The Kentucky Geological Survey Landslide Program: An Overview

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2015 Geohazards in Transportation

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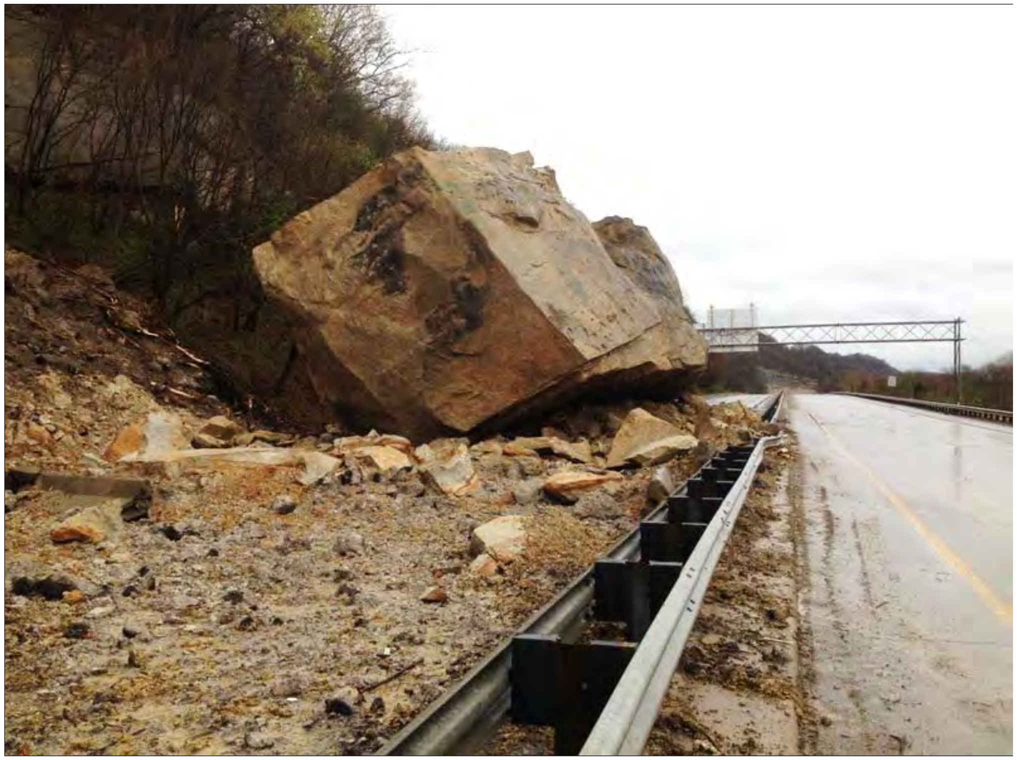
UK
UNIVERSITY OF
KENTUCKY
Kentucky Geological Survey

Outline

- National background
- Landslides in Kentucky
- 2015 landslides YTD in Ky.
- Research and data delivery
  - ➢ Landslide inventory
  - ➢ Landslide Information Map
  - ➢ Research projects
- Summary



Rockfall, 4/2015, Hwy52, OH

- Responsible for $2-3 billion in damages annually (direct & indirect), rivaling annual flood losses

- Deadliest landslide in U.S. history, March 2014, Oso, WA

- No systematic catalog of occurrence or impact maintained in U.S.
  - Damage is poorly documented, considered part of another triggering event (flood, earthquake, tropical storm)
  - No insurance plans exist

- Hazard assessment is difficult:
  - No standard model for hazard assessment. No earthquake model.
  - Quantifying risk and loss reduction strategies are different for different types of landslides (variability in site conditions and slide behavior)

- USGS Landslides Hazards Program is funded ~3.5 million/year

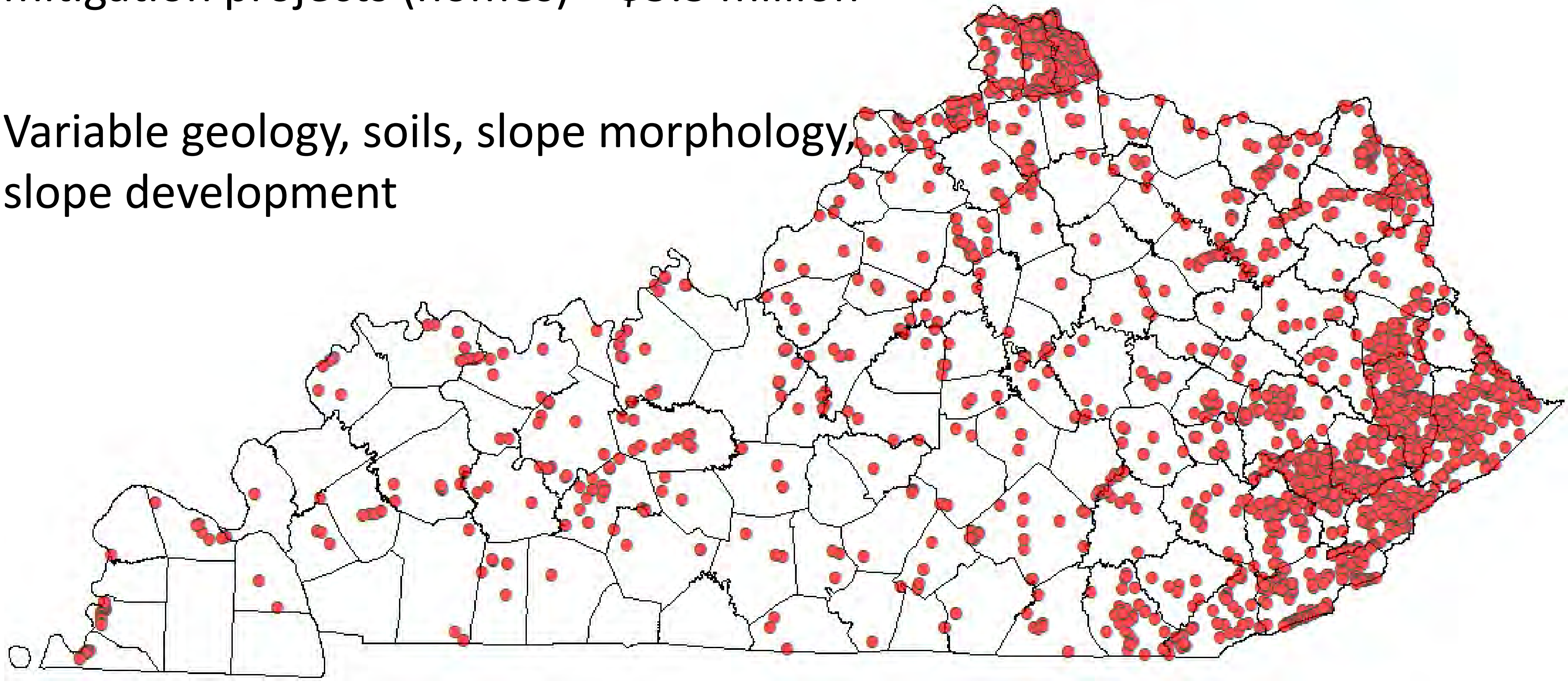
- State geological surveys COMBINED spending on landslides is ~$900k per yr.

Landslides in Kentucky

- KY spends ~$10 million/yr. on landslide mitigation and repair (mostly direct)

- 2003-2013 KYEM-FEMA landslide mitigation projects (homes) ~ $5.3 million

- Variable geology, soils, slope morphology, slope development



Hickman, KY., Fulton Co. along the Mississippi River

1996-2000

$17 million in federal funding

Soil nails, shotcrete, deep anchors, aggregate geogrid

Translational slide / Debris avalanche

Harlan Co.
6/13/13

Nola Sizemore – Harlan Daily Enterprise

Google Image of same area

Breathitt Co., eastern Ky.
March 2015

WYMT News

Translational slide

Carroll Co.
4/2014

Carter Co. ,2015

Campbell Co., northern KY.

Recycled railroad rail

Rockfall, 2015

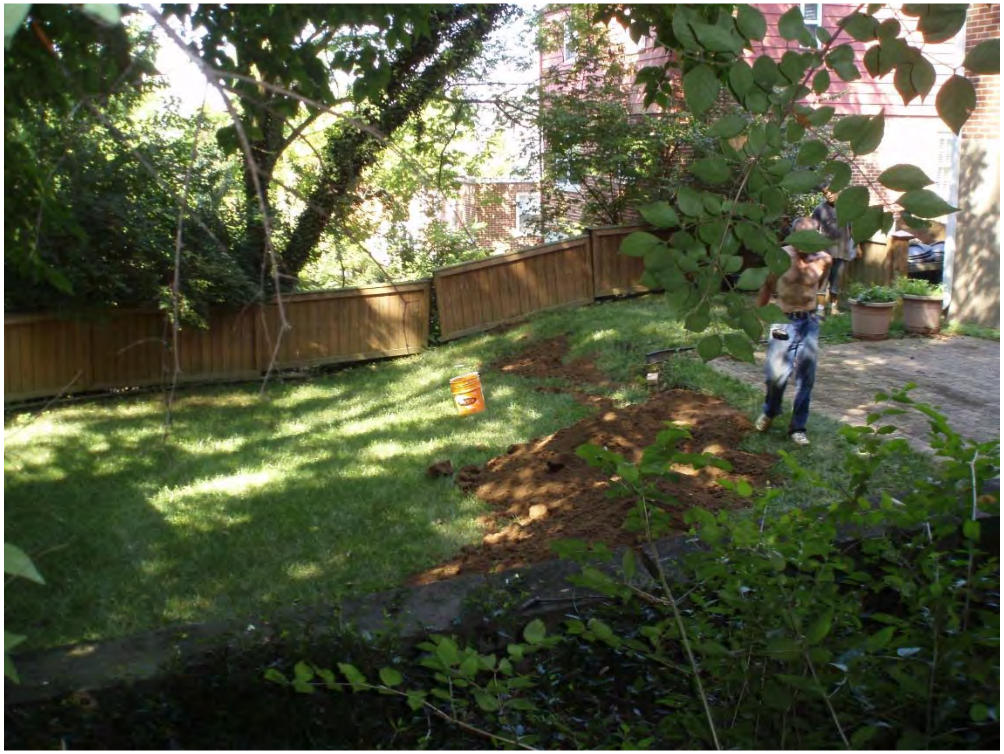
Breathitt Co., eastern KY.

2008

Campbell Co.

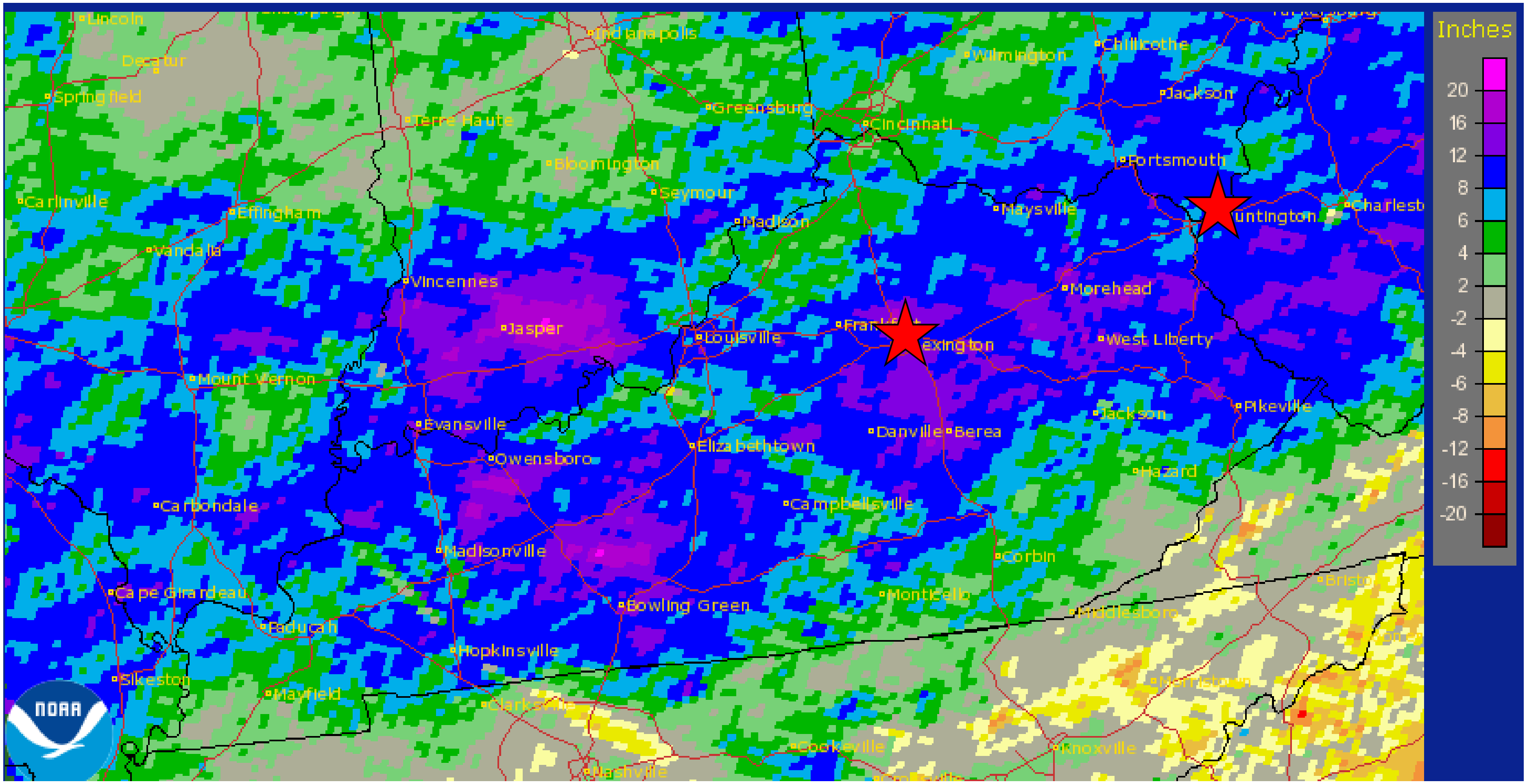
Urban landslides

2011



2015 Landslides, YTD

Precipitation departure for first half of year – 8 to 15”
Rainfall YTD, 39.3” in Jackson, KY



- March-April totals
  - 13.3 Johnson Co
  - 13.3 Knox Co

- July 2015, wettest on record
  - 9.73” in Johnson Co
  - 11.23” in London, KY.

- ~100 landslides to date
  - Debris flows
  - Slumps
  - Rockslides
  - Rockfalls
  - Road washouts

Haywood Branch, Floyd Co., eastern KY.

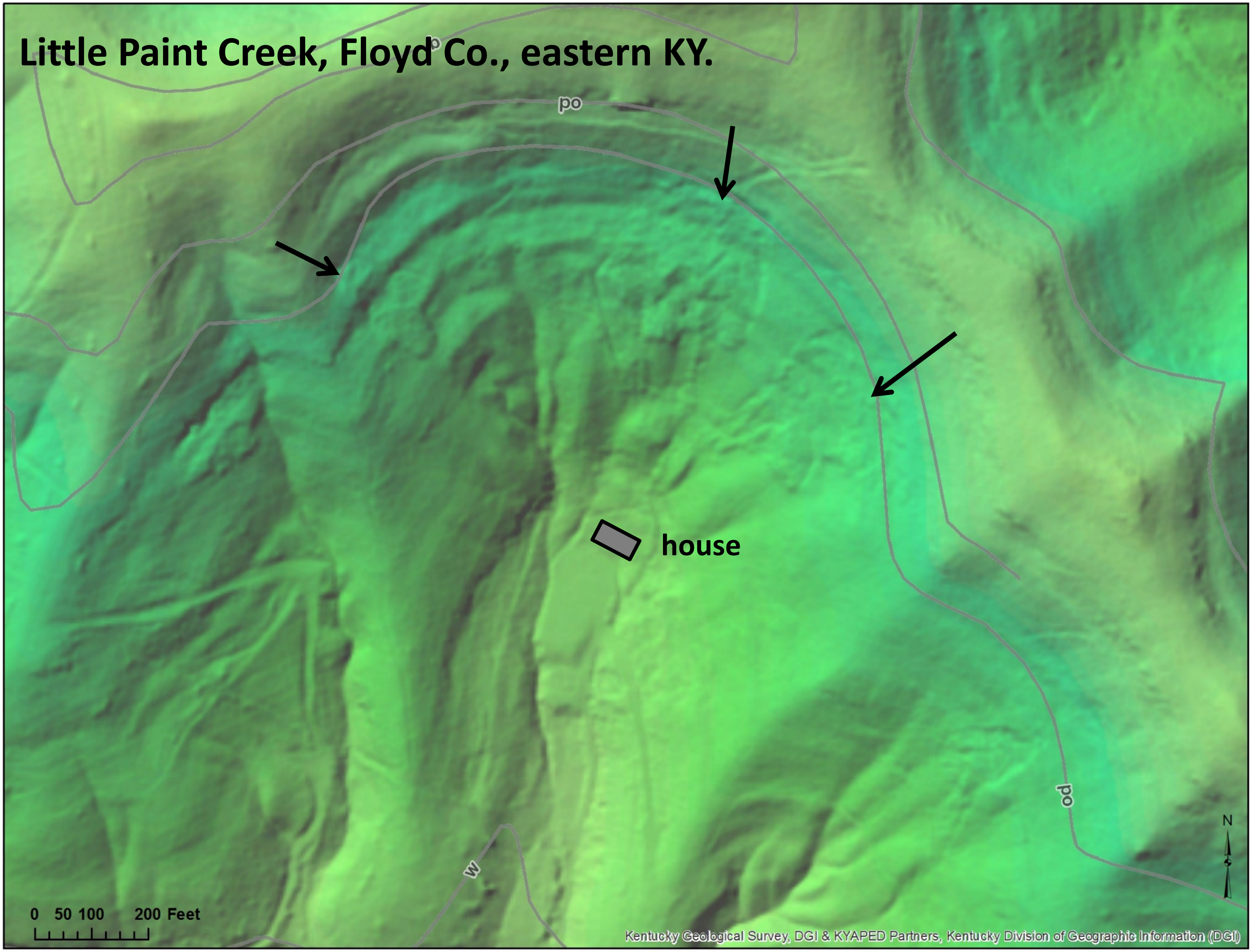
Haywood Branch, Floyd Co., eastern KY.

Official Hollow, Floyd Co., eastern KY.

Official Hollow, Floyd Co., eastern KY.

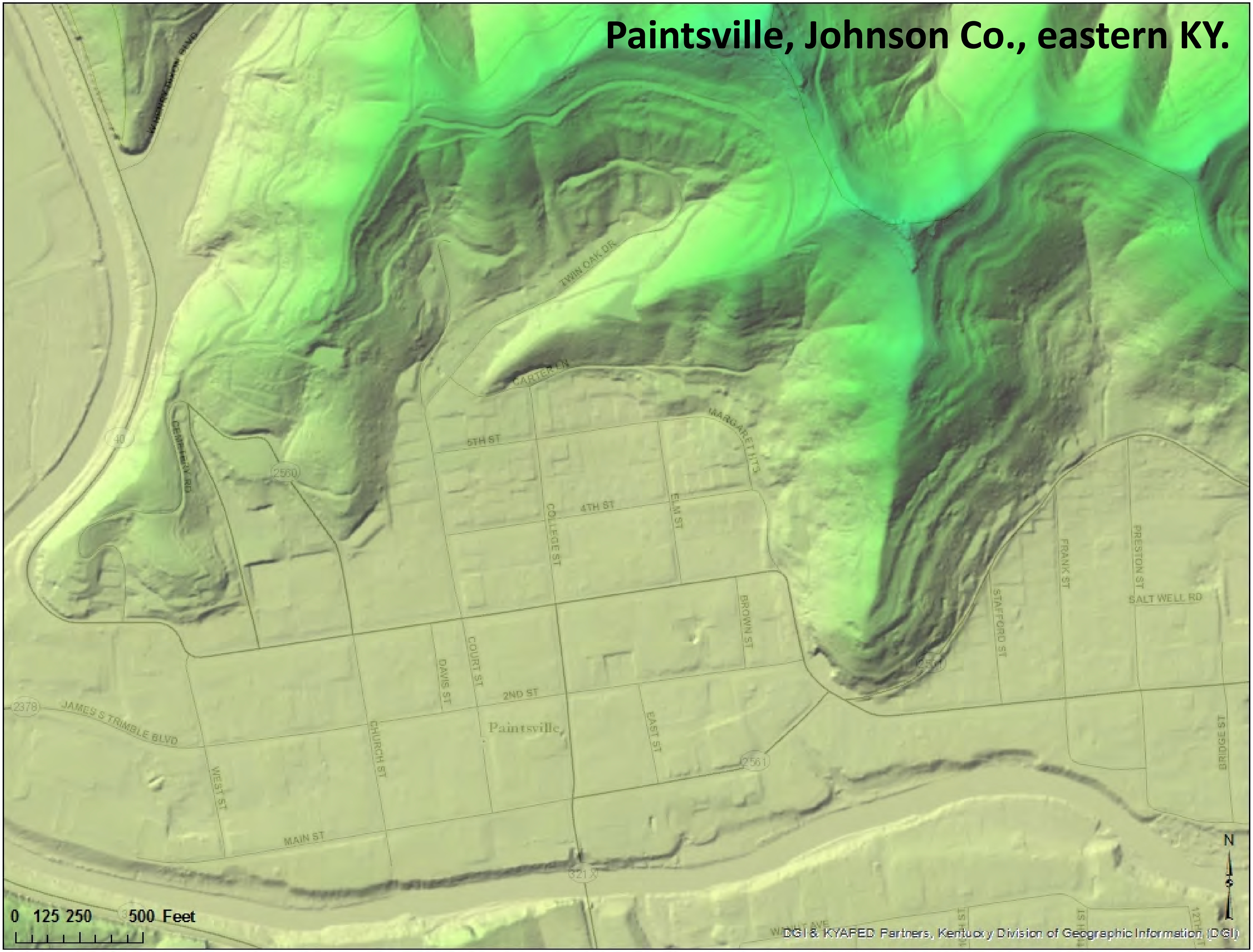
Little Paint Creek, Floyd Co., eastern KY.

Little Paint Creek, Floyd Co., eastern KY.

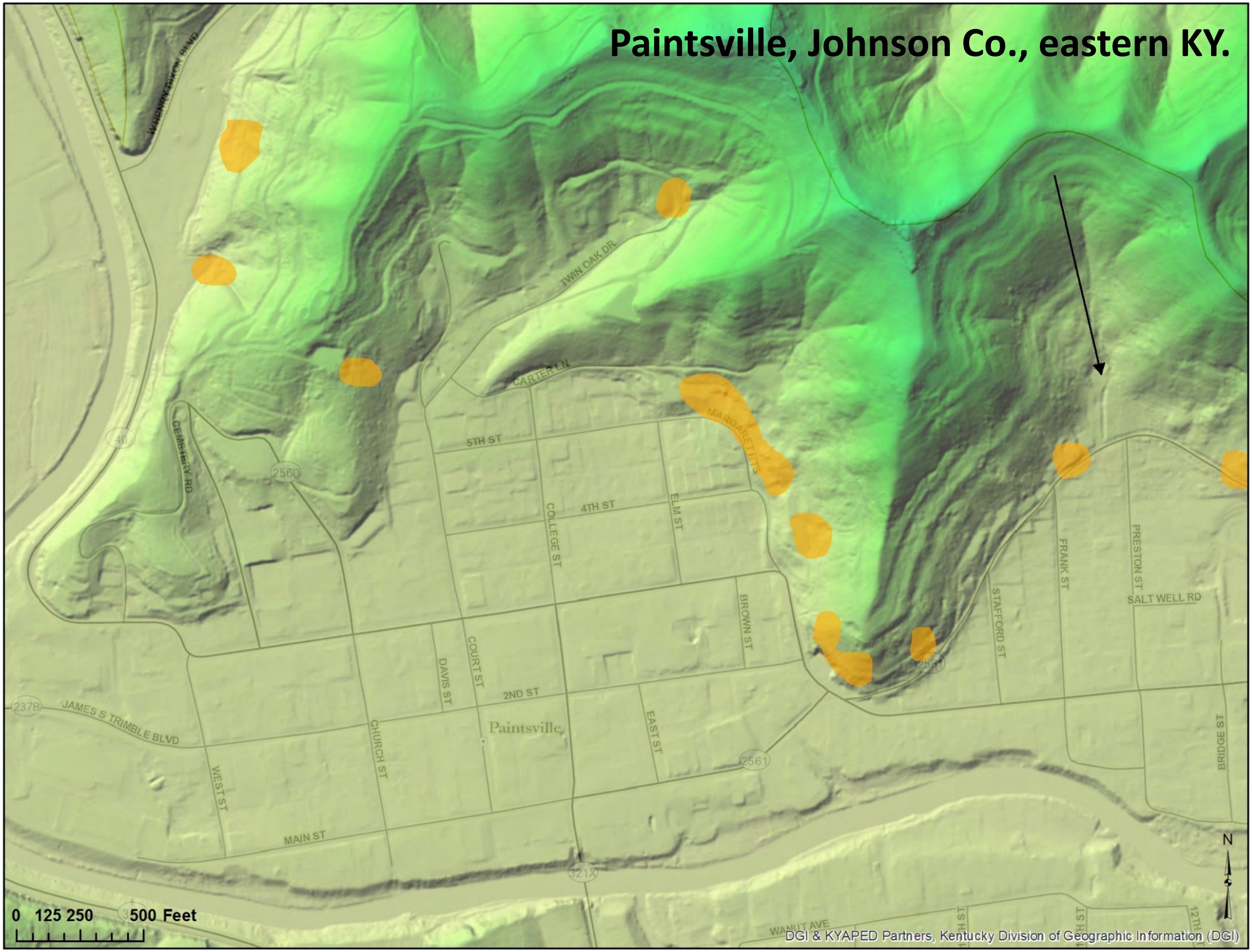


Kentucky Geological Survey, DGI & KYAPED Partners, Kentucky Division of Geographic Information (DGI)

Paintsville, Johnson Co., eastern KY.



DGI & KYAPED Partners, Kentucky Division of Geographic Information (DGI)



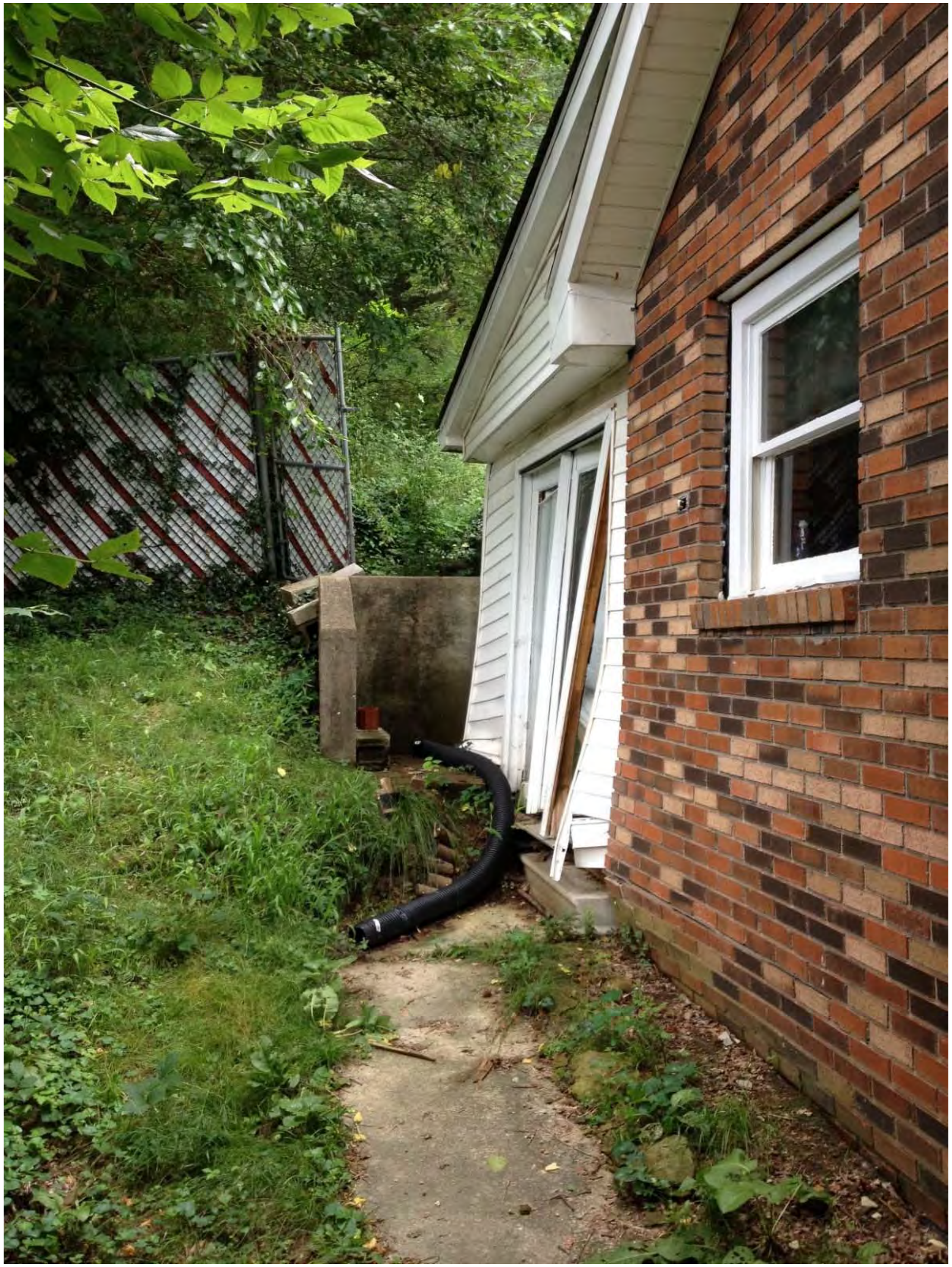
Paintsville, Johnson Co., eastern KY.

DGI & KYAPED Partners, Kentucky Division of Geographic Information (DGI)

Paintsville, Johnson Co., eastern KY.

Above homes

Below homes



Paintsville, Johnson Co.

Perry Co., 2015 eastern KY.

Cut and fill, old landslide

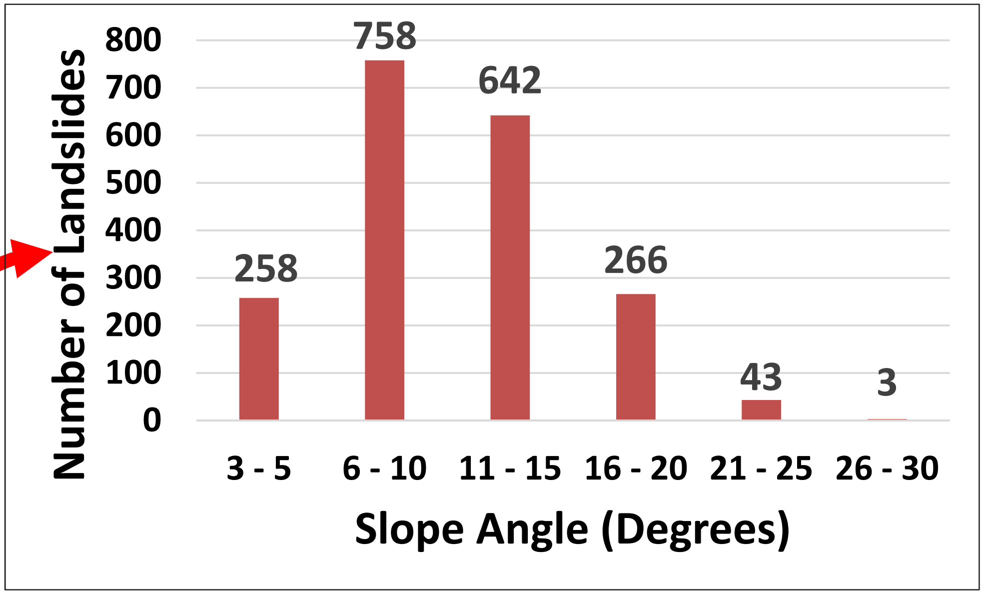
Pike Co., eastern KY.

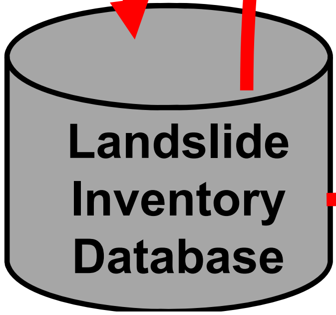
Debris flow; destroyed church and damaged home

Research and Data Delivery

Landslide Inventory Database

- Known landslide locations
- Areas susceptible to debris flows
- Various sources
- Various attributes



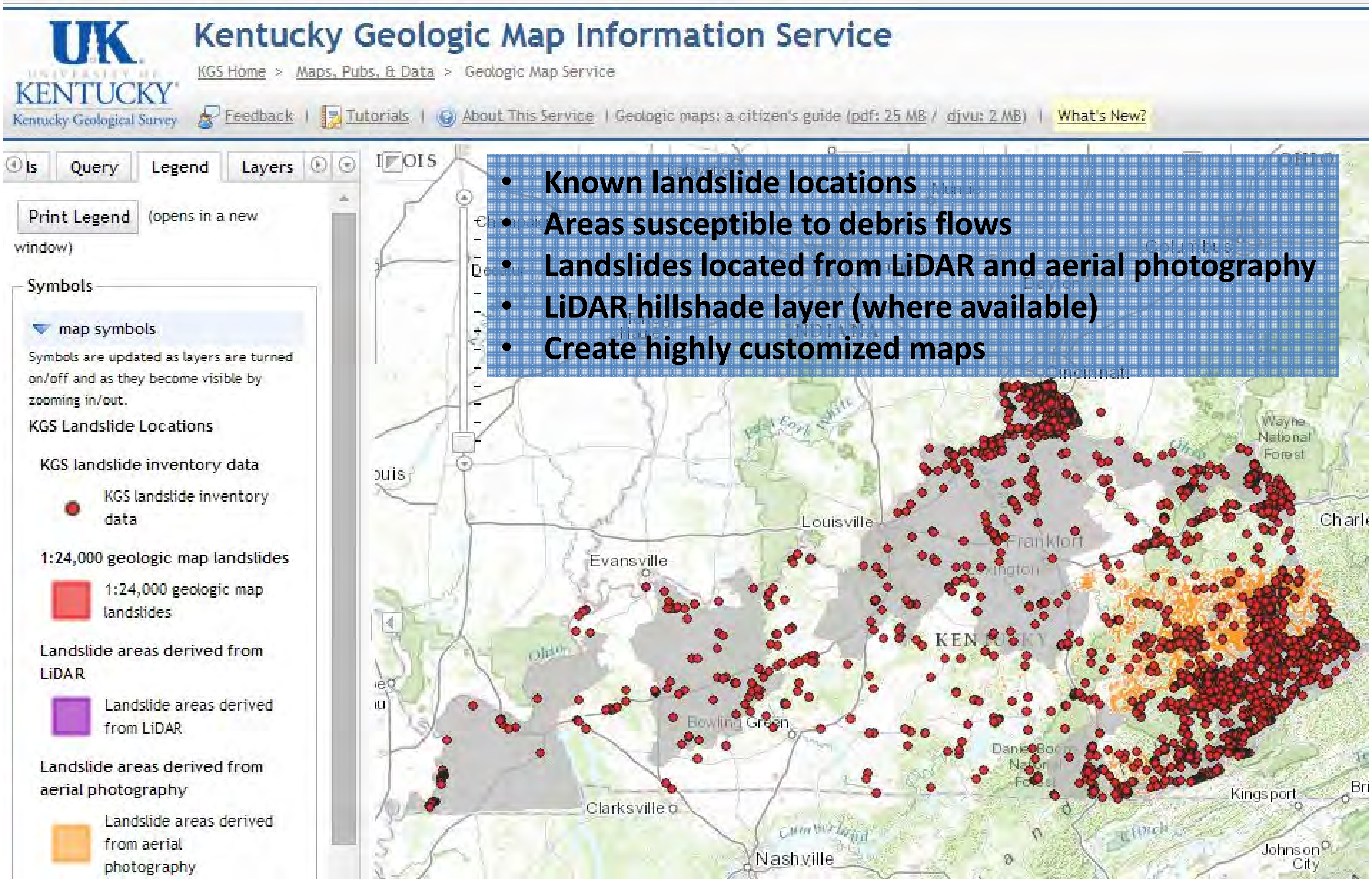


Total = 2,443

Geologic Formation	Landslides
Pikeville Formation	474
Kope Formation	334
Hyden Formation	285
Landslide deposits	186
Four Corners Formation	156
Grundy Formation	68
Fairview Formation	62
Clays Ferry Formation	43
Princess Formation	53
Bull Fork Formation	27
Borden Formation	21
Paragon Formation	19

“bad actors”

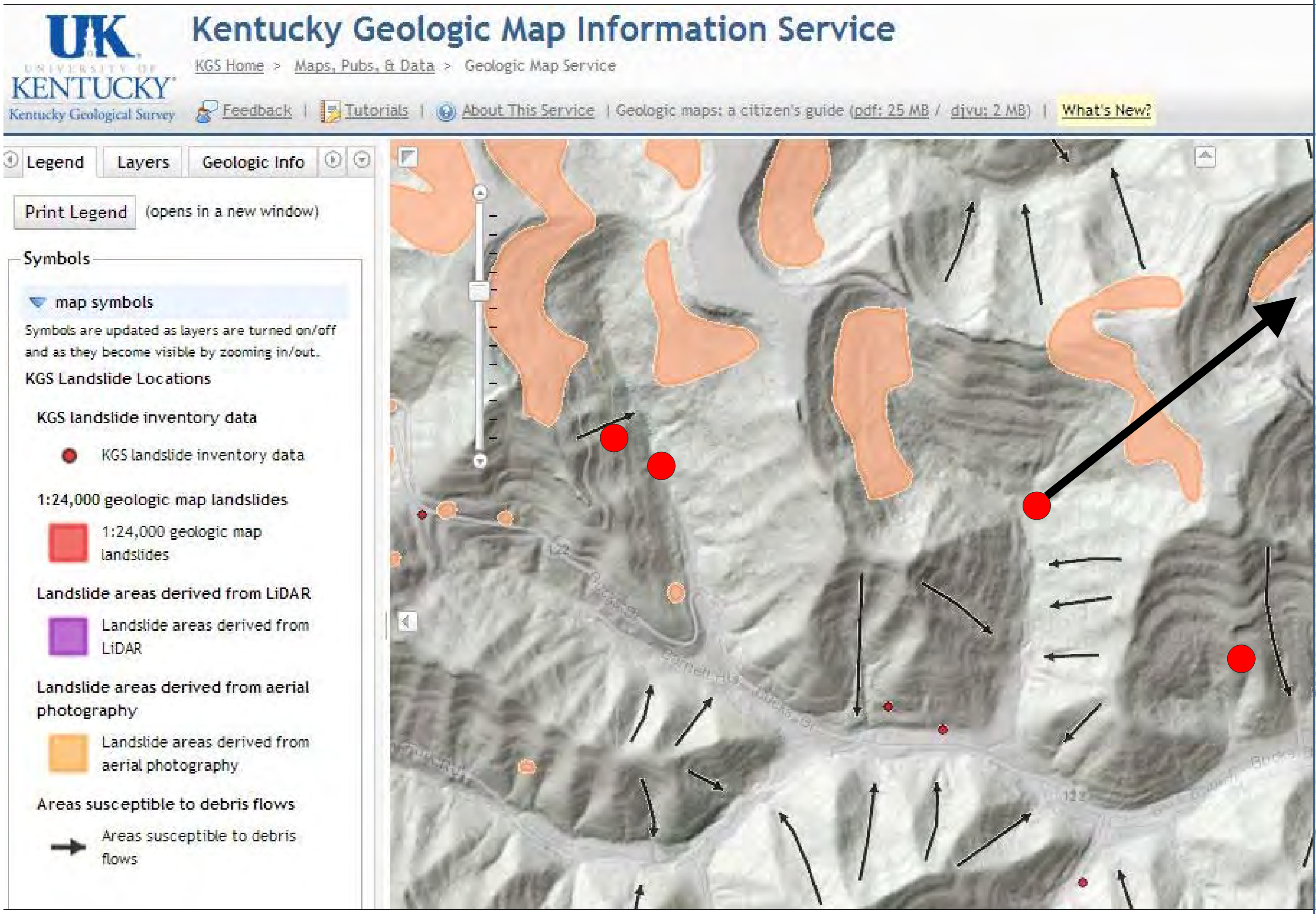
KGS Landslide Information Map



- Known landslide locations
- Areas susceptible to debris flows
- Landslides located from LiDAR and aerial photography
- LiDAR hillshade layer (where available)
- Create highly customized maps

Symbols are updated as layers are turned on/off and as they become visible by zooming in/out.

Landslide Information Map



Kentucky Geologic Map Information Service

KGS Home > Maps, Pubs, & Data > Geologic Map Service

Feedback | Tutorials | About This Service | Geologic maps: a citizen's guide (pdf: 25 MB / djvu: 2 MB) | What's New?

Legend | Layers | Geologic Info

Print Legend (opens in a new window)

Symbols

map symbols

Symbols are updated as layers are turned on/off and as they become visible by zooming in/out.

KGS Landslide Locations

KGS landslide inventory data

● KGS landslide inventory data

1:24,000 geologic map landslides

🟥 1:24,000 geologic map landslides

Landslide areas derived from LiDAR

🟪 Landslide areas derived from LiDAR

Landslide areas derived from aerial photography

🟧 Landslide areas derived from aerial photography

Areas susceptible to debris flows

→ Areas susceptible to debris flows

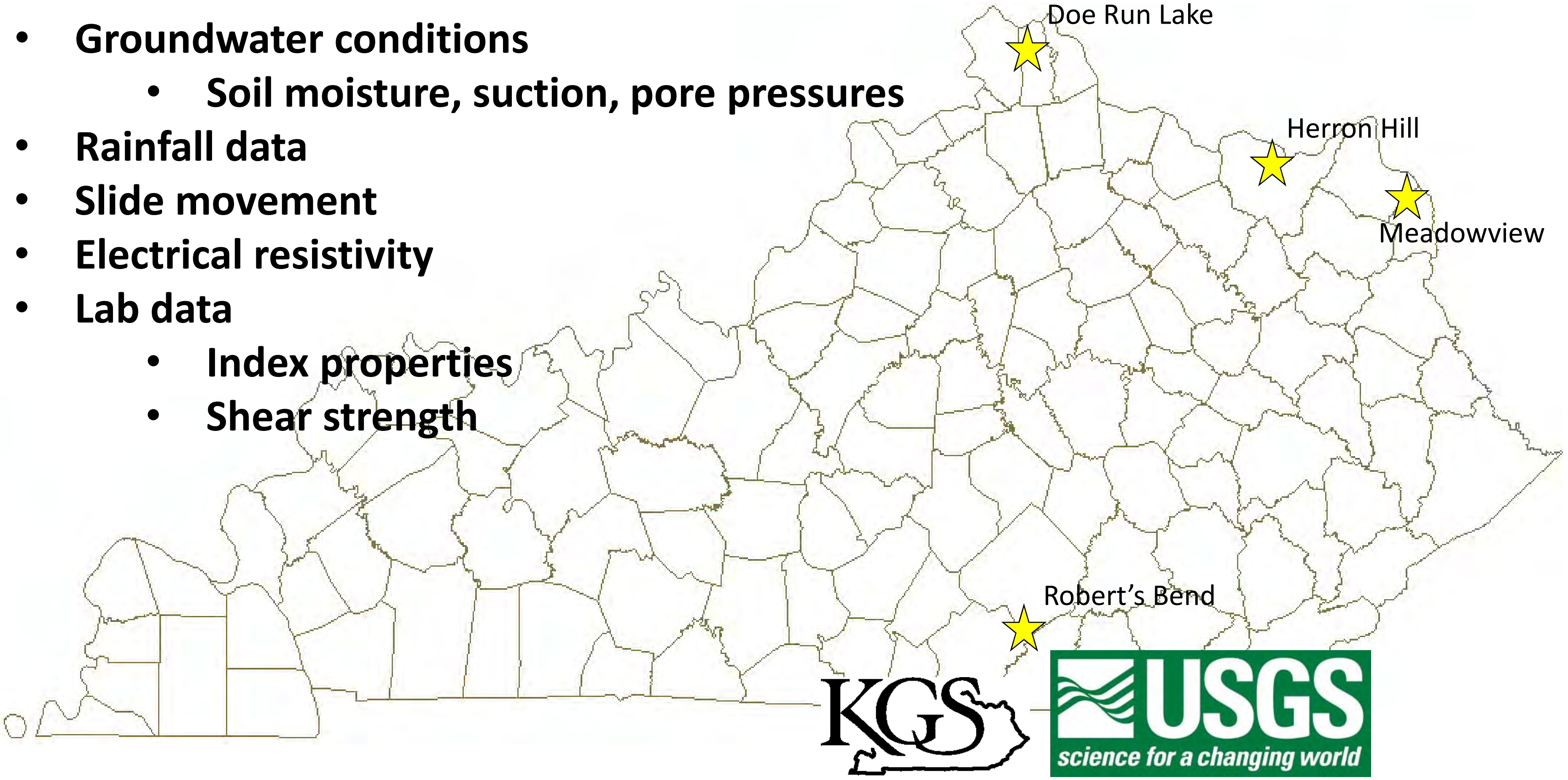
Landslide attributes

- *Source desc*
- *SourceID*
- *County*
- *Quad*
- *Latitude83*
- *Longitude83*
- *Route*
- *Date Observed*
- *Failure Date*
- *Field Checked*
- *Material*
- *Failure Type*
- *Track Length*
- *Width*
- *Head scarp height*
- *Slip surface depth*
- *Geomorphic position*
- *Bedrock Formation*
- *Failure location*
- *Contributing factor*
- *Damage*
- *Comments*

Research Projects

Geologic, geotechnical, geophysical landslide investigations

- Landslide characterization
- Groundwater conditions
    - Soil moisture, suction, pore pressures
- Rainfall data
- Slide movement
- Electrical resistivity
- Lab data
    - Index properties
    - Shear strength

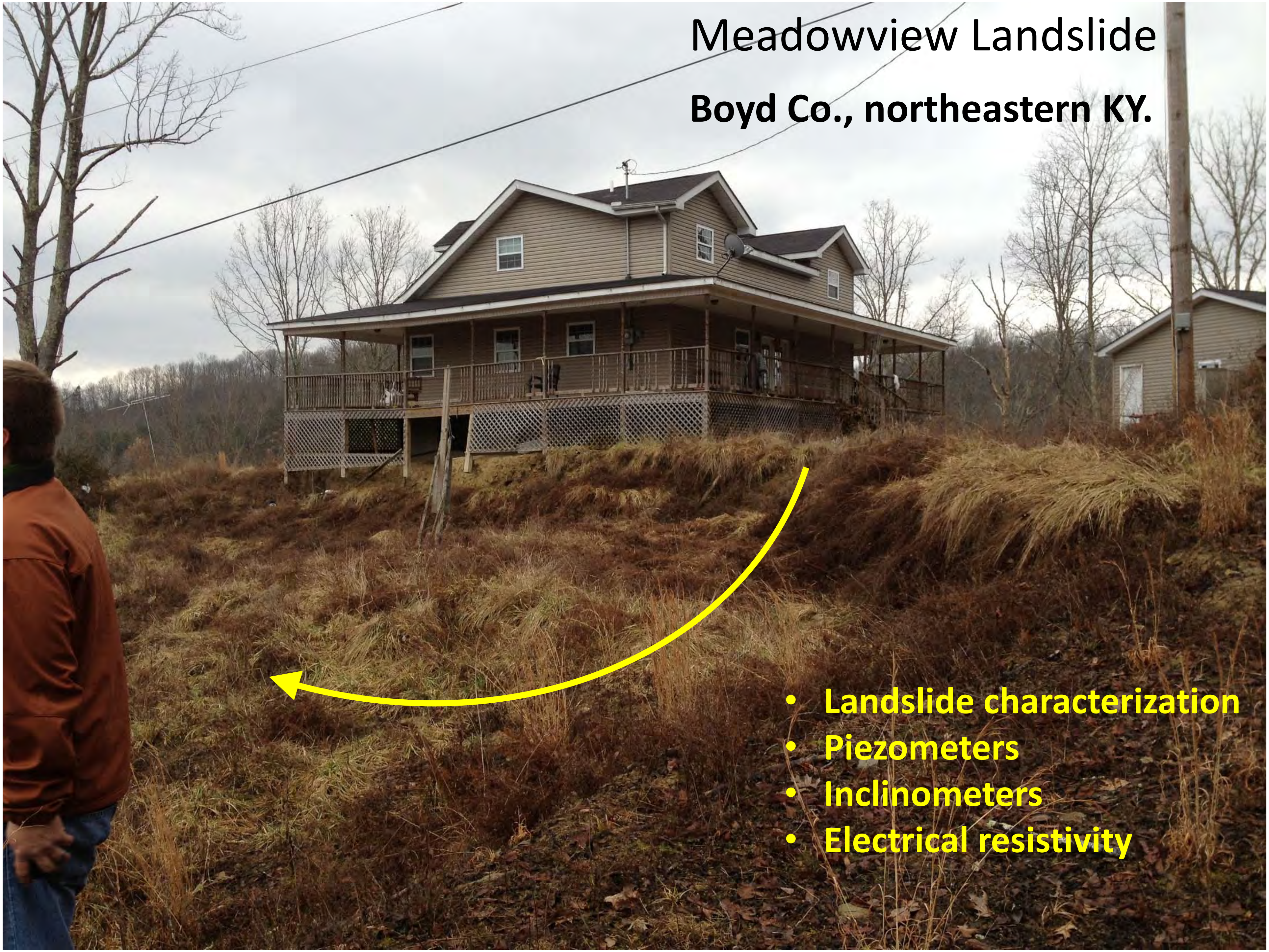


KGS

USGS science for a changing world

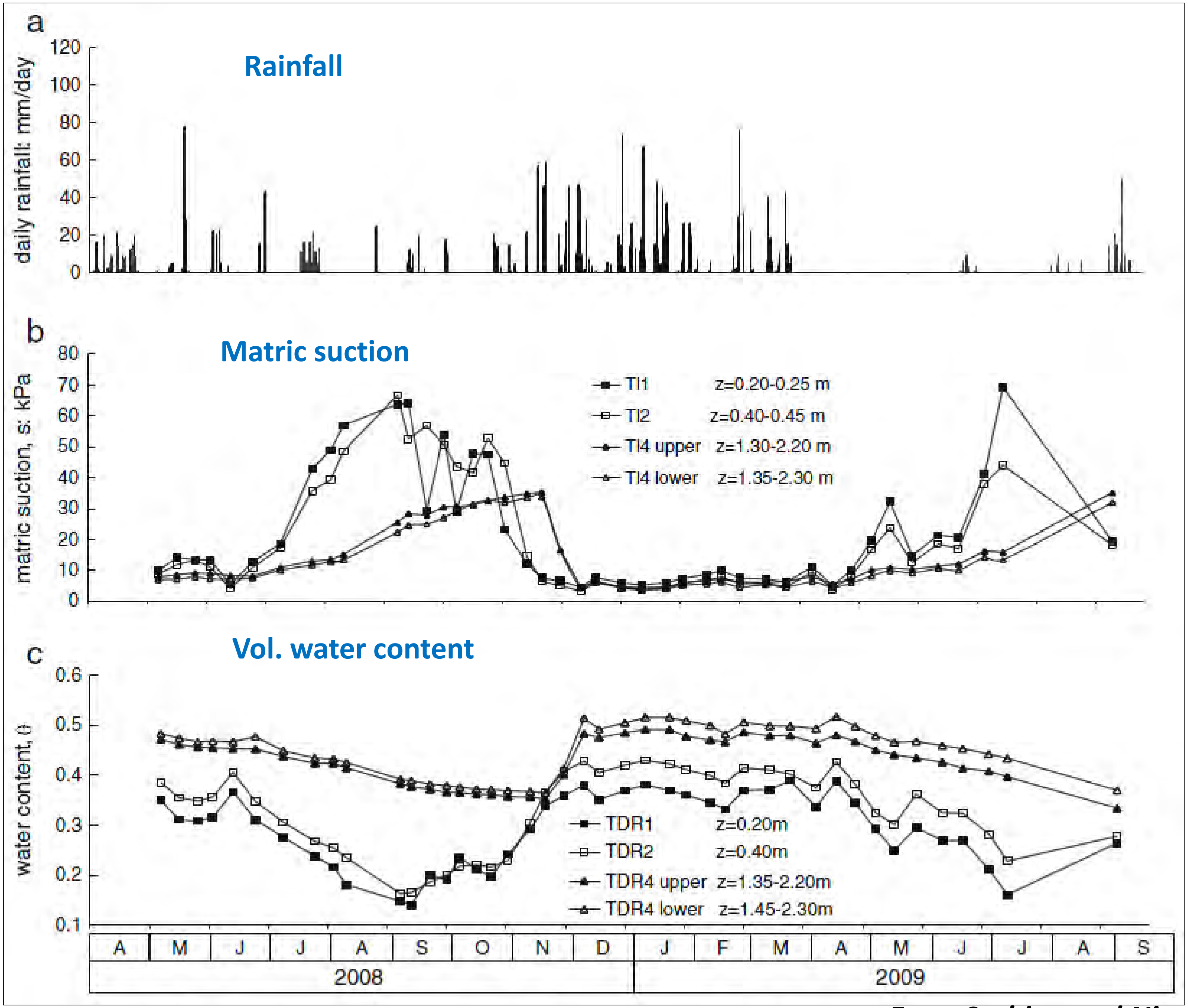
Meadowview Landslide

Boyd Co., northeastern KY.



- Landslide characterization
- Piezometers
- Inclinometers
- Electrical resistivity

Doe Run Landslide, Kenton County



Rainfall

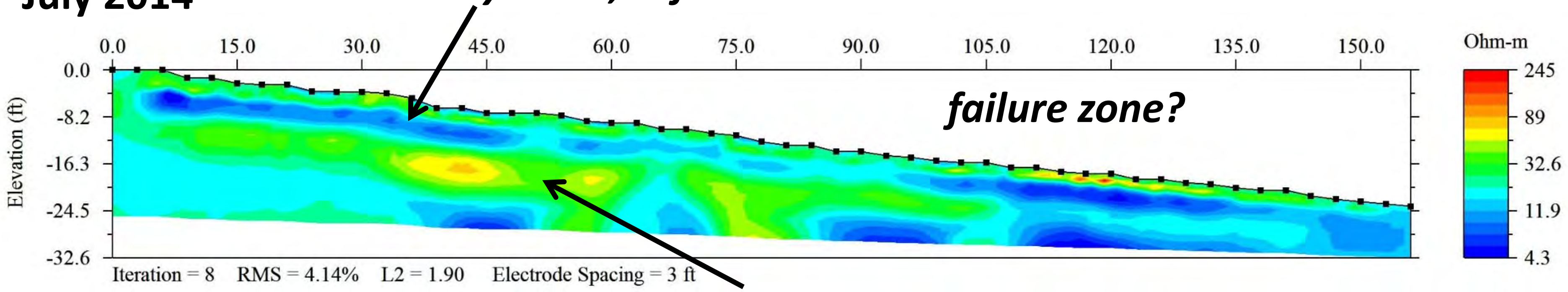
Matric suction

Vol. water content

From Sorbino and Nicotera, 2013

Inverted electrical resistivity sections, Herron Hill landslide

July 2014

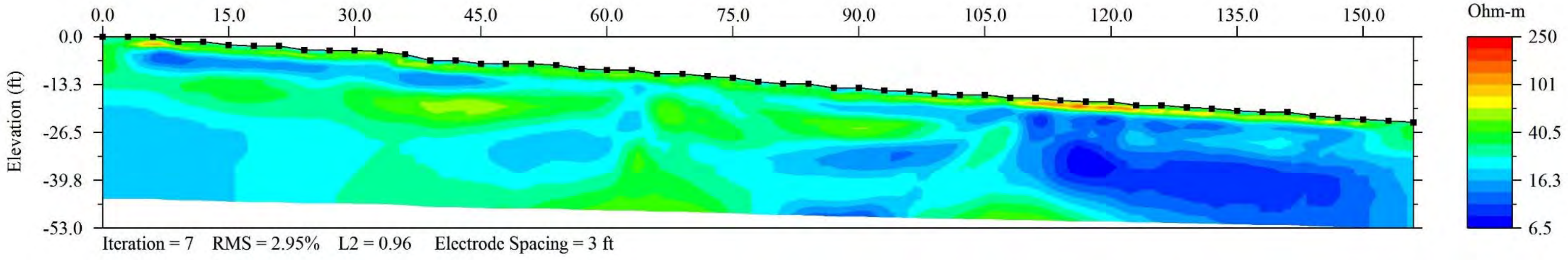


Clay shale, soft

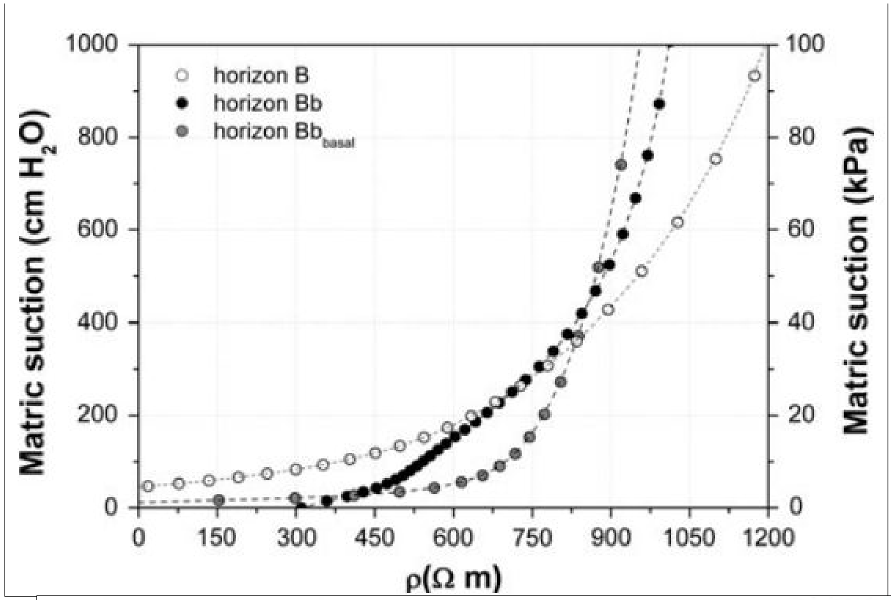
failure zone?

Weathered shale

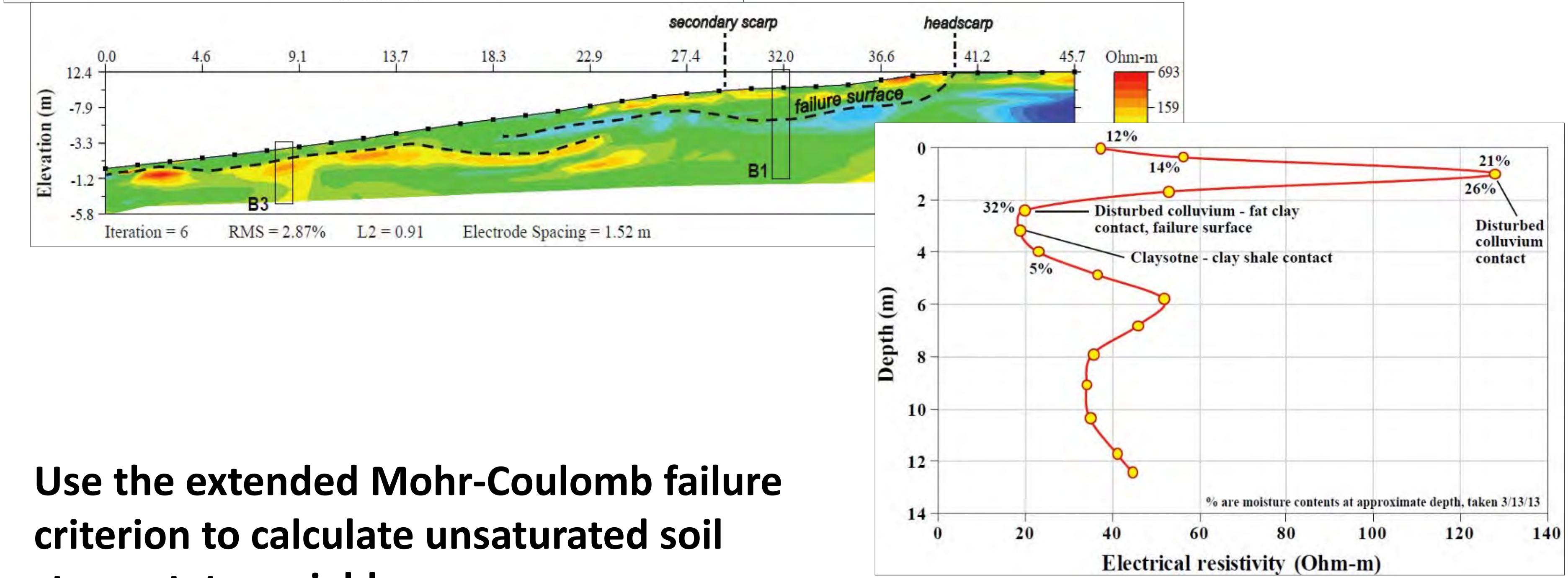
March 2015



Need more time-lapse ER data

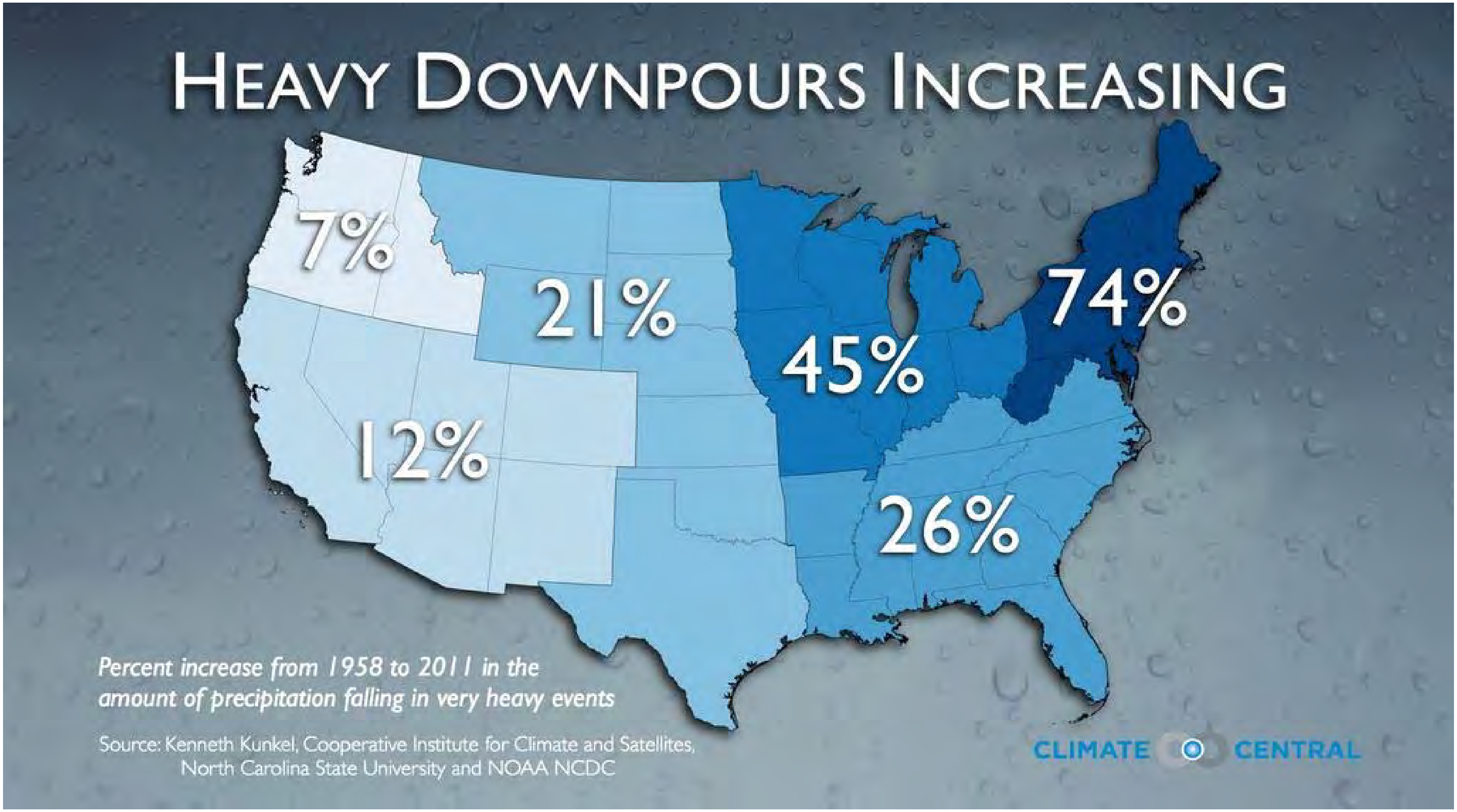


From Devita and others, 2012



Use the extended Mohr-Coulomb failure criterion to calculate unsaturated soil stress state variables

$$\tau_f = c' + (\sigma - u_a)tan\varphi' + (u_a - u_w)tan\varphi^b$$



What is a "heavy downpour?" A 2-day precip total that is exceeded on avg. once in a 5-yr period.

