	Pond pine saturated forest
	I.A.8.N.g.040	Slash pine saturated forest
	I.C.3.N.c.012	Slash pine-sweet bay-pondcypress-swamp blackgum saturated forest
	II.A.3.N.f.010	Slash pine saturated woodland
	II.A.3.N.f.040	Longleaf pine saturated woodland

*CISC=Continuous inventory of stand conditions

**Ecological community = Forest and woodland alliance

Table 46. *Attributes of the southern wet pine forest, woodland, and savanna old-growth forest community type (Harms 1996).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Minimum age	Longleaf pine - 150 - 200 yrs	Chapman 1909; Wahlenberg 1946;
	Slash pine - 80 - 100 yrs	Hebb and Clewell 1976;
	Pond pine - 60 - 100 yrs	Schumacher and Coile 1960
2. Average stand d.b.h.	Longleaf pine - 20 inches	Chapman 1909; Wahlenberg 1946;
	Slash pine - 21 inches	Hebb and Clewell 1976;
	Pond pine - 9 inches	Schumacher and Coile 1960
3. Minimum stand density	Longleaf pine - 61*	Chapman (1909), Wahlenberg (1946)
	Slash pine - 61*	Hebb & Clewell (1976)
	Pond pine - 81*	Schumacher and Coile (1960)
4. Stand basal area	N/A	
5. Number of standing snags per acre	N/A	
6. Volume of downed logs	N/A	
7. Stand structure	Forest - hardwood understory present Woodland - shrub understory dominant Savanna - grass-herb understory dominant	

*Trees per acre
N/A = Not available

Montane and Allied Spruce and Spruce-Fir Forest Old-Growth Forest Community Type 31

Community Description

Montane and allied spruce and spruce-fir forests typically occur at middle-to-high elevations in the Appalachians from Maine to North Carolina (table 47). This old-growth forest community type occurs on the highest mountains of the southern Appalachians, where it caps many of the highest peaks. Site conditions are usually severe, including short frost-free seasons and shallow, poorly developed soils that erode easily on steep slopes. The montane and allied spruce and spruce-fir forest community type typically occurs in fog-shrouded locations where moisture is obtained through direct cloud contact (Tyrrell and others, in preparation).

Table 47. *The potential distribution of the montane and allied spruce and spruce-fir old-growth forest community type.*

Ecological Province	Ecological Section	National Forest
Central Appalachian Broadleaf-Coniferous Forest Meadow	Northern Ridge and Valley	George Washington-Jefferson
	Blue Ridge Mountains	Nantahala-Pisgah Cherokee George Washington-Jefferson (Mount Rogers NRA*)

*NRA = National recreation area

Red spruce (Picea rubens), yellow birch (Betula alleghaniensis), mountain ash (Sorbus americana), and mountain maple (Acer spicatum) are commonly found in this forest community (table 48). Other typical tree species are Fraser fir (Abies fraseri) and pin cherry (Prunus pensylvanica). Hobble bush (Viburnum alnifolium) and bearberry (Vaccinium erythrucarpum) are common understory plants (Tyrrell and others, in preparation). Table 49 contains old-growth attributes for the montane and allied spruce and spruce-fir forest community type.

Table 48. *The relationship of the montane and allied spruce and spruce-fir old-growth forest community type to the forest classification systems of the National Forest System and the Society of American Foresters, and the International Classification of Ecological Communities of The Nature Conservancy.*

Classification	Code	Forest Type
National Forest CISC*		
cover type	6	Fraser fir
	7	Red spruce-Fraser fir
Society of American Foresters		
forest type code	32	Red spruce
	34	Red spruce-Fraser fir
The Nature Conservancy		
International Classification of		
Ecological Communities**	I.A.8.N.c.010	Fraser fir-(red spruce)
	I.A.8.N.c.030	Red spruce
	I.C.3.N.a.045	Red spruce-yellow birch

*CISC = Continuous inventory of stand conditions
**Ecological communities = Forest alliance

Disturbance

Disturbances are usually intense and affect large areas of this forest community type. Because of exposure and limited rooting depth, these forests are susceptible to large-scale blowdowns during storms. Tree mortality may occur in waves across the landscape.

Insect outbreaks, including the balsam woolly adelgid, can cause widespread devastation.

Tree mortality due to windthrow or insect attack can predispose these areas to fire during droughts (Tyrrell and others, in preparation).

Concerns about spruce decline have been raised due to pollution such as acid deposition. While this decline has been documented for this community type in the northeast portion of its range, the detection of decline is problematic due to disturbances from insects (SAMAB 1996).

Representative Montane and Allied Spruce and Spruce-Fir Forest Old-Growth Stands

Black Mountain Research Natural Area, Yancey Co., North Carolina
Mount Pisgah, near Blue Ridge Parkway, North Carolina
Northwest side of Roan High Bluff, Tennessee

Table 49. *Attributes of the montane and allied spruce and spruce-fir old-growth forest community type (Tyrrell and others, in preparation).*

Old-Growth Attribute	**Old-Growth Parameters**	**Data Sources**
1. Average age of large trees	Red spruce - 81-390 yrs Balsam fir - 40-130 yrs Yellow birch - 140-225 yrs	N/A
2. DBH of largest trees	Red spruce - 13-36 inches Balsam fir - 8-24 inches Fraser fir - 9-24 inches Yellow birch - 18-48 inches	N/A
3. Stand density	D.b.h. ≥ 4 inches - 30-529*	N/A
4. Stand basal area	D.b.h. ≥ 4 inches - 99-276**	N/A
5. Number of standing snags per acre	D.b.h. ≥ 2 inches - 133-445 D.b.h. ≥ 8 inches- 14-67	N/A
6. Volume of downed logs	9,875 to 13,591 ft^3 per acre	N/A
7. Number of canopy layers	1 to 3	N/A
8. Number of 4” dbh classes	4 to 22	N/A

*Trees per acre
**Ft^2 per acre
N/A = Not available

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GLOSSARY

Basal area (BA) - the area, in square feet, of the cross section of a single tree, or all of the trees in a stand, measured at 4.5 feet above ground, usually expressed as square feet per acre.

Biodiversity - the variety of life in an area, including the variety of genes, species, plant and animal communities, and ecosystems, as well as the interactions of these elements.

Diameter of breast height (d.b.h.) - the standard method for measuring tree diameter at 4 1/2 feet from the ground.

Continuous inventory of stand conditions (CISC) - the USDA Forest Service, Southern Region's forest stand database containing descriptive and prescriptive data about mapped stands of forest land.

Ecological classification system (ECS) - a hierarchical system used in classifying ecological types and ecological units for making comparisons. The system is ecologically based and integrates existing data about site conditions, such as climate, topography, geology, soil, hydrology, and vegetation. It includes four planning and analysis scales of ecological units (from largest to smallest): ecoregion, subregion, landscape, and land unit. These ecological units are then subdivided as follows: ecoregion - domain, division, and province; subregion - section and subsection; landscape - landtype association; and land unit - landtype, landtype phase, and site**.**

Ecological section - an area with a similar geomorphic process, geologic origin, drainage network, topography, and regional climate. Such areas are often inferred by relating geologic maps to potential natural vegetation. Boundaries of ecological sections approximate those of geomorphic provinces, as recognized by geologists.

Even-aged - a stand of trees which originated at a single point in time, so that the individual trees are approximately the same age or a regeneration system designed to produce such a stand.

Existing old growth - individual stands on a national forest currently recognized as meeting the parameters of the old-growth operational definitions (table 2).

Forests - an area of trees with overlapping crowns (generally forming a 60 to 100 percent cover).

Future old growth - areas on national forests that have been allocated to old-growth restoration through land management decisions.

Habitat - the physical and biological environment for a plant or animal in which all the essentials for its development, existence, and reproduction are present.

Habitat linkage - vegetation or other conditions, that permit a species to move between habitat areas without encountering barriers.

Late seral (successional) stage - the stage of forest development during which the age of trees is usually greater than 80 years depending on the composition of tree species. Small gaps become more common as some trees die allowing full sunlight to reach the mid- and understories. This stage contains the largest trees within a forest and provides the highest capability for large snags, large live cavities, and den tree production. The presence of large, downed, woody material is highest during this period. Old-growth forests occur during the later periods of the seral stage.

Mesic - pertaining to or adapted to an area that has a balanced supply of water; neither wet nor dry.

Mid seral (successional) stage - the stage of forest development during which distinct overstory, midstory, and understory canopies are present. The age of trees range from about 20 years to about 90 years depending on the composition of tree species. The trees are usually greater than 10 inches in d.b.h. This stage provides capability for hard mast production, large standing snags, and live cavities. During this period, tree species reach economic maturity.

Montane - relating to the zone of relatively moist, cool, upland slopes characterized by the presence of large evergreen trees as a dominant life form.

Natural plant community - an association of plant species which are endemic to an area and whose characteristics have not been adversely affected by human disturbance.

Obligate species - a plant or animal species which occurs naturally only in a specific type of habitat.

Old-growth forests - an ecosystem distinguished by old trees and related structural attributes. Old growth encompasses the later stages of stand development that typically differ from earlier stages in a variety of characteristics including tree size, accumulation of large dead woody material, number of canopy layers, species composition, and ecosystem function. Old growth is not necessarily virgin or primeval. It can develop over time following human disturbances, just as it does following natural disturbances. Old growth encompasses both older forests dominated by early seral species and forests in later successional stages dominated by shade tolerant species.

Possible old growth - areas with the highest probability of being existing or future old growth based on the preliminary inventory criteria.

Rare community - an association of plant and animal species which occurs only on a very small portion of the overall ecosystem.

Savannas - an open area with trees covering less than 25 percent and with herbaceous species dominating.

Seral stage - a developmental, transitory stage in the ecological succession of a biotic community.

Terrestrial - of, or pertaining to, land as distinct from water.

Uneven-aged - a stand of trees in which the individual trees originated over a long period of time and, thus, differ widely in age; a regeneration system designed to produce such as stand.

Virgin forests - an eastern forest characterized as being unaltered by European settlers; a forest in its original state.

Woodlands - an open stand of trees with crowns not usually touching (generally forming a 25 to 60 percent cover).

Xeric - characterized by a lack of moisture.

EXAMPLES OF FOREST PLAN DECISIONS RELATED TO OLD GROWTH

APPENDIX A

Three national forests have specifically addressed old-growth issues through forest plan revisions or amendments.

George Washington National Forest - The forest plan provides an interim policy, until the regional policy is developed. These interim directions address old-growth management through a series of forest-wide standards and guidelines. The plan states:

- no silvicultural practices will be scheduled in stands identified as “present old growth” in the “preliminary inventory” and located on lands classified as unsuitable for timber management in any of the old-growth forest community type.

- no regeneration harvest practices will be scheduled in stands identified as “present old growth” in the “preliminary inventory” and located on lands classified as suitable for timber production in 9 of the 10 old-growth forest community types that occur on the forest.

- prior to scheduling any silvicultural practices in stands identified as “present old growth” in the “preliminary inventory” and located on lands classified as suitable for timber production in old-growth forest community type 21, the area will be inventoried according to the interim forest definition.

Ouachita National Forest - Approximately 40 percent of the 1.6 million acres is classified as unsuitable for timber production, including wilderness areas, scenic areas, riparian areas along streams, rocky ridgetops, and almost all lands where hardwoods are dominant. These areas, predominantly mature or approaching maturity, include upland and mixed oak-pine forest community types. Under the current plan directions, and without substantial disturbances, these areas will develop old-growth conditions. The pine-grass types maintained by fire is an ecological gap in community type representation.

A management area was created to restore fire-dependent, old-growth communities, and developed management area prescriptions for the restoration of old-growth pine-grass communities that would be allocated to continuous areas between around 600 to 6,000 acres in size. The acres within this management prescription could be either suitable (replacement stands) or unsuitable (core areas) for timber production based upon a specified set of conditions. The replacement stands are managed on a 160-year rotation.

Nantahala-Pisgah National Forests - The desired future condition (DFC) for old growth was defined as a network of small-, medium-, and large-sized old-growth areas that are representative of sites, elevation gradients, and landscapes and that are well dispersed and interconnected by forested lands. These areas should meet the following criteria: (1) high-quality old-growth characteristics; (2) unique species diversity; (3) community, soil type, aspect, elevation, ecological land unit, etc.; and (4) other specific resource concerns and management objectives.

The Nantahala-Pisgah National Forests used the following approach to develop a network of old-growth areas:

- Designated a series of large-sized areas (2,500+ contiguous acres), which will serve as reservoirs of biological diversity. The intent is to restore functional old-growth ecosystems at the subregional, forest, and landscape scales.

- Designate a series of medium-sized areas resulting in a series of old-growth areas that are each around 100 to 2,500 acres in size. They are located in each watershed or ecological subregion, or in whatever identifier unit is used for the scale of analysis. These medium-sized areas will serve as reservoirs of biological diversity. The intent is to restore functioning old-growth ecosystems at the landscape and Forest scales.

- Designated a series of small-sized areas resulting in a series of old-growth areas that are each around 50 to 100 acres in size. They are located in each compartment, or in whatever identifier unit is used for this scale of analysis. These small-sized areas will serve to increase biological diversity and to provide structural components of old growth at the stand and landscape levels.

AN EXAMPLE FIELD INVENTORY FORM FOR USE IN OLD-GROWTH VALIDATION MONITORING

APPENDIX B

KENTUCKY ENERGY & ENVIRONMENT CABINET

THE OFFICE OF
KENTUCKY NATURE PRESERVES

Endangered, Threatened, and Special Concern Plants, Animals, and Natural Communities of Kentucky

Office of Kentucky Nature Preserves
Kentucky Energy and Environment Cabinet
300 Sower Boulevard – 4th Floor
Frankfort, KY 40601

eec.ky.gov/Nature-Preserves

Key to Status and Rank Information

Office of Kentucky Nature Preserves

Status

USESA Status: U.S. Fish and Wildlife status

C	Candidate
LT	Listed as Threatened
LE	Listed as Endangered
SOMC	Species of Management Concern
LTNL	Listed Threatened in part of its range, but not listed in Kentucky
N or blank	None
Delisted	Delisted

State Status: Office of Kentucky Nature Preserves status

E	Endangered
T	Threatened
S	Special Concern
H	Historic
X	Extirpated
N	None

Ranks

State Rank: Estimate of species abundance in Kentucky

S1	Extremely Rare
S2	Rare
S3	Uncommon
S4	Many Occurrences
S5	Very Common
SH	Historically known in State
SX	Extirpated from State
SU	Unrankable due to conflicting or lack of information
SNR	Unranked, conservation status not yet assessed
S#S#	Numeric range rank denoting rank uncertainty
S#?	Denotes inexact numeric rank
S#B	Rank refers to breeding population in Kentucky
S#N	Rank refers to non-breeding population in Kentucky

Global Rank: Estimate of species abundance on a global scale

G1	Extremely Rare
G2	Rare

G3	Uncommon
G4	Common
G5	Very Common
GH	Historically known and expected to be Rediscovered
GX	Extinct
GU	Unrankable due to conflicting or lack of information
GNR	Unranked, conservation status not yet assessed
G#G#	Numeric range rank denoting rank uncertainty
G#?	Denotes inexact numeric rank
G#Q	Questionable taxonomy that may reduce conservation priority
G#T#	T rank denotes rarity of subspecies

The data from which this report is generated is continually updated. The date on which the report was created is in the report footer. Please note that the quantity and quality of data collected by the Office of Kentucky Nature Preserves is dependent on the research and observations of many individuals and organizations. In most cases, this information is not the result of comprehensive or site-specific field surveys; many natural areas in Kentucky have never been thoroughly surveyed, and new species of plants and animals are still being discovered. For these reasons, the Office of Kentucky Nature Preserves cannot provide a definitive statement on the presence, absence, or condition of biological elements in any part of Kentucky. Heritage reports summarize the existing information known to the Office of Kentucky Nature Preserves at the time this report was generated. It should not be regarded as a final statement on the elements being considered, nor should it be substituted for on-site surveys required for environmental assessments.

The Office of Kentucky Nature Preserves appreciates the submission of any endangered species data for Kentucky from field observations. For information on data reporting or other data services provided by the Office of Kentucky Nature Preserves, please contact the Office of Kentucky Nature Preserves at:

Office of Kentucky Nature Preserves
300 Sower Boulevard – 4th Floor
Frankfort, KY 40601

eec.ky.gov/Nature-Preserves

Endangered, Threatened, and Special Concern Plants, Animals, and Natural Communities of Kentucky
Office of Kentucky Nature Preserves

Scientific Name	Common Name	USESA Status	State Status	State Rank	Global Rank
Lichens					
Phaeophyscia leana	Lea's Bog Lichen		E	S1?	G2
Mosses					
Abietinella abietina	Wire Fern Moss		T	S2?	G5
Anomodon rugelii	Rugel's anomodon moss		T	S2?	G5
Brachythecium populeum	Matted Feather Moss		E	S1?	G5
Bryum cyclophyllum	Round-Leaved Bryum		E	S1?	G4G5
Bryum miniatum	Glossy red bryum moss		E	S1?	G4G5
Cirriphyllum piliferum	Hair pointed Feather-moss		T	S2?	G5
Dicranodontium asperulum	Orange Bow-moss		E	S1?	G4G5
Entodon brevisetus	Short-stalk Shiny Moss		E	S1?	G4?
Herzogiella turfacea	Flat Stump Moss		E	S1?	G5
Neckera pennata			T	S2?	G5
Oncophorus raui	Grout Oncophorus Moss		E	S1?	G3
Orthotrichum diaphanum	White-tipped Bristle-moss		E	S1?	G5
Plagiochila caduciloba	Gorge Leafy Liverwort		E	S1?	G3
Polytrichum pallidisetum	A Hair Cap Moss		T	S2?	G5
Polytrichum piliferum	Bristly Haircap		E	S1	G5
Polytrichum strictum	Strict Haircap		E	S1?	G5
Sphagnum quinquefarium	Five-ranked Bogmoss		E	S1?	G5
Tortula norvegica	Tortula		E	S1?	G5
Vascular Plants					
Acer spicatum	Mountain Maple		E	S1S2	G5
Aconitum uncinatum	Blue Monkshood		E	S1S2	G4
Actaea rubifolia	Appalachian Bugbane	SOMC	T	S2	G3
Adiantum capillus-veneris	Southern Maidenhair-fern		T	S2S3	G5
Adlumia fungosa	Allegheny-vine		H	SH	G4
Aesculus pavia var. pavia	Red Buckeye		T	S2S3	G5T5
Agalinis auriculata	Earleaf False Foxglove		E	S1	G3
Agalinis decemloba	Ten-lobed False Foxglove		E	S1	G3G4
Agalinis skinneriana	Pale False Foxglove		H	SH	G3G4
Ageratina luciae-brauniae	Lucy Braun's White Snakeroot	SOMC	S	S3	G3
Agrimonia gryposepala	Tall Hairy Groovebur		T	S1S2	G5
Amelanchier sanguinea	Roundleaf Serviceberry		E	S1	G5
Amelanchier stolonifera	Running Serviceberry		E	S1	G5
Amianthium muscitoxicum	Fly Poison		E	S1	G4G5
Angelica atropurpurea	Great Angelica		E	S1?	G5
Angelica triquinata	Filmy Angelica		E	S1S2	G4
Apios priceana	Price's Potato-bean	LT	E	S1	G3
Arabidopsis lyrata ssp. lyrata	Lyre-leaf Rockcress		E	S1S2	G5
Arabis patens	Spreading Rockcress		E	S1	G3
Aralia nudicaulis	Wild Sarsaparilla		T	S2S3	G5
Aristida ramosissima	Branched Three-awn Grass		H	SH	G5

Scientific Name	Common Name	USESA Status	State Status	State Rank	Global Rank
Asclepias hirtella	Prairie milkweed		T	S2	G5
Astragalus canadensis var. canadensis	Canadian Milk-vetch		S	S2	G5T5
Aureolaria patula	Spreading False Foxglove		S	S3	G3
Avenella flexuosa	Crinkled Hairgrass		T	S2	G5
Baptisia australis var. minor	Blue Wild Indigo		S	S2S3	G5T5
Baptisia leucophaea var. leucophaea	Cream Wild Indigo		S	S3	G4G5T4T5
Baptisia tinctoria	Yellow Wild Indigo		T	S1S2	G5
Bartonia virginica	Yellow Screwstem		T	S2	G5
Berberis canadensis	American Barberry		E	S1	G3G4
Berchemia scandens	Supple-jack		T	S1S2	G5
Boechera missouriensis	Missouri Rockcress		H	SH	G5
Boechera perstellata	Braun's Rockcress	LE	T	S2	G2
Bolboschoenus fluviatilis	River Bulrush		E	S1S2	G5
Botrychium matricariifolium	Matricary Grape-fern		E	S1	G5
Bouteloua curtipendula var. curtipendula	Side-oats Grama		S	S3?	G5T5
Boykinia aconitifolia	Brook Saxifrage		E	S1S2	G4
Cabomba caroliniana	Carolina Fanwort		T	S2	G5
Calamagrostis canadensis var. macouniana	Blue-joint Reedgrass		H	SH	G5T5?
Calamagrostis porteri ssp. insperata	Bent Reedgrass	SOMC	E	S1S2	G4T3
Calamagrostis porteri ssp. porteri	Porter's Reedgrass		T	S2S3	G4T4
Callicarpa americana	American Beautyberry		E	S1	G5
Calopogon tuberosus var. tuberosus	Grass-pink		E	S1	G5T5
Calycanthus floridus var. glaucus	Eastern Sweetshrub		T	S2	G5T5
Capnoides sempervirens	Rock Harlequin		S	S3?	G5
Carex aestivalis	Summer Sedge		E	S1	G4
Carex alata	Broadwing Sedge		T	S1S2	G5
Carex appalachica	Appalachian Sedge		T	S2?	G4
Carex austrocaroliniana	Tarheel Sedge		S	S3	G4
Carex buxbaumii	Brown Bog Sedge		E	S1	G5
Carex comosa	Bristly Sedge		H	SH	G5
Carex corrugata	Prune-fruit sedge		S	S3?	G5?
Carex crawei	Crawe's Sedge		S	S3	G5
Carex crebriflora	Coastal Plain Sedge		E	S1?	G4
Carex decomposita	Epiphytic Sedge		T	S2	G3G4
Carex fraseriana	Fraser's Sedge		E	S1	G4
Carex gigantea	Large Sedge		E	S1S2	G4
Carex howei	Prickly Bog Sedge		E	S1S2	G5T5?
Carex hystericina	Porcupine Sedge		H	SH	G5
Carex joorii	Cypress-swamp Sedge		E	S1S2	G4G5
Carex juniperorum	Juniper Sedge		E	S1S2	G3
Carex leptonervia	Finely-nerved Sedge		E	S1	G5
Carex ouachitana	Ouachita Sedge		E	S1	G4
Carex pellita	Woolly Sedge		H	SH	G5

Scientific Name	Common Name	USESA Status	State Status	State Rank	Global Rank
Carex reniformis	Reniform Sedge		E	S1?	G4?
Carex roanensis	Roan Mountain Sedge		E	S1	G2G3
Carex rugosperma	Umbel-like Sedge		T	S2?	G5T5
Carex seorsa	Weak Stellate Sedge		T	S2	G5
Carex stipata var. maxima	Stalkgrain Sedge		H	SH	G5T5?
Carex straminea	Straw Sedge		T	S2?	G5
Carex tetanica	Rigid Sedge		E	S1?	G4G5
Carex timida	Timid Sedge		T	S2	G2G4
Carex venusta	Dark Green Sedge		E	S1	G4
Carya aquatica	Water Hickory		T	S2S3	G5
Castanea dentata	American Chestnut		E	S1?	G4
Castanea pumila	Allegheny Chinkapin		T	S2	G5
Castilleja coccinea	Scarlet Indian Paintbrush		E	S1	G5
Cayaponia quinqueloba	Five-lobe Cucumber		E	S1?	G4
Ceanothus herbaceus	Prairie Redroot		T	S2	G5
Cerastium velutinum var. velutinum	Starry Grasswort		E	S1S2	G5T4?
Chelone obliqua var. obliqua	Red Turtlehead		E	S1	G4T3T4Q
Chelone obliqua var. speciosa	Rose Turtlehead		S	S3	G4T3
Chrysogonum virginianum var. brevistolon	Green-and-gold		E	S1	G5TNR
Chrysosplenium americanum	American Golden-saxifrage		T	S2?	G5
Circaea alpina ssp. alpina	Small Enchanter's Nightshade		S	S3	G5T5
Clematis catesbyana	Satin-curls		E	S1	G4G5
Clematis crispa	Blue Jasmine Leather-flower		T	S2	G5
Clematis glaucophylla	White-leaved Leather-flower		T	S2?	G4?
Collinsonia verticillata	Whorled Horse-balm		E	S1?	G3G4
Comptonia peregrina	Sweet-fern		E	S1	G5
Conradina verticillata	Cumberland Rosemary	LT	E	S1	G3
Convallaria montana	American Lily-of-the-valley		E	S1	G4?
Corallorhiza maculata	Spotted Coralroot		E	S1	G5
Coreopsis pubescens var. pubescens	Star Tickseed		S	S2S3	G5?T4T5
Crocanthemum bicknellii	Plains Frostweed		E	S1S2	G5
Crocanthemum canadense	Canada Frostweed		E	S1?	G5
Cyperus plukenetii	Plukenet's Cyperus		H	SH	G5
Cypripedium candidum	Small White Lady's-slipper		E	S1	G4
Cypripedium kentuckiense	Kentucky Lady's-slipper	SOMC	E	S1S2	G3
Cypripedium parviflorum var. parviflorum	Small Yellow Lady's-slipper		T	S2	G5T3T5
Dalea candida	White Prairie-clover		S	S3	G5
Dalea purpurea	Purple Prairie-clover		S	S3?	G5
Delphinium carolinianum ssp. calciphilum	Carolina Larkspur		T	S1S2	G5T2T4
Deschampsia cespitosa	Tufted Hairgrass		E	S1S2	G5
Desmodium ochroleucum	Cream Tick-trefoil		E	S1	G2
Dichanthelium lucidum	Shining rosette grass		S	S1?	G4
Didiplis diandra	Water-purslane		E	S1S2	G5

Scientific Name	**Common Name**	**USESA Status**	**State Status**	**State Rank**	**Global Rank**
Drosera brevifolia	Dwarf Sundew		E	S1	G5
Drosera intermedia	Spoon-leaved Sundew		E	S1	G5
Dryopteris carthusiana	Spinulose Wood Fern		S	S3	G5
Echinodorus berteroi	Burhead		T	S2	G5
Edrastima uniflora	Clustered Bluets		E	S1	G5
Eleocharis flavescens	Bright Green Spikerush		S	S1?	G5
Elodea nuttallii	Western Waterweed		T	S2?	G5
Elymus svensonii	Svenson's Wildrye	SOMC	T	S2S3	G3
Eriogonum harperi	Harper's Wild Fleabane		H	SH	G4T2
Eriophorum virginicum	Tawny Cotton-grass		E	S1?	G5
Eryngium integrifolium	Blue-flower Coyote-thistle		E	S1	G5
Erysimum capitatum var. capitatum	Western Wallflower		E	S1?	G5T5
Erythronium rostratum	Yellow Troutlily		S	S2S3	G5
Eubotrys recurvus	Red-twig Doghobble		E	S1	G4G5
Eupatorium maculatum var. maculatum	Spotted Joe-pye Weed		H	SH	G5T5
Eupatorium semiserratum	Small-flower Thoroughwort		E	S1?	G5
Euphorbia mercurialina	Mercury Spurge		T	S1S2	G4
Eurybia hemispherica	Tennessee Aster		E	S1	G4
Eurybia radula	Rough-leaved Aster		E	S1?	G5
Eurybia saxicastellii	Rockcastle Aster	SOMC	T	S1S2	G1G2
Eutrochium steelei	Steele's Joe-pye-weed		T	S2	G4
Fimbristylis perpusilla	Harper's fimbry		S	S1?	G2
Fimbristylis puberula var. puberula	Hairy Fimbristylis		T	S2	G5T5
Forestiera ligustrina	Upland Privet		T	S2S3	G4G5
Gaylussacia ursina	Bear huckleberry		T	S1S2	G4
Gentiana alba	Yellow Gentian		E	S1S2	G4
Gentiana decora	Showy Gentian		S	S3	G4?
Gentiana puberulenta	Prairie Gentian		E	S1	G4G5
Glandularia canadensis	Rose Mock-vervain		E	S1?	G5
Gleditsia aquatica	Water Locust		S	S3?	G5
Glyceria acutiflora	Sharp-scaled Manna-grass		E	S1S2	G5
Goodyera repens	Lesser rattlesnake-plantain		E	S1S2	G5
Gratiola quartermaniae	Quarterman's Hedge-hyssop		E	S1	G3
Gratiola viscidula	Short's Hedgehyssop		S	S3	G4G5
Gymnopogon ambiguus	Bearded Skeleton-grass		S	S2S3	G4
Gymnopogon brevifolius	Shortleaf Skeleton-grass		E	S1	G5
Halesia tetraptera	Common Silverbell		E	S1S2	G5
Hedeoma hispida	Rough Pennyroyal		T	S2	G5
Helanthium tenellum	Dwarf Burhead	SOMC	E	S1	G5?
Helianthus eggertii	Eggert's Sunflower		T	S2	G3
Helianthus silphioides	Silphium Sunflower		E	S1	G4
Heracleum lanatum	Cow-parsnip		H	SH	G5
Heteranthera dubia	Grassleaf Mud-plantain		S	S3	G5

Scientific Name	Common Name	USESA Status	State Status	State Rank	Global Rank
Heteranthera limosa	Blue Mud-plantain		S	S2S3	G5
Heterotheca latifolia var. latifolia	Broad-leaf Golden-aster		T	S2	G5T5
Hexastylis contracta	Southern Heartleaf	SOMC	E	S1	G3
Hieracium longipilum	Hairy Hawkweed		T	S2	G4G5
Houstonia serpyllifolia	Michaux's Bluets		E	S1	G4?
Hydrocotyle americana	American Water-pennywort		E	S1	G5
Hydrocotyle ranunculoides	Floating Pennywort		E	S1S2	G5
Hydrocotyle verticillata	Whorled Marsh-pennywort		E	S1	G5
Hydrolea ovata	Ovate Fiddleleaf		E	S1	G5
Hydrolea uniflora	One-flower Fiddleleaf		E	S1	G5
Hydrophyllum virginianum	Eastern Waterleaf		T	S2?	G5
Hylotelephium telephioides	Allegheny Stonecrop		T	S2	G4
Hypericum adpressum	Creeping St. John's-wort	SOMC	H	SH	G3
Hypericum crux-andreae	St. Peter's-wort		T	S2S3	G5
Hypericum gymnanthum	Claspingleaf St. John's-wort		E	S1	G4
Iris brevicaulis	Zigzag Iris		T	S1S2	G4
Iris fulva	Copper Iris		E	S1	G5
Isoetes butleri	Butler's Quillwort		E	S1	G4
Isoetes melanopoda ssp. melanopoda	Blackfoot Quillwort		E	S1	G5TNR
Juglans cinerea	White Walnut	SOMC	T	S2S3	G4
Juncus articulatus	Jointed Rush		S	S2S3	G5
Juncus elliottii	Bog Rush		H	SH	G4G5
Juncus filipendulus	Ringseed Rush		T	S2?	G5
Juniperus communis var. depressa	Ground Juniper		T	S1	G5T5
Koeleria macrantha	Prairie Junegrass		E	S1	G5
Krigia occidentalis	Western Dwarf Dandelion		E	S1?	G5
Lathyrus palustris	Vetchling Peavine		T	S2	G5
Lathyrus venosus	Smooth Veiny Peavine		S	S2S3	G5
Leavenworthia exigua var. laciniata	Kentucky Gladecress	LT	E	S1S2	G4T1T2
Leavenworthia torulosa	Necklace Gladecress		T	S2	G4
Lespedeza angustifolia	Narrowleaf Bush-clover		E	S1	G5
Lespedeza capitata	Round-head Bush-clover		S	S3	G5
Lespedeza stuevei	Tall Bush-clover		T	S2S3	G4?
Liatris cylindracea	Slender Blazingstar		T	S2S3	G5
Lilium philadelphicum var. philadelphicum	Wood Lily		T	S2S3	G5T4T5
Lilium superbum	Turk's Cap Lily		T	S1S2	G5
Limnobium spongia	American Frog's-bit		T	S2S3	G4
Liparis loeselii	Loesel's Twayblade		T	S2S3	G5
Listera australis	Southern Twayblade		E	S1	G4
Listera smallii	Kidney-leaf Twayblade		T	S2	G4
Lithospermum molle	Soft-hairy False-gromwell		H	SH	G4G5
Lithospermum occidentale	Western False Gromwell		E	S1	G4G5T4?
Lithospermum parviflorum	Hairy False Gromwell		E	S2	G4G5T4

Scientific Name	Common Name	USESA Status	State Status	State Rank	Global Rank
Lobelia gattingeri	Gattinger's Lobelia		E	S1	G4G5T4
Lobelia nuttallii	Nuttall's Lobelia		T	S2	G4G5
Lonicera dioica var. orientalis	Wild Honeysuckle		E	S1	G5TNRQ
Lonicera reticulata	Grape Honeysuckle		T	S2	G5
Ludwigia hirtella	Rafinesque's seedbox		E	S1	G5
Lycopodiella appressa	Southern Bog Clubmoss		E	S1	G5
Lycopodiella inundata	Northern Bog Clubmoss		E	S1S2	G5
Lycopodium clavatum	Running Pine		E	S1?	G5
Lysimachia borealis	Northern Starflower		E	S1	G5
Lysimachia minima	Chaffweed		S	S2	G5
Lysimachia radicans	Trailing Loosestrife		E	S1	G4G5
Lysimachia terrestris	Swamp Candles		E	S1	G5
Magnolia pyramidata	Pyramid Magnolia		H	SH	G4
Maianthemum canadense	Wild Lily-of-the-valley		T	S2	G5
Maianthemum stellatum	Starflower False Solomon's-seal		E	S1	G5
Malus ioensis	Iowa Crabapple		S	S2?	G4G5
Malvastrum hispidum	Hispid Falsemallow		T	S2?	G3G5
Marshallia grandiflora	Barbara's Buttons	SOMC	E	S1	G3
Matelea carolinensis	Carolina Anglepod		E	S1?	G4
Melampyrum lineare var. latifolium	American Cowwheat		T	S2	G5T5
Melampyrum lineare var. pectinatum	American Cow-wheat		H	SH	G5T5
Melanthera nivea	Snow Squarestem		S	S3?	G5
Melanthium parviflorum	Appalachian Bunchflower		T	S2	G4?
Melanthium virginicum	Virginia Bunchflower		E	S1	G5
Melanthium woodii	Wood's Bunchflower		T	S2	G5
Micranthes micranthidifolia	Lettuce-leaf Saxifrage		E	S1	G5
Micranthes petiolaris	Michaux's Saxifrage		T	S2	G4G5
Mirabilis albida	Pale Umbrella-wort		H	SH	G5
Mononeuria cumberlandensis	Cumberland Sandwort	LE	E	S1	G3
Mononeuria glabra	Appalachian Sandwort		T	S1S2	G4
Monotropsis odorata	Sweet Pinesap	SOMC	T	S2	G3
Muhlenbergia bushii	Bush's Muhly		E	S1S2	G5
Muhlenbergia cuspidata	Plains Muhly		T	S2	G5
Muhlenbergia glabrifloris	Hair Grass		S	S2S3	G4?
Myriophyllum heterophyllum	Broadleaf Water-milfoil		S	S3?	G5
Myriophyllum pinnatum	Cutleaf Water-milfoil		H	SH	G5
Myriopteris alabamensis	Alabama Lipfern		H	SH	G4G5
Myriopteris gracilis	Fee's Lipfern		E	S1	G5
Myzorrhiza ludoviciana	Louisiana Broomrape		H	SH	G5
Nabalus albus	White Rattlesnake-root		E	S1	G5
Nabalus asper	Rough Rattlesnake-root		E	S1	G4?
Nabalus crepidineus	Nodding Rattlesnake-root		S	S3	G4
Nabalus racemosus	Glaucous Rattlesnake-root		S	S1S2	G5