Source: Kenneth Kunkel, National Climate Assessment, Cooperative Institute for Climate and Satellites-NC

Summary

- Landslides in Kentucky damage roadways and infrastructure with mitigation costing millions of dollars per year in damages
- KGS landslide inventory and map service assists investigations and allows for better determination of where future landslides may occur
- KGS conducts research projects investigating hydrologic conditions, movement, and structure, and how geophysics may be used as a tool to support slope stability assessments.

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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

Phillip Lee Arant

Lexington, Kentucky

Director: Dr. Michael J. Lacki, Professor of Wildlife Ecology and Management

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

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

By: Phillip Lee Arant

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August 20, 2020

Date

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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.

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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.

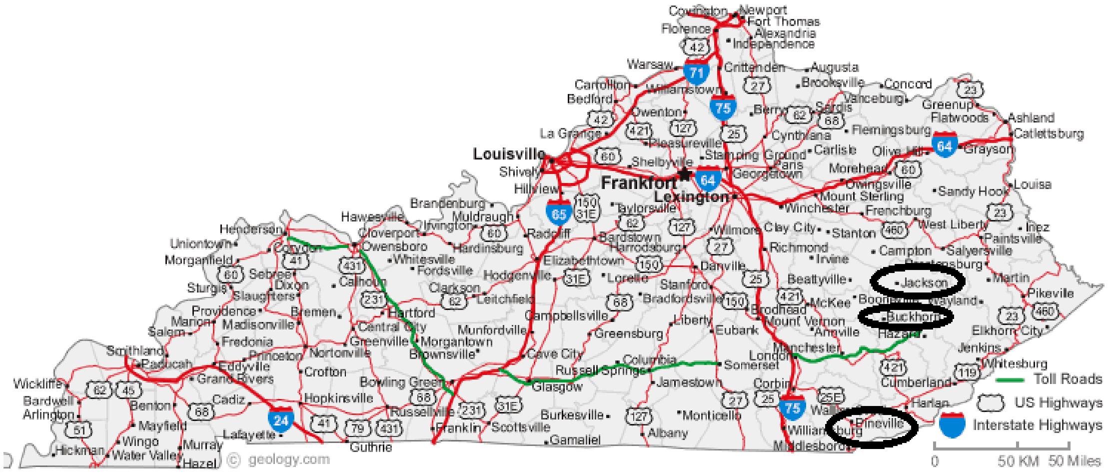


Figure 1. Map of field sites in Kentucky. Laurel Ridge rests within Robinson Forest near Buckhorn, KY, the Beech site is outside of Jackson, KY, and Kentucky Ridge is outside of Pineville, KY.

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.

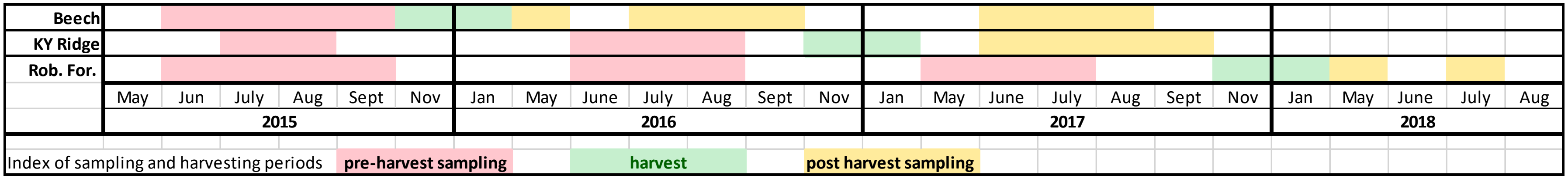
Pre-treatment acoustic sampling took place in summer 2015 at all three study sites. Activity was monitored using Song Meter 3 units and SMU-1 microphones (Wildlife Acoustics, Maynard, MA). The SM3 units were housed within pelican cases, with microphones placed within PVC pipe and tied to a tree at 1.5-m 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.



Beech		🟥	🟥	🟥	🟥	🟩	🟩	🟨		🟨	🟨	🟨				🟨	🟨	🟨							
KY Ridge			🟥	🟥					🟥	🟥	🟥		🟩	🟩		🟨	🟨	🟨	🟨						
Rob. For.		🟥	🟥	🟥	🟥				🟥	🟥	🟥				🟥	🟥	🟥			🟩	🟩	🟨		🟨	
	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
	2015						**2016**							**2017**							**2018**				

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.

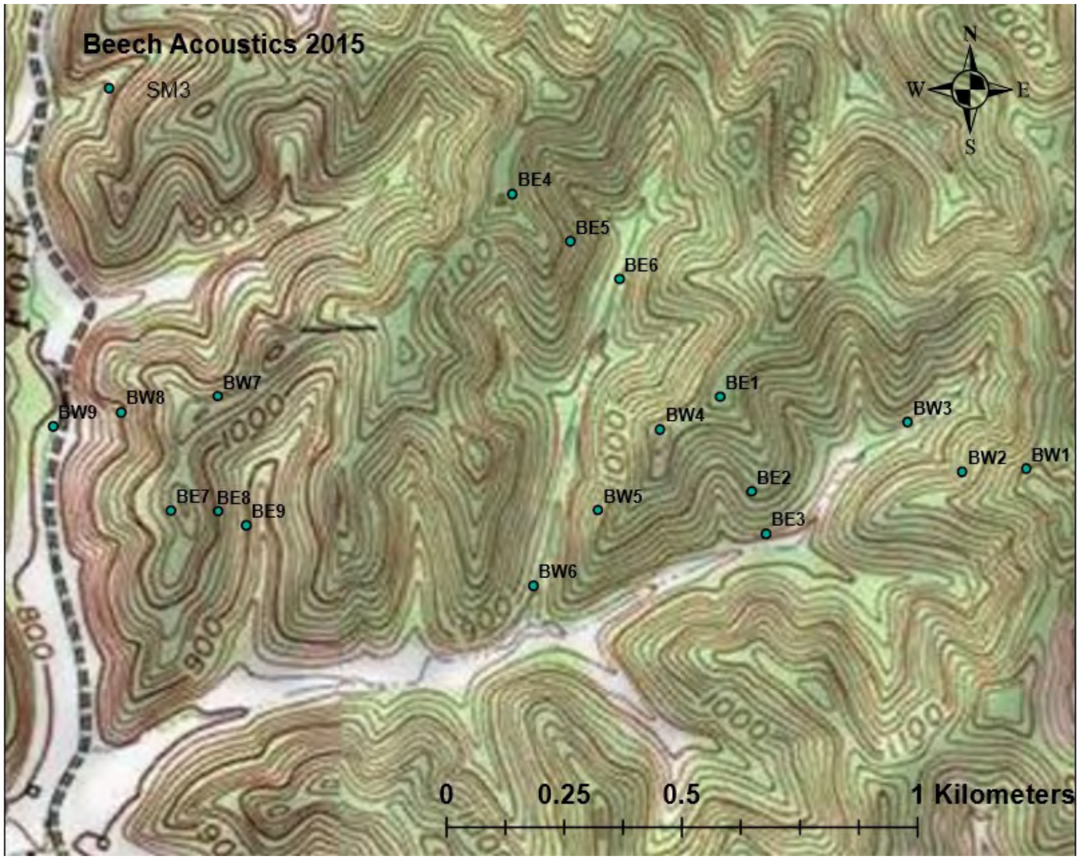


Figure 4. Pre-harvest (2015) acoustic transects at the Beech tract.

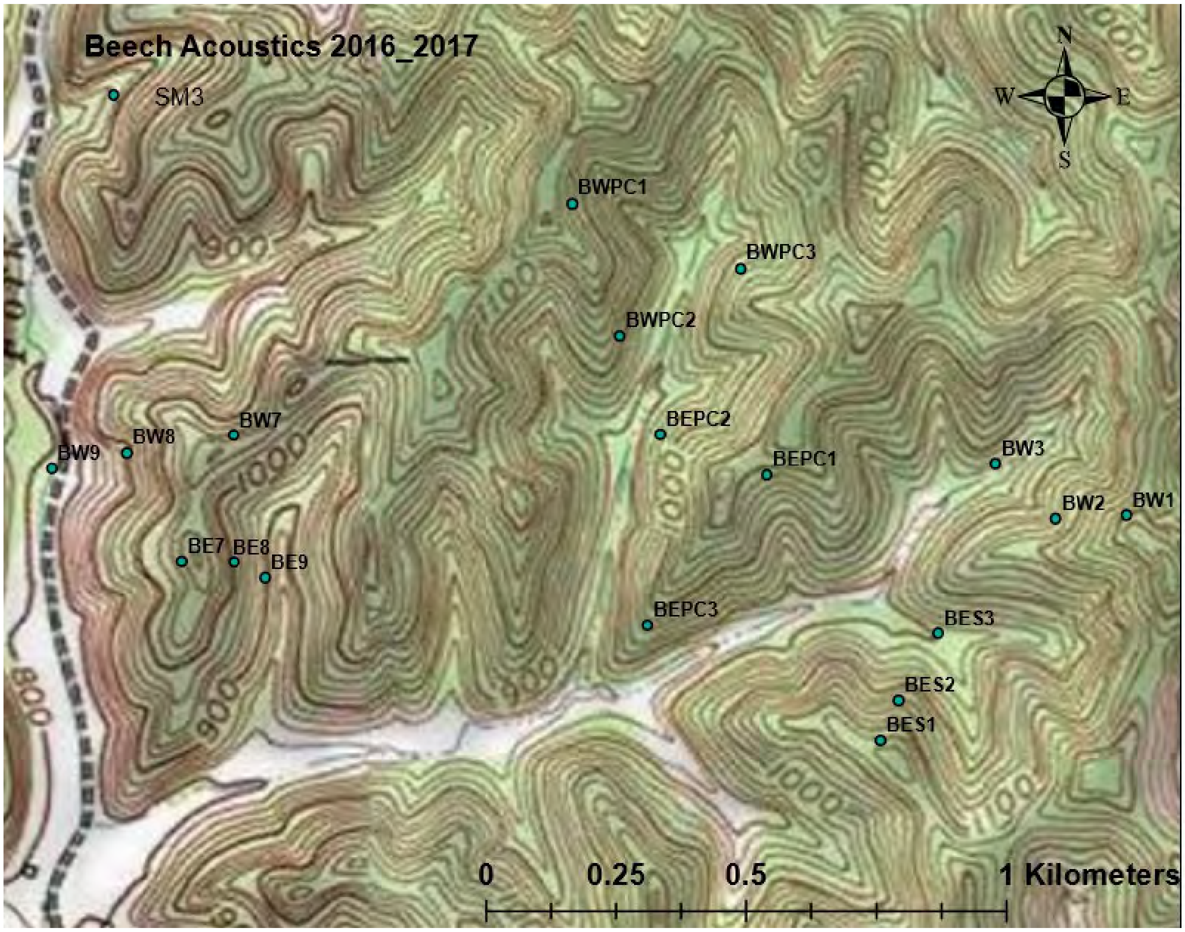


Figure 5. Post-harvest (2016-17) acoustic transects at the Beech tract.

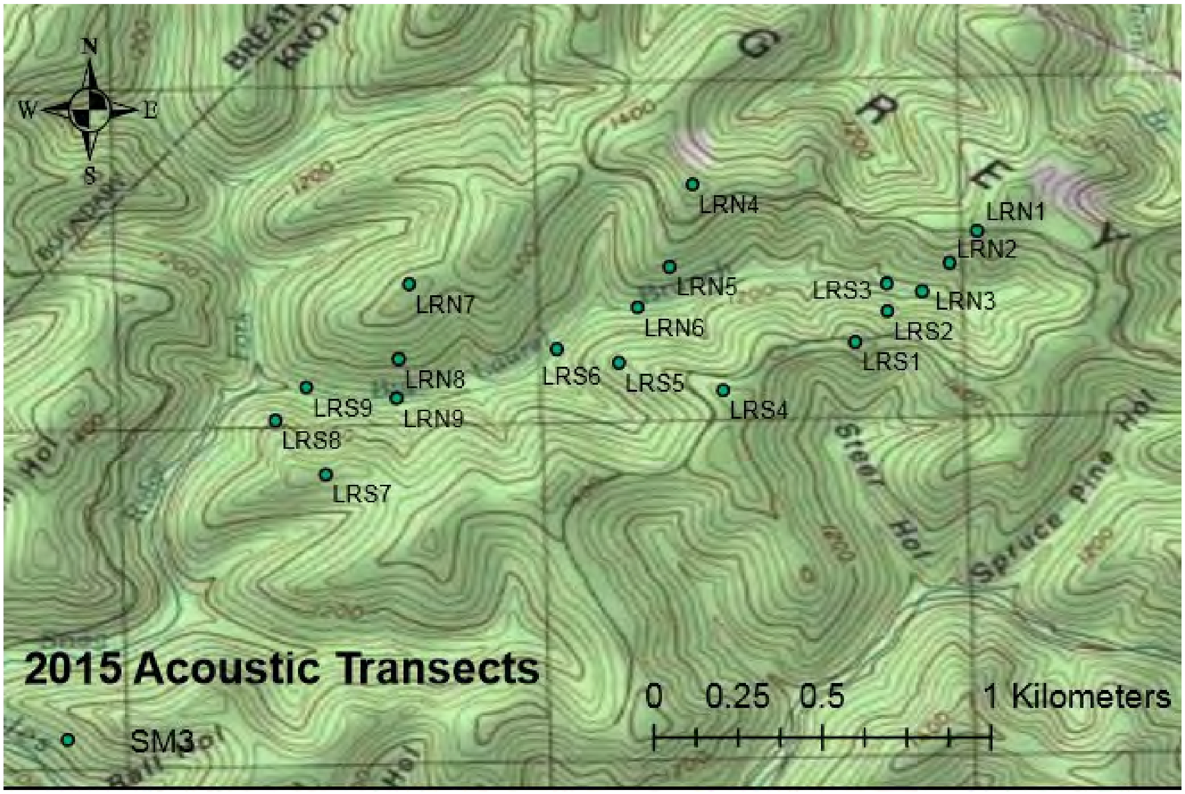


Figure 6. Pre-harvest (2015) acoustic transects at the Laurel Ridge tract, Robinson Forest.

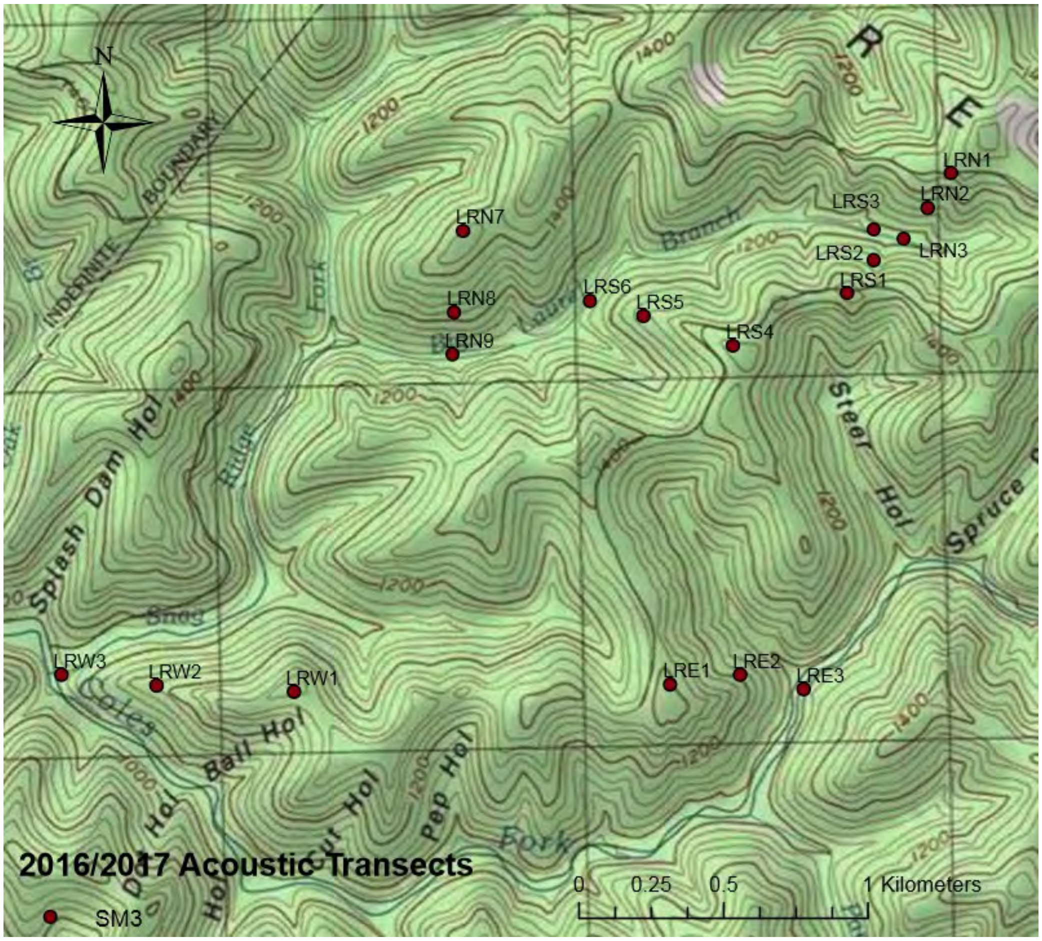


Figure 7. Pre-harvest (2016-17) acoustic transects at the Laurel Ridge tract, Robinson Forest.

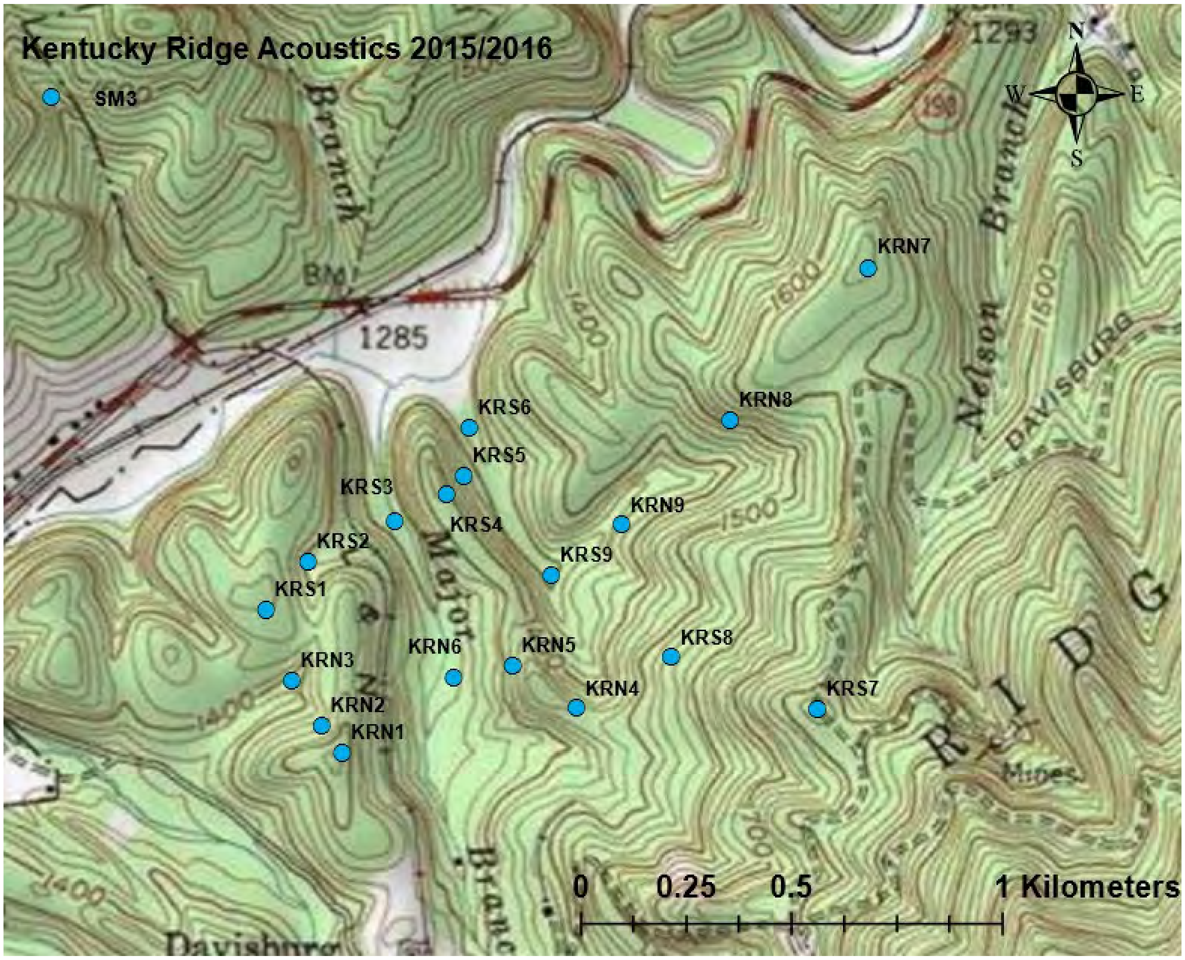


Figure 8. Pre-harvest (2015-16) acoustic transects at the Kentucky Ridge tract.

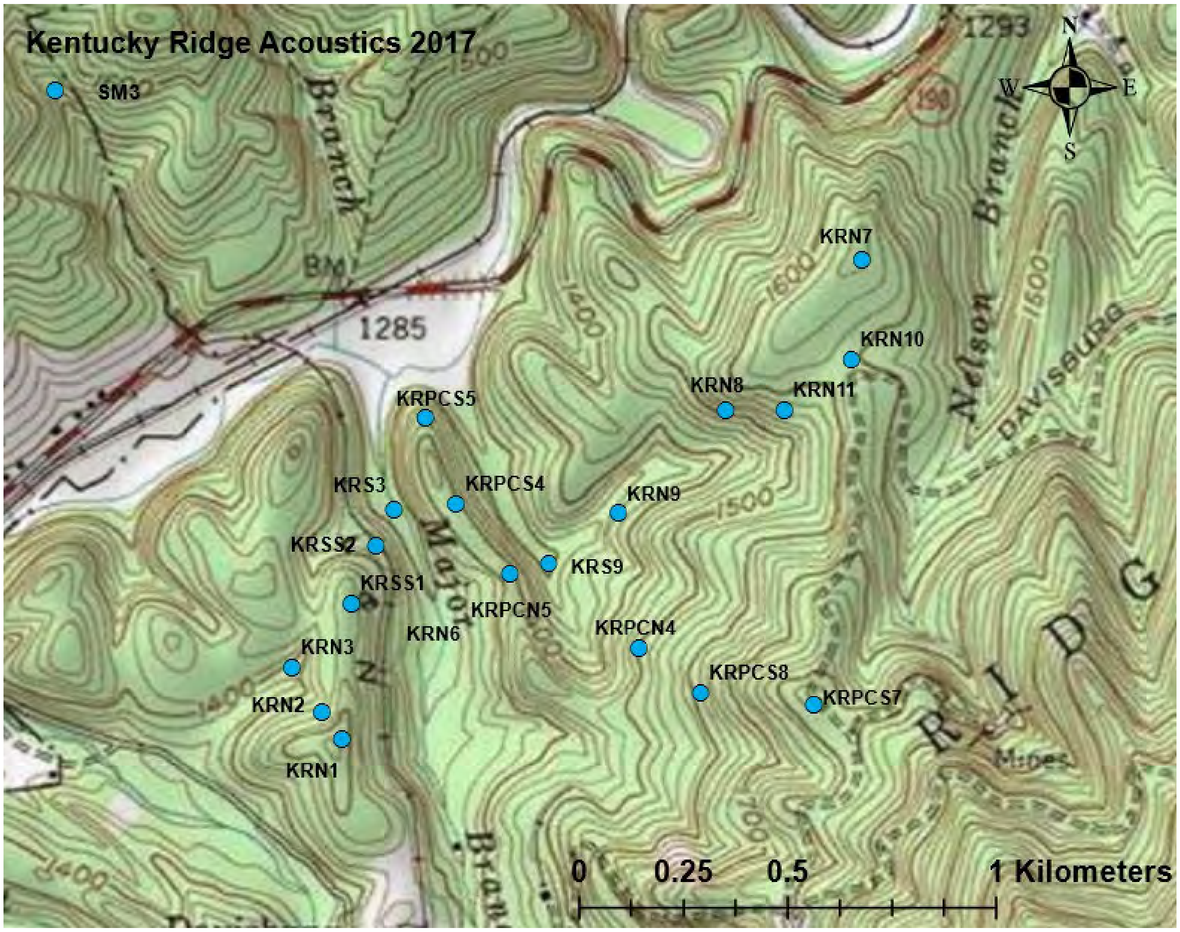


Figure 9. Post-harvest (2017) acoustic transects at the Kentucky Ridge tract.

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.

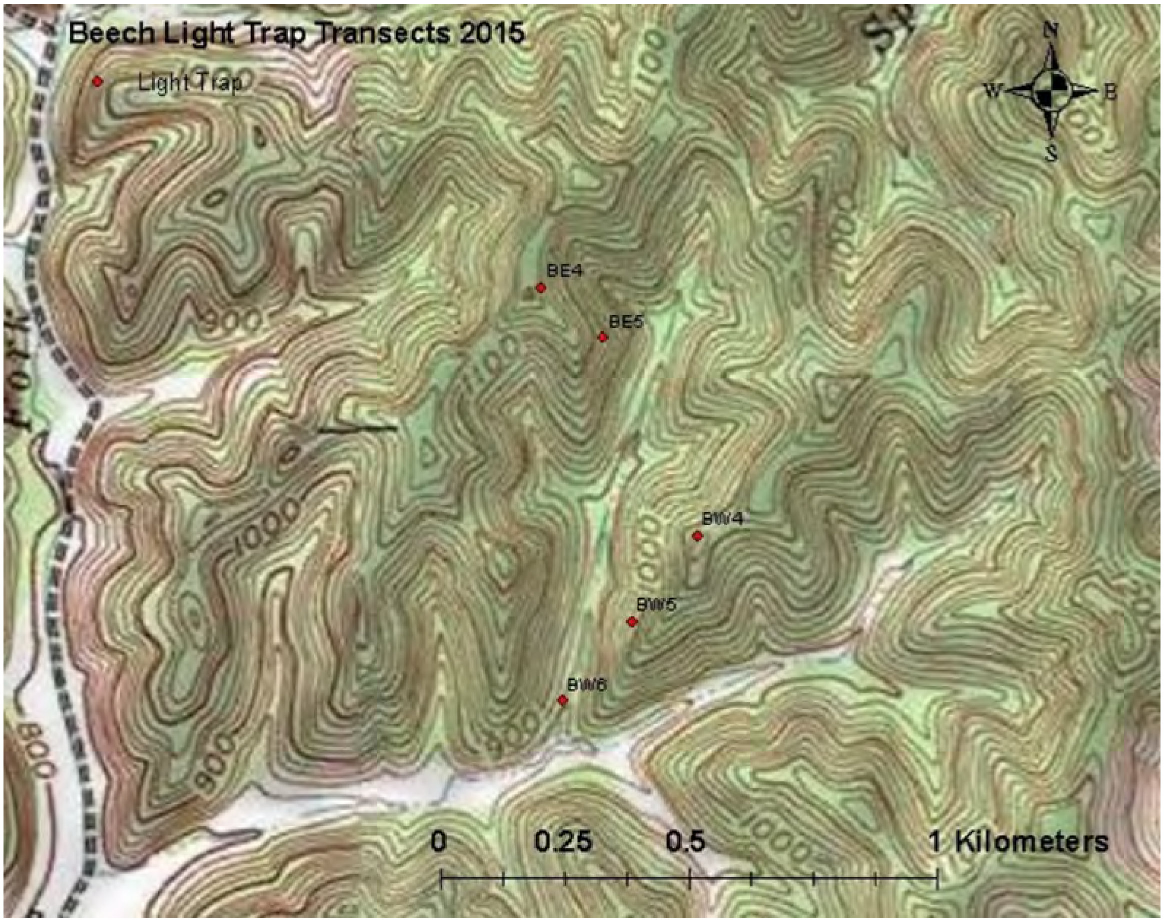


Figure 10. Pre-harvest (2015) light trap transects at the Beech tract.

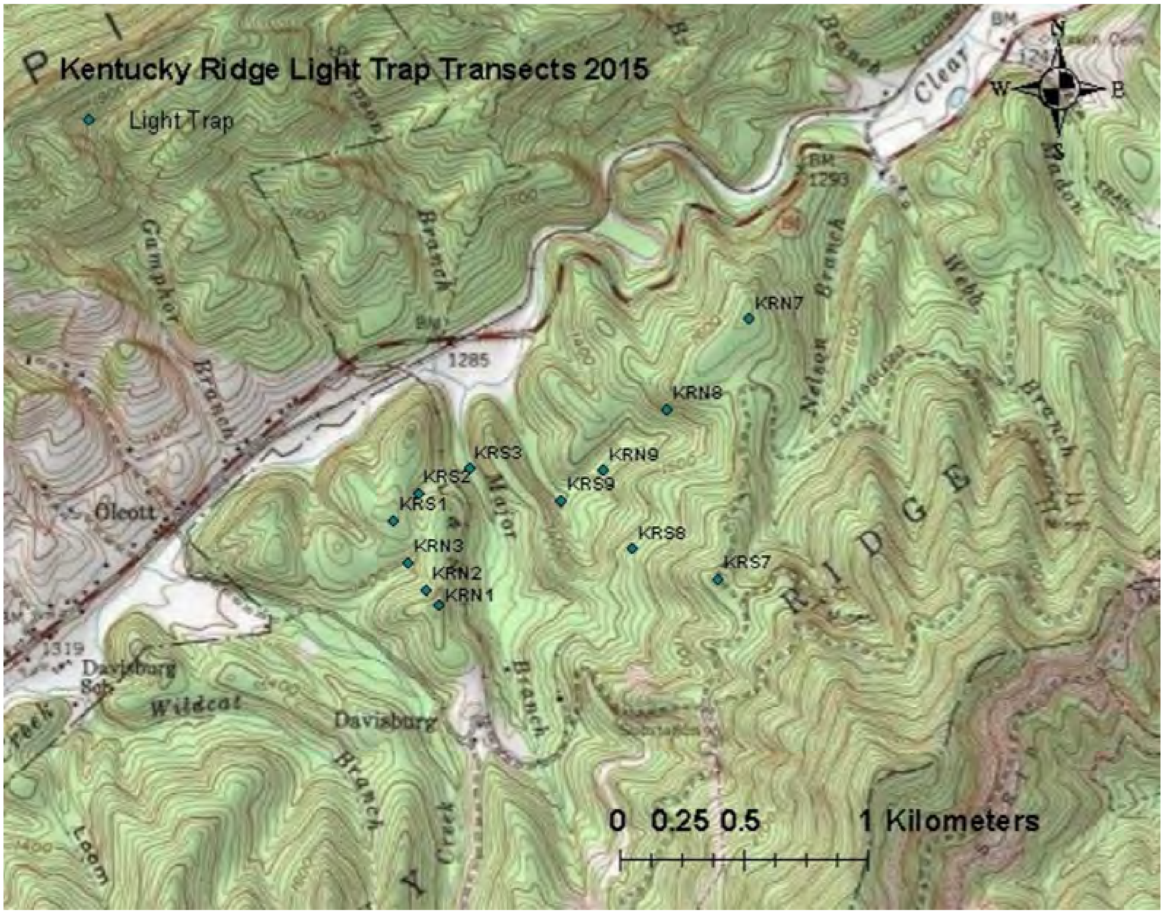


Figure 11. Pre-harvest (2015) light trap transects at the Kentucky Ridge tract.

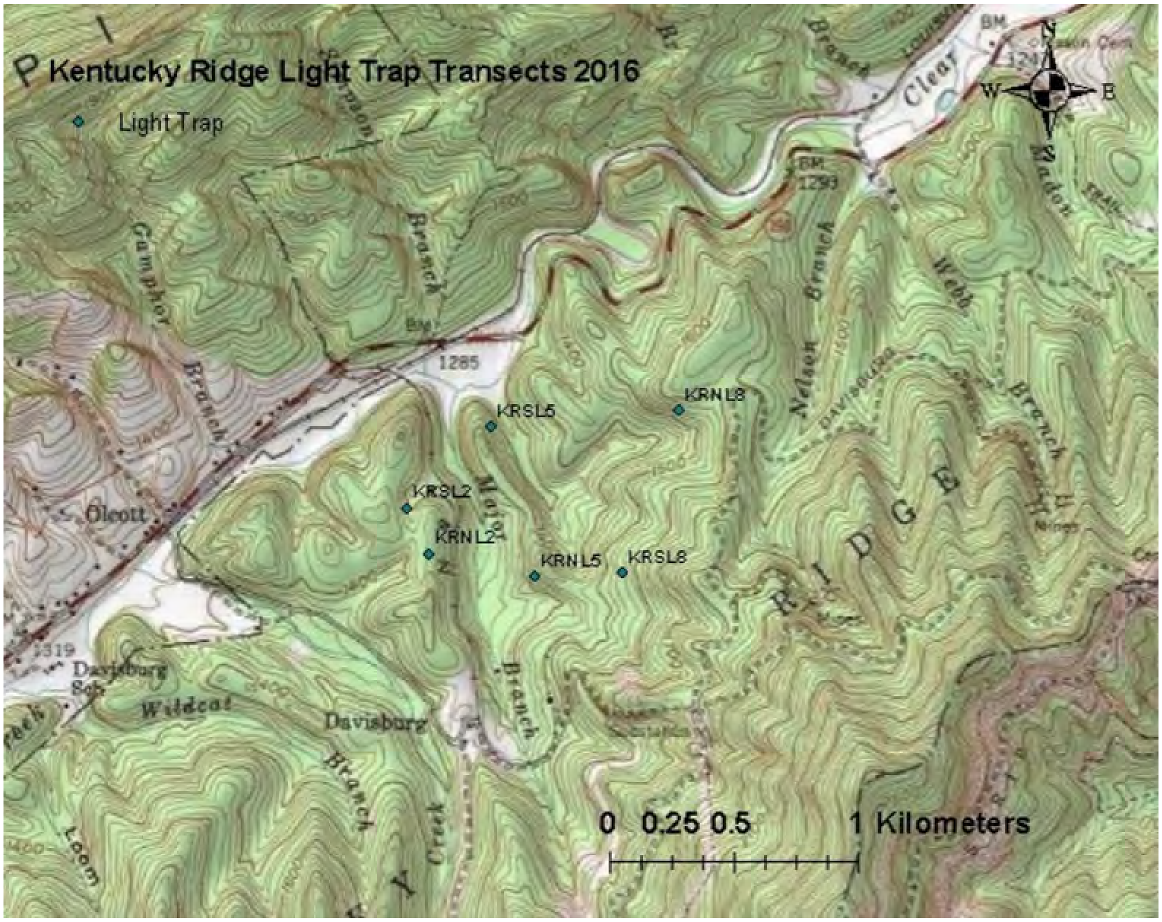


Figure 12. Pre-harvest (2016) light trap transects at the Kentucky Ridge tract.

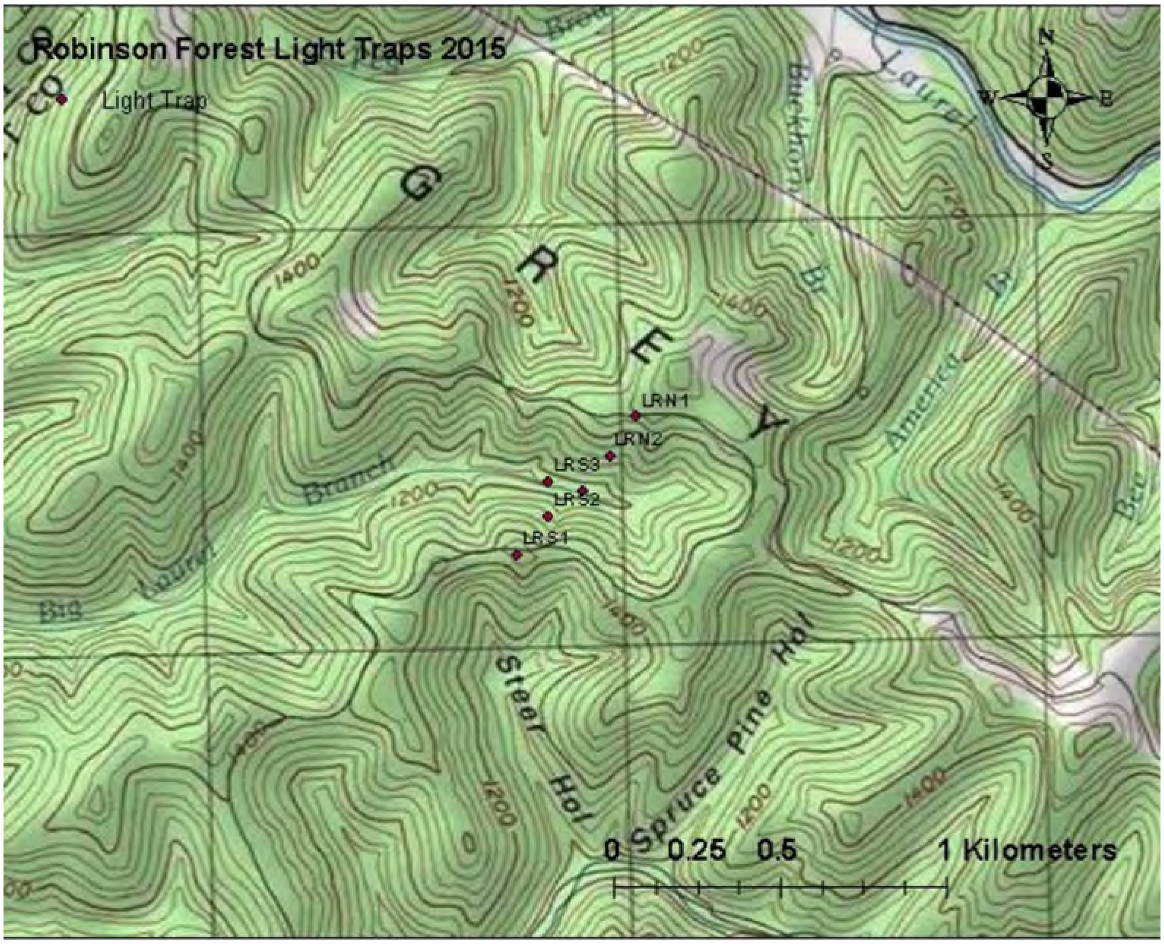


Figure 13. Pre-harvest (2015) light trap transects at the Laurel Ridge tract, Robinson Forest.

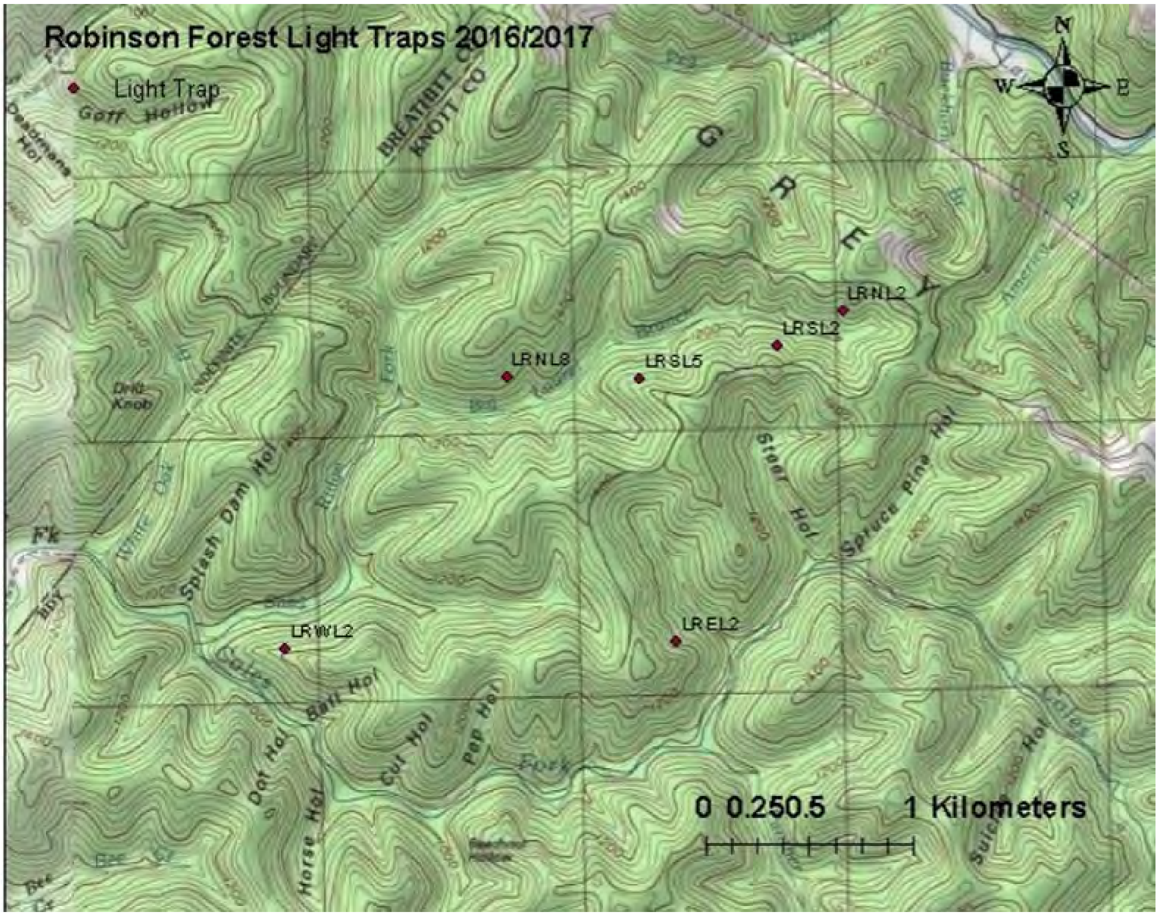


Figure 14. Pre-harvest (2016-17) light trap transects at the Laurel Ridge tract, Robinson Forest.

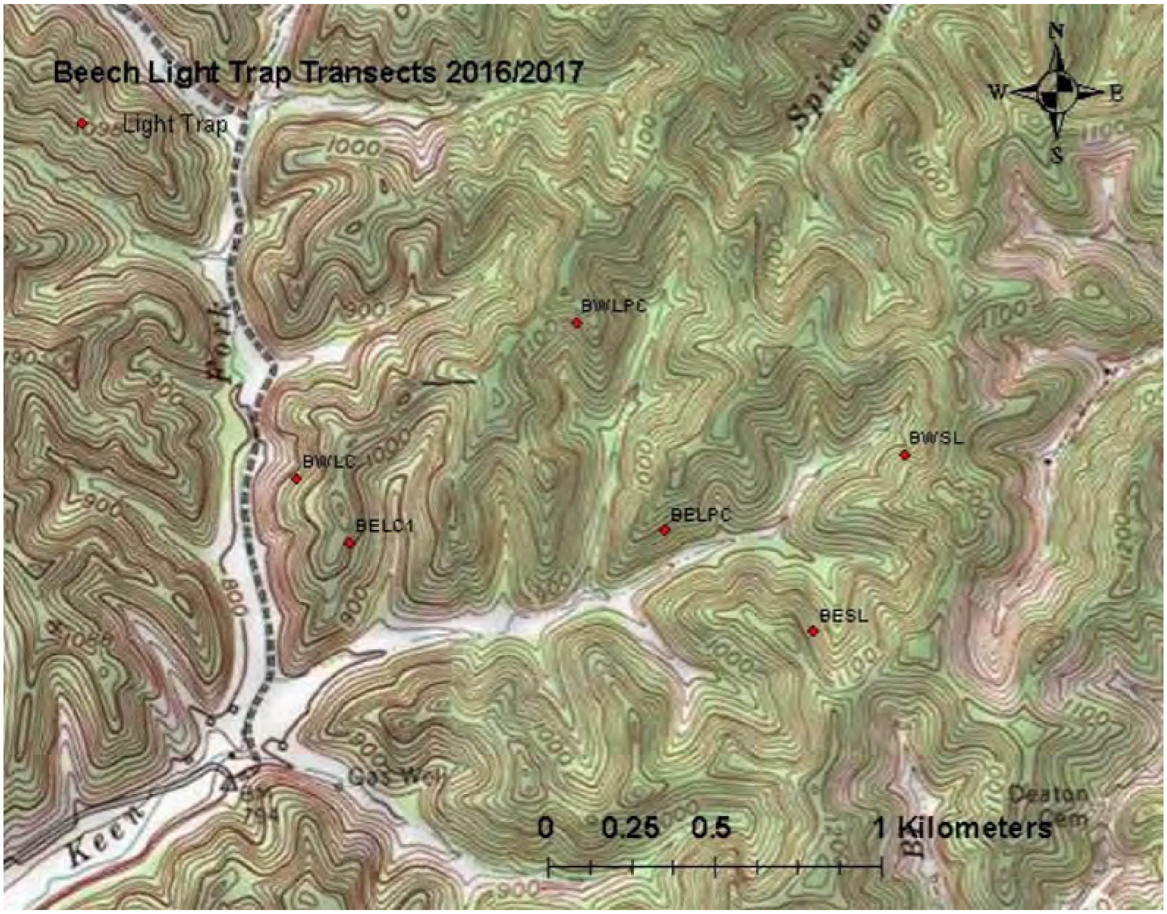


Figure 15. Post-harvest (2016-17) light trap transects at the Beech tract.

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

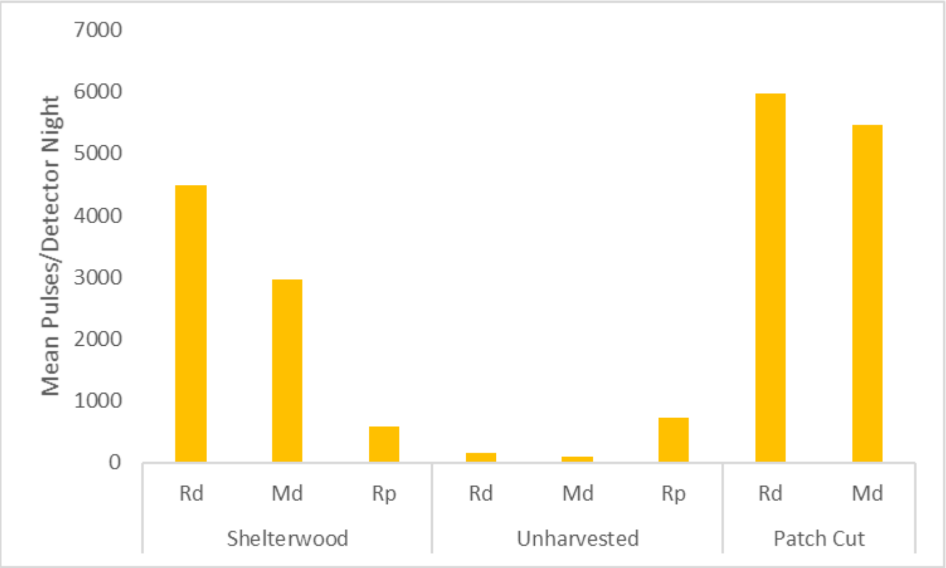
Acoustic sampling occurred in pre-harvest sites from late July 2015 thru early September 2017. During 2015, 310 nights of acoustic sampling data were collected from the Beech, Kentucky Ridge, and Laurel Ridge tracts. Data were used to determine the pre-harvest assemblage of bats present. Significant 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.

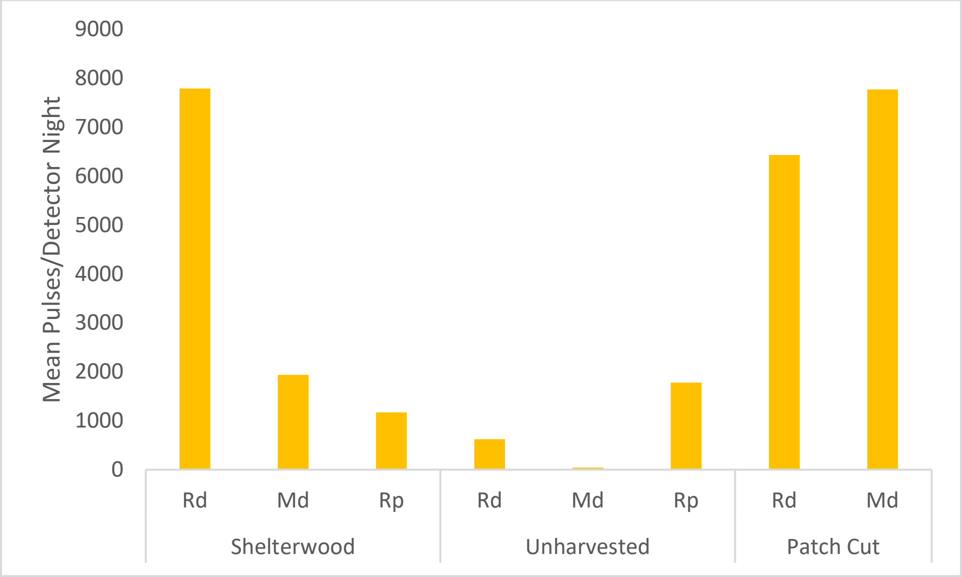
A quasi-poisson model comparing years showed significant increase in activity post-harvest at the Kentucky Ridge (649 acoustic nights) and Beech properties (492 acoustic nights). A quasi-poisson model comparing slope positions post-harvest, showed differences between shelterwood slope positions. At the 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.



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

a.



Mean Pulses/Detector Night
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
Rd
Md
Rp
Rd
Md
Rp
Rd
Md
Shelterwood
Unharvested
Patch Cut

b.

c.

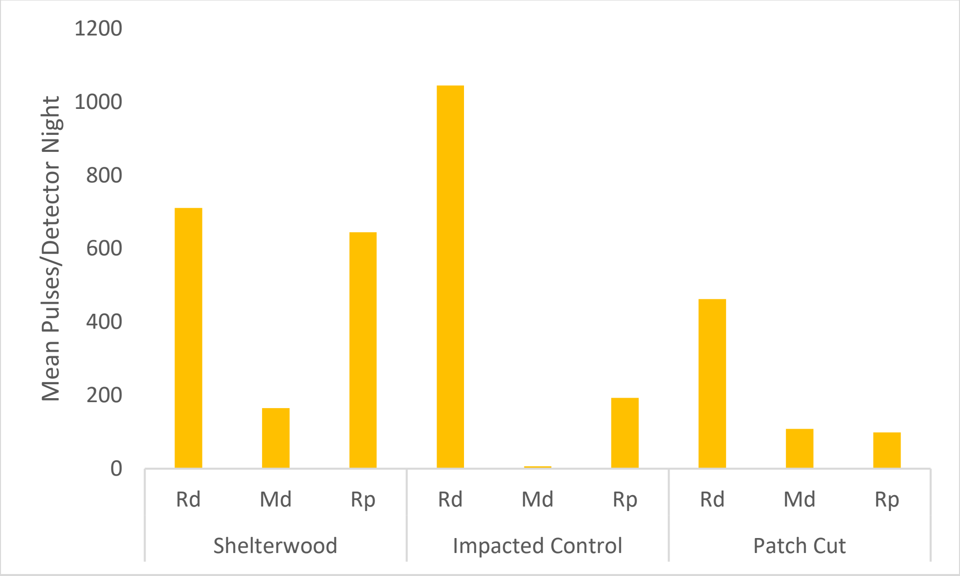
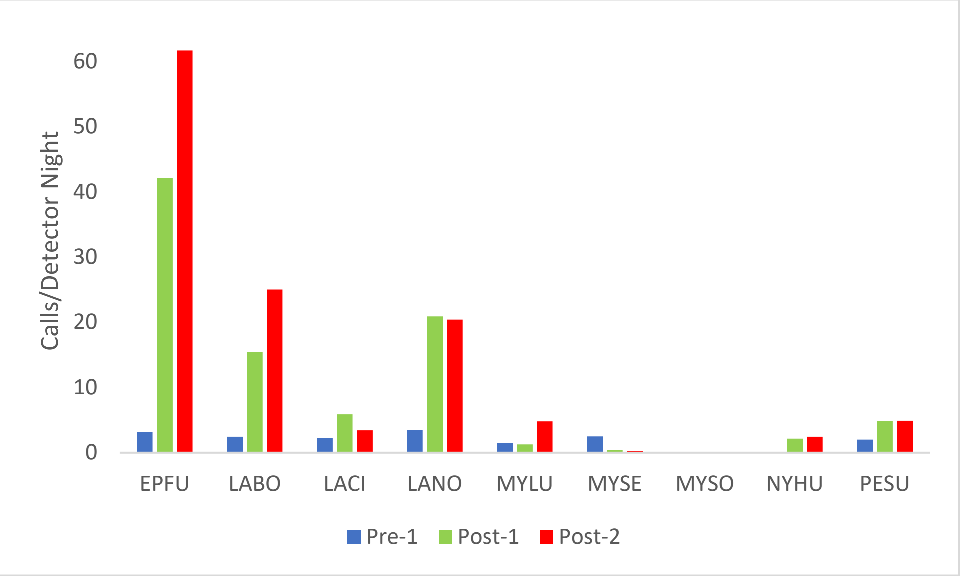
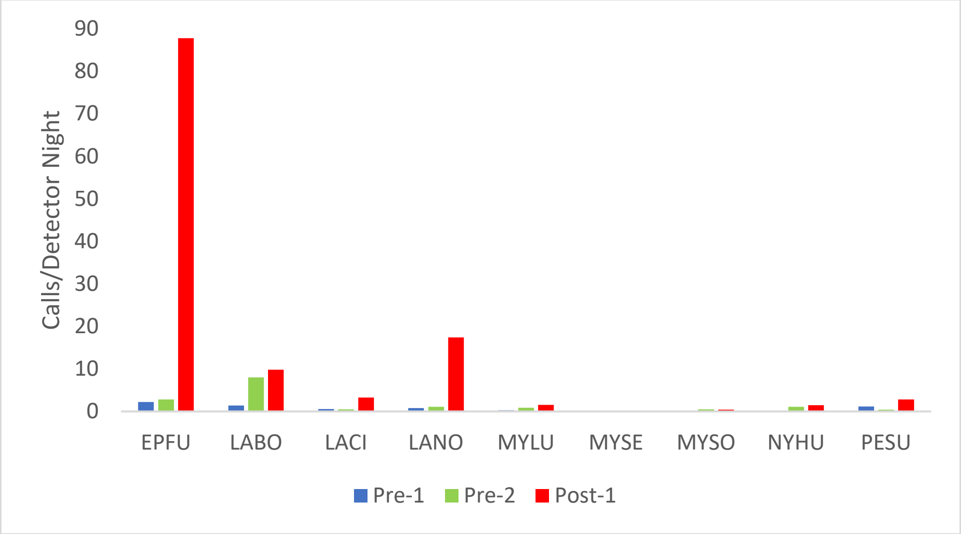


Figure 17. Comparison of activity of bats in different treatments and slope positions; ridgetop (rd), mid-slope (md), and riparian (rp). Beech (a), Kentucky Ridge (b), and Laurel Ridge (c) tracts in eastern Kentucky.

a.



b.



c.

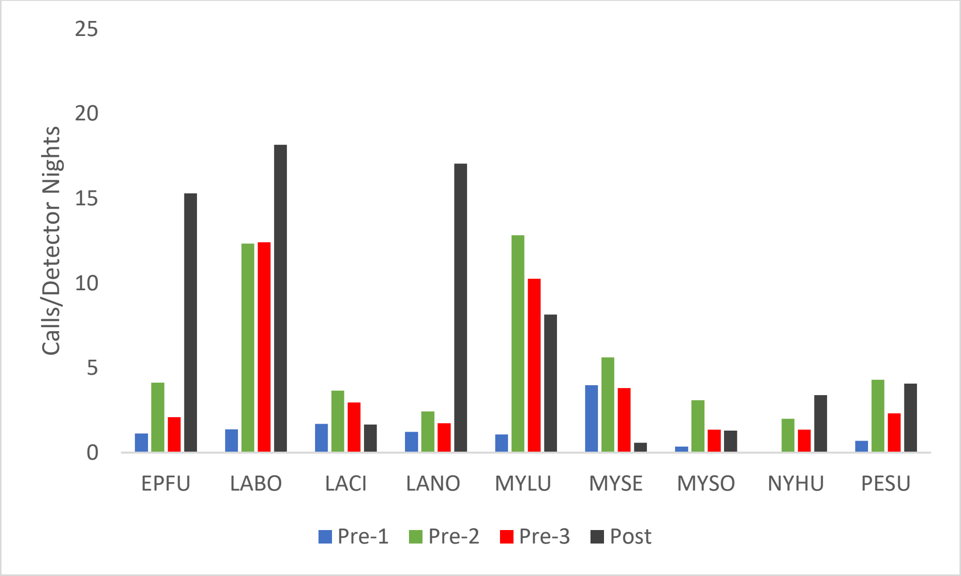


Figure 18. Activity of bat species pre-and post-harvest at; Beech (a), Kentucky Ridge (b), and Laurel Ridge (c) tracts in eastern Kentucky. (Blue (2015), Green (2016), Red (2017), and Black (2018). The pre-x designation denotes the site had not yet been harvested and the number of seasons the site has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

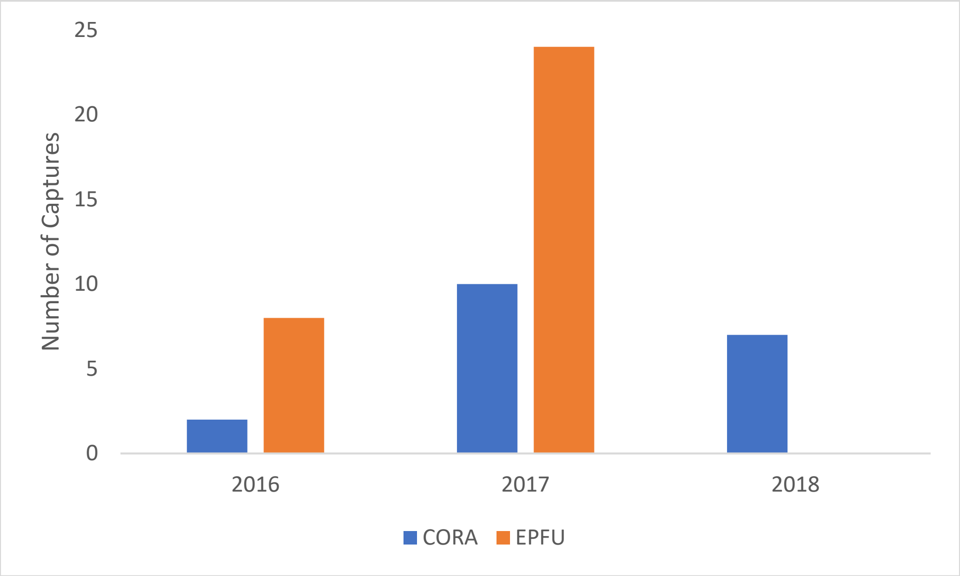
The camp at Robinson Forest has several maternity colonies of bats. A maternity colony of big brown bats numbering around 100 individuals roosted within the attics in two separate cabins. The office had a small bachelor colony of big brown bats, along with a small bachelor colony of Rafinesque big-eared 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.


25
20
15
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5
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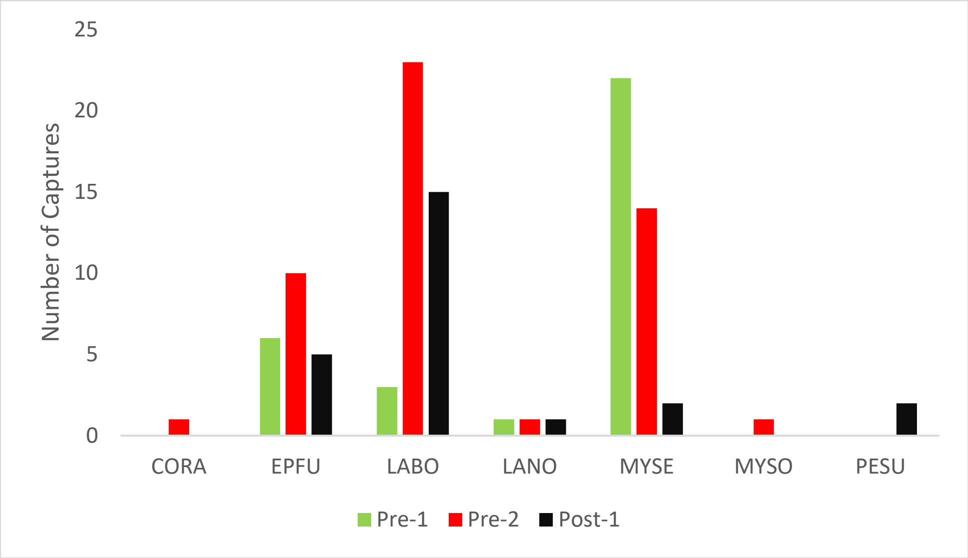
Number of Captures
2016
2017
2018
CORA
EPFU

b.


25
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Number of Captures
CORA
EPFU
LABO
LANO
MYSE
MYSO
PESU
Pre-1
Pre-2
Post-1

c.

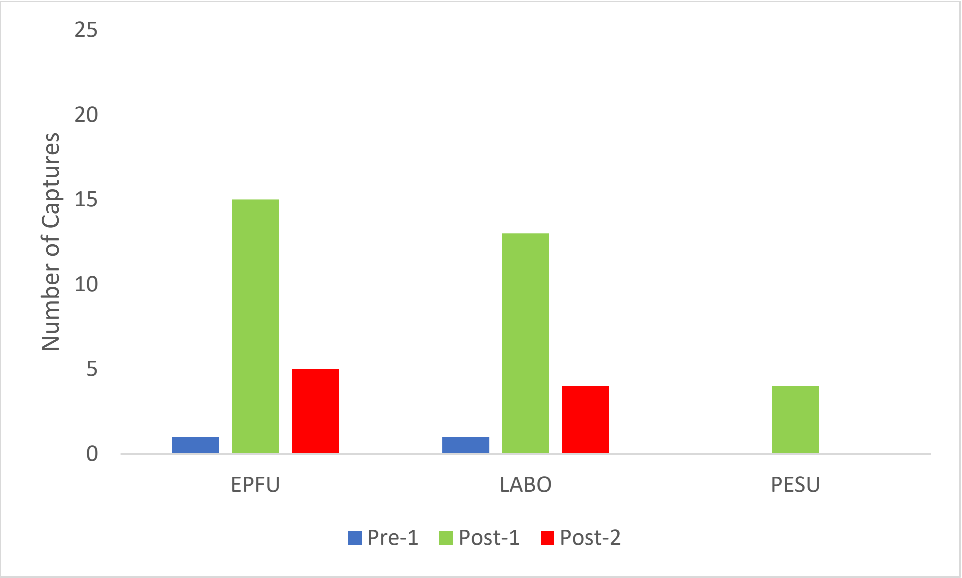

Figure 19. Results of bats captured during mist netting efforts. (a) Bats captured during mist netting efforts at Robinson Forest's camp. (b) Bats captured during surveys on Robinson Forest. (c) Bats captured during surveys on the Beech tract. (Blue (2015), Green (2016), Red (2017), and Black (2018).

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.

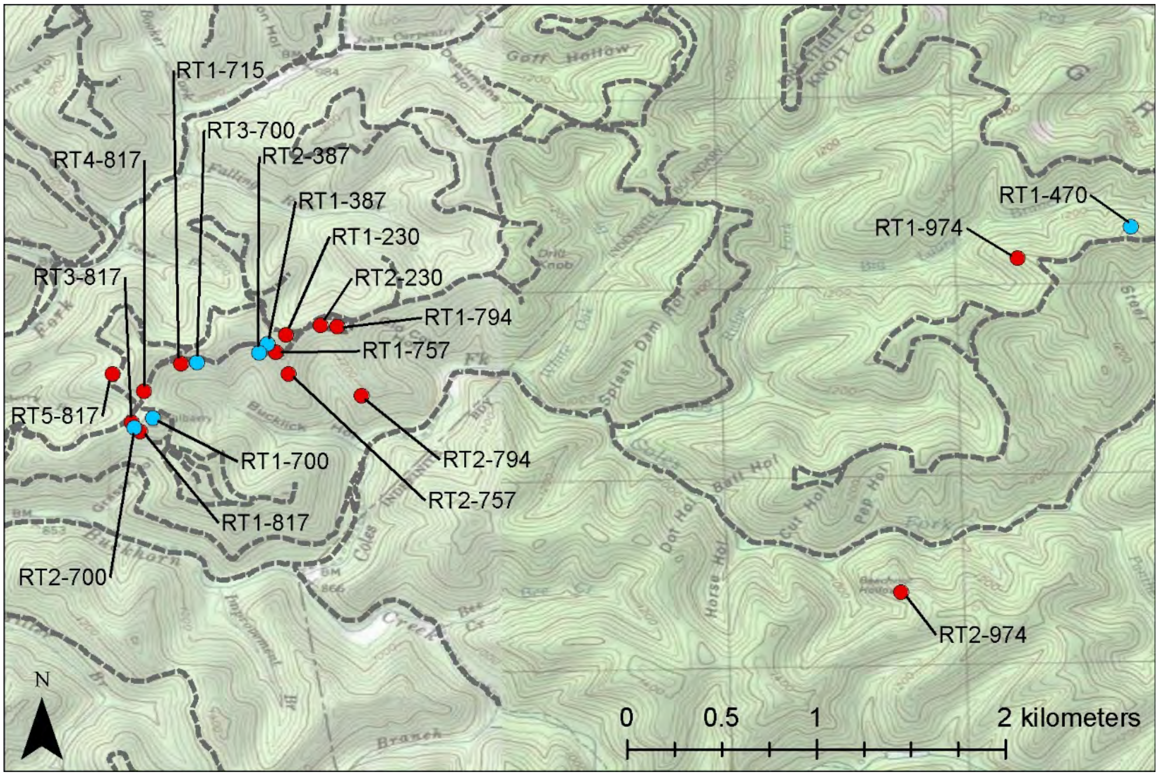

Figure 20. Roost trees located at Robinson Forest during tracking efforts from 2016-2017. Red dots are maternity roosts used by pregnant or lactating females. Blue dots are roost trees used by bats. The grey dotted line is the maintained closed canopy forest road. RT2-794 and RT2-974 both have non-maintained 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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Professional Positions

Scientist, Environmental Solutions and Innovations	2019 – 2020
Bat Biologist/Environmental Scientist I, Allstar Ecology, LLC	2018
Research/Teaching Assistant, University of Kentucky	2015 – 2018
Protein Analyst Technician, Aerotek/Kentucky Bioprocessing	2015
Acoustic Technician, Missouri Department of Conservation	2014
Bat Technician, West, Inc.	2014
Metrology Technician, Premier Scales and Systems	2014
Microbiology Technician, Aerotek/Mead Johnson Nutrition	2013
Intermittent Worker, DNR Fish and Wildlife	2012

Presentations

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PLOS SUSTAINABILITY AND TRANSFORMATION

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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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.

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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,

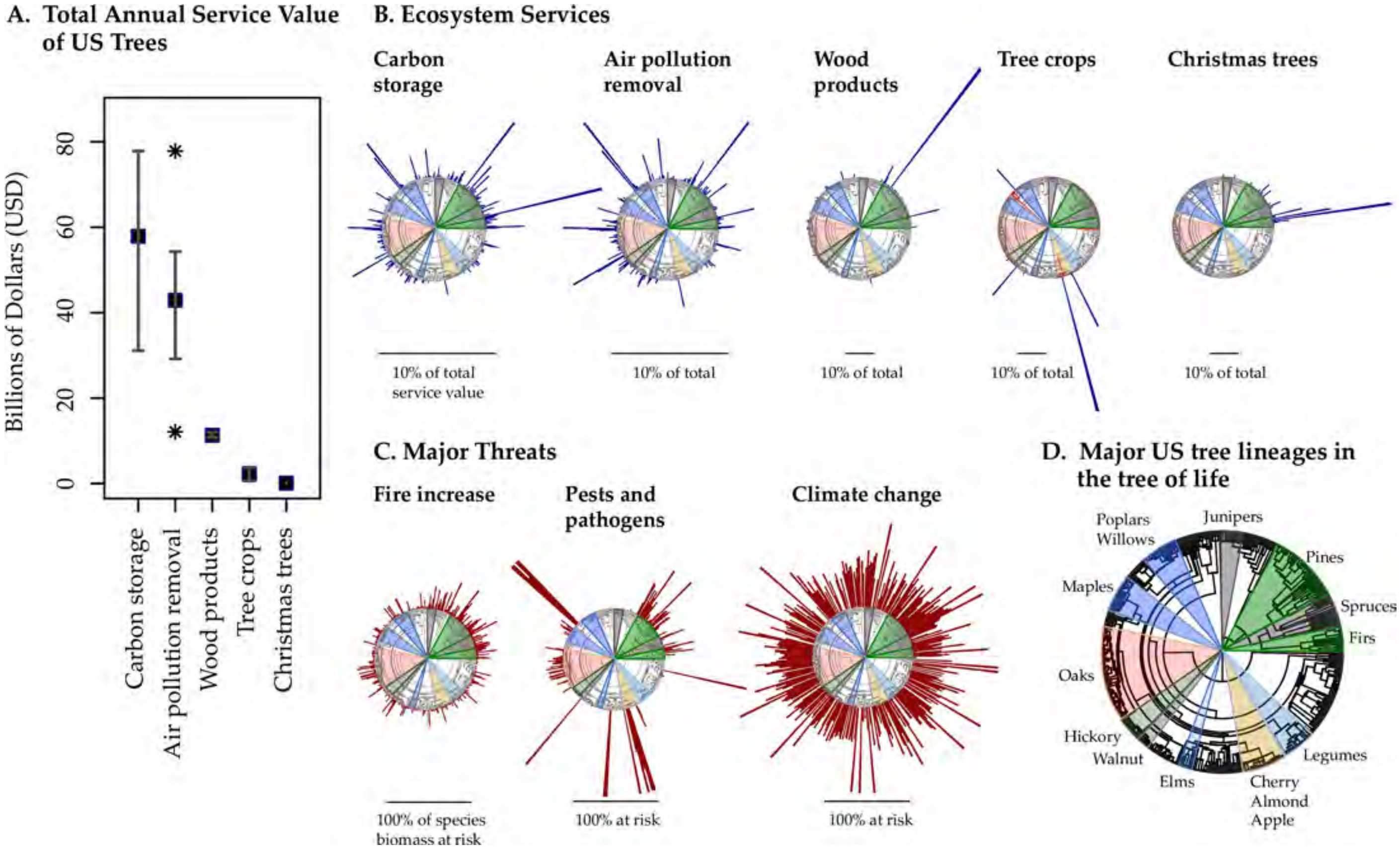

Fig 1. (A) Total net annual ecosystem service values provided by contiguous US trees between 2010 and 2012. The squares give mean estimated value and the error bars show the range in expected values. (B) Ecosystem service annual value (blue bars) and (C) potential threats (brown bars) for tree species 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.

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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

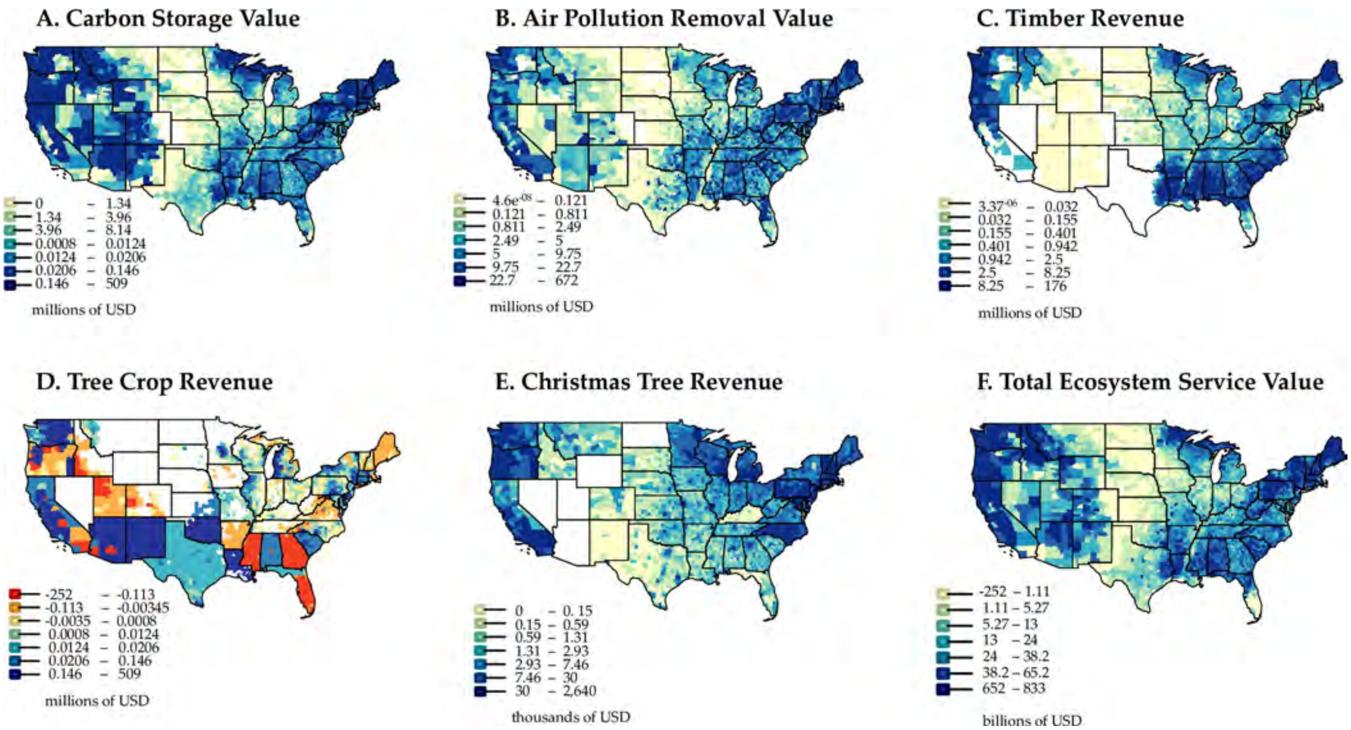

Fig 2. Annual net ecosystem service value generated between 2010 and 2012 (in 2010 USD) (A) climate regulation via carbon storage, (B) air quality regulation via human health damages avoided by tree-based filtering of air pollution (C), wood product net revenue (D) tree crop net revenue, (E) Christmas 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).

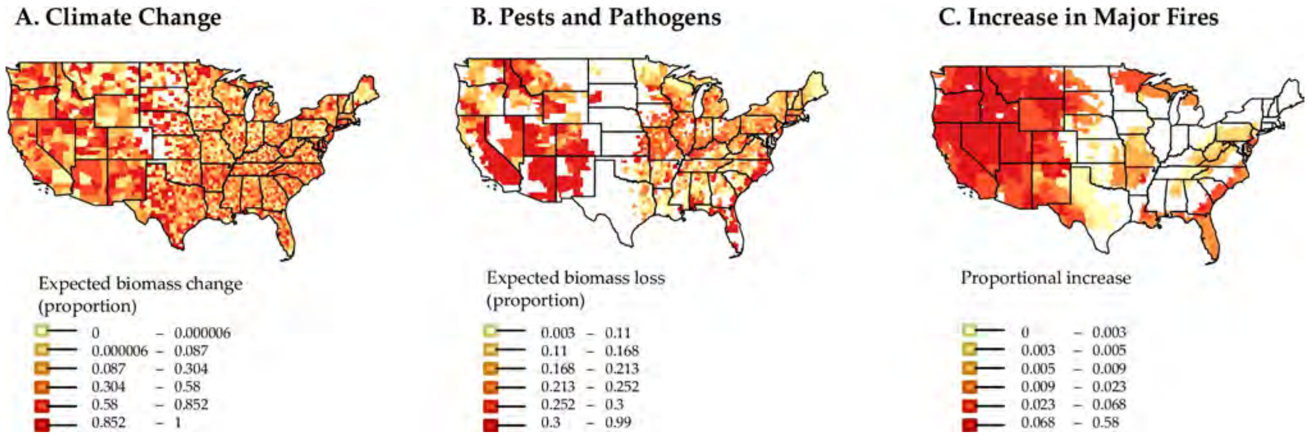

Fig 3. Magnitude of county-level threats across the contiguous US. Darker colors indicate greater threat to the biomass currently located in the county. Missing data are indicated in white. (A) Proportion of current total tree biomass in each county that is expected to be exposed to climatic regimes (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.

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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.

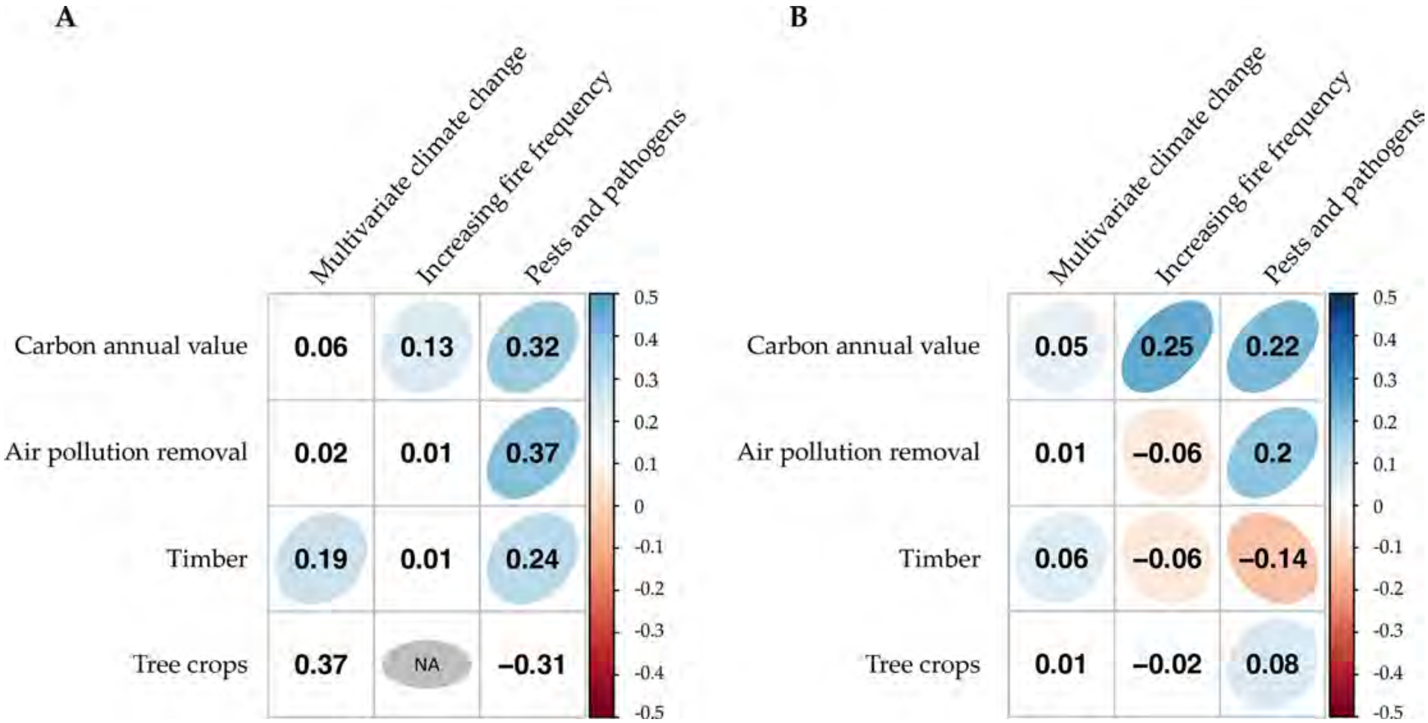

Fig 5. Associations between annual net ecosystem service values of tree species in the US and their predicted threats and drivers of change based on Spearman's rank-order correlations. A) Species-level correlation coefficients (rho) between annual net ecosystem service value and predicted threats. B) 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 μg/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 \$/μg/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 μg/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)

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Disturbance-Mediated Accelerated Succession in Two Michigan Forest Types

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ABSTRACT. In northern lower Michigan, logging accelerated sugar maple (*Acer saccharum*) dominance in a northern white cedar (*Thuja occidentalis*) community, and clear-cutting and burning quickly converted certain sites dominated by mature jack pine (*Pinus banksiana*) to early-successional hardwoods, including *Prunus*, *Populus*, and *Quercus*. In both forest types the succeeding hardwoods should continue to increase in the future at the expense of the pioneer conifer species. In the cedar example, sugar maple was also increasing in an undistrubed, old-growth stand, but at a much reduced rate than in the logged stand. Traditionally, disturbance was thought to set back succession to some earlier stage. However, our study sites and at least several other North American forest communities exhibited accelerated succession following a wide range of disturbances, including logging, fire, ice storms, wind-throw, disease, insect attack, and herbicide spraying. FOR. SCI. 35(1):42–49.

ADDITIONAL KEY WORDS. Northern white cedar, jack pine, sugar maple, logging, fire, old-growth.

FOR A SIGNIFICANT PORTION OF THIS CENTURY, Clements' ideas on succession and climax dominated much of the ecological thinking. Clements (1916) described succession as a universal orderly process of progressive change under the control of the regional climate (the superorganism community concept). The idea that recurring natural disturbance was a widespread phenomenon in many North American plant communities was not emphasized. Nonetheless, Cooper (1913) reported that the native vegetation of Isle Royale was a mosaic or patchwork of burned and wind-throw areas of varying ages and species composition. Gleason (1926), who pioneered the individualistic concept of the plant association, also recognized that disturbances shape the spatial and temporal boundaries of associations. In the 1940s, evidence increased that fire and wind-throw pervade in forest communities (Maissurow 1941, Watt 1947, Stearns 1949). In his classic study of beechwoods in England, Watt (1947) recognized that tree death from storms, fire, drought, epidemics, and old-age cause gaps in the forest, to which regeneration is confined. Egler (1954) developed an "initial floristic composition" model for old-field succession, in which a field receives propagules of many species prior to abandonment. Successional development then unfolds from this initial flora without significant additions from later invasion. Egler hypothesized that succession could be arrested by disturbance if the woody species that would dominate the mature community were killed at some earlier stage. After 1970, the role of disturbance as a normal, recurring influence on the structure and maintenance of numerous plant communities worldwide became widely accepted (Loucks 1970,

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Sprugel 1976, White 1979, Oliver 1981, Sousa 1984). Moreover, it was recognized that disturbances profoundly affect succession and may promote the occurrence of multiple successional pathways on a variety of sites (Cattelino et al. 1979, West et al. 1981, Abrams et al. 1985).

Despite the historic effort to describe and understand succession, we feel that at least one idea has not been well developed in the ecological literature, namely, disturbance-mediated accelerated succession. We believe that, following disturbance, certain early successional forest communities dominated by pioneer tree species can be converted to later successional associations at an accelerated rate. This contrasts with the traditional idea that disturbance sets back succession to some earlier seral stage. In this paper evidence of disturbance-mediated accelerated succession is presented for northern white cedar (*Thuja occidentials* L.) and jack pine (*Pinus banksiana* Lamb.) communities in Michigan.

Methods

This study was conducted in two different areas in northern lower Michigan, where disturbed and undisturbed northern white cedar and jack pine communities were found. White cedar and jack pine are both considered early successional species that typically invade lowland swamps or open dunes and burned-over or clearcut sandy soils, respectively (Fowells 1965, Abrams et al. 1985, Scott and Murphy 1986). Two adjacent white cedar dune communities were examined on South Manitou Island in Leelenau County. The soil of the study area is a Deer Park sand, classified as mixed, frigid, Spodic Udipsamment. One community was a 10 ha old-growth (>175 yr) stand. The other community (3.4 ha) was logged for large cedar between 1890–1900 and is presently dominated by sugar maple (*Acer saccharum* Marsh.). Prior to logging, differences in the density and basal area of cedar between the two communities were not significant (Scott 1985). Four undisturbed, mature jack pine stands (>55 yr) and two prescribe-burned jack pine clearcuts (surveyed from ages 4–6 yr) were studied in Roscommon, Crawford, Oscoda, and Ogemaw counties (Abrams 1982). All six jack pine sites occurred on the Grayling sand soil series (a mixed, frigid, Typic Udipsamment), characterized by its loose consistency, incoherent structure, and low nutrient and water holding capacity.

Stand description for the two white cedar communities was obtained using 22 randomly located 100 m^2 quadrats from which the following information was collected for each tree $\geq$2.5 cm dbh: (1) species; (2) live or dead; (3) dbh; and (4) tree height. Two increment cores were extracted from each of several live trees per quadrat over the observed size ranges for each species (35 trees per stand). Relative dominance, density, frequency, and importance values were calculated for each species (Muller-Dombois and Ellenberg 1974). In addition, dbh measurements were taken on all down-stems encountered in the quadrats. All cedar and maple mortality (standing and down-stems) identifiable by bark and wood characteristics was assumed to have occurred after 1890. This assumption is supported by the observation that cedar stumps in the second-growth stand had lost all traces of bark and were beginning to fragment. In terms of basal area, cedar in the old-growth stand accounted for >99% of this mortality. To examine shifts in the relative dominance of cedar and maple in both stands following logging (1890), basal area changes corrected for growth and mortality were estimated for each decade between 1900 and 1980 (cf. Oliver and Stevens 1977). Using tree growth information obtained from cores, average stem growth rates per plot were estimated for each species in 10 cm size classes. These growth increments were subtracted on a per plot basis from the diameters of each cedar or maple in the appropriate size class for each successive decade in the growth record. Basal area for post-logging mortality was added to estimates of stand basal area for cedar and maple in 1900, and factored out over the subsequent decades. We were unable to accurately quantify mortality decade by decade and consequently total observed mortality was factored out by assuming uniform mortality over time. While this assumption does not influence our initial and final basal area estimates, it likely simplifies the pattern of basal area change over time.

In the jack pine communities, cover was estimated for all understory vegetation (plants ≤ 1.5 m tall or <2.5 cm dbh) by summing the canopy distance intersected by each species along three 20 m transects (Abrams et al. 1985). The transects were oriented to best include the entire area to be surveyed.

Results and Discussion

The old-growth northern white cedar stand was dominated by cedar, but sugar maple, white ash (*Fraxinus americana* L.) and mountain maple (*Acer spicatum* Lam.) had relatively high importance values (Table 1). In contrast, the second-growth stand was clearly dominated by sugar maple, with much lesser amounts of cedar and paper birch (*Betula papyrifera* Marsh.). For 80 years after logging (1900–1980), basal area increased dramatically in the second-growth stand mainly due to increases in sugar maple (Figure 1). In the old-growth stand, basal area decreased from 1900 to 1930, after which it gradually increased through 1980 to approximately the same value determined for 1900. This increase in basal area after 1930 was due to sugar maple growth exceeding losses by cedar.

Total cover of tree species in the four mature jack pine understories was much lower than that in the two burned clearcut cites (Table 2). The greater tree cover on the disturbed sites was mainly due to increased black cherry (*Prunus serotina* Ehrl.) and trembling aspen (*Populus tremuloides* Michx.). Scattered areas of trembling aspen were present on site 2 prior to clearcutting and burning (Abrams 1982). Jack pine cover was low on all sites, which may be attributed to its low tolerance to understory conditions and the destruction of advanced seedlings and stored seed in the logging debris following clearcutting and burning. The well-developed early successional hardwood and shrub canopy on the two disturbed sites will probably pre-

TABLE 1. Importance values for tree species (≥2.5 cm dbh) in an old-growth (>175 yr) and a second-growth (logged in 1890s) northern white cedar community on South Manitou Island, MI.

Species	Old-growth	Second-growth
Thuja occidentalis	114	37
Acer saccharum	77	217
Fraxinus americana	41	6
Acer spicatum	33	—
Betula papyrifera	—	19
Prunus virginiana	9	6
Tilia americana	8	8
Cornus alternifolia	6	—
Ostrya virginiana	6	6
Abies balsamea	5	—

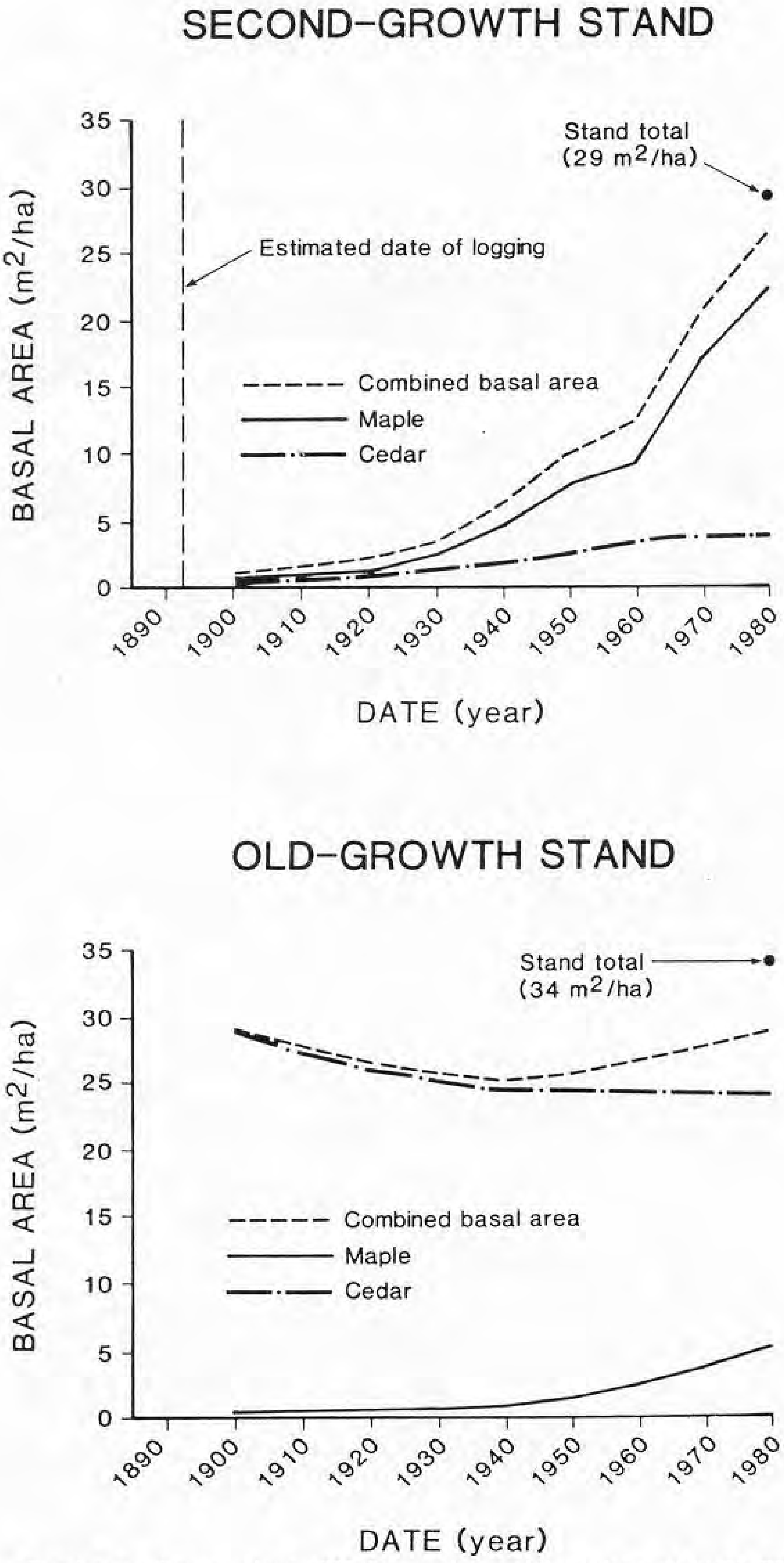

FIGURE 1. Basal area changes since 1900 for northern white cedar and sugar maple in a second-growth and old-growth cedar stand on South Manitou Island, MI.

clude any substantial increase in jack pine in the future. An increase in northern red oaks, red maple (*Acer rubrum* L.) and black cherry on these sites seems more likely to occur (Abrams et al. 1985). Conversion of older clearcut and burned jack pine sites to oak has been observed in some area forests (Don Grant, Michigan Department of Natural Resources, pers. comm.). It is important to note that other clearcut and/or burned jack pine sites in the study area were quickly converted to *Carex* meadows with very low hardwood and shrub cover and may be experiencing arrested succession (Abrams et al. 1985).

Data presented for the northern white cedar and jack pine communities suggest that disturbance can accelerate succession to later associations. For example, advanced sugar maple regeneration was present in the cedar stand prior to logging, but most of this species' recruitment into the tree size class and basal area growth took place relatively soon after logging (Scott 1985). In our examples, disturbance promoted the development of species that were likely to replace the pioneer conifer overstories in the long-term absence of disturbance. This is especially apparent in cedar communities, where sugar maple is considered a potential climax species (Gates 1926, Fowells 1965). Gradual replacement of cedar by sugar maple was evident in the old-growth stand. Increased basal area in that stand after 1930 was due to sugar maple growth exceeding losses by cedar. However, the rate of sugar maple increase in the old-growth stand was much lower than that in the logged stand, and it appeared to represent a tree-by-tree replacement.

The jack pine example is more complex because of the extreme soil conditions that limited the development of mesic, later successional tree species (Abrams et al. 1985). We believe, however, that the cherry-aspen-oak canopy developing on the disturbed sites will inhibit jack pine and facilitate continued hardwood expansion. These same species and several others (e.g., white pine, sugar maple, and balsam fir) may dominate overmature jack pine stands in the long-term absence of fire (Eyre and LeBarron 1944).

Although the idea of disturbance-mediated accelerated succession has not been well developed in the literature, several direct and indirect inferences have been made concerning this phenomenon. In Appalachian hardwood stands, the creation of gaps by ice storms has been considered an agent in accelerated forest succession (Carvell et al. 1957, Lemon 1961, Whitney and Johnson 1984, Boerner et al. 1988). Spurr (1956) indicated that hurricane damage to a white pine forest in New Hampshire eliminated early successional species and released advanced regeneration of hemlock, beech, and red maple. In northern Wisconsin, wind has been implicated in the acceleration of sugar maple and red maple, and the replacement of paper birch, in

TABLE 2. Absolute cover (%) of understory tree species (≤1.5 m tall or <2.5 cm dbh) in four mature (>55 yr) jack pine stands ($\bar{x}$ ± s.e.) and in two jack pine clearcuts surveyed at years 4–6 after prescribe burning in northern lower Michigan.

Tree species	Mature stands	Prescribe burns 1	2
Crataegus sp.	0.2 ± 0.2	2.1	0.2
Pinus banksiana	0.3 ± 0.2	2.6	0.3
Populus tremuloides	—	2.6	17.7
Prunus serotina	0.6 ± 0.3	12.8	2.9
Quercus spp.	0.8 ± 0.5	1.0	2.5
Salix glaucophylloides	—	—	3.0
Total	1.9 ± .6	21.1	26.6

birch–maple forests (Kapustka and Koch 1979). Logging of old-growth stands with advance reproduction of later successional species can speed the process of successional replacement (Spurr and Barnes 1973, p. 258). Early logging of white pine and hemlock in Michigan promoted a conversion to sugar maple on those sites (Whitney 1987). Various silvicultural studies have demonstrated that the creation of different size openings in a forest canopy can promote either early- or late-successional species, thus setting back or accelerating succession, respectively (Minckler and Woerheide 1965, Smith 1986). Future disturbance to a pine and oak forest in eastern Texas will likely accelerate succession to beech and magnolia, because of their dominance in the understory (Glitzenstein et al. 1986). Moreover, patches created by oak wilt and gypsy moth may convert to sugar maple or red maple in eastern and Lake State forests (Collins 1961, Tryon et al. 1983, Menges and Loucks 1984). Gaps caused by the death of gallery forest oak species after herbicide spraying in Kansas were quickly dominated by hackberry, eastern redbud, and/or elm (M. D. Abrams, personal observation). These species may also replace oak during succession in relatively undisturbed gallery forests (Abrams 1986). Similarly, cutting in certain Midwestern oak forests can speed succession to more mesophytic species, such as sugar maple (Lorimer 1985).

A hypothetical example of disturbance-mediated accelerated succession is presented in Figure 2. An open area is dominated by seedlings of a pioneer tree species A. As these individuals mature and dominate the overstory, they may temporarily exclude the development of younger stems (cf. Oliver 1981). Eventually, advanced regeneration of more tolerant, later successional species B and C become established and dominate the understory. The length of time for understory reinitiation to begin may be a function of the overstory species tolerance, resource availability in the understory, and rate of migration of tolerant species to the site (cf. Oliver 1981). If a stand in the understory reinitiation stage is disturbed and the tolerant understory species survive (as undisturbed advanced regeneration and/or sprouts) and

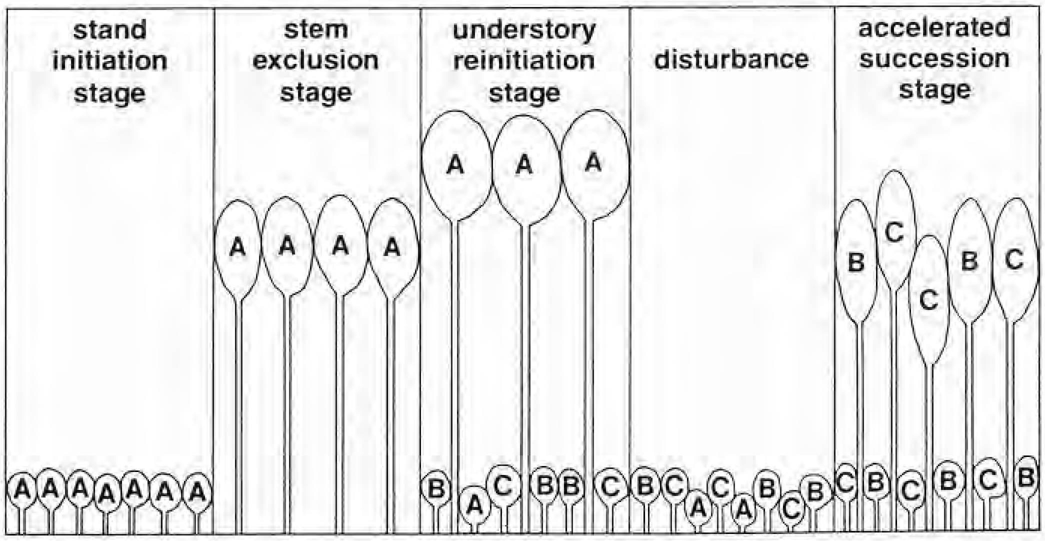

FIGURE 2. Schematic diagram of disturbance-mediated accelerated succession in a pioneer forest community. The first three stages of stand development have been outlined by Oliver (1981). Species A is a pioneer tree, whereas B and C are later successional tree species. Disturbances may include logging, fire, ice storms, wind-throw, insect attack, disease, and herbicide spraying.

can quickly adapt to a high light environment, we believe that accelerated succession should occur.

Conclusion

Even though the idea of disturbance-mediated accelerated succession has not been well developed in the ecological literature, at least several North American forest communities have exhibited this phenomenon. A wide range of natural and anthropogenic disturbance types may be involved, including logging, fire, ice storms, wind-throw, disease, insect attack, and herbicide spraying. In most cases, disturbance destroyed part of the dominant pioneer overstory, which released advanced reproduction of later successional species. Many of these succeeding species are hardwoods capable of sprouting and quickly reestablishing themselves on the site even if disturbed. In our examples, jack pine and northern white cedar do not sprout and were unable to successfully reestablish themselves on the disturbed sites. We have presented evidence that logging accelerated sugar maple dominance in a northern white cedar community, and that clearcutting and burning quickly converted sites dominated by mature jack pine to early successional hardwoods. Traditionally, disturbance was thought to set succession back to some earlier stage. In addition to this, however, we believe that disturbance can accelerate succession to a more advanced stage.

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

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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 ecomorphological 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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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

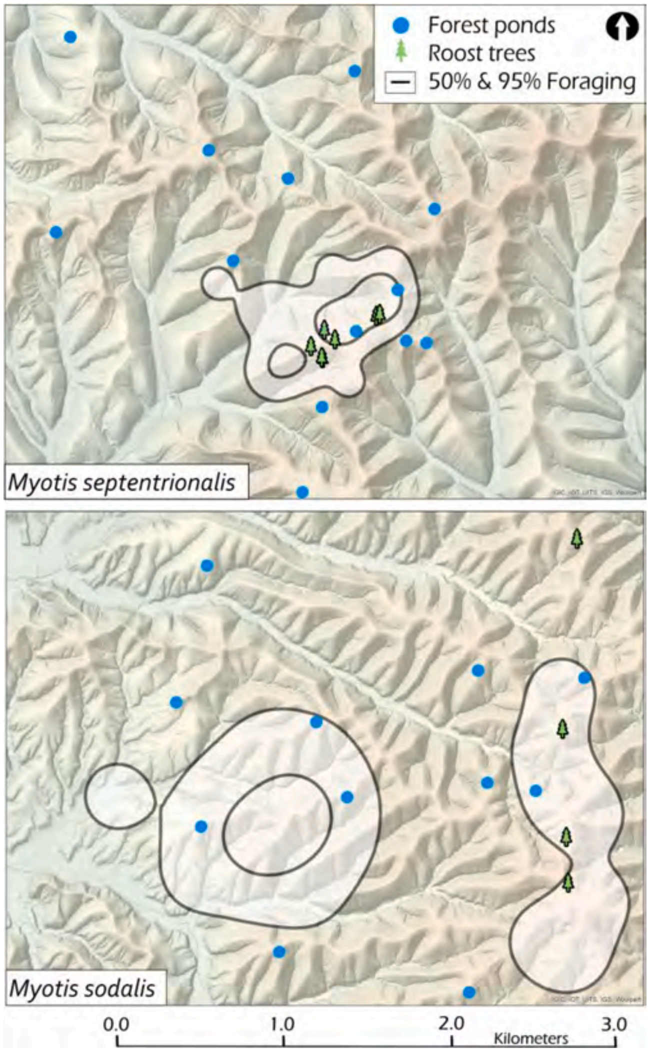

Fig. 1. Examples of roosting-foraging proximity. Northern long-eared bat (*Myotis septentrionalis*) roosts were typically near the center of foraging areas, as shown for one pregnant *M. septentrionalis* (top panel). Indiana bat (*Myotis sodalis*) roost sites were often disjunct from foraging areas, 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* =

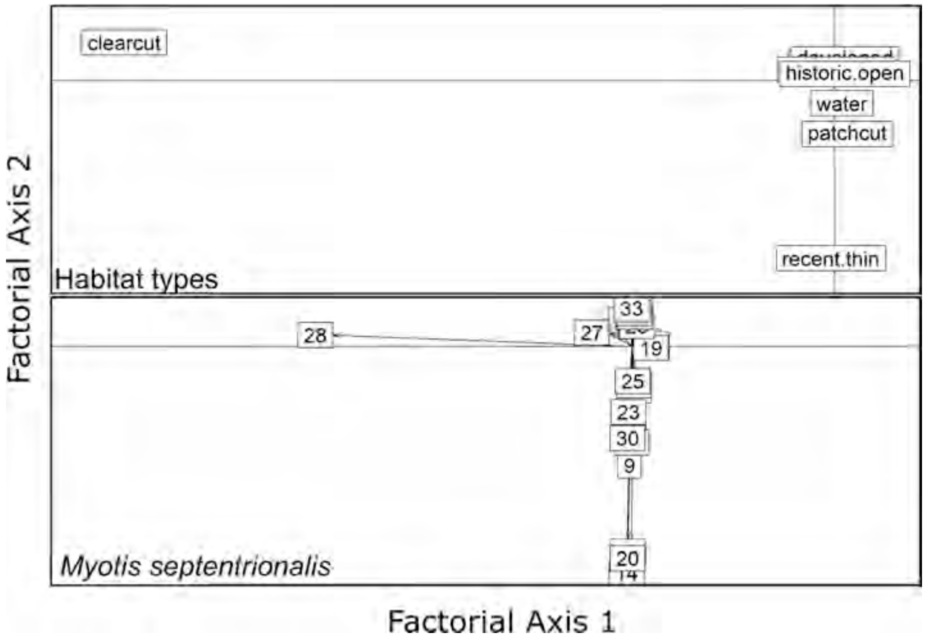

Fig. 2. Eigenanalysis of habitat selection ratios for 33 northern long-eared bats (*Myotis septentrionalis*). The top panel displays habitat loadings along the first two factorial axes and the bottom panel displays habitat preferences of individual bats in the same factorial space.

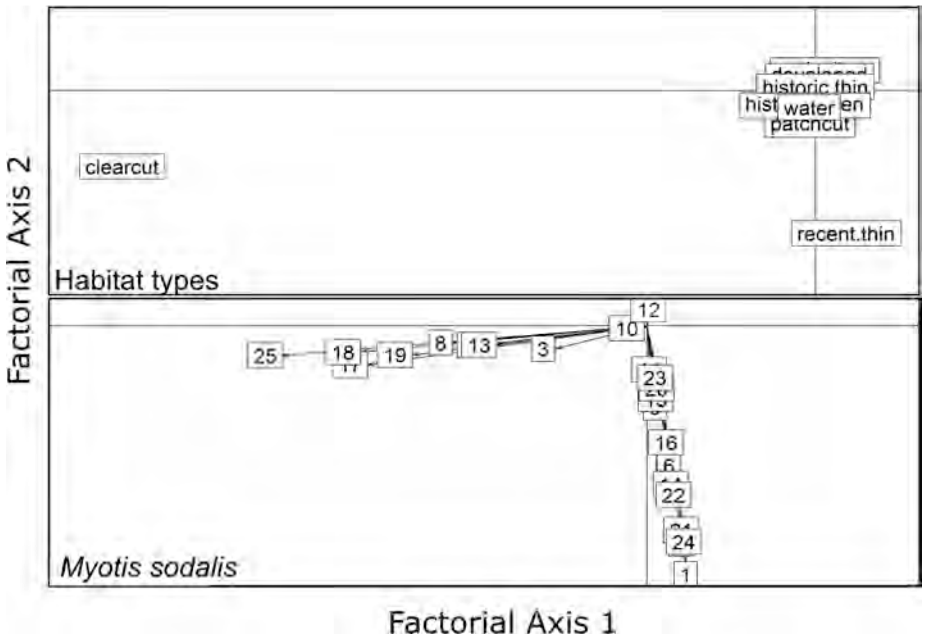

Fig. 3. Eigenanalysis of habitat selection ratios for 25 Indiana bats (*Myotis sodalis*). The top panel displays habitat loadings along the first two factorial axes and the bottom panel displays habitat preferences of individual bats in the same factorial space.

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.

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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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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.

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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).

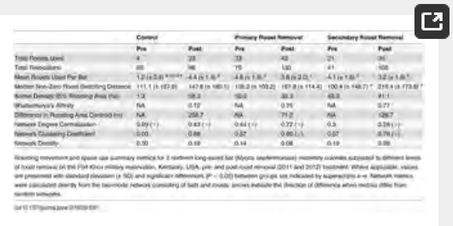

Table 1. Summary of female northern long-eared bat roost use patterns.

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

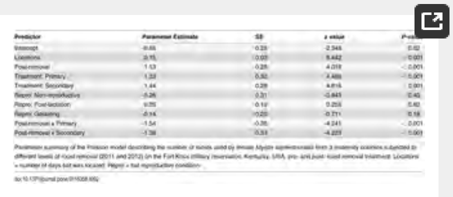

Table 2. Factors influencing the number of roosts used by individual female northern long-eared bats.

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.

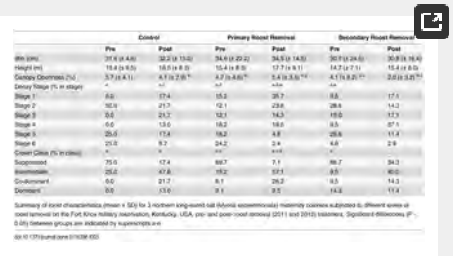

Table 3. Summary of female northern long-eared bat roost characteristics.
https://doi.org/10.1371/journal.pone.0116356.t003

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).

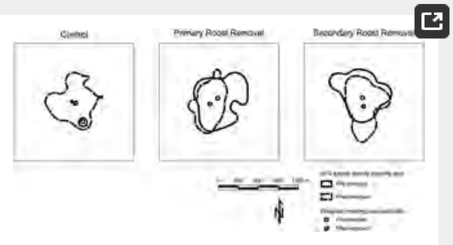

Figure 1. Northern long-eared bat maternity colony roosting areas.
Roosting areas (95% utilization distribution) of 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies subjected to different levels of roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post- roost removal (2011 and 2012)
https://doi.org/10.1371/journal.pone.0116356.g001

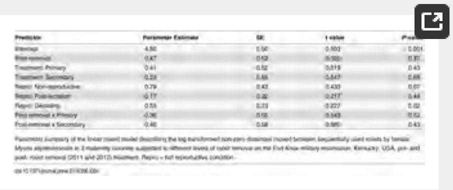

Table 4. Factors influencing distances moved between roosts by female northern long-eared bats.
https://doi.org/10.1371/journal.pone.0116356.t004

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).

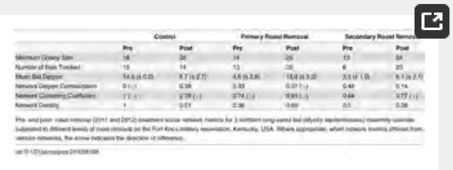

Table 5. Northern long-eared bat maternity colony social network metrics.
https://doi.org/10.1371/journal.pone.0116356.t005

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).

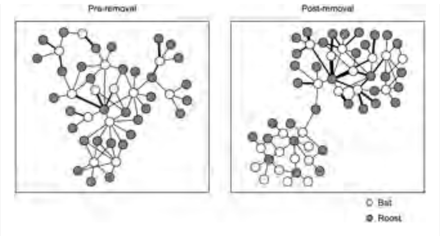

Figure 2. Northern long-eared bat maternity colony roost network map.

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.

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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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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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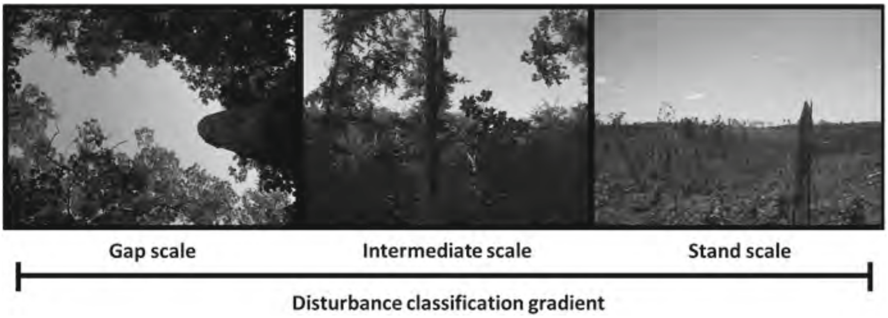

Fig. 2.1 Disturbance classification gradient based on spatial extent and magnitude of a discrete disturbance event (Photographs by author)

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.

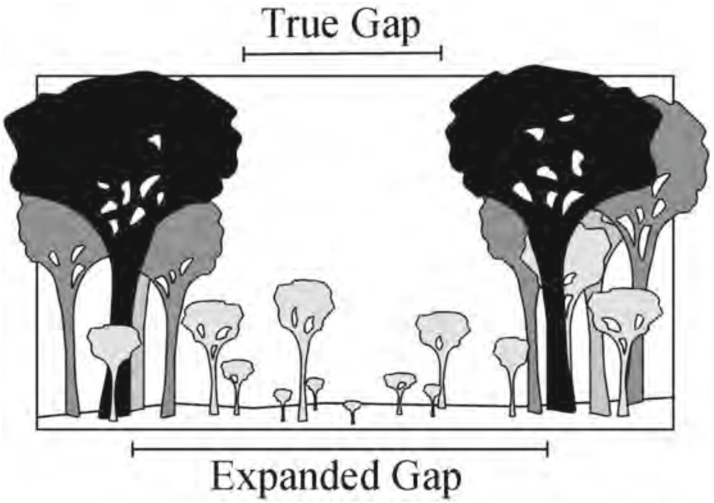

Fig. 2.2 The true gap (also called observed or light gap) and expanded gap (also called extended gap) environments. The *black* trees represent canopy dominants along the periphery of the gap

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.

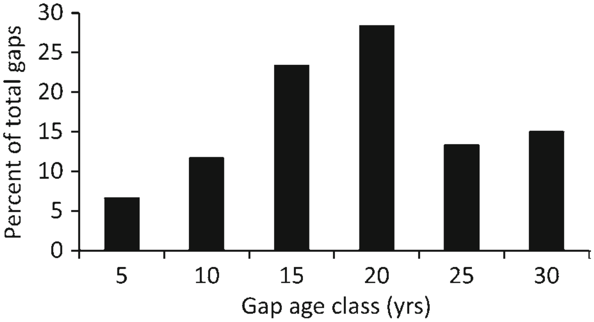

Fig. 2.3 Distribution of 60 canopy gaps by five-year age class bins in upland hardwood stands on the Bankhead National Forest, Alabama (Adapted from Richards and Hart 2011)

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.

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LETTER

Meeting GHG reduction targets requires accounting for all forest sector emissions

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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

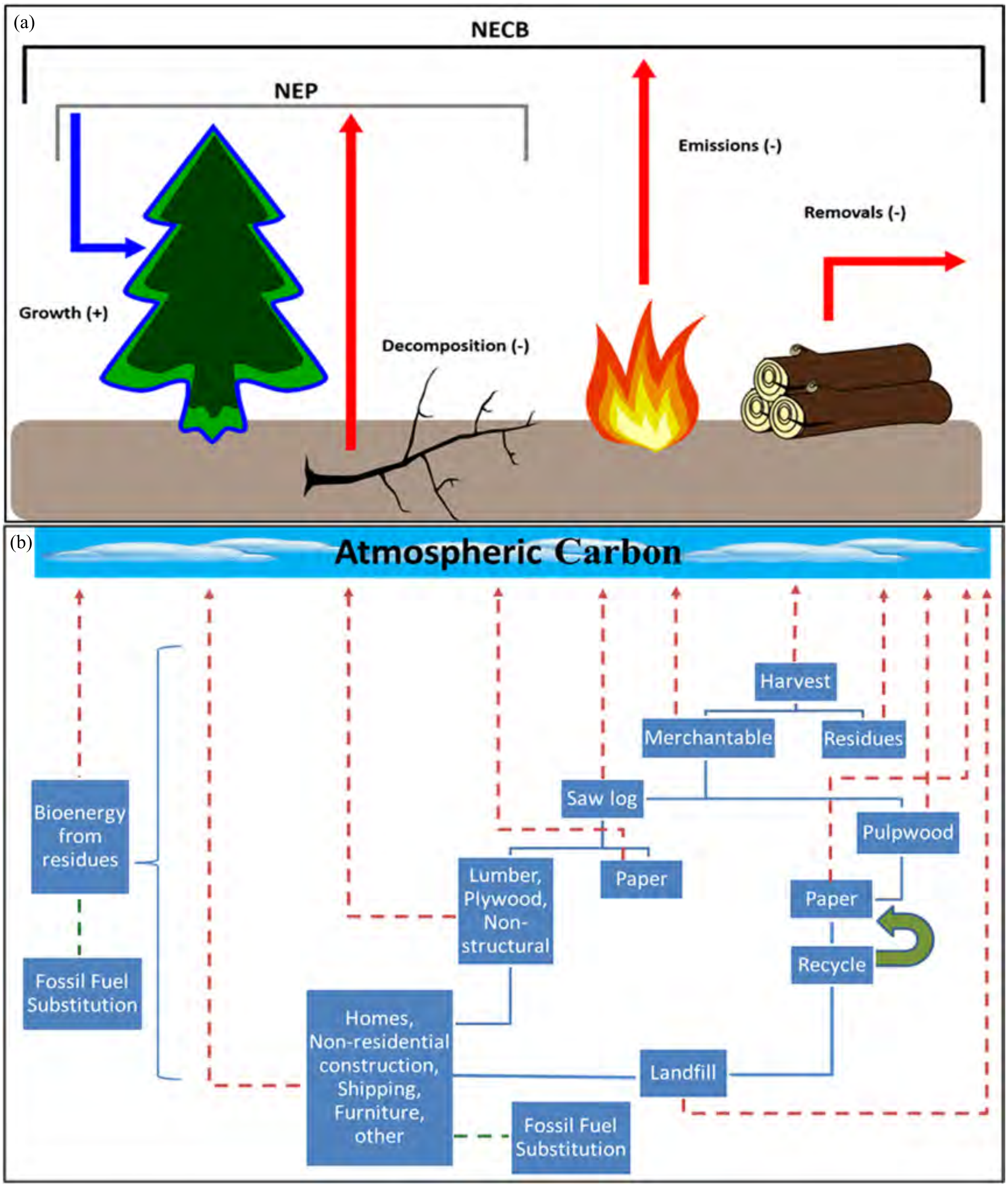

Figure 1. Conceptual diagram of Forest-GHG (a) describes the natural, land-based forest carbon sink where the net of growth and decomposition is net ecosystem production (NEP), and after accounting for removals from fire and harvest, the balance is net ecosystem carbon balance (NECB), (b) describes the 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

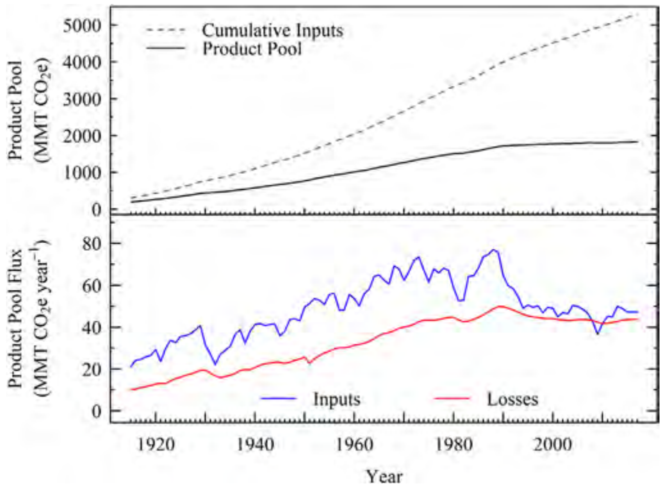

Figure 2. Wood product inputs and outputs from 1900 to 2016 for Washington, Oregon, and California. (A) Cumulative production in MMT CO_2e per year assuming no losses over time (dotted grey line) versus the realized in-use wood product pool over time after accounting for decay (losses). (B) Yearly product 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

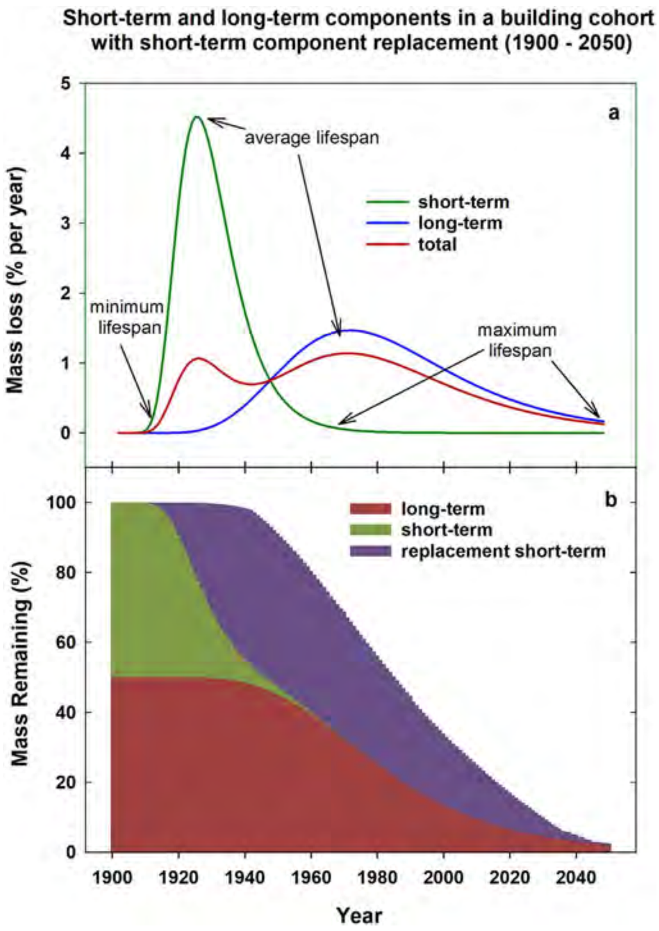

Figure 3. Conceptual models of the Forest-GHG cohort-component method for: (a) mass loss in a cohort of buildings with a 75 year average life span that accounts for the short and long-term portions of buildings and (b) mass remaining in a single building cohort over time (with replacement). Data presented 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 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

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.

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Land use strategies to mitigate climate change in carbon dense temperate forests

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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.

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The authors declare no conflict of interest.

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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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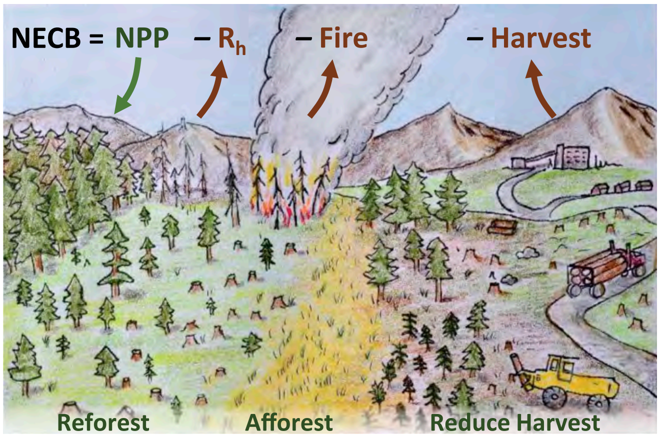

Fig. 1. Approach to assessing effects of mitigation strategies on forest carbon and forest sector emissions. NECB is productivity (NPP) minus Rh and losses from fire and harvest (red arrows). Harvest emissions include those associated with wood products and bioenergy.

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).

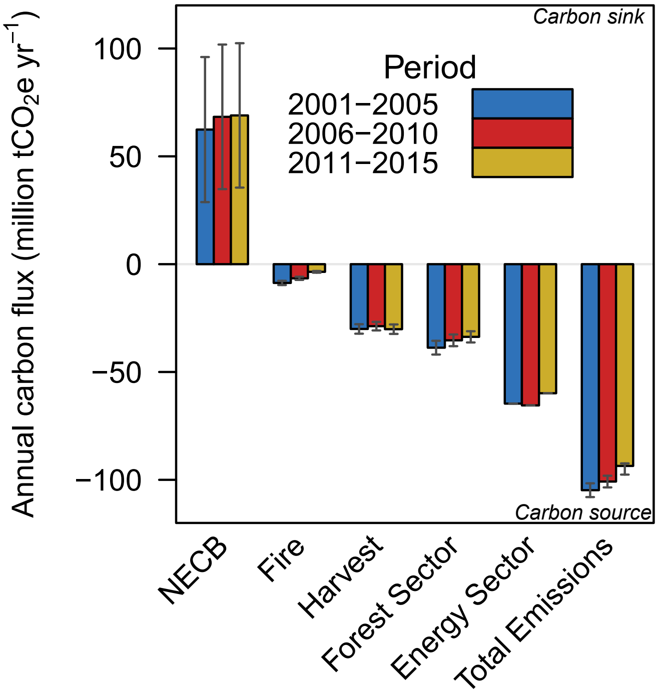

Fig. 2. Oregon's forest carbon sink and emissions from forest and energy sectors. Harvest emissions are computed by LCA. Fire and harvest emissions sum to forest sector emissions. Energy sector emissions are from the Oregon Global Warming Commission (14), minus forest-related emissions. Error bars are 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 $m^3 \cdot y^{-1}$ 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 $mm \cdot y^{-1}$ and 516 $mm \cdot y^{-1}$. Under current climate conditions, the observations suggest an increase in annual water availability of 260 billion $m^3 \cdot y^{-1}$ 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,

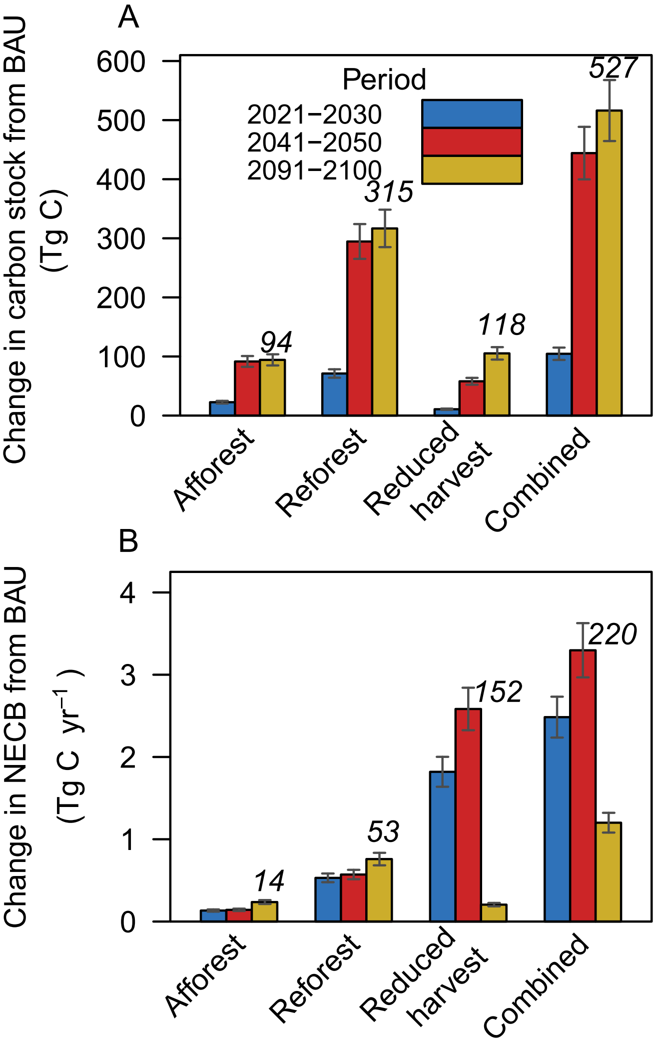

Fig. 3. Future change in carbon stocks and NECB with mitigation strategies relative to BAU management. The decadal average change in forest carbon stocks (*A*) and NECB relative to BAU (*B*) are shown. Italicized numbers over bars indicate mean forest carbon stocks in 2091–2100 (*A*) and cumulative change 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.