Scientific Name	Common Name	USESA Status	State Status	State Rank	Global Rank
Najas gracillima	Thread-like Naiad		S	S2S3	G5?
Nemophila aphylla	Small-flower Baby-blue-eyes		T	S2?	G5
Nestronia umbellula	Conjurer's-nut		E	S1	G4
Oclemena acuminata	Whorled Aster		T	S2S3	G5
Oenothera linifolia	Thread-leaf Sundrops		E	S1S2	G5
Oenothera oakesiana	Evening Primrose		H	SH	G5
Oenothera perennis	Small Sundrops		E	S1S2	G5
Oenothera serrulata	Yellow Evening Primrose		H	SH	G5
Oenothera triloba	Stemless Evening-primrose		T	S1S2	G4
Orontium aquaticum	Golden Club		T	S2	G5
Oxalis macrantha	Price's Yellow Wood Sorrel		E	S2?	GNR
Packera paupercula var. paupercula	Balsam Ragweed		T	S2?	G5
Packera paupercula var. pseudotomentosa	Ozark ragwort		T	S2	G5TNR
Parnassia asarifolia	Kidneyleaf Grass-of-parnassus		E	S1	G4
Parnassia grandifolia	Large-leaved Grass-of-parnassus		E	S1	G3
Paronychia argyrocoma	Silverling		E	S1	G4
Paspalum boscianum	Bull Paspalum		S	S2S3	G5
Paxistima canbyi	Canby's Mountain-lover	SOMC	T	S2	G2?
Paysonia lescurii	Lescur's Bladderpod		H	SH	G4
Pediomelum tenuiflorum	Few-flowered Scurf-pea		E	S1	G5
Perideridia americana	Eastern Yampah		T	S2	G4
Phacelia ranunculacea	Blue Scorpion-weed		S	S3	G4
Phemeranthus calcaricus	Limestone Fameflower		E	S1	G3
Phemeranthus teretifolius	Roundleaf Fameflower		E	S1	G4
Philadelphus inodorus	Mock Orange		T	S1S2	G4G5
Philadelphus pubescens	Hoary Mock Orange		E	S1	G5?
Phlox bifida ssp. bifida	Cleft Phlox		T	S1S2	G5?T5?
Phlox bifida ssp. stellaria	Starry-cleft Phlox	SOMC	E	S1	G5?T3
Physaria globosa	Globe Bladderpod	LE	E	S1	G2
Platanthera cristata	Yellow-crested Orchid		T	S1S2	G5
Platanthera integrilabia	White Fringeless Orchid	LT	E	S1	G2G3
Platanthera psycodes	Small Purple-fringed Orchid		E	S1	G5
Poa saltuensis	Drooping Bluegrass		E	S1S2	G5T5
Podostemum ceratophyllum	Threadfoot		S	S3	G5
Pogonia ophioglossoides	Rose Pogonia		E	S1	G5
Polygala cruciata	Crossleaf Milkwort		E	S1	G5
Polygala nuttallii	Nuttall's Milkwort		H	SH	G5
Polygala polygama	Racemed Milkwort		T	S2	G5
Polygaloides paucifolia	Gaywings		E	S1?	G5
Polymnia laevigata	Tennessee Leafcup		E	S1S2	G3
Pontederia cordata	Pickerel-weed		T	S1S2	G5
Potamogeton amplifolius	Large-leaf Pondweed		E	S1?	G5
Potamogeton illinoensis	Illinois Pondweed		S	S2	G5

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Potamogeton pulcher	Spotted Pondweed		T	S1S2	G5
Primula frenchii	French's Shooting Star		S	S3	G3?
Prosartes maculata	Nodding Mandarin		S	S3?	G4
Pseudognaphalium micradenium	Small Rabbit-tobacco		H	SH	G4G5T3?
Ptilimnium capillaceum	Mock Bishop's-weed		T	S1S2	G5
Ptilimnium costatum	Eastern Mock Bishop's-weed		E	S1?	G4
Ptilimnium nuttallii	Nuttall's Mock Bishop's-weed		E	S1S2	G5?
Pycnanthemum albescens	Whiteleaf Mountainmint		H	SH	G5
Pycnanthemum muticum	Blunt Mountainmint		E	S1	G5
Quercus ilicifolia	Scrub oak		H	SH	G5
Quercus nigra	Water Oak		T	S2?	G5
Quercus texana	Nuttall's Oak		T	S2S3	G4G5
Ranunculus ambigens	Waterplantain Spearwort		S	S3	G4
Rhododendron canescens	Hoary Azalea		E	S1	G5
Rhynchosia tomentosa	Hairy Snoutbean		E	S1S2	G5
Rhynchospora macrostachya	Tall Beaked-rush		E	S1	G4
Rhynchospora recognita	Globe Beaked-rush		S	S3	G5?
Ribes americanum	Eastern Black Currant		T	S2?	G5
Rorippa aquatica	Lakecress		T	S1S2	G4?
Rubus canadensis	Smooth Blackberry		E	S1?	G5
Rudbeckia subtomentosa	Sweet Coneflower		E	S1	G5
Ruellia pedunculata	Stalked Wild-petuna		E	S1	G5
Sabatia brachiata	Narrow-leaf Pink		E	S1	G5?
Sabatia campanulata	Slender Marsh Pink		E	S1	G5
Sabulina fontinalis	Water Stitchwort		E	S1S2	G3
Sagittaria graminea	Grassleaf Arrowhead		T	S1S2	G5
Sagittaria platyphylla	Delta Arrowhead		E	S1	G5
Sagittaria rigida	Sessile-fruited Arrowhead		E	S1	G5
Salix amygdaloides	Peach-leaved Willow		H	SH	G5
Salix discolor	Pussy Willow		H	SH	G5
Salvia urticifolia	Nettle-leaf Sage		E	S1	G5
Sambucus racemosa ssp. pubens	Red Elderberry		E	S1S2	G5T5
Sanguisorba canadensis	Canada Burnet		E	S1	G5
Sceptridium oneidense	Blunt-lobe Grape-fern		H	SH	G4
Schisandra glabra	Bay Starvine		E	S1	G3
Schizachne purpurascens	Purple Oat		T	S2	G5
Schoenoplectiella hallii	Hall's Bulrush	SOMC	E	S1	G2G3
Schoenoplectus heterochaetus	Slender Bulrush		H	SH	G5
Schwalbea americana	Chaffseed	LE	H	SH	G2
Scirpus expansus	Woodland Beakrush		E	S1S2	G4
Scutellaria arguta	Hairy Skullcap		E	S1S2	G1?Q
Scutellaria saxatilis	Rock Skullcap		T	S2S3	G3G4
Senecio suaveolens	Sweet-scented Indian-plantain		S	S3	G4

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Sida hermaphrodita	Virginia Mallow		T	S2S3	G3
Silene ovata	Ovate Catchfly	SOMC	E	S1	G3
Silene regia	Royal Catchfly		E	S1	G3
Silphium laciniatum	Compassplant		T	S2	G5
Silphium pinnatifidum	Tansy Rosinweed		S	S3	G3Q
Silphium wasiotense	Appalachian Rosinweed	SOMC	S	S3	G3
Solidago albopilosa	White-haired Goldenrod	Delisted	T	S2	G2
Solidago austrina	Southern Bog Goldenrod		T	S2?	GNR
Solidago buckleyi	Buckley's Goldenrod		S	S2S3	G4
Solidago curtisii	Curtis' Goldenrod		S	S3	GNR
Solidago puberula	Downy Goldenrod		S	S2	G5
Solidago racemosa	Rand's Goldenrod		S	S3	G5T3?
Solidago roanensis	Roan Mountain Goldenrod		T	S1S2	G4G5
Solidago shortii	Short's Goldenrod	LE	E	S1	G1
Solidago squarrosa	Squarrose Goldenrod		H	SH	G4G5
Sophronanthe pilosa	Shaggy Hedgehyssop		T	S2	G5?
Sparganium eurycarpum	Large Bur-reed		E	S1?	G5
Sphenopholis pensylvanica	Swamp Wedgescale		S	S1S2	G4
Spiraea alba	Narrow-leaved Meadow-sweet		H	SH	G5
Spiraea virginiana	Virginia Spiraea	LT	T	S2	G2
Spiranthes lucida	Shining Ladies'-tresses		T	S2S3	G4
Spiranthes magnicamporum	Great Plains Ladies'-tresses		T	S2	G3G4
Spiranthes ochroleuca	Yellow Nodding Ladies'-tresses		T	S2?	G4
Spiranthes odorata	Sweetscent Ladies'-tresses		E	S1	G5
Sporobolus arcuatus	Cumberland sandgrass		E	S1	G2G3
Sporobolus clandestinus	Rough Dropseed		T	S2S3	G5
Sporobolus heterolepis	Northern Dropseed		E	S1	G5
Stachys nuttallii	Nuttall's Hedge-nettle		H	SH	G5?
Stellaria longifolia	Longleaf Stitchwort		S	S2S3	G5
Stenanthium gramineum	Eastern Featherbells		T	S2S3	G4G5
Streptopus lanceolatus var. lanceolatus	Rosy Twisted-stalk		E	S1	G5T5
Styrax grandifolius	Bigleaf Snowbell		E	S1S2	G5
Symphoricarpos albus var. albus	Snowberry		E	S1	G5T5
Symphyotrichum concolor	Eastern Silvery Aster		T	S2	G5
Symphyotrichum pratense	Barrens Silky Aster		S	S3	G4?
Symphyotrichum priceae	White Heath Aster		E	S1	G3G5
Symphyotrichum texanum	Hairy Heart-leaved Aster		H	SH	G5T3T4
Taxus canadensis	Canadian Yew		T	S2S3	G5
Tephrosia spicata	Spiked Hoary-pea		E	S1S2	G4G5
Thaspium pinnatifidum	Cutleaf Meadow-parsnip	SOMC	T	S2S3	G2G3
Thermopsis mollis	Soft-haired Thermopsis		E	S1	G3G4
Thuja occidentalis	Northern White Cedar		T	S2S3	G5
Tomostima cuneifolia	Wedge-leaf Whitlow-grass		E	S1	G5

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Torreyochloa pallida var. pallida	Pale Manna Grass		H	SH	G5T5?
Toxicodendron vernix	Poison Sumac		E	S1	G5
Tragia urticifolia	Nettle-leaf Noseburn		E	S1?	G5
Trepocarpus aethusae	Trepocarpus		S	S3	G4G5
Trichophorum planifolium	Bashful Bulrush		E	S1?	G4G5
Trichostema setaceum	Narrowleaved Bluecurls		E	S1	G5
Tridens chapmanii	Chapman's Tridens		E	S1	G5T3
Trifolium kentuckiense	Kentucky Clover		E	S1	G1
Trifolium reflexum	Buffalo Clover		E	S1S2	G3G4
Trifolium stoloniferum	Running Buffalo Clover	LE	T	S2S3	G3
Trillium nivale	Snow Trillium		E	S1	G4
Trillium pusillum	Least Trillium	SOMC	E	S1	G3
Trillium undulatum	Painted Trillium		T	S2	G5
Ulmus serotina	September Elm		S	S3	G4
Utricularia macrorhiza	Greater Bladderwort		E	S1	G5
Vaccinium erythrocarpum	Southern Mountain Cranberry		E	S1?	G5
Vallisneria americana	Eelgrass		S	S2S3	G5
Veronica americana	American Speedwell		H	SH	G5
Viburnum lantanoides	Alderleaved Viburnum		E	S1?	G5
Viburnum molle	Kentucky Arrow-wood		S	S3?	G5
Viburnum nudum	Possumhaw		E	S1	G5
Viola egglestonii	Eggleston's Violet		S	S3	G4
Viola walteri	Walter's Violet		T	S2	G4G5
Vitis labrusca	Northern Fox Grape		T	S2S3	G5
Vitis rupestris	Sand Grape		T	S2	G3
Woodsia appalachiana	Appalachian Woodsia		E	S1	G4
Xyris difformis	Carolina Yellow-eyed-grass		E	S1?	G5
Zizania palustris var. interior	Indian Wild Rice		H	SH	G5T4T5
Zizaniopsis miliacea	Southern Wild Rice		T	S1S2	G5
Snails					
Anguispira rugoderma	Pine Mountain Tigersnail		E	S2	G2
Antroselates spiralis	Shaggy Cavesnail		S	S2	G3
Appalachina chilhoweensis	Queen Crater		S	S2	G4
Fumonelix wetherbyi	Clifty Covert		S	S2	G2G3
Glyphyalinia raderi	Maryland Glyph	SOMC	S	S1	G2
Glyphyalinia rhoadsi	Sculpted Glyph		T	S2	G5
Helicodiscus notius specus	A Terrestrial Snail		T	S1	G5T2
Helicodiscus punctatellus	Punctate Coil		S	S1	G1
Leptoxis praerosa	Onyx Rocksnail	SOMC	S	S3S4	G5
Lioplax sulculosa	Furrowed Lioplax		S	S3S4	G5
Lithasia armigera	Armored Rocksnail	SOMC	S	S3S4	G3G4
Lithasia geniculata	Ornate Rocksnail	SOMC	S	S1	G3Q
Lithasia salebrosa	Muddy Rocksnail	SOMC	S	S2S4	G2G3Q

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Lithasia verrucosa	Varicose Rocksnail	SOMC	S	S3S4	G4Q
Mesomphix rugeli	Wrinkled Button		T	S2	G4
Neohelix dentifera	Big-tooth Whitelip		T	S2	G5
Paravitrea lapilla	Gem Supercoil		H	SH	G2
Patera panselenus	Virginia Bladetooth		S	S2	G3
Pilsbryna vanattai	Honey Glyph		E	S1	G2G3
Pleurocera alveare	Rugged Hornsnail	SOMC	S	S3S4	G3
Pleurocera curta	Shortspire Hornsnail	SOMC	S	S2	G2
Rabdotus dealbatus	Whitewashed Rabdotus		T	S1S2	G5
Rhodacme elatior	Domed Ancylid		S	S1	G1
Vertigo bollesiana	Delicate Vertigo		E	S1	G4G5
Vertigo clappi	Cupped Vertigo		E	S1	G1G2
Vitrinizonites latissimus	Glassy Grapeskin		T	S2	G4
Webbhelix multilineata	Striped Whitelip		T	S2	G5
Freshwater Mussels					
Actinonaias pectorosa	Pheasantshell		S	S2S3	G4
Alasmidonta atropurpurea	Cumberland Elktoe	LE	E	S1	G1G2
Alasmidonta marginata	Elktoe	SOMC	T	S2	G4
Alasmidonta viridis	Slippershell Mussel		S	S3S4	G4G5
Anodontoides denigrata	Cumberland Papershell	SOMC	E	S1	G1
Anodontoides ferussacianus	Cylindrical Papershell		S	S3S4	G5
Cyprogenia stegaria	Fanshell	LE	E	S1	G1Q
Dromus dromas	Dromedary Pearlymussel	LE	E	S1	G1
Elliptio crassidens	Elephantear		S	S3S4	G5
Epioblasma brevidens	Cumberlandian Combshell	LE	E	S1	G1
Epioblasma capsaeformis	Oyster Mussel	LE	E	S1	G1
Epioblasma obliquata	Catspaw	LE,XN	E	S1	G1
Epioblasma rangiana	Northern Riffleshell	LE	E	S1	G2
Epioblasma triquetra	Snuffbox	LE	E	S1	G3
Epioblasma walkeri	Tan Riffleshell	LE	E	S1	G1
Fusconaia subrotunda	Longsolid		S	S3	G3
Lampsilis abrupta	Pink Mucket	LE	E	S1	G2
Lampsilis hydiana	Louisiana Fatmucket		S	S1	G4Q
Lampsilis ovata	Pocketbook		E	S1	G5
Lasmigona compressa	Creek Heelsplitter		E	S1	G5
Leaunio lienosus	Little Spectaclecase		T	S2S3	G5TNR
Leaunio ortmanni	Kentucky Creekshell	SOMC	E	S1S2	G2
Leaunio pataecus	Dwarf Rainbow		E	S1	GNR
Leaunio vanuxemensis	Mountain Creekshell		E	S1S2	GNR
Ligumia recta	Black Sandshell		S	S4	G4G5
Margaritifera monodonta	Spectaclecase	LE	E	S1	G3
Medionidus conradicus	Cumberland Moccasinshell		E	S1S2	G3G4
Obovaria retusa	Ring Pink	LE	E	S1	G1

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Obovaria subrotunda	Round Hickorynut		T	S2S3	G4
Pegias fabula	Littlewing Pearlymussel	LE	E	S1	G1
Plethobasus cooperianus	Orangefoot Pimpleback	LE	E	S1	G1
Plethobasus cyphyus	Sheepnose	LE	E	S1	G3
Pleurobema clava	Clubshell	LE	E	S1	G1G2
Pleurobema oviforme	Tennessee Clubshell	SOMC	E	S1	G2G3
Pleurobema plenum	Rough Pigtoe	LE	E	S1	G1
Pleurobema rubrum	Pyramid Pigtoe	SOMC	E	S1	G2G3
Potamilus capax	Fat Pocketbook	LE	T	S2	G2
Potamilus purpuratus	Bleufer		E	S1	G5
Ptychobranchus subtentus	Fluted Kidneyshell	LE	E	S1	G2
Simpsonaias ambigua	Salamander Mussel	SOMC	T	S2S3	G3
Theliderma cylindrica	Rabbitsfoot	LT	E	S2	G3G4
Toxolasma lividum	Purple Lilliput	SOMC	E	S1	G3Q
Toxolasma texasiense	Texas Lilliput		T	S2	G4
Venustaconcha troostensis	Cumberland Bean	LE	E	S1	GNR
Crustaceans					
Barbicambarus cornutus	Bottlebrush Crayfish		S	S2S3	G4
Bryocamptus morrisoni elegans	A Copepod		T	S1	G3G4T3T4
Caecidotea barri	Clifton Cave Isopod	SOMC	E	S1	G1
Cambarellus puer	Swamp Dwarf Crayfish		E	S1	G5
Cambarellus shufeldtii	Cajun Dwarf Crayfish		S	S2S3	G5
Cambarus adustus	Dusky Mudbug		E	S1S2	GNR
Cambarus angularis	Angled Crayfish		S	S3	G3
Cambarus bouchardi	Big South Fork Crayfish		E	S1S2	G2
Cambarus buntingi	Longclaw Crayfish		T	S2S3	G4Q
Cambarus callainus	Big Sandy Crayfish	LT	T	S1	G2
Cambarus deweesae	Valley Flame Crayfish		S	S3S4	G4
Cambarus friaufi	Hairy Crayfish		S	S3S4	G4
Cambarus guenteri	Redbird Crayfish		S	S3	GNR
Cambarus hazardi	Brawny Crayfish		S	S3	GNR
Cambarus jezerinaci	Poweel River Crayfish		S	SU	G3
Cambarus parvoculus	Mountain Midget Crayfish		S	S2	G5
Cambarus sciotensis	Teays River Crayfish		S	SNR	G5
Cambarus taylori	Cutshin Crayfish		S	S3	GNR
Cambarus theepiensis	Coalfields Crayfish		S	S4	GNR
Crangonyx caecus	An Amphipod		T	S1	G1
Crangonyx castellanum	An Amphipod		E	S1	G1
Crangonyx lewisi	Lewis Cave Amphipod		T	S1S2	G2
Crangonyx longidactylus	An Amphipod		T	S2	G2
Crangonyx specus	An Amphipod		E	S1	G1
Faxonius bellator	Screaming Eagle Crayfish		S	SNR	G1
Faxonius bisectus	Crittenden Crayfish	SOMC	T	S1	G1

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Faxonius burri	Blood River Crayfish		T	S2	G2
Faxonius durelli	Saddle Crayfish		S	S4	G5
Faxonius jeffersoni	Louisville Crayfish	SOMC	E	S1	G1
Faxonius kentuckiensis	Kentucky Crayfish		T	S2?	G4
Faxonius lancifer	Shrimp Crayfish		E	S1	G5
Faxonius margorectus	Livingston Crayfish		S	S2	G2
Faxonius palmeri palmeri	Gray-Speckled Crayfish		E	S1	G5T5
Faxonius pardalotus	Leopard Crayfish		S	SNR	G1
Faxonius rafinesquei	Rough River Crayfish		S	S2	G3
Faxonius sanbornii	Sanborn's Crayfish		S	SU	G5
Gammarus bousfieldi	Bousfield's Amphipod	SOMC	E	S1	G1
Lacunicambarus chimera	Crawzilla Crawdad		S	S4	GNR
Lacunicambarus ludovicianus	Painted Devil Crayfish		T	SU	G5
Macrobrachium ohione	Ohio Shrimp		E	S1	G4
Orconectes barri	Cumberland Plateau Cave Crayfish		T	S2	G2
Orconectes inermis inermis	Ghost Crayfish		S	S3	G5T4
Orconectes packardi	Appalachian Cave Crayfish		T	S2S3	G2
Orconectes pellucidus	Mammoth Cave Crayfish	SOMC	S	S3	G4
Palaemonias ganteri	Mammoth Cave Shrimp	LE	E	S1	G1
Procambarus viaeviridis	Vernal Crayfish		T	S1S2	G5
Pseudocandona jeanneli	Jeannel's Cave Ostracod		E	S1	G2
Sagittocythere stygia	An Ectocommensal Ostracod		T	S1	G1
Stygobromus vitreus	An Amphipod		S	S1	G4
Insects					
Acroneuria hitchcocki	Kentucky Stone		T	S1S2	G1G2
Acroneuria kosztarabi	Virginia Stone		T	S1S2	G1G2
Allocapnia cunninghami	Karst Snowfly		T	S1S2	G1G2
Amphiagrion saucium	Eastern Red Damsel		E	S1S2	G5
Arigomphus maxwelli	Bayou Clubtail		T	S1S2	G5
Batriasymmodes quisnamus	A Cave Obligate Beetle		H	SH	G3
Batrisodes henroti	A Cave Obligate Beetle		H	SH	G2G3
Batrisodes hubrichti	A Cave Obligate Beetle		H	SH	G1
Bombus affinis	Rusty-patched Bumble Bee	LE	H	SH	G2
Calephelis borealis	Northern Metalmark		T	S2	G3G4
Calephelis muticum	Swamp Metalmark		E	S1	G3
Callophrys irus	Frosted Elfin		E	S1	G3
Calopteryx dimidiata	Sparkling Jewelwing		E	S1S2	G5
Celithemis verna	Double-ringed Pennant		H	SH	G5
Cheumatopsyche helma	Helma's Net-spinning Caddisfly	SOMC	H	SH	G3
Chlosyne gorgone	Gorgone Checkerspot		T	S1S2	G5
Dannella provonshai	An Ephemerellid Mayfly		H	SH	G3G4
Dryobius sexnotatus	Six-banded Longhorn Beetle	SOMC	T	S2	GNR
Erora laeta	Early Hairstreak		E	S1	GU

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Euphyes dukesi	Dukes' Skipper		T	S2	G3
Gomphurus hybridus	Cocoa Clubtail		E	S1	G4
Habrophlebiodes celeteria	A Leptophlebiid Mayfly		H	SH	G2G4
Hansonoperla hokolesqua	Splendid Stone		S	S2	G2
Hystrichophora loricana	An Olethreutine Moth		T	S1S2	G2G4
Lepidostoma etnieri	A Lepidostomatid Caddisfly		E	S1S2	G1G2Q
Litobrancha recurvata	A Burrowing Mayfly		S	S1	G5
Lordithon niger	Black Lordithon Rove Beetle	SOMC	H	SH	GU
Lytrosis permagnaria	A Geometrid Moth	SOMC	E	S1S2	G3G4
Maccaffertium bednariki	A Heptageniid Mayfly		S	S2	G2G4
Manophylax butleri	Bottle Cap Caddisfly		S	S2	G2
Mesamia straminea	Helianthus Leafhopper		E	S1	GNR
Nannothemis bella	Elfin Skimmer		E	S1	G4G5
Nehalennia irene	Sedge Sprite		E	S1	G5
Nixe flowersi	A Heptageniid Mayfly		H	SH	G1G3
Ophiogomphus aspersus	Brook Snaketail		H	SH	G4
Ophiogomphus howei	Pygmy Snaketail	SOMC	E	S1S2	G3
Ophiogomphus mainensis	Maine Snaketail		E	S1	G4G5
Papaipema beeriana	Blazing Star Stem Borer		T	S2	G2G3
Papaipema eryngii	Rattlesnake-master Borer Moth	C	E	S1	G1G2
Papaipema leucostigma	Columbine Borer Moth		T	S1S2	G4G5
Papaipema silphii	Silphium Borer Moth		E	S1	G3G4
Papaipema sp. 5	Rare Cane Borer Moth		T	S1S2	G1G2
Papaipema speciosissima	Osmunda Borer Moth		T	S2	G4
Phyciodes batesii	Tawny Crescent	SOMC	H	SH	G5
Poanes viator	Broad-winged Skipper		E	S1	G5
Polygonia faunus	Green Comma		H	SH	G5
Polygonia progne	Gray Comma		H	SH	G5
Prairiana kansana	A Cicadellid Leafhopper		E	S1	GNR
Pseudanophthalmus abditus	Concealed Cave Beetle		H	SH	G3
Pseudanophthalmus audax	Bold Cave Beetle	SOMC	H	SH	G1G2
Pseudanophthalmus caecus	Clifton Cave Beetle		T	S1	G1
Pseudanophthalmus calcareus	Limestone Cave Beetle	SOMC	E	S1	G1
Pseudanophthalmus catoryctos	Lesser Adams Cave Beetle		E	S1	G1
Pseudanophthalmus cnephosus	A Cave Obligate Beetle		T	S1S2	G1G2
Pseudanophthalmus conditus	Hidden Cave Beetle	SOMC	T	S1S2	G1G2
Pseudanophthalmus elongatus	A Cave Obligate Beetle		H	SH	G1G2
Pseudanophthalmus exoticus	Exotic Cave Beetle	SOMC	H	SH	G1
Pseudanophthalmus frigidus	Icebox Cave Beetle		E	S1	G1
Pseudanophthalmus globiceps	Round-headed Cave Beetle	SOMC	E	S1	G1
Pseudanophthalmus horni	Garman's Cave Beetle	SOMC	S	S2S3	G3
Pseudanophthalmus hypolithos	Ashcamp Cave Beetle	SOMC	E	S1	G1
Pseudanophthalmus inexpectatus	Surprising Cave Beetle		T	S1S2	G1G2

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Pseudanophthalmus major	Beaver Cave Beetle	SOMC	T	S1	G1
Pseudanophthalmus parvus	Tatum Cave Beetle	SOMC	H	SH	GH
Pseudanophthalmus pholeter	Greater Adams Cave Beetle		E	S1	G1
Pseudanophthalmus pubescens intrepidus	A Cave Obligate Beetle		T	S1S2	G3T3
Pseudanophthalmus puteanus	Old Well Cave Beetle	SOMC	T	S1S2	G1G2
Pseudanophthalmus rogersae	Rogers' Cave Beetle	SOMC	T	S1	G1
Pseudanophthalmus scholasticus	Scholarly Cave Beetle	SOMC	T	S1	G1
Pseudanophthalmus simulans	Cub Run Cave Beetle	SOMC	H	SH	G1
Pseudanophthalmus solivagus	A Cave Obligate Beetle		H	SH	G1G2
Pseudanophthalmus tenebrosus	Stevens Creek Cave Beetle	SOMC	H	SH	G1
Pseudanophthalmus transfluvialis	A Cave Obligate Beetle		H	SH	G1G2
Pseudanophthalmus troglodytes	Louisville Cave Beetle	SOMC	S	S1	G1
Pseudosinella espanita	A Cave Obligate Springtail		S	S1S2	G1
Pygmarrhopalites altus	A Cave Obligate Springtail		H	SH	G2G3
Pygmarrhopalites bimus	A Cave Obligate Springtail		H	SH	G3G4
Raptoheptagenia cruentata	A Heptageniid Mayfly		H	SH	G4
Rasvena terna	Vermont Sallfly		S	S1S3	G4
Rhyacophila appalachia	A Rhyacophilid Caddisfly		H	SH	G3
Satyrium favonius ontario	Northern Oak Hairstreak		S	S2	G4G5T4
Soyedina calcarea	A Nemourid Stonefly		E	S1	G1
Stylurus notatus	Elusive Clubtail	SOMC	E	S1	G3
Stylurus scudderi	Zebra Clubtail		E	S1S2	G5
Tomocerus missus	A Cave Obligate Springtail		T	S1S2	G4
Traverella lewisi	A Leptophlebiid Mayfly		H	SH	G1G3
Tychobythinus hubrichti	A Cave Obligate Beetle		H	SH	G1G2
Other Invertebrates					
Belba bulbipedata	A Cave Obligate Mite		H	SH	G1
Galumna alata	A Cave Obligate Mite		H	SH	G1G2
Geocentrophora cavernicola	A Cave Obligate Planarian		T	S1S2	G1G2
Hesperonemastoma inops	A Cave Obligate Harvestman		H	SH	G1G2
Kleptochthonius attenuatus	A Cave Obligate Pseudoscorpion		H	SH	G1
Kleptochthonius cerberus	A Cave Obligate Pseudoscorpion		H	SH	G1
Kleptochthonius erebicus	A Cave Obligate Pseudoscorpion		H	SH	G1
Kleptochthonius hageni	A Cave Obligate Pseudoscorpion		S	S1S2	G1G2
Kleptochthonius hubrichti	A Cave Obligate Pseudoscorpion		H	SH	G1G2
Kleptochthonius microphthalmus	A Cave Obligate Pseudoscorpion		H	SH	G1G2
Macrocheles stygius	A Cave Obligate Mite		H	SH	G1G2
Macrocheles troglodytes	A Cave Obligate Mite		H	SH	G1G2
Pseudotremia amphiorax	A Cave Obligate Milliped		H	SH	G1G2
Pseudotremia carterensis	A Cave Obligate Milliped		S	S1S2	G2G3
Pseudotremia merops	A Cave Obligate Milliped		H	SH	G1
Pseudotremia spira	A Cave Obligate Milliped		S	S1S2	G1
Pseudotremia unca	A Cave Obligate Milliped		H	SH	G1

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Sphalloplana buchanani	A Cave Obligate Planarian		T	S1S2	G1G2
Tyrannochthonius hypogeus	A Cave Obligate Pseudoscorpion		S	S1S2	G1
Fishes					
Acipenser fulvescens	Lake Sturgeon	SOMC	E	S1	G3G4
Alosa alabamae	Alabama Shad	SOMC	E	S1	G2G3
Amblyopsis spelaea	Northern Cavefish	SOMC	S	S3	G2G3
Ammocrypta clara	Western Sand Darter	SOMC	E	S1	G3
Atractosteus spatula	Alligator Gar	SOMC	E	S1	G3G4
Chrosomus cumberlandensis	Blackside Dace	LT	T	S2	G2
Cyprinella camura	Bluntface Shiner		E	S1	G5
Cyprinella venusta	Blacktail Shiner		S	S3	G5
Erimystax insignis	Blotched Chub	SOMC	E	S1	G4
Erimyzon sucetta	Lake Chubsucker		T	S2	G5
Esox niger	Chain Pickerel		S	S3	G5
Etheostoma chienense	Relict Darter	LE	E	S1	G1
Etheostoma fusiforme	Swamp Darter		E	S1	G5
Etheostoma lemniscatum	Tuxedo Darter	LE	E	S1	G1
Etheostoma lynceum	Brighteye Darter		E	S1	G5
Etheostoma maculatum	Spotted Darter	SOMC	T	S2	G2G3
Etheostoma maydeni	Redlips Darter	SOMC	S	S3	GNR
Etheostoma microlepidum	Smallscale Darter	SOMC	E	S1	G2G3
Etheostoma nebra	Buck Darter		E	S1	G1
Etheostoma parvipinne	Goldstripe Darter		E	S1	G4G5
Etheostoma proeliare	Cypress Darter		T	S2	G5
Etheostoma pyrrhogaster	Firebelly Darter	SOMC	E	S1	G2G3
Etheostoma sagitta	Cumberland Arrow Darter		S	S3	G3
Etheostoma spilotum	Kentucky Arrow Darter	LT	T	S2	G2G3
Etheostoma susanae	Cumberland Darter	LE	E	S1	G1G2
Etheostoma swaini	Gulf Darter		E	S1	G5
Etheostoma tecumsehi	Shawnee Darter	SOMC	S	S2S3	G2G3
Fundulus chrysotus	Golden Topminnow		E	S1	G5
Fundulus dispar	Starhead Topminnow		E	S1	G4
Hemitremia flammea	Flame Chub		E	S1	G3
Hybognathus hayi	Cypress Minnow		E	S1	G4G5
Hybognathus placitus	Plains Minnow	SOMC	S	S1	G4
Hybopsis amnis	Pallid Shiner	SOMC	E	S1	G4
Ichthyomyzon castaneus	Chestnut Lamprey		S	S2	G4
Ichthyomyzon fossor	Northern Brook Lamprey		T	S2	G4
Ichthyomyzon gagei	Southern Brook Lamprey		E	S1	G5
Ichthyomyzon greeleyi	Mountain Brook Lamprey		T	S2	G4
Ictiobus niger	Black Buffalo		S	S3	G5
Lampetra sp. 1	Undescribed Terrapin Creek brook lamprey		E	S1	GNR
Lepomis marginatus	Dollar Sunfish		E	S1	G5