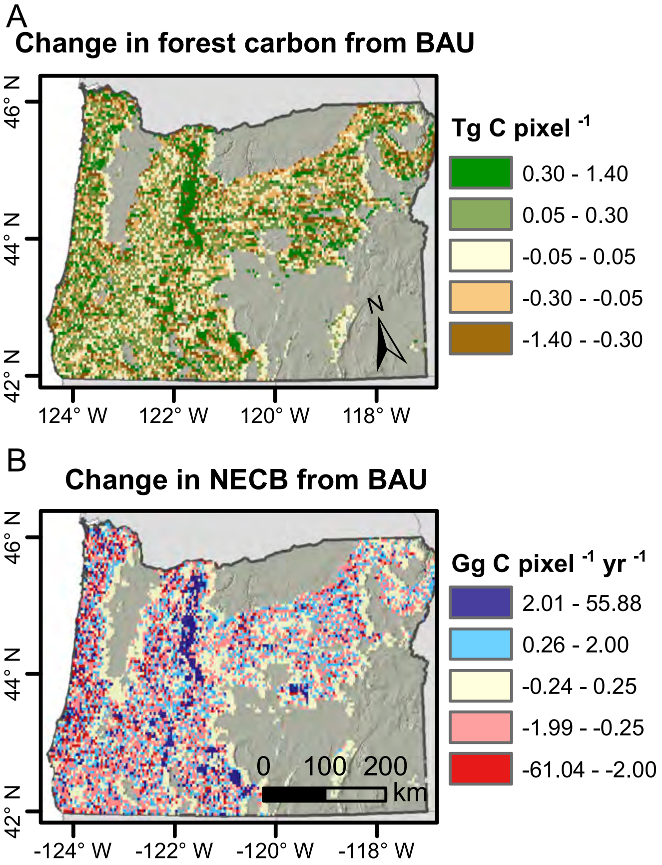

Fig. 4. Spatial patterns of forest carbon stocks and NECB by 2091–2100. The decadal average changes in forest carbon stocks (*A*) and NECB (*B*) due to afforestation, reforestation, protected areas, and lengthened harvest cycles relative to continued BAU forest management (red is increase in NECB) are shown.

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.

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).

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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

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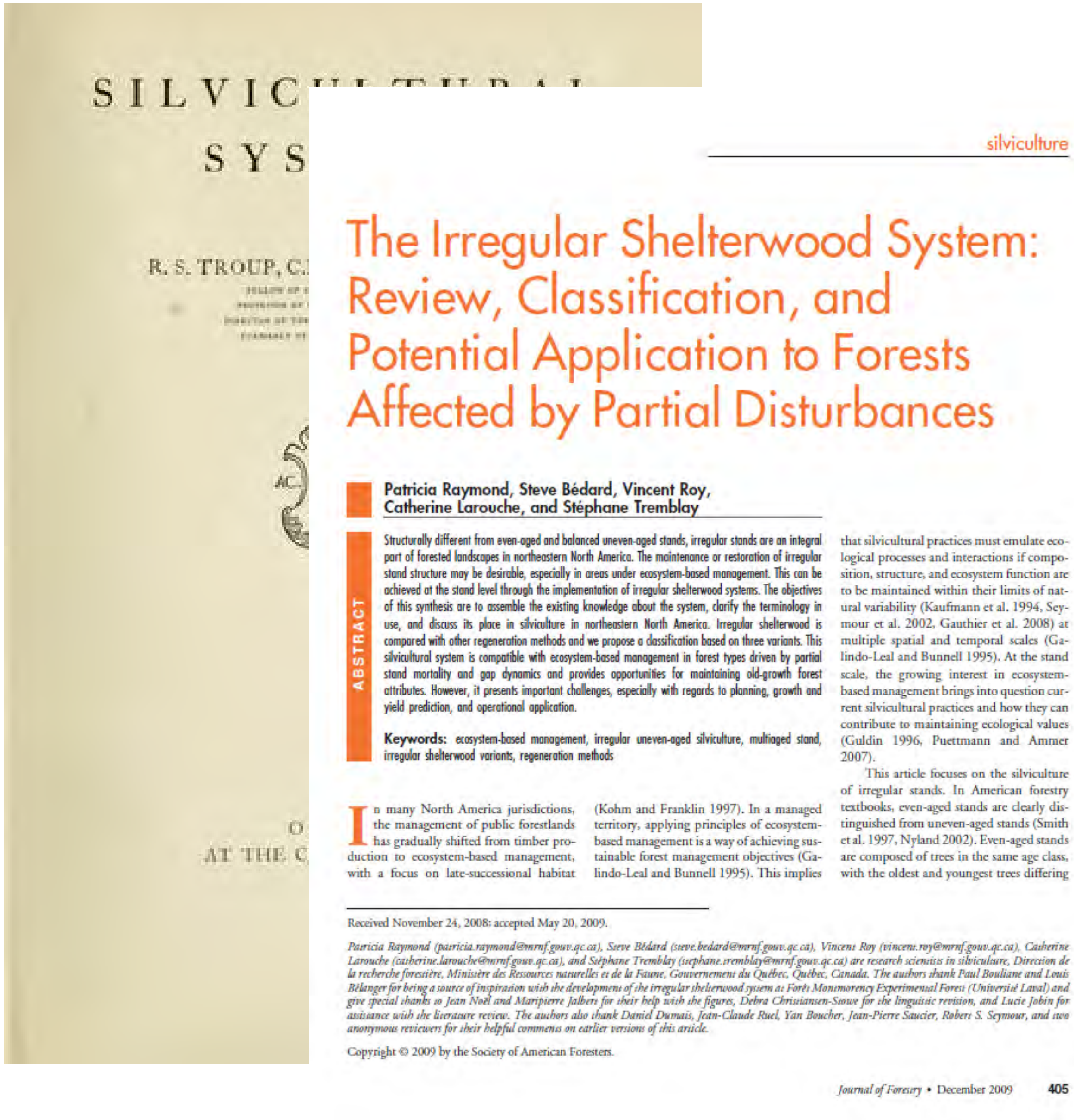
Historical Context



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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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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.

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.

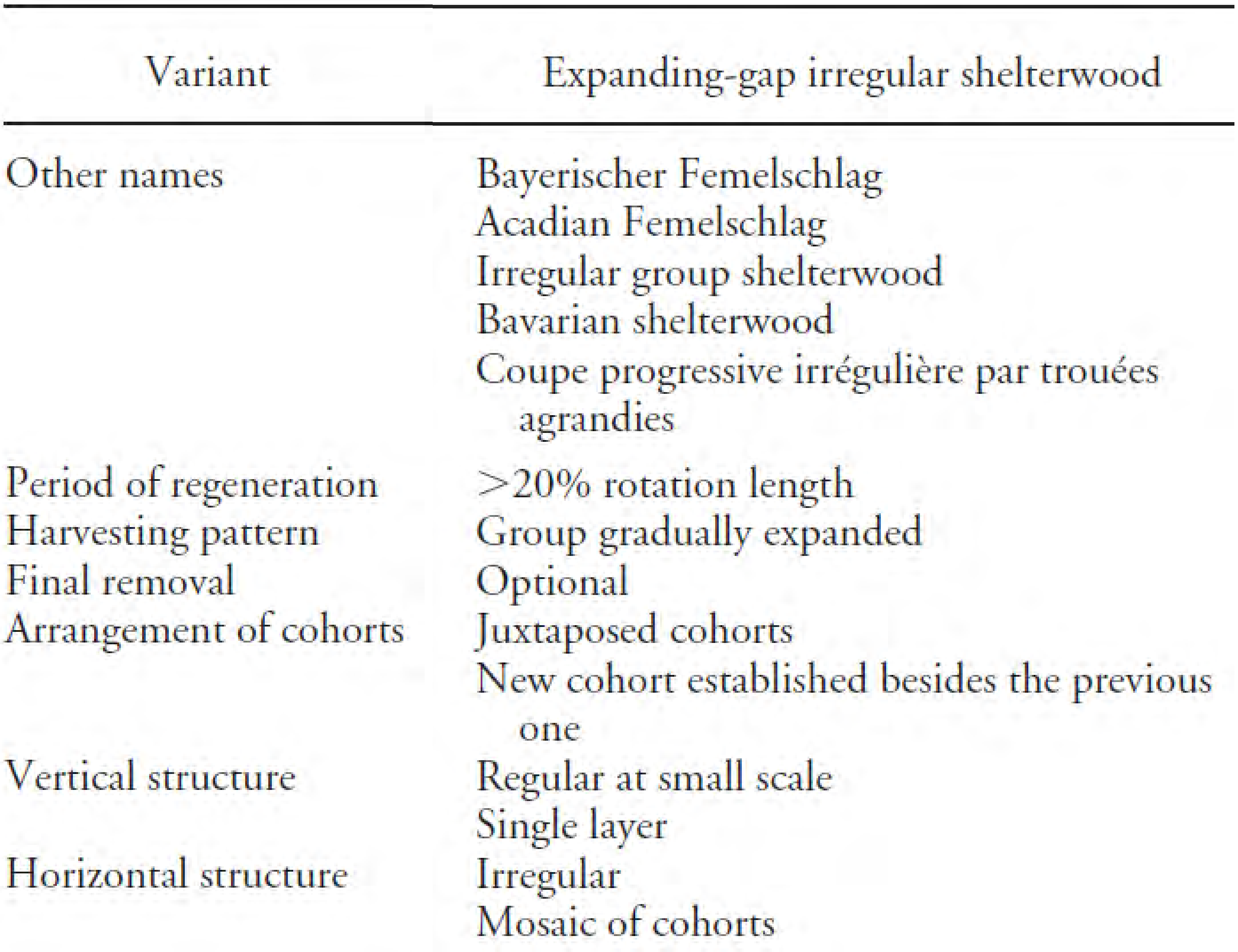
Irregular Shelterwood System Defined

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.

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

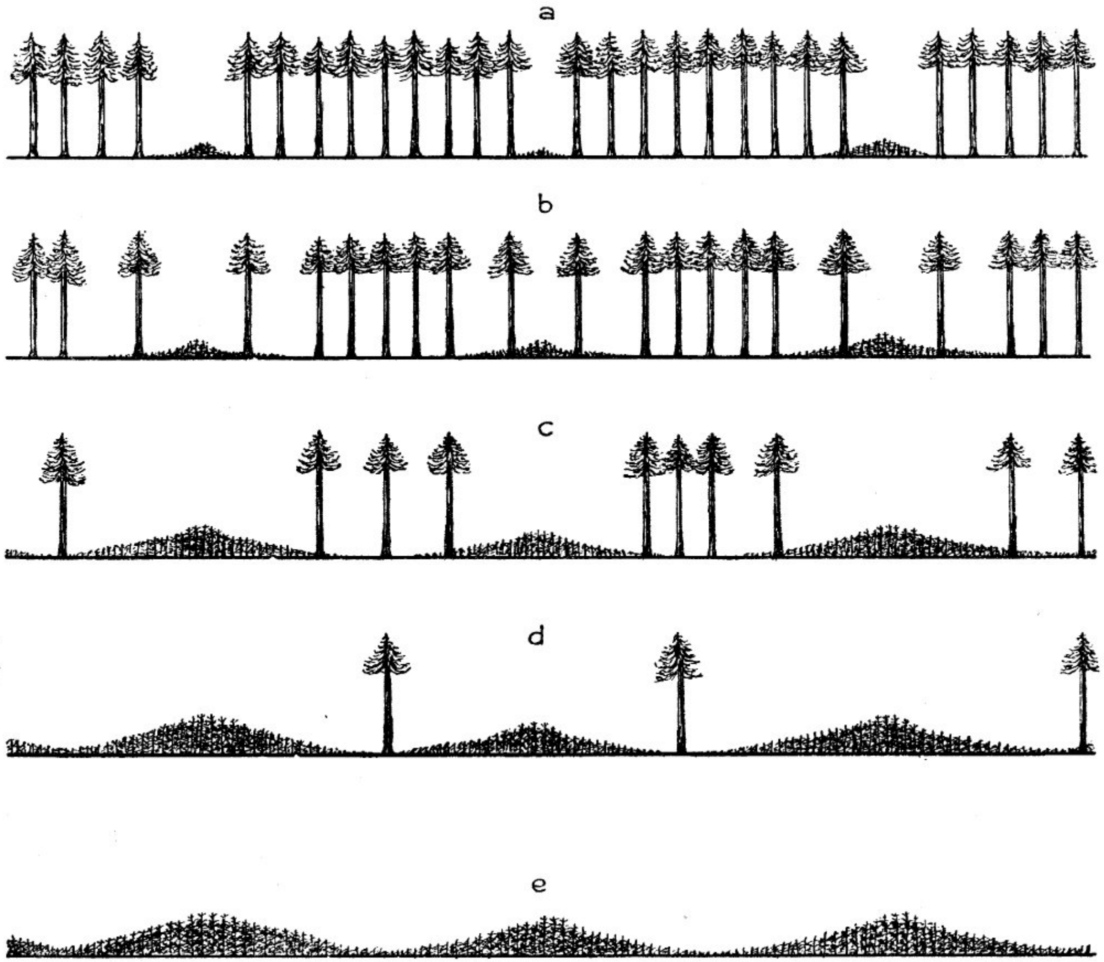
Irregular Shelterwoods and *Quercus* Forests

- *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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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

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

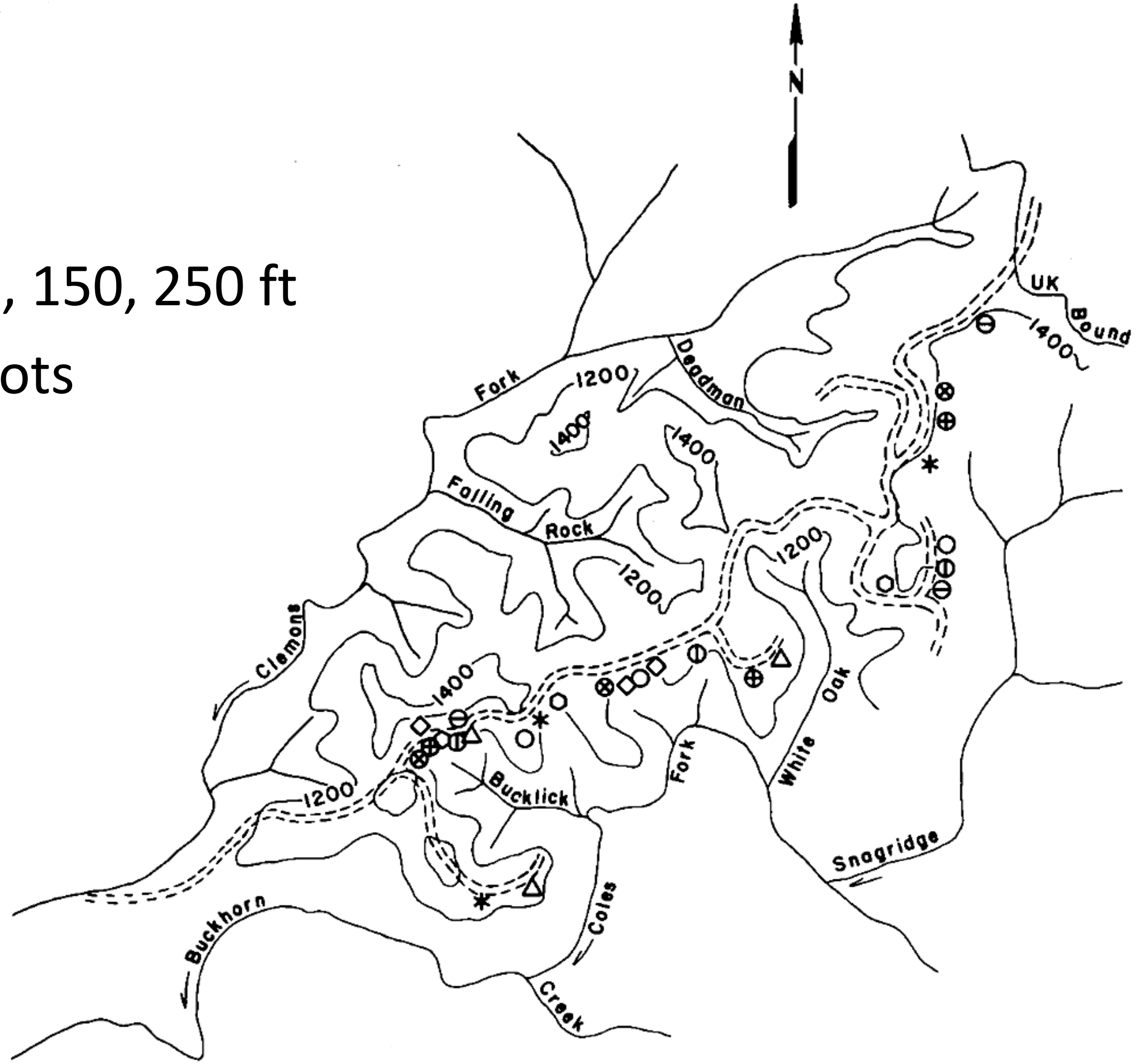
Lhotka and Stringer (In Review) characterized the relationship between distance from anthropogenically created edge and the height and density of oak reproduction

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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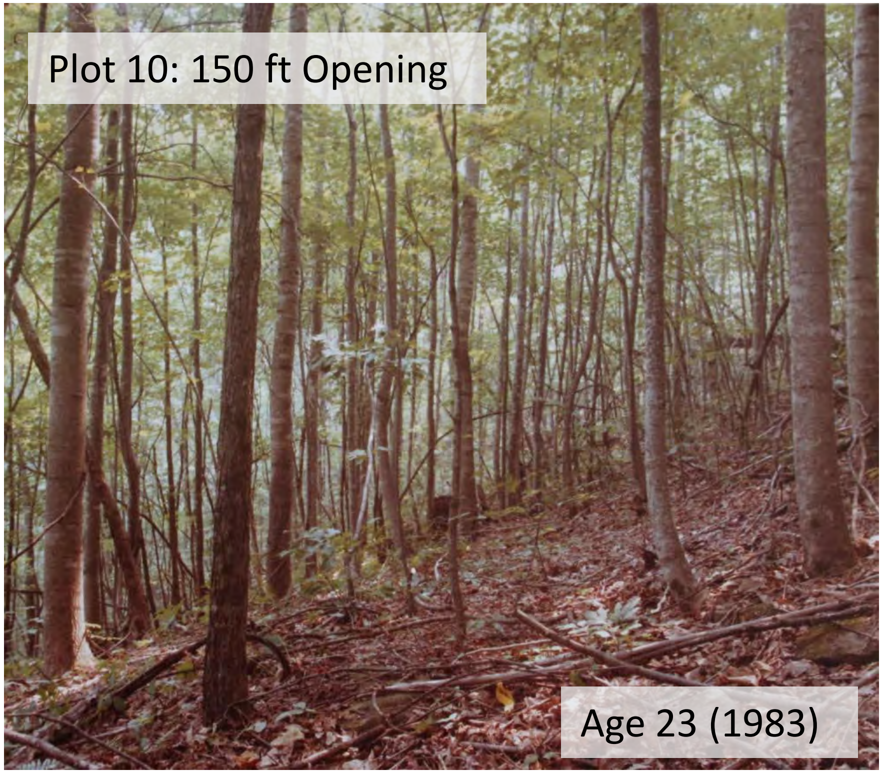
Robinson Forest Gap Size Study

Hill and Muller (UK): 1981, 1985, 1987
USDA Forest Service: 1991



Plot 10: 150 ft Opening

Age 23 (1983)

Lhotka: 2008
*Thanks to Matt Strong

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 ($\alpha = 0.05$)

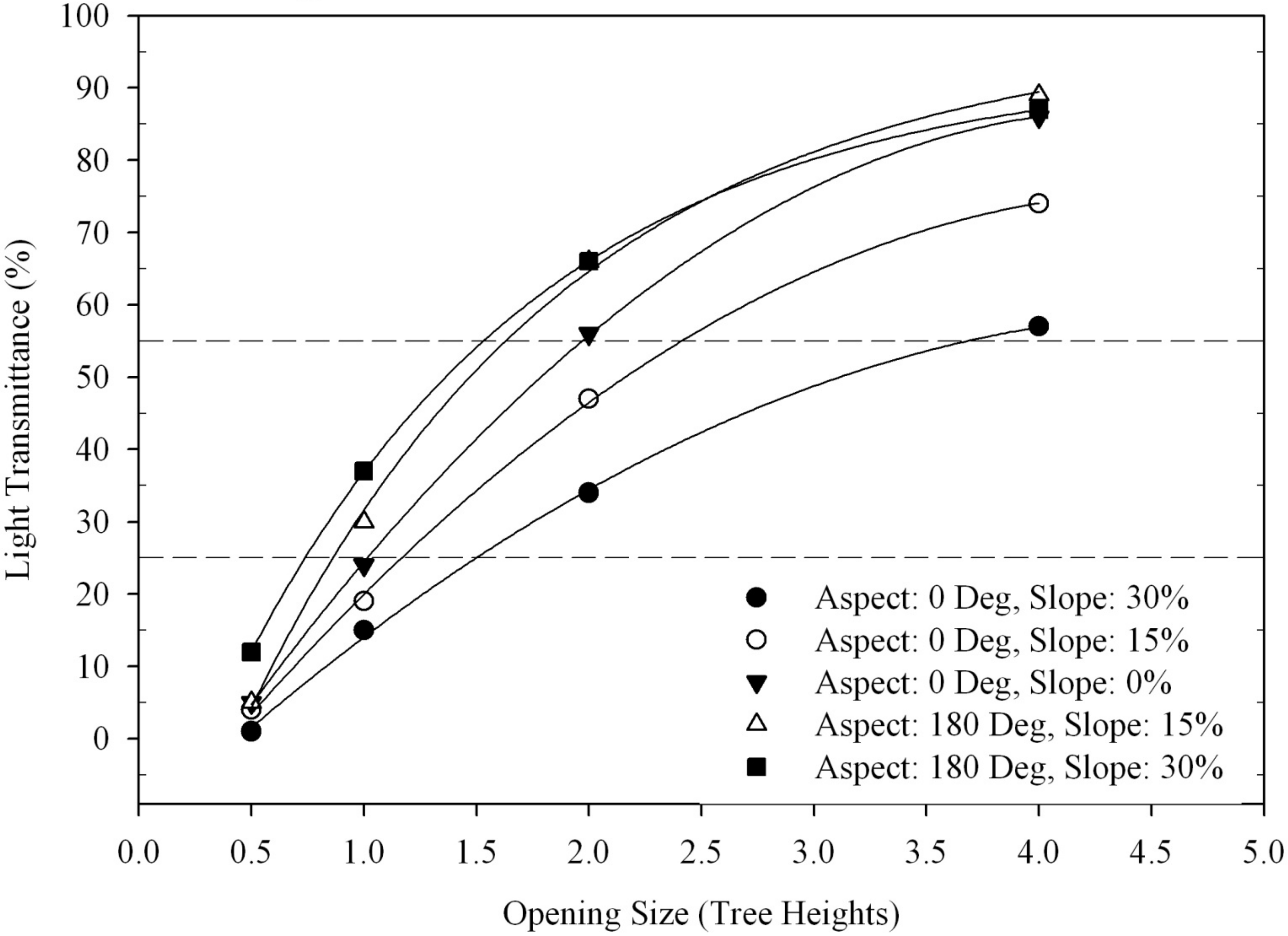
Robinson Forest Gap Size Study - Summary

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

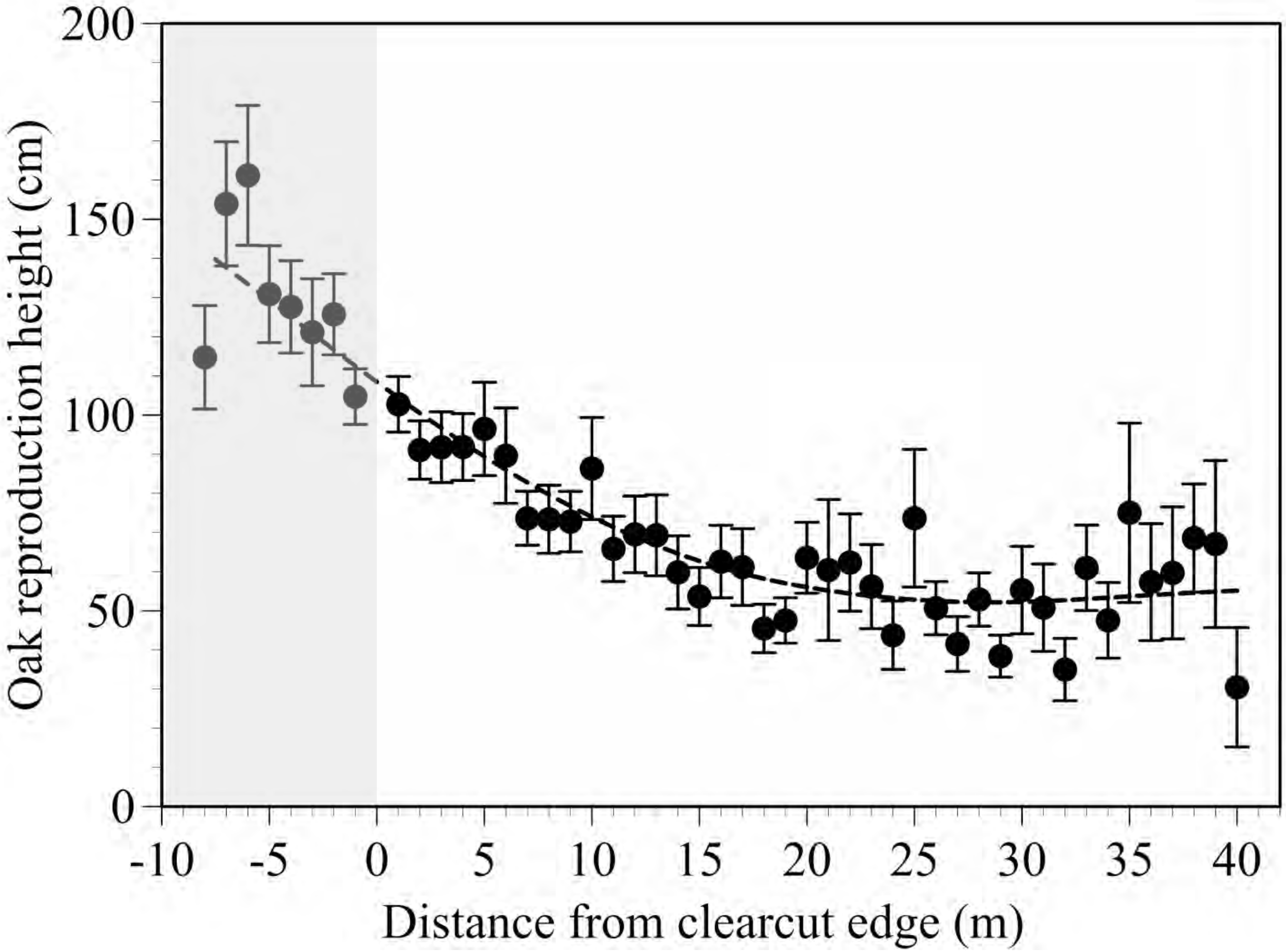
From: Fischer, B.C. 1981. Designing Forest Openings of the Group Selection Method. SO-GTR-34. pp 274-277.



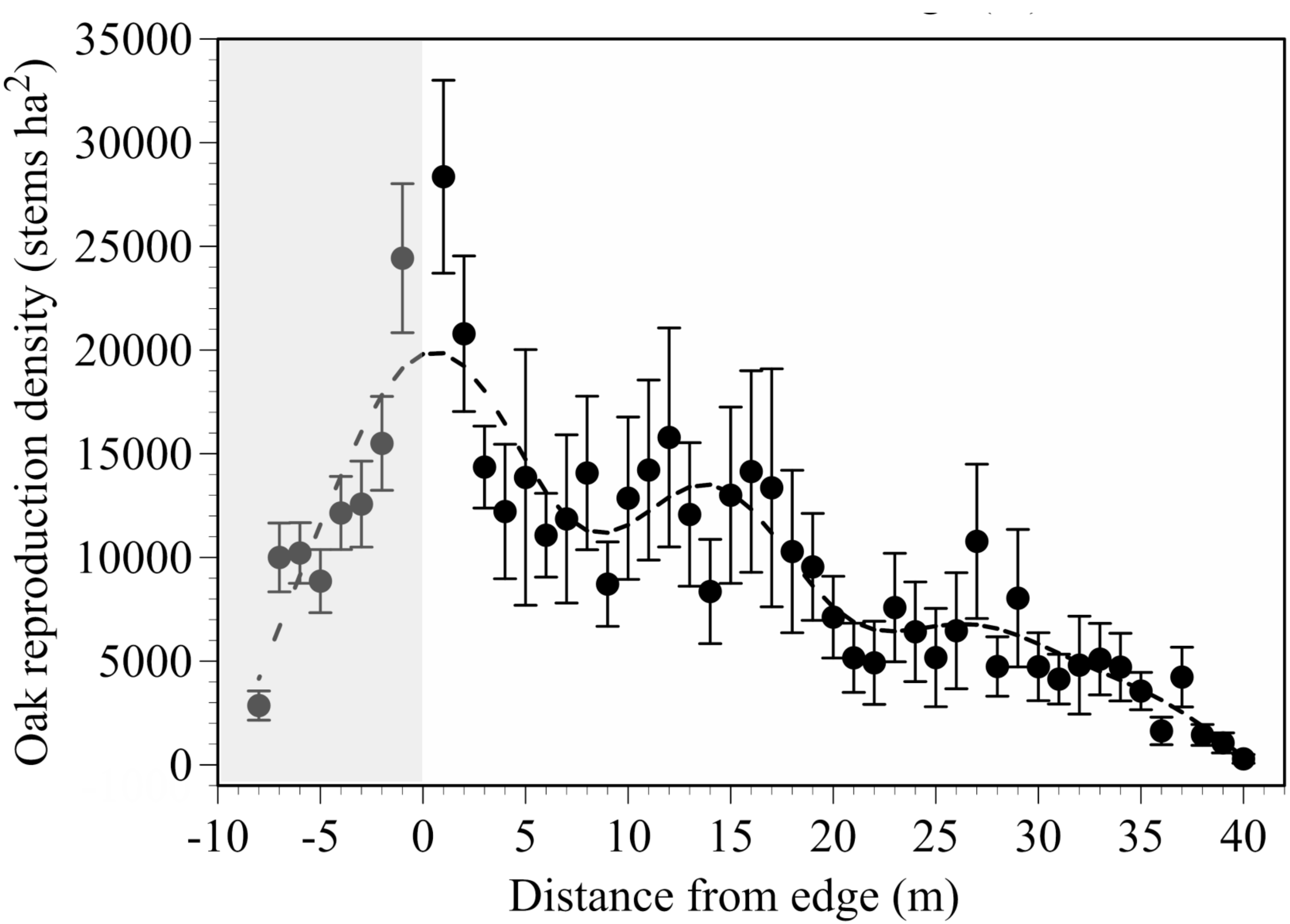
Berea Forest Edge Effects Study

- 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



Berea Forest Edge Effects Study – Seedling Density



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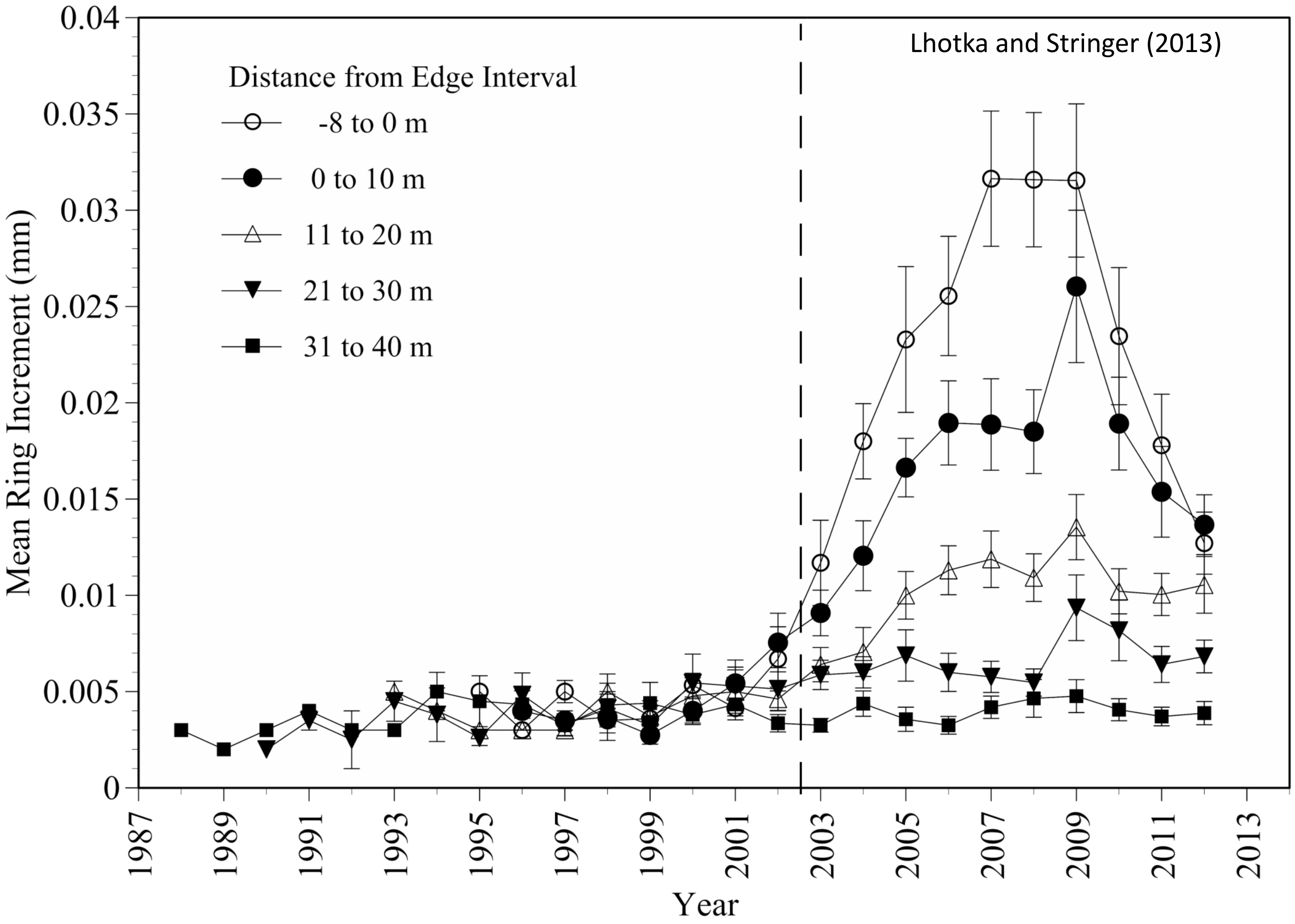
Edge Environment: Seedling Radial Growth



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

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?

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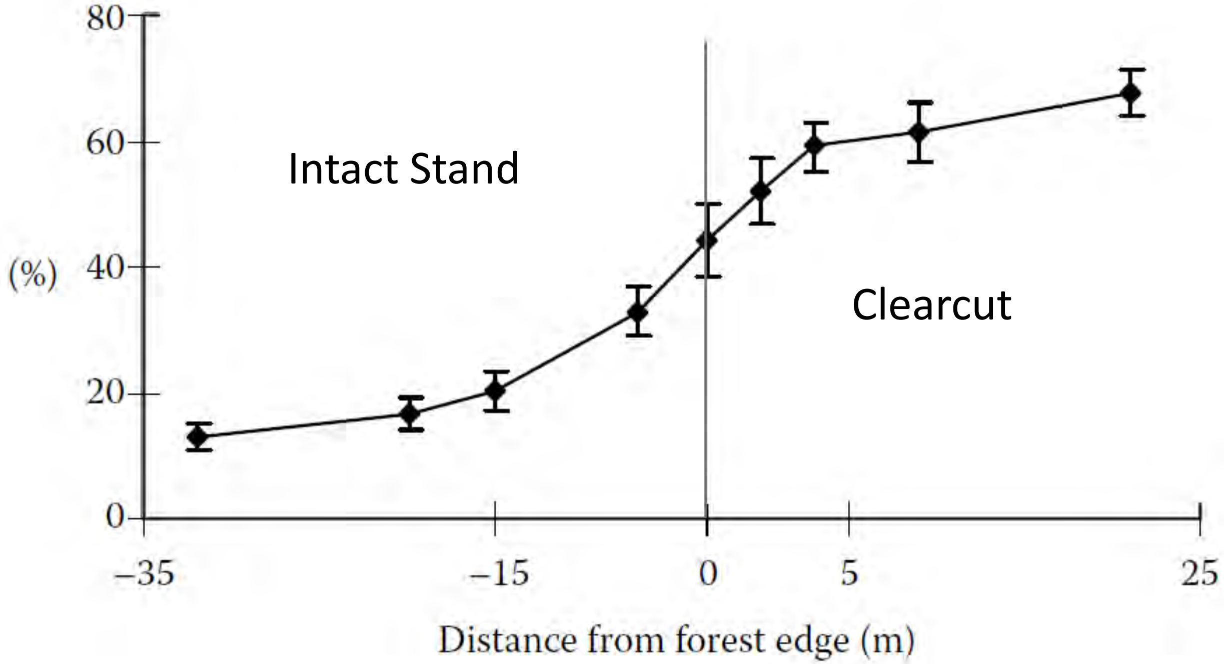
An Expanding-Gap Approach for Oak

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

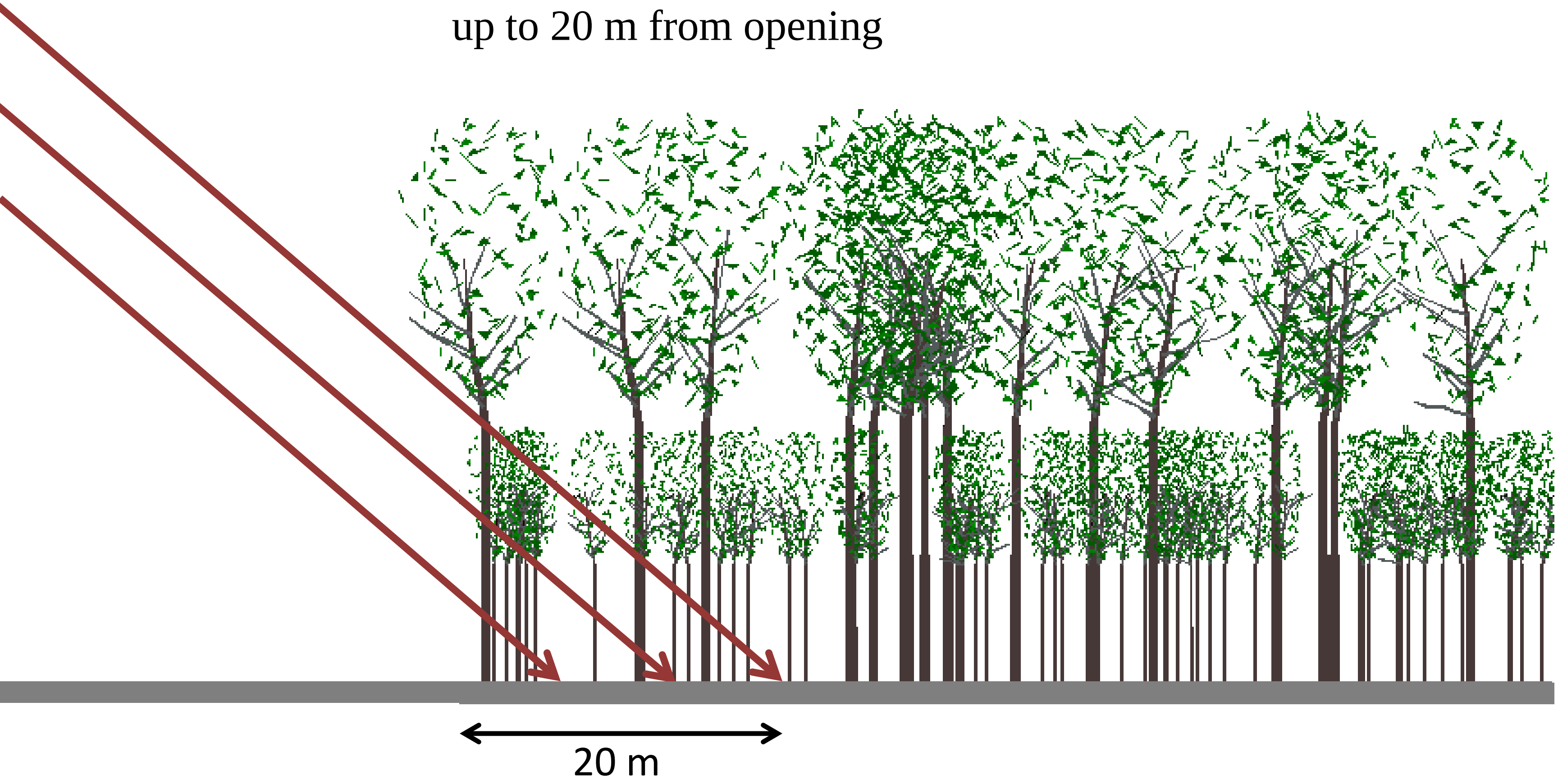
What about edge effects and forest structure in matrix?



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



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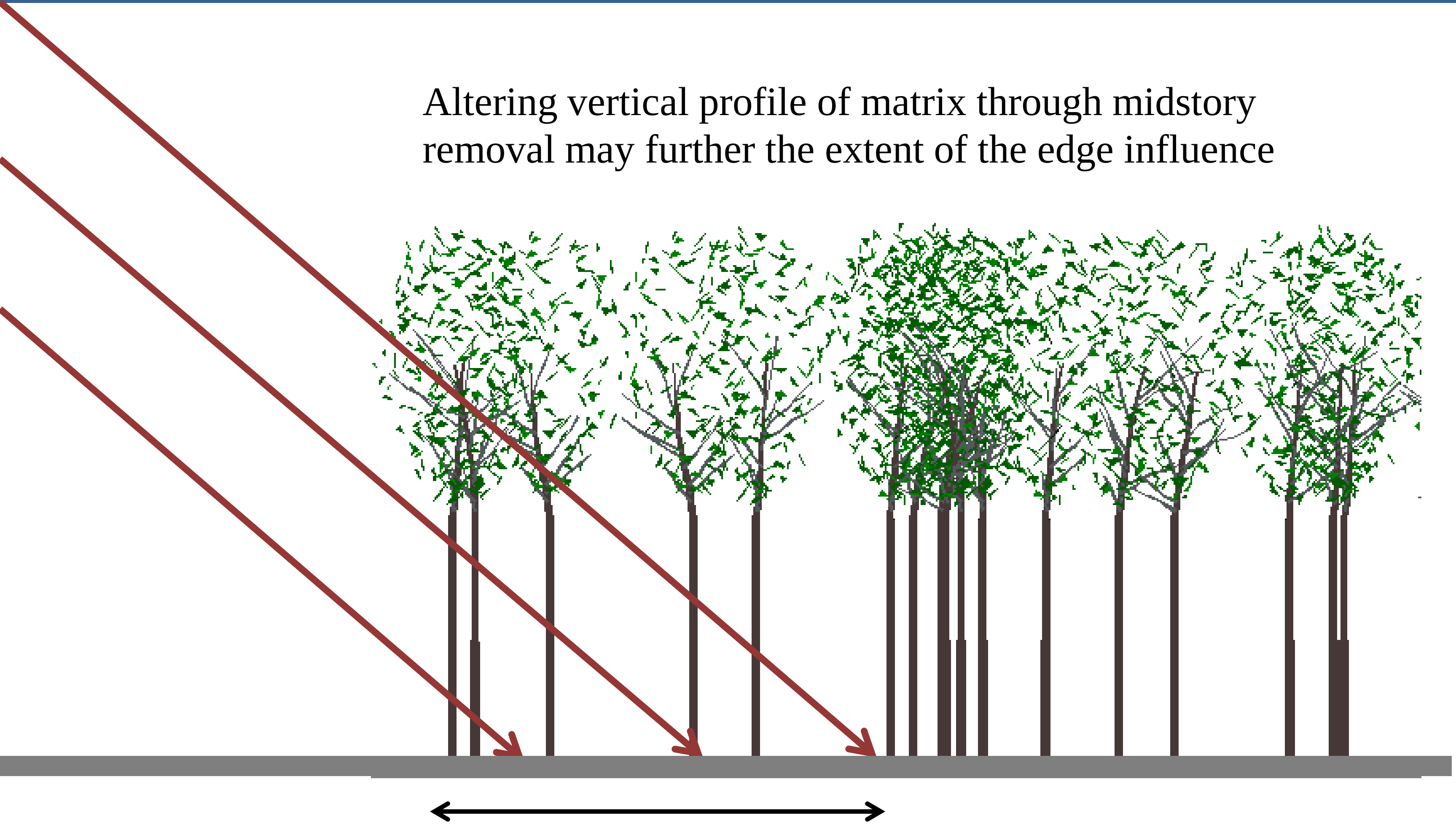
What about edge effects and forest structure in matrix?

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:

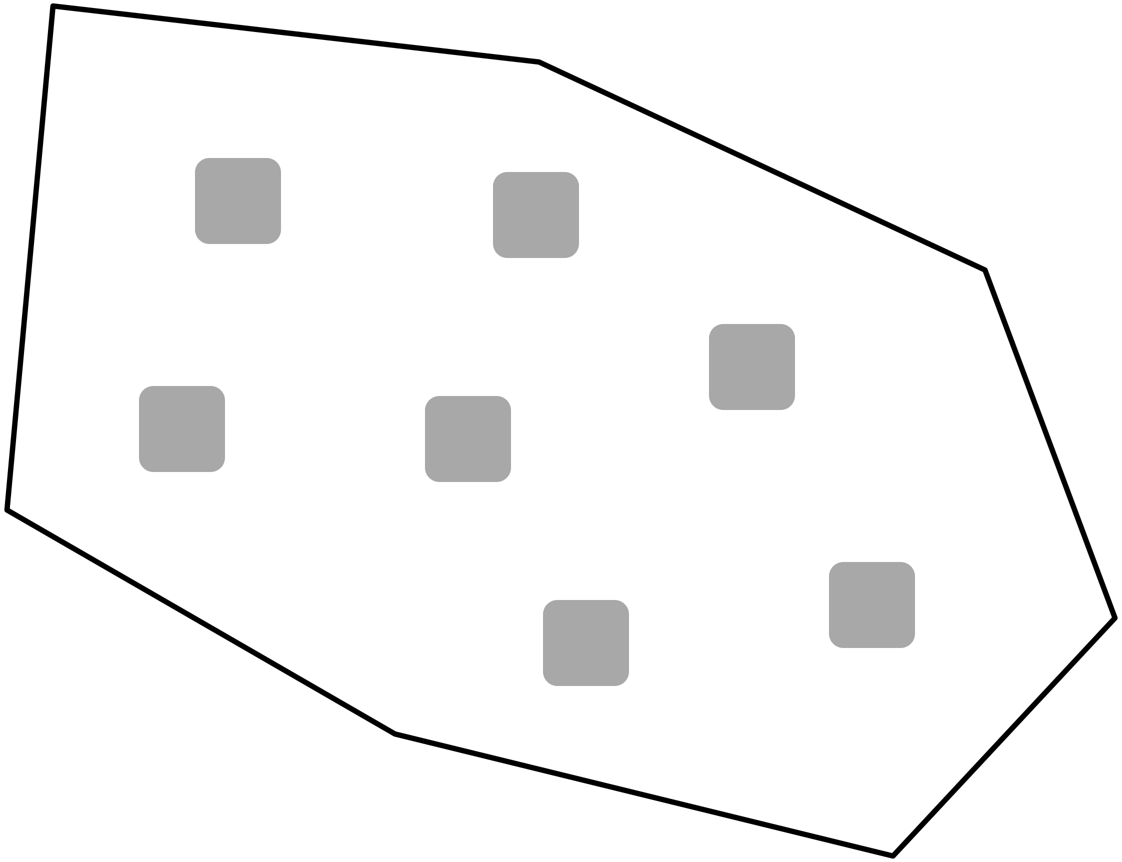
1. Improve oak survival and growth in areas to be released during subsequent gap expansions
2. Extend the enhancement effect of the edge environment on oak reproduction further in the forest matrix

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



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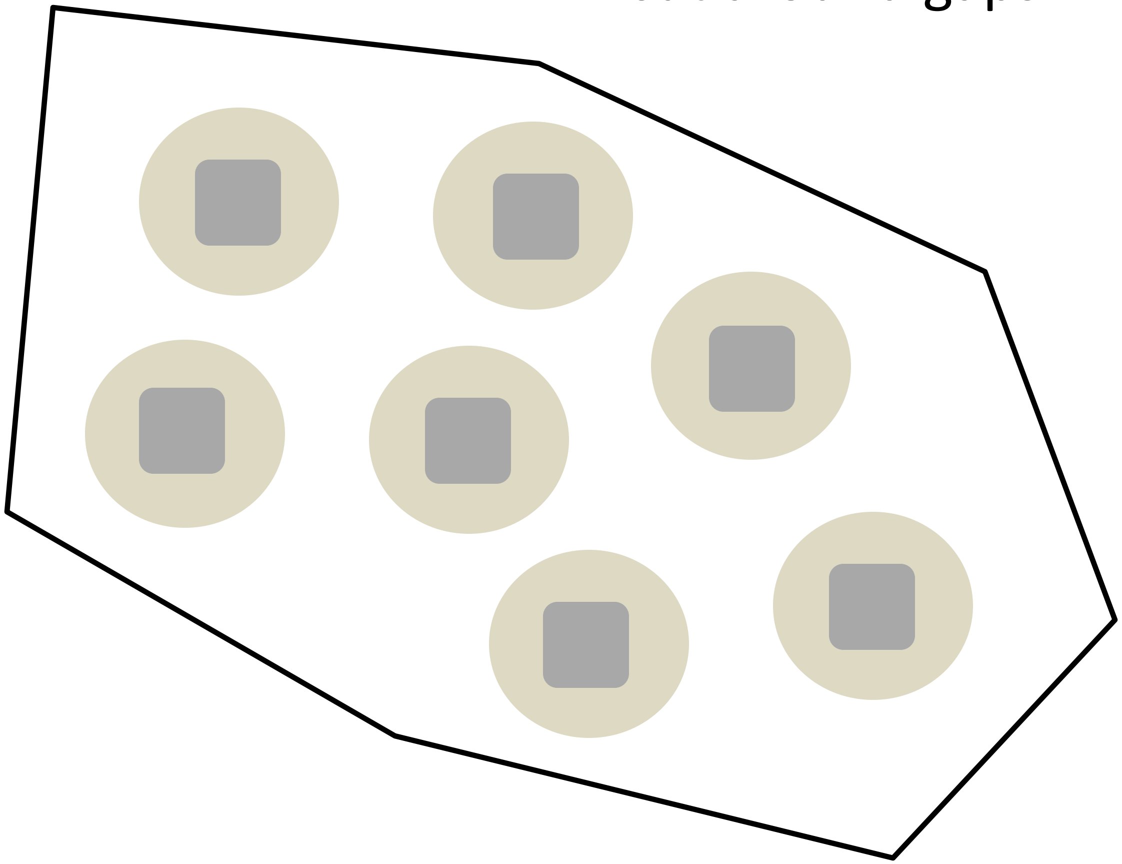
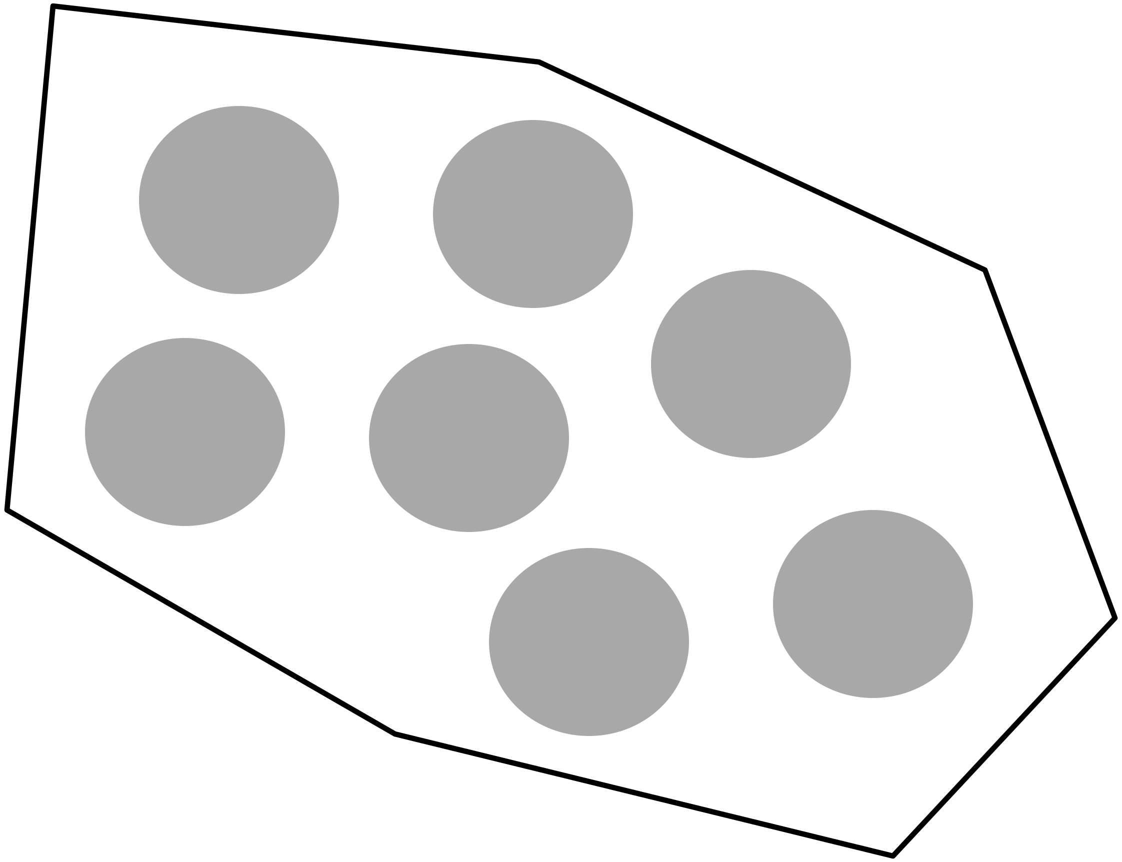
Expanding-Gap Irregular Shelterwood for Oak

Midstory removal as preparatory cut around gaps

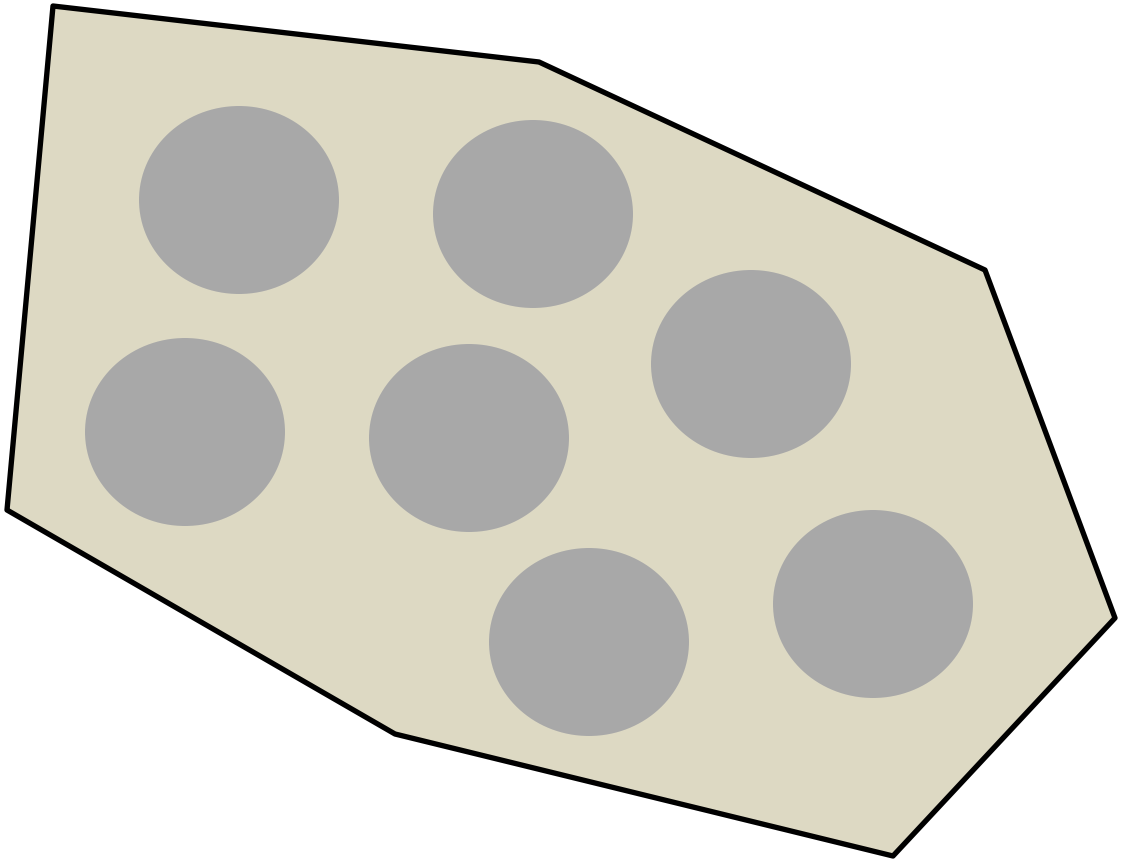


Expanding-Gap Irregular Shelterwood for Oak



Subsequent gap expansion into midstory removal areas based upon oak reproduction development

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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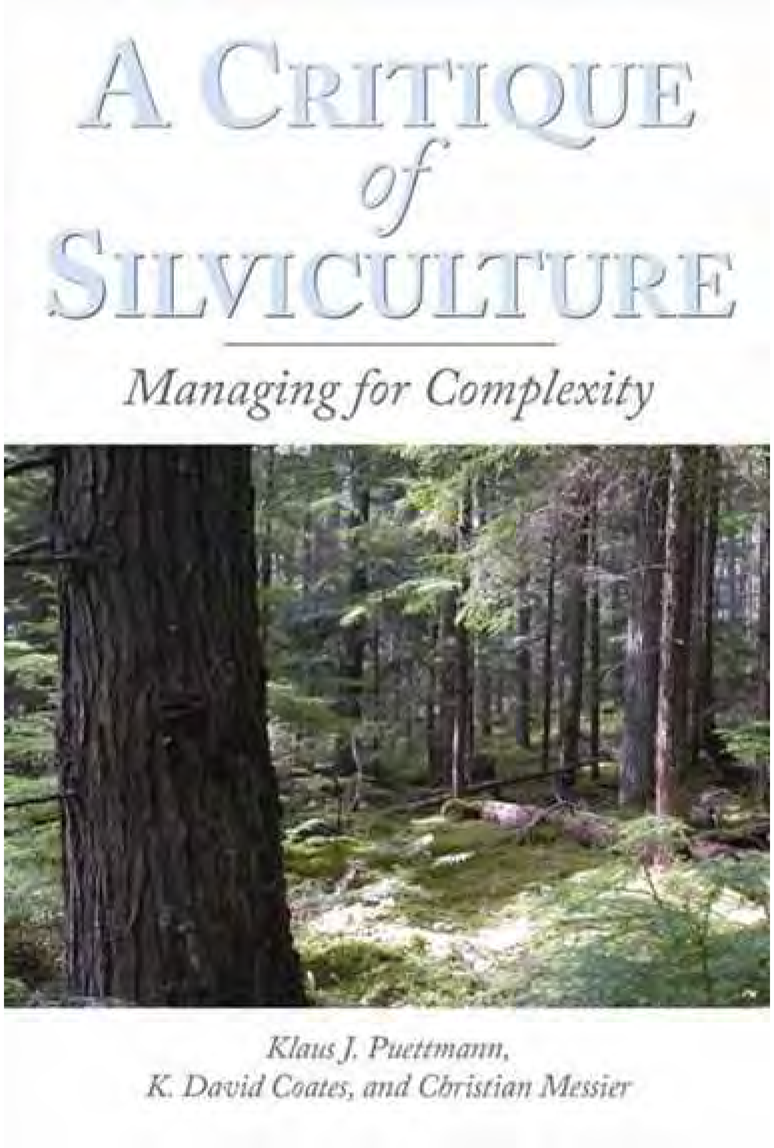
Future Extensions



A Critique of Silviculture

Managing for Complexity

Klaus J. Puettmann,
K. David Coates, and Christian Messier

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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)

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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

Doi: 10.1111/avsc.12060

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).

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-

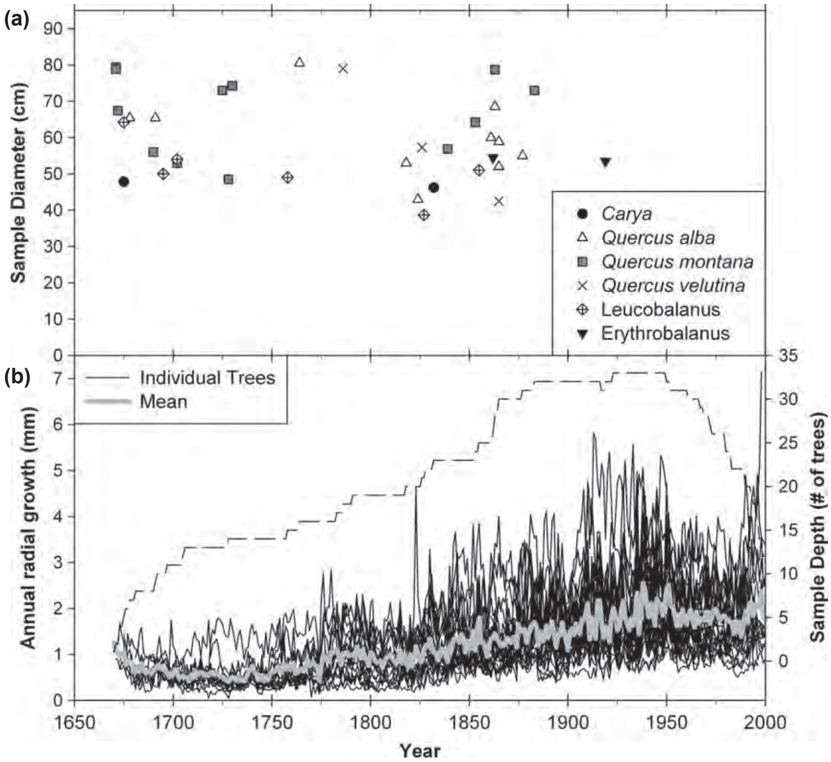

Fig. 1. Diameter and initiation dates **(a)** and annual growth **(b)** of tree cross-sections collected in an old-growth temperate deciduous forest, central Appalachian Mountains, USA.

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).

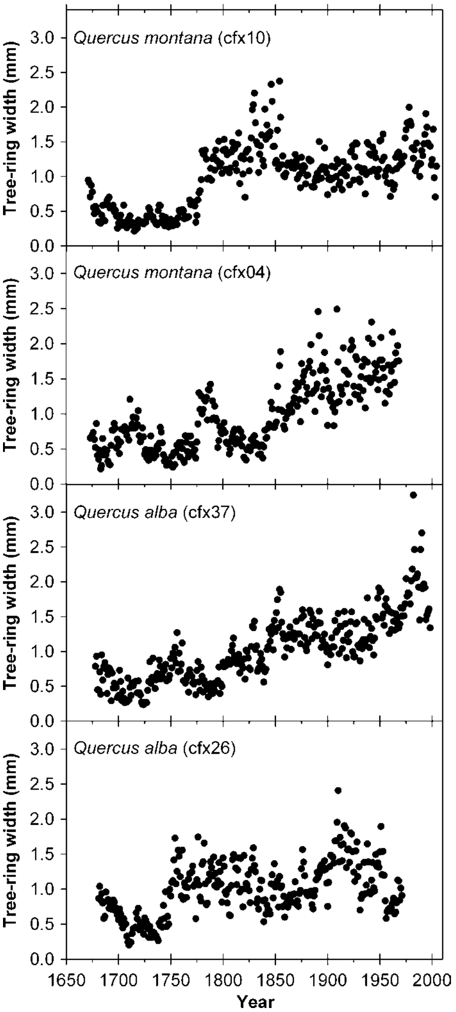

Fig. 2. Long-term growth patterns of the four oldest trees sampled as part of a fire history collection made in an old-growth temperate deciduous forest, central Appalachian Mountains, USA.

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.

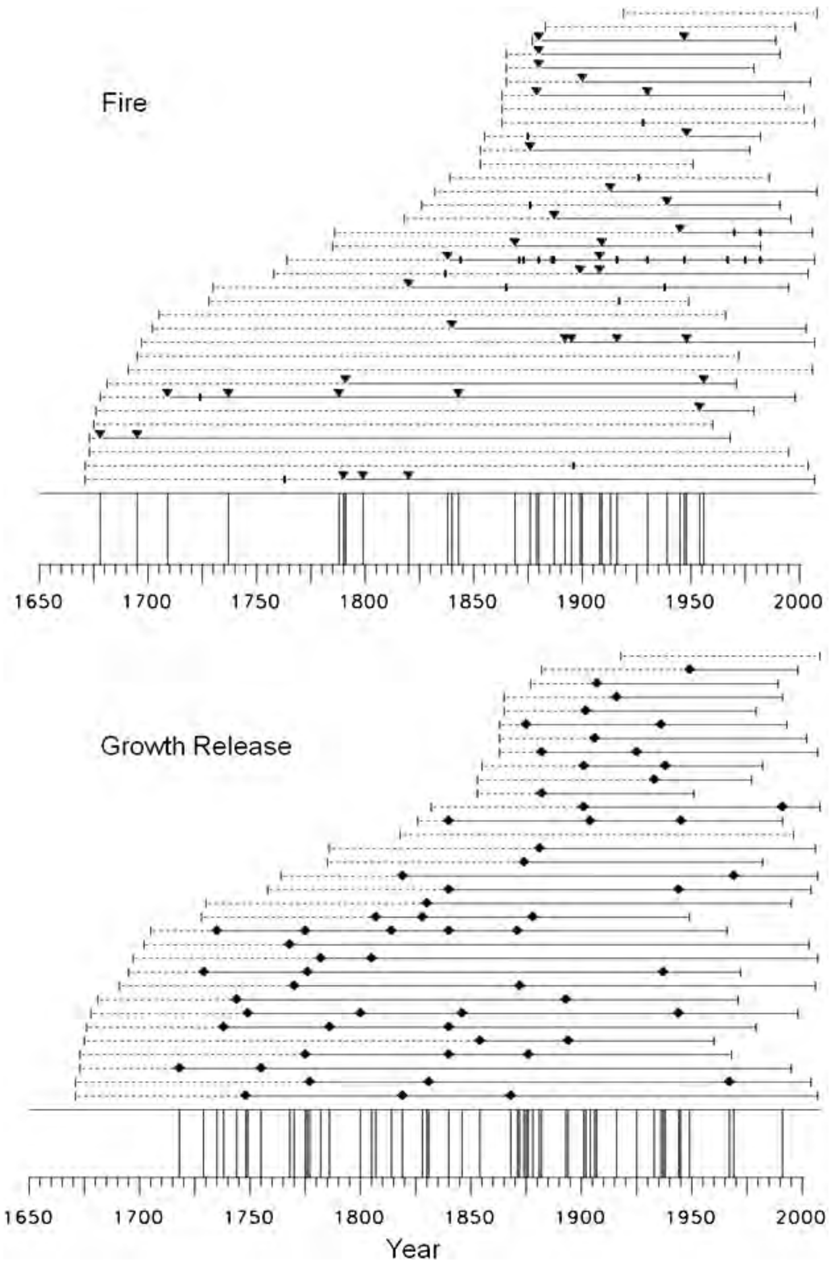

Fig. 3. Fire history and growth release from trees in an old-growth temperate deciduous forest, central Appalachian Mountains, USA. Horizontal lines represent the individual tree chronologies. In top panel, triangles indicate fire scars and dashes represent non-fire wound events. In bottom panel, diamonds 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).

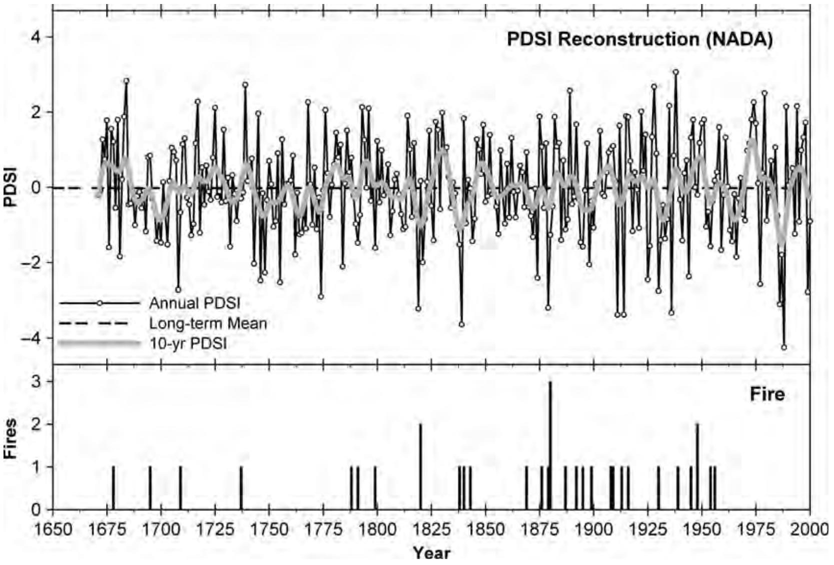

Fig. 4. Climate and fire in an old-growth temperate deciduous forest, central Appalachian Mountains, USA. Palmer Drought Severity Index (PDSI) indicates moisture levels on the landscape where negative values are dry years. Fire histograms (bottom panel) represent the number of trees recording a fire 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.

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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*	-

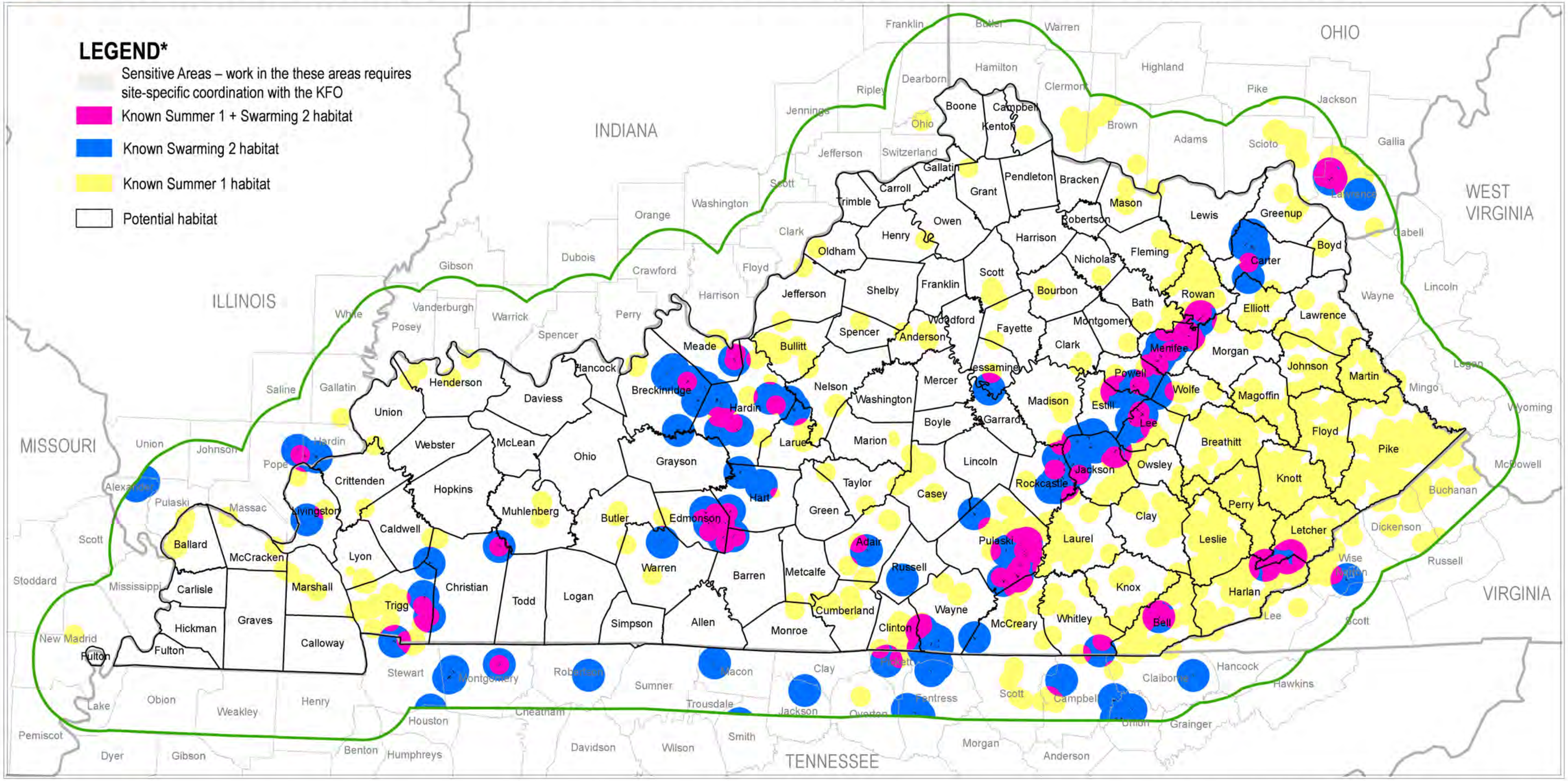
Supplemental Table 2.

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

U.S. Fish & Wildlife Service

Known northern long-eared bat habitat in Kentucky and within 20 miles (August 2019)



LEGEND*

▢ Sensitive Areas – work in the these areas requires site-specific coordination with the KFO

🟪 Known Summer 1 + Swarming 2 habitat

🟦 Known Swarming 2 habitat

🟨 Known Summer 1 habitat

☐ Potential habitat

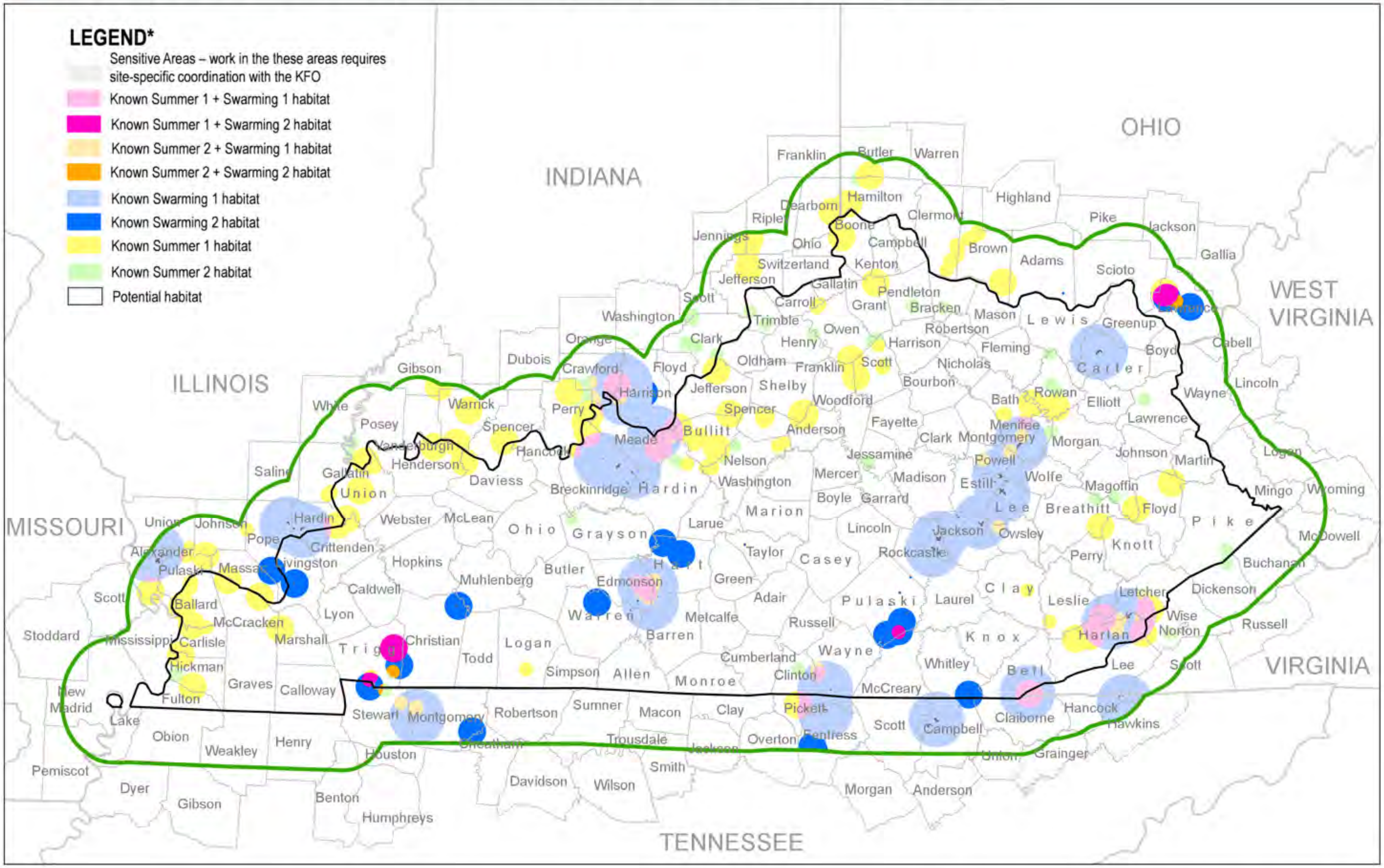
NOTE: This map is based on species occurrence information and is subject to change as new data become available. Please contact our office at 502/695-0468 to ensure you are working with the most current version.

*For an explanation of terms, please see the Conservation Strategy for Forest-Dwelling Bats in the Commonwealth of Kentucky.

The USFWS makes no warranty for use of this map and cannot be held liable for actions or decisions based on map content. This map was produced as an appendix to the Conservation Strategy for Forest-Dwelling Bats in the Commonwealth of Kentucky and should only be used in the context of this Strategy.

U.S. Fish & Wildlife Service

Known Indiana bat habitat in Kentucky and within 20 miles (August 2019)



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0 100 Miles

Kilometers 0 100

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Datum: NAD 83

Professional Hardwood Notes
Technical Information on Hardwood Silviculture for Foresters

UT Extension
SP676

Oak Shelterwood: A Technique to Improve Oak Regeneration

Jeff Stringer, Extension Professor of Hardwood Silviculture, Department of Forestry, University of Kentucky

The oak shelterwood method has been developed to enhance the regeneration potential of oaks growing on intermediate and high-quality sites. The method involves a well-timed mid-story removal to improve the number and vigor of oak advance regeneration and a subsequent overstory removal to facilitate regeneration of the stand (Figure 1).

Oak Regeneration Dynamics

Successful regeneration of oak on intermediate and high-quality sites (upland oak site index > 65 to 70 feet) is limited due to the lack of the vigorous advance regeneration and/or saplings/pole-sized trees that are capable of sprouting. Vigorous advance regeneration and/or stump sprouters are required at the time of regeneration on intermediate and high-quality sites, due to the abundance of competing species. Oak advance regeneration that is small in stature and low in vigor can quickly become overtopped by co-occurring species after a regeneration event. On poorer-quality sites, oaks are subjected to less competition, and often contain an adequate pool of advance regeneration or trees that are capable of sprouting.

In many instances, oak stands on intermediate and high-quality sites contain well-developed, mid- and under-stories of shade-tolerant species typically composed of red maple, sugar maple and American beech. This stand structure leads to light levels at

Untreated with well-developed mid-story.

First growing season after mid-story removal.

Figure 1. Oak shelterwood method and the implementation of the mid-story removal treatment in a typical upland oak stand.

SREF
Tennessee Forestry Department of Agriculture
Cooperative Extension Service
UK
University of Kentucky College of Agriculture

the forest floor that are not sufficient to provide for the long-term growth and development of oak advance regeneration. When a cohort of new seedlings is established under an intact canopy with a well-developed mid-story, the cohort languishes. The seedlings peak in height growth between 6 inches and 2 feet and mortality quickly reduces numbers. Ultimately, their ability to respond to increased light levels from a canopy disturbance is limited or non-existent.

The more shade-intolerant the species of oak, the more pronounced the effect. Figure 2 shows the height growth and survival of a cohort of northern red oak, one of the most shade-intolerant oaks, which has established and grown under an intact canopy on a high-quality site. After 10 years, only 10 percent of the original cohort is left, with an average height of less than 1 foot. Figure 3 shows similar height growth development for white oak, one of the most shade-tolerant oaks, on an intermediate-quality site. Both of these indicate that under undisturbed canopies with well-developed mid- and under-stories, the cohort establishes, grows negligibly in height and over time dies off. This process repeats itself throughout the life of the forest unless a disturbance occurs at the right time to break the cycle.

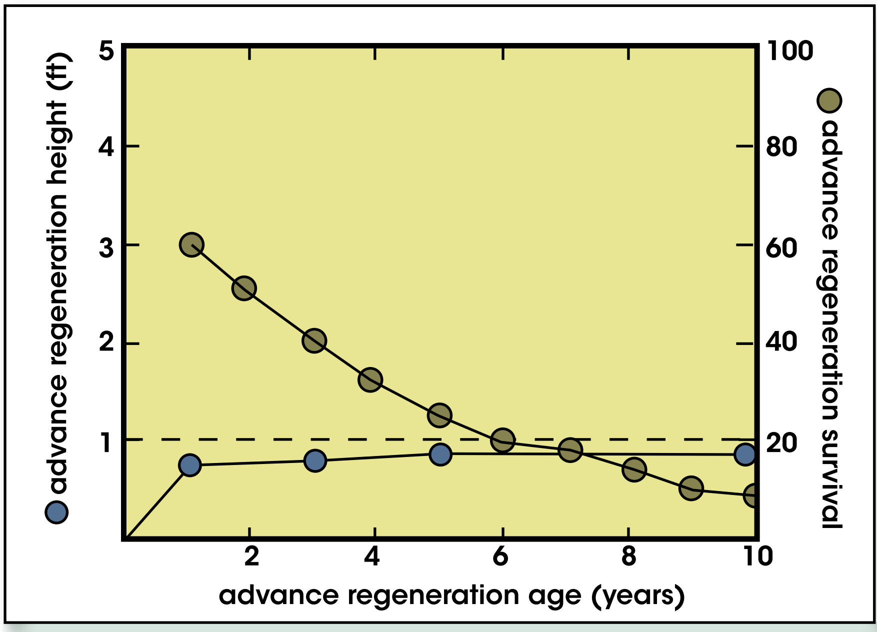

Figure 2. Northern red oak advance regeneration cohort height growth and survival under a typical mid-story on a mesic site.

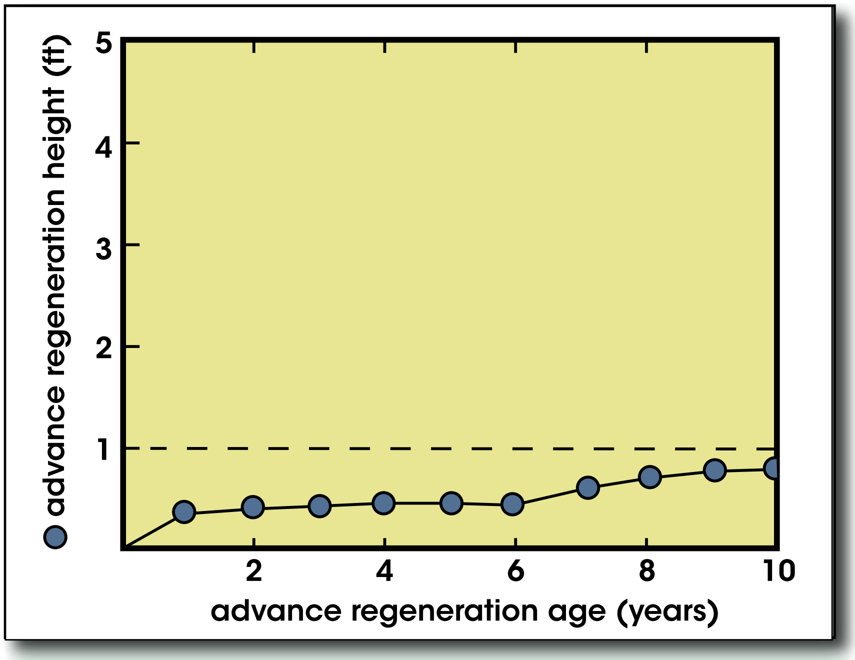

Figure 3. Height of white oak advance regeneration growing under a typical red maple mid-story.

Basics of the Oak Shelterwood Method

The oak shelterwood method has been developed to culture vigorous oak advance regeneration. It accomplishes this through a well-timed mid-story removal, improving light levels for adequate oak advance regeneration development, followed by a canopy release after the advance regeneration has reached a height where it can compete successfully with co-occurring species. The basic science behind the oak shelterwood method is well-documented. While species- and site-specific information for this method is under development, enough is known that recommendations can be made regarding its use in many oak-dominated stands.

The methods concept is simple. After the initial establishment of a cohort of oak seedlings, the mid- and under-stories are removed using herbicides. Typically, approximately 20 percent of the total stand basal area is removed, starting from the smallest trees that can be operationally treated (typically ½ to 1 inch dbh) increasing in diameter but stopping short of removing trees that would open holes in the main canopy. The removal of leaf area close to the ground without opening up the canopy increases diffuse light levels to a point where the newly established seedlings are not severely suppressed and can maintain continued height growth. Survival of the cohort will also improve.

It is important to note that opening the canopy can easily allow for sufficient amounts of direct sunlight to reach the forest floor, spawning the regeneration of many co-occurring species. Many of these species can quickly overtop small oak advance regeneration and lead to their demise. Therefore, it is imperative that the mid-story removal is aimed at increasing diffuse light levels and minimizing main canopy openings.

The ultimate aim of the mid-story treatment is to provide for an adequate number of high-vigor oak advance regeneration that can successfully compete when the overstory is finally removed. If the numbers and size of advance regeneration are sufficient, site preparation treatments at the time of overstory removal will not be required.

Figure 4. Suppressed oak advance regeneration.

Vigor of Advance Oak Regeneration

Vigor, as used in the context of the oak shelterwood method, describes the ability of the advance regeneration to respond quickly in height growth at the time of its full release, typically associated with some type of regeneration harvest. While all aspects of vigor are not thoroughly understood, vigorous advance regeneration is typically indicated by height and stem diameter and form. In turn, these provide clues to the strength of the root system that is a function of its size and available carbohydrate supply. Ultimately, it is this factor that has much to do with the success of advance regeneration upon full release.

While it is true that the sprouting nature of oak can lead to root systems that are older and can be much larger than indicated by the top, there is a general relationship between height, root mass and root carbohydrate stores for a young developing cohort of oak seedlings. As a cohort languishes under a dense mid-story, root carbohydrate reserves are reduced and stems lose apical dominance. Figure 4 shows an advanced regeneration white oak that has been suppressed under a red maple mid-story for 14 years. It is less than 2 feet in height and has lost apical dominance.

The key to the mid-story removal is to implement it directly after seedlings are established and to provide seedlings with enough light to generate root systems stocked with carbohydrates, allowing them to maintain apical dominance. The vigorous root system is especially necessary to ensure good sprouting if the stem is severed during a regeneration event. Even if the stem remains intact after a regeneration event, the crown must quickly develop a main leader and the root system must be well-developed to allow the advance regeneration stem to rapidly increase in height. At a minimum, oak advance regeneration stems should be 3 to 4 feet tall. It is also helpful if the oak advance regeneration possesses apical dominance. However, this latter attribute can be overcome if the root system is vigorous enough.

Which Stands Can Benefit

The system has been developed for stands that currently have oak-dominated overstories on intermediate to high-quality sites (site index > 65 to 70 feet for upland oak). Generally, these are bottomland sites with well-drained, silty loam soils. Upland high-quality sites are found in coves and north or northeast slopes with significant A horizons. Intermediate-quality sites are common on upper east- and lower south- and southeast-facing slopes. When site indices drop below 65 feet on upland sites, oaks are generally capable of regenerating themselves. This is because these stands carry less leaf area and the under-stories are generally higher in diffuse lighting, allowing for the development of vigorous advance regeneration. Also, poorer-quality sites have less vigorous competition from co-occurring species.

On sites above 65 to 70 feet site index, mid-stories are much more developed, limiting advance regeneration growth. Also, the challenge from co-occurring species can be significant upon full-canopy release. Bottomland sites are highly variable and may or may not contain well-developed mid-stories. When mid-stories are present, these stands can benefit from the oak shelterwood treatment.

Typically, this system has been used in stands where the overstory has the potential to provide adequate acorn crops of appropriate oak species and develop advance regeneration. However, when oak advance regeneration is lacking, this system has the potential to be used with underplantings of oak seedlings. Oak seedlings can be planted directly after the mid-story treatment and have been shown to respond well to mid-story removal. The overstory should be removed after the seedlings have acclimated to the environment and obtained heights of at least 6 feet.

There may be stands where the oak advance regeneration occurs in groups or clumps. In these cases, implementation of the mid-story removal treatment should only occur in and around the areas where the oak regeneration exists. It should be noted that there may be reasons to treat all unwanted mid-story species throughout the stand, even in areas where no advance regeneration is present. This could be done to remove or reduce unwanted species and might be advantageous for long-term management and reducing the need for a site preparation treatment in association with a regeneration event.

Timing of the Treatments

This system was designed to be implemented when oak advance regeneration is present. Implementing the mid-story removal prior to the establishment of an oak cohort is risky. If abundant numbers of seedlings are not established within a year or two after the mid-story removal, the advance regeneration of shade-tolerant species (typically present in most oak-dominated stands) will respond to the treatment, and oaks that establish themselves after the treatment will be in jeopardy. Recent studies also indicate that implementing the mid-story removal when the seedlings have been suppressed for several years may severely limit their ability to respond quickly to the treatment. These studies indicate that the seedlings lose vigor quickly. When provided improved diffuse lighting from the mid-story removal, it takes several years for the seedling to respond with detectable height and diameter growth. Generally, the longer the period of suppression of individual cohorts of seedlings, the smaller their numbers, the less vigor they have and the longer they take to respond, if at all.

Implementation of the Oak Shelterwood Method

Step 1. Candidate Stands

Implementation of this method should start with the identification of stands that could benefit from the method. Selection criteria include:

- intermediate to high-quality sites (> 65 to 70 feet site index for upland oak, or the equivalent),
- co-dominant and dominant oaks present (unless underplanting is possible)
- management objectives require maintenance of an oak component
- requiring regeneration now or in the near future

Step 2. Determining Oak Regeneration Potential of Candidate Stands

Once candidate stands have been defined, they should be scouted for their oak regeneration potential. Regeneration targets for maintenance of an oak-dominated canopy typically require a minimum of 50 to 100 dominant or co-dominant oaks at the time of canopy closure after a regeneration event (typically 10 to 15 years after regeneration). This requires that stands contain, prior to a regeneration event, advance regeneration at least 3 to 4 feet tall or sapling/pole oak stems that have the ability to stump sprout. The latter should be trees less than 10 inches in diameter and 65 years old for white oaks and 35 years old for red oaks.

Due to differences in competition pressure and condition of the advance regeneration, it is difficult to determine the exact number of advance regeneration stems per acre that are required to successfully regenerate an oak-dominated stand. However, if advance regeneration is non-existent or less than 2 feet tall (regardless of the numbers), then the stand is lacking in oak regeneration potential and the oak shelterwood method could be employed to improve this condition. If there are less than 100 advance oak regeneration greater than 3 to 4 feet in height and/or stump sprouters per acre (normally 100 to150 per acre), then some successful oak regeneration can be expected. Use of the oak shelterwood method in these stands would improve the oak percentage in the regenerating canopy. If stands contain the proper advance regeneration pool and/or adequate stump sprouters, then a regeneration harvest can be scheduled immediately and the oak shelterwood method is not required.

As indicated previously, this system could also be used with artificial regeneration. This would involve the underplanting of seedlings prior to a regeneration event and the oak shelterwood method used to improve their vigor prior to a regeneration harvest. Research has indicated that bare-root seedlings cultured in this fashion do have the ability to positively respond to the system.

Step 3. Timing the Mid-Story Removal

Proper timing of the mid-story removal is important for the overall success of this method. If an abundant acorn crop in the last several years has generated a large number of seedlings that still have apical dominance, then the mid-story removal treatment should be implemented as soon as possible (see below). If the seedlings are few in number, are extremely small (≤ 2 foot in height) with the majority of them having

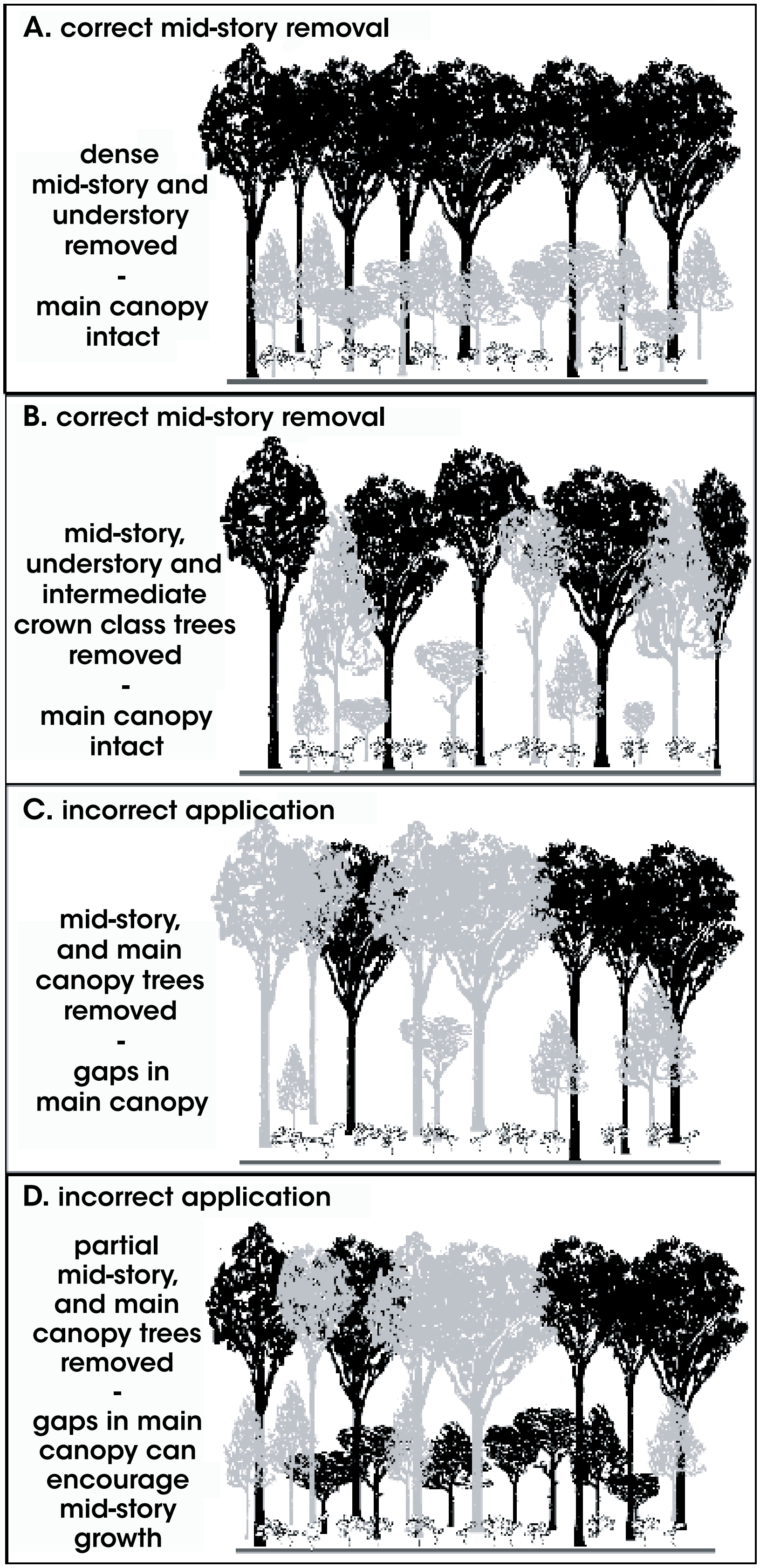

Figure 5. Correct and incorrect application of mid-story removal.

lost apical dominance, then the mid-story removal should be delayed until an abundant acorn crop produces a new cohort. The small, poorly formed advance regeneration present may not be capable of a reasonable response to the mid-story treatment, and waiting for a new cohort to develop may be required. Once a cohort of seedlings has established, implement the mid-story removal.

As a general recommendation, if there is no advance regeneration present, do not attempt the mid-story removal. There are two reasons for this. First, there is no evidence that implementing the treatment will improve oak seedling establishment. Second, the improved light conditions from the mid-story removal will stimulate the advance regeneration of competing species if present. Even if a good acorn crop occurs several years after a pre-emptive mid-story removal, the newly established cohort may be significantly behind in height growth, ultimately leading to its demise.

It is important to note that under conditions where there is no competing advance regeneration and there is reason to expect a reasonable mast crop in the next year or two, the pre-emptive mid-story removal might prove beneficial. However, caution should be exercised in implementing the mid-story removal prior to establishment of oak advance regeneration. The only other situation that would reasonably allow for a mid-story removal without the presence of advance regeneration is if oak is artificially established in the stand. This is typically accomplished using 1-0 or 2-0 bare-root seedlings.

Step 4. Implementing the Mid-Story Removal

The objective of the treatment is to remove the mid-story and understory to provide a significant increase in diffuse lighting without opening up the main canopy. Typically, a target removal of approximately 20 percent of the stand basal area should be planned. While determining the basal area removal is good for planning purposes, typically the treatment is implemented by removing sub-canopy trees, starting with the smallest trees that can be treated. Begin with the smallest, and move up in size but stop short of removing co-dominant or dominant trees (Figure 5).

In some stands, the under- and mid-story may all be overtopped crown class trees and they can be completely removed (Figure 5a). In some cases, the under- and mid-story trees may include overtopped and intermediate crown class trees. Removal of intermediate crown class trees can occur as long as co-dominant or dominant crown-sized gaps are not created (Figure 5b). Figures 5c and 5d show cases where main canopy openings were created, allowing direct radiation to enter the forest. Figure 5d shows a mid-story that was left intact coupled with openings in the main canopy. Under these conditions, the remaining mid-story trees will flourish and increase their leaf area and crown size, further decreasing light levels on the ground.

In almost all cases, the under- and mid-story trees should be treated with herbicides. Simply cutting shade-tolerant under- and mid-story trees will lead to sprouting and cause a greater shade problem for advance oak regeneration than if they had been left standing as single stems. Using herbicides ensures the elimination or significant reduction of competing species and also has the added bonus of removing or reducing the seed source of competing species from the stand. Because oak advance regeneration can not be harmed, individual tree treatments must be used. Methods usually include tree injection, hack and squirt, or basal bark application. Selection of herbicides is generally not critical. However, there have been instances where a significant number of trees per acre have been treated with herbicides with soil activity and some effects on the advance regeneration pool have been observed. Conduct the mid-story removal during the season that is most appropriate for the herbicide treatment prescribed.

Step 5. Monitoring the Advance Regeneration

In the years after the mid-story removal, inspect the stand to ensure that the oak advance regeneration is progressing in growth and to determine if any competition problems have arisen. If there is a seed source of shade-tolerant species in the area, then new advance regeneration of these competing species may establish. These can be taken care of as appropriate through a follow-up herbicide treatment.

Unfortunately, oak seedlings may take some time to respond to the treatment. Response may occur the first year or two after the treatment, especially if the seedlings are of a fast-growing species, are young and exhibiting good apical dominance, and are growing on a good-quality site. Examples of these species and sites would be northern red oak on mesic upland sites or cherrybark oak on bottomland alluvial sites. It may take several years for a slower-growing species such as white oak on an intermediate-quality site to respond.

Step 6. Full Release

The timing of the final release treatment, usually a regeneration harvest, should coincide with the oak advance regeneration attaining a height of 3 to 4 feet or more, the taller the better. The more intense the competition is estimated to be upon release, the larger the advance regeneration should be. Once the advance regeneration has reached the appropriate size, the overstory can be removed by the most appropriate regeneration harvest. Complete clearcuts, patch clearcuts or group openings are generally recommended. Regardless of regeneration harvest, make sure that enough overstory is removed to ensure vigorous regeneration response. If necessary, a site preparation treatment for natural regeneration can be employed to aid in regeneration success. However, successful implementation of the oak shelterwood treatment would negate the need for this treatment.

Other Considerations

There is evidence that oak advance regeneration that has been suppressed for a number of years can respond positively to coppicing. This allows for the root system to produce a top with apical dominance and possibly in better balance with the root system. However, thorough testing of this technique has not been conducted.

The role of prescribed fire in the oak shelterwood method is also a question. Prescribed fire can be used to top-prune poorly formed advance regeneration. However, the intensity of prescribed fire that could be used would only top kill under- and mid-story shade-tolerant trees, resulting in significant sprouting and ultimate interference with oak advance regeneration development. It is possible to combine a prescribed fire with herbicides (either pre- or post-fire treatment). However, the results of this method of competition control have not been thoroughly tested. There have been instances where prescribed fire has been used to successfully remove competing species that were shade-intolerant (ex. yellow-poplar) or where the shade-tolerant competition was newly established from seed. Regardless, prescribed fire might have potential to use in this method, but the risks, benefits and the specific stand and competition conditions must be closely evaluated.

Summary

The oak shelterwood method is a useful tool to help improve the ability of oak to regenerate. Proper timing and implementation are critical for the effective use of this method. Application steps include:

- Determination of appropriate stands based on site quality, oak dominance and oak regeneration potential
- Proper timing of the mid-story removal treatment to ensure that oak advance regeneration is present prior to implementation
- Proper removal of under- and mid-story trees so as not to open the main canopy and to kill treated trees
- Implementation of the final regeneration harvest after the advance regeneration has reached adequate size.

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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 long-standing 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].

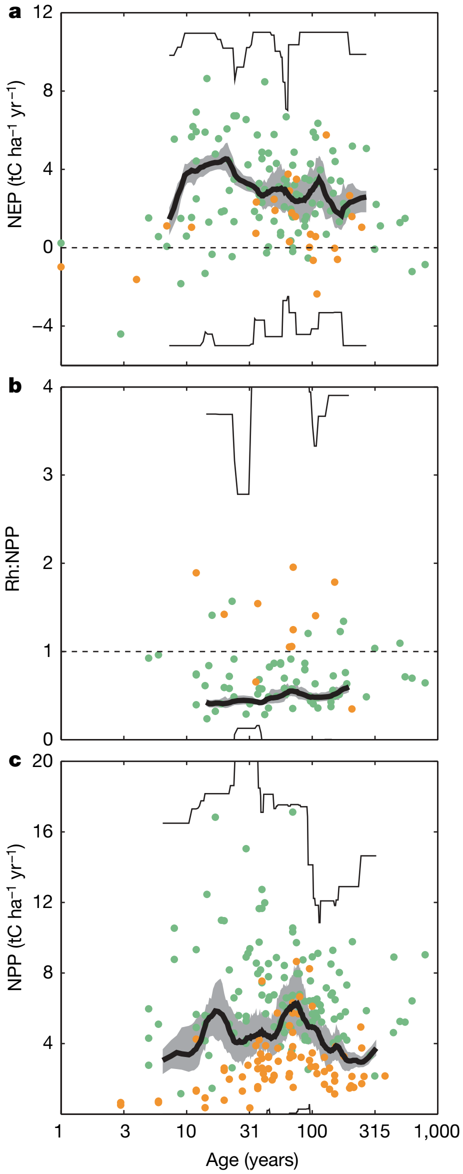

Figure 1 | Changes in carbon fluxes as a function of age. a, Observed NEP versus age; positive values indicate carbon sinks and negative values indicate carbon sources. **b**, Observed ratio of heterotrophic respiration (Rh) to NPP versus age; Rh:NPP < 1 indicates a carbon sink. **c**, Observed NPP versus 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).

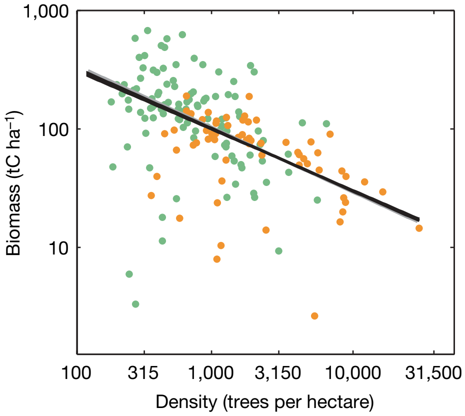

Figure 2 | Biomass accumulation as a function of stand density. Each data point represents a different forest, many of which have different growing conditions and tree species. Not all growing conditions and species compositions allow for the accumulation of the global maximum observed biomass. Self-thinning, 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.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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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:

$$F_{il} = \sum_{j=1}^{k} \left(w_{ijl} \times F_{ijl} \Big/ \sum_{j=1}^{k} w_{ijl} \right) \tag{2}$$

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:

$$F_i = \sum_{l=1}^{m} \left(w_{il} \times F_{il} \Big/ \sum_{l=1}^{m} w_{il} \right) \tag{4}$$

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:

$$W = c \cdot n^{\gamma - 1} \tag{4}$$

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 ΔL:$\Delta Bgross$ 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.

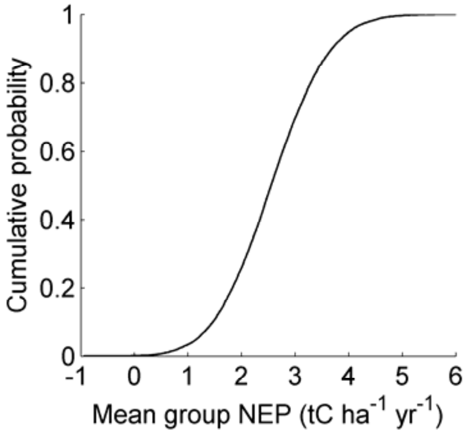

Cumulative probability
0
0.2
0.4
0.6
0.8
1
-1
0
1
2
3
4
5
6
Mean group NEP (tC ha^{-1} yr^{-1})

Figure S1

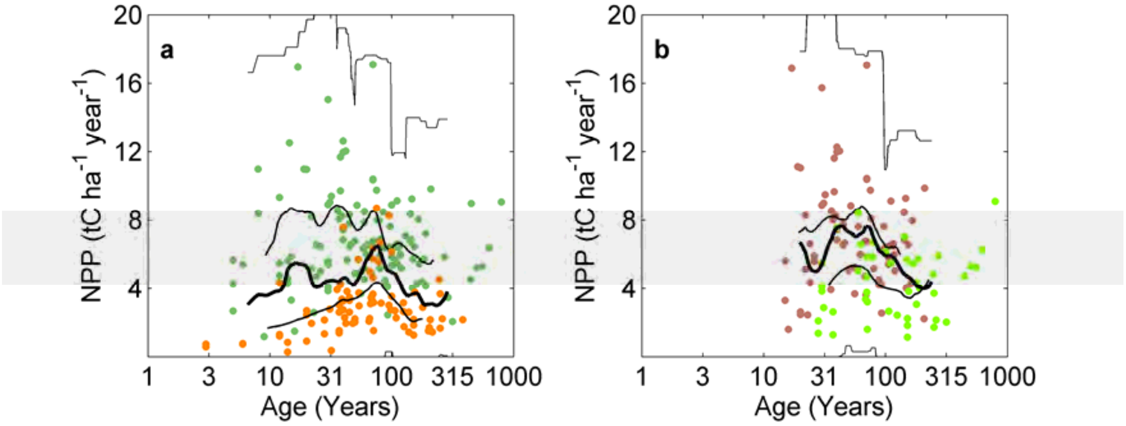


Figure S2

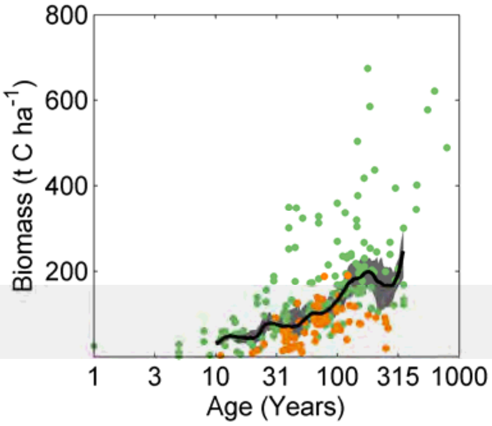


Figure S3

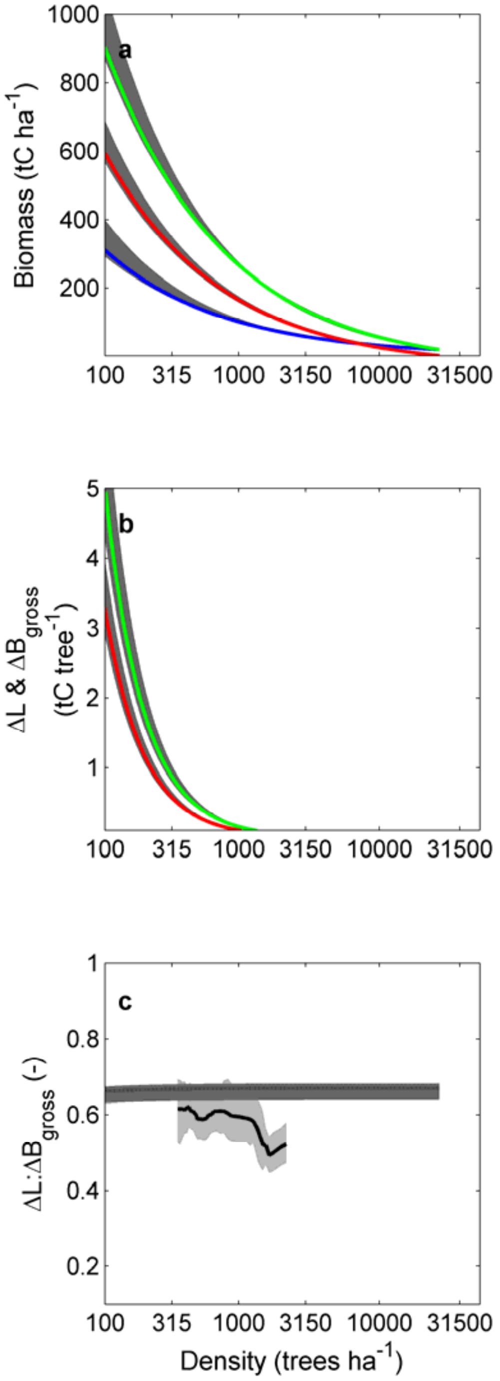
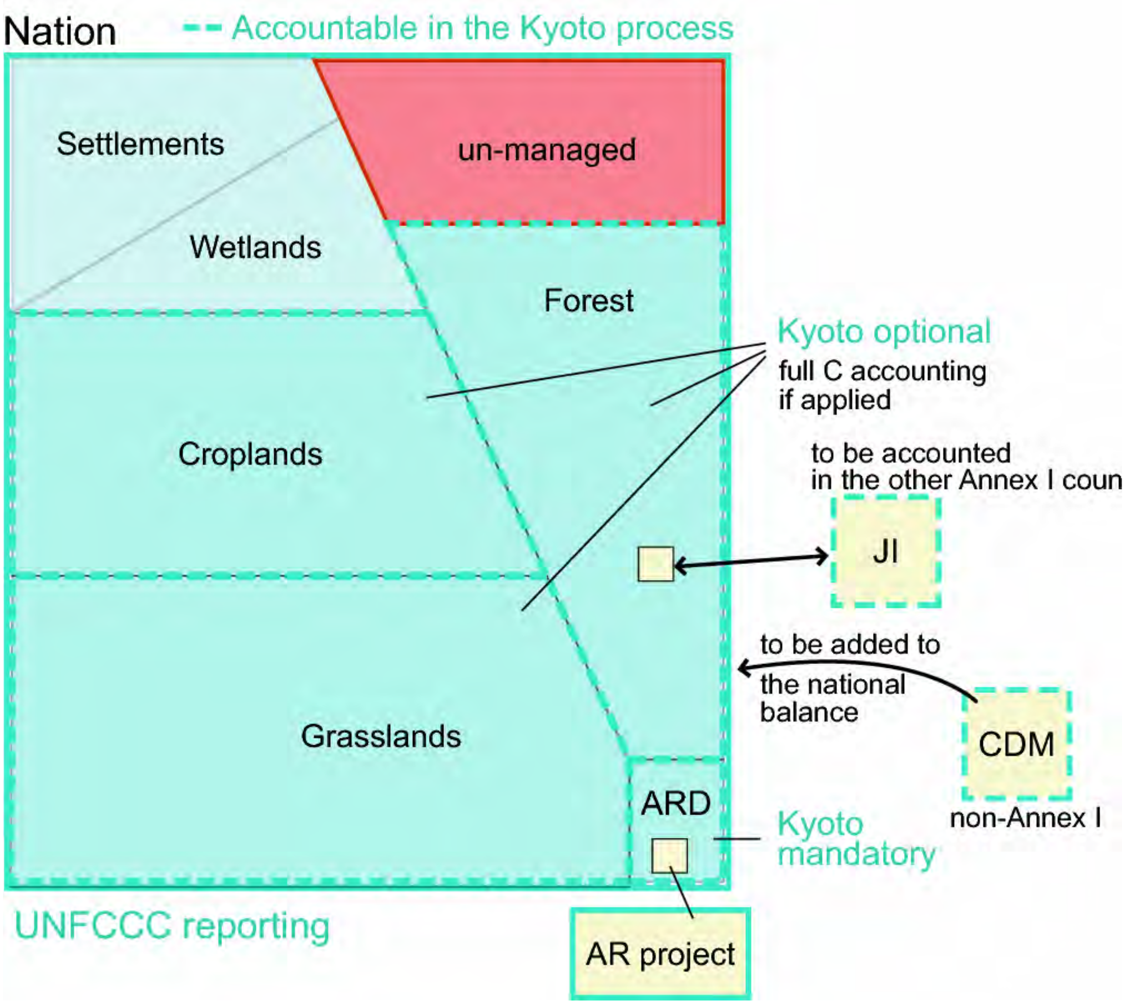

a
Biomass (tC ha^{-1})
1000
800
600
400
200
100
315
1000
3150
10000
31500
b
ΔL & ΔB$_{gross}$ (tC tree^{-1})
5
4
3
2
1
100
315
1000
3150
10000
31500
c
ΔL:ΔB$_{gross}$ (-)
1
0.8
0.6
0.4
0.2
100
315
1000
3150
10000
31500
Density (trees ha^{-1})

Figure S4


Nation
Accountable in the Kyoto process
Settlements
un-managed
Wetlands
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Croplands
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JI
Grasslands
to be added to
the national
balance
CDM
ARD
non-Annex I
Kyoto
mandatory
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.

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[7] Kelly, P., 2009. A Greenhouse Gas Inventory of Oregon's Forests. Salem, OR: Oregon Global Warming Commission, Oregon Department of Energy.

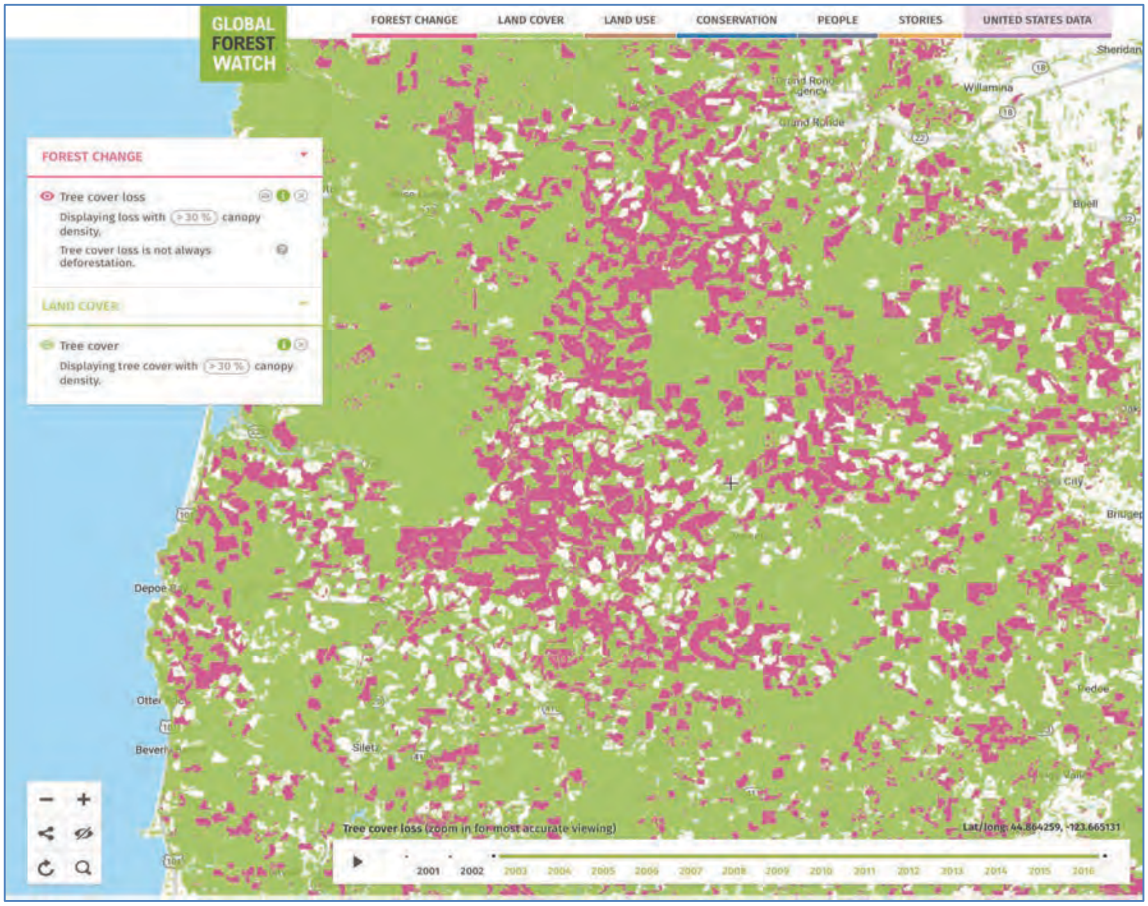
[8] Air Resources Board. 2014. Staff Report: Initial Statement of Reasons for Proposed Rulemaking. Appendix I, Detailed Analysis for Indirect Land Use Change. Sacramento, CA: California Environmental Protection Agency.

[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*)



Tree cover loss
Displaying loss with >30 % canopy density.
Tree cover loss is not always deforestation.

Tree cover
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)

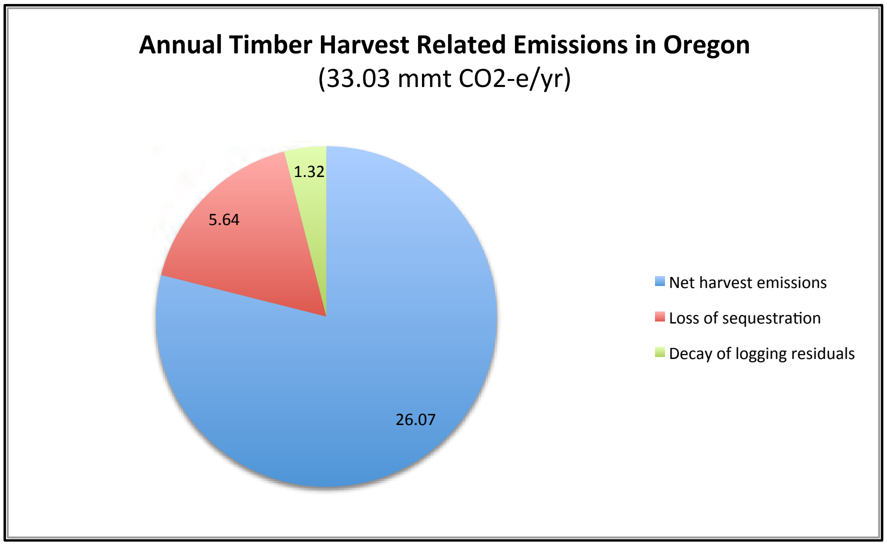
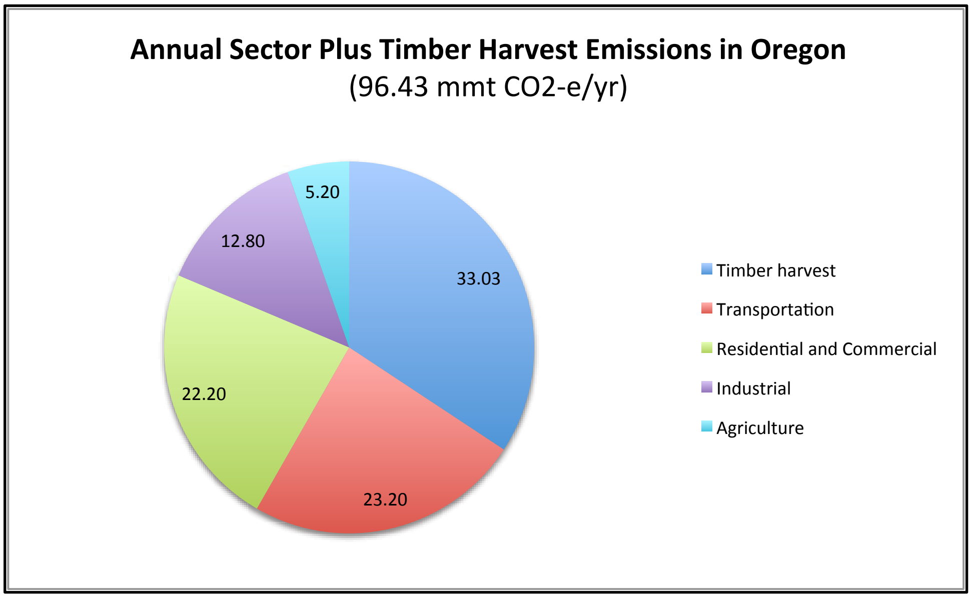


Figure 3: Timber harvest is by far the largest source of GHG emissions in Oregon each year



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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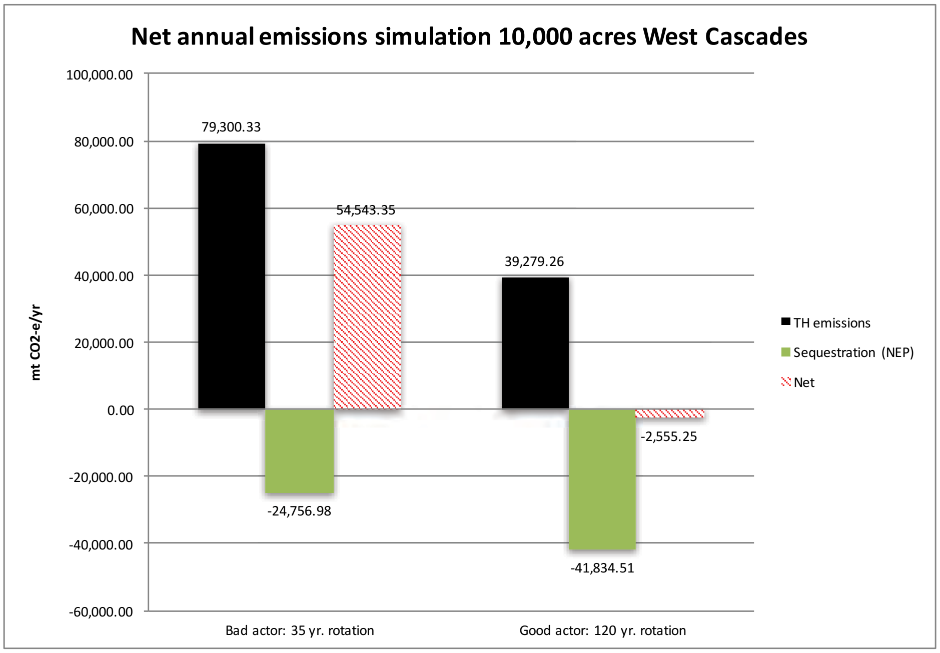
[45] Curtis, R.O., 1997. "The role of extended rotations." Chapter 10 in Kohm, K.A., Franklin, J.F., eds. Creating a Forestry for the 21st Century. Washington, DC: Island Press.

[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

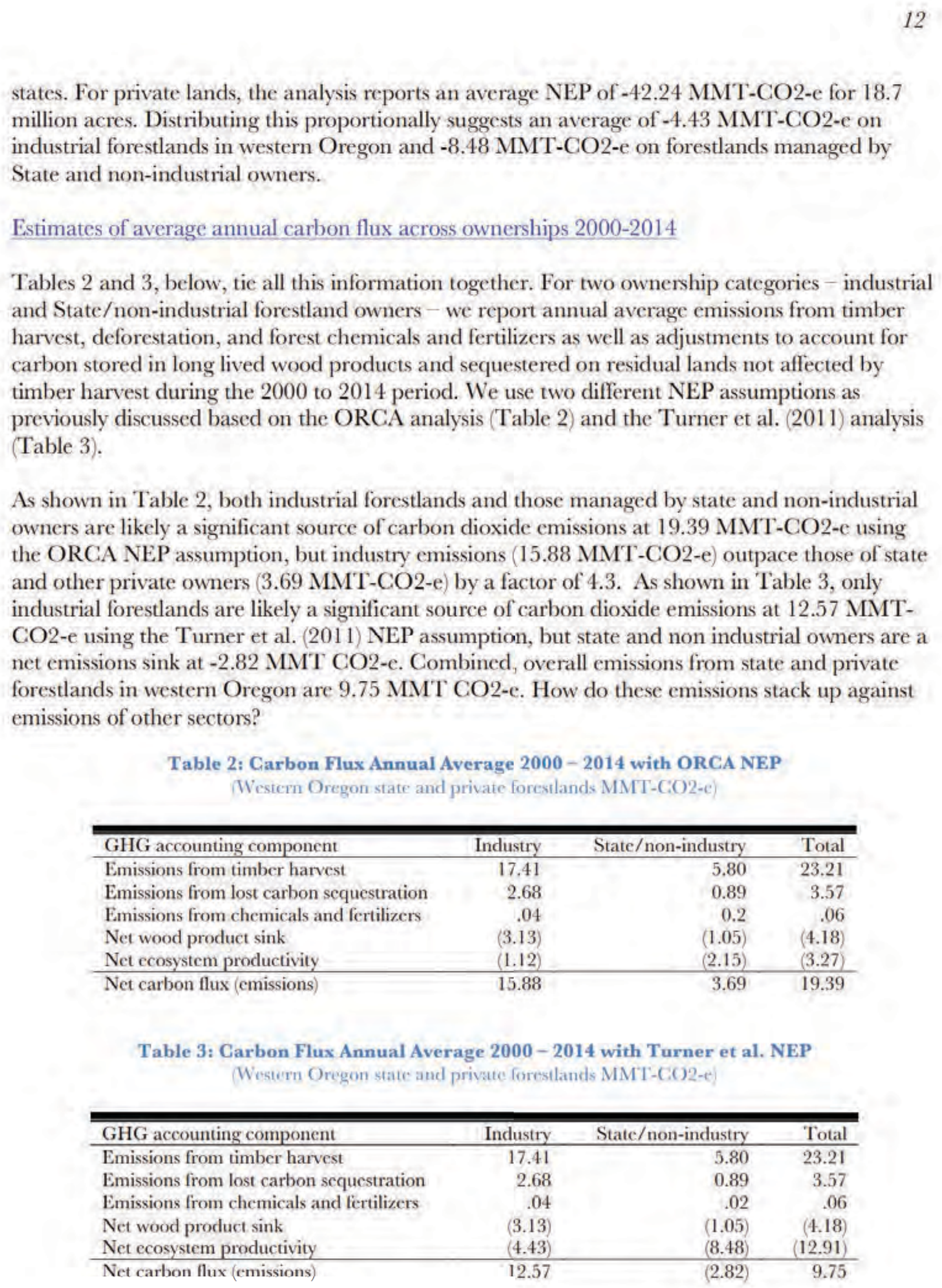
Table 2A. Growth, Removals and Mortality of CO2 equivalent, by ecoregion

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

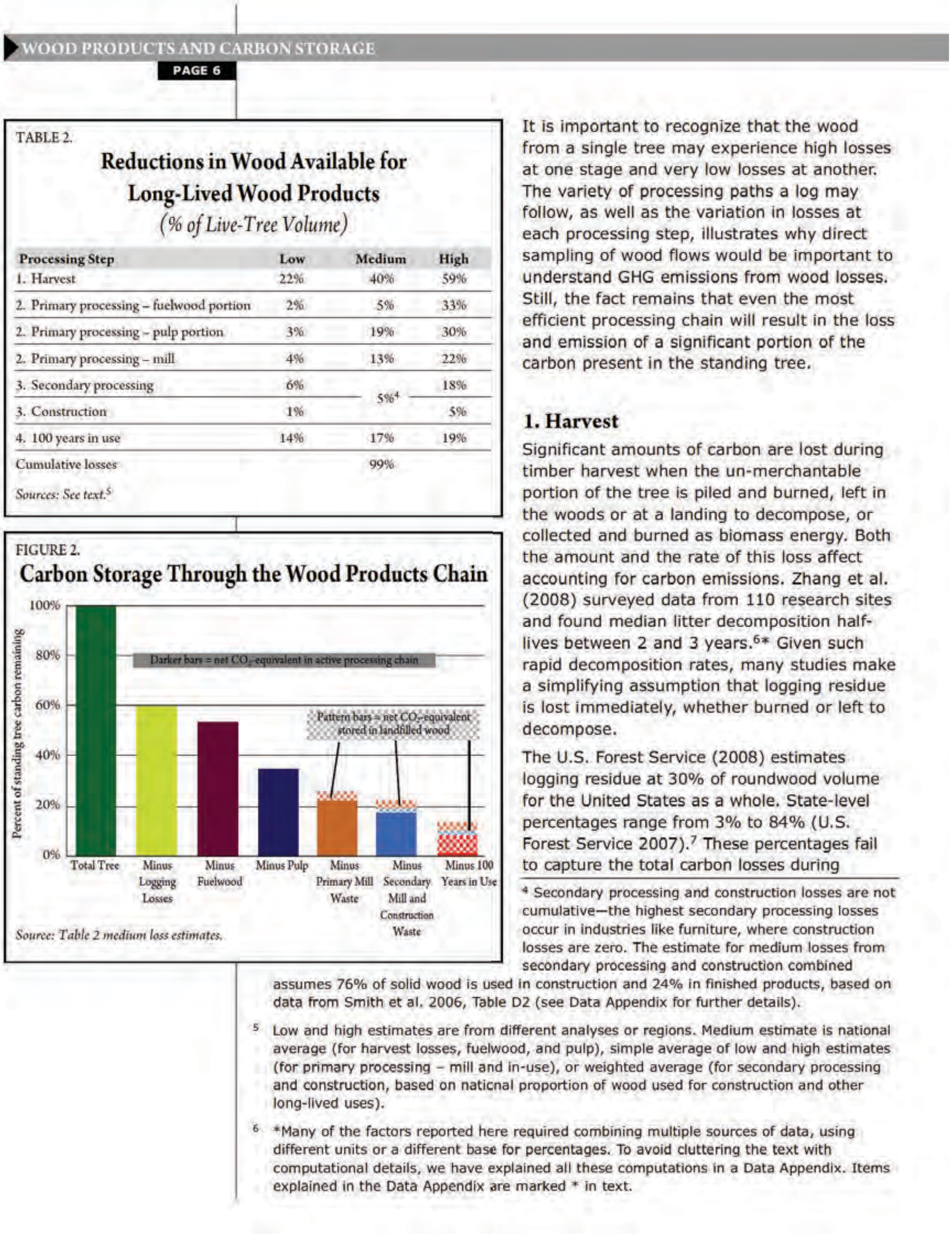


TABLE 2.