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Lepomis miniatus	Redspotted Sunfish		T	S2	G5
Lethenteron appendix	American Brook Lamprey		T	S2	G4
Lota lota	Burbot		S	S2	G5
Macrhybopsis gelida	Sturgeon Chub		E	S1	G3
Macrhybopsis meeki	Sicklefin Chub		E	S1	G3
Menidia audens	Inland Silverside		T	S2	G5
Moxostoma poecilurum	Blacktail Redhorse		E	S1	G5
Nocomis biguttatus	Hornyhead Chub		S	S2	G5
Notropis albizonatus	Palezone Shiner	LE	E	S1	G1
Notropis dorsalis	Bigmouth Shiner		S	S3	G5
Notropis hudsonius	Spottail Shiner		S	S2	G5
Notropis maculatus	Taillight Shiner		T	S2S3	G5
Notropis sp. 4	Sawfin Shiner		E	S1	G4
Noturus exilis	Slender Madtom		E	S1	G5
Noturus hildebrandi	Least Madtom		E	S1	G5
Noturus phaeus	Brown Madtom		E	S1	G4
Noturus stigmosus	Northern Madtom	SOMC	S	S2S3	G3
Percina macrocephala	Longhead Darter	SOMC	E	S1	G3
Percina squamata	Olive Darter	SOMC	E	S1	G3
Percopsis omiscomaycus	Trout-perch	SOMC	S	S3	G5
Phenacobius uranops	Stargazing Minnow		S	S2S3	G4
Platygobio gracilis	Flathead Chub	SOMC	S	S1	G5
Scaphirhynchus albus	Pallid Sturgeon	LE	E	S1	G2
Thoburnia atripinnis	Blackfin Sucker	SOMC	S	S2	G3
Typhlichthys subterraneus	Southern Cavefish	SOMC	S	S2S3	G4
Umbra limi	Central Mudminnow		T	S2S3	G5
Amphibians					
Amphiuma tridactylum	Three-toed Amphiuma		E	S1	G5
Cryptobranchus alleganiensis alleganiensis	Eastern Hellbender	SOMC	S	S2S3	G3T2
Eurycea guttolineata	Three-lined Salamander		T	S2	G5
Hyla versicolor	Gray Treefrog		S	S2S3	G5
Lithobates areolatus circulosus	Northern Crawfish Frog		S	S3	G4T4
Lithobates blairi	Plains Leopard Frog		E	S1	G5
Lithobates pipiens	Northern Leopard Frog		S	S3	G5
Plethodon cinereus	Redback Salamander		S	S2S3	G5
Plethodon wehrlei	Wehrle's Salamander		E	S1	G4
Reptiles					
Aspidoscelis sexlineata	Six-lined Racerunner		S	S3	G5
Cemophora coccinea	Scarlet Snake		S	S3	G5
Chrysemys dorsalis	Southern Painted Turtle		T	S2	G5
Clonophis kirtlandii	Kirtland's Snake	SOMC	T	S2	G2
Farancia abacura reinwardtii	Western Mud Snake		S	S3	G5T5
Lampropeltis elapsoides	Scarlet Kingsnake		E	S1	G5

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Macrochelys temminckii	Alligator Snapping Turtle	SOMC	E	S1	G3G4
Nerodia cyclopion	Green Water Snake		E	S1	G5
Nerodia fasciata confluens	Broad-banded Water Snake		E	S1	G5T5
Ophisaurus attenuatus longicaudus	Eastern Slender Glass Lizard		T	S2	G5T5
Pantherophis guttatus	Corn Snake		S	S3	G5
Pituophis melanoleucus melanoleucus	Northern Pine Snake	SOMC	E	S1	G4T4
Plestiodon anthracinus	Coal Skink		E	S1	G5
Plestiodon inexpectatus	Southeastern Five-lined Skink		S	S2S3	G5
Sistrurus miliarius streckeri	Western Pygmy Rattlesnake		E	S1	G5T5
Tantilla coronata	Southeastern Crowned Snake		T	S2	G5
Thamnophis proximus proximus	Western Ribbon Snake		E	S1	G5T5
Thamnophis sauritus sauritus	Eastern Ribbon Snake		S	S3	G5T5
Breeding Birds					
Accipiter striatus	Sharp-shinned Hawk		S	S3B,S4N	G5
Actitis macularius	Spotted Sandpiper		E	S1B	G5
Ardea alba	Great Egret		T	S2B	G5
Asio flammeus	Short-eared Owl		E	S1B,S2N	G5
Asio otus	Long-eared Owl		E	S1B,S1S2N	G5
Bartramia longicauda	Upland Sandpiper		H	SHB	G5
Botaurus lentiginosus	American Bittern		H	SHB	G5
Bubulcus ibis	Cattle Egret		S	S1S2B	G5
Cardellina canadensis	Canada Warbler		S	S3B	G5
Centronyx henslowii	Henslow's Sparrow	SOMC	S	S3B	G4
Certhia americana	Brown Creeper		T	S1S2B,S4S5N	G5
Chondestes grammacus	Lark Sparrow		S	S2S3B	G5
Circus hudsonius	Northern Harrier		T	S1S2B,S4N	G5
Cistothorus platensis	Sedge Wren		S	S3B	G5
Corvus corax	Common Raven		T	S1S2	G5
Corvus ossifragus	Fish Crow		S	S3B	G5
Dolichonyx oryzivorus	Bobolink		S	S2S3B	G5
Egretta caerulea	Little Blue Heron		E	S1B	G5
Egretta thula	Snowy Egret		E	S1B	G5
Empidonax minimus	Least Flycatcher		E	S1B	G5
Falco peregrinus	Peregrine Falcon	SOMC	E	S1B	G4
Fulica americana	American Coot		E	S1B	G5
Gallinula galeata	Common Gallinule		T	S1S2B	G5
Haliaeetus leucocephalus	Bald Eagle	Delisted	S	S3B,S3S4N	G5
Ictinia mississippiensis	Mississippi Kite		S	S2S3B	G5
Ixobrychus exilis	Least Bittern		T	S1S2B	G4G5
Junco hyemalis	Dark-eyed Junco		S	S2S3B,S5N	G5
Lanius ludovicianus	Loggerhead Shrike	SOMC	S	S3S4B,S4N	G4
Lophodytes cucullatus	Hooded Merganser		T	S2B,S3S4N	G5
Nyctanassa violacea	Yellow-crowned Night-heron		T	S2B	G5

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Nycticorax nycticorax	Black-crowned Night-heron		T	S1S2B	G5
Pandion haliaetus	Osprey		S	S3S4B	G5
Passerculus sandwichensis	Savannah Sparrow		S	S2S3B,S2S3N	G5
Peucaea aestivalis	Bachman's Sparrow	SOMC	E	S1B	G3
Phalacrocorax auritus	Double-crested Cormorant		S	S2B	G5
Pheucticus ludovicianus	Rose-breasted Grosbeak		S	S3S4B	G5
Podilymbus podiceps	Pied-billed Grebe		E	S1B,S4N	G5
Pooecetes gramineus	Vesper Sparrow		E	S1B	G5
Rallus elegans	King Rail		E	S1B	G4
Riparia riparia	Bank Swallow		S	S3B	G5
Setophaga fusca	Blackburnian Warbler		T	S1S2B	G5
Sitta canadensis	Red-breasted Nuthatch		E	S1B	G5
Spatula clypeata	Northern Shoveler		E	S1B	G5
Spatula discors	Blue-winged Teal		T	S1S2B	G5
Sternula antillarum athalassos	Interior Least Tern	LE	E	S1S2B	G4T3Q
Thryomanes bewickii	Bewick's Wren	SOMC	H	SHB	G5
Tyto alba	Barn Owl		S	S3	G5
Vermivora chrysoptera	Golden-winged Warbler	SOMC	E	S1B	G4
Vireo bellii	Bell's Vireo	SOMC	S	S2S3B	G5
Mammals					
Corynorhinus rafinesquii	Rafinesque's Big-eared Bat	SOMC	S	S3	G3G4
Corynorhinus townsendii virginianus	Virginia Big-eared Bat	LE	E	S1	G4T4
Mustela nivalis	Least Weasel		S	S2S3	G5
Myodes gapperi maurus	Kentucky Red-backed Vole	SOMC	S	S3	G5T3T4
Myotis austroriparius	Southeastern Myotis	SOMC	S	S3	G4
Myotis grisescens	Gray Myotis	LE	T	S2	G4
Myotis leibii	Eastern Small-footed Myotis	SOMC	T	S2	G4
Myotis lucifugus	Little Brown Bat		T	S2	G3
Myotis septentrionalis	Northern Long-Eared Bat	LT	E	S1	G1G2
Myotis sodalis	Indiana Bat	LE	E	S1S2	G2
Perimyotis subflavus	Tricolored Bat		T	S2	G2G3
Peromyscus gossypinus	Cotton Mouse		T	S2	G5
Sorex cinereus	Cinereus Shrew		S	S3	G5
Sorex dispar blitchi	Long-tailed Shrew		E	S1	G4T3T4
Spilogale putorius	Eastern Spotted Skunk		S	S2S3	G4
Communities					
Acid seep/bog			S	S2S3	GNR
Appalachian seep/bog			T	S1S2	GNR
Bluegrass mesophytic cane forest			E	S1	GNR
Bluegrass woodland			E	S1	GNR
Bottomland hardwood forest			S	S3	GNR
Bottomland lake			S	S2S3	GNR
Bottomland marsh			T	S1S2	GNR

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Bottomland ridge/terrace forest			E	S1	GNR
Bottomland slough			T	S2	GNR
Calcareous seep/bog			E	S1	GNR
Coastal Plain forested acid seep			E	S1	GNR
Coastal Plain mesophytic cane forest			T	S2S3	GNR
Coastal Plain slough			T	S2	GNR
Cumberland Mountains pitch pine woodland			E	S1	GNR
Cumberland Plateau gravel/cobble bar			E	S1S2	GNR
Cumberland Plateau sandstone glade			E	S1	GNR
Cumberland highlands forest			E	S1	G2
Cypress (tupelo) swamp			E	S1	GNR
Dolomite glade			E	S1	GNR
Limestone barrens (open woodland)			T	S2	GNR
Limestone flat rock glade			E	S1	GNR
Limestone slope glade			S	S2S3	GNR
Limestone/dolomite prairie			E	S1	GNR
Sand bar			S	S3?	GNR
Sandstone barrens (open woodland)			E	S1	GNR
Sandstone prairie			E	S1	GNR
Shawnee Hills sandstone glade			T	S1S2	GNR
Shrub swamp			T	S2S3	GNR
Sinkhole/depression marsh			E	S1S2	GNR
Sinkhole/depression pond			T	S2	GNR
Tallgrass prairie			E	S1	GNR
Wet bottomland hardwood forest			T	S2	GNR
Wet depression/sinkhole forest			T	S1S2	GNR
Wet meadow			E	S1	GNR
Wet prairie			E	S1	GNR
Xerohydric flatwoods			E	S1S2	GNR

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LETTER

doi:10.1038/nature12914

Rate of tree carbon accumulation increases continuously with tree size

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Forests are major components of the global carbon cycle, providing substantial feedback to atmospheric greenhouse gas concentrations[1]. Our ability to understand and predict changes in the forest carbon cycle—particularly net primary productivity and carbon storage—increasingly relies on models that represent biological processes across several scales of biological organization, from tree leaves to forest stands[2,3]. Yet, despite advances in our understanding of productivity at the scales of leaves and stands, no consensus exists about the nature of productivity at the scale of the individual tree[4–7], in part because we lack a broad empirical assessment of whether rates of absolute tree mass growth (and thus carbon accumulation) decrease, remain constant, or increase as trees increase in size and age. Here we present a global analysis of 403 tropical and temperate tree species, showing that for most species mass growth rate increases continuously with tree size. Thus, large, old trees do not act simply as senescent carbon reservoirs but actively fix large amounts of carbon compared to smaller trees; at the extreme, a single big tree can add the same amount of carbon to the forest within a year as is contained in an entire mid-sized tree. The apparent paradoxes of individual tree growth increasing with tree size despite declining leaf-level[8–10] and stand-level[10] productivity can be explained, respectively, by increases in a tree's total leaf area that outpace declines in productivity per unit of leaf area and, among other factors, age-related reductions in population density. Our results resolve conflicting assumptions about the nature of tree growth, inform efforts to undertand and model forest carbon dynamics, and have additional implications for theories of resource allocation[11] and plant senescence[12].

A widely held assumption is that after an initial period of increasing growth, the mass growth rate of individual trees declines with increasing tree size[4,5,13–16]. Although the results of a few single-species studies have been consistent with this assumption[15], the bulk of evidence cited in support of declining growth is not based on measurements of individual tree mass growth. Instead, much of the cited evidence documents either the well-known age-related decline in net primary productivity (hereafter 'productivity') of even-aged forest stands[10] (in which the trees are all of a similar age) or size-related declines in the rate of mass gain per unit leaf area (or unit leaf mass)[8–10], with the implicit assumption that declines at these scales must also apply at the scale of the individual tree. Declining tree growth is also sometimes inferred from life-history theory to be a necessary corollary of increasing resource allocation to reproduction[11,16]. On the other hand, metabolic scaling theory predicts that mass growth rate should increase continuously with tree size[6], and this prediction has also received empirical support from a few site-specific studies[6,7]. Thus, we are confronted with two conflicting generalizations about the fundamental nature of tree growth, but lack a global assessment that would allow us to distinguish clearly between them.

To fill this gap, we conducted a global analysis in which we directly estimated mass growth rates from repeated measurements of 673,046 trees belonging to 403 tropical, subtropical and temperate tree species, spanning every forested continent. Tree growth rate was modelled as a function of log(tree mass) using piecewise regression, where the independent variable was divided into one to four bins. Conjoined line segments were fitted across the bins (Fig. 1).

For all continents, aboveground tree mass growth rates (and, hence, rates of carbon gain) for most species increased continuously with tree mass (size) (Fig. 2). The rate of mass gain increased with tree mass in each model bin for 87% of species, and increased in the bin that included the largest trees for 97% of species; the majority of increases were statistically significant (Table 1, Extended Data Fig. 1 and Supplementary Table 1). Even when we restricted our analysis to species achieving the largest sizes (maximum trunk diameter >100 cm; 33% of species), 94% had increasing mass growth rates in the bin that included the largest trees. We found no clear taxonomic or geographic patterns among the 3% of species with declining growth rates in their largest trees, although the small number of these species (thirteen) hampers inference. Declining species included both angiosperms and gymnosperms in seven of the 76 families in our study; most of the seven families had only one or two declining species and no family was dominated by declining species (Supplementary Table 1).

When we log-transformed mass growth rate in addition to tree mass, the resulting model fits were generally linear, as predicted by metabolic scaling theory[6] (Extended Data Fig. 2). Similar to the results of our main

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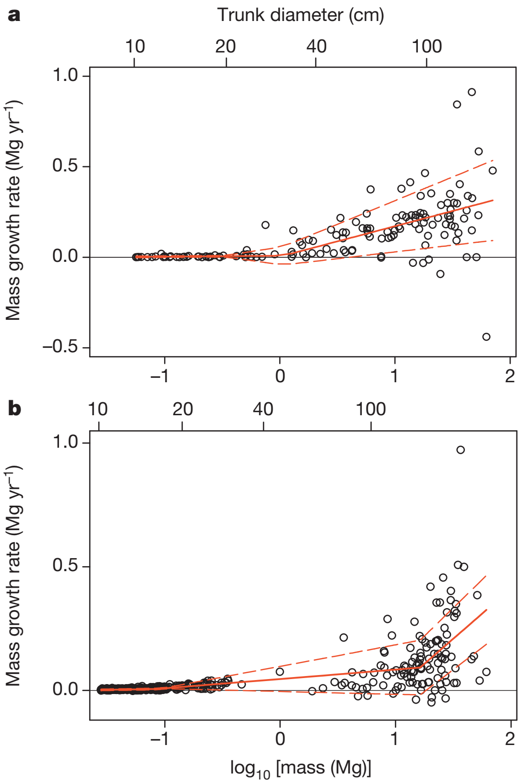

Figure 1 | Example model fits for tree mass growth rates. The species shown are the angiosperm species (*Lecomtedoxa klaineana*, Cameroon, 142 trees) (**a**) and gymnosperm species (*Picea sitchensis*, USA, 409 trees) (**b**) in our data set that had the most massive trees (defined as those with the greatest cumulative aboveground dry mass in their five most massive trees). Each point represents a single tree; the solid red lines represent best fits selected by our model; and the dashed red lines indicate one standard deviation around the predicted values.

analysis using untransformed growth, of the 381 log-transformed species analysed (see Methods), the log-transformed growth rate increased in the bin containing the largest trees for 96% of species.

In absolute terms, trees 100 cm in trunk diameter typically add from 10 kg to 200 kg of aboveground dry mass each year (depending on species), averaging 103 kg per year. This is nearly three times the rate for trees of the same species at 50 cm in diameter, and is the mass equivalent to adding an entirely new tree of 10–20 cm in diameter to the forest each year. Our findings further indicate that the extraordinary growth recently reported in an intensive study of large *Eucalyptus regnans* and *Sequoia sempervirens*[7], which included some of the world's most massive individual trees, is not a phenomenon limited to a few unusual species. Rather, rapid growth in giant trees is the global norm, and can exceed 600 kg per year in the largest individuals (Fig. 3).

Our data set included many natural and unmanaged forests in which the growth of smaller trees was probably reduced by asymmetric competition with larger trees. To explore the effects of competition, we calculated mass growth rates for 41 North American and European species that had published equations for diameter growth rate in the absence of competition. We found that, even in the absence of competition, 85% of the species had mass growth rates that increased continuously with tree size (Extended Data Fig. 3), with growth curves closely resembling those in Fig. 2. Thus, our finding of increasing growth not only has broad generality across species, continents and forest biomes (tropical, subtropical and temperate), it appears to hold regardless of competitive environment.

Importantly, our finding of continuously increasing growth is compatible with the two classes of observations most often cited as evidence of declining, rather than increasing, individual tree growth: with increasing tree size and age, productivity usually declines at the scales of both tree organs (leaves) and tree populations (even-aged forest stands).

First, although growth efficiency (tree mass growth per unit leaf area or leaf mass) often declines with increasing tree size[8–10], empirical observations and metabolic scaling theory both indicate that, on average, total tree leaf mass increases as the square of trunk diameter[17,18]. A typical tree that experiences a tenfold increase in diameter will therefore undergo a roughly 100-fold increase in total leaf mass and a 50–100-fold

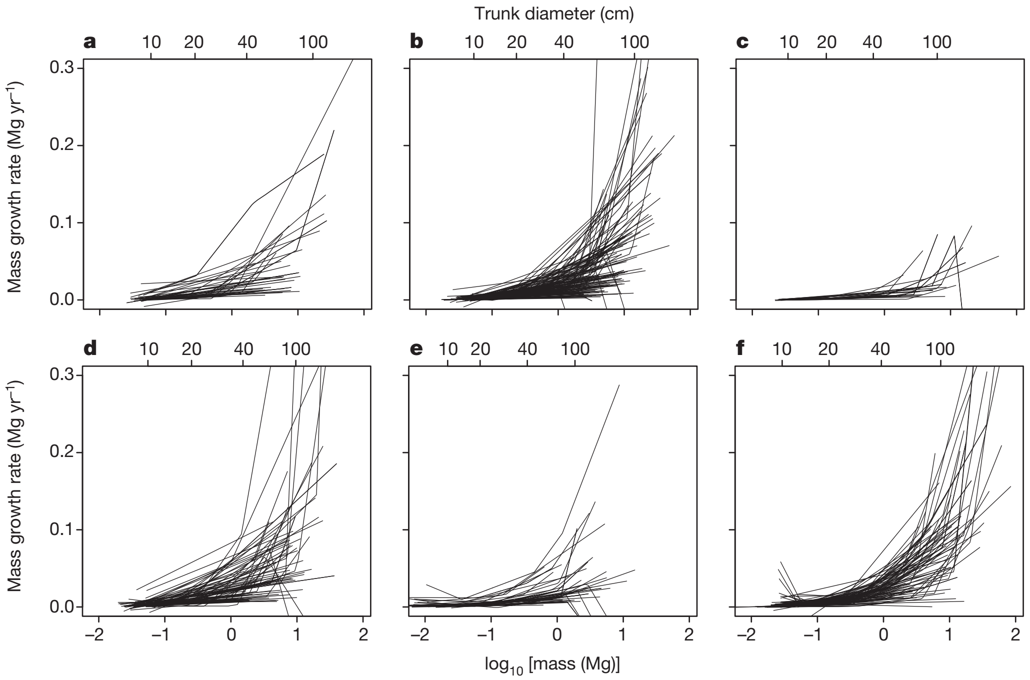

Figure 2 | Aboveground mass growth rates for the 403 tree species, by continent. **a**, Africa (Cameroon, Democratic Republic of the Congo); **b**, Asia (China, Malaysia, Taiwan, Thailand); **c**, Australasia (New Zealand); **d**, Central and South America (Argentina, Colombia, Panama); **e**, Europe (Spain); and **f**, North America (USA). Numbers of trees, numbers of species and percentages with increasing growth are given in Table 1. Trunk diameters are approximate values for reference, based on the average diameters of trees of a given mass.

Table 1 | Sample sizes and tree growth trends by continent

Continent	Number of trees	Number of species	Percentage of species with increasing mass growth rate in the largest trees (percentage significant at $P \leq 0.05$)
Africa	15,366	37	100.0 (86.5)
Asia	43,690	136	96.3 (89.0)
Australasia	45,418	22	95.5 (95.5)
Central and South America	18,530	77	97.4 (92.2)
Europe	439,889	42	90.5 (78.6)
North America	110,153	89	98.9 (94.4)
Total	673,046	403	96.8 (89.8)

The largest trees are those in the last bin fitted by the model. Countries are listed in the legend for Fig. 2.

increase in total leaf area (depending on size-related increases in leaf mass per unit leaf area[19,20]). Parallel changes in growth efficiency can range from a modest increase (such as in stands where small trees are suppressed by large trees)[21] to as much as a tenfold decline[22], with most changes falling in between[8,9,19,22]. At one extreme, the net effect of a low (50-fold) increase in leaf area combined with a large (tenfold) decline in growth efficiency would still yield a fivefold increase in individual tree mass growth rate; the opposite extreme would yield roughly a 100-fold increase. Our calculated 52-fold greater average mass growth rate of trees 100 cm in diameter compared to those 10 cm in diameter falls within this range. Thus, although growth efficiency often declines with increasing tree size, increases in a tree's total leaf area are sufficient to overcome this decline and cause whole-tree carbon accumulation rate to increase.

Second, our findings are similarly compatible with the well-known age-related decline in productivity at the scale of even-aged forest stands. Although a review of mechanisms is beyond the scope of this paper[10,23], several factors (including the interplay of changing growth efficiency and tree dominance hierarchies[24]) can contribute to declining productivity at the stand scale. We highlight the fact that increasing individual tree growth rate does not automatically result in increasing stand productivity because tree mortality can drive orders-of-magnitude reductions in population density[25,26]. That is, even though the large trees in older, even-aged stands may be growing more rapidly, such stands have fewer trees. Tree population dynamics, especially mortality, can thus be a significant contributor to declining productivity at the scale of the forest stand[23].

For a large majority of species, our findings support metabolic scaling theory's qualitative prediction of continuously increasing growth at the scale of individual trees[6], with several implications. For example, life-history theory often assumes that tradeoffs between plant growth and reproduction are substantial[11]. Contrary to some expectations[11,16], our results indicate that for most tree species size-related changes in reproductive allocation are insufficient to drive long-term declines in growth rates[6]. Additionally, declining growth is sometimes considered to be a defining feature of plant senescence[12]. Our findings are thus relevant to understanding the nature and prevalence of senescence in the life history of perennial plants[27].

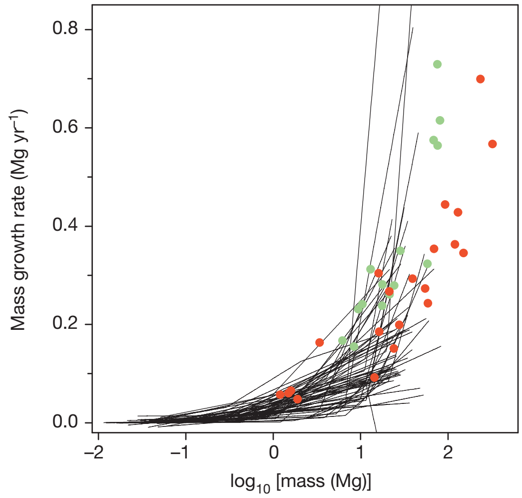

Figure 3 | Aboveground mass growth rates of species in our data set compared with *E. regnans* and *S. sempervirens*. For clarity, only the 58 species in our data set having at least one tree exceeding 20 Mg are shown (lines). Data for *E. regnans* (green dots, 15 trees) and *S. sempervirens* (red dots, 21 trees) are from an intensive study that included some of the most massive individual trees on Earth[7]. Both axes are expanded relative to those of Fig. 2.

Finally, our results are relevant to understanding and predicting forest feedbacks to the terrestrial carbon cycle and global climate system[1–3]. These feedbacks will be influenced by the effects of climatic, land-use and other environmental changes on the size-specific growth rates and size structure of tree populations—effects that are already being observed in forests[28,29]. The rapid growth of large trees indicates that, relative to their numbers, they could play a disproportionately important role in these feedbacks[30]. For example, in our western USA old-growth forest plots, trees >100 cm in diameter comprised 6% of trees, yet contributed 33% of the annual forest mass growth. Mechanistic models of the forest carbon cycle will depend on accurate representation of productivity across several scales of biological organization, including calibration and validation against continuously increasing carbon accumulation rates at the scale of individual trees.

METHODS SUMMARY

We estimated aboveground dry mass growth rates from consecutive diameter measurements of tree trunks—typically measured every five to ten years—from long-term monitoring plots. Analyses were restricted to trees with trunk diameter ≥10 cm, and to species having ≥40 trees in total and ≥15 trees with trunk diameter ≥30 cm. Maximum trunk diameters ranged from 38 cm to 270 cm among species, averaging 92 cm. We converted each diameter measurement (plus an accompanying height measurement for 16% of species) to aboveground dry mass, M, using published allometric equations. We estimated tree growth rate as $G = \Delta M/\Delta t$ and modelled G as a function of $\log(M)$ for each species using piecewise regression. The independent variable $\log(M)$ was divided into bins and a separate line segment was fitted to G versus $\log(M)$ in each bin so that the line segments met at the bin divisions. Bin divisions were not assigned a priori, but were fitted by the model separately for each species. We fitted models with 1, 2, 3 and 4 bins, and selected the model receiving the most support by Akaike's Information Criterion for each species. Our approach thus makes no assumptions about the shape of the relationship between G and $\log(M)$, and can accommodate increasing, decreasing or hump-shaped relationships. Parameters were fitted with a Gibbs sampler based on Metropolis updates, producing credible intervals for model parameters and growth rates at any diameter; uninformative priors were used for all parameters. We tested extensively for bias, and found no evidence that our results were influenced by model fits failing to detect a final growth decline in the largest trees, possible biases introduced by the 47% of species for which we combined data from several plots, or possible biases introduced by allometric equations (Extended Data Figs 4 and 5).

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 5 August; accepted 27 November 2013.

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Supplementary Information is available in the online version of the paper.

Acknowledgements We thank the hundreds of people who have established and maintained the forest plots and their associated databases; M. G. Ryan for comments on the manuscript; C. D. Canham and T. Hart for supplying data; C. D. Canham for discussions and feedback; J. S. Baron for hosting our workshops; and Spain's Ministerio de Agricultura, Alimentación y Medio Ambiente (MAGRAMA) for granting access to the Spanish Forest Inventory Data. Our analyses were supported by the United States Geological Survey (USGS) John Wesley Powell Center for Analysis and Synthesis, the USGS Ecosystems and Climate and Land Use Change mission areas, the Smithsonian Institution Global Earth Observatory—Center for Tropical Forest Science (CTFS), and a University of Nebraska-Lincoln Program of Excellence in Population Biology Postdoctoral Fellowship (to N.G.B.). In addition, X.W. was supported by National Natural Science Foundation of China (31370444) and State Key Laboratory of Forest and Soil Ecology (LFSE2013-11). Data collection was funded by a broad range of organizations including the USGS, the CTFS, the US National Science Foundation, the Andrews LTER (NSF-LTER DEB-0823380), the US National Park Service, the US Forest Service (USFS), the USFS Forest Inventory and Analysis Program, the John D. and Catherine T. MacArthur Foundation, the Andrew W. Mellon Foundation, MAGRAMA, the Council of Agriculture of Taiwan, the National Science Council of Taiwan, the National Natural Science Foundation of China, the Knowledge Innovation Program of the Chinese Academy of Sciences, Landcare Research and the National Vegetation Survey Database (NVS) of New Zealand, the French Fund for the Global Environment and Fundación ProYungas. This paper is a contribution from the Western Mountain Initiative, a USGS global change research project. Any use of trade names is for descriptive purposes only and does not imply endorsement by the USA government.

Author Contributions N.L.S. and A.J.D. conceived the study with feedback from R.C. and D.A.C., N.L.S., A.J.D., R.C. and S.E.R. wrote the manuscript. R.C. devised the main analytical approach and wrote the computer code. N.L.S., A.J.D., R.C., S.E.R., P.J.B., N.G.B., D.A.C., E.R.L., W.K.M. and N.R. performed analyses. N.L.S., A.J.D., R.C., S.E.R., P.J.B., D.A.C., E.R.L., W.K.M., E.Á., C.B., S.B., G.C., S.J.D., Á.D., C.N.E., O.F., J.F.F., H.R.G., Z.H., M.E.H., S.P.H., D.K., Y.L., J.-R.M., A.M., L.R.M., R.J.P., N.P., S.-H.S., I-F.S., S.T., D.T., P.J.v.M., X.W., S.K.W. and M.A.Z. supplied data and sources of allometric equations appropriate to their data.

Author Information Fitted model parameters for each species have been deposited in USGS's ScienceBase at http://dx.doi.org/10.5066/F7JS9NFM. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to N.L.S. (nstephenson@usgs.gov).

METHODS

Data. We required that forest monitoring plots provided unbiased samples of all living trees within the plot boundaries, and that the trees had undergone two trunk diameter measurements separated by at least one year. Some plots sampled minimally disturbed old (all-aged) forest, whereas others, particularly those associated with national inventories, sampled forest stands regardless of past management history. Plots are described in the references cited in Supplementary Table 1.

Our raw data were consecutive measurements of trunk diameter, D, with most measurements taken 5 to 10 years apart (range, 1–29 years). D was measured at a standard height on the trunk (usually 1.3–1.4 m above ground level), consistent across measurements for a tree. Allometric equations for 16% of species required, in addition to consecutive measurements of D, consecutive measurements of tree height.

We excluded trees exhibiting extreme diameter growth, defined as trunks where D increased by $\geq 40\,\mathrm{mm\,yr^{-1}}$ or that shrank by $\geq 12s$, where s is the standard deviation of the D measurement error, $s = 0.9036 + 0.006214D$ (refs 31, 32); outliers of these magnitudes were almost certainly due to error. By being so liberal in allowing negative growth anomalies, we erred on the side of reducing our ability to detect increases in tree mass growth rate. Using other exclusion values yielded similar results, as did a second approach to handling error in which we reanalysed a subset of our models using a Bayesian method that estimates growth rates after accounting for error, based on independent plot-specific data quantifying measurement error[33].

To standardize minimum D among data sets, we analysed only trees with $D \geq 10$ cm at the first census. To ensure adequate samples of trees spanning a broad range of sizes, we restricted analyses to species having both ≥40 trees in total and also ≥15 trees with $D \geq 30$ cm at the first census. This left us with 673,046 trees belonging to 403 tropical and temperate species in 76 families, spanning twelve countries and all forested continents (Supplementary Table 1). Maximum trunk diameters ranged from 38 cm to 270 cm among species, and averaged 92 cm.

Estimating tree mass. To estimate each tree's aboveground dry mass, M, we used published allometric equations relating M to D (or for 16% of species, relating M to D and tree height). Some equations were species-specific and others were specific to higher taxonomic levels or forest types, described in the references in Supplementary Table 1. The single tropical moist forest equation of ref. 34 was applied to most tropical species, whereas most temperate species had unique species-specific equations. Most allometric equations are broadly similar, relating log(M) to log(D) linearly, or nearly linearly—a familiar relationship in allometric scaling of both animals and plants[35]. Equations can show a variety of differences in detail, however, with some adding log(D) squared and cubed terms. All equations make use of the wood density of individual species, but when wood density was not available for a given species we used mean wood density for a genus or family[36].

Using a single, average allometry for most tropical species, and mean wood density for a genus or family for several species, limits the accuracy of our estimates of M. However, because we treat each species separately, it makes no difference whether our absolute M estimates are more accurate in some species than in others, only that they are consistent within a species and therefore accurately reveal whether mass growth rates increase or decrease with tree size.

For two regions—Spain and the western USA—allometric equations estimated mass only for a tree's main stem rather than all aboveground parts, including branches and leaves. But because leaf and stem masses are positively correlated and their growth rates are expected to scale isometrically both within and among species[18,37,38], results from these two regions should not alter our qualitative conclusions. Confirming this, the percentage of species with increasing stem mass growth rate in the last bin for Spain and the western USA (93.4% of 61 species) was similar to that from the remainder of regions (97.4% of 342 species) ($P = 0.12$, Fisher's exact test).

Modelling mass growth rate. We sought a modelling approach that made no assumptions about the shape of the relationship between aboveground dry mass growth rate, G, and aboveground dry mass, M, and that could accommodate monotonically increasing, monotonically decreasing, or hump-shaped relationships. We therefore chose to model G as a function of log(M) using piecewise linear regression. The range of the x axis, $X = \log(M)$, is divided into a series of bins, and within each bin G is fitted as a function of X by linear regression. The position of the bins is adaptive: it is fitted along with the regression terms. Regression lines are required to meet at the boundary between bins. For a single model-fitting run the number of bins, B, is fixed. For example, if $B = 2$, there are four parameters to be fitted for a single species: the location of the boundary between bins, X_1; the slope of the regression in the first bin, S_1; the slope in the second bin, S_2; and an intercept term. Those four parameters completely define the model. In general, there are $2B$ parameters for B bins.