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

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[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 national 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.

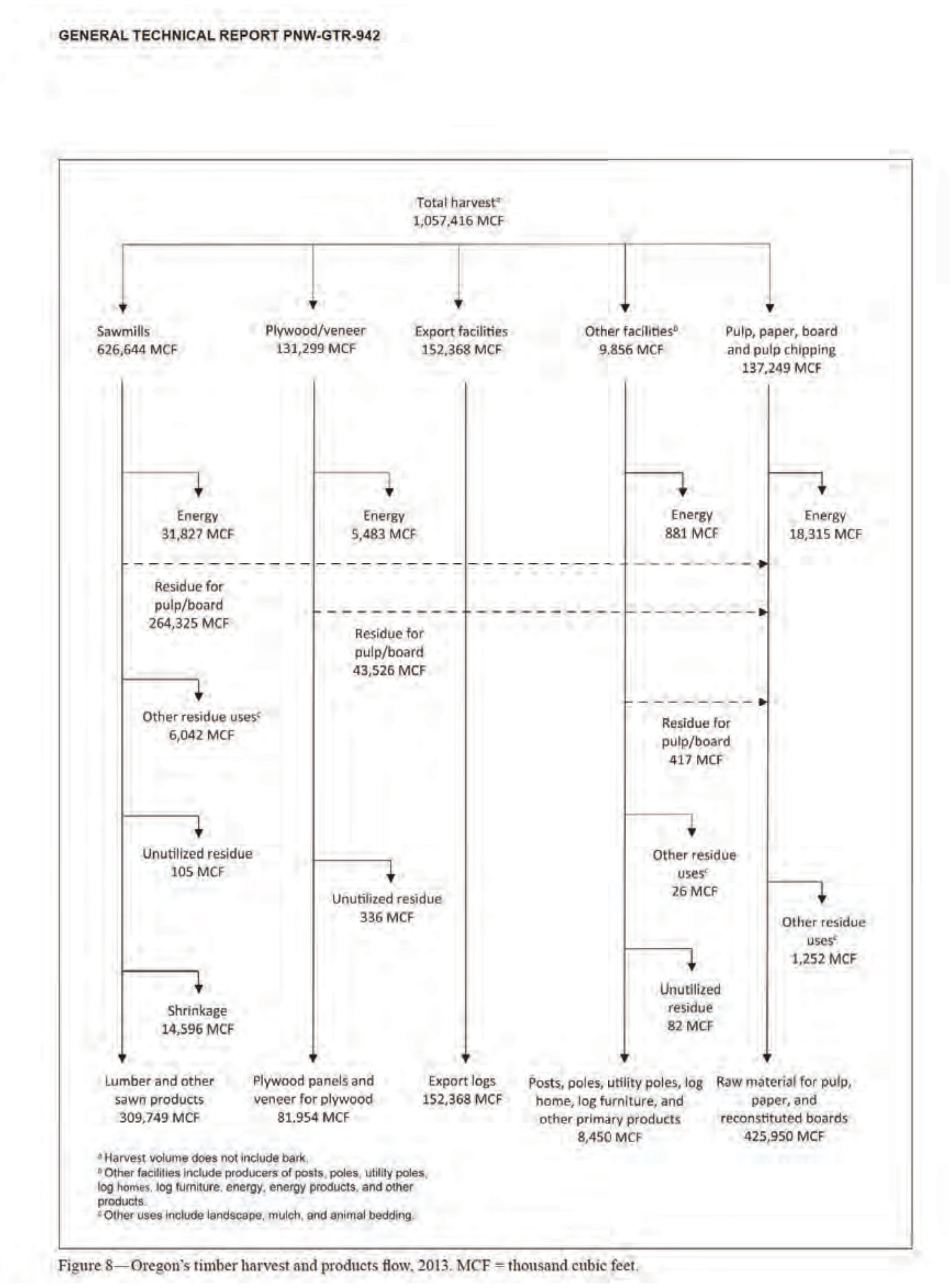
Appendix D

Table 6.—continued

	Pacific Northwest, West, Softwoods							
	Saw log				Pulpwood			
Year after production	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

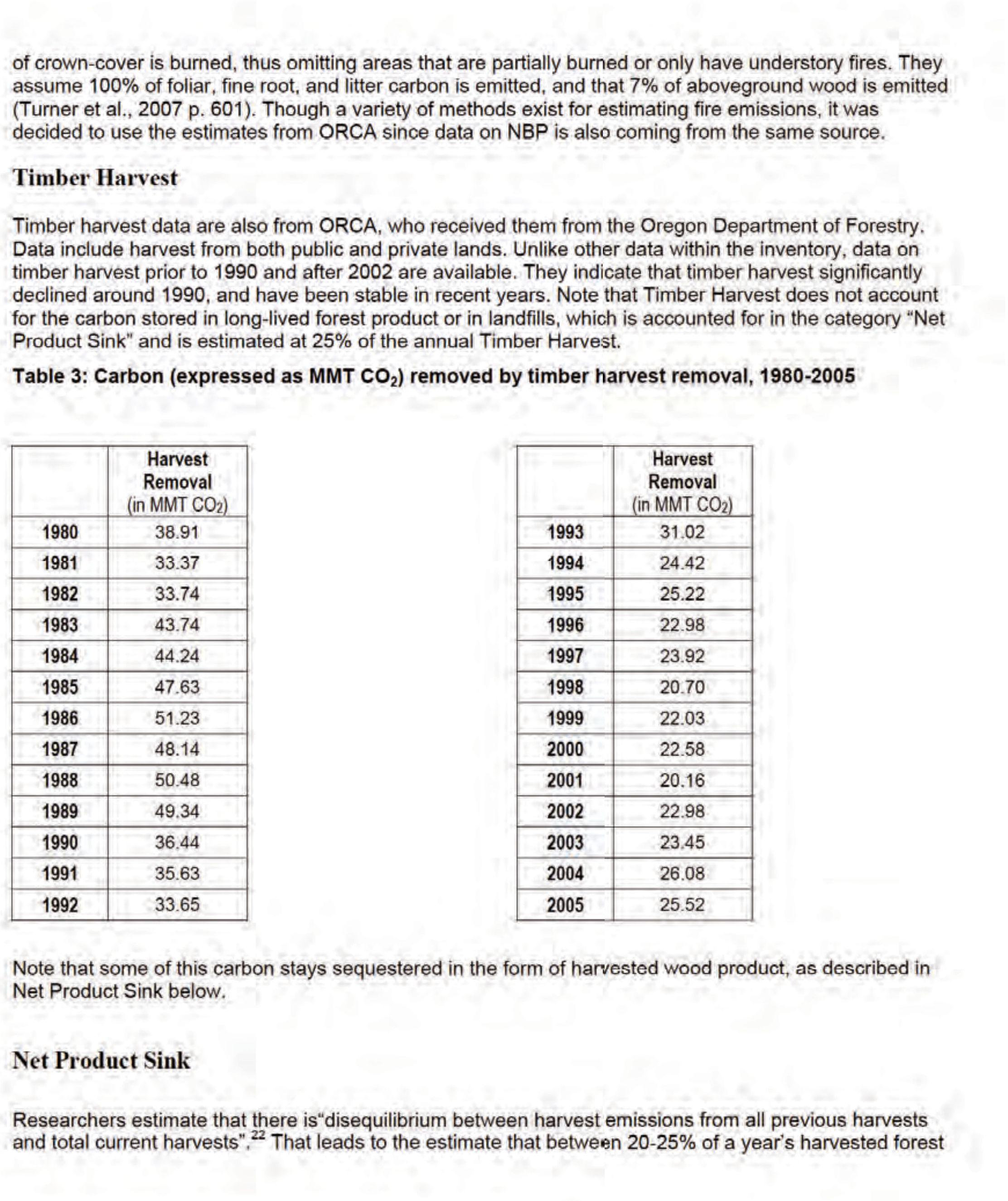
Appendix E



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.



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

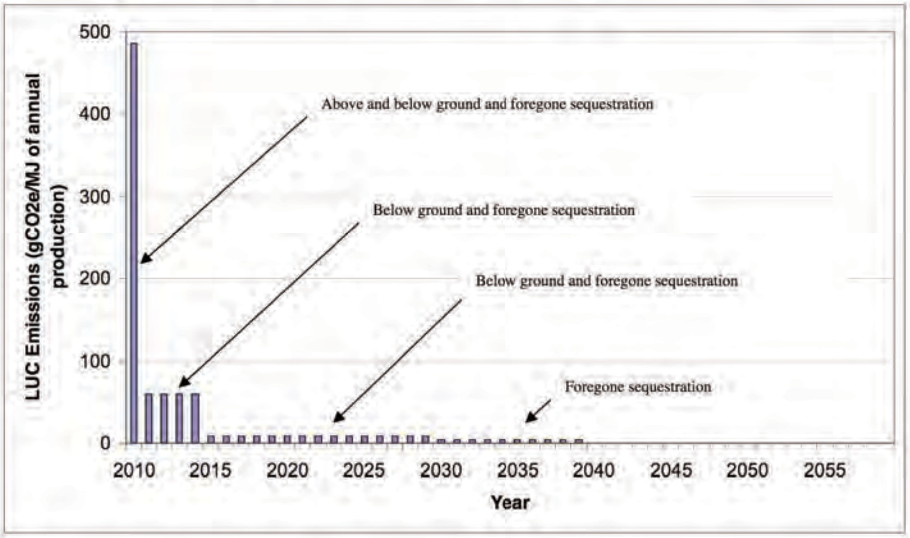
Note that some of this carbon stays sequestered in the form of harvested wood product, as described in Net Product Sink below.

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

- 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

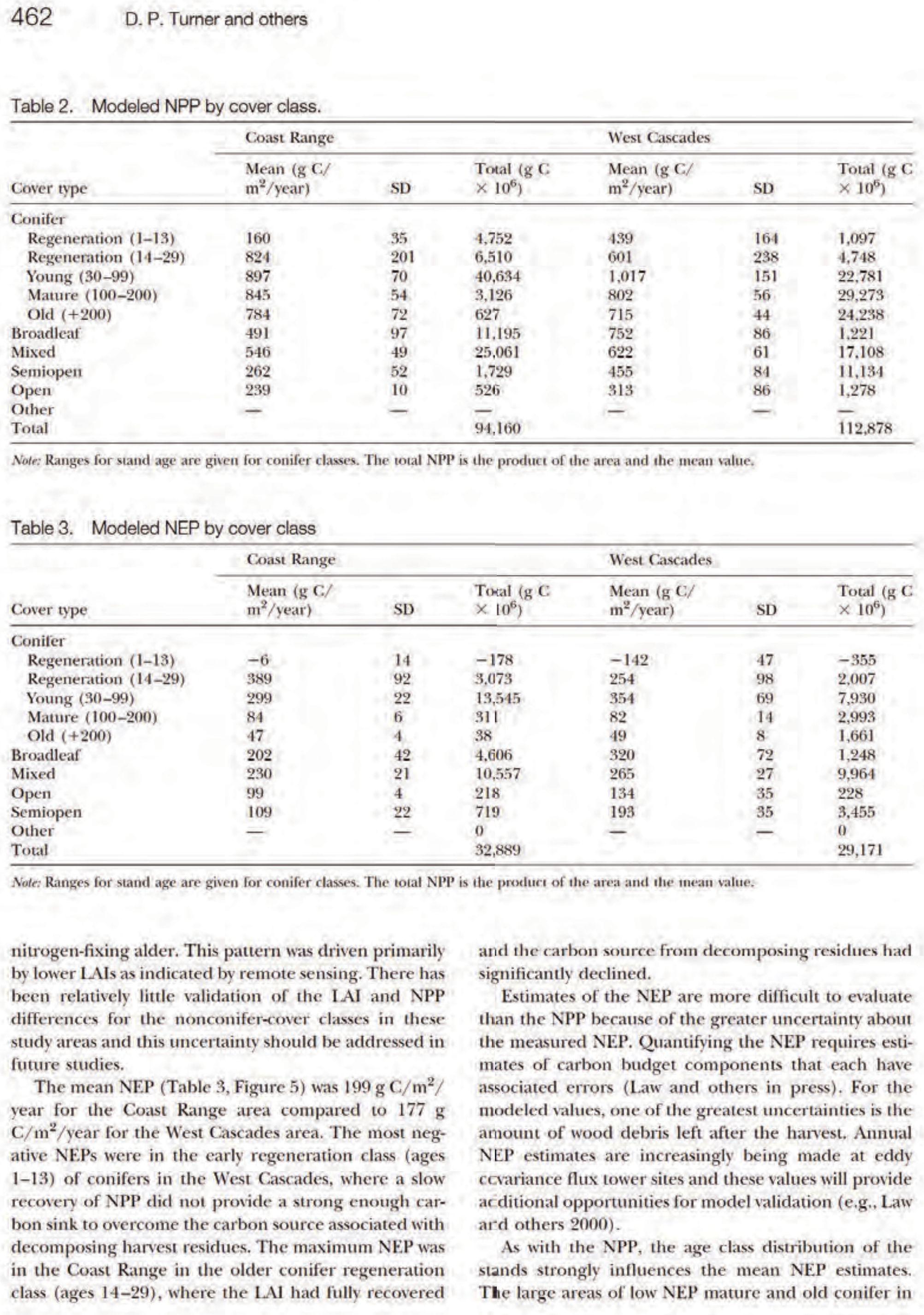


Table 2. Modeled NPP by cover class.

	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.

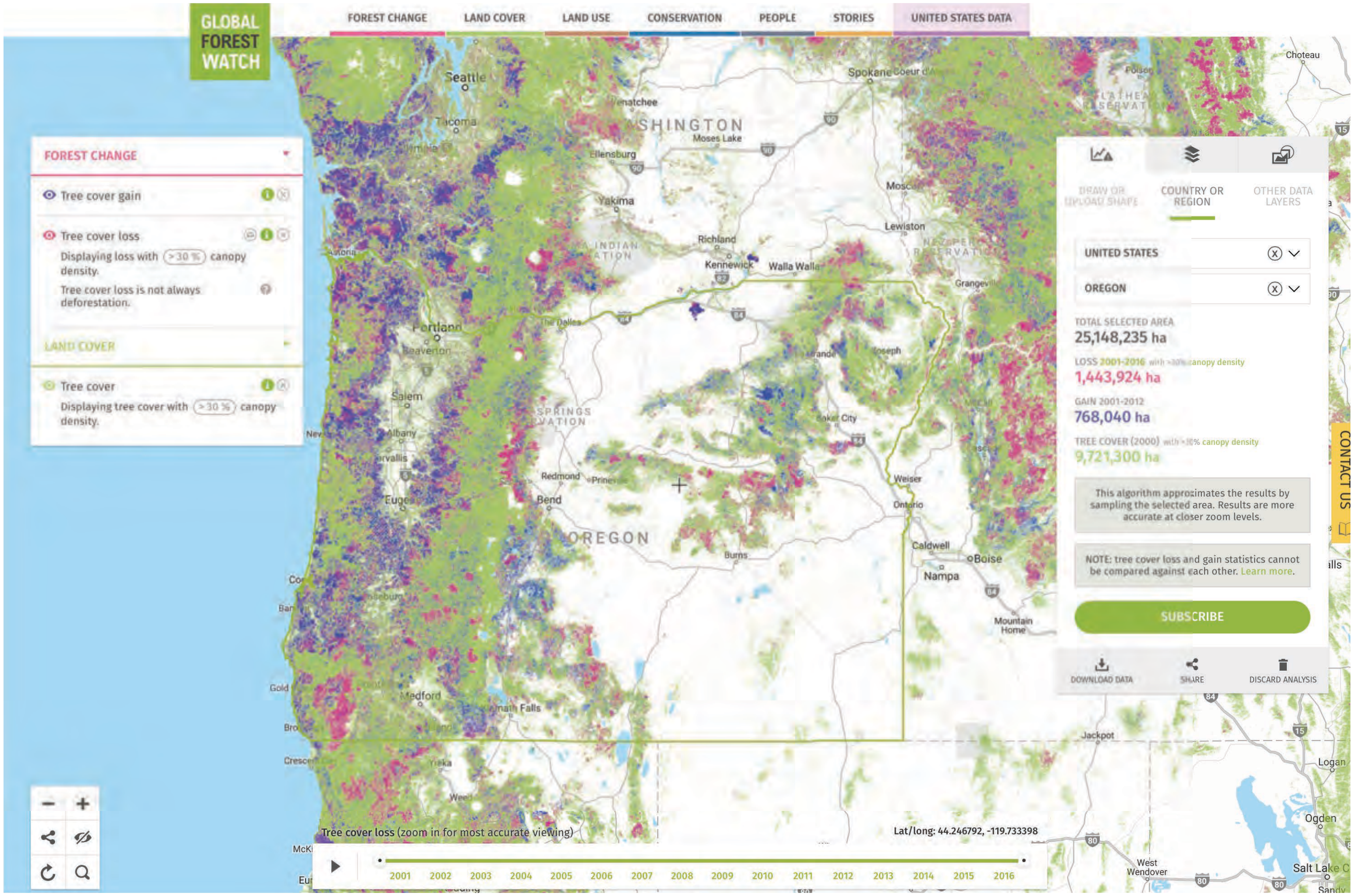
nitrogen-fixing alder. This pattern was driven primarily by lower LAIs as indicated by remote sensing. There has been relatively little validation of the LAI and NPP differences for the nonconifer-cover classes in these study areas and this uncertainty should be addressed in future studies.

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

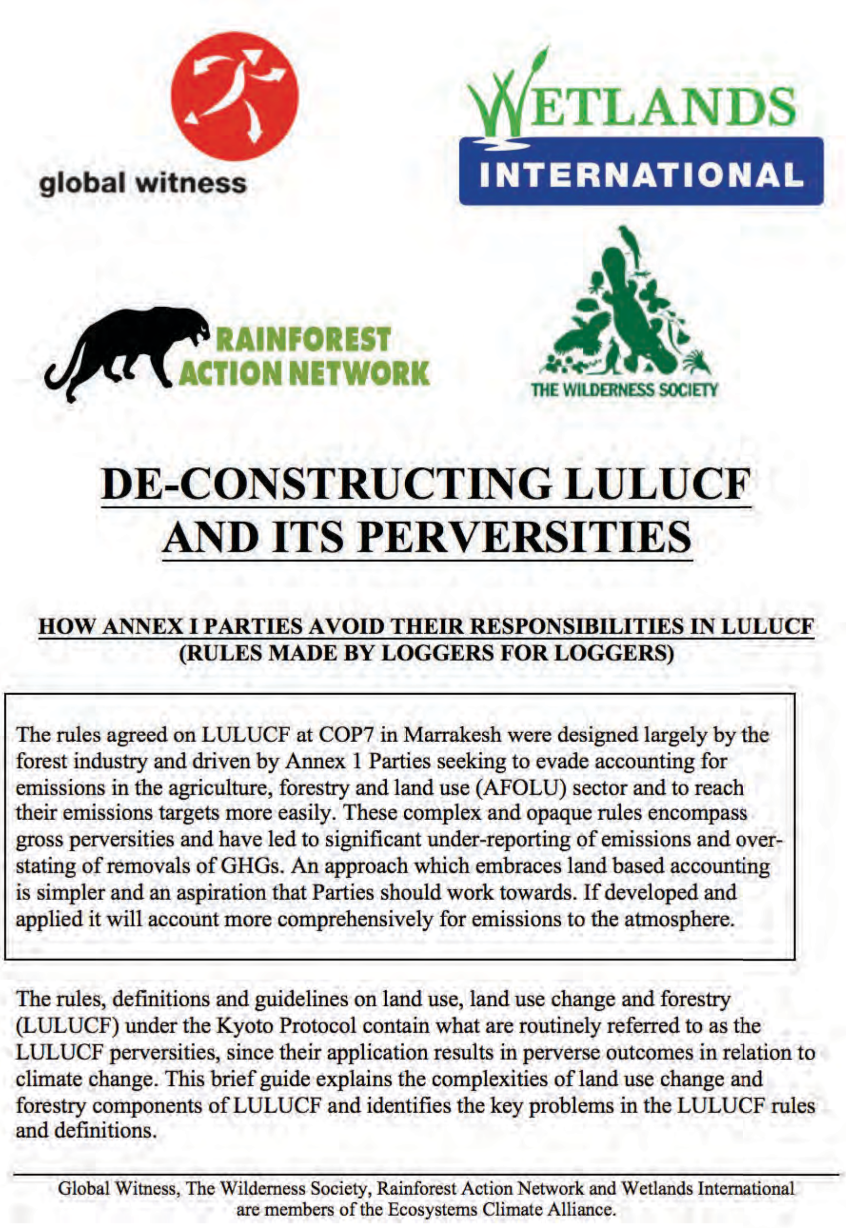
This algorithm approximates the results by sampling the selected area. Results are more accurate at closer zoom levels.

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



global witness

WETLANDS INTERNATIONAL

RAINFOREST ACTION NETWORK

THE WILDERNESS SOCIETY

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.

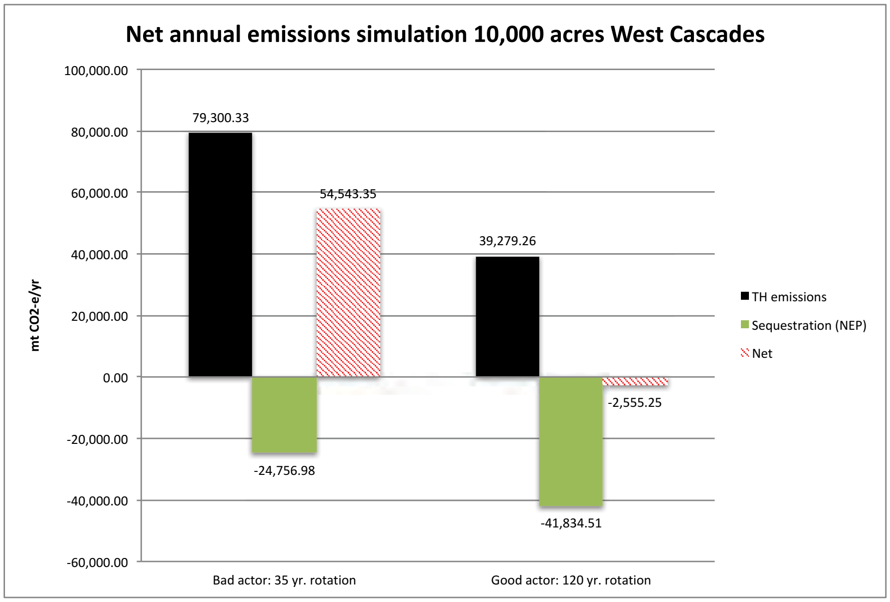
Appendix K

Good actor bad actor bar chart - West Cascades

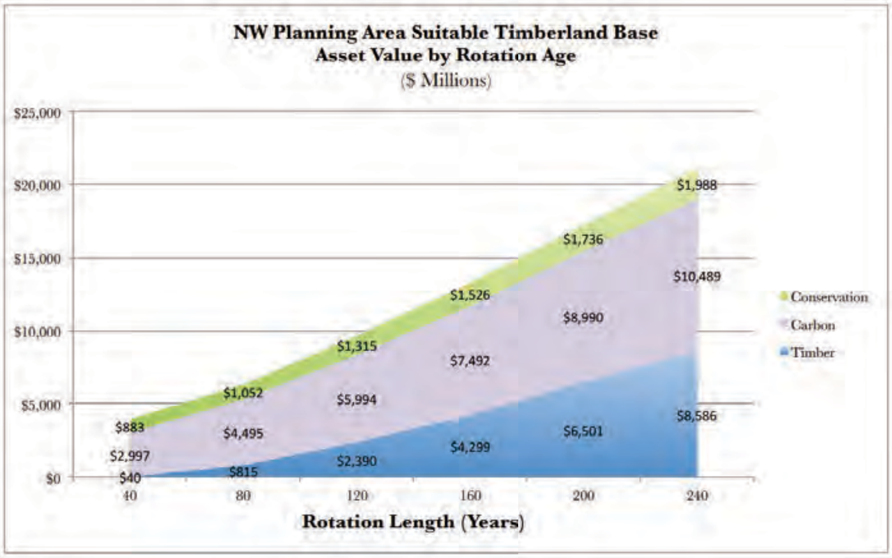
	TH emissions	Sequestration (NEP)	Net
Bad actor: 35 yr. rotation	79,300.33	-24,756.98	54,543.35
Good actor: 120 yr. rotation	39,279.26	-41,834.51	-2,555.25

	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

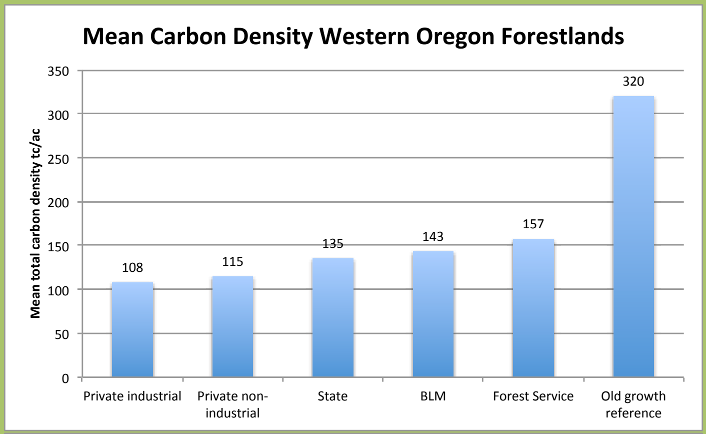


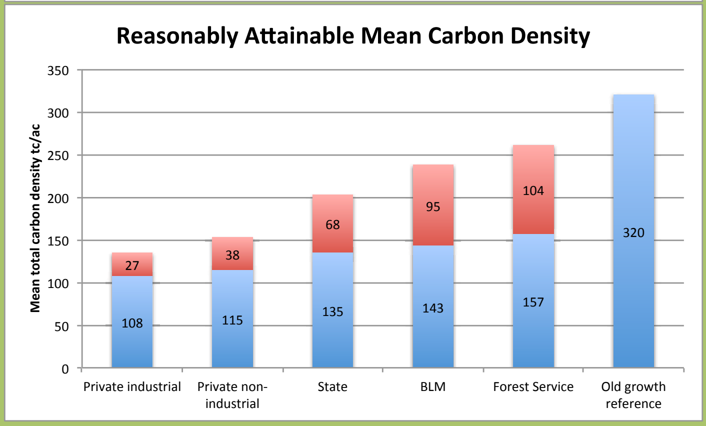
Key assumptions:

- 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

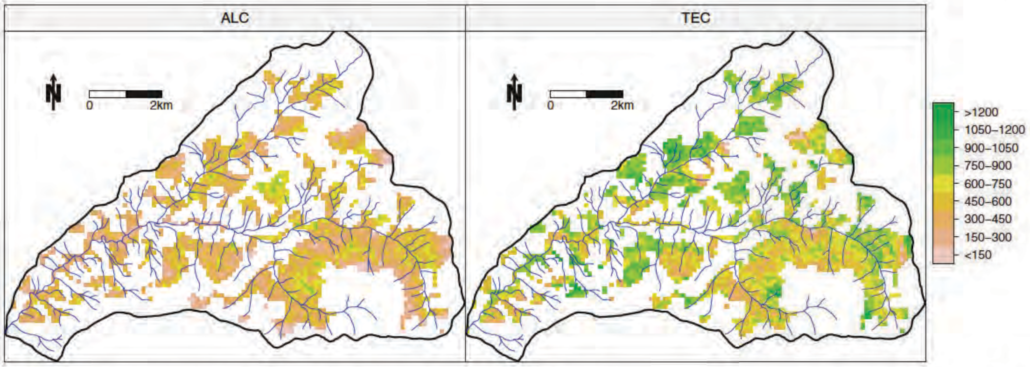


Figure 3. Aboveground live carbon (ALC, derived from Lidar) and total ecosystem carbon (TEC, simulated with iLand) in old-growth forests at the HJ Andrews Experimental Forest (Mg C ha^{-1}). (Color figure online)

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

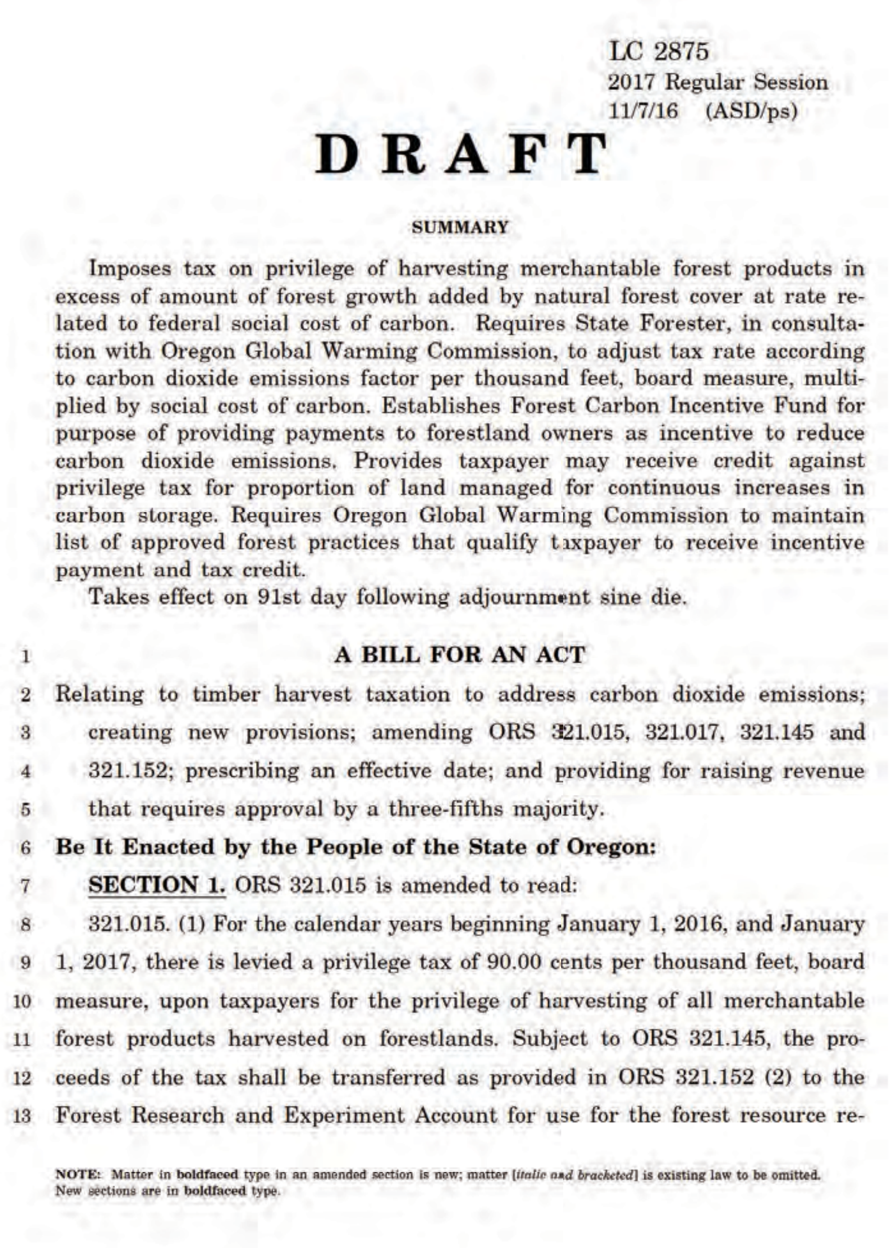
Lidar-based ALC densities were only weakly correlated with individual environmental drivers, with radiation and effective soil rooting depth being the most prominent factors (Figure 4). A stronger relationship was found with individual indicators of stand structure, with Lidar-based ALC moderately correlated 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	🟥

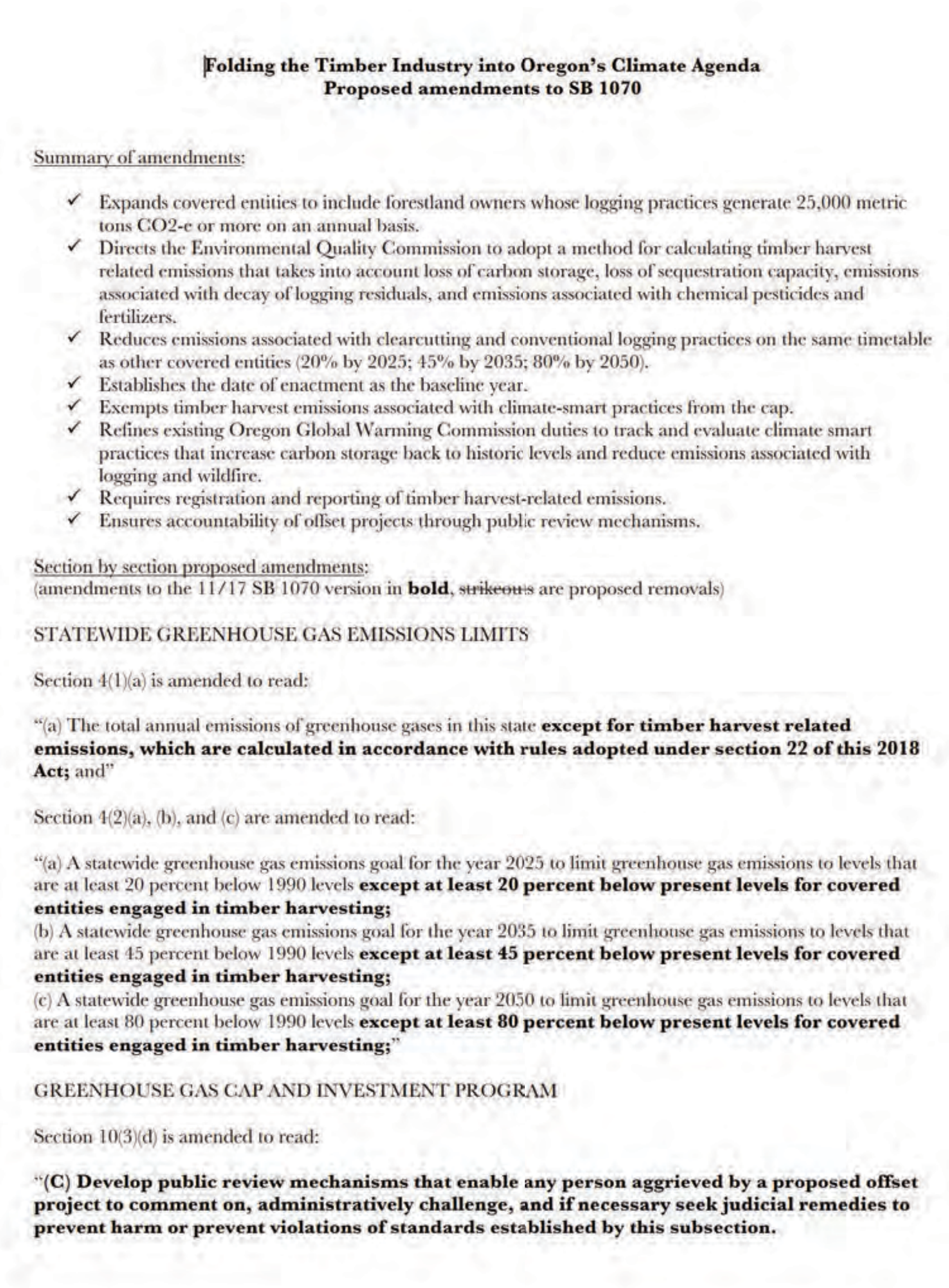
Region:	Western
Ownsership:	Pvt Industry

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.

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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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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

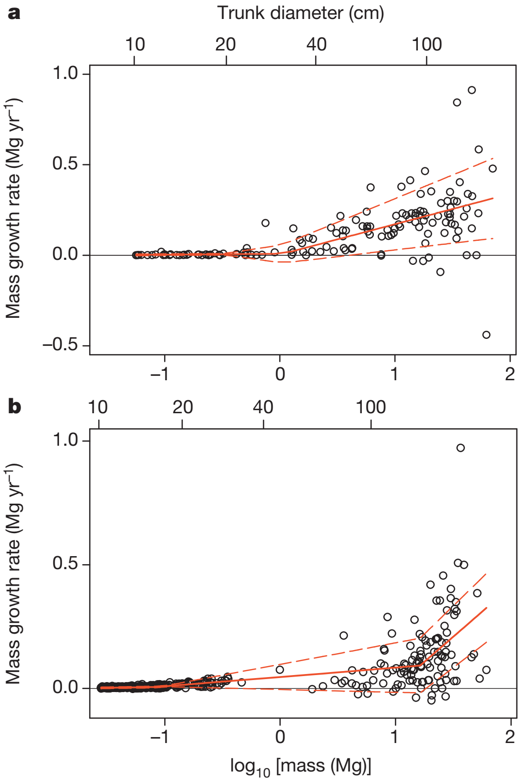

Figure 1 | Example model fits for tree mass growth rates. The species shown are the angiosperm species (*Lecomtedoxa klaineana*, Cameroon, 142 trees) (**a**) and gymnosperm species (*Picea sitchensis*, USA, 409 trees) (**b**) in our data set that had the most massive trees (defined as those with the 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.

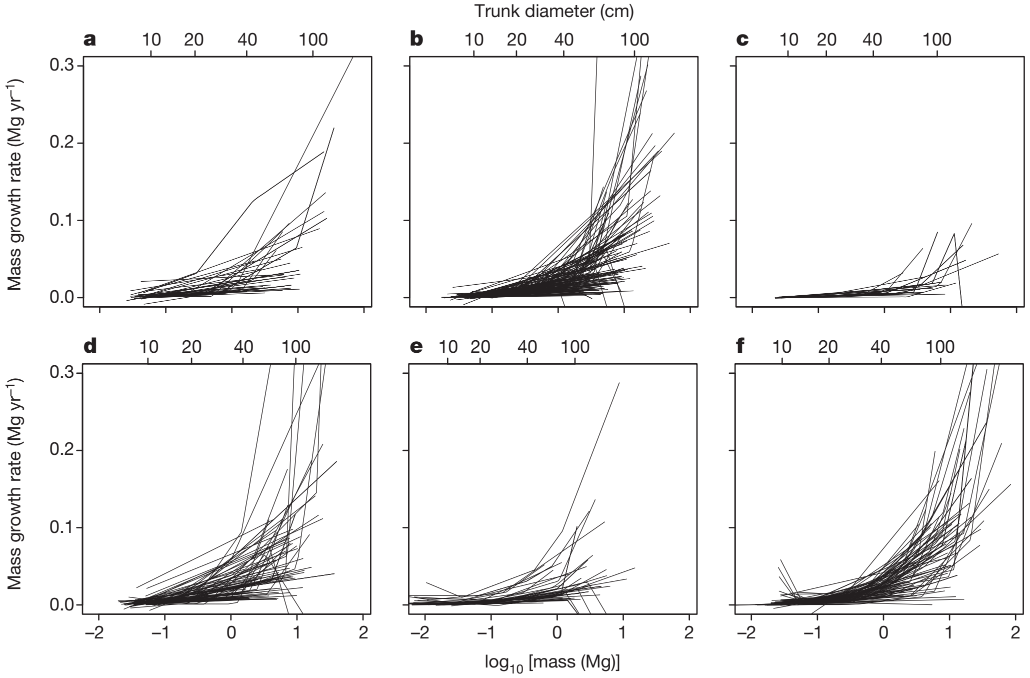

Figure 2 | Aboveground mass growth rates for the 403 tree species, by continent. **a**, Africa (Cameroon, Democratic Republic of the Congo); **b**, Asia (China, Malaysia, Taiwan, Thailand); **c**, Australasia (New Zealand); **d**, Central and South America (Argentina, Colombia, Panama); **e**, Europe (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].

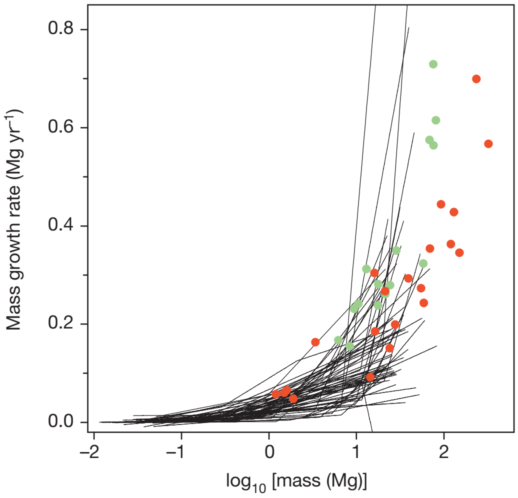

Figure 3 | Aboveground mass growth rates of species in our data set compared with *E. regnans* and *S. sempervirens*. For clarity, only the 58 species in our data set having at least one tree exceeding 20 Mg are shown (lines). Data for *E. regnans* (green dots, 15 trees) and *S. sempervirens* (red dots, 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 $\geq$10 cm, and to species having $\geq$40 trees in total and $\geq$15 trees with trunk diameter $\geq$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.

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Supplementary Information is available in the online version of the paper.

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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., A.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 underrepresented 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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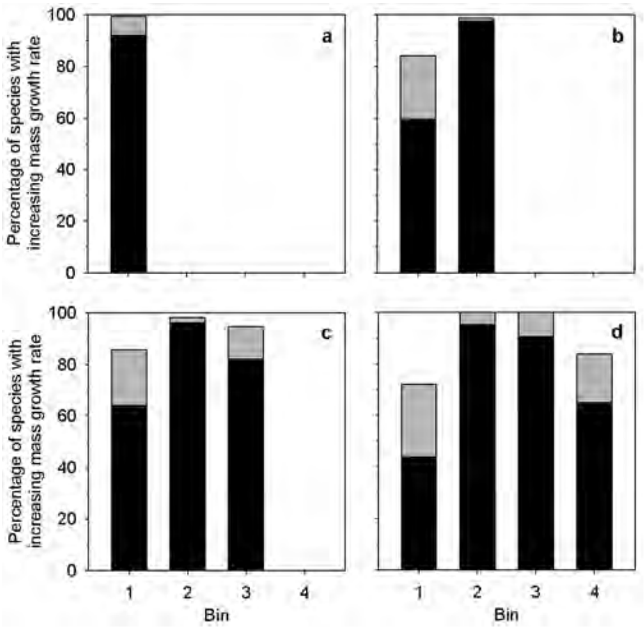
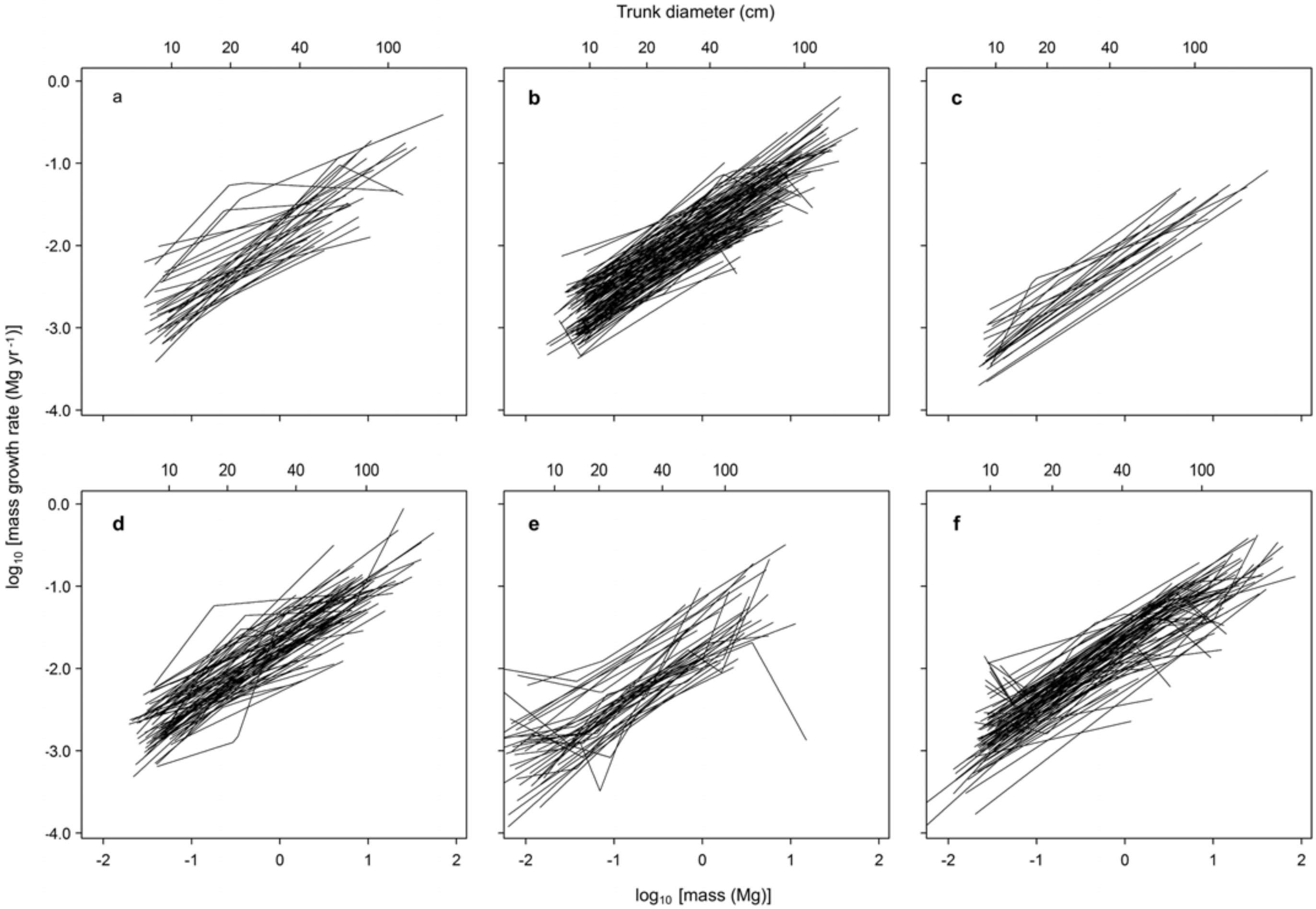
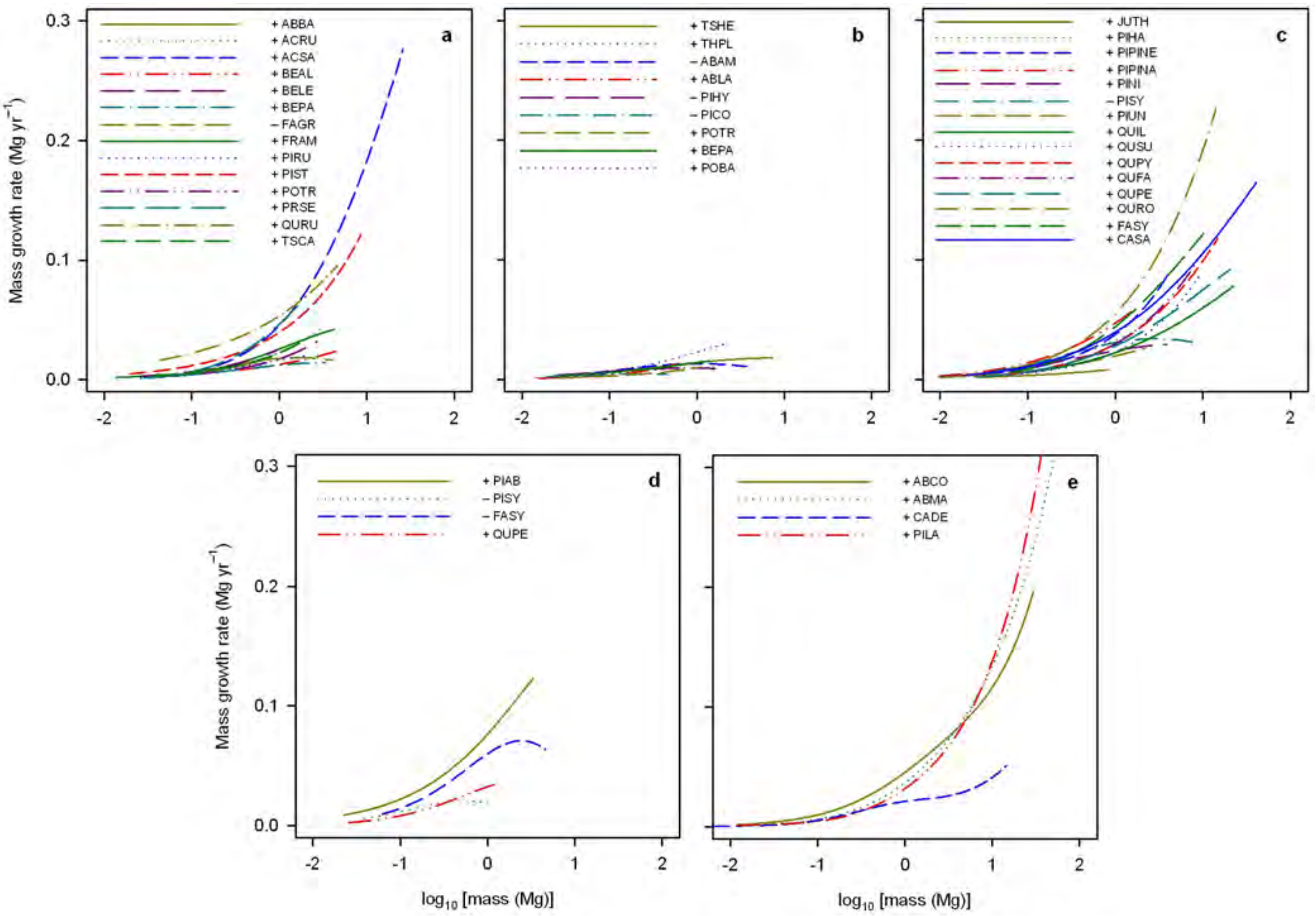


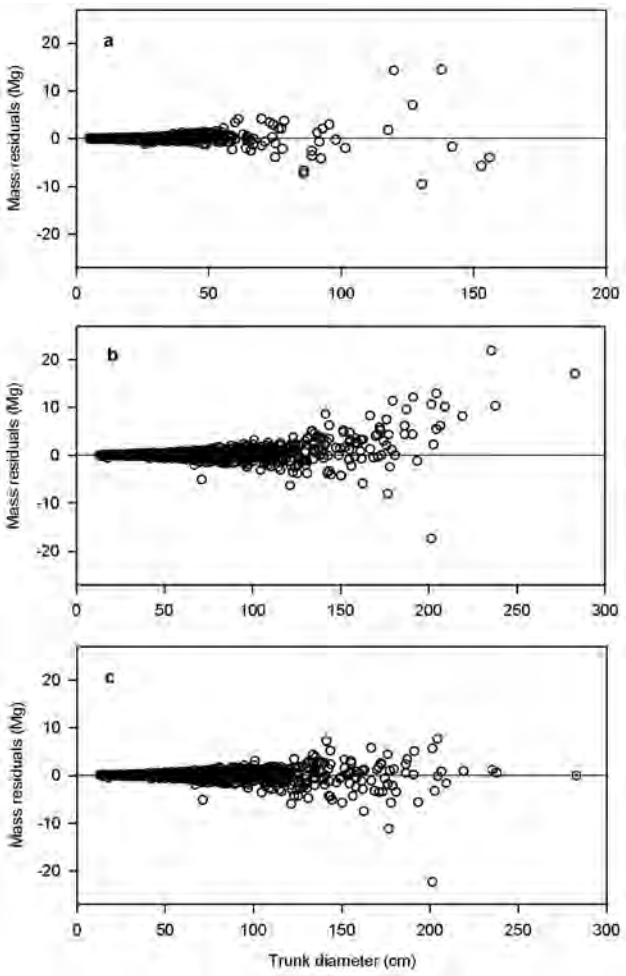
Extended Data Figure 1 | Summary of model fits for tree mass growth rates. Bars show the percentage of species with mass growth rates that increase with tree mass for each bin; black shading indicates percentage significant at $P \leq 0.05$. Tree masses increase with bin number. **a**, Species fitted 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).



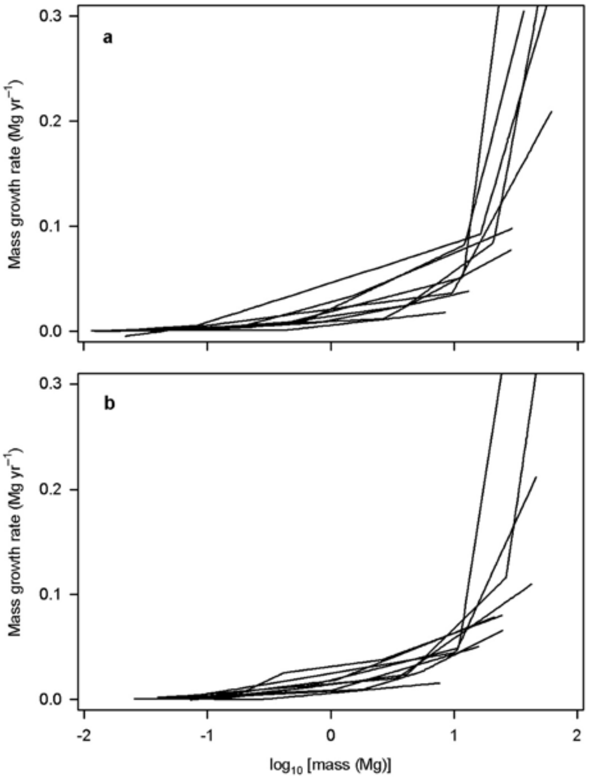
Extended Data Figure 2 | Log–log model fits of mass growth rates for 381 tree species, by continent. Trees with growth rates ≤ 0 were dropped from the analysis, reducing the number of species meeting our threshold sample size for analysis. **a**, Africa (33 species); **b**, Asia (123 species); **c**, 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.

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Ruffed Grouse Habitat Use, Reproductive Ecology, and Survival in Western North Carolina

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University of Tennessee - Knoxville

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To the Graduate Council:

I am submitting herewith a dissertation written by Benjamin Colter Jones entitled "Ruffed Grouse Habitat Use, Reproductive Ecology, and Survival in Western North Carolina." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

Craig A. Harper, Major Professor

We have read this dissertation and recommend its acceptance:

David A. Buehler, Frank T. van Manen, Arnold M. Saxton

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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David A. Buehler

Frank T. van Manen

Arnold M. Saxton

Accepted for the Council:

Anne Mayhew
Vice Chancellor and Dean of
Graduate Studies

(Original signatures are on file with official student records.)

RUFFED GROUSE HABITAT USE, REPRODUCTIVE ECOLOGY, AND SURVIVAL IN WESTERN NORTH CAROLINA

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee

Benjamin Colter Jones
December 2005

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Wildlifers tend to be an obsessive lot in our careers and associated hobbies. My wife Michelle Lynne has inspired me to be the best possible husband and father above all else. Thanks are not enough.

ABSTRACT

Ruffed grouse populations are lower in the Appalachians compared to the Great Lakes states, the geographic core of grouse distribution. Theories to explain lower numbers in the Appalachians include inadequate foods, lower reproduction, lower survival, and loss of habitat. To provide insight into ruffed grouse ecology in the Appalachians, habitat use, reproduction, and survival were studied on Nantahala National Forest in western North Carolina. Radiotagged grouse (*n* = 276) were monitored through the year. Seasonal 75% kernel home ranges (*n* = 172) averaged 15–59 ha across sexes, ages, and seasons. Home range size was related to habitat with smaller ranges occurring where 6–20-year-old mixed oak (SUBXER2) and forest roads (ROAD) were interspersed with other habitats. Across seasons, sexes and ages, SUBXER2 and ROAD were among preferred habitats. Compared to males, females used greater diversity of habitats, including >40-year-old stands. Use of older stands may have been influenced by food availability (i.e., hard mast). Nests (*n* = 44) were located to determine fate. The majority of nests (86%) were on mid and upper slopes in mature stands >40-years old. Proportion of successful nests was 81%. Mayfield nest survival was 0.83 (± 0.084 SE) and did not differ between juveniles and adults. Nesting rate was 73% and did not differ between juveniles and adults. One female renested, though high nest success precluded opportunities for documenting extent of renesting. Mean first nest clutch was 10.1 eggs. Broods (*n* = 35) were monitored intensively following hatch. Brood sites had greater herbaceous ground cover, vertical cover, midstory stem density, and invertebrate density compared to random sites. Mean home range size was 24.3 ha (±4.0 SE) using 75% kernel methods and 40.0 ha (± 4.0 SE) using MCP. Preferred habitats were mixed oak

0–5, 6–20, and >80-years old, forest roads, and edges of maintained clearings. Mean annual survival of grouse >3 months old was 0.39 (± 0.052 SE). Of mortalities, 43% were from mammalian predators, 27% avian, 13% unknown predation, 11% hunter harvest and 7% other causes. Scavenging prior to transmitter recovery may have inflated mammalian predation rates. Relatively low hunter harvest did not appear to be additive to natural mortality. Spring population density, estimated from drumming counts, decreased from 11.4 grouse/100ha in 2000 to 5.88 grouse/100 ha in 2004. Fall population density indexed by catch per unit effort also decreased during the study from 0.96 grouse/100 trap-days in 1999 to 0.19 grouse/100 trap-days in 2003. The fall population index was inversely related to annual survival ($r^2 = 0.76$, $P = 0.054$). The inverse relationship may have been a function of habitat availability. Annual recruitment indexed by proportion of juveniles in fall captures was less than reports from the northern core of ruffed grouse range. Overall percentage of juveniles in fall captures was 59.6%, ranging from 46.2–66.7%. Recommendations to increase grouse density include creating a diversity of forest types and age classes interspersed across the landscape. Alternative regeneration techniques such as shelterwood, irregular shelterwood, and group selection can be used to intersperse food and cover, thus improving grouse habitat.

PREFACE

Data presented here were collected over 5 years (1999–2004) on Wine Spring Creek Ecosystem Management Area (WSC) in Macon County, North Carolina. In addition to addressing local topics of interest, data collected from April 1999 to September 2002 were contributed to a regional research effort, the Appalachian Cooperative Grouse Research Project (ACGRP). Of 12 ACGRP study sites in 8 states (Kentucky, Maryland, North Carolina, Ohio, Pennsylvania, Rhode Island, Virginia, and West Virginia), WSC was at the most southerly extent of ruffed grouse range.

University of Tennessee graduate students, Carrie Schumacher and Jennifer Fettinger, presented partial reports from data collected 1999–2001 in their Master's theses. I led field data collection from August 2001 through study completion and analyzed the complete data set for presentation herein. The primary focus of this research was to investigate ruffed grouse habitat use, particularly as it related to forest management practices. Radiotagging ruffed grouse also presented opportunities to investigate other aspects of population ecology, including reproduction and survival. While investigating these parameters, efforts were made to relate results to habitat quality and identify potential for improvements. Chapters of this dissertation were submitted individually to peer-reviewed journals, and each represents an aspect of ruffed grouse ecology.

TABLE OF CONTENTS

Part Page

I. USE OF SPRING DRUMMING COUNTS TO INDEX RUFFED GROUSE POPULATIONS IN THE SOUTHERN APPALACHIANS

Methods

Discussion

LIST OF TABLES

LIST OF FIGURES

PART I.

USE OF SPRING DRUMMING COUNTS TO INDEX RUFFED GROUSE POPULATIONS IN THE SOUTHERN APPALACHIANS

ABSTRACT

Drumming surveys are used as an index to monitor ruffed grouse (*Bonasa umbellus*) populations across the species' range; however, most reports of drumming behavior are from the Great Lakes Region. Ruffed grouse drumming behavior was studied in the southern Appalachian Mountains of North Carolina. Drumming counts were conducted from late March through mid-April, 2002 – 2004. Concurrent with drumming counts, radio-tagged males (*n* = 30) were monitored to determine proportion of males drumming. Drumming activity increased from late March (20% of males drumming) to a peak in mid-April (56 – 69% of males drumming). Consistent drumming coincided with mean nest initiation date by females (12 April, *n* = 44). Drumming count results suggested a decreasing population trend similar to fall trapping success on the study area. Drumming counts appear to be an effective tool to monitor grouse population trends in the southern Appalachians. In North Carolina, drumming counts should be conducted during the peak drumming period of 9–16 April.

Key words: Appalachians, *Bonasa umbellus*, drumming, North Carolina, population index, ruffed grouse.

INTRODUCTION

In the southeastern United States, ruffed grouse are distributed across 190,000 km^2 of forest in the Appalachian Mountains of Alabama, Georgia, Kentucky, Maryland, North Carolina, South Carolina, Tennessee, Virginia and West Virginia (Cole and Dimmick 1991). Ruffed grouse are associated with a mosaic of early-, mid-, and late-successional habitats. During the past decade, forest maturation and reduced forest management have resulted in contiguous areas lacking early successional components, causing population declines (Dessecker 2001).