Growth rates, while approximately normally distributed, were heteroskedastic, with the variance increasing with mass (Fig. 1), so an additional model was needed for the standard deviation of G, σ_G, as a function of log(M). The increase of σ_G with log(M) was clearly not linear, so we used a three-parameter model:

$$\sigma_G = k \qquad (\text{for } \log(M) < d)$$

$$\sigma_G = a + b\log(M) \qquad (\text{for } \log(M) \geq d)$$

where the intercept a is determined by the values of k, d and b. Thus σ_G was constant for smaller values of log(M) (below the cutoff d), then increased linearly for larger log(M) (Fig. 1). The parameters k, d and b were estimated along with the parameters of the growth model.

Parameters of both the growth and standard deviation models were estimated in a Bayesian framework using the likelihood of observing growth rates given model predictions and the estimated standard deviation of the Gaussian error function. A Markov chain Monte Carlo chain of parameter estimates was created using a Gibbs sampler with a Metropolis update[39,40] written in the programming language R (ref. 41) (a tutorial and the computer code are available through http://ctfs.arnarb.harvard.edu/Public/CTFSRPackage/files/tutorials/growthfitAnalysis). The sampler works by updating each of the parameters in sequence, holding other parameters fixed while the relevant likelihood function is used to locate the target parameter's next value. The step size used in the updates was adjusted adaptively through the runs, allowing more rapid convergence[40]. The final Markov chain Monte Carlo chain describes the posterior distribution for each model parameter, the error, and was then used to estimate the posterior distribution of growth rates as estimated from the model. Priors on model parameters were uniform over an unlimited range, whereas the parameters describing the standard deviation were restricted to >0. Bin boundaries, X_i, were constrained as follows: (1) boundaries could only fall within the range of X, (2) each bin contained at least five trees, and (3) no bin spanned less than 10% of the range of X. The last two restrictions prevented the bins from collapsing to very narrow ranges of X in which the fitted slope might take absurd extremes.

We chose piecewise regression over other alternatives for modelling G as a function of M for two main reasons. First, the linear regression slopes within each bin provide precise statistical tests of whether G increases or decreases with X, based on credible intervals of the slope parameters. Second, with adaptive bin positions, the function is completely flexible in allowing changes in slope at any point in the X range, with no influence of any one bin on the others. In contrast, in parametric models where a single function defines the relationship across all X, the shape of the curve at low X can (and indeed must) influence the shape at high X, hindering statistical inference about changes in tree growth at large size.

We used log(M) as our predictor because within a species M has a highly non-Gaussian distribution, with many small trees and only a few very large trees, including some large outliers. In contrast, we did not log-transform our dependent variable G so that we could retain values of $G \leq 0$ that are often recorded in very slowly growing trees, for which diameter change over a short measurement interval can be on a par with diameter measurement error.

For each species, models with 1, 2, 3 and 4 bins were fitted. Of these four models, the model receiving the greatest weight of evidence by Akaike Information Criterion (AIC) was selected. AIC is defined as the log-likelihood of the best-fitting model, penalized by twice the number of parameters. Given that adding one more bin to a model meant two more parameters, the model with an extra bin had to improve the log-likelihood by 4 to be considered a better model[42].

Assessing model fits. To determine whether our approach might have failed to reveal a final growth decline within the few largest trees of the various species, we calculated mass growth rate residuals for the single most massive individual tree of each species. For 52% of the 403 species, growth of the most massive tree was underestimated by our model fits (for example, Fig. 1a); for 48% it was overestimated (for example, Fig. 1b). These proportions were indistinguishable from 50% ($P = 0.55$, binomial test), as would be expected for unbiased model fits. Furthermore, the mean residual (observed minus predicted) mass growth rate of these most massive trees, $+0.006\,\mathrm{Mg\,yr^{-1}}$, was statistically indistinguishable from zero ($P = 0.29$, two-tailed t-test). We conclude that our model fits accurately represent growth trends up through, and including, the most massive trees.

Effects of combined data. To achieve sample sizes adequate for analysis, for some species we combined data from several different forest plots, potentially introducing a source of bias: if the largest trees of a species disproportionately occur on productive sites, the increase in mass growth rate with tree size could be exaggerated. This might occur because trees on less-productive sites—presumably the sites having the slowest-growing trees within any given size class—could be under-represented in the largest size classes. We assessed this possibility in two ways.

First, our conclusions remained unchanged when we compared results for the 53% of species that came uniquely from single large plots with those of the 47% of species whose data were combined across several plots. Proportions of species with increasing mass growth rates in the last bin were indistinguishable between the two groups (97.6% and 95.8%, respectively; $P = 0.40$, Fisher's exact test). Additionally, the shapes and magnitudes of the growth curves for Africa and Asia, where data for each species came uniquely from single large plots, were similar to those of Australasia, Europe and North America, where data for each species were combined across several plots (Table 1, Fig. 2 and Extended Data Fig. 2). (Data from Central and South America were from both single and combined plots, depending on species.)

Second, for a subset of combined-data species we compared two sets of model fits: (1) using all available plots (that is, the analyses we present in the main text), and (2) using only plots that contained massive trees—those in the top 5% of mass for a species. To maximize our ability to detect differences, we limited these analyses to species with large numbers of trees found in a large number of plots, dispersed widely across a broad geographic region. We therefore analysed the twelve Spanish species that each had more than 10,000 individual trees (Supplementary Table 1), found in 34,580 plots distributed across Spain. Massive trees occurred in 6,588 (19%) of the 34,580 plots. We found no substantial differences between the two analyses. When all 34,580 plots were analysed, ten of the twelve species showed increasing growth in the last bin, and seven showed increasing growth across all bins; when only the 6,588 plots containing the most massive trees were analysed, the corresponding numbers were eleven and nine. Model fits for the two groups were nearly indistinguishable in shape and magnitude across the range of tree masses. We thus found no evidence that the potential for growth differences among plots influenced our conclusions.

Effects of possible allometric biases. For some species, the maximum trunk diameter D in our data sets exceeded the maximum used to calibrate the species' allometric equation. In such cases our estimates of M extrapolate beyond the fitted allometry and could therefore be subject to bias. For 336 of our 403 species we were able to determine D of the largest tree that had been used in calibrating the associated allometric equations. Of those 336 species, 74% (dominated by tropical species) had no trees in our data set with D exceeding that used in calibrating the allometric equations, with the remaining 26% (dominated by temperate species) having at least one tree with D exceeding that used in calibration. The percentage of species with increasing G in the last bin for the first group (98.0%) was indistinguishable from that of the second group (96.6%) ($P = 0.44$, Fisher's exact test). Thus, our finding of increasing G with tree size is not affected by the minority of species that have at least one tree exceeding the maximum value of D used to calibrate their associated allometric equations.

A bias that could inflate the rate at which G increases with tree size could arise if allometric equations systematically underestimate M for small trees or overestimate M for large trees[43]. For a subset of our study species we obtained the raw data—consisting of measured values of D and M for individual trees—needed to calibrate allometric equations, allowing us to determine whether the particular form of those species' allometric equations was prone to bias, and if so, the potential consequences of that bias.

To assess the potential for allometric bias for the majority (58%) of species in our data set—those that used the empirical moist tropical forest equation of ref. 34—we reanalysed the data provided by ref. 34. The data were from 1,504 harvested trees representing 60 families and 184 genera, with D ranging from 5 cm to 156 cm; the associated allometric equation relates $\log(M)$ to a third-order polynomial of $\log(D)$. Because the regression of M on D was fitted on a log–log scale, this and subsequent equations include a correction of $\exp[(\mathrm{RSE})^2/2]$ for the error in back-transformation, where RSE is the residual standard error from the statistical model[44]. Residuals of M for the equation revealed no evident biases (Extended Data Fig. 4a), suggesting that we should expect little (if any) systematic size-related biases in our estimates of G for the 58% of our species that used this equation.

Our simplest form of allometric equation—applied to 22% of our species—was $\log(M) = a + b\log(D)$, where a and b are taxon-specific constants. For nine of our species that used equations of this form (all from the temperate western USA: *Abies amabilis, A. concolor, A. procera, Pinus lambertiana, Pinus ponderosa, Picea sitchensis, Pseudotsuga menziesii, Tsuga heterophylla* and *T. mertensiana*) we had values of both D and M for a total of 1,358 individual trees, allowing us to fit species-specific allometric equations of the form $\log(M) = a + b\log(D)$ and then assess them for bias. Residual plots showed a tendency to overestimate M for the largest trees (Extended Data Fig. 4b), with the possible consequence of inflating estimates of G for the largest relative to the smallest trees of these species.

To determine whether this bias was likely to alter our qualitative conclusion that G increases with tree size, we created a new set of allometric relations between D and M —one for each of the nine species—using the same piecewise linear regression approach we used to model G as a function of M. However, because our goal was to eliminate bias rather than seek the most parsimonious model, we fixed the number of bins at four, with the locations of boundaries between the bins being fitted by the model. Our new allometry using piecewise regressions led to predictions of M with no apparent bias relative to D (Extended Data Fig. 4c). This new, unbiased allometry gave the same qualitative results as our original, simple allometry regarding the relationship between G and M: for all nine species, G increased in the bin containing the largest trees, regardless of the allometry used (Extended Data Fig. 5). We conclude that any bias associated with the minority of our species that used the simple allometric equation form was unlikely to affect our broad conclusion that G increases with tree size in a majority of tree species.

As a final assessment, we compared our results to those of a recent study of *E. regnans* and *S. sempervirens*, in which M and G had been calculated from intensive measurements of aboveground portions of trees without the use of standard allometric equations[7]. Specifically, in two consecutive years 36 trees of different sizes and ages were climbed, trunk diameters were systematically measured at several heights, branch diameters and lengths were measured (with subsets of foliage and branches destructively sampled to determine mass relationships), wood densities were determined and ring widths from increment cores were used to supplement measured diameter growth increments. The authors used these measurements to calculate M for each of the trees in each of the two consecutive years, and G as the difference in M between the two years[7]. *E. regnans* and *S. sempervirens* are the world's tallest angiosperm and gymnosperm species, respectively, so the data set was dominated by exceptionally large trees; most had $M \geq 20$ Mg, and M of some individuals exceeded that of the most massive trees in our own data set (which lacked *E. regnans* and *S. sempervirens*). We therefore compared *E. regnans* and *S. sempervirens* to the 58 species in our data set that had at least one individual with $M \geq 20$ Mg. Sample sizes for *E. regnans* and *S. sempervirens*—15 and 21 trees, respectively—fell below our required ≥40 trees for fitting piecewise linear regressions, so we simply plotted data points for individual *E. regnans* and *S. sempervirens* along with the piecewise regressions that we had already fitted for our 58 comparison species (Fig. 3).

As reported by ref. 7, G increased with M for both *E. regnans* and *S. sempervirens*, up to and including some of the most massive individual trees on the Earth (Fig. 3). Within the zone of overlapping M between the two data sets, G values for individual *E. regnans* and *S. sempervirens* trees fell almost entirely within the ranges of the piecewise regressions we had fitted for our 58 comparison species. We take these observations as a further indication that our results, produced using standard allometric equations, accurately reflect broad relationships between M and G.

Fitting log–log models. To model $\log(G)$ as a function of $\log(M)$, we used the binning approach that we used in our primary analysis of mass growth rate (described earlier). However, in log-transforming growth we dropped trees with $G \leq 0$. Because negative growth rates become more extreme with increasing tree size, dropping them could introduce a bias towards increasing growth rates. Log-transformation additionally resulted in skewed growth rate residuals. Dropping trees with $G \leq 0$ caused several species to fall below our threshold sample size, reducing the total number of species analysed to 381 (Extended Data Fig. 2).

Growth in the absence of competition. We obtained published equations for 41 North American and European species, in 46 species-site combinations, relating species-specific tree diameter growth rates to trunk diameter D and to neighbourhood competition[45–49]. Setting neighbourhood competition to zero gave us equations describing estimated annual D growth as a function of D in the absence of competition. Starting at $D_0 = 10$ cm, we sequentially (1) calculated annual D growth for a tree of size D_t, (2) added this amount to D_t to determine D_{t+1}, (3) used an appropriate taxon-specific allometric equation to calculate the associated tree masses M_t and M_{t+1}, and (iv) calculated tree mass growth rate G_t of a tree of mass M_t in the absence of competition as $M_{t+1} - M_t$. For each of the five species that had separate growth analyses available from two different sites, we required that mass growth rate increased continuously with tree size at both sites for the species to be considered to have a continuously increasing mass growth rate. North American and European allometries were taken from refs 17 and 50, respectively, with preference given to allometric equations based on power functions of tree diameter, large numbers of sampled trees, and trees spanning a broad range of diameters. For the 47% of European species for which ref. 50 had no equations meeting our criteria, we used the best-matched (by species or genus) equations from ref. 17.

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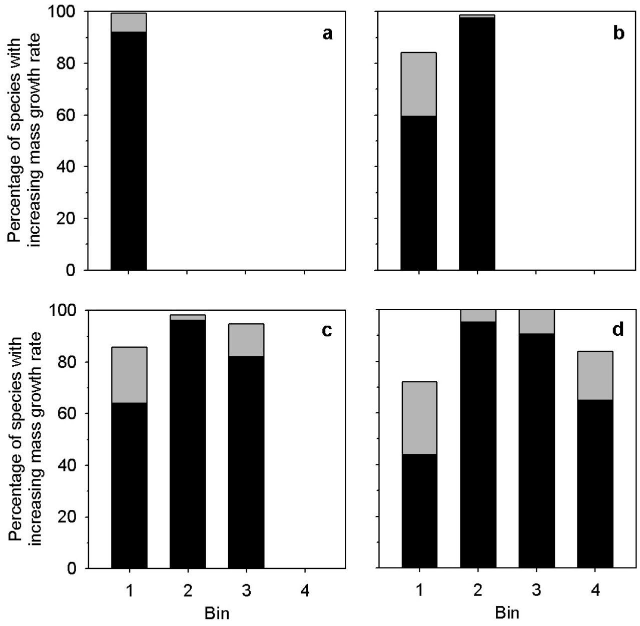
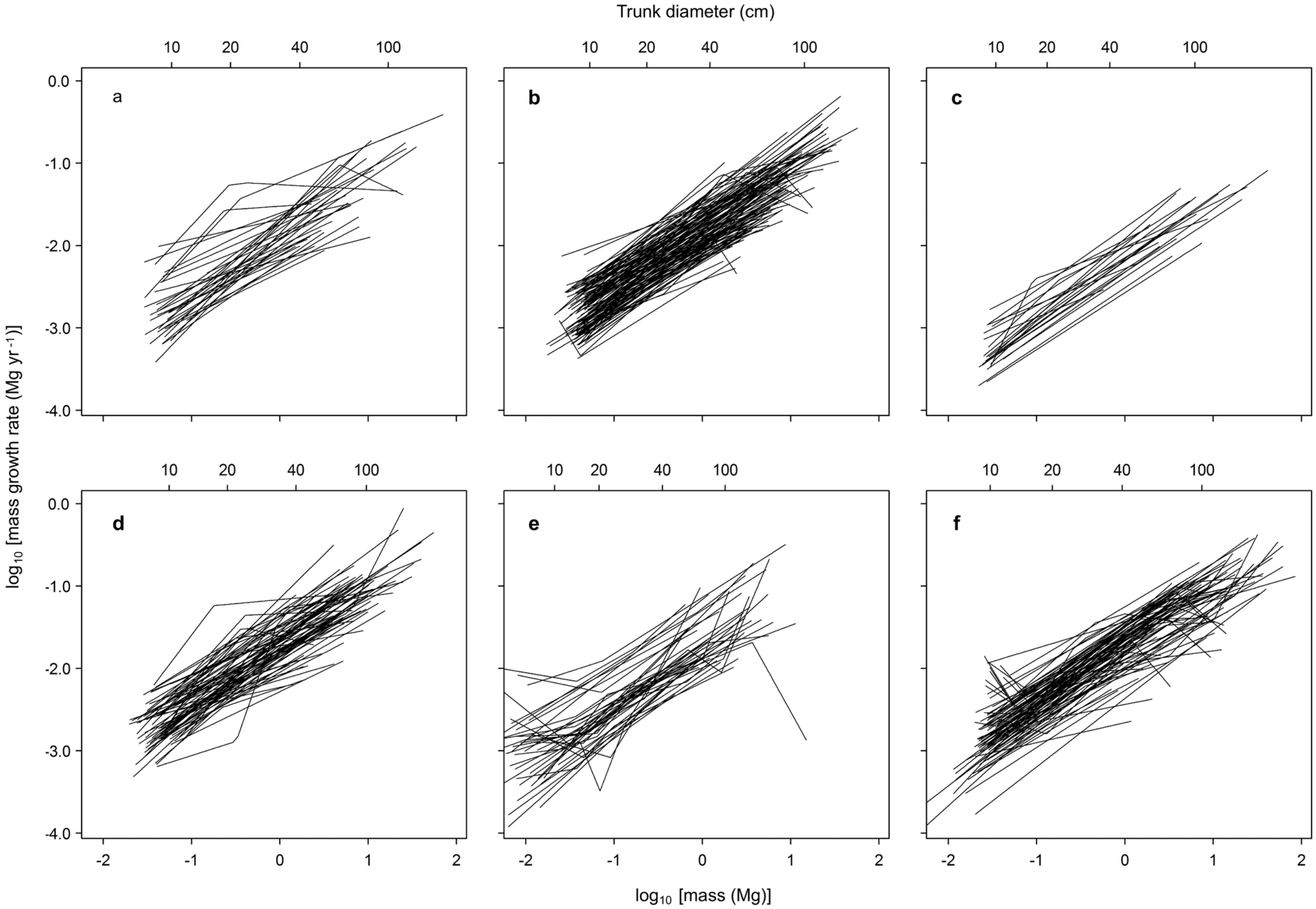
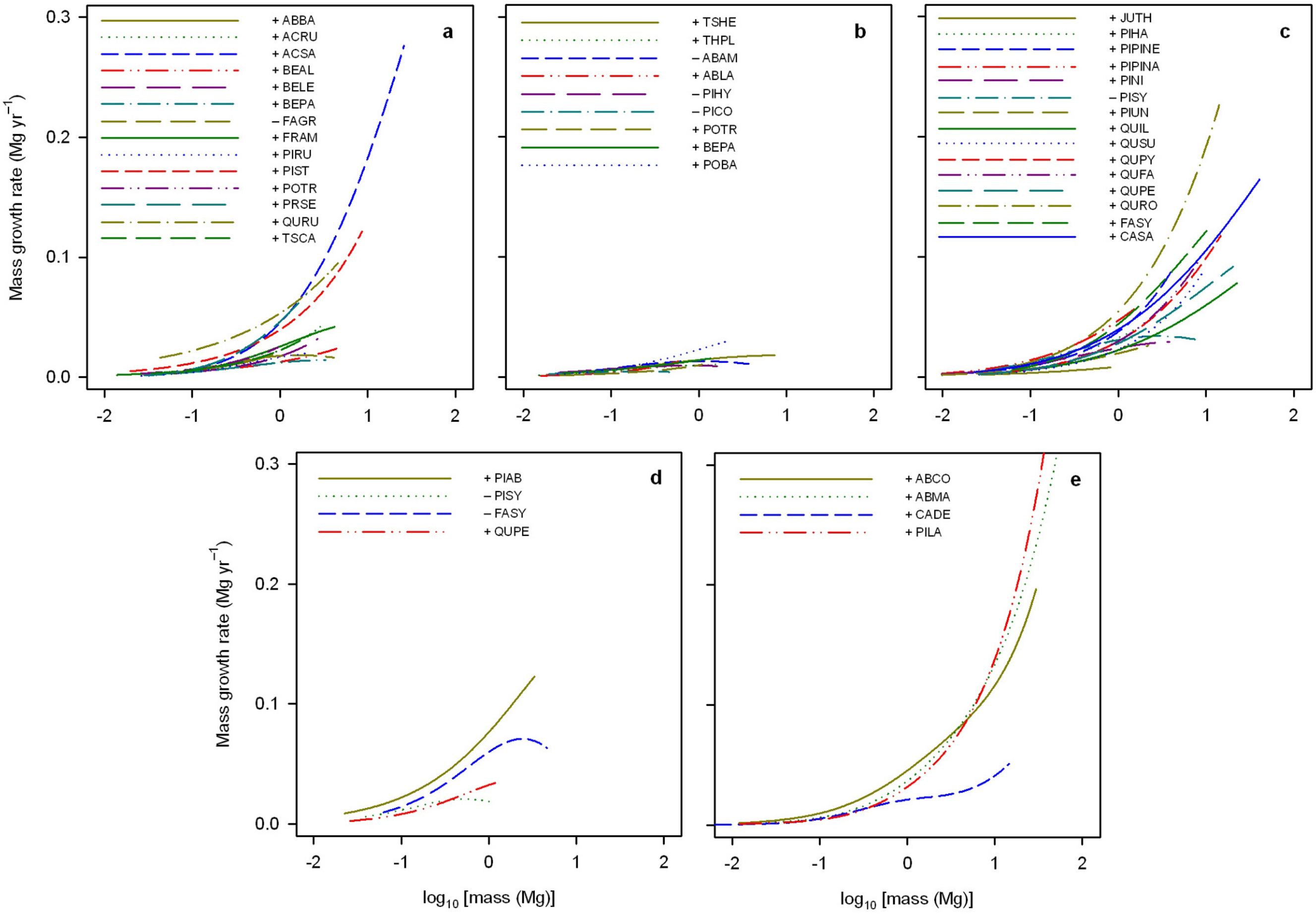


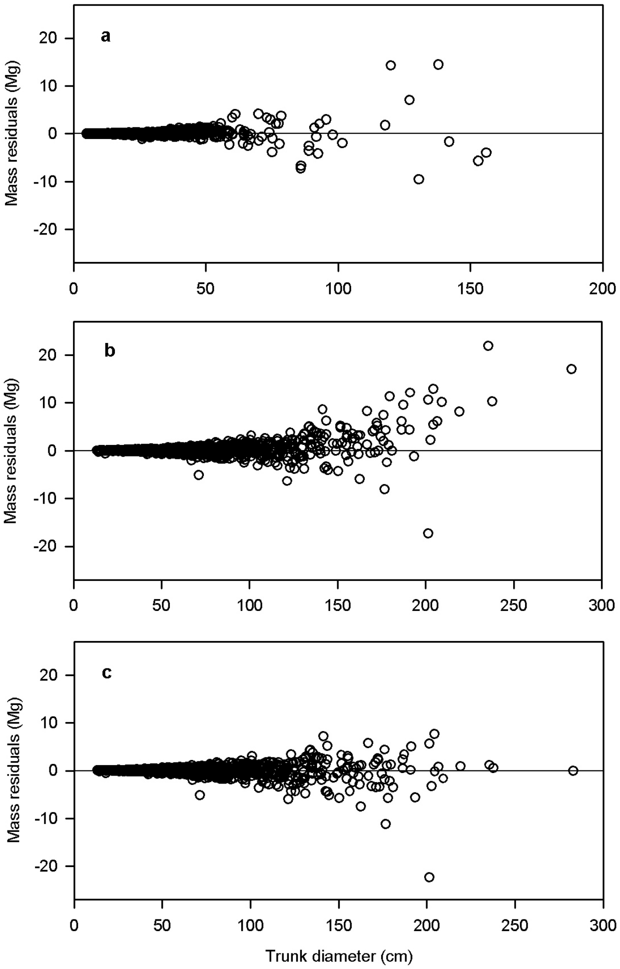
Extended Data Figure 1 | Summary of model fits for tree mass growth rates. Bars show the percentage of species with mass growth rates that increase with tree mass for each bin; black shading indicates percentage significant at $P \leq 0.05$. Tree masses increase with bin number. **a**, Species fitted with one bin (165 species); **b**, Species fitted with two bins (139 species); **c**, Species fitted with three bins (56 species); and **d**, Species fitted with four bins (43 species).



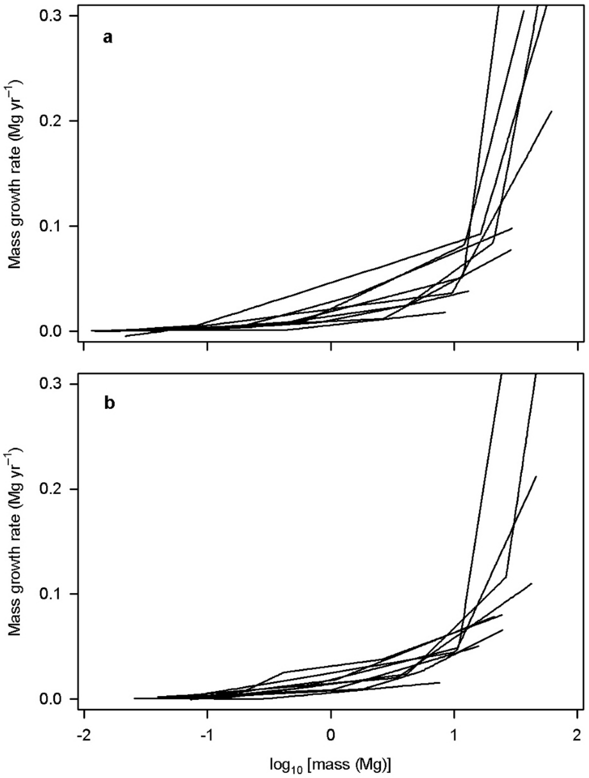
Extended Data Figure 2 | Log–log model fits of mass growth rates for 381 tree species, by continent. Trees with growth rates ≤ 0 were dropped from the analysis, reducing the number of species meeting our threshold sample size for analysis. **a**, Africa (33 species); **b**, Asia (123 species); **c**, Australasia (22 species); **d**, Central and South America (73 species); **e**, Europe (41 species); and **f**, North America (89 species). Trunk diameters are approximate values for reference, based on the average diameters of trees of a given mass.



Extended Data Figure 3 | Aboveground mass growth rates for 41 tree species in the absence of competition. The '+' or '–' symbol preceding each species code indicates, respectively, species with mass growth rates that increased continuously with tree size or species with mass growth rates that declined in the largest trees. Sources of the diameter growth equations used to calculate mass growth were: **a**, ref. 45; **b**, ref. 46; **c**, ref. 48; **d**, ref. 47; and **e**, ref. 49. ABAM, *Abies amabilis*; ABBA, *Abies balsamea*; ABCO, *Abies concolor*; ABLA, *Abies lasiocarpa*; ABMA, *Abies magnifica*; ACRU, *Acer rubrum*; ACSA, *Acer saccharum*; BEAL, *Betula alleghaniensis*; BELE, *Betula lenta*; BEPA, *Betula papyrifera*; CADE, *Calocedrus decurrens*; CASA, *Castanea sativa*; FAGR, *Fagus grandifolia*; FASY, *Fagus sylvatica*; FRAM, *Fraxinus americana*; JUTH, *Juniperus thurifera*; PIAB, *Picea abies*; PICO, *Pinus contorta*; PIHA, *Pinus halepensis*; PIHY, *Picea* hybrid (a complex of *Picea glauca*, *P. sitchensis* and *P. engelmannii*); PILA, *Pinus lambertiana*; PINI, *Pinus nigra*; PIPINA, *Pinus pinaster*; PIPINE, *Pinus pinea*; PIRU, *Picea rubens*; PIST, *Pinus strobus*; PISY, *Pinus sylvestris*; PIUN, *Pinus uncinata*; POBA, *Populus balsamifera* ssp. *trichocarpa*; POTR, *Populus tremuloides*; PRSE, *Prunus serotina*; QUFA, *Quercus faginea*; QUIL, *Quercus ilex*; QUPE, *Quercus petraea*; QUPY, *Quercus pyrenaica*; QURO, *Quercus robar*; QURU, *Quercus rubra*; QUSU, *Quercus suber*; THPL, *Thuja plicata*; TSCA, *Tsuga canadensis*; and TSHE, *Tsuga heterophylla*.



Extended Data Figure 4 | Residuals of predicted minus observed tree mass. **a**, The allometric equation for moist tropical forests[34]—used for the majority of tree species—shows no evident systematic bias in predicted aboveground dry mass, *M*, relative to trunk diameter (n = 1,504 trees). **b**, In contrast, our simplest form of allometric equation—used for 22% of our species and here applied to nine temperate species—shows an apparent bias towards overestimating *M* for large trees (n = 1,358 trees). **c**, New allometries that we created for the nine temperate species removed the apparent bias in predicted *M*.



Extended Data Figure 5 | Estimated mass growth rates of the nine temperate species of Extended Data Fig. 4. Growth was estimated using the simplest form of allometric model [$\log(M) = a + b\log(D)$] (**a**) and our allometric models fitted with piecewise linear regression (**b**). Regardless of the allometric model form, all nine species show increasing G in the largest trees.

NATURE | NEWS

Tree growth never slows

Idea debunked that young trees have the edge on their older siblings in carbon accumulation.

Jeff Tollefson

15 January 2014

Richard Schultz/Corbis

Trees — including California's giant redwoods — add an increasing amount of mass every year.

Many foresters have long assumed that trees gradually lose their vigour as they mature, but a new analysis suggests that the larger a tree gets, the more kilos of carbon it puts on each year.

“The trees that are adding the most mass are the biggest ones, and that holds pretty much everywhere on Earth that we looked,” says Nathan Stephenson, an ecologist at the US Geological Survey in Three Rivers, California, and the first author of the study, which appears today in *Nature*[1]. “Trees have the equivalent of an adolescent growth spurt, but it just keeps going.”

The scientific literature is chock-full of studies that focus on forests' initial growth and their gradual move towards a plateau in the amount of carbon they store as they reach maturity[2]. Researchers have also documented a reduction in growth at the level of individual leaves in older trees[3].

In their study, Stephenson and his colleagues analysed reams of data on 673,046 trees from 403 species in monitored forest plots, in both tropical and temperate areas around the world. They found that the largest trees gained the most mass each year in 97% of the species, capitalizing on their additional leaves and adding ever more girth high in the sky.

Although they relied mostly on existing data, the team calculated growth rates at the level of the individual trees, whereas earlier studies had typically looked at the overall carbon stored in a plot.

Estimating absolute growth for any tree remains problematic, in part because researchers typically take measurements at a person's height and have to extrapolate the growth rate higher up. But the researchers' calculations consistently showed that larger trees added the most mass. In one old-growth forest plot in the western United States, for instance, trees larger than 100 centimetres in diameter comprised just 6% of trees, but accounted for 33% of the growth.

The findings build on a detailed case study published in 2010, which showed similar growth trends for two of the world’s tallest trees — the coast redwood (*Sequoia sempervirens*) and the eucalyptus (*Eucalyptus regnans*)[4], both of which can grow well past 100 metres in height. In that study, researchers climbed, and took detailed measurements of, branches and limbs throughout the canopy to calculate overall tree growth. Stephen Sillett, a botanist at Humboldt State University in Arcata, California, who led the 2010 study, says that the latest analysis confirms that his group's basic findings apply to almost all trees.

Nature Podcast

Noah Baker spoke about the findings with Nathan Stephenson, an ecologist at the US Geological Survey.

You may need a more recent browser or to install the latest version of the Adobe Flash Plugin.

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Decline in efficiency

The results are consistent with the known reduction in growth at the leaf level as trees age. Although individual leaves may be less efficient, older trees have more of them. And in older forests, fewer large trees dominate growth trends until they are eventually brought down by a combination of fungi, fires, wind and gravity; the rate of carbon accumulation depends on how fast old forests turn over.

"It's the geometric reality of tree growth: bigger trees have more leaves, and they have more surface across which wood is deposited," Sillett says. "The idea that older forests are decadent — it's really just a myth."

The findings help to resolve some of these contradictions, says Maurizio Mencuccini, a forest ecologist at the University of Edinburgh, UK. The younger trees may grow faster on a relative scale, he says, meaning that they take less time to, say, double in size. "But on an absolute scale, the old trees keep growing far more."

The study has broad implications for forest management, whether in maximizing the yield of timber harvests or providing old-growth habitat and increasing carbon stocks. More broadly, the research could help scientists to develop better models of how forests function and their role in regulating the climate.

Nature | doi:10.1038/nature.2014.14536

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Frequency and Magnitude of Selected Historical Landslide Events in the Southern Appalachian Highlands of North Carolina and Virginia: Relationships to Rainfall, Geological and Ecoh...

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Chapter 9
Frequency and Magnitude of Selected Historical Landslide Events in the Southern Appalachian Highlands of North Carolina and Virginia: Relationships to Rainfall, Geological and Ecohydrological Controls, and Effects

Richard M. Wooten, Anne C. Witt, Chelcy F. Miniat, Tristram C. Hales, and Jennifer L. Aldred

Abstract Landsliding is a recurring process in the southern Appalachian Highlands (SAH) region of the Central Hardwood Region. Debris flows, dominant among landslide processes in the SAH, are triggered when rainfall increases pore-water pressures in steep, soil-mantled slopes. Storms that trigger hundreds of debris flows occur about every 9 years and those that generate thousands occur about every 25 years. Rainfall from cyclonic storms triggered hundreds to thousands of debris

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C.H. Greenberg, B.S. Collins (eds.), *Natural Disturbances and Historic Range of Variation*, Managing Forest Ecosystems 32,
DOI 10.1007/978-3-319-21527-3_9

flows in 1916, 1940, 1969, 1977, 1985, and 2004. Debris flows have caused loss of life and property, and severely affected forest lands by altering forest structure and disrupting aquatic ecosystems. Forests on mountain slopes are critical in mitigating the impacts of recurring landslide events. Forest cover is an important stabilizing factor on hillslopes by intercepting precipitation, increasing evapotranspiration, and reinforcing roots. Precipitation and hillslope-scale landforms have a controlling effect on soil moisture, root strength, and debris flow hazards. Anthropogenic influences have increased the frequency of mass wasting for a given storm event above historical natural levels through changes in vegetation and disturbances on mountain slopes. Climate change that results in increased occurrences of high intensity rainfall through more frequent storms, or higher intensity storms, would also be expected to increase the frequency of debris flows and other forms of mass-wasting in the SAH. The interdisciplinary technical and scientific capacity exists to investigate, analyze, identify and delineate landslide prone areas of the landscape with increasing reliability.

Keywords Debris flow • Ecohydrological • Landslide • Blue Ridge Mountains • Southern Appalachian Highlands

9.1 Introduction

Landsliding is a recurring process of mass wasting and sediment transport in the landscape evolution of the southern Appalachian Highlands (SAH) of the USA. The SAH encompasses the Blue Ridge Mountains, and adjoining mountainous and high relief areas of the Central Appalachians, Ridge and Valley, and Piedmont Ecoregions (Greenberg et al. Chap. 1, Fig. 1.1). In comparing the relative frequency of disturbances among ecoregions of the Central Hardwood Region (CHR), White et al. (2011) found that the remnants of hurricanes (tropical cyclones) and, consequently, landslides are more common disturbances in the Blue Ridge Mountains, Ridge and Valley, and Central Appalachians ecoregions. Here we concentrate on the Blue Ridge Mountains and adjacent Piedmont of North Carolina and Virginia where previous and recent landslide mapping and studies have helped quantify the extent and magnitude of major historical landslide events. These events have caused loss of life, damage and destruction of homes, property and transportation networks, and have had major impacts on forest structure and hydrologic systems (Fig. 9.1). Future debris flow events in the SAH are certain and will have similar impacts.

The term landslide refers to a variety of gravity-driven ground movements of soil and/or rock materials. Landslides may be swift and catastrophic (i.e., rockfalls and debris flows) or may travel slowly and incrementally downslope (i.e., some soil slides). Landslide incidence and susceptibility occurs in nearly all of the high-relief areas of the USA including the CHR (Fig. 9.2). Although many types of landslides occur throughout the SAH, debris flow is the dominant landslide process in the Blue Ridge Mountains of North Carolina and Virginia, and the SAH, and will be the

Fig. 9.1 Damaged and destroyed homes, and debris flow erosion and deposition along the run out zone (lower track) of the September 16, 2004 Peeks Creek debris flow in Macon County, North Carolina. The debris flow triggered by rainfall from Hurricane Ivan claimed five lives and destroyed 16 homes (September 19, 2004 NCGS photo). Refer to Fig. 9.17 for location

focus of this chapter. A debris flow is a water-laden (i.e., liquefied) moving mass of rock fragments and soil (debris) in which the majority of soil particles are sand-sized or larger (Cruden and Varnes 1996). Debris flows move rapidly downslope, attaining speeds in excess of 50 km per hour, and are capable of destroying or damaging everything in their paths. A typical debris flow pathway consists of an upper initiation site or source area, a main track or path along a drainage way or stream channel, and a lower depositional area or run out zone on mountain footslopes (Clark 1987; Cruden and Varnes 1996). The present SAH landscape includes many remnants of prehistoric (Pleistocene and older) debris flow deposits (Leigh Chap. 8). These features are typically composite, recording multiple episodes of prehistoric and historic mass wasting in mountain coves and foot slopes. Importantly, these deposits indicate areas that may be affected by future debris flow activity, as modern debris flows generally deposit sediment in areas occupied by past debris flow deposits.

The primary trigger for debris flows is heavy rainfall (generally greater than 125–250 mm in 24 h) that results in excess pore-water pressures in relatively thin soil on steep slopes. From 1916 to 2006 seven major cyclonic storms tracked over the SAH, setting off hundreds to thousands of debris flows in multi-county areas in the North Carolina, Virginia and West Virginia. In addition, rainfall associated with

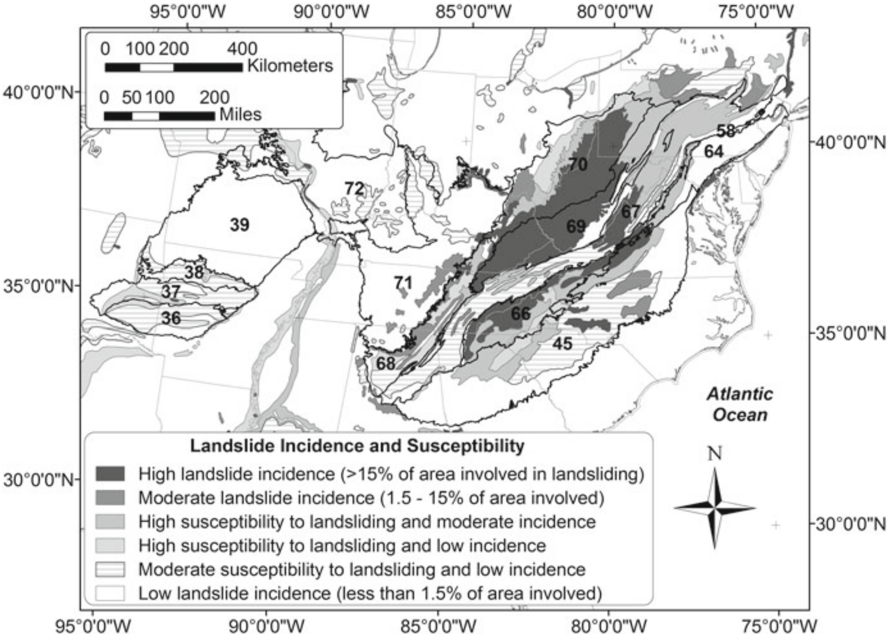

Fig. 9.2 Generalized map of landslide incidence and susceptibility (From Godt (1997) shown for the CHR and ecoregions within it. Within the CHR the Appalachians have the overall highest landslide incidence and susceptibility. Landslide incidence is the percentage of the area involved in landsliding. Susceptibility is defined as the probable degree of the areal response of rocks and soil to natural or artificial cutting or loading of slopes, or to anomalously high precipitation. Ecoregions shown with *bold outlines*: 36 = Ouachita Mountains, 37 = Arkansas Valley, 38 = Boston Mountains, 39 = Ozark Highlands, 45 = Piedmont, 58 = Northeastern Highlands, 64 = Northern Piedmont, 66 = Blue Ridge Mountains, 67 = Ridge and Valley, 68 = Southwestern Appalachians, 69 = Central Appalachians, 70 = Western Allegheny Plateau, 71 = Interior Plateau, 72 = Interior Valleys and Hills

low pressure systems, and localized storms, especially when coincident with periods of above average rainfall can trigger tens to hundreds of debris flows. From 1876 to 2013, at least 16 of these storm events generated tens to hundreds of debris flows.

The majority of landslides in the SAH occur in the Blue Ridge Mountains of North Carolina and Tennessee, the northern Blue Ridge Mountains of Virginia, and the Ridge and Valley of Virginia and West Virginia (Figs. 9.3 and 9.4). The concentration of landslide activity in the North Carolina Blue Ridge Mountains and adjacent portions of the Great Smoky Mountains National Park (GSMNP) in Tennessee is partly the result of the high relief and ruggedness of the terrain, and partly owing to the more frequent impacts of cyclonic storms in this region (9 of 13 storms). Although there are fewer documented landslide events for the Blue Ridge Mountains, and Ridge and Valley of Virginia and West Virginia, rainfall events there have

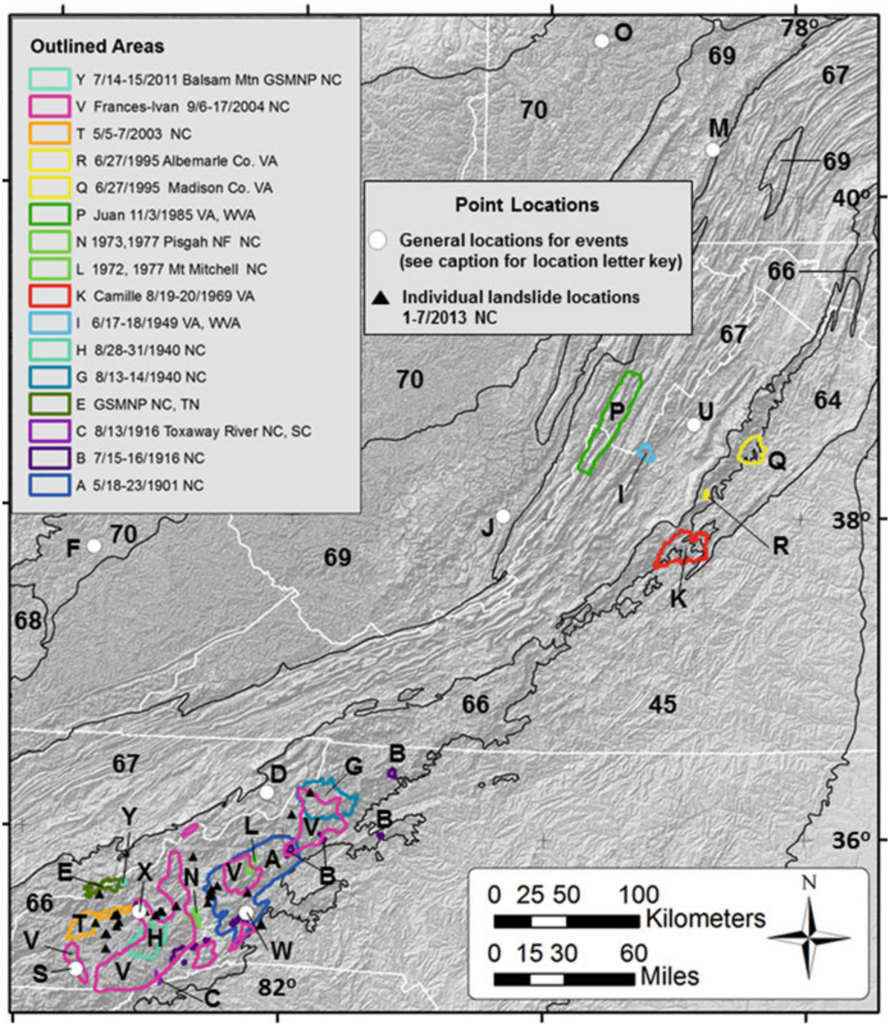

Fig. 9.3 Shaded relief map showing ecoregions and areas of selected past debris flow events in the SAH and other selected locations in the CHR. Lettered locations correspond to events in Table 9.1. General point locations: D = 6/3/1924 Carter Co. TN, F = 7/4-5/1939 KY, J = Camille 8/19-20/1969 Greenbrier C. WV, M = 7/19/1977 PA, O = 8/14/1980 PA, S = Opal 10/3-5/1995 NC, U = Isabel 9/18-19/2003 NC, W = Cindy 7/7/2005 NC, X = Ernesto 8/3/2006 NC. Ecoregion number designation: 45 = Piedmont, 64 = Northern Piedmont, 66 = Blue Ridge Mountains, 67 = Ridge and Valley, 68 = Southwestern Appalachians, 69 = Central Appalachians, 70 = Western Allegheny Plateau, 71 = Interior Plateau

triggered the greatest numbers of documented landslides. The remnants of Hurricane Camille in 1969 generated a total of 5,377 documented landslides (mainly debris flows) in Virginia and West Virginia making it the largest magnitude, well-documented landslide event in the SAH.

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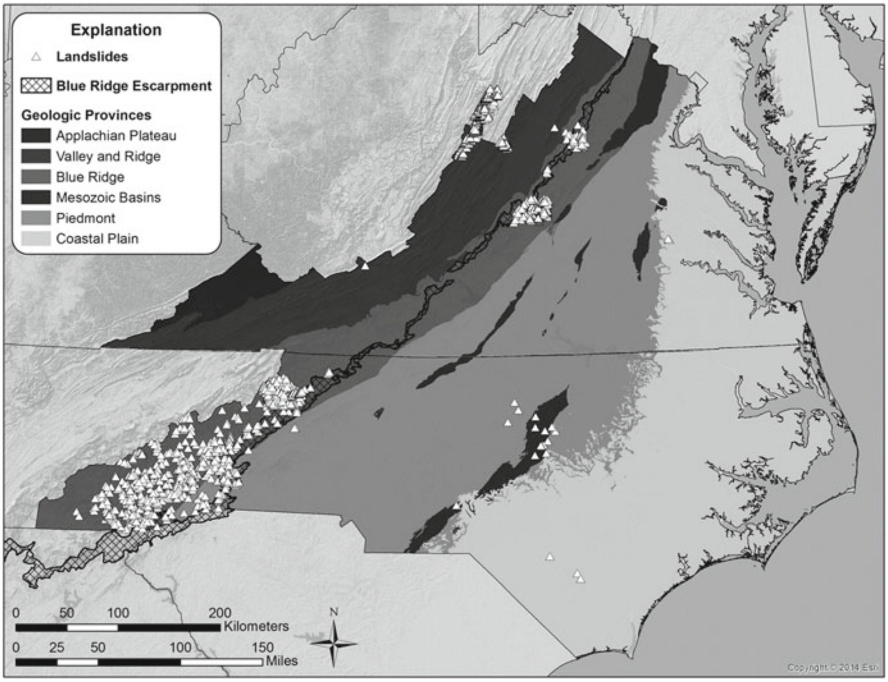

Fig. 9.4 Geologic provinces of North Carolina and Virginia, the Blue Ridge Escarpment, and landslide locations in landslide geodatabases of the North Carolina Geological Survey and Virginia Department of Mines Minerals and Energy. Clustered distribution of landslides results from detailed mapping in some areas of major landslide events, and incomplete mapping in other areas

Geologic, geomorphic, and meteorological conditions influence where debris flows are most likely to initiate on the landscape. Orographic enhancement of rainfall can occur as an air mass or storm moves over a high mountain range from lower elevations. This phenomenon is caused by the lifting and cooling of the air mass as it travels over a high elevation area and often produces excess precipitation. Heavy rainfall, when combined with the high-relief areas of certain landforms (i.e., the multi-basin scale Blue Ridge Escarpment and the watershed-scale Nantahala Mountains Escarpment) and erosional reentrants into them, are more prone to debris flow activity. Geologically, intersecting bedrock structural discontinuities (e.g., fracture, foliation, and bedding planes) and differential weathering control the locations and subsurface morphologies of convergent landforms (i.e., colluvial hollows) where debris flows typically initiate. Less frequently, soil on planar or divergent (i.e., convex) slopes such as ridge noses, also controlled by bedrock discontinuities, serve as debris flow initiation zones. Bedrock geology is dynamically coupled with hillslope geomorphology, hydrology, soil, and vegetation, all of which influence hillslope stability. In addition to these factors, ground disturbance from human activity, such as poorly constructed or maintained cut and fill slopes, and drainage systems, can further destabilize hillsides making them more susceptible to damaging debris flows.

Forest cover is an important stabilizing factor on steep upland hillslopes through precipitation interception, evapotranspiration, and root biomass (e.g., root reinforcement). Debris flows often initiate where the reinforcing ability of plant roots is at a minimum, either through reduced root biomass and/or tensile strength, and/or less connectivity between roots and the bedrock substrate. The reinforcement provided by the roots of forest plants reflects hillslope-scale differences in belowground biomass and tensile strength, and is directly affected by precipitation and soil moisture. Systematic differences in forest structure driven by differences in soil moisture and nutrient distributions, combined with the expansion of weakly rooted species such as the shrub Rhododendron (*Rhododendron maximum*), appear to influence the size of individual landslides and possibly regional landsliding events. Studies of SAH woody species show responses of root tensile strength to changes in precipitation and soil moisture. Roots are weaker in convergent compared to divergent geomorphic features, and roots in wetter soils, i.e., after rain events, become weaker compared to when soils are drier. Precipitation, therefore, has a controlling effect on soil moisture, root tensile strength, and debris flow hazards. Although forest cover is beneficial, forested slopes are a common location for debris flows triggered by storm events in the SAH.

9.1.1 Methods

In North Carolina and Virginia, earlier landslide mapping has been integrated into a geographic information system (GIS) environment for ease of data entry and for statistical analyses. Field studies and the development of similar statewide, GIS-based, landslide geodatabases by the North Carolina Geological Survey (NCGS) and the Virginia Department of Mines, Minerals and Energy – Division of Geology and Mineral Resources (DGMR), capture and help to quantify the frequency and severity of debris flow events of various magnitudes in the SAH (Fuemmeler et al. 2008; Bauer et al. 2012; Witt and Heller 2014). The NCGS geodatabase currently has over 3,400 landslide points and over 3,200 landslide deposit (mainly debris) polygons, located primarily in the four counties with completed landslide hazard maps. The DGMR geodatabase currently has over 5,200 landslide points and associated data. Digital elevation models, including those derived from LiDAR, coupled with archival aerial photography and recent orthophotography have advanced the capability to identify, map, and analyze prehistoric and historic landslide features within the context of the current landscapes and land covers. Currently, the NCGS and DGMR do not actively map landslides and landslide deposits, but landslide features are added to the geodatabases on an as-needed basis

A compilation of existing landslide information and new mapping of landslide features in a GIS environment by the NCGS began in 2003 in the western North Carolina Blue Ridge Mountains (Wooten et al. 2005) and was funded in part by the Federal Emergency Management Agency (FEMA). New mapping and data collection in North Carolina included a geologic hazards inventory along the North

Carolina portion of Blue Ridge Parkway (Latham et al. 2009), and completion of landslide hazard maps for Macon, Watauga, Buncombe and Henderson Counties (Wooten et al. 2006, 2008b, 2009b, 2011). The NCGS has also responded to requests for technical assistance in over 85 landslide events in which field data were collected during investigations. In a 1-year FEMA funded pilot project, the Virginia DGMR mapped landslides and prehistoric landslide deposits in Page County, Virginia (Witt and Heller 2012, 2013, 2014; Witt et al. in press).

9.2 General Geologic and Geomorphic Setting

The bedrock geology of the Blue Ridge Mountains in North Carolina and Virginia and the adjacent Piedmont includes metasedimentary slate, phyllite, marble, schist, and gneiss, and metaigneous amphibolite and greenstone (metabasalt), granitic gneiss, and relatively unmetamorphosed granitic rock (Fig. 9.4). Protoliths of these rocks were deposited or crystallized during distinct periods spanning the last 1.8 billion years (Hatcher 2010; Ownby et al. 2004). The oldest rocks, Mesoproterozoic gneisses, are highly metamorphosed igneous and sedimentary rocks formed between 1.8 and 1 billion years ago. These gneisses comprised the edge of the ancient North American craton upon which early Paleozoic sediments were deposited in rift and ocean basins. During the Paleozoic, at least three continental collisional events subjected all of these rocks to high temperatures and differential pressures, creating complex folding, faulting, and widespread metamorphism. Igneous activity associated with the Paleozoic orogenies emplaced numerous granitic plutons into the surrounding country rock. Thrusting along low angle faults folded and transported these rock packages tens to hundreds of km to the northwest, placing them on top of and deforming younger, low-grade to unmetamorphosed, folded and faulted Paleozoic sedimentary rocks of the Valley and Ridge province (Hatcher 1989). The multiple episodes of metamorphism, folding, thrust faulting, and fracturing during the southern Appalachian orogen have resulted in complex ductile (e.g., foliation and shear zones) and brittle (e.g., fractures) bedrock structures that are reflected in the topography at scales from a single outcrop to the region.

Later, Cenozoic uplift and subsequent post-orogenic erosion and denudation, enhanced by climatic variations from repeated glacial and interglacial intervals, have resulted in many of the Quaternary geomorphic features seen in the Appalachian Mountains today (Kochel and Johnson 1984; Kochel 1987,1990; Soller and Mills 1991). The most extensive regional landform in the SAH is the Blue Ridge Escarpment (BRE) (Hack 1982; Clark 1993), which is also referred to the as the eastern Blue Ridge front in Virginia. This high relief, erosional feature extends from northeast Georgia to northwest Virginia, generally corresponds with the Eastern Continental Divide, and marks the boundary between the mountainous Blue Ridge Mountains and the rolling foothills of the Piedmont physiographic province to the east (Fig. 9.4).

Ancient and modern deposits from debris flows and other types of landslides on mountain footslopes and in coves record a long history of mass wasting from early Miocene to the present, reflecting the ongoing landscape evolution of the SAH. These accumulations of unconsolidated, matix- or clast-supported, clay- to boulder-sized sediment (i.e., composite diamictons) are referred to by various names, including debris fans, alluvial fans, and piedmont cove deposits (Kochel and Johnson 1984; Kochel 1987, 1990; Mills 1982, 1998; Mills et al. 1987; Whittecar and Ryter 1992; Mills and Allison 1995a, b). The morphology and composition of these deposits varies greatly depending on their age, topographic setting, and past and present depositional processes. These deposits are typically composites of several generations of debris flows reworked and incised by alluvial action. Individual fan-shaped deposits occur at outlets of first and second order drainages. Coalescing fans can form continuous apron-like deposits, along footslopes, and fill valley floors where topographically constrained (Fig. 9.5). These deposits collectively will be referred to here as debris deposits or debris fans. In North Carolina and Virginia, large debris deposits are often found in the Blue Ridge Mountains, but extend into

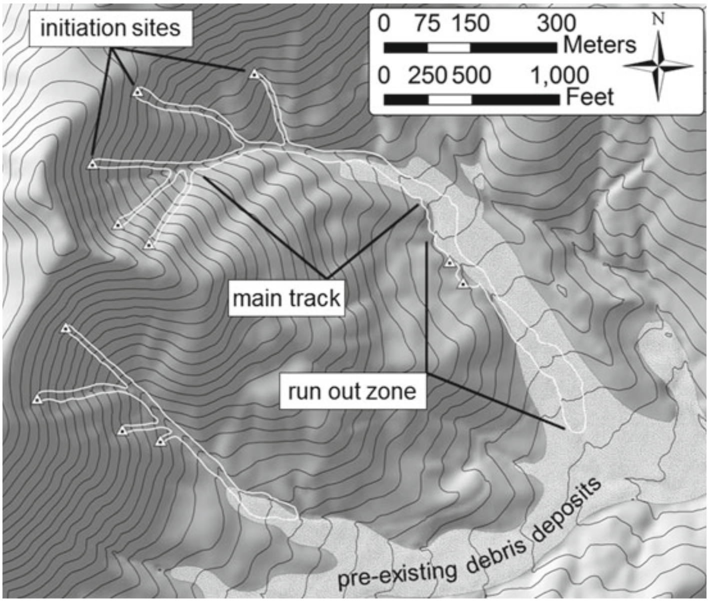

Fig. 9.5 Tracks of 1977 debris flows (*white outlines*) and pre-existing debris deposits (stippled polygons) in the Rocky Branch area, Bent Creek Experimental Forest, Pisgah National Forest, in Buncombe County North Carolina. Initiation sites (*triangles*), main track, and run out zone labels show typical components of a debris flow. The 1977 debris flows deposited material in areas underlain by pre-existing debris flow deposits. Topographic contours (*black lines*) and the shaded relief map are derived from a 6 m-pixel resolution LiDAR digital elevation model (DEM). Contour interval = 6.1 m (20 ft). Elevation ranges from 1,152 to 762 m, with lower elevations in the southeast portion of the map (Derived from Wooten et al. 2009b) (Location N in Fig. 9.3 and Table 9.1)

the adjoining Piedmont along footslopes of the BRE. These deposits also occur along the eastern border of the Ridge and Valley in Virginia.

Recent dating of a large, deeply weathered debris fan in the Big Levels 7.5-min quadrangle in the western Virginia Blue Ridge Mountains was completed using the cosmogenic ^{26}Al/^{10}Be burial decay method (Heller et al. 2014). Two samples determined the age of the fan to be early Miocene: sampling at 20 m below the land surface yielded an age of 7.94 ± 2.4 Mega-annum (one million years), while a higher fan layer 15 m below the surface yielded an age of 6.90 ± 1.7 Mega-annum. This age range is much older that those derived using radiocarbon dating on slope deposits exposed by a 1995 storm in Madison County, Virginia (Eaton et al. 2003a) and on debris fans in Nelson County, Virginia (Kochel and Johnson 1984). Eaton et al. (2003a) found that stratified slope deposits in Madison County were formed in the late Pleistocene (15.8–27.4 Kilo-annum, 1,000 years), while maximum ages for debris flow deposits were found to be >50 Kilo-annum. Kochel and Johnson (1984) dated basal units of debris fans in the Davis Creek area of Nelson County to the start of the Holocene (10.7 Kilo-annum).

In the North Carolina Blue Ridge Mountains, large, composite debris deposits are characterized by variation in relative fan-surface ages as reflected by physical differences (e.g., variation in soil matrix color, topographic position, and clast weathering rinds) indicating relative ages that range from Early Pleistocene to Holocene (Mills 1982; Mills and Allison 1995a). Mills and Allison (1995b) used paleomagnetism to determine a minimum relative age of early Pleistocene (78 Kilo-annum) for weathered debris deposits in Watauga County. Subsequently Mills and Grainger (2002) used cosmogenic ^{26}Al/^{10}Be to date a debris fan deposit on the slopes of Rich Mountain, also in Watauga County, as early Pleistocene (1.45 ± 0.17 Mega-annum). Late Holocene debris deposits are also present in the region. Radiocarbon dating of charcoal beneath a debris flow deposit at a site near the Nantahala River in Swain County, North Carolina, indicates the debris flow postdates 4,441–4,797 years before present (Leigh 2009; see also Leigh Chap. 8).

Older debris deposits can indicate areas that can be affected by modern debris flows. In the eastern Blue Ridge Mountains of Virginia heavy rainfall in 1969 and 1995 triggered debris flows on older debris fan material in Nelson County (Williams and Guy 1973; Kochel and Johnson 1984) and Madison County (Morgan et al. 1997; Eaton et al. 2003a), respectively. Field studies and mapping in Macon County in the North Carolina Blue Ridge Mountains determined that debris deposits of various ages cover about 4,500 ha or 3.3 % of the land area there (Wooten et al. 2006). These pre-existing debris deposits were identified at all of the 62 relatively recent debris-flow sites in Macon County, evidence that prior debris flow events had occurred at the same locations, in many cases multiple times (Wooten et al. 2008a). The common occurrence of modern debris flow deposition in areas with past debris flow deposits was also identified by landslide mapping in Watauga, Buncombe and Henderson Counties in the North Carolina Blue Ridge Mountains (Wooten et al. 2008b, 2009b, 2011). These studies found that modern debris flows typically affect areas where streams have incised into, or flow around the margins of older deposits. In relatively rare cases modern debris deposition has occurred on fan surfaces outside of stream channels (Fig. 9.5).

On the west slope of the Virginia Blue Ridge Mountains, debris fans tend to be larger, better developed, and more weathered than those along the eastern Blue Ridge front. These west-facing fans appear to be dominated by alluvial and fluvial processes, having more of the characteristics of a braided stream deposit (Kochel 1990; Heller et al. 2014). Debris flow activity tends to be confined to the upper-to-middle reaches of these fans and to active channels (Whittecar and Ryter 1992; Eaton et al. 2003a; Heller et al. 2014). In the western portion of Page County, no modern landslides (post-1950) were found within or along ancient debris fans originating from the western flank of the Blue Ridge Mountains (Witt and Heller 2013, 2014).

9.3 Temporal Frequency and Magnitude of Debris Flow Events Related to Regional and Localized Rainfall Events

9.3.1 Rainfall Scenarios

Building on the work of Scott (1972), Clark (1987), Witt (2005), and Wieczorek et al. (2009), we have compiled existing data and reported new data for a total of 31 landslide events listed in Table 9.1, and shown graphically in Fig. 9.6. Figure 9.3 shows the general locations for the major events. In summary, tropical cyclones and an extratropical cyclone tracked over the SAH, setting off tens to thousands of debris flows in multi-county areas in North Carolina in 1916, 1940, 1977 and 2004, and in Virginia and West Virginia in 1969 and 1985. These cyclonic storms have resulted in the most widespread and numerous flooding and landslide events in the SAH. From 1916 to 2004, 13 cyclonic storms have impacted the SAH, on average, approximately every 7 years. Five of these storms (Agnes, Opal, Isabel, Cindy and Ernesto) generated relatively few landslides in the region. Although no landslides were reported for the July 7, 1916 tropical cyclone, it was significant because it created high antecedent moisture prior to a July 15–16, 1916 tropical cyclone, which was the storm of record for the French Broad watershed of North Carolina.

The short duration between Hurricanes Frances and Ivan in September 2004 was significant in that it established a pattern of back-to-back major storms within 6–20 days of each other causing flooding and triggering debris flows in Blue Ridge Mountains of North Carolina. Three such scenarios have occurred over an 88-year period from 1916 to 2004 (Witt 2005). Work by the US Geological Survey (1949), Tennessee Valley Authority (1964), Scott (1972), and Witt (2005) established that similar weather patterns had triggered regional flooding and debris flows in July of 1916 and August 1940. Following Frances and Ivan, the average frequency of such weather scenarios in western North Carolina is 29 years.

In addition to tropical cyclones, rainfall associated with low pressure systems and localized storms, especially when coincident with periods of above normal rainfall, have triggered from a few to hundreds of landslides in each of the 18 events

Table 9.1 Selected examples of landslide (mainly debris flow) events induced by rainfall in the SAH, and other selected locations in the Central Hardwood Region. Letters in the first column correspond with locations shown in Fig. 9.3. *TC* tropical cyclone, *ETC* extratropical cyclone, *EANR* period of extended of above normal rainfall. Number in parentheses in 'Total Area of Tracks' column represents number of landslides used to determine track area where less than the total number of reported landslides. Other abbreviations used in the table: *NCGS* NC Geological Survey, *TVA* Tennessee Valley Authority, *USDA* US Department of Agriculture, *USGS* US Geological Survey

Lettered location Fig. 9.3	Type of rainfall event	Rainfall total (mm)	Time of most intense rainfall	Landslide dates mm/day/year	Landslides reported	Total track area (ha)	General location ecoregion	Reported landslide locations	Notes – References
–	Storm	165	?	6/15/1876				Macon, Jackson Co., NC	Clingman 1877; Witt 2005
A	Storm	228	?	5/21-22/1901	>17		Blue Ridge Mountains, Piedmont	Buncombe, Henderson, Mitchell, McDowell Co., NC	Holmes 1917; Myers 1902; Scott 1972; USDA 1902; Witt 2005
–	TC (unnamed)		1 day	7/9/1916 (rainfall)	0		Blue Ridge Mountains	Western NC	Henry 1916; Scott 1972
B	TC (unnamed)	564	24 h	7/15-16/1916	Many, >45		Blue Ridge Mountains	Western NC	Bell 1916; Scott 1972; Witt 2005
C	Storm	584	24 h	8/13/1916	1	122.1	Blue Ridge Mountains	Toxaway River, Transylvania Co., NC	Dam failure – debris flow; Wooten et al. 2003a, b
D	Thunderstorm	380	2 days	6/13/1924	~100		Blue Ridge Mountains	Carter Co., TN	Slides from 8/13-14/1940 storm also here (Hack and Goodlett 1960); Scott, 1972
E	Cloudburst	305	4 h	8/4-5/1938	>100		Blue Ridge Mountains	Webb Mountain, TN (GSMNP)	Within concentrated debris flow area in Southworth et al. 2012; Scott 1972
F	Thunderstorm	508	2 days	7/4-5/1939	4		Western Allegheny Plateau	Wolfe, Breathitt Co., KY	Total number of landslides not reported; Schrader, 1945

G	TC (unnamed)	254	6 h	8/13-14/1940	2,120	368	Blue Ridge Mountains	Watauga, Ashe, Allegheny, Avery, Wilkes, Caldwell Co., NC; Unicoi County, TN	USGS 1949; Wieczorek et al. 2004; Witt et al. 2007a; Wooten et al. 2008b
H	Storm	330	2 days	8/28-31/1940	>200			Macon, Jackson (location 6) and Haywood Counties, NC	TVA 1940; USGS 1949; NCGS landslide geodatabase
–	Storm	381	24 h	Winter 1942	Numerous		Blue Ridge Mountains	Watauga Co., NC	Gryta and Bartholomew 1983
I	Cloudburst	400	1 day	6/17-18/1949	466		Ridge and Valley	Augusta and Rockingham Co., VA; Highland County, WV	Hack and Goodlett 1960
E	Cloudburst	100	1 h	9/1/1951			Blue Ridge Mountains	Mt. LeConte, TN (GSMNP)	Within concentrated debris flow area in Southworth et al. 2012; Bogucki 1976; Clark et al. 1987
J	TC Camille	635	8 h	8/19-20/1969 9/5-6/1969	1,584		Central Appalachians	Spring Creek, Greenbrier County, WV	Schneider 1973
K	TC Camille	710–800	8 h	8/19-20/1969	3,793	1,200	Blue Ridge Mountains, Piedmont	Albemarle, Amherst, Nelson Co., VA	Williams and Guy 1971, 1973; Morgan et al 1999a
L	TC Agnes	203	2 days	6/20-21/1972	?		Blue Ridge Mountains	Mt. Mitchell area (location L), Waterrock Knob, Haywood Co., NC.	Bailey et al. 1975; Clark 1987
H, N	Thunderstorms	196	1 h	5/26-28/1973	Many, 8 documented		Blue Ridge Mountains	Tuckasegee watershed, Jackson Co., NC (location H), Pisgah NF, NC (location M)	Young 1973; Zeedyk 1973; NCGS landslide geodatabase

(continued)

Table 9.1 (continued)

Lettered location Fig. 9.3	Type of rainfall event	Rainfall total (mm)	Time of most intense rainfall	Landslide dates mm/day/year	Landslides reported	Total track area (ha)	General location ecoregion	Reported landslide locations	Notes – References
M	Thunderstorm or Cloudburst	300	9 h	7/19-20/1977	Several hundred		Central Appalachians	Johnstown area, western PA	Pomeroy, 1980
L	ETC (unnamed)	300	2 days	11/5-7/1977	13	25.2	Blue Ridge Mountains	Mt. Mitchell, Black Mtns., Yancey Co., NC	Eschner and Patrick 1982; Wooten et al. this chapter
N	ETC (unnamed)	150	2 days	11/5-7/1977	83	32.8	Blue Ridge Mountains	Pisgah NF, Buncombe, Henderson Co., NC.	Neary and Swift 1987; Pomeroy 1991; Otteman 2001; Wooten et al. 2009b, 2011
O	Thunderstorm	115	14 days	8/14/1980	62		Western Allegheny Plateau	East Brady along Allegeny River, PA	Pomeroy 1984
P	TC Juan	350	3 days	11/3-5/1985	3,000		Ridge and Valley	Pendleton Co., WV; Highland Co., VA	Jacobson, 1993
–	Storm	60	1 day	12/23/1990	4	2.57	Blue Rige Mountains	Nantahala NF in Swain, Cherokee, Clay Co., NC	Wooten et al. 2007
Q	Storm	770	14 h	6/27/1995	629	600	Blue Rige Mountains	Madison Co., VA	Eaton et al. 2004; Morgan et al. 1997, 1999b; Wieczorek et al. 1995, 2000
R	Storm	635	1 day	6/27/1995	72	49.8	Blue Ridge Mountains	Albemarle Co., VA	Morgan and Wieczorek 1996
S	TC Opal	274	1 h	10/3-5/1995	2	1.4	Blue Ridge Mountains	Poplar Cove, Macon Co., NC	Wooten et al. 2008a
T	Storm	187	1 day	5/5-7/2003	10	4.5	Blue Ridge Mountains	Swain Co., NC	Wooten and Latham 2004

U	TC Isabel	513	1 day	9/18-19/2003	6		Ridge and Valley	Shennandoah Valley, VA	Wieczorek et al. 2004
V	TC Frances	599	2 days	9/6-8/2004	400+	81.3 (184)	Blue Ridge Mountains	Western NC	Reported landslide total for Frances and Ivan; Collins 2008; Wooten et al. 2008a; Wieczorek et al. 2009; Collins 2014; Roth 2015
	TC Ivan	432	2 days	9/16-17/2004					
W	TC Cindy	110	2 days	7/7/2005	1	0.05	Blue Ridge Mountains	Buncombe Co., NC	Rockslide; Wooten et al. 2007
X	TC Ernesto	168	12 h	8/31/2006	1	1.1	Blue Ridge Mountains	Haywood Co., NC	Wooten and Latham 2006
–	Storm	152	24 h	1/7/2009	2	1.5	Blue Ridge Mountains	Haywood Co., NC	Embankment failures-debris flows; Wooten et al. 2009a
–	Storm	35	4 h	2/5/2010	1	2.6	Blue Ridge Mountains	Maggie Valley, Haywood Co., NC	Witt et al. 2012; Wooten et al. this chapter
Y	Thunderstorm	125	4 h	7/14-15/2011	21	12.9	Blue Ridge Mountains	Balsam Mountain, NC (GSMNP)	Lee et al. 2011; Miller et al. 2012; Wooten et al. this chapter
Point locations	Storm (within EANR period)	388	2 days	1/14-17/2013	Numerous 268 confirmed	5.2 (18)	Blue Ridge Mountains	Western NC	Gibbs 2013; Jennifer Bauer personal comm.; Wooten et al. 2014, and this chapter
Point locations	Storm (within EANR period)	168	2 days	5/4-6/2013	Numerous 50 confirmed	1.3 (8)	Blue Ridge Mountains	Western NC	Gibbs 2013; Wooten et al. this chapter
Point locations	Storm (within EANR period)	250	2 days	7/2-9/2013	Numerous 9 confirmed	5.0 (7)	Blue Ridge Mountains	Western NC	Wooten et al. 2014; and this chapter

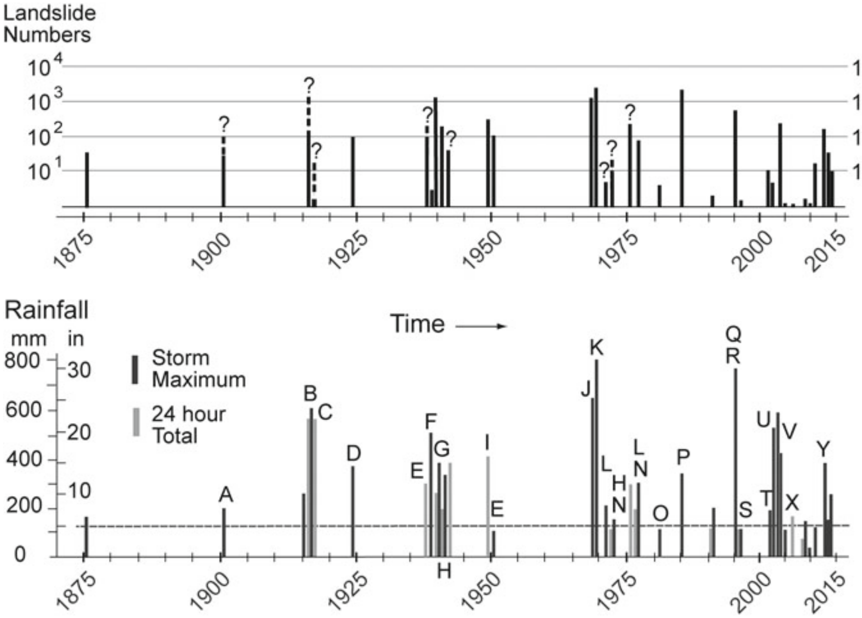

Fig. 9.6 Chart showing the landslide numbers and rainfall associated with tropical cyclones and other storms that triggered landslides in the SAH and other selected locations in the CHR. The 24-h rainfall threshold of 125 mm for triggering debris flows from Eschner and Patrick (1982) shown by a *dashed line*. Single letter in parentheses corresponds with locations in Fig. 9.3, and Table 9.1 (Adapted and expanded from Wooten et al. 2007)

documented for the SAH in Table 9.1. Six events in this category each generated 100 or more reported landslides. The June 27, 1995 storm event in Madison County produced 629 landslides (mainly debris flows) making it the largest event in this category. During a period of above normal rainfall throughout western North Carolina from January to August 2013, four storms collectively triggered more than 300 landslides. Landslides from three of these storms are documented here. Undoubtedly many other landslide events of this nature have occurred throughout the SAH that are not reported here (e.g., Crawford 2014) and not documented in the literature.