Because of their close association with early seral stages, ruffed grouse (hereafter, grouse) are a Management Indicator Species (MIS) on many National Forests. The National Forest Land and Resource Management Plan requires that MIS be monitored to index population responses to habitat management (U.S. Department of Agriculture Forest Service 1982). State wildlife agencies often work in cooperation with the Forest Service on such monitoring efforts. Further, as grouse have gained popularity among hunters following a regional decline in northern bobwhite (*Colinus virginianus*), state agencies are interested in monitoring grouse population trends to assist in setting hunting seasons and bag limits (Cole and Dimmick 1991).

Drumming behavior of male grouse provides a basis for estimating their numbers. From telephone surveys with state agency personnel in the southern portion of grouse range, it was determined spring drumming counts were used to varying extents in Georgia, Kentucky, North Carolina, Ohio, Virginia, and West Virginia and a proposal for their use has been drafted in Tennessee. Drumming count methodology has been well described (Petraborg et al. 1953, Dorney et al. 1958, Gullion 1966). In short, number of grouse heard drumming along survey routes is recorded and reported as density per unit area sampled. Frequently, results are extrapolated to a population estimate with assumptions made regarding sex ratio, sampling area, and proportion of males drumming over time. Although these assumptions have been studied in the Great Lakes states (Gullion 1981, Rodgers 1981), no studies have explored chronology of spring drumming and efficacy of drumming counts to index grouse populations in the Southeast.

Objectives were to: (1) estimate drumming intensity from late March through April, (2) determine period of peak drumming activity, and (3) examine efficacy of drumming counts as a population index in the southern Appalachians.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (WSC) within the Nantahala National Forest in Macon County, North Carolina. The area is within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1644 m. Terrain was typical of the southern Blue Ridge with broad ridges, steep valleys and long connecting slopes (McNab and Browning 1993). Mean annual temperature was 10.4º C, and mean annual precipitation was 192 cm. Mixed deciduous hardwood, primarily oak (*Quercus* spp.) with some northern hardwoods on north and east aspects above 1219m elevation dominated (>99%) the area. Rhododendron (*Rhododendron maximum*) was a primary midstory component along stream drainages while mountain laurel (*Kalmia* spp.) and huckleberry (*Gaylussacia* spp.) were present on drier upland sites. The U.S. Forest Service purchased the Wine Spring area in 1912. Since then, timber has been harvested on an 80–100-year rotation, making it representative of most Forest Service lands within the southern Appalachians. Approximately 9% of the area was in the 6–20-year age class.

Grouse Capture and Population Monitoring

Grouse were captured using intercept traps (Liscinsky and Bailey 1955) during August –November and March–April, 1999–2003, fitted with 12-g necklace-style radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota) and released at capture sites. Two hundred seventy six grouse were radiotagged.

Spring drumming counts were conducted 24 March to 30 April 2001–2004. Observers walked designated routes (i.e., gated forest roads) on two consecutive mornings beginning 30 minutes before sunrise and ending three hours after sunrise. The starting point on the second morning was the endpoint from the first morning. Routes were selected across the area such that approximately 20% of the study area was sampled. Drumming counts were cancelled when winds were >13 km/h because of reduced ability of observers to hear drumming. Observers listened for drumming while walking continuously at a steady pace. When a drumming male was heard, distance to drummer, time, and an azimuth to the bird were recorded. Approximate location for each drumming grouse was plotted on a geographic information system (GIS). Drumming male locations were buffered by 150 m because grouse may use alternate drumming sites (Lovallo et al. 2000). If two locations from consecutive days fell within the same 150 m buffer, they were considered the same bird.

Population estimates (grouse/100 ha) were calculated by doubling number of drumming males heard to account for females under the assumption of a 1:1 breeding season sex ratio (Bump et al. 1947, Gullion and Marshall 1968, Rusch and Keith 1971). For these density estimates, it was necessary to determine effective sampling area. This was achieved by estimating radius of audibility, the maximum distance at which drumming grouse could be heard (Petraborg et al. 1953). Audibility trials ($n = 10$) were conducted opportunistically during routine fieldwork. When a drumming grouse was located, one observer remained close to the drumming site and raised a flag when drumming occurred. A second observer moved away from the drumming site in 25 m increments until drumming could no longer be heard. When visibility was limited between observers, hand-held radios were used to retain contact. Radius of audibility may vary with changes in topography and hearing ability of observers; however, time did not permit replication necessary to identify these sources of variation. The estimate should be viewed as a general, conservative estimate of audibility. Consistent with Petraborg et al. (1953), 200 m was determined as the maximum audibility distance; therefore, 400 m buffers around each route (i.e., 200 m on each side) defined sampling area.

In 2001, one drumming count was conducted during the week of 9–16 April (period 3). During 2002–2004, counts were conducted during each of the weekly periods, 24–31 March (period 1), 1–8 April (period 2), and 9–16 April (period 3). In 2004, additional counts were conducted 17–24 April (period 4), and 25 April–2 May (period 5). Population estimates were calculated for each period to identify temporal changes in drumming. This allowed comparison of estimates among periods within the same year. Because grouse populations should not fluctuate greatly (especially increase) over 4 weeks in April, it was assumed variation within the same spring was a result of changes in drumming behavior.

Drumming intensity is the percentage of radiotagged males heard drumming during a specific morning (Gullion 1966). To determine drumming intensity, radiotagged males were located and approached them within 50 m using care not to disturb the bird. After an initial quiet-down period of one minute, occurrence or non-occurrence of drumming was recorded during a 5-minute interval. A distance of 50 m was used a because it was well within the audible range of drumming, but not so close as to disturb the bird.

Observations were concurrent with drumming count periods in 2002 and 2003, allowing examination of within year changes in drumming intensity.

Porath and Vohs (1972) suggested peak of drumming in northeastern Iowa corresponded with copulation. To explore this relationship, telemetry data were used to estimate mean nest (*n* = 44) initiation date (Chapter II). Copulation occurs 3–7 days prior to laying the first egg (Bump et al. 1947); therefore, mean copulation date was estimated by subtracting this range from mean nest initiation date. Estimated copulation range was then compared graphically to drumming chronology.

Across year population trends were compared from Period 3 drumming counts to several data sources, including grouse hunter surveys, ancillary observations, and trapping success the following fall. The North Carolina Wildlife Resources Commission collects grouse hunter surveys annually. To identify population trends from those data, number of grouse flushed per hunter hour on public lands was calculated within the southern mountain region of North Carolina during the 2001–2004 hunting seasons. The 16-county southern mountain region included the WSC study area. Ancillary observations were recorded by research technicians on WSC. During routine radiotracking, technicians recorded kilometers driven and grouse observed along roads. Grouse seen per 100 km during the period, 15 March–30 April were compared to drumming counts. Fall trapping success on WSC, measured by grouse captured/100 trap-days, also was compared to drumming count data. Pearson correlation coefficients were calculated between drumming count population estimates and other indices using SAS (SAS Institute, Cary, North Carolina, USA).

RESULTS

Within each year, more drumming males were heard during period 3 than in periods 1 and 2. In 2004, number of drumming males heard decreased through periods 4 and 5, suggesting peak drumming activity in period3 (Figure 1.1; tables and figures are located in the Appendix). Population estimates from period 3 were 243%, 38%, and 242% greater than those from period 1 in 2002, 2003, and 2004, respectively.

Similar to drumming counts, drumming intensity generally increased from period 1 through period 3. In 2002, proportion of radiotagged males drumming was 20% (n = 15) in period1, 67% (n = 13) in period 2, and 69% (n = 9) in period 3. In 2003, proportion of radiotagged males drumming was 20% (n = 10), 18% (n = 11), and 56% (n = 9) in periods 1, 2, and 3, respectively. When further delineated by age, the above sample sizes were too small to detect meaningful differences in drumming intensity between juveniles and adults.

Estimated copulation was 5–9 April, just prior to annual peaks in drumming. Greatest drumming activity coincided more closely with nest initiation ($\bar{x}$ = 12 April, 10–14 April 95% CI) than mean copulation date across years.

Fall trapping success and drumming counts suggested decreasing population trends from 2001–2003 (Table 1.1). Pearson’s correlation coefficient between these methods was not significant (P = 0.332). Lack of significance was likely a function of small sample size (n = 3 years). Hunter flush rates were consistent across years, and did not indicate population change. Ancillary observations suggested overall decline from

2001–2004, with an apparent population increase in 2003. Drumming counts were not correlated with hunter flush rates (*R* = 0.351, *P* = 0.649) or ancillary observations (*R* = 0.225, *P* = 0.775).

DISCUSSION

Of the four methods examined, all but hunter flush rates indicated population decline. There may be several reasons hunter surveys did not indicate population change. First, surveys were conducted across 16 counties, and decreasing population trends may not have been as pronounced regionally as they were on WSC; however, conversations with hunters and U.S. Forest Service personnel suggested grouse numbers were decreasing across North Carolina’s southern mountain region. Second, hunter surveys may be insensitive to population changes as hunters continually return to areas where they experience success, rather than “sampling” new or unproductive coverts. Perceived population changes from hunter surveys may reflect shifting hunter patterns as old coverts mature and new ones are discovered.

Ancillary observations suggested a decline in grouse numbers between 2001 and 2004 despite a population spike in 2003 that was not apparent in drumming counts or trapping success (Table1.1). Ancillary observations can be sensitive to changes in observer travel patterns. While radiotracking a female grouse in 2003, frequent trips were made through an area where grouse often were observed along a forest road. These daily travels may have positively biased 2003 ancillary data. Data collected by wildlife agency and U.S. Forest Service personnel during fieldwork may be similarly biased as their travel routes probably would not be consistent over time. Amman and Ryel (1963) reported grouse observations made by U.S. Postal Service employees were an effective population index because mail carriers traveled the same distances and routes; however, in western North Carolina, mail carriers seldom travel through higher elevations that constitute grouse range in the region.

Drumming counts have been used extensively to monitor population trends and responses to habitat management in the Appalachians and across ruffed grouse range (Kubisiak 1985, Wiggers et al. 1992, McCaffery et al. 1996, Dimmick et al. 1998, Storm et al. 2003). Drumming counts conducted in mid-April can provide an effective means to monitor population trends in North Carolina. Due to non-drumming males, drumming surveys tend to underestimate number of birds on an area (Gullion 1966). Fortunately for managers attempting to inventory grouse populations, error remains rather constant across years until maximum population densities are reached (Gullion 1981). The greatest proportion of males drumming on any morning on WSC was 69%. Without a method to estimate proportion of males drumming concurrent with counts (i.e., radiotelemetry), it is not possible for managers to extrapolate accurate spring population estimates; therefore, drumming counts are best used as an index to population trends over time.

There are two main drumming count techniques; the walking method described for this study and others (Rodgers 1981, Dimmick et al. 1998), and roadside counts developed by Petraborg et al. (1953). Roadside counts involve driving a route and stopping at predefined listening points for 4–5 minutes before proceeding to the next point. Roadside counts are an effective method to determine population trends and allow coverage of a large area with relatively few observers (Petraborg et al. 1953, Stoll 1980). Walked routes are better suited to sampling smaller, specific areas of interest, such as wildlife management areas or research study sites. The utility of either technique to determine population trends depends on consistency of methods and timing of counts. Peaks of drumming activity occur at approximately the same time each spring (Gullion 1966); therefore, identifying peak periods and planning counts accordingly lends to consistency across years.

Earliest onset of spring drumming was recorded 9 March 2002. Ruffed grouse drumming activity on WSC peaked during the week of 9–16 April. Beyond the mid-April peak, drumming had nearly ceased by the first week in May. Studies in Minnesota and Wisconsin identified plateaus in drumming within 7 days of 1 May (Dorney et al. 1958, Gullion 1966). In Ohio and Iowa, drumming peaked between 15 and 25 April (Donohoe 1965, Porath and Vohs 1972). Hale et al. (1982) reported drumming activity began in mid-March in northern Georgia, but did not indicate when peak drumming occurred. Those data support the contention of Bump et al. (1947) that onset and peak of drumming behavior occur earlier in southerly latitudes.

Because drumming counts were conducted once each week, within-period error could not be assessed; however, field observations provided insight into variability over time. During all years, drumming remained sporadic through the end of March and during that period, occurred only on clear days with no precipitation and little wind. By mid-April (period 3), drumming became more consistent and males drummed despite overcast skies, precipitation and other inclement weather, including snow. Managers may not have flexibility to schedule drumming counts according to weather; therefore, planning surveys during peak drumming appears most advantageous. Nonetheless, high winds hinder the ability of observers to hear drumming, and surveys should be suspended if winds exceed 13 km/h (Petraborg et al. 1953).

On WSC, peak drumming coincided with nest initiation by females. Drumming behavior serves a dual purpose, to advertise territories and attract females (McBurney 1989). As females became preoccupied with nesting, males may have spent greater time on drumming logs attempting to attract mates. Incubation chronology compiled by Devers (2005) for the Appalachian Cooperative Grouse Research Project was backdated to estimate regional nest initiation dates (Table 1.2). Regional nest initiation dates should provide insight to managers regarding peak drumming for their area of interest.

Prompted by population declines in the southern extent of ruffed grouse range, managers are developing strategic plans for grouse in the Appalachians. Monitoring population trends and response to habitat manipulation over time is an integral part of any strategy. With appropriate planning and consistency, spring drumming counts provide an effective population index. Roadside counts and walked routes are equally viable techniques and choice of method depends on scale of area to be sampled (i.e., regional vs. management area). To reduce within- and across-year variability, surveys should be planned to coincide with peak drumming periods.

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APPENDIX

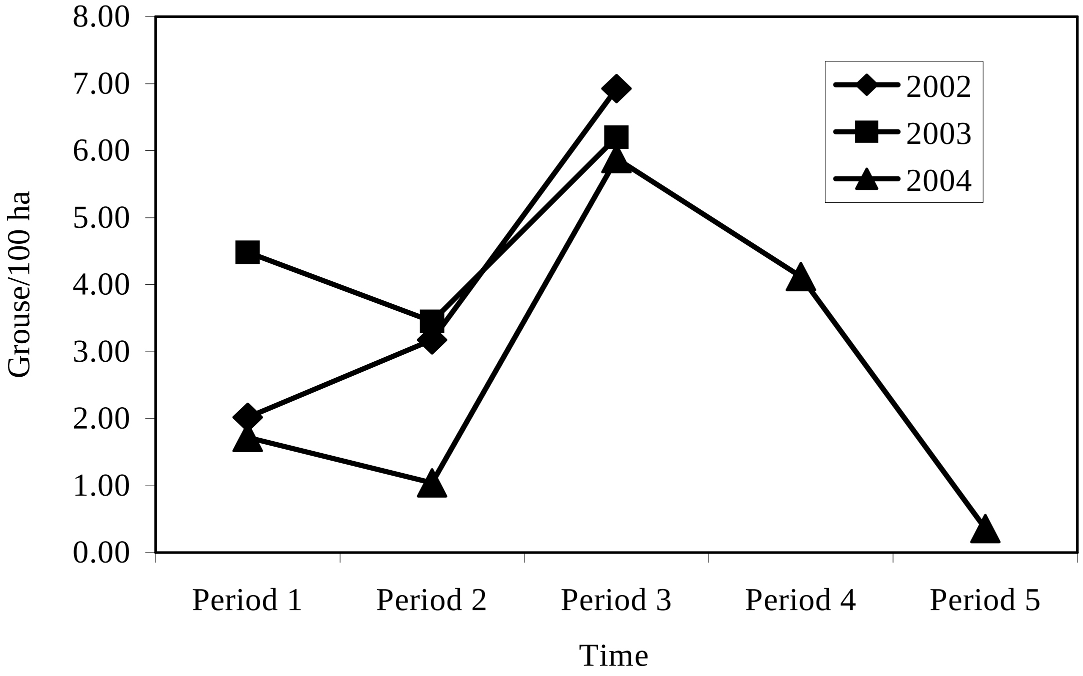

Figure 1.1. Ruffed grouse population estimates extrapolated from drumming counts conducted 24–31 March (period 1), 1–8 April (period 2), 9–16 April (period 3), 17–24 April (period 4), and 25 April–2 May (period 5), 2002–2004, on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina.

Table 1.1. Ruffed grouse population indices from drumming counts (grouse/100 ha), trapping success (grouse/100 trap-days), ancillary observations (grouse/100 km), and hunter surveys (flushes/hour), 2001–2004 on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina.

	Year			
Index	2001	2002	2003	2004
Drumming counts	11.40	6.93	6.20	5.88
Trapping success	0.68	0.48	0.19	NA
Ancillary observations	4.64	3.69	6.15	2.90
Hunter surveys	0.56	0.56	0.54	0.55

Table 1.2. Nest initiation dates and associated 95% confidence intervals for ruffed grouse on Appalachian Cooperative Grouse Research Project study sites, 1997–2002, adapted from Devers (2005).

State	County	Nest initiation	95% CI
Rhode Island	Washington	25 April	20–30 April
Pennsylvania	Clearfield	23 April	21–25 April
Ohio	Coshocton	10 April	4–15 April
Ohio	Athens	8 April	6–10 April
Maryland	Garrett	17 April	15–19 April
West Virginia	Randolph	16 April	13–19 April
West Virginia	Greenbrier	15 April	10–21 April
Kentucky	Lawrence	8 April	5–12 April
Virginia	Augusta	15 April	11–18 April
Virginia	Botetourt	14 April	11–16 April
Virginia	Smyth, Washington	17 April	15–19 April
North Carolina	Macon	12 April	10–14 April

PART II.

RUFFED GROUSE REPRODUCTIVE ECOLOGY AND NESTING HABITAT IN WESTERN NORTH CAROLINA

ABSTRACT

Poor reproduction may be responsible for lower ruffed grouse (*Bonasa umbellus*) populations in the southern Appalachians compared with northern parts of the species' range. Nutritional stress imposed by poor quality habitat and greater nest predation have been cited as negative influences on reproduction in the region. From 1999–2004, ruffed grouse reproductive ecology was studied in the Appalachian Mountains of North Carolina. Female grouse (n = 138) were radio tagged and monitored through the year. Nests (n = 44) were located to determine fate and habitat characteristics. Mayfield estimated nest survival was 0.83 (± 0.084 SE). Proportion of successful nests was 81%, among the greatest reported across ruffed grouse range; however, nesting rate (73%) was lower than many reports. Only 1 female (1/9) attempted a renest. Mean first nest clutch size of 10.1 eggs was within the range reported for the Appalachians, but less than those reported for the Great Lakes states. Females nested in various forest types, and microhabitat at nests did not differ from paired, random locations. Nesting habitat did not appear to be limiting; however, improvements in winter and early spring habitat quality could improve physical condition of females prior to nesting, potentially increasing nesting rate.

Key words: Appalachians, *Bonasa umbellus*, clutch, habitat, nest, reproduction, ruffed grouse, weather.

INTRODUCTION

In southern portions of their range, ruffed grouse (*Bonasa umbellus*) generally are generally less abundant than in northern latitudes (Bump et al. 1947). Several theories have been proposed to explain lower grouse numbers in the Appalachians, including additive mortality during extended hunting seasons (Stoll and Culbertson 1995), nutritionally inadequate foods (Servello and Kirkpatrick 1987), and loss of early successional habitat (Dessecker and McAuley 2001). Together, these factors may contribute to lower annual reproductive output in the Appalachians compared with the core of grouse range (Stewart 1956, Haulton 1999, Dobony 2000).

Understanding reproductive parameters is necessary to evaluate management scenarios for ground-nesting birds (Peterson et al. 1998). Nesting rate, clutch size, and nest success are important factors in grouse population ecology. Improving reproductive success could be a focus of management strategies (Bergerud 1988*a*). Habitat manipulation may affect reproduction by enhancing physical condition of females prior to nesting (Devers 2005), and decreasing nest predation (Tirpak and Giuliano 2004).

In addition to habitat, extrinsic factors such as weather may play a role in reproduction (Larsen and Lahey 1958, Ritcey and Edwards 1963). Although climatic conditions may seem out of the proximate control of managers, Larsen and Lahey (1958:67) stated, “The correlation between grouse density and maximum temperature pattern does not imply that the correlation is with maximum temperature alone, but rather that it is with those environmental conditions that maximum temperature patterns induce or reflect.” To provide a comprehensive management strategy for ruffed grouse in the Appalachians, managers require estimates of reproduction and insight into environmental conditions that can be altered to enhance reproductive success.

Until recently, most reproduction studies were conducted in the core of ruffed grouse range. As part of the Appalachian Cooperative Grouse Research Project (ACGRP), Devers (2005) examined population ecology on study sites across the central and southern Appalachian region; however only partial data (2 of 4 years) from this study site in western North Carolina were included. Tirpak (in press) reported nesting habitat characteristics for ACGRP sites, but omitted data from North Carolina because unique forest associations typical of the southern Blue Ridge amplified variability of the data set. Additional insight can be gained from this study, as the North Carolina site was the most southerly and is the first study to provide comprehensive estimates of reproduction at the southern extent of ruffed grouse range. Objectives were to (1) estimate reproductive parameters including nesting rate, nest success, clutch size, hatchability, hen success, and brood survival; (2) identify microhabitat characteristics of nest sites; and (3) examine associations among weather and reproductive parameters.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (WSC, 3,230 ha), within the Nantahala National Forest in western Macon County, North Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1,644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges that connect upper elevations to narrow valley floors (Whittaker 1956). Mean annual temperature was 10.4ºC, and mean annual precipitation was 160 cm. The area was predominantly forested with <1% coverage in small openings. The U.S. Forest Service purchased WSC in 1912 after it was logged. Since then, forest management practices included salvage harvest of blight-killed American chestnut (*Castanea dentata*), thinning, clearcutting, and diameter-limit cutting (McNab and Browning 1993). In 1997, 9 stands were harvested (3 shelterwood, 3 two-age, and 3 group selection) to study the effects of alternative regeneration techniques on vegetation response and wildlife habitat.

Habitats were classified by a combination of vegetative community type and stand age. Communities were stratified into 3 land classes (xeric, subxeric, and mesic) defined by elevation, landform, soil moisture, and soil thickness (McNab and Browning 1993; Table 2.1; tables are located in the Appendix). Additional land classes included gated forest roads (ROAD) and wildlife openings (WLO). Gated forest roads were defined by a buffer width of 5 m from road center on each side. The 10-m width included the road and adjacent berm maintained by mowing. Wildlife openings were small, open areas (0.50 ± 0.12 ha SE, $n = 24$) and also were maintained by mowing. Stand ages were determined by years since harvest or stand establishment in categories deemed important to ruffed grouse (0–5, 6–20, 21–39, 40–80, >80). Gated forest roads, wildlife openings and rhododendron (*Rhododendron maximum*)-dominated understory were not assigned age categories because they are in a state of arrested succession and their structural characteristics do not change appreciably over time (Phillips and Murdy 1985).

Habitat types were delineated in a geographic information system (GIS) developed for the study site. Oak and mixed oak-hickory stands in the >80-year age class (SUBXER5) made up the greatest proportion of the study site (31.5%) and wildlife openings (WLO) made up the least (0.2%; Table 2.2). Early successional habitats in the 6–20-year age class (XERIC2 and SUBXER2) occupied 9.3% of the area. The 0–5, 6–20, and 21–39-year age classes were not represented on mesic sites. There were 52.6 km of gated forest roads (1.1% of total area).

Capture and Telemetry

Grouse were captured using interception traps (Gullion 1965) during two annual periods, late August–early November, and early March–early April, 1999–2003. Gender and age (juvenile or adult) were assessed by feather characteristics and molt patterns (Kalla and Dimmick 1995). Grouse tagged as juveniles in fall graduated to be adults at the end of the following summer. Grouse were weighed, leg-banded, fitted with 12-g necklace-style radiotransmitters with a 3-hour mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA), and released at capture sites. Tagged birds (n = 276) were located $\geq$3 times per week from permanent telemetry stations. To adequately represent diurnal time periods, an equal number of locations were recorded during the periods, morning (0700–1100), mid-day (1101–1500), and evening (1501–1900). Stations were geo-referenced using a Trimble Global Positioning System (Trimble Navigation Limited Inc., Sunnyvale, CA). Transmitter signals were received using Telonics TR-2 receivers (Telonics Inc., Mesa, AZ), Clark model H7050 headphones (David Clark Company Inc., Worcester, MA), and hand-held 3-element yagi antennas.

Beginning in April, females were located daily to monitor nesting activity. When 2 consecutive locations occurred within a 0.25-ha area for an individual, she was assumed to be nesting. During the second week of continuous incubation, the nest was examined briefly to determine clutch size. Thereafter, nests were remotely monitored to minimize disturbance at the nest site. If a female was located away from the nest for >24 hours, the nest site was examined within 1 day to determine fate and clutch size. For successful nests, number of eggs hatched was determined by eggshell fragments. For unsuccessful nests, cause of nest failure was categorized as predation or abandonment. Unsuccessful females were monitored daily after failure to determine renesting effort.

Nest Microhabitat

Microhabitat data were collected in nested, circular plots centered on the nest site within 2 days of hatch or nest destruction. For comparison, a corresponding site was sampled 100 m in a random direction from each nest. Basal area was estimated from plot center with a 2.5 m^2/ha prism. Overstory composition of trees $\geq$11.4 cm diameter at breast height (DBH) was recorded within a 0.04-ha plot. Species and number of midstory saplings and shrubs <11.4 cm DBH and $\geq$1.4 m height was recorded for 4 DBH classes (<2.54 cm, 2.54–5.08 cm, 5.09–7.62 cm, and 7.63–11.4 cm) within a 0.01-ha plot. Woody seedlings <1.4 m in height were recorded within a 0.004-ha plot.

Nest Macrohabitat

Locations of nest and random sites were determined with a Trimble Global Positioning System (Trimble Navigation Limited Inc., Sunnyvale, California, USA) and incorporated in the GIS. Patch Analyst 3.0 (Elkie et al. 1999) was used to calculate edge density (m/ha) within 100-m radius buffers around nests and random sites used for microhabitat sampling. Distance to nearest opening also was measured from these points. Openings included forest roads, wildlife openings, and 0–5-year-old forest. Small canopy gaps created by natural disturbance of one or a few trees were not included, as these features were not available in the GIS stand coverage. At the study area scale, additional points were generated within a nesting habitat availability polygon to compare distances from random and nest sites to preferred brood-rearing habitats. The availability polygon was defined by merging fall and winter home ranges of females because female ruffed grouse are thought to sample potential nesting habitats during these seasons (Bergerud and Gratson 1988). Home ranges (95% fixed kernel) were calculated in ArcView GIS 3.2 (Environmental Systems Research Institute Inc., Redlands, California, USA) using the Animal Movement Extension to ArcView with least squares cross validation (Hooge and Eichenlaub 1997). Ninety-five percent kernel estimates were used because they incorporate home range periphery (Seaman et al. 1999) as available nesting habitat. Brood habitats were identified through intensive telemetry from hatch to 5 weeks post-hatch. Relative preference of SUBXER1, SUBXER2, SUBXER5, and ROAD within SUBXER5 stands for brood rearing was determined through compositional analysis (Aebischer et al. 1993, Chapter III). For distance measurements, points that fell within a preferred brood habitat were assigned a value of 0.

Nesting Chronology and Reproductive Parameters

Onset of continuous incubation was calculated by subtracting 24 days from the hatch date (Bump et al. 1947). Nest initiation dates were calculated by adding the number of incubation days (24) with the number of egg laying days (number of eggs in clutch * 1.5 days) and subtracting the sum from the hatch date (Bump et al. 1947). Nesting rate was the proportion of females alive in the 3 April radio-marked population known to reach incubation of an initial nest. April 3 was used because it was the earliest nest initiation date recorded on WSC. Nest success was the proportion of females that successfully hatched $\geq$1 egg in an initial nesting attempt. Renesting rate was the proportion of females, unsuccessful in an initial nesting attempt that reached incubation of a second nest. Renest success was the proportion of renesters that successfully hatched $\geq$1 egg. Hen success was the proportion of females alive in the 3 April radio-marked population that successfully hatched ≥1 egg in an initial or renesting attempt. Annual reproductive parameters were calculated across individuals within each year. Mean parameters and standard errors were calculated across years. Small sample sizes precluded calculation of annual reproductive parameters for juveniles and adults separately, therefore age-specific reproductive parameters were calculated with years pooled. Clutch size was the mean number of eggs in initial nests, determined by flushing the female once during the second week of incubation. Hatchability was the proportion of eggs in successful nests that hatched. Nest initiation date, nesting rate, clutch size, and nest success were compared across years between juveniles and adults.

Nest survival also was estimated using methods described by Mayfield (1975). Mayfield daily nest survival was calculated by dividing number of nests lost by total number of days nests were observed and subtracting from 1. Daily nest survival raised to a power of 24 (total incubation days) provided a survival estimate over the entire incubation period. An estimate of nest survival during laying and incubation was calculated by adding laying days to incubation days. During laying, female ruffed grouse lay approximately 1 egg every 1.5 days (Bump et al. 1947); therefore, laying days were estimated by multiplying mean clutch size by 1.5. Daily nest survival during laying and incubation was raised to a power of 39 (mean laying days + incubation days).

Weather

Coweeta Long Term Ecological Research Station (Coweeta LTER, Otto, North Carolina, USA) recorded weather data at a permanent weather station on the study site. Minimum and maximum temperature and precipitation (tipping bucket) were recorded daily. Weather data collected between 12 April (mean nest initiation date) and 21 May (mean hatch date) were used to explore correlations with annual nest success. Variables of interest included mean maximum temperature (MAXTEMP), mean minimum temperature (MINTEMP), number of days with temperatures <7°C (COLDAYS), total rainfall (RAIN), and number of days with rainfall events (RAINDAYS).

Data Analysis

Mean reproductive parameters were calculated by averaging across individuals within each year, then averaging across years. An information-theoretic approach (Burnham and Anderson 1998) was used to evaluate differences in habitat characteristics between nest and random sites. A set of a-*priori* candidate models (Table 2.3) was created using combinations of microhabitat characteristics (basal area, midstory stem density, understory stem density) and landscape features (edge density, distance to opening). An estimate of ĉ was calculated from the global model to test for over dispersion of the data. Data were not over dispersed (ĉ = 0.515); therefore, bias-corrected Akaike's Information Criterion (AIC_c) and weight of evidence (w_i) were used to rank and select model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). Logistic regression was used to calculate 2log-likelihood values for each model with nest sites = 1 and random sites = 0 (Procedure GLM, SAS Institute, Cary, North Carolina, USA.). Log-likelihoods were then used to calculate Akaike's Information Criterion.

Difference in clutch size between juveniles and adults and distance to brood habitat were analyzed using the Generalized Linear Models (GLM) procedure in SAS. Nest survival was compared between juveniles and adults using chi-square methods described by Mayfield (1975). Relationships of weather data with nest success were examined using multiple regression (Procedure REG) in SAS.

RESULTS

Reproductive Parameters

One hundred thirty-eight female ruffed grouse were radio-tagged. Fate was recorded for 44 nests (35 successful, 9 unsuccessful). Mean annual nesting rate was 73% (6.8 SE), ranging from 50–92% across years (Table 2.4). Mean annual nest success was 81% (6.4 SE), based on proportion of nests that hatched $\geq$1 egg. Nests were observed for a total of 850 nest-days. Mayfield nest survival during incubation across years was 0.83 ($\pm$ 0.084 SE). Nest survival during laying and incubation across years was 0.84 ($\pm$ 0.076 SE).

Only 1 female of 9 (a juvenile) reached incubation of a second nest after an initial nesting attempt failed. Mean hen success was 61% (8.2 SE), ranging from 33% to 75%. Mean clutch size was 10.1 eggs (0.17 SE) with a mean hatchability of 97% (1.2 SE). Clutch size did not differ between juveniles ($\bar{x}$ = 9.4 $\pm$ 0.37 SE) and adults ($\bar{x}$ = 10.6 $\pm$ 0.53 SE, P = 0.0654, Table 2.5). Overall nesting rate was 74% (29/39) for juveniles and 88% for adults (15/17). Overall nest success was 87% (13/15) for adults and 76% (22/29) for juveniles. Nest survival did not differ between juvenile and adults (χ_2^2 = 1.42, $P >$ 0.500).

Nesting Chronology

Females initiated first nests on a mean date of 12 April (0.84 days SE; Table 2.6). Mean dates were similar between juveniles ($\bar{x}$ = 14 April $\pm$ 1.35 SE) and adults ($\bar{x}$ = 13 April $\pm$ 2.36 SE). Nest initiation dates ranged over a 3-week period from 3 April–26 April. Start of continuous incubation occurred 21 April–10 May ($\bar{x}$ = 27 April $\pm$ 0.74

days SE). Mean hatch date was 21 May (0.74 days SE) with 80% of hatch occurring during the 10-day period of 17 May–27 May.

Nest Habitat

The majority of nests (86%) were on mid and upper slopes in mature sawtimber stands >40-years old (Table 2.7). Two nests (5%) were in 6–20-year-old stands, 2 (5%) were in rhododendron, 1 was in a 5-year-old two-aged stand, and 1 was in a 21–39-year-old pole stand. Small sample size of nests relative to habitat types resulted in expected habitat use values <1, preventing statistical analysis of use versus availability at the stand scale. Weight of evidence was low ($\omega_i \leq 0.217$) for all microhabitat nest site selection models, and Δ_i values indicated similar strength of evidence among members of the candidate set (Table 2.8). Habitat variable means were similar between nest and random sites; 95% confidence intervals overlapped for all variables (Table 2.9). Stem density at nest sites was 5,732 stems/ha (4,041–7,420, 95% CI) in the midstory, and 19,000 stems/ha (9,610–28,389, 95% CI) in the understory. Mean basal area was 18m^2/ha (15–20, 95% CI), and mean distance to edge was 195 m (115–275, 95% CI). Total edge density within 100-m buffers around nests was 394 m/ha (352–435, 95% CI), compared to 399 m/ha (344–454, 95% CI) for random sites. All nests were situated next to an object, 43% against stumps or fallen trees, 35% against standing trees, and 22% against rocks. Mean distance to preferred brood-rearing habitats did not differ between nests ($\bar{x}$ = 61 $\pm$ 19.0 m SE) and random points ($\bar{x}$ = 83 $\pm$ 11.3 m SE, $P = 0.327$).

Habitat models for nest fate were not created because sample size of unsuccessful nests was small (n = 9); however, mean habitat values were similar between successful and unsuccessful nests (Table 2.10). Annual nest success was not related to MINTEMP

($r^2 = 0.864$, $P = 0.136$, $n = 5$), COLDAYS ($r^2 = 0.627$, $P = 0.323$, $n = 5$), RAIN ($r^2 = 0.377$, $P = 0.623$, $n = 5$), RAINDAYS ($r^2 = 0.070$, $P = 0.930$, $n = 5$) or MAXTEMP ($r^2 = 0.865$, $P = 0.070$, $n = 5$).

DISCUSSION

Nesting Chronology

Increasing day length activates physiological changes that prepare ruffed grouse for reproduction, though annual variation in nesting phenology can be influenced by latitude and weather (Bump et al. 1947). Ruffed grouse in southern portions of their range nested earlier than those in northern areas. On WSC, incubation began on a mean date of 27 April across years. By comparison, incubation began approximately 17 May in northern Michigan (Larson et al. 2003), 14 May in Minnesota (Maxson 1978), and 7 May in New York (Bump et al. 1947). Across the Appalachians, Devers (2005) noted earlier nesting on more southerly sites, with incubation onset occurring 10 May in Rhode Island, 8 May in Pennsylvania, 29 April in southern West Virginia, and 27 April in central Virginia.

Nesting phenology in southerly latitudes may be driven by early occurrence of warming spring temperatures compared with northern areas. In New York, Bump et al. (1947) attributed annual fluctuations in nesting to weather. They noted advanced nesting dates when average minimum temperature during the pre-nesting period was above normal. Data from WSC support this contention, as the earliest mean incubation date (in 2001), coincided with greatest mean minimum temperature during pre-nesting (15

March–14 April). Although photoperiod determines the general timing of reproduction, annual and latitudinal fluctuations may in part be determined by climate.

Clutch Size and Hatchability

Mean clutch size of 10.1 eggs was within the range of 9.2–11.3 reported by Devers (2005) for the Appalachians. Clutches in the northern United States and southern Canada were generally larger, with reports of 11.4 in Ontario (Cringan 1970), 11.6 in Alberta (Rusch and Keith 1971), 11.5 in New York (Bump et al. 1947), 11.0 in Wisconsin (Small et al. 1996), and 12.7 in Michigan (Larson et al. 2003). Hatchability of 97% on WSC was similar to the 95% average from northern studies, but greater than the mean of 86% for ACGRP (Devers 2005).

Variation in clutch size has been related to latitude in many bird species (Kulesza 1990, Gaese et al. 2000). Within the Appalachians, Devers (2005) attributed differences in clutch size to latitude, with smaller clutches occurring on more southerly study areas. Variation in clutch size with latitude may be related to food availability (Cody 1966, Perrins and Jones 1974, James 1983, Findlay and Cook 1987). Food availability plays the greatest role in clutch size on marginal or poor habitats (Nager et al. 1997). For ruffed grouse, females in poor physiological condition tend to lay smaller clutches (Beckerton and Middleton 1982). In the Appalachians, habitats with nutritionally inadequate foods can cause physiological stress prior to nesting (Servello and Kirkpatrick 1987) that may result in decreased egg production. This presents an opportunity for management to improve reproductive output. Habitat manipulations that improve nutrition, especially in winter and early spring may alleviate stress and positively influence clutch size and other reproductive parameters.

Nesting Rate

Estimates of nesting rate and nest success from telemetry studies tend to be biased because most nests are not located prior to onset of continuous incubation. Nesting rate may be negatively biased, as nests destroyed during laying are not discovered. For the same reason, nest success estimates may be artificially high. Larson et al. (2003) suggested the extent of bias in nest success reports can differ among areas, and comparisons among study sites may be inappropriate. Mayfield (1975) outlined several potential problems in reports of apparent nest survival, including a mixture of nests discovered early and late, nests with unknown outcomes, and observer bias in ability to locate nests. By using intensive radio telemetry during this study, nests were located within 3 days of incubation onset, and once located, fate was determined for all nests. Use of radio telemetry minimizes observer bias among observers, and methodology on WSC was consistent with other ruffed grouse studies in Minnesota (Maxson 1978), Wisconsin (Small et al. 1996), and the Appalachian region (Devers 2005). For consistency with other research, reports herein included apparent nesting rate and apparent nest success as well as Mayfield nest survival.

Nesting rates averaged 73%, which was lower than estimates of 100% from the Great Lakes States (Maxson 1978, Small et al. 1996). In New York, Bump et al. (1947) used systematic nest searching methods to estimate rates of 75–100%, with all females attempting to nest in all but 3 of 13 years. Of 11 study sites in the central and southern Appalachians, nesting rates were 69–100% (Devers 2005). Only one area, located in northern Virginia (VA1), had rates lower than those reported here (Devers 2005). Seven ACGRP study sites (KY1, MD1, OH1, OH2, PA, RI1, and VA3) had nesting rates of

100%, while 3 (WV1, VA2, WV2) reported 98%, 96%, and 85%, respectively (see Devers 2005 for study site locations and acronyms).

Habitat quality and resultant food availability may influence physiological condition and nesting by ruffed grouse in the Appalachians (Servello and Kirkpatrick 1987, Long et al. 2004). Devers (2005) proposed nesting rate was lower on ACGRP sites dominated by oak-hickory forest, where grouse are dependent on annually variable hard mast production, compared with mixed mesophytic forests where alternate food sources, such as herbaceous plants, were plentiful. The WSC study area was classified as mixed mesophytic by ACGRP; however, nesting rates were lower than similarly classed sites in Maryland, Pennsylvania, West Virginia, and Virginia (Devers 2005). Larson (1998) believed that despite an apparent nesting rate of 65% in Michigan, all hens attempted to nest, with some losses occurring prior to incubation. The nesting rate on WSC may have reflected habitat quality, nest predation during the laying period, or a combination of these factors.

Nest Success

Although nesting rates on WSC were lower, nest success (81%) was greater than the range of 47–78% reported from 10 ACGRP study areas (Devers 2005). Only 1 ACGRP site had nest success >81% (92%, Augusta County, Virginia). Estimates also were greater than those from the core of grouse range. Using telemetry techniques, Maxson (1978), Larson et al. (2003), and Small et al. (1996) reported apparent nest success of 75%, 70% and 46% in Minnesota, Wisconsin, and Michigan, respectively. Nest success on WSC likely was biased high because nests were not located prior to incubation; however, methods were similar to other studies and relative comparisons seem appropriate.

Nest survival rates calculated using the Mayfield method were available from 1 other study (Larson et al. 2003). Their survival of first nests (0.44) was considerable lower than a survival rate of 0.83 on WSC. No other studies have estimated nest survival through the laying and incubation periods.

Correlations between weather variables and nest success were not identified. Devers (2005) found a positive relationship between ACGRP nest success and mean minimum temperature in April and May, and proposed colder temperatures necessitate females to make more frequent feeding trips away from the nest. In New York, Bump et al. (1947) concluded weather had a negligible effect on nest success, despite frequent bouts of cold spring weather coupled with snow during their 13-year study period. Results from WSC support the latter contention, as no relationship of nest success with mean minimum temperature and maximum temperature was observed.

Age may influence nest success, as nesting experience gained by juveniles could benefit future attempts (Bergerud 1988*b*). Supporting this contention, Small et al. (1996) found greater adult nest success compared with juveniles in Wisconsin. Conversely, success did not differ with age in northern Michigan (Larson et al. 2003), or across the central and southern Appalachians (Devers 2005). Similar to the latter studies, nest survival on WSC did not differ between juveniles and adults. Availability of nesting habitat (i.e., mature forest) may have resulted in greater opportunity for successful nesting for both juveniles and adults.

Renesting Rate

Renesting was recorded for one female (a juvenile). High success of initial nests precluded the opportunity to document subsequent attempts. Bump et al. (1947) argued renesting contributes little to annual reproductive output. Renesting rates determined by radio telemetry were 46% in Michigan (Larson 1988) and 56% in Wisconsin (Small et al. 1996). In the Appalachians, Devers (2005) reported 23% renesting rate with a range of 0–50%.

Physiological condition largely determines the reproductive capacity of female ruffed grouse (Beckerton and Middleton 1982). In the absence of quality winter forage, Appalachian grouse experience nutritional deficiencies that can result in lower reproductive potential (Servello and Kirkpatrick 1987, Long et al. 2004). Nutritionally stressed grouse in the Appalachians may put more emphasis on initial nesting attempts because low physiological reserves make production of a second clutch difficult. Bergerud and Gratson (1988) suggested that, if disturbed, female grouse should abandon a nest and initiate another attempt, "…if certainty of a current loss outweighs the unpredictability of the loss of a future effort." On WSC, all females were flushed during the first 2 weeks of incubation to determine clutch size; however, no females abandoned nests after these disturbances. This may indicate grouse in the southern Appalachians put more effort in an initial nesting attempt, as opposed to abandoning a first attempt and renesting.

The probability of second nesting efforts also may decrease with increased time invested in an initial nest (Bump et al. 1947, Bergerud and Gratson 1988). In Minnesota, when nests were destroyed during incubation, females did not initiate a second attempt (Maxson 1978). Because nests were not located prior to incubation, potential existed to mistake renests (i.e., those following destruction during laying) for first attempts; however, second clutches are generally smaller (Bump et al. 1947, Maxson 1978, Larson et al. 2003, Devers 2005). Based on numbers reported in the literature, clutch sizes on WSC were not indicative of renests.

Hen Success

Mean annual hen success (63%) was within the range of 47–92% reported across ACGRP study areas (Devers 2005). Of 10 study sites, the WSC estimate was greater than PA1 and VA2, similar to MD1 and WV2, and less than KY1, OH1, OH2, RI, VA1, VA3, and WV1. Hen success has not been reported on other ruffed grouse research studies.

Hen success was defined as the proportion of females alive at the beginning of the reproductive period that successfully hatched ≥1 egg in an initial or renesting attempt. This definition differed from that provided by Vangilder and Kurzejeski (1995) for wild turkeys, as they considered only females that attempted to nest or survived through the reproductive season. As calculated here, hen success represents cumulative contributions of nesting rate, nest success, renesting rate, and renest success to annual reproductive output. On WSC, high nest success offset relatively low nesting and renesting rates.

Nest Habitat

Nesting habitat, particularly placement of nests in relatively open, mature forest, was similar to reports from across grouse range (Bump et al. 1947, Gullion 1977, Maxson 1978, Thompson et al. 1987). These studies and others (Larson et al. 2003, Tirpak et al. in press) suggested females conceal nests against trees or other objects in stands that permit detection of advancing predators. Inability to detect microhabitat differences may have been a function of proximity, as nests and random points (100 m distant) were usually within the same forest type.

Female grouse may select nesting sites based on predation risk (Bergerud and Gratson 1988). Habitat characteristics on WSC were similar between successful and unsuccessful nests; however, given high success rates, few unsuccessful nests were sampled. In Michigan, Larson et al. (2003) could not relate variability in microhabitat structure to nest fate. Conversely, Tirpak et al. (in press) described a positive relationship among nest success, basal area, and coarse woody debris. To decrease predator efficiency, they suggested females nest against trees or debris in stands with numerous potential nest sites. Results from WSC support this contention, as females nested in areas of contiguous habitat against objects, including trees, stumps, and fallen logs, and experienced high success rates.

MANAGEMENT IMPLICATIONS

Recent studies of ruffed grouse in the Appalachians suggest annual productivity is a limiting factor, and habitat management has been recommended to improve nest success and physiological condition of females prior to nesting (Whitaker 2003, Devers 2005, Tirpak et al. in press). Nest success on WSC was among the highest reported for the species, and nesting habitat did not appear to be limiting. Nesting rates, however, were lower than those reported for other areas and may be a function of habitat quality and nutrition.

Habitat manipulations that increase interspersion of quality food sources with suitable protective cover could improve pre-breeding condition of females resulting in greater nesting rates and larger clutches. Topography of the Appalachians creates diverse vegetation communities defined by changes in soil type, thickness, and moisture

(Whitaker 1956). With heterogeneity in soil characteristics, various communities and associated ecotones often occur in close proximity, presenting unique opportunities to intersperse forest types. The greatest diversity often occurs on midslope transition zones between xeric uplands and mesic lower slopes (Berner and Gysel 1969, McNab and Browning 1993). By placing timber harvests on midslope positions, managers can take advantage of diverse food sources while creating early successional cover in close proximity. Timber harvest on midslopes also can create corridors between upper and lower elevation habitats and connect disjunct patches. Such interspersion of cover types also would provide brood habitat in close proximity to stands used for nesting and could ultimately provide the greatest benefit to annual productivity.

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APPENDIX

Table 2.1. Forest stand associations, understory characteristics, and corresponding USDA Forest Service (USFS) and Society of American Foresters (SAF) codes for land classifications used to define ruffed grouse habitats on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina 1999–2004. Adapted from McNab and Browning (1993).

Land class	Moisture gradient	Forest associations	Understory	USFS	SAF
Xeric	Xeric	Pitch pine-oak	>75% ericaceous	59	NA
	.	Scarlet oak	>75% ericaceous	15	45
	.	Chestnut oak-scarlet oak	50-75% ericaceous	60	NA
	Subxeric	Chestnut oak	50-75% ericaceous	52	44
Subxeric	Subxeric	Chestnut oak	25-50% ericaceous	52	44
	.	White oak-red oak-hickory	25-50% ericaceous	55	52
	.	Northern red oak	Herbaceous	53	55
	Submesic	Yellow poplar-white oak-red oak	Herbaceous	56	59
Mesic	Submesic	Yellow poplar	Herbaceous	50	57
	.	Sugar maple-beech-yellow birch	Herbaceous	81	25
	.	Basswood-yellow buckeye	Herbaceous	41	26
	Mesic	Hemlock	75-100% rhododendron	8	23

Table 2.2. Land class, stand age (years), resultant ruffed grouse habitat types, number of stands (*n*), mean stand size (ha) and study area coverage (%) of Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Land class	Age	Habitat type	*n*	Mean ± SE	Coverage
Mesic	40-80	MESIC4	23	21 ± 5.3	9.7
Mesic	>80	MESIC5	12	37 ± 8.7	9.1
Mesic	NA	RHODO	18	53 ± 20.3	19.6
Subxeric	0-5	SUBXER1	30	2 ± 0.4	0.8
Subxeric	6-20	SUBXER2	40	10 ± 0.6	8.1
Subxeric	21-39	SUBXER3	7	11 ± 1.7	1.6
Subxeric	40-80	SUBXER4	8	16 ± 3.9	2.7
Subxeric	>80	SUBXER5	43	36 ± 4.3	31.5
Xeric	6-20	XERIC2	4	15 ± 4.4	1.2
Xeric	40-80	XERIC4	6	20 ± 3.4	2.4
Xeric	>80	XERIC5	15	39 ± 11.2	11.9
Roads	NA	ROAD	NA	NA	1.1
Openings	NA	WLO	24	0.5 ± 0.1	0.2

Table 2.3. A-*priori* candidate models used to evaluate nest site selection by ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Model structure	Model definition
USTEM[a]	Nest site selection a function of understory stem density
MDSTEM	Nest site selection a function of midstory stem density
MDSTEM+USTEM	Nest site selection a function of midstory and understory stem density
BASAL	Nest site selection a function of basal area
MDSTEM+BASAL	Nest site selection a function of midstory stem density and basal area
MDSTEM+USTEM+BASAL	Nest site selection a function of midstory and understory stem density, and basal area
ED	Nest site selection a function of edge density within 100 m radius buffer
ED+BASAL	Nest site selection a function of edge density and basal area
DIST	Nest site selection a function of distance to opening
ED+BASAL+MDSTEM	Nest site selection a function of edge density, basal area, and midstory stem density
ED+BASAL+MDSTEM+USTEM+DIST	Nest site selection a function of edge density, basal area, midstory stem density, and distance to opening

[a] USTEM = density of woody seedlings <1.4 m in height within 0.004-ha plots
MDSTEM = density of woody seedlings >1.4 m in height and <11.4 cm dbh within 0.004-ha plots
BASAL = basal area (m^2/ha)
DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year old forest
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites

Table 2.4. Annual and mean reproductive parameters for female ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

	Year						
Parameter	2000	2001	2002	2003	2004	Mean	SE
Nesting rate (%)	71 (5/7)	92 (11/12)	79 (15/19)	83 (10/12)	50 (3/6)	73	6.8
Nest success (%)	100 (5/5)	82 (9/11)	67 (10/15)	90 (9/10)	67 (2/3)	81	6.4
Renest rate (%)	0	50 (1/2)	0	0	0	10	9.8
Renest success (%)	NA	0 (0/1)	NA	NA	NA	NA	NA
Hen success (%)	71 (5/7)	75 (9/12)	53 (10/19)	75 (9/12)	33 (2/6)	61	8.2
Clutch size (eggs)	9.8	10.5	10.4	9.4	8.5	9.72	0.4
Hatchability (%)	98	93	95	97	100	97	1.2

Table 2.5. Reproductive parameters by age class (juvenile or adult) with years pooled for female ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

	Age	
Parameter	Juvenile	Adult
Nesting rate (%)	74 (29/39)	88 (15/17)
Nest success (%)	76 (22/29)	87 (13/15)
Hen success (%)	56 (22/39)	76 (13/17)
Clutch size (eggs)	9.4 ± 0.37	10.6 ± 0.53
Initiation Date	14 April ± 1.35	13 April ± 2.36

Table 2.6. Nest initiation, incubation, and hatch dates and ranges for ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Year	Initiation	Range	Incubation	Range	Hatch	Range
2000	10 Apr	7 Apr–14 Apr	25 Apr	21 Apr–28 Apr	19 May	15 May–22 May
2001	13 Apr	9 Apr–18 Apr	29 Apr	26 Apr–3 May	23 May	20 May–27 May
2002	8 Apr	3 Apr–13 Apr	24 Apr	22 Apr–3 May	18 May	16 May–27 May
2003	15 Apr	11 Apr–16 Apr	28 Apr	26 Apr–3 May	22 May	20 May–27 May
2004	21 Apr	16 Apr–26 Apr	4 May	28 Apr–10 May	28 May	22 May–3 June
All Years	12 Apr	3 Apr–26 Apr	27 Apr	21 Apr–10 May	21 May	15 May–3 June

Table 2.7. Nesting habitat use and availability for ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Habitat	Number nests	Use (%)	Availability (%)
XERIC2	0	0	1
XERIC4	2	5	2
XERIC5	4	9	12
SUBXER1	1	2	1
SUBXER2	2	5	8
SUBXER3	1	2	2
SUBXER4	3	7	3
SUBXER5	16	37	32
MESIC4	8	19	10
MESIC5	4	9	9
RHODO	2	5	20
ROAD	0	0	1
WLO	0	0	<1

[a]XERIC2 = xeric uplands in 6–20-year age class
XERIC4 = xeric uplands in 40–80-year age class
XERIC5 = xeric uplands in >80-year age class
SUBXER1 = subxeric to submesic forest in 0–5-year age class
SUBXER2 = subxeric to submesic forest in 6–20-year age class
SUBXER3 = subxeric to submesic forest in 21–39-year age class
SUBXER4 = subxeric to submesic forest in 40–80-year age class
SUBXER5 = subxeric to submesic forest in >80-year age class
MESIC4 = mesic forest in 40–80-year age class
MESIC5 = mesic forest in >80-year age class
RHODO = forest with >75% midstory coverage in rhododendron
ROAD = gated forest roads
WLO = wildlife openings

Table 2.8. Comparison of Akaike's Information Criterion (AIC_c), differences in AIC_c, and model weights (w_i) for ruffed grouse nest site selection models on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Model	AICc	ΔAICc	*w*i
MDSTM	96.845	0.000	0.217
BASAL	97.198	0.353	0.182
DIST	98.348	1.503	0.102
USTEM	98.401	1.556	0.100
ED	98.425	1.580	0.099
MDSTM + USTEM	98.703	1.858	0.086
ED + MDSTEM	99.032	2.187	0.073
ED + BASAL	99.231	2.386	0.066
BASAL + MDSTM + USTEM	100.372	3.527	0.037
ED + BASAL + MIDSTEM	100.519	3.674	0.035
BASAL + MDSTEM + USTEM + DIST + ED	105.068	8.223	0.004

[a] USTEM = density of woody seedlings <1.4 m in height within 0.004-ha plots
MDSTEM = density ofwoody seedlings >1.4 m in height and <11.4 cm dbh in 0.004-ha plots
BASAL = basal area (m^2/ha)
DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year old forest
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites

Table 2.9. Means and 95% confidence intervals for habitat variables at nest and paired random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Variable	Sampling site			
	Nest		Random	
	Mean	95% CI	Mean	95% CI
USTEM	19,000	9,610-28,389	20,455	11,187-29,274
MDSTM	5,732	4,041-7,420	4,414	3,113-5,716
BASAL	18	15-20	19	17-22
DIST	195	115-275	213	128-299
ED	394	352-435	399	344-454

[a] USTEM = density of woody seedlings <1.4 m in height/ha
MDSTEM = density ofwoody seedlings >1.4 m in height and <11.4 cm dbh/ha
BASAL = basal area (m^2/ha)
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites
DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year old forest

Table 2.10. Means and 95% confidence limits for habitat variables at successful and unsuccessful nest sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Variable	Nest Fate			
	Successful		Unsuccessful	
	Mean	95% CI	Mean	95% CI
USTEM	18,024	7,768-28,281	27,550	10,464-44,636
MDSTM	7,371	2,444-12,298	5,480	3,339-7,621
BASAL	17	15-20	21	15-26
DIST	216	122-311	189	32-346
ED	407	358-457	378	290-465

[a]USTEM = density of woody seedlings <1.4 m in height/ha
MDSTEM = density ofwoody seedlings >1.4 m in height and <11.4 cm dbh/ha
BASAL = basal area (m^2/ha)
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites
DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year old forest

PART III.

RUFFED GROUSE BROOD HOME RANGE AND HABITAT USE IN WESTERN NORTH CAROLINA

ABSTRACT

Ruffed grouse brood habitat is an important consideration in management of the species.We measured brood habitat characteristics at forest stand and microhabitat scales in the Appalachian Mountains of western North Carolina. From 2000–2004, radiotagged females with broods (N = 36) were monitored from hatch to 5 weeks post-hatch, resulting in 372 microhabitat plots (186 brood, 186 random). Brood sites had greater percent herbaceous ground cover, greater percent vertical cover 0–2 m, greater density of midstory stems <11.4 cm DBH, and greater invertebrate density compared with random. Seventeen broods survived the 5-week post-hatch period and were available for home range analysis. Mean 75% kernel home range was 24.3 ha. Top-ranked habitats for relative preference were mixed oak in the 0–5, 6–20, and >80-year age classes, forest roads, and edges of maintained wildlife openings. Broods often were associated with managed stands, and forest management may be used to further enhance brood habitat in the southern Appalachians.

Key words: Appalachians, *Bonasa umbellus*, broods, habitat use, home range, ruffed grouse.

INTRODUCTION

Provision of brood habitat is an important aspect of ruffed grouse (*Bonasa umbellus*) management. Female grouse promote chick survival by seeking areas that allow optimal foraging near the safety of protective cover (Bergerud and Gratson 1988). Realizing the inherent relationship between cover and chick survival, Bump et al. (1947) suggested brood habitat quality ultimately determines an area’s reproductive potential.

Prompted by population declines, biologists in the central and southern Appalachians (CSA) are developing management strategies to address ruffed grouse habitat needs. Provision of quality brooding areas may be a cornerstone of such plans, as fulfilling specific brood requirements also improves conditions for adults throughout the year. The reverse, however, may not be true, as broods are less able to adjust to unfavorable conditions (Berner and Gysel 1969).

Characteristics of brood habitat during the first few weeks after hatch are well documented from the core of ruffed grouse range. Requirements include ample invertebrates, a diversity of moderately dense, herbaceous groundcover and a high density of midstory shrubs and woody stems (Berner and Gysel 1969, Porath and Vohs 1972, Godfrey 1975, Gullion 1977, Kubisiak 1978, Maxson 1978). The diversity of forest stands exhibiting these conditions included lowland speckled alder (*Alnus rugosa*, Godfrey 1975), mature alder-aspen (*Populus tremuloides*, *P. grandidentata*, Kubisiak 1978), and various combinations of forest openings and edge habitats (Berner and Gysel 1969, Porath and Vohs 1972, Maxson 1978).

Several studies have examined brood habitat in the CSA (Stewart 1956, Scott et al. 1998, Haulton et al. 2003); however, conflicting reports exist regarding forest types preferred by grouse broods in the region. Similar to other areas within grouse range, results emphasized importance of diverse herbaceous cover with varying descriptions of forest stand types and ages that provided optimal conditions. In Virginia and West Virginia, broods frequented mature, closed canopy hardwoods (Haulton et al. 2003). Also in Virginia, Stewart (1956) located broods in moist forest ravines and near canopy gaps in otherwise mature forest. On an intensively managed mixed oak (*Quercus* spp.) forest in Pennsylvania, brood hens selected 10-year-old clearcuts (Scott et al. 1998). The range of forest types reportedly used by grouse broods, from closed canopy mature stands to young clearcuts, may complicate decision-making for managers choosing among silvicultural options for improving ruffed grouse brood habitat in the CSA.

Most forest management plans are implemented at stand and compartment scales. Within forest stands, vegetation characteristics (i.e., microhabitat) are altered by natural disturbances and management activities including timber harvest and prescribed burning. Within compartments, or multiple stands, habitat is influenced albeit at a coarser resolution. Habitat selection can occur at one or both of these scales (Johnson 1980); therefore, a comprehensive understanding of forest management effects on wildlife can be gained through habitat investigations at multiple spatial scales. Such a study could provide valuable information pertinent to forest management for ruffed grouse in the CSA.

Ruffed grouse brood habitat was studied in the southern Appalachian Mountains of North Carolina. Objectives were to (1) compare habitat use versus availability at the forest stand scale; (2) examine vegetation structure of brood habitat; (3) investigate invertebrate availability in brood habitats; and (4) identify forest management options for creating, maintaining, and improving brood habitat in the CSA.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (WSC; 3,230 ha), within Nantahala National Forest in western Macon County, North

Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges connecting upper elevations to narrow valley floors (Whittaker 1956). Mean annual temperature was 10.4ºC, and mean annual precipitation was 160 cm. The area was predominantly forested with <1% coverage in small openings. The U.S. Forest Service purchased WSC in 1912 after it was logged. Since then, forest management practices included salvage harvest of blight-killed American chestnut (*Castanea dentata*), thinning, clearcutting, and diameter-limit cutting (McNab and Browning 1993).

Habitats were classified by a combination of vegetative community type and stand age. Communities were stratified into 3 land classes (i.e., xeric, subxeric, and mesic) defined by elevation, landform, soil moisture, and soil thickness (McNab and Browning 1993; Table 3.1; tables are located in the Appendix). Within communities, variation in plant species occurrence existed along a moisture continuum, similar to that described by Whittaker (1956). Xeric communities were on high elevation, steep, south and west aspects characterized by shallow, dry soils. Tree species included scarlet oak (*Quercus coccinea*), black oak (*Q. velutina*), pitch pine (*Pinus rigida*) and chestnut oak (*Q. prinus*) in the overstory with ericaceous plants including huckleberry (*Gaylussacia baccata*), lowbush blueberry (*Vaccinium vacillans*), and mountain laurel (*Kalmia latifolia*) in the understory. Subxeric communities were at middle elevations and upper elevations on less exposed aspects. Soil characteristics were between xeric and mesic, or subxeric and submesic (Whittaker 1956). Overstory was dominated by chestnut oak, white oak (*Q. alba*), hickory (*Carya* spp.), northern red oak (*Q. rubra*), red maple (*Acer* *rubrum*), and yellow poplar (*Liriodendron tulipifera*). Ericaceous understory occupied 25–50% groundcover on drier microsites, whereas herbaceous plants occupied more mesic sites. Mesic communities occurred on north and east aspects, on lower slopes, and in sheltered coves. Stands were comprised of yellow poplar, eastern hemlock (*Tsuga canadensis*), northern hardwoods including sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and birch (*Betula* spp.), and mixed mesophytic obligates including American basswood (*Tilia americana*) and yellow buckeye (*Aesculus octandra*). Understory was herbaceous except where rhododendron (*Rhododendron maximum*) inhibited groundcover. Sites with 75–100% cover in rhododendron were placed in a separate habitat classification (RHODO).

Additional land classes included gated forest roads (ROAD) and wildlife openings (WLO). Gated forest roads were defined by a buffer width of 5m from road center on each side. The 10-m width included the road and adjacent berm. Wildlife openings were small, permanent clearings (0.50 ± 0.12 ha SE). Management of roads and openings included an initial planting of orchardgrass (*Dactylis glomerata*), tall fescue (*Festuca arundinacea*) and white-dutch clover (*Trifolium repens*) maintained by annual or biennial mowing.

Stand ages were determined by years since harvest or stand establishment in categories deemed important to ruffed grouse (0–5, 6–20, 21–39, 40–80, >80). Grouse reportedly begin use of regenerating mixed hardwood and oak stands approximately six years after harvest (Kubisiak 1987, Thompson and Dessecker 1997). At approximately 20 years of age, habitat quality decreases as the upper canopy closes and woody stem density and herbaceous ground cover decrease (Kubisiak 1987, Storm et al. 2003). Mixed hardwood stands remain in this “pole stage” for up to 40 years. By age 40, most oak species have reached reproductive maturity and are capable of producing significant acorn crops (Guyette et al. 2004). By 80–120 years, oak stands are considered full rotation age (U.S. Forest Service 1994). Beyond 120 years, natural mortality of upland oaks increases (Guyette et al. 2004), resulting in canopy gaps. Wildlife openings, roads and rhododendron-dominated understory were not assigned age categories because they are in a state of arrested succession and their structural characteristics do not change appreciably over time (Phillips and Murdy 1985).