9.3.2 *Characterization of Triggering Rainfall*

Total storm rainfall is an important factor in debris flow initiation. As can be seen from Table 9.1 and Fig. 9.6, the majority of events fall within 125–250 mm per day precipitation thresholds presented by Eschner and Patrick (1982) needed to generate debris flows on forested slopes in the SAH. Fuhrmann et al. (2008) found that landslide activity in western North Carolina is strongly related to antecedent precipitation over a 90-day period. Other studies in the SAH of North Carolina and

Virginia have demonstrated that rainfall rate (intensity) and duration is a critical factor in debris flow initiation. Areas of high-intensity rainfall promote the development of debris flows and slides as evident in the 1969 Nelson County storm (Williams and Guy 1973) and the 1995 Madison County storm (Wieczorek et al. 2000). Neary and Swift (1987) concluded that rainfall rates on the order of 90–100 mm per hour (188 mm storm total) initiated debris flows in the Bent Creek area near Asheville, North Carolina, during a November 3–5, 1977 storm, but they do not report specific durations associated with these rates. Wieczorek et al. (2000, 2009) present a rainfall intensity-duration threshold curve for the Central Blue Ridge Mountains of Virginia that ranges from approximately 90 mm per hour for 1 h, to 10 mm per hour for 24 h. Wieczorek et al.(2004) reported that 254 mm of rain within 6 h (42 mm per hour average) triggered over 700 debris flows during the August 13–14, 1940 storm in the Deep Gap area of Watauga County, North Carolina, a value that plots above the Virginia threshold curve. An average rate of 25 mm per hour for the 4.65 h period of peak cumulative rainfall (5.5 mm per hour for the 33.2 h storm total) during Ivan preceded the Peeks Creek and Wayah debris flows in Macon County, North Carolina (Wooten et al. 2008a). This value falls below the Virginia curve threshold; however, the North Carolina debris flows occurred with high antecedent moisture conditions from the passage of the remnants of Hurricane Frances the previous week. An average rainfall rate of 57 mm per hour for 2 h generated the 2011 Balsam Mountain debris flows in the GSMNP (Miller et al. 2012; Tao and Barros 2014), a value that plots below the Virginia threshold curve.

In two North Carolina cases, less rainfall was required to generate debris flows on slopes with evidence of prior instability related to human activity, when compared to debris flows generated on unmodified, forested slopes as described above (Wooten et al. 2009a, 2010b). In 2009, peak rainfall of ~6.4 mm per hour for 1.2 h (3.3 mm per hour for 23.5 h storm total) triggered a debris flow in fill material that destroyed a home. In 2010, peak rainfall of ~3.4 mm per hour for 2 h (4.4 mm per hour for 13.3 h rain total on snow) contributed to a retaining wall failure that mobilized into a debris flow which damaged three homes (Witt et al. 2012). This limited number of cases indicates that the destabilizing effects of human activity likely decreases the requisite rainfall needed to initiate debris flows on some modified slopes in contrast with rainfall amounts needed to generate debris flows on forested slopes not modified by human activity.

9.4 Summary of Selected Major Historical Events

9.4.1 July 1916: North Carolina

The storm of record for the French Broad watershed at Asheville occurred on July 15–16, 1916 when a hurricane made landfall near Charleston, South Carolina and moved northwest over western North Carolina causing extensive flooding and triggering numerous landslides (Bell 1916; Holmes 1917; Scott 1972; Witt 2005).

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The storm set the 24-h rainfall record for North Carolina of 564 mm at Altapass on the crest of the BRE in Mitchell County. Preceding the mid-July storm, a tropical cyclone produced 100–250 mm of rain over western North Carolina on July 8 and 9, 1916 (Henry 1916; Scott 1972). Although no landslides were reported for this early July storm, it created high antecedent moisture conditions in advance of the July 15–16, 1916 storm. While only 45 landslides were reported for this storm, they occurred over a widespread extent. Landslides were reported in a 200 km-long corridor of the Blue Ridge Mountains and Piedmont from Brevard in Transylvania County, northeast to Basin Creek in Alleghany and Wilkes Counties (in what is now Doughton Park) and were the direct cause of in 22 fatalities. Devastated by fatalities and destruction from flooding and landslides, the Basin Creek community never recovered.

9.4.2 *August 13–17, 1940: North Carolina*

During August 10–17, 1940, the remnants of a landfalling hurricane caused flooding throughout much of the southeastern USA (US Geological Survey 1949). Rainfall, totaling 340 mm in Watauga and adjacent counties in the North Carolina Blue Ridge Mountains, triggered numerous debris flows during August 13–14, 1940 (Fig. 9.7), during which time as much as 254 mm of rain may have fallen within a 6 h period (Wieczorek et al. 2004). Landslides caused 14 deaths, damaged or destroyed 32 structures in Watauga County, and destroyed transportation networks there and in neighboring counties (Witt et al. 2007a). Over 700 debris flows triggered by this storm were identified in the Deep Gap area of southeastern Watauga County by Wieczorek et al. (2004). Upon completion of the landslide hazard maps for Watauga County, 2,120 landslides, mainly debris flows and debris slides, attributed to this storm were identified and mapped (Wooten et al. 2008b). Of the 2,120 landslides, 2,099 occurred throughout Watauga County, but were generally concentrated in the Deep Gap area (Fig. 9.7) and in a highly dissected, mountainous area in the northwest part of the county. The remaining 21 debris flows occurred in adjacent portions of Wilkes and Ashe Counties mainly along the BRE. Given the magnitude of the debris flow event in Watauga County, and the widespread nature of the heavy rainfall along other nearby areas of the BRE, we speculate that this storm likely triggered many more debris flows in northwestern North Carolina.

Debris flows ranged widely in size from 2 m wide and 12–15 m long, upwards to 60–90 m wide and 400–800 m long. The largest debris flows were in an area of 600 m of relief in the Deep Gap area of the BRE, where the longest track measured from 1940 aerial photography was nearly 2,100 m long (Witt et al. 2008). Within Watauga County, the total area of mapped debris flow tracks was 368 ha in mainly first order and some second order drainages (Witt et al. 2008; Wooten et al 2008b). Although 368 ha is only about 0.5 % of the 819.5 km^2 (81,950 ha) area of Watauga County, it is a significant component of the riparian area. Many of the 1940 debris flows deposited sediment in footslope areas where pre-existing debris deposits were mapped (Wooten et al. 2008b). Examination of the locations of the 1940 debris flow

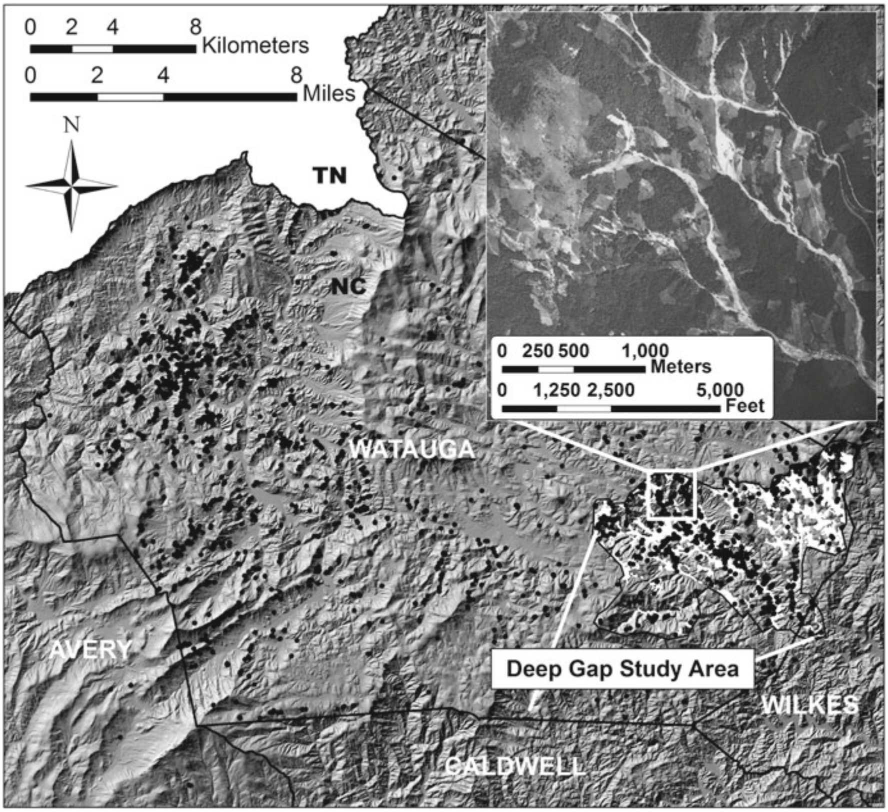


Fig. 9.7 Shaded relief map of Watauga County and the Deep Gap study area (see also Sect. 9.8), *black dots* are point locations for the over 2,100 landslide (mainly debris flow) initiation sites in Watauga and adjacent Wilkes Counties triggered by the August 13–14, 1940 tropical cyclone (from Wooten et al. 2008b). Inset image *upper right* shows debris flow tracks visible as linear high reflectance areas on September 29, 1940 aerial photography. Unforested slopes in the Deep Gap study area are shown in white; remaining slopes within the Deep Gap study area are forested. Shaded relief map derived from a 6 m-pixel resolution LiDAR DEM (Location G in Fig. 9.3 and Table 9.1)

tracks with 2005 orthophotography revealed two findings with respect to current land use patterns and the built environment: (1) since 1940, 136 structures, mainly residences, have been built in the tracks of 1940 debris flows; and (2) 521 tracks of 1940 debris flows cross existing roads (Witt et al. 2007a).

Additional mapping identified another 154 landslides of various types that had occurred in Watauga County since 1940 (Wooten et al. 2008b). Nearly 60 of these landslides were triggered by the remnants of Hurricanes Frances and Ivan in September 2004. Fifteen of the September 2004 debris flow sites were located at, or very near to 1940 initiation sites. Although some of the reactivated sites had been modified by human activity (e.g., fills) since 1940, this finding indicates that the recurrence interval for some landslide prone sites could be on the order of decades, rather than on millennial scales as found in the Virginia Blue Ridge Mountains (Kochel 1987; Eaton et al. 2003a).

9.4.3 *August 28–30, 1940: North Carolina*

A second major storm struck western North Carolina in August 1940. This storm, a low-pressure system, occurred during August 28–31, and affected mainly the Little Tennessee watershed of Jackson, Macon and Swain Counties, and the French Broad watershed in Haywood County (Tennessee Valley Authority 1940; US Geological Survey 1949; Witt 2005). The Tennessee Valley Authority (Tennessee Valley Authority 1940) reported the heaviest rainfall in the headwaters of the Tuckasegee River in Jackson County where 241–305 mm fell over a 24 h period. The high intensity rainfall over a relatively small area of 388 km^2 triggered more than 200 debris flows which claimed six lives in Jackson and Haywood Counties (Tennessee Valley Authority 1940). High antecedent moisture conditions from the earlier mid-August 1940 likely contributed to the severity of the flooding and debris flows near the center of the late August storm.

9.4.4 *August 19–20, 1969 Camille: Virginia, West Virginia*

The landslides and flooding associated with the remnants of Hurricane Camille on the night of August 19–20, 1969, was one of the worst natural disasters experienced in Virginia. Approximately 710 mm of rain fell in a span of roughly 8 h, mostly in rural, forested Nelson County in the Blue Ridge Mountains of central Virginia (Williams and Guy 1973). Debris flows and slides permanently altered the landscape and created deep scars in mountainsides that are still visible on aerial photography today. The storm caused the deaths of over 150 people, the majority of whom were killed by blunt force impact related directly to landslides (Simpson and Simpson 1970).

Based on mapping by Morgan et al. (1999a) and Bartholomew (1977), over 3,700 landslides (mostly debris flows and slides) have been identified as occurring during the August 1969 storm. The greatest concentration of debris flows occurred in Nelson County (Figs. 9.8 and 9.9), covering approximately 40 % of the county. Slides were also identified in northern Amherst County and southern Albemarle County. In total, approximately 1,200 ha were damaged by landslide scarring and deposition. Most of this area is comprised of agricultural land and temperate broadleaf and mixed forests with varieties of oak, poplar, and ash (Williams and Guy 1971). The total area stated here is probably a low estimate, as the most recent mapping of these debris flows occurred in 1999 at a scale of 1:24,000 (Morgan et al.

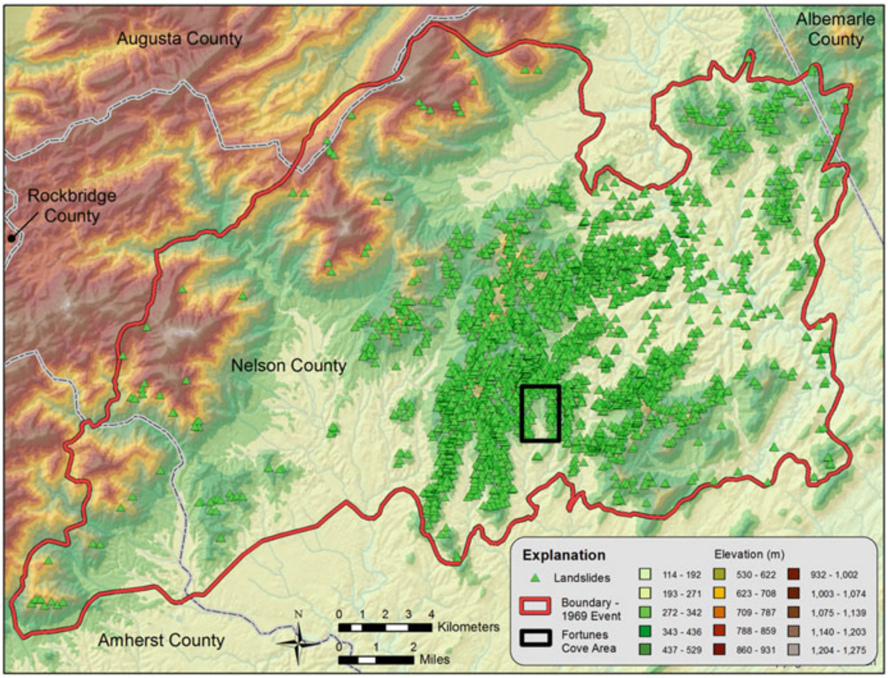


Fig. 9.8 Landslide (mainly debris flow) initiation sites triggered by Hurricane Camille from August 19–20, 1969 in Nelson County Virginia. Camille triggered over 3,700 landslides in this area, impacting 1,200 ha. Map base is a shaded relief map, color-coded by elevation derived from a 30 m digital elevation model. *Black outline* shows the location of the Fortunes Cove area in Fig. 9.9 (Location K in Fig. 9.3 and Table 9.1)

1999a). Re-evaluation of aerial photography, coupled with LiDAR mapping when it becomes available, will likely increase the total amount of land area disturbed.

The greatest number of debris flows occurred along Davis Creek where nearly every first- and second-order stream, and many mountain coves, failed. Along this drainage, over 400 coalescing debris flows and slides destroyed 290 ha. Of the 25 houses along this drainage, 23 were destroyed (Williams and Guy 1971). Along Davis Creek and other heavily damaged drainages, headscarps and scour in the upper portion of the debris flow track frequently left the bedrock exposed. At the headscarps, vegetative cover, including large trees, was completely removed and boulders up to 3 m in length were transported (Williams and Guy 1973). Further downstream, excessive stream discharge scoured even small drainages deeply. The amount of sediment transport and denudation from hillsides and drainages in this area was enormous for a single event. Williams and Guy (1973) studied three watersheds to the south and west of Davis Creek and extrapolated the average denudation for these areas to be approximately 360–500 mm. In comparison, average denudation rates in the Blue Ridge Mountains are estimated to be 150–360 mm per 1,000 years (Judson and Ritter 1964).

Fig. 9.9 Outlines of numerous debris flow tracks that occurred during Camille from August 19 to 20, 1969 and affected nearly every drainage in the Fortunes Cove area of Nelson County Virginia. The outlines are superimposed onto 2009 orthophotography illustrating the progress of vegetative recovery along the debris flow tracks since 1969 (Location K in Fig. 9.3 and Table 9.1)

Forest recovery at the debris flow sites in Nelson County varies depending on the morphology of the headscarp scar (Fig. 9.9). Where bedrock was exposed along debris flow initiation sites, forest recovery has been exceedingly slow and scars are still visible on the landscape today. Until colluvium fills in these areas, vegetation will not return. Where debris flows occurred within colluvium, forest regrowth occurred quickly and may be fully reestablished today (Kochel 1987).

Schneider (1973) reported 1,584 landslides during Camille in the central Appalachians of Greenbrier County, West Virginia. When combined with the 3,793 landslides documented in Virginia, a total of 5,377 landslides resulted from Camille, making it the storm that triggered the greatest number of documented landslides in the SAH.

9.4.5 November 5–7, 1977: North Carolina

During November 2–7, 1977 an extratropical cyclone that originated in the Gulf of Mexico passed over western North Carolina causing extensive flooding and triggering debris flows over a multi-county region (Neary and Swift 1987). Although the total storm rainfall in the area was 150 mm, intense convective downpours on the night of November 5–6, 1977 set off debris flows in the Bent Creek Experimental Forest within the Pisgah National Forest near Asheville in southwestern Buncombe County (Neary and Swift 1987) (Figs. 9.5, 9.10, and 9.11). Pomeroy (1991) mapped 72 debris flows in the Bent Creek area, and Otteman (2001) incorporated his mapping into GIS as part of a study of the area's debris flow susceptibility. Landslide mapping in Buncombe County (Wooten et al. 2009b) and adjacent Henderson County (Wooten et al. 2011) identified 11 additional debris flows attributed to this event bringing the total number of debris flows from the 1977 storm in this area to 83.

Rainfall from the 1977 storm also triggered debris flows on the slopes of Mount Mitchell and the Black Mountains in the Pisgah National Forest (Eschner and Patrick 1982). Total rainfall from the storm was 300 mm in the vicinity of Mount Mitchell (Neary and Swift 1987) which at elevation 2,037 m is the highest peak in eastern North America. The upper tracks from these debris flows are still visible on the southeast facing slopes of Mt. Mitchell and the Black Mountains (Fig. 9.12). Silver (2003) relates a personal account of a resident who witnessed one of these debris flows along Shuford Creek that originated on Celo Knob. The upper portion of the track of the Shuford Creek debris flow is visible in 2013 aerial photography. An evaluation of several vintages of aerial photography dating from 1993 to 2013 reveal at least three episodes of debris flows occurring on the southeast-facing

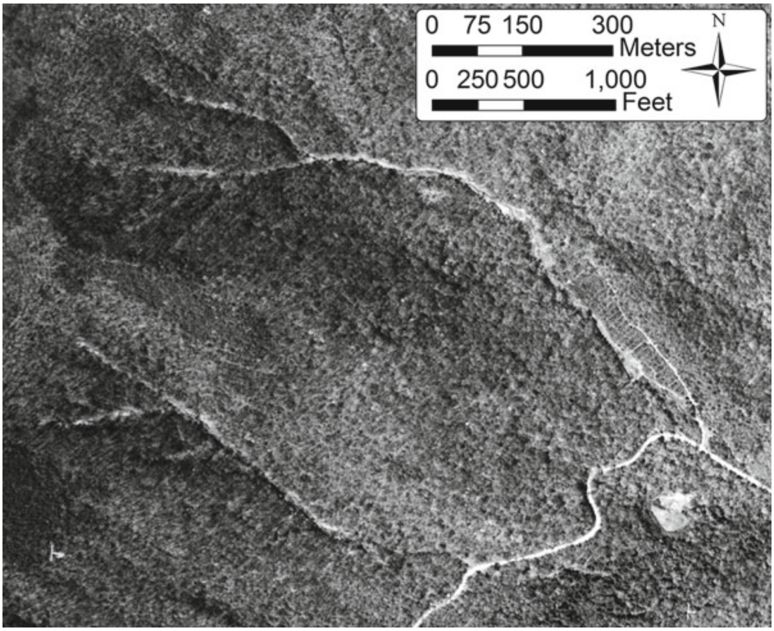


Fig. 9.10 Sparsely vegetated tracks of 1977 debris flows visible in 1983 aerial photography of the Rocky Branch area, Bent Creek Experimental Forest, Pisgah National Forest, in Buncombe County North Carolina. Elevation ranges from 1,152 to 762 m, with lower elevations in the southeast portion of the map. Same view as Fig. 9.5 (Location N in Fig. 9.3 and Table 9.1)

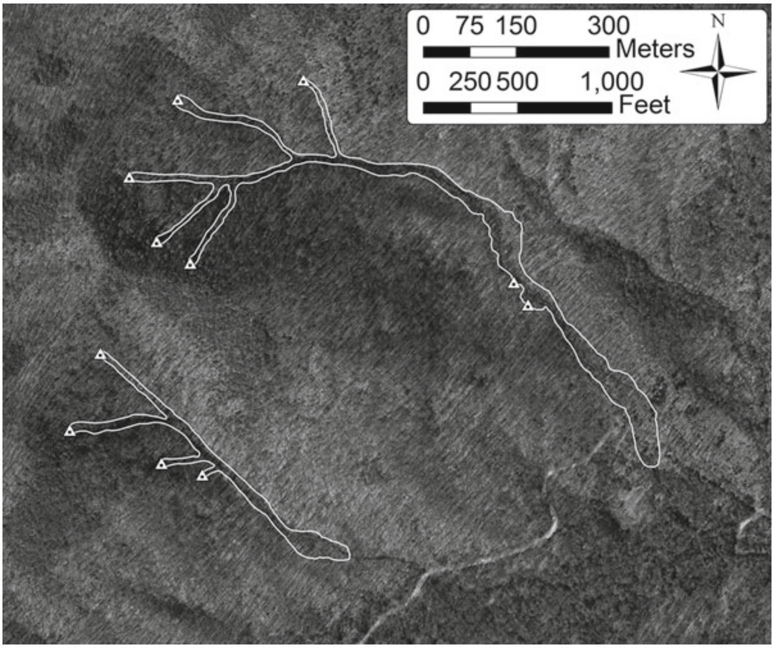


Fig. 9.11 Outlines of tracks of 1977 debris flows visible in 2010 orthophotography of the Rocky Branch area, Bent Creek Experimental Forest, Pisgah National Forest, in Buncombe County North Carolina Debris flow initiation sites shown by triangles (From Wooten et al. 2009b). Vegetative recovery has progressed in the tracks since 1977, and since 1983 as visible in Fig. 9.10. Elevation ranges from 1,152 to 762 m, with lower elevations in the southeast portion of the map. Same view as Figs. 9.5 and 9.10 (Location N in Fig. 9.3 and Table 9.1)

slopes of Mount Mitchell and the Black Mountains. These flows appear to correspond with the occurrence of four separate tropical cyclones in 1972, 1977, 1994 or 1995, and 2004. Clark (1987) reported debris flows during a hurricane in June of 1972 (Agnes) in the area of Mount Mitchell, although the exact location was not specified. As many as 13 of the debris flow tracks are attributable to the 1977 event. Three tracks may correspond with the passage of tropical cyclone Beryl in 1994 or Opal in 1995, and one track probably corresponds with the remnants of Hurricanes Frances and Ivan in September 2004.

The total area of the 83 debris flow tracks for the November 1977 event for the Bent Creek area is 32.8 ha. The 13 tracks on Mount Mitchell and the Black Mountains affected 25.2 ha resulting in a total of 58 ha for the November 1977 event. As in other study areas, the 1977 and 2004 debris flows in the Bent Creek area deposited sediment in areas of pre-existing debris deposits. Neary et al. (1986) point out that although debris avalanching (flows) are destructive events and are major contributors to long term erosion rates, they lead to formation of some of the more productive forest soils. Although the tracks of the 1977 debris flows are still discernable in the Bent Creek area where maximum elevations are on the order of

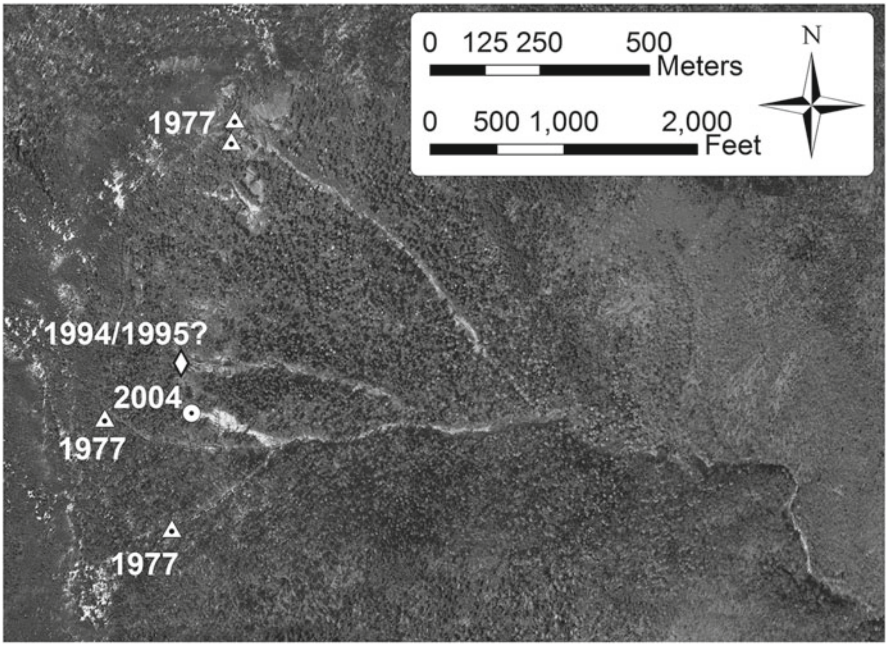


Fig. 9.12 Sparsely vegetated upper portions of tracks from three generations of debris flows in the Black Mountains near Mount Mitchell, North Carolina shown on 2010 orthophotography (initiation sites: *1977 = triangles*, *1994/1995? = diamond*, *2004 = circle*). Debris flow recurrence at steep, high elevation sites can be on decadal time scales; whereas vegetative recovery can be on decadal to centennial time scales. Downslope direction is from west (elev. 2,005 m) to east (elev. 1,260 m) (Location L on Fig. 9.3)

1,150 m; the tracks of 1977 debris flows are more readily visible on the upper slopes of Mount Mitchell and the Black Mountains were elevations range from 2,037 to 1,500 m.

9.4.6 *June 27, 1995: Madison County and Albemarle County Virginia*

On June 27, 1995, a series of severe rainstorms struck the high relief areas of the Blue Ridge Mountains in central Virginia. Approximately 630–770 mm of rain fell over a period of 16 h causing severe flooding and debris flows and slides in rural Madison County in northwestern Virginia (Fig. 9.13) (Morgan et al. 1997). Flooding and landslides destroyed or damaged 1,700–2,000 residential buildings; property damage was estimated to be $112 million. One fatality was also attributed to a debris flow (Wieczorek et al. 1995).

Landslides related to the June 1995 storm were originally mapped by Morgan et al. (1999b). To improve the inventory of debris flows and tracks for the Madison

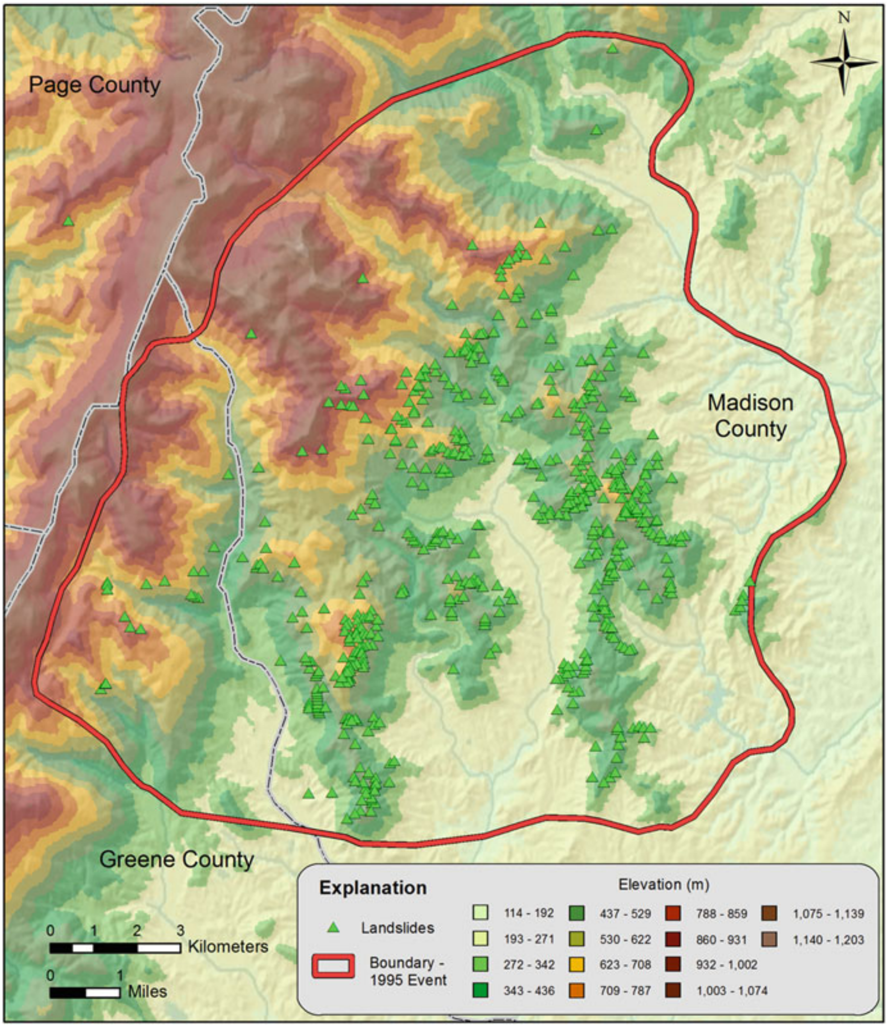


Fig. 9.13 Point locations for 629 landslide (mainly debris flow) sites triggered by the June 27, 1995 storm in Madison County Virginia. Debris flows inundated approximately 600 ha of land here. Map base is a shaded relief map, color-coded by elevation derived from a 30 m digital elevation model (Landslide locations from Morgan and Wieczorek (1996)) (Location Q on Fig. 9.3 and Table 9.1)

County area, we digitized the Morgan et al. (1999b) mapping and identified additional debris flows using 1998 infrared photography and 2002 orthophotography. Based on this work, a total of 629 landslide headscarps or initiation sites were found in both Madison County and northern Greene County occupying an area of about 240 km^2 (24,000 ha) Approximately 600 ha of land were inundated by debris flows and slides.

The largest debris flow occurred along Kinsey Run which damaged a total of 43 ha and contains 29 individual headscarps from multiple coalescing debris flows. The volume of deposited debris attributed to the Kinsey Run debris flow was estimated to be 570,000 m^3 (Mazza and Wieczorek 1997). Much like in the 1969 Nelson County storm, the upper portions of the debris flows exposed bedrock and denuded hillsides of soil, causing significant sediment transport during a single catastrophic event. Eaton et al. (2003a) estimated that the average basin-denudation rates for the upland areas in Madison County were approximately 330 mm during the storm, accounting for 27–65 % of the long-term denudation that would have occurred in 2,500 years.

Numerous debris flows stripped vegetation from the hillsides, sometimes along the entire length of larger debris flows. The rapidly moving flows had sufficient force to snap meter-wide trees at their base (Wieczorek et al. 2000). This vegetative material added significantly to the volume of debris, causing log jams and backups along paths (Wieczorek et al. 2000). The recovery rate of various plant species along the Kinsey Run debris flow was studied and it was found that pioneer species like black locust (*Robinia pseudoacacia)* and (non-native) tree-of-heaven (*Ailanthus altissima*) were the first woody plant types to reestablish and compete with other native species (Eaton and Reynolds 2002).

Landslides were also reported later in the evening on June 27 about 45 km southwest of Madison County along the North Fork of the Moormans River within Shenandoah National Park in western Albemarle County. While no official storm totals exist, eye-witness accounts indicate that rainfall totals varied from 279 to 635 mm (Morgan and Wieczorek 1996; Eaton et al. 2003b). Mapping and field work completed by Morgan and Wieczorek (1996) identified 72 initiation sites of debris flows and slides, many of which were hidden by thick forest cover. Additional interpretation of the area using 1997 infrared photography and 2002 orthophotography allowed for more detailed mapping of individual tracks. Within the 13 km^2 (1,300 ha) watershed, we calculated that a nearly 50 ha area was inundated by debris flows, many of which coalesced into Moormans River. Debris surged downstream into the Sugar Hollow Reservoir, the main water source for Charlottesville, reducing its holding capacity by 15 % (Eaton et al. 2003b).

9.4.7 September 2004 Frances and Ivan: North Carolina

In September 2004, intense rainfall from the remnants of Hurricanes Frances (Sept. 7–8) and Ivan (Sept. 16–17) triggered at least 400 landslides that caused five deaths, destroyed at least 27 residential buildings, and disrupted transportation corridors throughout western North Carolina (Collins 2008, 2014; Witt 2005; Wooten et al. 2005, 2007). Nineteen western North Carolina counties were federally declared disaster areas as a result of flooding and landslide damage from the storms. Known landslide events occurred in a 200 km-long swath in the Blue Ridge Mountains from Macon County northeast to Watauga County North Carolina. Major damage

Fig. 9.14 Large woody debris and boulder deposits along the track the Bear Drive Creek fill failure-debris flow that occurred during Hurricane Frances, September 6–8, 2004. The debris flow initiated as a fill failure on the Blue Ridge Parkway and scoured 8.61 ha along a 2.44 km-long track. Location is in the Pisgah National Forest near Curtis Creek approximately 2 km downslope from the debris flow initiation site. Direction of flow to the right. Geologist at bottom right for scale (November 17, 2004 NCGS photo)

occurred on the Blue Ridge Parkway including three major debris flows that initiated from fill failures that scoured destructive paths downslope into the Pisgah National Forest (Collins 2008; Latham et al. 2009). Figure 9.14 shows imbricated boulder deposits and large woody debris along the track of the Bear Drive Creek fill failure-debris flow near Curtis Creek. Originating at elevations of 1,116, 1,412 (Bear Drive Creek), and 1,349 m along the crest of BRE, these debris flows scoured tracks 2.44, 3.05, and 3.27 km-long, creating canopy gaps of 6.1, 8.0 and 8.61 ha respectively in the headwaters of the Catawba River.

The deadliest of the September 2004 debris flows occurred along Peeks Creek which resulted in 5 deaths (including an unborn child), 2 serious injuries requiring amputation, and 16 destroyed residences (Latham et al. 2006, Witt 2005, Wooten et al. 2006, 2008a). Residents reported that the debris flow occurred at about 2110 EST on September 16, 2014, corresponding to the time of heaviest rainfall from a spiral rain band as it passed over Macon County. The debris flow began on the steep (33–55°) forested slopes of Fishhawk Mountain and traveled 1.5 km through the Nantahala National Forest before entering private land where the fatalities and destroyed homes occurred in the run out zone (Fig. 9.1). The 3.6 km-long track of the debris flow covered an area of 13.8 ha from the upper, northeast-facing slopes of Fishhawk Mountain (Fig. 9.17) downstream to the Cullasaja River. Calculated estimates of a peak velocity of 14.8 m per second, and discharge values ranging from 1,275 m^3 per second to 1,980 m^3 per second for the debris flow attest to its destructive power. Pre-existing debris deposits exposed along the path of the Peeks Creek debris flow indicate that at least two debris flows had occurred before the September 2004 event. Clingman (1877) reported 'water spouts' on the southwest and northeast sides of Fishhawk Mountain in 1876 that, from his description, were likely debris flows (Witt 2005).

Of the 48 landslides attributed to Frances and Ivan in Macon County, 33 were debris flows that initiated on relatively undisturbed forested slopes, mainly on the Nantahala National Forest. The total area of the 27 mapped debris flow tracks throughout Macon County is 26.9 ha, with over half of that being the 13.8 ha of the Peeks Creek debris flow. The tracks of the 184 mapped debris flows in western North Carolina attributed to Frances and Ivan constitute a total disturbed area of 83.1 ha. Of this total, 45.6 ha (54.8 %) resulted from debris flows that originated on slopes modified by human activity, whereas 37.1 ha (44.6 %) resulted from those that originated on forested slopes not modified by human activity.

9.4.8 July 14–15, 2011 Balsam Mountain Debris Flows: North Carolina

On the night of July 14–15, 2011, a stationary thunderstorm storm over the GSMNP caused flash flooding in Straight Fork and triggered debris flows on Balsam Mountain (Miller et al. 2012). The flash flooding resulted in major damage to the Eastern Band of Cherokee Indians fish hatchery on Straight Fork where damage estimates ranged from $30,000 to $50,000 (Lee et al. 2011). Rainfall measurements made from the high elevation Duke University GSMNP rain gage network (Tao et al., 2012) indicate that the storm produced intense rainfall of 125 mm in a 4-h period (Miller et al. 2012) and set off 21 debris flows on the slopes of Balsam Mountain (elevation 1827 m), upstream of Straight Fork (Fig. 9.15). Here the high elevation peaks and watershed divides of GSMNP likely contributed to orographic forcing of rainfall (Tao and Barros 2014) which in combination with steep slopes predisposes these locations to debris flow activity.

In September 2011, NCGS geologists made field investigations of three debris flows in the Gunter Fork watershed on the northeast slopes of the Balsam Mountain (Tao and Barros 2014). An additional 18 debris flows were also identified on the southwest slopes of Balsam Mountain through the analysis of 2013 aerial photography. Scoured tracks, downed trees in initiation sites, and accumulations of large woody debris along the tracks are visible in the 2013 imagery. The 18 debris flows on the southwest side of Balsam Mountain all fed in into the upper reaches of Balsam Corner Creek or its tributaries which then flow into Straight Fork. National Park Service staff confirmed that the damage from debris flows in Balsam Corner Creek occurred in the July 14–15, 2011 event. Southworth et al. (2012) previously

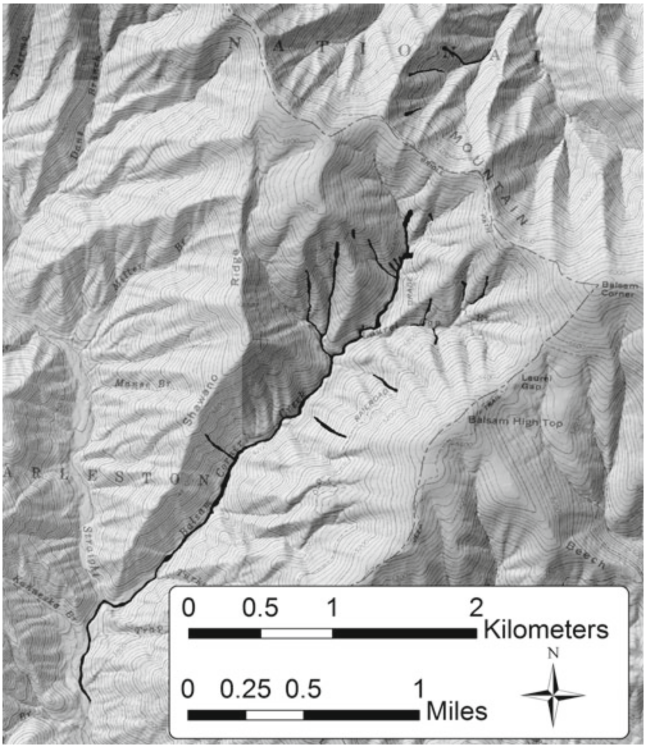


Fig. 9.15 Tracks of 21 debris flows (*black*) triggered by the July 14–15, 2011 storm near Balsam Mountain, GSMNP, North Carolina. Coalescing debris flows scoured a 4.6 km reach of Balsam Corner Creek. Map base is an excerpt of the USGS 7.5-min Luftee Knob quadrangle superimposed onto a 6 m-pixel resolution LiDAR Hillshade map (Location Y on Fig. 9.3 and Table 9.1)

mapped numerous pre-existing debris flows in the headwaters of Straight Fork immediately west of the headwaters of Balsam Corner Creek indicating that the area is prone to debris flow activity.

The track area for the Balsam Mountain debris flows measured from aerial photography is 13 ha, with 12 ha of that total contributed by the Balsam Corner debris flows. The damage to the riparian area from the main debris flow visible in the aerial imagery extends 4.6 km along Balsam Corner Creek. The debris flows in Balsam Corner Creek are significant not only because of the riparian damage along 12.9 ha of tracks, but because they likely contributed to the flooding at the Cherokee Fish hatchery 13.3 km downstream, and 760 m lower in elevation from the initiation sites. This event demonstrates that summer thunderstorms with the potential to trigger debris flows and flash flooding, can develop with little, if any, warning and cause significant damage to resources and communities located several km downstream.

9.4.9 2013 Extended Period of Above Normal Rainfall: North Carolina

Record amounts of rain fell in western North Carolina in between January and August of 2013. By the end of August, the National Weather Service had recorded 1,730 mm of cumulative rainfall for the year at the Asheville airport, 585 mm above a 30-year normal (Fig. 9.16). From July through August 2013, 335 reported landslides of various types occurred throughout western North Carolina (Gibbs 2013; Wooten et al. 2014). Six storms within this period triggered landslides, and the storm events of January 14–18, July 2–7 and July 27, 2013 were federally declared disasters for landslides and flooding. During this timeframe the NCGS, in response to requests for technical assistance, investigated 33 of the reported landslides that resulted in 5 destroyed or condemned homes, and damage to 4 other homes and 24 roads.

Information to date indicates that the vast majority of the 335 reported slope failures involved slopes modified by human activity, mainly embankment slope failures that mobilized into damaging debris flows. Only two landslides that occurred during this period are known to have originated on natural (i.e., unmodified by human activity) slopes. This finding indicates that although record rainfall amounts occurred throughout the region, rainfall was mostly below thresholds necessary to trigger slope failures on forested slopes not modified by human activity.

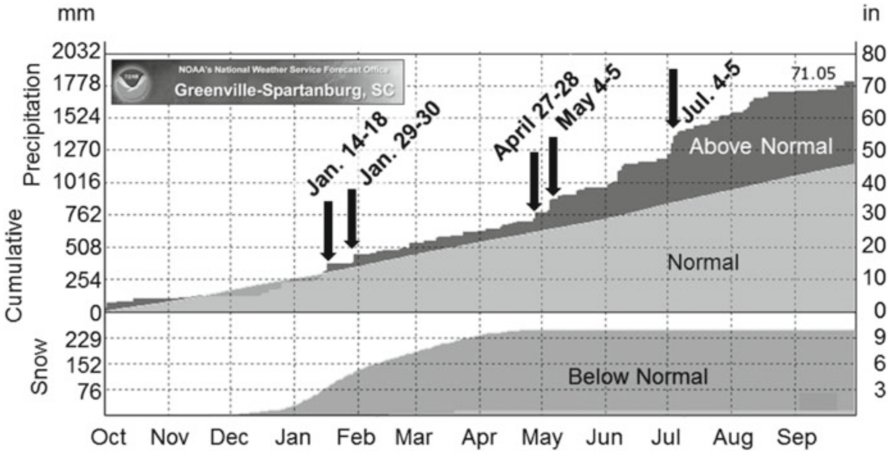


Fig. 9.16 Precipitation chart for the period October 2012 through September 2013 showing rainfall departure from the 30-year normal at the Asheville Regional Airport (KAVL) determined by the National Weather Service. The January 14–18, 2013 event began an extended period of above normal rainfall. *Black arrows* denote rainfall events that triggered landslides throughout western North Carolina (Note: Snow season typically ends in April. The graph shows below normal snow accumulation remained constant after April)

Two debris flows that occurred during this period are noteworthy with respect to impacts of forest structure and riparian areas. On December 16, 2013 a major debris flow occurred on US 441 in the GSMNP, cutting off the main transportation route through the Park from Cherokee, North Carolina to Gatlinburg Tennessee. Accounts by National Park Service staff and field investigations by the NCGS indicate that a debris slide began in road fill and mobilized into a rapidly moving debris flow. About 68,000 m^3 of road fill and the underlying colluvial deposits were involved in the debris flow that removed vegetation and scoured 1.4 ha of slopes that drain into the Beech Flats Prong of the Oconaluftee River. One of the two landslides that initiated on naturally forested slopes not modified by human activity was the July 4, 2013 debris flow on the Nantahala National Forest along Herron Branch, a tributary to the Tuckasegee River in western Jackson County. The scoured riparian area of the 2.1 km-long track was about 3.4 ha as mapped from field investigations. The debris flow did not damage any structures, but large dams of woody debris remained in the track near private homes built along Herron Branch.

A similar, but lesser period of above normal rainfall occurred between September 2009 and February 2010 (Bauer et al. 2010). Western North Carolina received about 1,060 mm of rain, approximately 400 mm above normal. Rain events during this period triggered over 40 landslides; 15 of those investigated by the NCGS were on slopes modified by human activity.

9.5 Landform-Geologic Controls on Debris Flows Initiation

Bedrock structure and to a lesser degree lithology influence the development of geomorphic features prone to debris flows at a variety of scales. At a regional, multi-basin scale the BRE extending from northeast Georgia to northeast Virginia (Fig. 9.4) makes it prone to debris flow activity. Although the geologic origins of the BRE have long been debated (Soller and Mills 1991) the overall southwest to northeast trend of major geologic features in the southern Appalachian orogen (Hatcher 2010; Hibbard et al. 2006) strongly influence the parallel trend in the BRE. The distribution of the generalized locations of areas affected by debris flows for the July 15–16, 1916 event, and the locations of mapped debris flows for the August 13–14, 1940 event in North Carolina, and the August 19–20, 1969 (Camille), the June 27, 1995 events in Virginia generally correspond with the BRE (Figs. 9.3 and 9.4). Geologically, the high relief, steep slopes, and highly dissected nature (a possible reflection of the spatial frequency of bedrock discontinuities) of the BRE make it susceptible to debris flows. Orographic forcing of rainfall along the BRE is shown by the greater rainfall totals along the BRE as compared to the surrounding regions for the storms of July 15–6, 1916 (Scott 1972, Witt 2005), August 10–17, 1940 (US Geological Survey 1949; Wieczorek et al. 2000, 2004; Witt 2005) and June 27, 1995 (Wieczorek et al. 2000, 2004). Steep topography in Madison County, Virginia along the Blue Ridge Mountains likely favored the development of heavy rainfall during the 1995 storm due to orographic lifting (Pontrelli et al. 1999), although the relation between orographic lifting and the heavy rainfall in Nelson County during Hurricane Camille remains unclear (Williams and Guy 1973).

Similar geologic controls on the configuration of landforms prone to debris flows occur in the mountain headwaters of river basins and individual watersheds. For example, the majority (25 of 33) of the debris flows related to the September 2004 rainfall from Frances and Ivan in Macon County, North Carolina occurred on the steep eastern flanks of the Nantahala Mountains Escarpment (NME) (Wooten et al. 2008a). Here, the 100 km^2, 25 km-long NME forms an abrupt topographic rise that contains the headwaters of east-flowing tributaries of the Little Tennessee River (Fig. 9.17). The main northwest and north trends, and secondary northeast trends of its different segments parallel numerous topographic lineaments with orientations similar to measured bedrock discontinuities in the area, reflecting the influence of bedrock structures on the NME. Wooten et al. (2008a) used the term 'structural-geomorphic domain' for such features. Orographic forcing of rainfall by the NME occurred during Hurricanes Frances and Ivan. The Mooney Gap rain gage (elevation

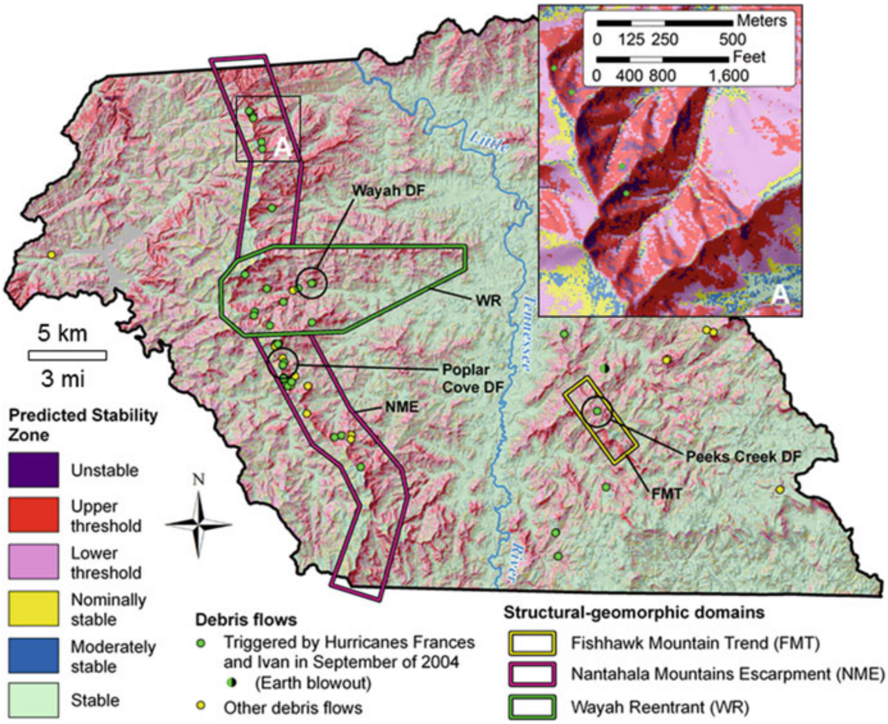


Fig. 9.17 Structural-geomorphic domains in relationship to debris flow locations for Macon County. Map base is a shaded relief 6 m LiDAR DEM overlain by a stability index map (Modified from Sheet 2 of Wooten et al. 2006). Unstable (*purple*) and upper threshold (*red*) stability zones portrayed on the map highlight the topographic features of the structural-geomorphic domains discussed in the text. Inset *A* shows enlarged area for color resolution (Reproduced from Wooten et al. (2008a)). DF = named debris flow location. Poplar Cove debris flow is location S on Fig. 9.3 and Table 9.1

1,364 m) on the crest of NME at the USDA Forest Service Coweeta Hydrologic Laboratory received 100 mm more rainfall in each storm than did several lower elevation gages in the area (Wooten et al. 2008a). At the watershed scale, the September 2004 debris flows were concentrated within the Wayah Creek and Poplar Cove erosional reentrants on the NME, which are likely controlled by bedrock structures that intersect the NME. The Fishhawk Mountain trend, where the 2004 Peeks Creek debris flow originated, has a similar orientation and configuration of geologic structures as the NME, but is a smaller-scale structural geomorphic domain. Perhaps the best example of where bedrock structure can be related to a concentrated debris flow activity is the Deep Gap area of Watauga County (Fig. 9.7, and Sect. 9.8), where 700 debris flows occurred during the August 13–14, 1940 storm (Wieczorek et al. 2004; Wooten et al. 2008b). Here, Elk Creek and its tributaries form a highly dissected erosional reentrant within the BRE that corresponds with WNW-trending ductile faults (Bryant and Reed 1970) and other WNW-trending topographic lineaments that intersect the BRE (Wooten et al. 2008a, b; Gillon et al. 2009).

At the hillslope scale, individual debris flows typically originate in convergent colluvial accumulation zones or catchments called hollows (Hack and Goodlett 1960) that occur on steep hillslopes above the highest extent of channelized streams in mountainous terrain (Fig. 9.18). Colluvial hollows are widely recognized geomorphic features known to be initiation sites for debris flows triggered by heavy rainfall in mountainous terrain (Kochel 1987; Reneau and Dietrich 1987). Residence time of colluvium within individual hollows between successive debris flow events can be more than 20,000 years. The two oldest radiocarbon ages for colluvium in hollows determined by Hales et al. (2011) were 23,989 ± 238 (S.D.) and 23,546 ± 265 radiocarbon years before present in one trench. Samples collected at higher levels in

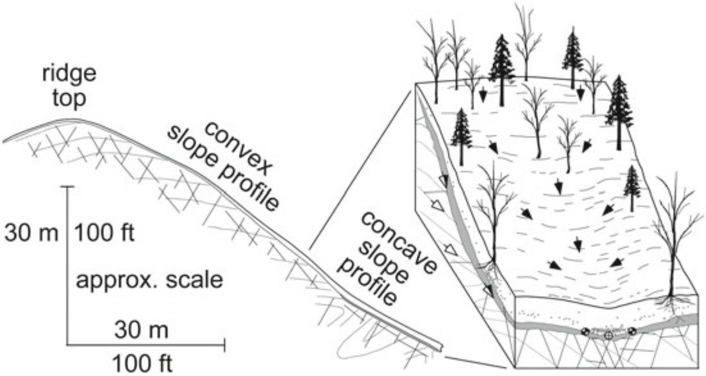


Fig. 9.18 Generalized conceptual model of a hillslope profile (*left*) and hollow (*right*) with colluvial soil layers overlying bedrock (shown with lines depicting curved and planar discontinuities). *Black arrows* depict directions of surface water flow; *black and white arrows* depict shallow groundwater seepage along the colluvium-bedrock contact; *white arrows* depict bedrock fracture flow. *Circles* depict out-of-plane seepage

the same trench had ages that ranged from 4,278 ± 129 to 569 ± 61 radiocarbon years before present. In another pit ages ranged from 8,065 ± 95 to 2,964 ± 112 radiocarbon years before present.

Workers have long recognized the influence of bedrock structure (e.g., planar discontinuities such as fractures, bedding and foliation planes) on the formation hollows in the SAH (Grant 1988; Wooten et al 2008a; Sas and Eaton 2008). Differential weathering of bedrock and enhanced weathering along intersecting discontinuities influences the formation of trough- or wedge-shaped depressions in bedrock surfaces that underlie hollows (Fig. 9.18). In some locations underlain by moderately dipping (less than 45°) layered metasedimentary rocks, the opposing slope (or scarp slope) of the landform is steeper, and contains more colluvial hollows than the slope that coincides with the dip direction (Wooten et al. 2003a). The convergent surface and subsurface geometries of hollows contribute to the accumulation of colluvial soil, which along with the build-up of excess pore-water pressures from infiltrating rainfall and fracture flow along bedrock discontinuities (Sas and Eaton 2008), combine to initiate debris flows. The relationships between topographic convergence in hollows, soil moisture content, and root cohesion are discussed in detail in Sect. 9.7.

Of the 880 debris flows and slides in the NCGS landslide geodatabase where the geomorphic shape of the initiation sites was categorized, 68 % (601) occur on concave slopes or hollows; 18 % (157) are on convex slopes; and 14 % (122) are on planar slopes. Although the majority of debris flows originate in colluvial soil, a lesser number initiate in residual soil derived from the in situ weathering of bedrock. Where detailed studies were done at 21 debris flow initiation sites in western North Carolina Wooten et al. (2012) found that soil at 65 % (15) of the debris flow detachment surfaces to be colluvial soil, and soil at 35 % (6) sites to be residual soil. Steep slopes and relatively thin soil characterize debris flow initiation zones. Slopes at the detailed study sites range from 22° to 40°; inferred detachment depths range from 0.6 to 3 m, which generally correspond with soil depth. Ground slopes (28–44°) and soil depths (0.5–2.4 m) were within similar ranges at 28 debris flow sites investigated in Macon County (Wooten et al. 2008a).

Relationships between bedrock type and debris flow occurrence are less clear. In the Virginia Blue Ridge Mountains, bedrock resistance to weathering contributes to the ruggedness of the topography and thus to the overall steepness of the area. Gryta and Bartholomew (1989) conclude that bedrock lithology is related to preferred debris flow initiation by contributing to topographic relief as a function of resistance to weathering in areas that experience heavy rainfall. In the Nelson County area, a majority of 1969 debris flows initiated in foliated biotite gneisses with steep topography. In contrast, low-relief areas with similar bedrock lithologies did not experience debris flows, even if heavy rainfall was recorded (Gryta and Bartholomew 1989). Morgan et al. (1997) concluded that bedrock type had a negligible effect on debris flow initiation during the 1995 Madison County storm, except in relation to soil and colluvial development. As in Nelson County, the bedrock underlying the areas of debris flows is primarily highly resistant bedrock, commonly granitoids and granitic gneisses, interspersed with high-strain mylonitic zones (Eaton et al. 2004).

There was, however, a minor correlation between the phyllitic metasedimentary units within the Catoctin Formation (metabasalts) and debris flow initiation in western Nelson County, although only a few debris flows failed in this area due to lesser rainfall totals (Gryta and Bartholomew 1989). A similar correlation was noted by Witt and Heller (2014) in Page County in the phyllitic units of the Catoctin Formation; two debris flows and one potential debris flow occurred in phyllites with a foliation dipping to the SE, parallel to slope. Clusters of August 1940 debris flows in western North Carolina correspond with highly dissected areas underlain by Proterozoic granitic gneisses in northwest Watauga County, and in the Deep Gap area of the BRE (Wooten et al. 2008b; Gillon et al. 2009). Further analysis is needed to determine if this apparent correlation results from bedrock lithologies, bedrock structure, meteorological affects, or some combination of factors.

Several investigators have documented slope instability associated with sulfidic rocks in the southern Appalachians. Clark et al. (1987) reported an increased severity of [debris] slides and flows in pyrite-rich rocks of the Anakeesta Formation in the GSMNP. During the May 5–7, 2003 storm in western North Carolina (location T, Fig. 9.3 and Table 9.1) six debris flows originated in embankments constructed with pyrite-bearing rock derived from the underlying sulfidic and graphitic metasedimentary rocks (Wooten and Latham 2004). Latham et al. (2009) reported on rock slides that involved sulfidic and graphitic rocks on the North Carolina portion of the Blue Ridge Parkway.

The weathering of sulfidic rocks can decrease the stability of slopes in several ways (Bryant et al. 2003). Sulfuric acid produced by the breakdown of the iron-sulfide minerals pyrite and pyrrhotite reduces the shear strength of rock and soil. The acid accelerates the rate of rock weathering, and over time the rock fragments in a fill will behave mechanically more like soil, and less like rock. The acid also attacks the clay mineral structure in soil and decreases the cohesion, thereby possibly reducing the shear strength of the soil component of the fill. Sulfidic materials are also susceptible to heaving due to mineral expansion as sulfide minerals oxidize when exposed to moisture. Heaving can increase the porosity and decrease the relative density of the material allowing for more infiltration and the destabilizing build-up of pore-water pressure. Graphite, typically present in sulfidic rocks in western North Carolina, may reduce the shear strength of rock and soil materials.

9.6 Anthropogenic Influences

Anthropogenic influences on hillslopes can have destabilizing effects (causes) which predispose them to slope failures in precipitation events (triggers). Inadequately constructed and maintained fill slopes are a well-documented source of debrisflows in mountainous terrain (Collins 2008; Wooten et al. 2009a, 2014) (Fig. 9.14). Excavations (i.e., cut slopes) into hillsides can also destabilize slopes (Collins 2008; Gillon et al. 2009; Latham et al. 2009); however, debris flows that originate from fill failures typically travel greater distances and impact larger areas. Of 3,267 landslides analyzed in the NCGS landslide geodatabase, 380 (11.6 %) are categorized as cut slope failures, and 421 (12.9 %) are embankment (fill) failures. The remaining 2,466 landslides are categorized as initiating on slopes not modified by ground-disturbing human activity; however 1,752 of those occurred on unforested slopes during the August 1940 storm in Watauga County. Forest cover is an important stabilizing factor, particularly on mountain slopes. This factor and consequences of forest removal are addressed in Sect. 8.8. Given that the vast majority of those unforested slopes likely resulted from human activity, as many as 78 % of the total of 3,267 landslides analyzed may have been influenced in one way or another by humans. Examples of landslides related to ground-disturbing activity follow to help illustrate their spatial impacts on the landscape.

The largest known single debris flow event related to human activity in western North Carolina occurred on August 13, 1916 when the original earthen dam at Lake Toxaway failed when a low pressure system dropped 584 mm of rain over Transylvania County (Wooten et al. 2003a, b). The catastrophic dam failure triggered a debris flow covering a minimum area of 122 ha along an 11.4 km reach of the Toxaway River where it flowed down the BRE and into the adjacent Piedmont of South Carolina (location C Figs. 9.3 and 9.6). The enormous outflow of the breached dam, calculated to be on the order of 8,665 m^3 per second (Wooten et al. 2010a) scoured the steep valley walls and transported boulders as large as 18 m long. Deposits from this event are preserved in Gorges State Park and beneath the upper portion of Lake Jocassee. The debris flow scoured to bedrock a 3.7 km length of the upper reach of the river from Lake Toxaway downstream to Wintergreen Falls, a condition that persists today. Boulder levees and other deposits left by the debris flow below Wintergreen Falls now support vegetation. Initial revegetation of the deposit areas probably began soon after the debris flow. Tree ring studies in Gorges State Park (Wooten et al. 2003a, b; 2004) show 1917 to be the beginning growth year for a pitch pine (*Pinus rigida*) now growing on the 1916 boulder deposits near the confluence of Bearwallow Creek and the Toxaway River.

Three major debris flows that damaged the Blue Ridge Parkway and slopes below on the Pisgah National Forest during Frances and Ivan in September 2004 originated as fill slope failures (Collins 2008, Latham et al. 2009). Collins (2014) assessed 105 of the hundreds of landslides on the Pisgah and Nantahala National Forests triggered by rainfall from the remnants of Frances and Ivan and found that 78 (74 %) were road-related failures, mainly fill slope failures. In 2010 a retaining wall failure that mobilized into a 0.82 km-long debris flow damaged three houses and 2.6 ha of mountain side riparian area in Haywood County, North Carolina (Witt et al. 2012). More recently, during the period of extended above average rainfall throughout western North Carolina in 2013 (Sect. 8.4.9) only two of the reported 335 landslides occurred on slopes not modified by human activity. Although the assessment of the 2013 landslides in western North Carolina is incomplete, this high proportion of landslides related to human activity points to the destabilizing influence that some slope modifications and vegetation removal can have.

9.7 Ecohydrological Controls on Debris Flows Initiation

The historical range of variation in landslides is important to consider in the context that the past may be an adequate predictor of the future. However when novel conditions occur, as are expected with changes in precipitation amount and distribution (Ford et al. 2011) and changes in species' ranges (Hansen et al. 2001; Burrows et al. 2014), it is important to consider the ecological and hydrological controls on landslide initiation. The large majority of landslides that initiate in the SAH are 'shallow' landslides that initiate in the soil column and often form debris flows. The spatial distribution of these shallow landslides and their frequency is strongly controlled by the cohesion of the soils (Crozier et al. 1990; D'Odorico and Fagherazzi 2003). Where soils have no cohesion, landslides are smaller and more frequent than in cohesive soils. Cohesive soils are thicker (i.e., can support a greater volume of soil), require larger precipitation events (usually tropical cyclones) to initiate slides that are of a greater volume (magnitude) (Gabet and Dunne 2003). In the southern Appalachians the steep, colluvial soils that initiate landslides typically have a low soil cohesion, so the cohesive strength provided by the roots (this is technically an apparent cohesion, see Schmidt et al. (2001) for a full derivation) of plants acts as a primary driver of the spatial and temporal distribution of shallow landslides. In addition to the provision of cohesive strength, there are a number of additional ways that vegetation affects landslide initiation including adding weight from the stem and aboveground biomass, altering shallow surface hydrology, and affecting soil structure particularly by adding macropores (Hales et al. 2009).

Because of the important role that vegetation plays in influencing the distribution and thickness of soils, landslides initiate where additional cohesion provided by roots is at a minimum (Roering et al. 2003; Hwang et al. 2015). The role that vegetation plays in controlling the initiation of southern Appalachian debris flows, can be challenging to generalize due to the interactions that occur among forest ecology and physiology, and hydrology (henceforth ecohydrology). Differences among species and forest structures are found not only in transpiration and interception rates (Ford et al. 2012), but also in root system architecture, root density, root strength, and how these change with local soil moisture conditions driven in-part by topography.

The additional soil shear strength provided by roots is a large proportion of total shear strength of the thin (average soil depth is 0.9 m), low (soil) cohesion, colluvial soil in the southern Appalachians (Band et al. 2011; Hales et al. 2009). For example, the apparent cohesion provided by roots can represent up to 100 % of the cohesive strength of hillslope soils (Abernethy and Rutherfurd 2001). Roots add shear strength through a frictional coupling with the surrounding soil particles (Schwarz et al. 2010). The shear strength provided by roots is an 'apparent' cohesion, or an additive force (of a magnitude between 0 and 50 kilopascals) when calculating the overall stability of a slope (Waldron 1977). Before a landslide can initiate, the total tensile strength of all roots crossing the slide plane must be exceeded (Schmidt et al. 2001). This is typically envisioned in terms of a dynamic bundle of roots with different elasticities and tensile strengths that break progressively (Pollen and Simon 2005; Schwarz et al. 2010). Thus higher below-ground biomass imparts higher soil cohesion. However, both the elasticity (Schwarz et al. 2010) and tensile strength (Hales et al. 2009) of roots vary with their diameter. The distribution of biomass by soil depth and root diameter is also is also important (Hales and Miniat 2015). While forest ecologists have long recognized the relationship between below-ground biomass, root diameter distribution and soil resources (Albaugh et al. 1998; Joslin et al. 2000; Keyes and Grier 1981), these relationships have been largely absent in the theoretical considerations of predicting whether slopes will fail.

Debris flows typically initiate on the steep upper slopes (Wooten et al. 2008a), above the highest extent of stream channels (0 order basins), where the topography is dissected into minor ridges called noses, and convergent colluvial accumulation zones (Fig. 9.18) called hollows (Hack and Goodlett 1960). Hollows are wetter and have roots that are weaker, with more even vertical root distributions when compared with noses (Figs. 9.19 and 9.20) (Hales et al. 2009). Although roots are exponentially distributed with depth in hollows and noses (Fig. 9.19), soils in hollows tend to have a higher number of roots at depths greater than 50 cm compared to noses. This greater number is important for slope stability, as the total strength of the soil is dependent upon the total tensile strength of roots crossing the failure plane. Hollows, in this case, would have a greater frequency of roots relative to other parts of the landscape. Tree root tensile strength is controlled by the amount of cellulose within the root structure; hence, larger diameter roots that have a greater number of cellulose microfibrils are stronger (Genet et al. 2005; Hales et al. 2009). This effect is modified by soil moisture content and wood structure (Fig. 9.20) (Hales et al. 2013). In the same way that wet wood is weaker than dry wood, root tensile strength decreases in wetter roots through the breakdown of electrostatic bonds between cellulose fibrils at the microscopic level (Winandy and Rowell 2005). The relationships among geology, topographic convergence, soil moisture content, and hollow stability provides a framework for estimating regional apparent root cohesion and how it might change with changing land cover and land use.

Plants also alter soil moisture primarily through transpiration and interception losses and the development of macropores that increase the transmissivity of the soil and reduce the magnitude of the pore pressures produced by any given storm (Selby 1993). During transpiration, plants remove water from the soil column as it is lost from leaf surfaces in the process of CO_2 uptake. In the soil, there is a concurrent increase in apparent cohesion through the addition of a matric suction force. Matric suction is the capillary stress formed in partially saturated soils and is dependent on the soil moisture content and soil matrix properties (Selby 1993). The total amount of apparent cohesion added to the soil by suction is reduced during large storms, as plants cease to transpire when leaves are wet and atmospheric humidity is near saturation. Interception losses are the amount of precipitation that is intercepted by plant and litter surfaces and subsequently evaporates. These losses reduce the total volume of water added to the soil during precipitation events. During a rain event, these losses introduce a lag in the time taken to reach maximum soil pore water pressure (Keim and Skaugset 2003). Landslide initiation tends to occur during large storms

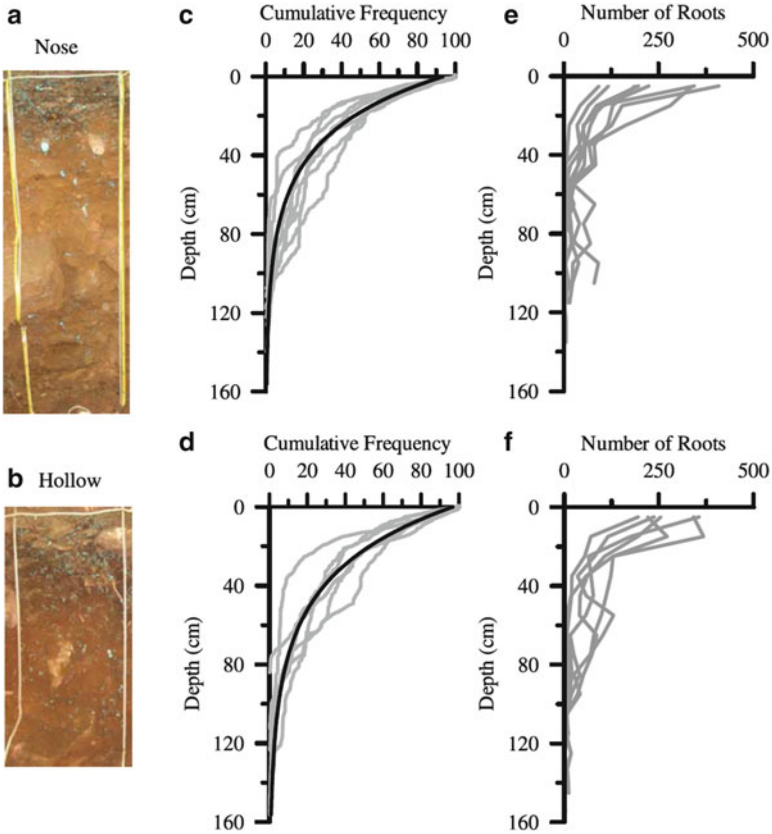


Fig. 9.19 The distribution of roots as a function of soil depth for 16 pits—9 were located on noses and 7 in hollows. (**a** and **b**) Photographs are vertical sections of two northern red oak (*Quercus rubra*) pits dug within 20 m of each other. The diameters of the blue painted roots (high reflectance areas) were measured in an image analysis program to calculate the depth distributions. (**c** and **d**) The cumulative frequency of the number of roots as a function of depth, with gray lines representing individual pits, while black lines are the modeled mean of all pits. (**e** and **f**) The absolute number of roots binned at every 10 cm depth interval, which provides an approximate measure of root area ratio. *Gray lines* are individual pits (From (Hales et al. 2009)

when transpiration is minimal and soils are at or near saturation and suction forces are low (Godt et al. 2009; Montgomery and Dietrich 1994). As a result, plants primarily affect soil shear strength through the added shear strength of roots distributed throughout the soil column rather than through transpiration and interception (Pollen and Simon 2005; Schwarz et al. 2010).

In summary, vegetation is a strong control on size, spatial distribution, and frequency of landsliding in the southern Appalachians. Vegetation serves to both mitigate and promote landslide initiation, with the primary driver of this being the support provided by the roots. Densely rooted forests are more resistant to the effects of large storms, despite having a larger stems that add more weight to the soil, because of the mitigating effects of a large, strong root mass, and more efficient

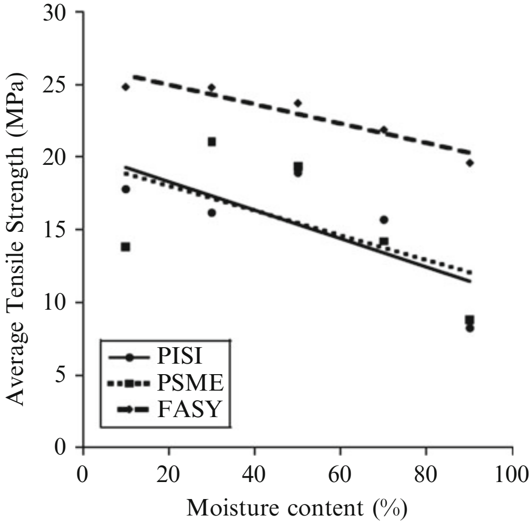


Fig. 9.20 Average root tensile strength as a function of laboratory-controlled root moisture content for species representing two main root xylem architecture types. European beech (FASY; *Fagus sylvatica*), a hardwood with more evolutionary advanced, stronger xylem; and Sitka spruce (PISI; *Picea sitchensis*) and Douglas fir (PSME; *Psuedotsuga menziesii*), coniferous trees with evolutionarily older, weaker xylem. Within each wood type, the wetter the root, the less force required to make the root fail (Modified from Hales et al. 2013)

transpiration. The large roots of trees also increase the porosity and permeability of soils through the development of macropores, reducing the likelihood of high pore pressures required to initiate landslides.

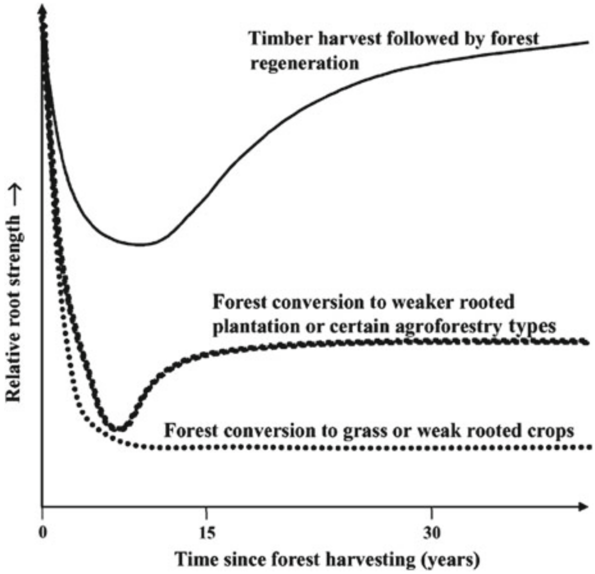
9.7.1 Southern Appalachian Land Use and Slope Stability

Humans have made extensive changes to land cover and land use in the southern Appalachians. Forest types have been affected by land-use change to varying degrees, with high-elevation, northern hardwood forests remaining less affected by development than lower elevation, cove hardwood forests. For example, up to 70 % of the lower elevation cove hardwood forests have been altered by various disturbance processes (Turner et al. 2003). Land-use changes have affected landslide distributions through changes in vegetative land cover. Forests, with deeply rooted trees on cohesive soils have been replaced with agricultural and pasture lands that have shallowly rooted grasses, crops, and shrubs on less cohesive, weak soils. Replacement of trees with grasses, crops and shrubs reduces the apparent root cohesion to values <10 kPa (Schmidt et al. 2001), meaning that shear strength of soils is dependent primarily on the cohesive and frictional properties of the soil particles. Reduction of apparent root cohesion can increase both the number and frequency of shallow landslide events (Gabet and Dunne 2003).

The species and age structure of forests has also changed, with invasive insects and pathogens causing mortality to specific tree species and with forest harvesting (Sakals and Sidle 2004). Recent introductions of two invasive species, the chestnut blight (*Cryphonectria parasitica*), and the hemlock woolly adelgid (*Adelges tsugae*), have functionally removed American chestnut (*Castanea dentata*) and eastern hemlock (*Tsuga canadensis*) trees from southern Appalachian forests. The species that is increasing more than any other in response to eastern hemlock loss is the rhododendron shrub (Ford et al. 2012). As shrubs generally have weaker roots than trees (Hales et al. 2009), soils likely will become weaker over time in these impacted forests. Observational records show that southern Appalachian landslide initiations appear to be strongly concentrated in areas containing this shrub. Additionally, harvesting changes the age structure of the forest and thus affects landslide -susceptibility (Fig. 9.21) (O'Loughlin and Watson 1979; Sidle et al. 2006). After harvest, tree root strength decays exponentially (Schmidt et al. 2001). Young trees with sparse, shallow root systems do not provide as much root reinforcement as mature trees. Therefore, after forest harvest a minima in root reinforcement exists, usually at around 10 years after forest harvest when harvested tree roots have decayed and the young forest is not old enough to provide significant root reinforcement (Fig. 9.21) (Sidle et al. 2006).

Considering all of the interacting factors affecting landslide susceptibility—including vegetation, hydrology, geology—requires an integrated modeling approach. Differences in below-ground biomass and the root strengths of different forest tree and shrub species affect the stability of steeper slopes. A transition from forests to shrub thickets or grasslands means the landscape will support thinner soils and require lower soil pore water pressures to trigger landslides (Gabet and Dunne 2003) (Fig. 9.22). Ecohydrology controls the spatial distribution of root strengths

Fig. 9.21 Conceptual diagram showing the temporal response of root cohesion to forest harvest and land use change (From Sidle et al. 2006)



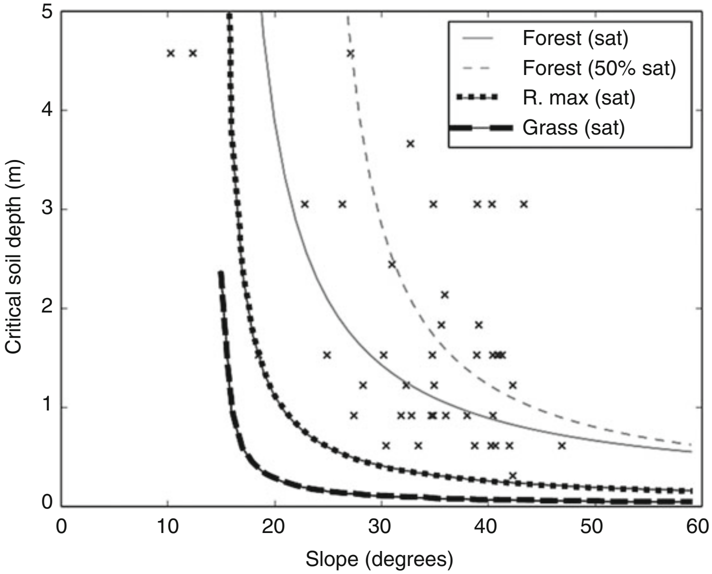


Fig. 9.22 Plot of the relationship between slope and soil depth (measured as the thickness of the landslide scarp) for landslides recorded in the North Carolina landslide database in Macon County, North Carolina. Blue crosses represent each individual landslide event. The four lines represent theoretical failure criteria for different vegetation and hydrologic conditions calculated using the infinite slope model, points that fall above the line should theoretically fail under these conditions. In this model we have maintained constant values of soil cohesion (0 kilopascals) and friction angle (30°) measured using triaxial tests. The *lines* represent failure criteria for average Appalachian hardwood forest (*solid line*, cohesion 6 kilopascals), *Rhododendron maximum*, a common shrub species associated with landslide initiation zones (*dotted line*, 2 kilopascals), and grass (*heavy dashed line*, 0.5 kilopascals) under fully saturated conditions. The *light gray dashed line* is for average Appalachian hardwood forest but with a soil that is 50 % saturated

within forested landscapes, with hollows having the lowest root cohesions. This results in increased landslide potential in these areas (Fig. 9.23). This is an area of significant future research. It is anticipated that more accurate maps of land surfaces and forest structures made using high resolution LiDAR data will lead to more accurate models of root cohesions.

9.8 Vegetation- Debris Flow Relationships: Deep Gap North Carolina

We empirically assessed the spatial relationship between vegetation type and debris flow occurrence in the Deep Gap area of Watauga County and adjoining Wilkes County. The Deep Gap study area was chosen because of the high concentration of debris flows triggered by rainfall from the remnants of a hurricane that passed over

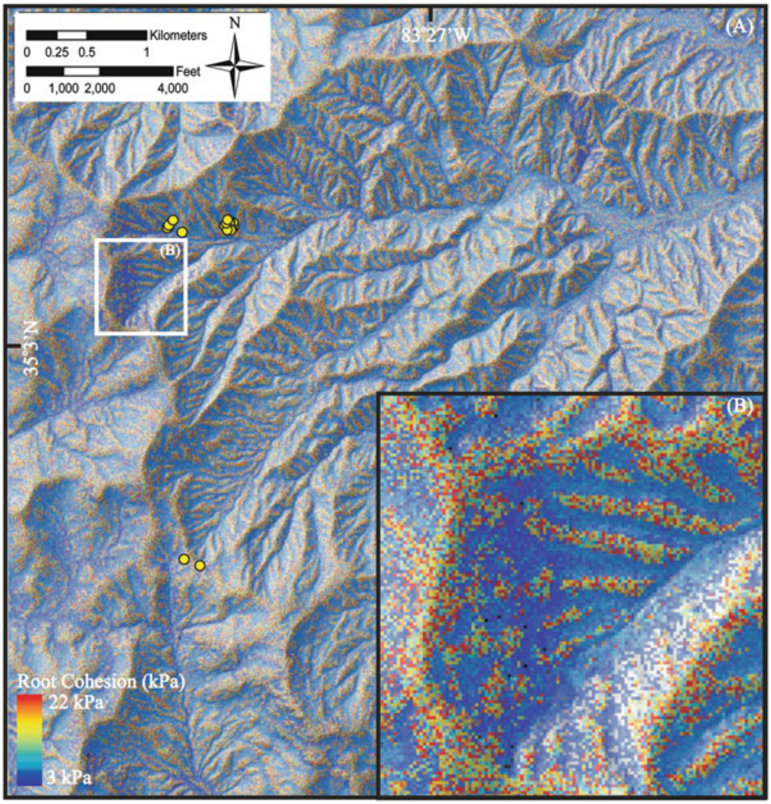


Fig. 9.23 Spatial model of the distribution of root cohesion across Coweeta Hydrological Laboratory in Macon County, North Carolina. *Yellow dots* represent the locations of pits and trenches sampled by Hales et al. (2009). The model is constructed by calculating profile curvature across the catchment. Root apparent cohesion values were assigned using a random uniform distribution of values for each topographic class (nose or hollow)

the area on August 13–14, 1940. The Deep Gap area is a highly dissected erosional reentrant on the BRE that coincides with the surface traces of west-northwest trending ductile thrust faults and topographic lineaments that transect the BRE. Figure 9.7 shows the Deep Gap study on the steep slopes of the BRE, and the landslide initiation sites identified on the landslide hazard maps of Watauga County (Wooten et al. 2008a).

Our approach was to determine the relative spatial frequency of debris flows that initiated on forested slopes versus unforested slopes. As part of landslide hazard mapping in Watauga County (Wooten et al. 2008a), September 29, 1940 vintage black and white aerial photographs (Fig. 9.7) were scanned and georegistered for use in GIS to identify and map the debris flow initiation sites and tracks. Approximately 10 % of the nearly 2100 debris flows, debris slides and blowouts identified as being triggered by the 1940 event were field verified. In this current study, forested slopes were defined as closed canopy, mixed conifer and hardwood

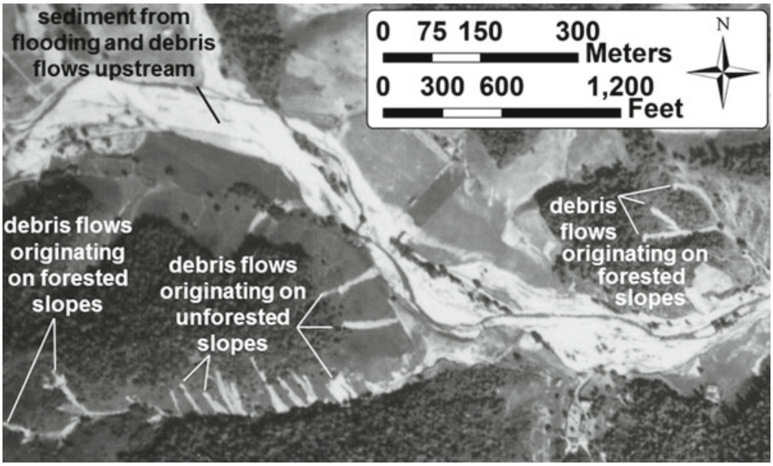


Fig. 9.24 Excerpt of a September 29, 1940 aerial photograph showing examples of August 13–14, 1940 debris flow initiation sites on forested and unforested slopes within the Deep Gap study area (Fig. 9.7). Analysis of 629 debris flow sites in the Deep Gap study area showed a nearly five-fold increase in debris flow initiation sites on unforested slopes over those on forested slopes

forest that were readily identifiable on the aerial photos by the dark color and distinct textural contrasts of foliage. Unforested slopes were defined as open areas that included grasses, shrubs, agricultural fields, areas of recently harvested timber, but also included small areas containing, isolated stands of trees, or bare earth. In general, the unforested slopes occurred in areas more readily suited for clearing and agriculture such as in valleys and toe slopes. Figure 9.7 shows the mapped forested and unforested slopes in the study area. Figure 9.24 shows examples of debris flows originating of forested vs. unforested slopes on 1940 aerial photography of the Deep Gap area.

Potential sources of error include misinterpreting the type of vegetation present at initiation sites and in mapping vegetation patterns. Individual photographs were georegistered, not ortho-rectified; therefore, planimetric areas of the map unit polygons are approximate give the high relief of the area. The numbers of debris flows within forested slopes may be underestimated because they were obscured by the forest canopy. The scoured tracks of debris flows, and sediment deposited in second and third order drainages by debris flows and flood waters obscured the vegetation types present prior to the storm event.

The results of the analysis are given in Table 9.2. Within the 78.2 km^2 study area, 629 debris flow initiation sites were mapped for an average of 8.0 initiation sites/km^2, and a total track area of 18.7 km^2 (1,870 ha). Forested slopes accounted for approximately 63.9 km^2 of the total area, whereas unforested slopes made up a significantly smaller area at approximately 14.3 km^2. On forested slopes there were 234 initiation sites representing 38.4 % of the total sites, resulting in an average of 3.8 sites per km^2. In contrast, 263 sites occurred on unforested slopes yielding an average of 19.5 sites per km^2, nearly a fivefold increase over those on forested

Table 9.2 Tabulated results from the Deep Gap area vegetation and debris flow study. Analysis of 629 debris flow sites in the Deep Gap study area showed a nearly fivefold increase in debris flow initiation sites on unforested slopes over those on forested slopes

	Area km^2	Number of debris flows	Percentage of total debris flows	Average debris flow frequency per km^2
Study area	78.2	629	100	8.0
Forested area	63.9	242	38.4	3.8
Unforested area	14.3	279	44.4	19.5
Boundary of forested – unforested area	–	108	17.2	–

slopes. Interestingly, 108 initiation sites (17.2 % of the total) were mapped as being on the boundary between forested and unforested slopes. This occurrence may reflect a change in slope conditions near the boundaries of forested and cleared land, perhaps the forested land being steeper and less suited for clearing and agriculture. Although there were several potential sources of error in the assessment, the nearly five-fold difference in the frequency of debris flows on unforested slopes over that on forested slopes supports the concept that deep rooted vegetation provides a greater stabilizing influence on slopes than shallow rooted vegetation.

9.9 Debris Flows Effects on Landscape and Forest Structure

Debris flows, in contrast with most other disturbances such as wind, fire, ice, insects and diseases in the SAH remove not only the forest, but the soil and land beneath the forest. Debris flows remove vegetation, scour surface soil, and disrupt aquatic ecosystems, creating linear canopy gaps and early successional habitats along their tracks. As noted in the Introduction chapter (Greenberg et al., Chap. 1) landslides (debris flows) can facilitate species diversity and lead to persistent patches of early successional vegetation in older forests (Seiwa et al. 2013). Debris flows evacuate sediment from their initiation zones and along their scoured paths in upland areas, and deposit it in their run out zones in footslope drainage valleys and channels, commonly in areas of older debris flow deposits (Fig. 9.5). The development of landslide geodatabases and the mapping of debris flows in a GIS (Bauer et al. 2012; Witt and Heller 2014; Crawford 2014) provide the framework for studying the geospatial and temporal aspects forest recovery from documented historical debris flow event in the SAH.

An individual debris flow may initiate with soil volumes on the order 10^1–10^2 m^3, but with entrainment and bulking of soil along its path, it may erode and transport in excess of 10^3–10^4 m^3 of soil. Vegetation recovery can begin rapidly in the depositional (i.e., run out) zones of debris flows. Even in the case of catastrophic events like the 11.4 km-long, 122 ha debris flow that resulted from the August 1916 failure of the Lake Toxaway Dam tree growth (pitch pine) began in boulder deposits the following year (Wooten et al. 2003a, b). Sediment from individual debris flows has a relatively short term negative impact on aquatic ecosystems. A positive aspect of debris flow activity over the long term is that in some areas of western North Carolina accumulated deposition in footslope areas leads to the formation of productive forest soils (Neary et al. 1986) at centennial and millennial time frames. Vegetative recovery in the steep, high elevation, upper portions of debris flow tracks, commonly scoured to bedrock (Fig. 9.12), would generally be slower than in debris deposition zones in the lower reaches of drainages and foot slope area (Fig. 9.5).

Major debris flow events induced by tropical cyclones can disturb large areas over multiple watersheds. Mapped debris flows from the August 13–14, 1940 event disturbed a minimum of 368 ha of riparian area in Watauga County not accounting for the large volume of sediment transported downstream below the BRE into Wilkes and Caldwell Counties. Mapped debris flows from Hurricane Camille in the Virginia Blue Ridge Mountains and Piedmont account for a minimum of 1,200 ha of disturbed riparian area, nearly every first and second order drainage in some watersheds. Smaller, though spatially concentrated events such as the Balsam Mountain debris flows triggered by a July 14–15, 2011 thunderstorm resulted in near source disturbances on the order of 13 ha. Impacts from this localized, but intense, storm event extended over 13 km downstream from the debris flow initiation sites.

9.10 Methods and Approaches to Debris Flow Susceptibility Mapping and Modeling

Quantitative methods for landslide hazard mapping geared toward debris flow mapping and susceptibility modeling are well established, readily available, and are continually being improved. Slope stability assessments are important not only for forest and watershed management, but are critical to help protect public health and safety on forest lands and at the interface of forest lands with private property in areas downslope from upland forests (Collins 2014; US Department of Agriculture 2014).

Physically-based computerized models that use a limit-equilibrium approach to slope stability analysis governed by variations of the infinite slope model incorporated into a GIS platform have been developed and in use since the 1990s. In evaluating the computer programs SINMAP (Pack et al. 1998) and SHALSTAB (Montgomery and Dietrich 1994) for use in the North Carolina landslide hazard mapping program Witt et al. (2007a) found the output results to be very similar. SINMAP has been used in North Carolina to model debris flow susceptibility at the county level (Fig. 9.17) (Witt et al. 2007a; Wooten et al. 2007). Modeling using SINMAP coupled with a GIS-based hydrologic routing model and field mapping of debris flows and deposits have been used together to model potential debris flow pathways (Fuemmeler et al. 2008; Witt et al. 2008). These steady-state hydrologic models can be used to forecast the spatial distribution of unstable slopes and landslide occurrence. Models that incorporate transient hydrologic responses (Baum et al. 2002) have the capability to assess spatial and temporal slope stability for varying precipitation scenarios. Morrissey et al. (2004) found such an approach useful in attempting to simulate the locations and timing of debris flow from the 1995 event in Madison County, Virginia.

Next generation models that are being developed and tested include the RHESSys (Regional HydroEcological Simulation System) model in which ecohydrological and geomorphic inputs are coupled to simulate spatial and temporal slope stability. The RHESSys model has undergone development and successfully applied at the watershed scale at the Coweeta Hydrologic Laboratory (Band et al. 2011). Development and application a hydro-mechanical model HILLSOPE FS2 (Lu et al. 2010) that incorporates soil capillary tension to model stability at the hillslope scale is to be tested in western North Carolina (Lewis et al. 2013) on the Nantahala National Forest and Coweeta Hydrologic Laboratory in Macon County, and at the Bent Creek Experimental Forest in Buncombe County. A hydrologic model used with a high elevation rain gage network to predict flood response and debris flow initiation has been applied to GSMNP and adjoining area of western North Carolina (Tao and Barros 2014).

The performance of models used to map slope instability at various spatial scales is highly dependent on the quality of the geologic, soil, geotechnical, hydrologic, and vegetative input parameters, and the quality of the landslide mapping and data used to calibrate them and evaluate their results (Witt et al. 2007b). Landslide and landslide deposit inventories are important not only for identifying areas affected by recent and past landslide activity, but serve as important means to calibrate debris flow susceptibility and run out models. Quality digital elevation data are critical to model performance. Where available 6 m- or higher (e.g., 1 m) pixel resolution LiDAR digital elevation models improve model results over standard 10 or 30 m digital elevation models. These models do not substitute for site-specific stability assessments by qualified earth scientists, but they provide a means for planning purposes to identify potentially at-risk areas where on-site analyses are warranted.

9.11 Summary

The term landslide refers to a variety of gravity-driven movements of soil or rock materials downslope. Landslides may be swift and catastrophic (i.e., rockfalls and debris flows) or may travel slowly and incrementally downslope (i.e., soil slides). Debris flows, the dominant landslide processes in the SAH, are a water-laden (i.e., liquefied) mass of rock fragments and coarse grained soil (debris). Debris flows can attain speeds in excess of 50 km per hour and are capable of destroying or damaging everything in their paths.

Debris flows originate on steep mountain slopes, mainly in areas of convergent topography known as colluvial hollows. Debris flows initiate when the shear stresses on a hillslope exceed the frictional and cohesion shear strength of the hillslope material, which is composed of soil, rock fragments, and roots. Many interrelated, chiefly geologic, factors contribute to debris flow occurrence, including steep slopes, landforms (i.e., their influence on rainfall patterns, runoff and infiltration in convergent topography), bedrock types and structure, soil types (i.e., mechanical and hydrologic properties), and vegetation (i.e., evapotranspiration and root cohesion). Excessive rainfall leading to elevated pore-water pressures (i.e., decreased shear strength) is the primary trigger for debris flows, especially when antecedent moisture conditions are high.

Debris flows and other forms of mass wasting are natural processes of landscape evolution in the SAH. The present landscape includes many remnants of prehistoric (Pleistocene and older) debris flow deposits. Native American and early European settlements were confined mainly to valleys and some mountain footslope areas that include debris flow run-out zones. In the twentieth and twenty-first centuries, however, anthropogenic influences on the landscape have increased the frequency of mass wasting for a given storm event above historical natural levels through changes in vegetation and disturbances on mountain slopes. Where forests with deeply rooted trees have been replaced with agricultural and pasture lands that have shallow-rooted grasses, crops, and shrubs, the stabilizing effects of precipitation interception, evapotranspiration and root cohesion by vegetation have been reduced. In the latter part of the twentieth century increased development on steep mountain slopes has resulted in ground-disturbing human activity where debris flows initiate. Poorly constructed and maintained cut and fill slopes are the primary destabilizing influences that increase the susceptibility of mountain slopes to debris flow initiation. This upslope development pattern combined with increased development in footslope areas within debris flow run-out zones has increased the overall societal risk from damaging debris flows.

Debris flows remove vegetation, remove surface soil and vegetation, and disrupt aquatic ecosystems, creating linear canopy gaps and early successional habitats along their tracks. The area affected by an individual debris flow originating on forested slopes ranges from less than 10 m^2 to 13.8 ha (2004 Peeks Creek debris flow). Coalescing debris flows can impact areas on the order of 16.5 ha or more. Human activity resulted in the largest area affected by a single debris flow in this study where the failure of the Lake Toxaway dam in 1916 disturbed a minimum of 122 ha along the Toxaway River in North and South Carolina. Recovery of areas impacted by debris flows to pre-disturbance conditions can be on decadal and centennial time scales. Vegetative recovery in the steep upper portions of debris flow tracks, commonly scoured to bedrock, would generally be slower than in debris deposition zones in the lower reaches of drainages and foot slope area.

In 1940, 1969 and 1985, each of three tropical cyclones that passed over the SAH generated thousands of documented debris flows. Given the magnitude of the July 15–16, 1916 storm, it is reasonable to conclude that this event triggered thousands of debris flows, bringing the total to four tropical cyclones that have had the greatest impacts on the SAH over the last century. The average frequency of these major events is about 25 years. Where documented by mapping, these catastrophic storms disrupt forest structure and/or hydrologic systems over areas ranging from about 368 to 1,200 ha. Major storms that have each generated hundreds of reported landslides in the SAH have occurred 10 times from 1924 to 2013 for an average frequency of about 9 years. Where documented by mapping, these major storms disrupt forest structure and/or hydrologic systems over areas ranging from about 70 to 600 ha. Collectively these catastrophic and major storms have an average frequency of 7 years over the period 1916–2013.

Sixteen smaller-scale storms that generated less than a hundred of debris flows have a maximum average frequency of 7–8 years over the period from 1876 to 2013. These smaller storms that have induced debris flows are undoubtedly more frequent, and many have not been recorded in the literature. Where documented by mapping, these lesser storms disrupt forest structure and/or hydrologic systems over areas ranging from about 1.4 to 50 ha. Taken together, the 31 landslide events documented here over the period from 1876 to 2013 have an average frequency of about 4 years.

Debris flow occurrence is strongly correlated with antecedent precipitation and rainfall intensity (i.e., rainfall rate and duration). Looking forward, should climate change result in increased occurrences of high intensity rainfall through more frequent storms, or less frequent, but higher intensity storms, then an increased frequency of debris flows and other forms of mass-wasting should be expected in the SAH (see Dale et al. Chap. 13). With regard to the difficulties and uncertainties in predicting the affects that climate change scenarios will have on landslide occurrence, Sidle and Ochiai (2006) conclude that a higher priority should be given to understanding the interactions between land use and landslides, and applying this knowledge in managing mountainous and unstable terrain. Given the importance of the stabilizing influences of forest cover, healthy forests on mountain slopes are critical in mitigating the impacts of recurring landslide events. Reducing losses from landslides are important from the perspectives of ecosystem and infrastructure integrity, but most importantly from the standpoint of public safety.

Quantitative methods for landslide hazard assessment geared toward debris flow mapping and susceptibility modeling are well established, readily available, and are continually being improved. Landslide and landslide deposit inventories are important not only for identifying areas affected by recent and past landslide activity, but serve as important means to calibrate landslide models. These models do not substitute for site-specific stability assessments by qualified earth scientists, but provide a means at the planning level to identify potentially at-risk areas where detailed on-site analyses are warranted. The interdisciplinary technical and scientific capacity exists now to investigate, analyze, identify and delineate landslide prone areas of the landscape with increasing reliability. The March 22, 2014 landslide near Oso, Washington that killed 41 people is yet another reminder of the destructive power of landslides of all types, and the ongoing need to identify and map landslide hazard zones in mountain slopes.

Acknowledgements Many people and agencies have contributed to this effort, but the dedicated work of Jennifer Bauer, Tommy Douglas, Stephen Fuemmeler, Ken Gillon, Rebecca Latham, and Anne Witt of the North Carolina Geological Survey landslide mapping team from 2005 to 2011 made it possible. Reviews by Francis Ashland, Bart Cattanach, Tom Collins, Matt Heller, Kenneth Taylor, and the editors, Beverly Collins and Cathryn Greenberg, resulted in many substantial improvements to the manuscript. Statistical and GIS support by Nick Bozdog and Zach West, and proof-reading and formatting by Rachael Pressley are gratefully acknowledged.

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