Stands in the 6–20-year age class were predominantly clearcuts (1.3–24.6 ha, *n* = 44) harvested in the late 1980s and early 1990s. Alternative regeneration harvests (i.e., shelterwood, irregular shelterwood, group selection) were cut 1996–1997, and represented the 0–5-year category (SUBXER1) for most of the study. Target residual basal area was 9.0 m^2/ha for shelterwood harvests. Prescriptions called for a final removal cut of residuals approximately 10 years after the initial harvest. Ruffed grouse data were collected prior to removal of residuals in these stands. Mean size of shelterwood stands was (5.56 ± 0.42 ha SE, *n*=3). For irregular shelterwood, target residual basal area was 5.0 m^2/ha. Residuals in irregular shelterwood were to be retained through the next rotation, resulting in 2-aged stands. Mean size of 2-aged stands created by irregular shelterwood was (4.68 ± 0.18 ha SE, *n* =3). Group selection was implemented in 3 stands with 4–9 groups/stand. Mean group size was 0.36 ha (± 0.05 SE). All shelterwood, irregular shelterwood, and group selection harvests were implemented on subxeric sites and represented the SUBXER1 habitat type.

Subxeric oak and mixed oak-hickory in the >80 year age class (SUBXER5) made up the greatest proportion of the study site (31.5%) and wildlife openings (WLO) made up the least (<1.0%; Table 3.2). Early successional habitats in the 6–20-year age class (XERIC2 and SUBXER2) occupied 9.3% of the area. The 6–20-year, and 21–39-year age classes were not represented on mesic sites. There were 52.6 km of gated forest roads (1.1% of total area).

Capture and Telemetry

Grouse were captured using intercept traps (Gullion 1965) during two annual periods, late August–early November and early March–early April, 1999–2003. Gender and age (juvenile or adult) were assessed by feather characteristics and molt patterns (Kalla and Dimmick 1995). Grouse were weighed, leg-banded, fitted with a 12-g necklace-style radiotransmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA) and released after processing.

Females with broods were monitored intensively from hatch to 5 weeks post-hatch, a critical period when chick mortality is greatest and survival may depend on habitat characteristics (Bump et al 1947, Larson et al. 2001). Brood females were located 1-2 times daily by triangulation and 2-3 times weekly by homing. Homing provided visual locations necessary to confirm brood survival and sites for vegetation and invertebrate sampling. Intensive monitoring continued as long as a female had $\geq$1 surviving chick or until 5 weeks post-hatch. When possible, flush counts were avoided, as frequent disturbance may influence brood movements and survival. Instead, broods were approached cautiously to determine presence or absence through observation of brooding behavior or direct observation of chicks. In this way, field personnel were successful in determining brood presence or absence without flushing chicks.

Microhabitat Sampling

Microhabitat data were collected in nested circular plots centered on brood locations. For comparison, corresponding random locations were sampled at a random distance (200–400 m) and azimuth (0–359°) from a location recorded the previous day. This allowed availability to differ among observations as broods moved within the study area (Arthur et al. 1996). The 200–400 m distance was chosen because it represented mean daily movement distance of grouse chicks (Godfrey 1975, Fettinger 2002).

Basal area was estimated from plot center with a 2.5 m^2/ha prism. Overstory composition of trees $\geq$11.4 cm diameter at breast height (DBH) was recorded within a 0.04-ha plot. Species and number of midstory saplings and shrubs <11.4 cm DBH and $\geq$1.4 m height was recorded for 4 DBH classes (<2.54 cm, 2.54–5.08 cm, 5.09–7.62 cm, and 7.63–11.4 cm) within a 0.01-ha plot. Woody seedlings <1.4 m in height were recorded within a 0.004-ha plot. Mean percent herbaceous groundcover was estimated from 3, 3.6-m transects (0°, 120°, 240°). Groundcover was expressed as a total and within the categories fern, forb, grass, and briar. Briar included blackberry, raspberry (*Rubus* spp.), and greenbriar (*Smilax* spp.). Vertical vegetation density was estimated using a 2.0 m vegetation profile board divided into 0.2-m sections (Nudds 1977). Mean percent vertical coverage of vegetation was estimated 10 m from plot center at 4 sample points, one for each cardinal direction. During 2002–2004, mean percent overstory canopy also was estimated from these points using a densiometer. Standard deviation of the 4 canopy measurements was calculated to measure canopy continuity.

Invertebrates were sampled within a 15 m radius of plot center using a 0.10-m^2 bottomless box and a terrestrial vacuum sampler (Harper and Guynn 1998). During 2000–2001, 5 subsamples were collected at each plot. After 2001, power analysis revealed 4 subsamples were adequate to estimate mean invertebrate density within plots (Fettinger 2002). Invertebrate samples were frozen pending sorting in the laboratory. Arthropods were sorted from leaf litter and detritus and identified to order according to Borror et al. (1989). After sorting, arthropods were placed in glass vials, oven-dried for 48 hours at 60°C (Murkin et al. 1996), and weighed by order. Orders frequently consumed by ruffed grouse chicks, including Araneae, Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, and Orthoptera, were grouped in a unique category (Bump et al. 1947, Stewart 1956, Kimmel and Samuel 1984).

Weather

Coweeta Hydrologic Lab (Coweeta LTER, Otto, North Carolina) recorded weather data at a permanent weather station on the study site. Minimum and maximum temperature and precipitation (tipping bucket) were recorded daily. Weather data collected between 25 May (mean hatch date) and 30 June each year were used to explore correlations with brood survival. Variables of interest included, mean maximum temperature (MAXTEMP), number of days with temperatures < 7^{o}C (COLDAYS), total rainfall (RAIN), and number of days with rainfall events (RAINDAYS). Linear relationships of weather data with 5-week brood survival were examined using the REG procedure in SAS.

Habitat Modeling

An information-theoretic approach (Burnham and Anderson 1998) was used to evaluate differences in habitat characteristics between brood and random sites. A set of a-*priori* candidate models was created using combinations of microhabitat characteristics previously determined important to ruffed grouse broods (Stewart 1956, Berner and Gysel 1969 Porath and Vohs 1972, Godfrey 1975, Kubisiak 1978, Maxson 1978, Kimmel and Samuel 1984, Thompson et al. 1987, Scott et al. 1998, Fettinger 2002, Haulton et al 2003). Variables included in models were percent total groundcover, percent vertical cover $\leq$2 m, midstory stems $\leq$11.4 cm DBH, and density of invertebrates in orders preferred by ruffed grouse chicks. Bias-corrected Akaike's Information Criterion (AIC_c) and weight of evidence (w_i) were used to rank and select the model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). Logistic regression was used to calculate 2log-likelihood values for each model with brood sites = 1 and random sites = 0 (Procedure GLM, SAS Institute, Cary, North Carolina, USA.). Log-likelihoods were then used to calculate Akaike's Information Criterion. Multicollinearity of explanatory variables was assessed for each model with variance inflation factor (VIF) output by the REG Procedure in SAS. Goodness of fit of the most parsimonious models was assessed with Hosmer and Lemeshow goodness of fit test (Hosmer and Lemeshow 1989).

Habitat characteristics were compared between broods that survived to 5-weeks post hatch and those that did not. Linear distance from nest sites to preferred brood habitats was measured for both categories. Nests located within a preferred brooding habitat were assigned a value of 0. Inherently small sample size of vegetation plots for non-surviving broods (n = 32) prevented model development. Therefore, habitat variable means and 95% confidence intervals were calculated for comparisons.

Second Order Habitat Selection

Habitat use was compared with availability at the study area scale (i.e., second-order selection; Johnson 1980). Use was represented by the proportion of habitats within brood home ranges. The Animal Movement Extension to ArcView GIS 3.2 (Environmental Systems Research Institute Inc., Redlands, CA; Hooge and Eichenlaub 1997) was used to calculate fixed kernel home ranges (Worton 1989). Estimates were based on 75 percent kernel contours to define central portions of a home range and exclude “occasional sallies” (Burt 1943, Seaman et al. 1999). To determine adequate sampling (minimum locations), home range area was plotted against number of locations to determine sampling level at which area variation decreased and became asymptotic. Only broods with $\geq$1 chick surviving at 5 weeks post-hatch and home ranges that became asymptotic were used for analysis.

Home ranges were overlaid on a Geographic Information System (GIS) created for the area using color infrared aerial photographs, 1:24,000 U.S. Geologic Survey 7.5-min quadrangles, U.S. Forest Service Continuous Inventory of Stand Condition (CISCS), and ground truthing. Home ranges were clipped from the coverage to determine proportional use of each habitat type. The Animal Movement Extension also was used to calculate home range size by 95% kernel and minimum convex polygon (MCP) methods for comparison with other studies.

Second-order habitat availability was defined by 1,200 m circular buffers around successful nest sites. Grouse chicks are capable of moving up to 1200 m during the 5 weeks following hatch (Godfrey 1975, Fettinger 2002); therefore, this distance represented habitats available to broods based on their movement potential. Use was compared with availability using compositional analysis (Aebischer et al. 1993). Relative ranks of habitat use were assigned by calculating pair-wise differences in use versus availability for corresponding habitat log-ratios. To control Type I error, data were examined for 0% observations in any available habitat (Bingham and Brennan 2004). Shapiro-Wilk's test was used to test for normality in log-ratio differences, and randomization tests were used to determine differences in use versus availability for non-normal data. Significance tests ($\alpha = 0.05$) were used to examine differences in relative preference among ranked habitats (Aebischer et al. 1993).

RESULTS

From 2000–2004, 36 brood females were monitored resulting in 372 microhabitat plots (186 brood, 186 random). Seventeen brood females had $\geq$1 chick alive at 5 weeks post-hatch. Whole brood survival varied across years with 0% (0/5), 100% (9/9), 70% (7/10), 22% (2/9), and 33% (1/3) surviving to 5 weeks post-hatch in 2000, 2001, 2002, 2003, and 2004, respetively. Annual brood survival was not correlated with MAXTEMP ($r^2 = 0.015$, $P = 0.984$), COLDAYS ($r^2 = -0.613$, $P = 0.387$), RAIN ($r^2 = 0.034$, $P = 0.966$), or RAINDAYS ($r^2 = 0.047$, $P = 0.953$).

Mean home range size was 24.3 ha (± 4.0 SE) using 75% kernel methods and 40.0 ha (± 4.0 SE) using MCP. At second order selection, log-ratio differences were non-normal (Wilk's $\lambda = 0.90$). Randomization tests recommended for non-normal log-ratios (n=10,000; Aebischer et al. 1993) indicated use differed from availability ($P < 0.001$).

Top-ranked habitats for relative preference were SUBXER1, SUBXER2, SUBXER5, ROAD, and WLO (Table 3.3). Lack of significant differences in use indicated ranks among these habitats were interchangeable.

The most parsimonious microhabitat model included an intercept term, percent total herbaceous groundcover, percent vertical cover, density of midstory stems <11.4 cm DBH, and preferred invertebrate density (AIC_c = 482.36, ω_i = 0.965; Table 3.4). Cross-validation revealed the model correctly classified 66.3 % of brood locations, and lack of fit was rejected by Hosmer and Lemeshow goodness of fit test (χ^2 = 6.02, P = 0.645; Hosmer and Lemeshow 1989). Explanatory variables in the best model were not linearly related (VIF <1.38).

Compared with random plots, brood sites had greater percent herbaceous groundcover (brood = 55.7 ± 2.0 SE, random = 44.8 ± 2.0 SE), greater percent vertical cover (brood = 52.3 ± 2.0 SE, random = 41.5 ± 2.0 SE), greater midstory stems/ha <11.4 cm DBH (brood = 6,250 ± 441 SE, random = 4,963 ± 355 SE), and greater number of invertebrates/m^2 (brood = 58.9 ± 5.0 SE, random = 44.3 ± 2.4 SE; Tables 3.5, 3.6). Herbaceous groundcover on both brood and random plots was evenly distributed between forb and fern with lesser amounts of grass and briar (Table 3.5). Vertical vegetation coverage 0–2 m in height also was evenly distributed across 0.4 m sections. The greatest difference in preferred invertebrate density was within the order Hymenoptera (i.e., bees, wasps, ants; Table 3.6). Mean Hymenopteran density was 13.5/m^2 (± 4.3 SE) on brood plots and 7.7/m^2 (± 1.5 SE) on random plots. Invertebrate biomass did not differ between brood and random plots (Table 3.7).

Microhabitat variables did not differ among plots measured for broods that survived to 5 weeks post-hatch and those that did not (Table 3.8). Mean linear distance from nest sites to brood habitats was 41 m (8–73 m, 95% CI) for surviving broods; and 90 m (16–165, 95%CI) for non-surviving broods; however, variability resulted in overlap between confidence intervals.

DISCUSSION

Whole brood survival varied widely from 0–100% across years; however, this statistic should not be viewed as a reliable indicator of chick survival. For example, if brood survival in a given year was 2/10 (20%) with 3 chicks/brood, the number of chicks surviving would actually be greater than during a year with 5/10 broods surviving (50%) with 1 chick/brood. Flush count data do not provide an alternative, as brood mixing and a wide range of observer bias may occur (Godfrey 1975*b*). Given difficulties in estimating chick survival without radiotagged individuals (Larson et al. 2001), whole brood longevity was the best estimator available on WSC.

Brood survival was not related to weather variables examined on WSC. It seems reasonable to theorize cold weather and rainfall would influence ruffed grouse chick survival during the first weeks after hatch when chicks are unable to thermo regulate and the brooding female provides protection from the elements. Spring weather has been shown to influence recruitment in other gallinaceous game birds including wild turkeys (*Meleagris gallopavo*, Roberts and Porter 1998) and northern bobwhite (*Colinus virgianus*, Lusk et al. 2001); however, such relationships have not been identified for ruffed grouse (Bump et al. 1947, Larson and Lahey 1958, Gullion 1970). As a northern species, ruffed grouse may have adapted to efficiently brood chicks during periods of inclement spring weather frequently encountered in northern latitudes. In the CSA, there may be even less of an impact as weather extremes are less severe compared with northern parts of their range.

Brood MCP home ranges were smaller than those reported from other studies in mixed oak forests. On 2 study sites in Virginia and West Virginia, brood home ranges averaged 90 ha (Haulton 1999). In Pennsylvania, Scott et al. (1998) reported overall home range of 84 ha, with smaller ranges occurring on intensively managed sections of the study area. Although home range size may be a function of habitat quality (Schoener 1968, Smith and Shugart 1987, Renken and Wiggers 1989), larger use areas reported from other studies may have resulted from these researchers monitoring broods through late summer when ranges often shift to take advantage of diverse food sources. Home ranges in this study were estimated during the early brood period, ending in early July. Nonetheless, considerably smaller estimates from the core of ruffed grouse range of 12.9 ha (Godfrey 1975) and 16.0 ha (Maxson 1978) may indicate more desirable habitat conditions in mixed hardwood-aspen forests of the Great Lakes Region.

With respect to forest types, broods used mixed oak stands in the 0–5, 6–20, and >80-year age classes. Site conditions were submesic to subxeric with northern red oak and red maple dominant in the overstory and flame azalea, American chestnut sprouts, red maple, serviceberry, and northern red oak, in the midstory (Tables 3.9, 3.10). The 0–5-year class was represented by use of 3–4-year-old group selection cuts and edges of 2 recently harvested irregular shelterwood (i.e., 2-aged) stands. Broods also utilized edges of 6–20-year-old mixed oak clearcuts, but seldom ventured into their interior.

There may be an apparent contradiction between use of younger age classes and >80-year-old mixed oaks. During the mid-1980s an extensive drought in the southeastern United States resulted in increased overstory tree mortality and canopy gap formation in late-rotation oak forests (Clinton et al. 1993). These canopy openings promoted localized patches of early successional structure similar to that found in younger stands. Broods often were associated with such canopy openings as evidenced by greater variability in canopy closure at brood locations (Table 3.5).

In addition to the aforementioned forest types, broods used other openings, including edges of permanent clearings (i.e., wildlife openings) and forest roads. All wildlife openings and roads used by broods were located within late-rotation mixed oak stands. Management included an initial planting of orchardgrass (*Dactylis glomerata*), tall fescue (*Festuca arundinacea*) and white-dutch clover (*Trifolium repens*) maintained by annual or biennial mowing. Dense understory conditions created by perennial cool-season grasses prevented chick movement through these areas; however, broods were observed foraging along their periphery. Herbaceous and woody stem cover provided by various forbs, brambles, shrubs, and regenerating hardwoods created desirable conditions for foraging and concealment along margins of clearings. Microclimates created by moderate forb cover in conjunction with overstory shrubs create ideal conditions for both grouse chicks and their invertebrate prey (Kimmel and Samuel 1984). Maxson (1978) also noted broods foraging along field edges and within hardwood strips between open fields and hardwood forest. In Virginia, Stewart (1956) observed broods using linear openings created by forest roads. These studies and ours suggest permanent clearings and forest roads can be managed to create and improve brood habitat in oak forests.

With the exception of Haulton et al. (2003), most habitat studies in mixed oaks have noted an association of ruffed grouse broods with forest openings. In Missouri, Freiling (1985) found broods near canopy gaps in mature sawtimber stands. Porath and Vohs (1972) and Stewart (1956) gave similar reports from Iowa and Virginia, respectively. In New York, Bump et al. (1947:140) cited brood use of “spot-lumbered hardwoods.” These areas seem to be similar to group selection stands on WSC. A common theme across studies is the young age and diversity of vegetation in brood habitats.

Microhabitats selected by broods had greater vertical vegetation cover, herbaceous groundcover, and midstory stem density compared to availability. Random plots were frequently within the same stand type as use locations, suggesting broods selected within stand microsites based on vegetation structure. Other brood habitat studies in mixed-oak forests emphasized the importance of 0.0–2.0 m vertical cover (Scott et al. 1998, Haulton et al. 2003) and percent groundcover in the 50–60% range (Porath and Vohs 1972, Thompson et al. 1987, Scott et al. 1998, Haulton et al. 2003); however, there is disagreement regarding importance of midstory stem density. Supporting desirability of high stem density, Scott et al. (1998) found broods used 10-year-old clearcuts with 21,100 stems/ha. In Missouri, Thompson et al. (1987) reported moderate stem density of 5,558 stems/ha at brood locations. Conversely, in Virginia and West Virginia, Haulton et al. (2003) suggested broods preferred more open conditions (i.e., 3,581–3,822 stems/ha) though more dense stands were available. Discrepancies in stem density reports may be a function of herbaceous cover conditions. Broods may select sites based on herbaceous structure with midstory stems providing additional cover when available. On WSC, desirable herbaceous cover and moderate stem density (6,250 stems/ha) occurred along edges of timber harvests and in canopy gaps.

Differences in habitat structure were not observed between surviving and non-surviving broods. Conditions that created canopy gaps were widespread (Clinton et al. 1993), resulting in patches of desirable cover across ≥80-year-old subxeric mixed oak stands. Interspersion of 3, 5–12 ha clearcuts and 1, 5 ha two-aged harvest created additional habitat on a 513 ha ridge used by 14 broods. This together with moderate overall brood survival (53%) may suggest brood habitat for the first 5 weeks following hatch was not limiting on WSC; however, to maintain habitat quality, continued disturbance may be necessary as clearcut stands were nearing pole-stage and gaps created 17–20-years prior were nearing closed canopy conditions.

Invertebrates are a primary food source for grouse chicks <5 weeks old (Bump et al. 1947, Stewart 1956, Kimmel and Samuel 1984). Density of preferred orders, primarily ants (Hymenoptera) and leafhoppers (Homoptera), was greater on brood plots compared to random (Table 3.6). Using human-imprinted ruffed grouse chicks, Kimmel and Samuel (1984) observed ants and leafhoppers were the most frequently consumed invertebrates. They also noted herbaceous cover that presents feeding opportunities and protective cover provide optimal habitat conditions.

Rather than selecting habitats based on food availability, birds may use proximate cues related to prey abundance (Schoener 1968, Smith and Shugart 1987). Based on microhabitat characteristics at use locations, broods appeared to select sites based on vegetation structure. This structure also provided invertebrates (especially those of the order Hymenoptera) as a food source. For wild turkey poults, which consume similar invertebrates to ruffed grouse chicks, authors have recommended forest management practices that may increase invertebrate density by promoting herbaceous communities (Hurst 1978, Rogers 1985, Pack et al. 1980). On WSC, Harper et al. (2001) also recommended habitat evaluations focus on vegetation structure to improve invertebrate density.

MANAGEMENT IMPLICATIONS

A comprehensive understanding of forest management effects on wildlife can be gained through habitat investigations at multiple spatial scales. Information is provided on forest stand types and microhabitat characteristics within stands used by ruffed grouse broods. Similar to other studies, vertical cover, herbaceous groundcover, and midstory stem density were important components of brood habitat on WSC. These requirements were met where openings in the forest canopy encouraged herbaceous plant growth and woody stem regeneration. Interspersion of forest age classes creates areas of desirable cover in close proximity (Sharp 1963, Berner and Gysel 1969, Gullion 1977, Kubisiak 1978). Where mature, undisturbed forests have closed canopies, timber management activities including group selection harvests, thinning, shelterwood, and irregular shelterwood harvests and prescribed burning can promote improved cover conditions. In mature (>40 years), mixed oak stands with closed canopies, timber management activities will allow sunlight to reach the forest floor, resulting in diverse understory communities favored by grouse broods. On forest roads and permanent clearings, eliminating perennial cool season grasses and maintaining forb communities through minimal maintenance should be a priority (Healy and Nenno 1983, Harper et al. 2001).

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APPENDIX

Table 3.1. Forest stand associations, understory characteristics, and corresponding USDA Forest Service (USFS) and Society of American Foresters (SAF) codes for land classifications used to define ruffed grouse habitats on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina 1999–2004. Adapted from McNab and Browning (1993).

Land class	Moisture	Forest associations	Understory	USFS	SAF
Xeric	Xeric	Scarlet oak	>75% ericaceous	59	NA
	.	Pitch pine-oak	>75% ericaceous	15	45
	.	Chestnut oak-scarlet oak	50-75% ericaceous	60	NA
	Subxeric	Chestnut oak	50-75% ericaceous	52	44
Subxeric	Subxeric	Chestnut oak	25-50% ericaceous	52	44
	.	White oak-red oak-hickory	25-50% ericaceous	55	52
	.	Northern red oak	herbaceous	53	55
	Submesic	Yellow poplar-white oak-red oak	herbaceous	56	59
Mesic	Submesic	Yellow poplar	Herbaceous	50	57
	.	Sugar maple-beech-yellow birch	Herbaceous	81	25
	.	Basswood-yellow buckeye	Herbaceous	41	26
	Mesic	Hemlock	75-100% rhododendron	8	23

Table 3.2. Land class, stand age (years), resultant ruffed grouse habitat delineations, number of stands, mean stand size (ha) and study area coverage (%) of Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Land class	Age	Habitat	*n*	Mean ± SE	Coverage
Mesic	40-80	MESIC4	23	21 ± 5.3	9.7
Mesic	>80	MESIC5	12	37 ± 8.7	9.1
Mesic	NA	RHODO	18	53 ± 20.3	19.6
Subxeric	0-5	SUBXER1[a]	30	2 ± 0.4	0.8
Subxeric	6-20	SUBXER2	40	10 ± 0.6	8.1
Subxeric	21-39	SUBXER3	7	11 ± 1.7	1.6
Subxeric	40-80	SUBXER4	8	16 ± 3.9	2.7
Subxeric	>80	SUBXER5	43	36 ± 4.3	31.5
Xeric	6-20	XERIC2	4	15 ± 4.4	1.2
Xeric	40-80	XERIC4	6	20 ± 3.4	2.4
Xeric	>80	XERIC5	15	39 ± 11.2	11.9
Roads	NA	ROAD	NA	NA	1.1
Openings	NA	WLO	24	0.5 ± 0.1	0.2

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[a] Represented alternative regeneration treatments (i.e., shelterwood, irregular shelterwood, and group selection).

Table 3.3. Ranks of habitats used versus availability at the study area scale for female ruffed grouse with broods on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it with corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Wlo	Subxer2	Subxer5	Subxer1	Road	Rhodo	Mescov4	Mescov5	Subxer3	Xeric2	Xeric4	Subxer4	Xeric5	Rank
Wlo		+	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	1
Subxer2			+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	2
Subxer5				+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	3
Subxer1					+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	4
Road						+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	5
Rhodo							+	+	+	+ + +	+	+ + +	+	6
Mescov4								+	+	+	+	+ + +	+	7
Mescov5									+	+	+	+	+	8
Subxer3										+	+	+	+	9
Xeric2											+	+	+	10
Xeric4												+	+	11
Subxer4													+	12
Xeric5														13

Table 3.4. A-*priori* candidate models, number of parameters estimated (K), bias-corrected Akaike's Information Criterion (AIC_c), and model weights (w_i) used to evaluate ruffed grouse brood microhabitat on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model[a]	K	AICc	ΔAIC	w_i
Gcvr + lat + midstem + arthropods	4	482.358	0.000	0.965
Gcvr + lat	2	489.757	7.399	0.024
Gcvr + lat + midstem	3	491.246	8.888	0.011
Gcvr	1	502.026	19.668	0.000
Arthropods	1	502.212	19.854	0.000
Lat	1	502.935	20.577	0.000
Lat + midstem	2	504.821	22.463	0.000
Midstem	1	512.816	30.458	0.000

[a] Gcvr = percent herbaceous groundcover
Lat = percent vertical vegetation cover 0.0 – 2.0 m in height
Midstem = density of woody stems <11.4 cm dbh
Arthropods = density of invertebrates in orders preferred by ruffed grouse chicks

Table 3.5. Microhabitat variables measured at sites used by ruffed grouse females with broods (*n* = 35) and corresponding random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

	Brood				Random			
Variable	Mean	*n*	SE	95% CI	Mean	*n*	SE	95% CI
Basal area (m^2/ha)	17.0	186	0.7	15.5–8.5	17.9	186	0.8	16.4–19.4
Canopy cover (%)	76.3	90	2.0	72.4–80.3	82.0	90	1.8	78.5–85.5
Std. dev. (%)[a]	12.1	90	1.1	9.9–14.3	6.9	90	0.7	5.6–8.2
Stem density (/ha)	6250	186	441	5380–7120	4963	186	355	4263–5662
Shrub (/ha)	2947	186	379	2198–3695	2172	186	309	1562–2781
Hardwood (/ha)	3303	186	217	2875–3732	2791	186	186	2424–3159
Lateral cover (%)								
0.00-2.00 m	52.3	186	2.0	48.4–56.3	41.5	186	2.0	37.6–45.3
0.00-0.40 m	77.1	186	1.8	73.6–80.6	65.3	186	2.0	61.4–69.2
0.41-0.80 m	57.0	186	2.3	52.5–61.5	45.7	186	2.2	41.4–49.9
0.81-1.20 m	47.6	186	2.3	43.0–52.1	36.6	186	2.3	32.0–41.1
1.21-1.60 m	41.7	186	2.4	36.9–46.4	32.6	186	2.3	28.0–37.2
1.61-2.00 m	38.4	186	2.5	33.4–43.3	27.1	186	2.3	22.7–31.6
Ground cover (%)								
Forb	23.5	186	1.6	20.3–26.7	21.1	186	1.6	17.8–24.3
Fern	23.3	186	1.9	19.6–27.0	17.6	186	1.5	14.7–20.5
Grass	5.6	186	0.8	4.0–7.2	4.3	186	0.8	2.6–5.9
Briar[b]	3.3	186	0.7	2.0–4.6	1.9	186	0.4	1.1–2.7
Total	55.7	186	2.0	51.8–59.7	44.8	186	2.0	40.8–48.7

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[a] Standard deviation of 4 canopy measurements taken at each site

[b] included coverage in greenbriar (*Smilax* spp.), blackberry, and raspberry (*Rubus* spp.)

Table 3.6. Density of invertebrates (number/m^2) preferred by ruffed grouse chicks at sites used by females with broods (*n* = 35) and corresponding random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

		Brood (*n* = 186)			Random (*n* = 186)		
Class	Order	Mean	SE	95% CI	Mean	SE	95% CI
Arachnida							
	Araneae	13.1	0.8	11.4–14.8	12.4	0.7	11.1–13.7
Hexapoda							
	Coleoptera	4.8	0.4	3.9–5.7	3.5	0.3	2.9–4.2
	Diptera	15.5	1.4	12.7–18.3	12.4	1.2	10.2–14.7
	Hemiptera	1.3	0.2	1.0–1.7	1.5	0.4	0.7–2.3
	Homoptera	8.0	1.2	5.7–10.3	5.0	0.5	4.0–6.1
	Hymenoptera	13.5	4.3	5.1–21.9	7.7	1.5	4.9–10.6
	Lepidoptera (Adult)	0.5	0.1	0.3–0.7	0.5	0.1	0.3–0.7
	Lepidoptera (Larval)	1.6	0.2	1.1–2.1	0.8	0.1	0.6–1.1
	Orthoptera	0.5	0.1	0.3–0.7	0.3	0.1	0.1–0.4

Table 3.7. Biomass of invertebrates (grams/m^2) preferred by ruffed grouse chicks measured at sites used by ruffed grouse females with broods (*n* = 35) and corresponding random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

		Brood (*n* = 186)			Random (*n* = 186)		
Class	Order	Mean	SE	95% CI	Mean	SE	95% CI
Arachnida							
	Araneae	0.033	0.003	0.026–0.039	0.025	0.002	0.021–0.029
Hexapoda							
	Coleoptera	0.014	0.002	0.10–0.018	0.016	0.003	0.010–0.021
	Diptera	0.008	0.001	0.006–0.009	0.006	0.001	0.005–0.007
	Hemiptera	0.002	0.001	0.001–0.003	0.003	0.001	0.001–0.004
	Homoptera	0.007	0.001	0.005–0.009	0.005	0.001	0.003–0.007
	Hymenoptera	0.010	0.003	0.003–0.017	0.005	0.001	0.003–0.007
	Lepidoptera (Adult)	0.002	0.001	0.000–0.004	0.003	0.001	0.000–0.005
	Lepidoptera (Larval)	0.014	0.004	0.007–0.021	0.009	0.003	0.003–0.014
	Orthoptera	0.011	0.003	0.004–0.017	0.012	0.004	0.004–0.021

Table 3.8. Means, associated standard error, and 95% confidence intervals for microhabitat variables, and density (number/m^2), and biomass (grams/m^2) of invertebrates preferred by ruffed grouse chicks measured at sites used by successful ($\geq$1 chick alive at 5 weeks post-hatch) and unsuccessful broods on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

	Successful (*n* = 63)			Unsuccessful (*n* = 34)		
Variable[a]	Mean	SE	95% CI	Mean	SE	95% CI
Basal Area (m^2/ha)	18.5	1.4	15.7–21.2	17.5	1.7	14.1–20.9
Stem Density (/ha)	4857	560	3,737–5,977	5,688	867	3,924–7,452
Lateral cover 0-2 m (%)	41.6	3.2	35.2–48.1	50.8	4.4	41.9–59.8
Ground cover (%)	52.8	3.0	46.7–58.9	45.6	5.1	35.4–55.9
Arthropod density	4.6	0.4	3.9–5.3	6.0	0.6	4.8–7.3
Arthropod biomass	0.0087	0.0009	0.0069–0.0105	0.0083	0.0018	0.0047–0.0119

[a] Stem desnity = density of woody stems <11.4 cm dbh/ha
Ground cover = percent herbaceous groundcover
Lateral cover = percent vertical vegetation cover 0–2 m in height
Arthropods = density of invertebrates in orders preferred by ruffed grouse chicks

Table 3.9. Frequency of occurrence (%) and percent of total stems $\geq$ 11.4 cm dbh measured on sites used by ruffed grouse females with broods on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Species	Percent occurrence in plots	Percent total stems
Quercus rubra	78.6	23.7
Acer rubrum	65.5	15.7
Amalanchier arborea	42.9	12.4
Fraxinus americana	35.7	7.7
Prunus serotina	35.7	6.1
Quercus alba	29.2	5.5
Betula alleghaniensis	22.6	4.1
Carya spp.	22.0	3.5
Robinia pseudoacacia	17.3	3.1
Betula lenta	12.5	2.7
Fagus grandifolia	11.3	2.5
Acer saccharum	10.1	1.5
Liriodendron tulipifera	6.5	1.9
Quercus montana	6.5	1.4
Tilia heterophylla	6.5	1.1
Magnolia acuminata	5.4	0.5
Halesia tetraptera	5.4	0.8
Aesculus flava	4.8	0.7
Quercus velutina	3.6	0.5
Prunus pennsylvanicum	2.4	0.2
Oxydendrum arboreum	1.8	0.3
Nyssa sylvatica	1.2	0.2
Sassafras albidum	1.2	0.0
Tsuga canadensis	1.2	2.5
Magnolia fraseri	0.6	1.5
Pinus strobus	0.6	0.0

Table 3.10. Frequency of occurrence (%) and percent of total stems ≤ 11.4 cm dbh measured on sites used by ruffed grouse females with broods on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Species	Percent occurrence in plots	Percent total stems
Castanea dentata	74.1	14.3
Acer rubrum	65.7	5.6
Amalanchier arborea	56.6	4.2
Quercus rubrum	55.9	4.3
Rhododendron calendulaceum	42.7	34.3
Acer pennsylvanicum	39.2	1.8
Rubus spp.	32.9	6.9
Ilex ambigua	30.8	1.9
Fraxinus americana	30.8	1.3
Robinia pseudoacacia	26.6	1.6
Carya spp.	26.6	1.5
Fagus grandifolia	25.9	4.8
Prunus serotina	24.5	1.3
Vaccinium spp.	23.1	2.8
Hamamelis virginiana	18.2	2.4
Magnolia acuminata	17.5	1.2
Sassafras albidum	16.8	1.4
Quercus alba	15.4	1.0
Betula alleghaniensis	14.0	1.1
Acer saccharum	13.3	1.1
Tsuga canadensis	9.8	0.4
Pyrularia pubera	9.1	0.5
Liriodendron tulipifera	7.0	0.4
Rhododendron maximum	6.3	1.0
Betula lenta	6.3	0.5
Kalmia latifolia	5.6	0.7
Gaylussacia ursina	5.6	0.2
Quercus montana	4.9	0.2

PART IV.

RUFFED GROUSE HABITAT USE AND INFLUENCE OF SEASON, SEX, AGE, AND LANDSCAPE CHARACTERISTICS ON HOME RANGE SIZE

ABSTRACT

Ruffed grouse (*Bonasa umbellus*) in the Great Lakes states (the geographic core of their distribution) have shown positive population responses to forest management. Because of differences in seasonal habitat requirements, forest management recommendations include interspersion of stand types to meet biological needs throughout the year. Managers in the southern Appalachians require an understanding of seasonal habitat use to manage for the species at the southern extent of its distribution. Ruffed grouse home ranges and habitat use were studied in the Appalachian Mountains of western North Carolina. The study area was divided into 3 distinct watersheds to examine effects of landscape characteristics on home range size. Habitat preference was determined through compositional analysis. Grouse (n = 276) were radiotagged and monitored $\geq$3 times/week. Seasonal 75% kernel home ranges (n =172) were estimated for 85 individuals. Mean home ranges were 15–59 ha depending on sex, age, and season. The best home range model included one explanatory variable, watershed ($AIC_c = 1,729.0$, $\omega_i > 0.999$). There was no support for models with sex, age, and season. The watershed with smallest home ranges had more patches of 6–20 year-old mixed oak with less distance among patches and greater interspersion compared to watersheds with larger home ranges. Forest roads and 6–20 year-old mixed oak were habitats preferred by all sex and age classes during all seasons. Early successional stands used by grouse had been harvested via clearcut, and alernative regeneration techniques (i.e., shelterwood and irregular shelterwood). Early successional forest is an important component of grouse habitat, though habitat quality may ultimately be determined by interspersion of young stands with other habitat types. Alternative regeneration techniques can be useful in interspersing habitat components.

Key words: Appalachians, *Bonasa umbellus*, habitat, home range, landscape characteristics, ruffed grouse.

INTRODUCTION

Home range is the area traversed by an animal during its normal activities over a specified period of time (Burt 1943, Kernohan et al. 2001). Home range size depends on individual traits, life history functions, environmental factors, and their interactions. For birds, home range size may be related to sex, age, food supply, breeding status, population density, and habitat distribution (Schoener 1968). McNab (1963) discussed home range size as a function of body size and food resource availability (i.e., bioenergetic demand). To optimize foraging and reduce risks associated with increased movement, animals should attempt to establish the smallest possible home range in habitats that meet all their needs (Badyaev et al. 1996); therefore, home range size may be a useful indicator of habitat quality, with smaller occupancy areas occurring on higher quality sites. Several studies of birds have shown inverse relationships between home range size and resource availability (Smith and Shugart 1987, Renken and Wiggers 1989, Whitaker 2003). Recent efforts have examined relationships of home range size with landscape features (Leary et al. 1998, Elchuck and Wiebe 2003).

Understanding landscape-scale habitat characteristics contributes information about ecological processes that impact wildlife (McGarigal and Marks 1995). Spatial characteristics including patch size, edge density, dispersion, interspersion, and juxtaposition have been shown to affect avian territory size, survival, and recruitment (e.g., Schmitz and Clark 1999, Hinsley 2000, Thogmartin and Schaeffer 2000, Elchuck and Wiebe 2003). Recently, Fearer and Stauffer (2003), and Whitaker (2003) identified landscape characteristics related to variations in home range size of ruffed grouse.

Ruffed grouse are forest-dwelling game birds distributed across boreal forests of Canada and the northern United States. In the eastern U.S., their range extends southward through the central and southern Appalachians. In the northern U.S. and southern Canada, where population densities are greatest, ruffed grouse are closely associated with aspen (*Populus tremuloides, P. grandidentata.*). Mature male aspen buds are an important winter food and regenerating stands of aspen provide year-round cover (Rusch and Keith 1971, Doer et al. 1974, Svoboda and Gullion 1972). South of the range of aspen, Appalachian grouse rely on a diversity of alternate food and cover resources (Servello and Kirkpatrick 1987).

Although forest types vary, a common characteristic of ruffed grouse habitat is dense woody cover with 17,000–34,000 stems/ha in hardwood saplings and brush considered optimal (Gullion 1984*a*). Suitable conditions often are found in young (5–20-year-old) forests created by timber harvest or natural disturbance; however, various age classes and forest types are used as biological activities and food availability changes through the year (Gullion 1972, Kubisiak et al. 1980, Whitaker 2003). Bump et al. (1947) advocated interspersion of habitats long before landscape analyses were commonplace. Since then, creating a mosaic of diverse habitat patches via forest management has been recommended throughout the literature (e.g., Berner and Gysel 1969, Gullion 1984*b*, Kubisiak 1998); however, most inferences are drawn from areas where aspen is a forest component.

Ruffed grouse studies in mixed oak forests have confirmed importance of early successional habitat (Stoll et al. 1995, Storm et al. 2003, Whitaker 2003). In the central and southern Appalachians (CSA), interspersion of forest types and age classes is especially important as grouse use diverse food sources (i.e., hard and soft mast, and herbaceous plants) in the absence of aspen (Whitaker 2003). Although clearcutting is generally recommended as a grouse habitat management practice, public land managers in the central and southern Appalachians are interested in use of esthetic alternatives to clearcutting. In addition to improved esthetics, techniques such as shelterwood, two-age, and group selection may be used to regenerate desirable species and influence hard mast production. Although these techniques have implications for creating grouse habitat, no studies have investigated their use by grouse in the CSA.

Managers require information regarding optimal size, shape, and placement of forest management units for ruffed grouse. Whitaker (2003) and Fearer and Stauffer (2003) studied relationships of home range size to habitat features in the Appalachian region. Both studies examined spatial features within home ranges, and found amount of edge and interspersion were indicators of habitat quality. Although these studies provided valuable insight into landscape composition effects on grouse home range size, many landscape measures of interest to managers, including patch size, patch shape, dispersion, interspersion, and juxtaposition were not included in home range models.

Ruffed grouse home range and habitat use were studied in the mountains of western North Carolina. Objectives were to (1) examine the relationship between sex and age on home range size; (2) determine temporal (seasonal) variability in home ranges; (3) estimate relative habitat preference; (4) identify landscape features of available habitats and their relationship to home range size; and (5) examine grouse use of stands harvested via alternative regeneration techniques.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (3,230 ha), within Nantahala National Forest in western Macon County, North Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges that connect upper elevations to narrow valley floors (Whittaker 1956). Wine Spring Creek, White Oak Creek, Cold Spring Creek, and surrounding ridges naturally divided the study site into 3 distinct watersheds. Mean annual temperature was 10.4º C, and mean annual precipitation was 160 cm. The area was predominantly forested with <1% coverage in small herbaceousopenings. The U.S.D.A. Forest Service purchased WSC in 1912 after it had been logged. Since then, forest management practices included salvage harvest of blight-killed American chestnut (*Castanea dentata*), thinning, clearcutting, and diameter-limit cutting (McNab and Browning 1993).

Habitats were classified by a combination of vegetative community type and stand age. Communities were stratified into 3 land classes (i.e., xeric, subxeric, and mesic) defined by elevation, landform, soil moisture, and soil thickness (McNab and

Browning 1993; Table 4.1; tables and figures are located in the Appendix). Within communities, variation in plant species occurred along a moisture continuum, similar to that described by Whittaker (1956). Xeric communities were on high elevation, steep, south and west aspects characterized by thin, dry soils. Tree species included, scarlet oak (*Quercus coccinea*), black oak (*Q. velutina*), pitch pine (*Pinus rigida*) and chestnut oak (*Q. prinus*) in the overstory with ericaceous plants including huckleberry (*Gaylussacia baccata*), lowbush blueberry (*Vaccinium vacillans*), and mountain laurel (*Kalmia latifolia*) in the understory. Subxeric communities were at middle elevations and upper elevations on less exposed aspects. Soil characteristics were between xeric and mesic, or subxeric and submesic (Whitaker 1956). Overstory was dominated by chestnut oak, white oak (*Q. alba*), hickory (*Carya* spp.), northern red oak (*Q. rubra*), red maple (*Acer rubrum*), and yellow poplar (*Liriodendron tulipifera*). Ericaceous understory occupied 25–50% groundcover on drier microsites whereas herbaceous plants occupied more mesic sites within this category. Mesic communities occurred on north and east aspects, on lower slopes, and in sheltered coves. Stands were comprised of yellow poplar, eastern hemlock (*Tsuga canadensis*), northern hardwoods, including sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), and mixed mesophytic obligates, including American basswood (*Tilia americana*) and yellow buckeye (*Aesculus octandra*). Understory was herbaceous except where rhododendron (*Rhododendron maximum*) inhibited groundcover. Sites with 75–100% cover in rhododendron were placed in a separate habitat classification (RHODO).

Additional land classes included gated forest roads (ROAD) and wildlife openings (WLO). Gated forest roads were defined by a buffer width of 5m from road center on each side. The 10-m width included the road and adjacent berm. Wildlife openings were small, permanent clearings (0.50 ± 0.12 ha SE). Management of roads and openings included an initial planting of orchardgrass (*Dactylis glomerata*), tall fescue (*Festuca arundinacea*) and white-dutch clover (*Trifolium repens*) maintained by annual or biennial mowing.

Stand ages were determined by years since harvest or stand establishment in categories deemed important to ruffed grouse (0–5, 6–20, 21–39, 40–80, >80). Grouse reportedly begin use of regenerating mixed hardwood and oak stands approximately six years after harvest (Kubisiak 1987, Thompson and Dessecker 1997). At 15–20 years of age, habitat quality decreases as the upper canopy closes and woody stem density and herbaceous ground cover decrease (Kubisiak 1987, Storm et al. 2003). Mixed hardwoods remain in a “pole stage” until 40 years of age, when most oak species have reached reproductive maturity and are capable of producing significant acorn crops (Guyette et al. 2004). By 80–120 years, oaks stands are considered full rotation age (U.S. Forest Service 1994). Beyond 120 years, natural mortality of upland oaks increases (Guyette et al. 2004), resulting in canopy gaps. Gated forest roads, wildlife openings and rhododendron-dominated understory were not assigned to age categories because they are in a state of arrested succession and their structural characteristics do not change appreciably over time (Phillips and Murdy 1985).

Stands in the 6–20-year age class were predominantly clearcuts (1.3–24.6 ha, n = 44) harvested in the late 1980s and early 1990s. Alternative regeneration harvests (i.e., shelterwood, irregular shelterwood, group selection) were cut 1996–1997, and represented the 0–5-year category (SUBXER1) for most of the study. Target residual basal area was 9.0 m^2/ha for shelterwood harvests. Prescriptions called for a final removal cut of residuals approximately 10 years after the initial harvest. Ruffed grouse data were collected prior to removal of residuals in these stands. Mean size of shelterwood stands was (5.56 ± 0.42 ha SE, n = 3). For irregular shelterwood (aka shelterwood with reserves), target residual basal area was 5.0 m^2/ha. Residuals in irregular shelterwood were to be retained through the next rotation, resulting in 2-aged stands. Mean size of 2-aged stands created by irregular shelterwood was (4.68 ± 0.18 ha SE, n = 3). Group selection was implemented in 3 stands with 4–9 groups/stand. Mean group size was 0.36 ha (± 0.05 SE). All shelterwood, irregular shelterwood, and group selection harvests were implemented on subxeric sites and represented the SUBXER1 habitat type.

Oak and mixed oak-hickory stands in the >80 year age class (SUBXER5) made up the greatest proportion of the study site (31.5%) and wildlife openings (WLO) made up the least (0.2%; Table 4.2). Early successional habitats in the 6–20-year age class (XERIC2 and SUBXER2) occupied 9.3% of the area. The 0–5, 6–20-year, and 21–39-year age classes were not represented on mesic sites. There were 52.6 km of gated forest roads (1.1% of total area).

Capture and Telemetry

Grouse were captured using intercept traps (Liscinsky and Bailey 1955, Gullion 1965) during two annual periods, late August–early November, and early March–early April, 1999–2003. Gender and age (juvenile or adult) were assessed by feather characteristics and molt patterns (Kalla and Dimmick 1995). Grouse tagged as juveniles in fall graduated to the adult age class at the end of the following summer. Grouse were weighed, leg-banded, fitted with 12-g necklace-style radiotransmitters with a 3-hour mortality switch (Advanced Telemetry Systems, Isanti, Minnesota), and released at capture sites. Tagged birds (*n* = 276) were located $\geq$3 times per week from permanent telemetry stations. To adequately represent diurnal time periods, an equal number of locations were recorded during the periods, morning (0700–1100), mid-day (1101–1500), and evening (1501–1900). Stations were geo-referenced using a Trimble Global Positioning System (Trimble Navigation Limited Inc., Sunnyvale, California, USA). Transmitter signals were received using Telonics TR-2 receivers (Telonics Inc., Mesa, Arizona, USA), Clark model H7050 headphones (David Clark Company Inc., Worcester, Massachusetts, USA), and hand-held 3-element yagi antennas. For each grouse location, time, azimuths (*n* = 3–5) to nearest degree, grouse activity (moving or still), and a relative measure of signal strength (1 = weakest, 5 = strongest) were recorded. A maximum of 20 minutes was allotted between first and last azimuths to minimize error from animal movement. While in the field, locations were plotted on paper maps to check precision of azimuths. Telemetry data were entered in Microsoft Excel and converted to x and y UTM coordinates using program LOCATE II (Nams 2000). Error was assessed by mean error ellipse of grouse locations and from test beacons (*n*=10) placed at central points (Jennrich and Turner 1969) in randomly selected grouse home ranges. Grouse locations with error ellipses >7 ha were culled from the data set. All field personnel triangulated beacons 4 times during March and June to account for potential foliage effects.

Home Range and Daily Movement

The Animal Movement Extension (Hooge and Eichenlaub 1997) to ArcView GIS 3.2 (Environmental Systems Research Institute Inc., Redlands, California, USA) with least squares cross validation was used to calculate seasonal fixed kernel home ranges (Worton 1989). Estimates were based on 75% kernel contours to define central portions of a home range (Seaman et al. 1999) and exclude the “occasional sallies” described by Burt (1943). To determine adequate sampling (minimum locations), home range area was plotted against number of locations to determine sampling level at which area variation decreased and became asymptotic. Only grouse with sufficient locations for home ranges to become asymptotic were used for analysis.

Four 91-day seasons were defined by plant phenology and grouse biology. Fall (15 September–14 December) was a period of food abundance and dispersal among juveniles. Winter (15 December–15 March) was defined by minimal food resources and physiological stress. Spring (16 March–14 June) coincided with vegetation green-up and breeding activity. Summer (15 June–14 September) was a period of low stress with maximum cover and food availability. Effect of breeding status on home range was evaluated by comparing spring (breeding) to fall and winter pooled (non-breeding). Summer was not included in seasonal analysis because only females with broods were monitored intensively in summer (Chapter III). In spring, home ranges of females known to nest included all locations prior to the onset of continuous incubation. To be included in a season, a grouse must have survived ≥75% of that season (68 days).

Daily movements were monitored by diurnal telemetry (focal runs). During a focal run, grouse were located once every 1.5–2.0 hours. Precision is necessary to ensure movements are reflective of grouse mobility, rather than a measure of telemetry error; therefore, focal locations with error ellipses >1 ha were excluded from analysis. To minimize error, grouse were monitored from proximate stations to prevent disturbing the bird and influencing its movement pattern. If a grouse was disturbed, the focal run was stopped and data were excluded from analysis. Data were collected for 10–20 grouse seasonally, fall 2000–spring 2004. Total daily movement for an individual was the sum of sequential travel distances (m/day), and movement rate was total daily movement divided by total locations (m/1.5 hrs).

Data Analysis

A geographic information system (GIS) was developed using color infrared aerial photographs, 1:24,000 U.S. Geologic Survey 7.5-min quadrangles, U.S. Forest Service Continuous Inventory of Stand Condition (CISCS), and ground truthing. Wine Spring (WSP; 842 ha), White Oak (WOC; 1,399 ha) and Cold Spring (CSP; 987 ha) watersheds were extracted from the GIS to examine landscape features of available habitat and their effects on home range size. Use of landform to define availability prevented spurious results that can be caused by geometric definition of landscapes (i.e., circular or square buffers). Grouse tended to remain within their watershed of capture. Birds that occupied >1 watershed (*n* = 3) were not included in analysis.

Program FRAGSTATS (McGarigal and Marks 1995) was used to calculate landscape metrics. FRAGSTATS output values at landscape, patch, and class (habitat) scales (Table 4.3). At the class scale, spatial characteristics of 6–20-year-old mixed oak (SUBXER2) and gated forest roads (ROAD) were examined because of their importance as grouse habitat in the Appalachians (Whitaker 2003). Metrics were chosen based on ability to describe features relevant to grouse habitat management and their relationships with each other (McGarigal and Marks 1995, Hargis et al. 1998). Of particular interest were metrics that described patch size, shape, dispersion, interspersion, and edge. Edges were weighted by contrast from 0 (low) to 1 (high) by increments of 0.25. For example, high contrast edges occurred along forest roads, wildlife openings, and boundaries between 0–20- and >40-year-old stands. Medium contrast edges occurred where 21– 39-year-old stands met 6–20-year-old and >40-year-old stands. Low contrast edges occurred between 40–80-and >80-year-old stands (Table 4.4). Vector data were converted to 10-m grids in ArcView 3.2. Analysis window size was defined by mean total daily movement distance of grouse.

An information-theoretic approach (Burnham and Anderson 1998) was used to evaluate sources of variation in home range size. A set of a-*priori* candidate models (Table 4.5) was created using combinations of sex, age, season, and watershed. A bias-corrected version of Akaike's Information Criterion (AIC_c), and weight of evidence (w_i), were used to rank and select the model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). The generalized linear models procedure (Proc GLM; SAS Institute Inc., Cary, North Carolina, USA) was used to calculate –2log-likelihood values for each model. Log-likelihoods were then used to calculate AIC_c. Generalized linear models also were used to test for effects of sex, age, and season on diurnal movements.

Habitat use was compared with availability at the study area scale (second-order selection; Johnson 1980). Use was defined by the proportion of habitats within home ranges. Availability was defined by topographic features surrounding the study area. Road systems facilitated access to most tagged grouse. If a bird traveled beyond the steep ridges surrounding the study area, use could not be measured; therefore, those areas were not included in availability. Use was compared with availability using compositional analysis (Aebischer et al. 1993). Relative ranks of habitat use were assigned by calculating pair-wise differences in use versus availability for corresponding habitat log-ratios. Shapiro-Wilk test was used to test for normality in log-ratio differences. An advantage of compositional analysis is that it allows testing for between group differences in habitat use. Differences were tested between age groups (juvenile and adult), within sexes and seasons. Significance tests ($\alpha = 0.05$) also were used to examine differences in relative preference among ranked habitats (Aebischer et al. 1993). To control Type I error, data were examined for 0% observations in any available habitat (Bingham and Brennan 2004). Wildlife openings had 0% observations and were <1% of available habitats; therefore, in the habitat coverage, openings were incorporated into the surrounding habitat type and excluded from analysis.

RESULTS

Home Range and Movements

Telemetry bearing error on beacons was ± 6.53^{o}. Mean grouse location error ellipse (n=6,656) was 1.9 ha (± 0.06 SE). Diurnal data were available for 24 grouse (6 adult female, 3 juvenile female, 7 adult male, 8 juvenile male) in fall, and 10 grouse (5 adult male, 5 juvenile male) in spring. Total mean daily movement (874 ± 72.1 m SE) did not differ between spring and fall or among sex and age classes ($F_5 = 0.9$, $P = 0.492$); therefore, 874 m was used as the analysis window for landscape analysis.

Seasonal home ranges (n=172) were estimated for 85 individuals (4.6). Mean locations/home range was 27 (± 3.1 SE). The most parsimonious home range model included one explanatory variable, watershed ($AIC_c = 1729.0$, $\omega_i > 0.999$). There was no evidence of support for home range models with sex, age, season, breeding status, and their interactions as explanatory variables (Table 4.7). Pooled seasonal home ranges were smallest on CSP (14.6 ± 2.8 ha SE) and greatest on WSP (36.2 ± 3.6 ha SE; Table 4.8). To examine effects of sex, age, season, and their interactions on home range size, an *a-posteriori* model of these variables was run in the absence of watershed. No variables in the model were significant ($P > 0.293$).

Landscape Features

There were differences in several landscape and patch metrics among watersheds (Tables 4.9, 4.10). Mean nearest neighbor distance (MNN) for 6–20 year old mixed oak stands (SUBXER2) was 31 m on CSP, 100 m on WOC, and 103 m on WSP, indicating less distance between neighboring SUBXER2 patches on CSP. Mean proximity index (MPI) of SUBXER2 was 142% and 198% greater on CSP compared with WOC and WSP, respectively, indicating more SUBXER2 patches within the analysis window on CSP. Interspersion juxtaposition index (IJI) of SUBXER2 was closer to the maximum of 100% on CSP (76%), compared with WOC (55%), and WSC (60%). Proportion (PROP), mean patch size (MPS), and mean shape index (MSI) of SUBXER2 were similar among watersheds. Gated access roads (ROAD) were not considered for MNN and MPI because roads were included as single linear patches in the GIS, and FRAGSTATS requires ≥2 patches of a corresponding type for these calculations. For ROAD, IJI was 85%, 76%, and 78% on CSP, WOC, and WSC, respectively, indicating similar interspersion of forest roads with other habitat types across watersheds. Proportion of ROAD also was similar on the 3 areas.

Fall Habitat Use

Differences in log-ratios were normally distributed for all sex and age classes within seasons (Shapiro-Wilk > 0.950, $P < 0.001$). Habitat use did not differ between juvenile and adult females ($P = 0.449$); therefore, female age classes were pooled for fall ($n = 29$). Habitat use by females differed from availability ($P < 0.001$). Top-ranked habitats were SUBXER1, SUBXER2, ROAD, RHODO, and MESIC4, with no difference among habitats (Table 4.11). Least ranked habitats were MESIC5 and XERIC4. Fall habitat use differed between adult and juvenile males ($P < 0.001$). There were fewer juvenile males than habitat types in the sample; therefore compositional analysis could not be used to assess habitat use by juvenile males. For adult males ($n = 30$), use differed from availability (P < 0.001). Greatest ranked habitats for adult males in fall were SUBXER2 and ROAD, with no difference between these types (Table 4.12). Least ranked habitats were SUBXER3, SUBXER4, XERIC4, XERIC5, and MESIC5.

Winter Habitat Use

Similar to fall, female habitat use in winter did not differ between juveniles and adults ($P = 0.460$); therefore female age classes were pooled. Female ($n = 28$) habitat use differed from availability ($P < 0.001$). Habitats preferred by females in winter were SUBXER1, SUBXER2, SUBXER5, ROAD, RHODO, and XERIC5 (Table 4.13). These habitats did not differ among each other. Least ranked habitats were XERIC4 and MESIC5, with no difference between them. For males in winter, habitat use did not differ between juveniles and adults ($P = 0.725$); therefore, age classes were pooled. Habitat use for males ($n = 28$) differed from availability ($P < 0.001$). Greatest ranked habitats were

SUBXER2 and ROAD with no difference between these types (Table 4.14). Least ranked habitats were XERIC4, XERIC5, and MESIC5.

Spring Habitat Use

Habitat use in spring did not differ between age classes for females ($P = 0.313$) or males ($P = 0.160$) in spring. Habitat use by females ($n = 32$) differed from availability ($P < 0.001$). Habitats preferred by females in spring were SUBXER1, SUBXER2, ROAD, and MESIC4, with no differences among habitats (Table 4.15). Least ranked habitats were XERIC4, SUBXER4, and MESIC5. Habitat use by males ($n = 34$) differed from availability ($P < 0.001$). The most preferred habitat for males in spring was ROAD (Table 4.16). Least ranked habitats were XERIC4, SUBXER4, and MESIC5, with no differences among habitats.

DISCUSSION

Habitat Use

Forest roads were among preferred habitats for all sex and age classes, during all seasons. Several studies cite the importance of roads as grouse habitat in the central and southern Appalachians (Stewart 1956, Endrulat 2003, Whitaker 2003). Roads can provide an herbaceous food source especially important during winter and early spring and in years of low mast production (Whitaker 2003). In Minnesota, where aspen nourishes grouse in winter, Gullion (1984*b*) suggested roads were a marginal habitat used when optimal areas were not available. In the Appalachians, herbaceous plants serve as quality forage for ruffed grouse (Stoll et al. 1980, Servello and Kirkpatrick 1987), and can provide a crucial winter food source in the absence of aspen. Cinquefoil (*Potentilla* spp.)

and wild strawberry (*Fragaria virginiana*) were plant protein sources especially important to females in the central and southern Appalachians prior to nesting (Long and Edwards 2004). These and other forbs often germinate from the seedbank following forest road closure. Preference of ROAD by males during the breeding season was influenced by their juxtapositon to other habitat types. Males on the study area established drumming territories on upper slopes and ridge tops with dense mid-story structure (Schumacher et al. 2001). Drumming sites often were in close proximity to ROAD, where males could attract females while remaining near safety of dense cover (Figure 4.1; Bergerud and Gratson 1988). In northern Georgia, Hale et al. (1982) also reported that drumming logs were in dense cover, close to forest openings (79% within 50 m of an opening).

Subxeric mixed oak in the 6–20-year age class was among habitats preferred by females in fall, winter, and spring, and by males in fall and winter. Association of ruffed grouse with early seral stages is well documented (Dessecker and McAuley 2001); however, interspersion of diverse forest types and age classes ultimately determines habitat quality (Bump et al. 1947, Berner and Gysel 1969, Gullion 1972, Kubisiak 1985). Interspersion of young stands for cover (i.e., high stem density) with mature stands for food (i.e., hard mast) is important, as grouse must optimize the balance between energy gain and predation risk (Cowie 1977). Nutritional constraints posed by reproduction may cause females to spend more time in foraging habitats, while males opt for cover (Whitaker 2003). Data from WSC support this contention. In fall and winter, adult males used fewer habitats compared to females, and selection for escape cover was evident in relative preference for 6–20-year-old subxeric mixed oak.

In fall, winter, and spring, females had $\geq$ 5 habitats ranked highest in preference, with no difference among them. Habitats that may have been preferred because of cover were RHODO, SUBXER1, and SUBXER2 in all seasons. Potential foraging habitats represented a topographic cross section and included MESIC4, ROAD, and SUBXER5 in fall, and ROAD, SUBXER5, and XERIC5 in winter. Inclusion of more xeric habitat in winter likely indicates a shift in diet to evergreen leaves such as laurel and trailing-arbutus (*Epigaea repens*) available on dry upper slopes (Servello and Kirkpatrick 1987).

Foraging habitats used by females were juxtaposed to escape cover (Figure 4.2.). Subxeric mixed oak stands in the 6–20-year age class provided cover and additional foraging opportunities between mature stands on upper and lower slopes. An example of juxtaposition as a proximate cue to females selecting foraging habitat was a high preference rank for MESIC4 and low preference for MESIC5 in fall. Food availability in terms of mast should be similar between these habitats; however, MESIC5 existed in several large patches, poorly interspersed with escape cover, whereas MESIC4 patches were irregularly shaped and juxtaposed to cover. Further, use of MESIC4 by females in spring was influenced by 6 females that used a stand selectively thinned to approximately 75% residual canopy cover in 1993, which likely resulted in increased midstory and herbaceous groundcover, and improved conditions for grouse in this stand.

With the exception of males in fall, habitat use did not differ between juveniles and adults. Juvenile males had greater proportions of ROAD, SUBXER1, SUBXER2, and MESIC5 in fall home ranges, compared with availability; however, sample size was insufficient ($n = 8$) to test differences statistically. After brood break-up in early fall, juvenile males disperse and seek potential breeding territories for the following spring (Hale and Dorney 1963, Small and Rusch 1989). The largest home ranges observed on this study were of juvenile males in fall (59.1 ± 27.4 ha SE). Relatively large home ranges and diverse habitat use may have resulted from occupation of unfamiliar areas and sampling of habitats for suitable spring territories. Such wandering was apparently complete by winter, when home range size decreased (21.5 ± 6.9 ha SE), and juvenile males selected habitats similar to those used by adults.

Use of shelterwood and 2-aged stands was indicated by inclusion of SUBXER1 among habitats preferred by females in fall, winter, and spring. Stands harvested via alternative regeneration techniques were restricted to the southern third of the study site (i.e., WSP watershed). Nonetheless, 22 of 89 grouse on WSP (7 juvenile females, 1 adult female, 7 juvenile males, 7 adult males) included shelterwood and 2-aged stands in their home ranges, although these stands were 0–5-years-old for most of the study and had not yet reached the 6–20-year age class. Grouse began using shelterwood and 2-aged stands 3 years after harvest and continued through the end of the study, 6 years post-harvest. Onset of use was consistent with findings of Stoll et al. (1999) in mixed oak-hickory clearcuts in Ohio, but earlier than reports of 7 years from Pennsylvania (Storm et al 2003) and Wisconsin (McCaffery et al. 1997). Gullion (1984) observed that grouse first utilized regenerating clearcuts when hardwood stems were naturally thinned to ≤37,000 stems/ha. Stem densities at 3 years post-harvest in this study were approximately 38,269 stems/ha and 49,117 stems/ha, in shelterwood and 2-aged stands, respectively (Elliott and Knoepp 2005). Group selection cuts were not used extensively in fall, winter or early spring; however, they were important brood habitats in late spring and summer (see Chapter III).

Shelterwood and 2-aged stands can provide sufficient regenerating stem densities for cover and mature mast-producing trees for food within the same stand. Studies in the central and southern Appalachians showed similar stem densities among shelterwood, 2-aged, and traditional clearcuts at 5–10 years after harvest (Beck 1986, Smith et al. 1989, Miller and Schuler 1995). Regarding food availability, acorns are a high quality food for Appalachian ruffed grouse (Servello and Kirkpatrick 1987). Two-aged stands moderate the time lag in acorn production that normally follows clearcutting (Beck 1986, Smith et al. 1989) and can increase number of acorns produced by individual trees (Stringer 2002). Shelterwood has a similar positive effect, though for a shorter time, prior to removal of residual overstory. Canopy disturbance and improved light conditions promote other grouse food sources in addition to acorns. In southwestern Virginia, herbaceous species richness increased following group selection, shelterwood, irregular shelterwood, and clearcutting (Wender et al. 1999). Miller and Schuler (1995) noted prevalence of wild grape (*Vitus* spp.), flowering dogwood (*Cornus florida*), pin cherry (*Prunus pennsylvanica*), and American hophornbeam (*Carpinus caroliniana*) in a 2-aged stand 10 years after harvest in West Virginia. Norman and Kirkpatrick (1984), and Servello and Kirkpatrick (1987) cited leaves of herbaceous plants and soft fruits as important foods for Appalachian grouse, and suggested silvicultural practices that encourage these foods may increase carrying capacity. Thus, compared to clearcutting, shelterwood and irregular shelterwood have the unique ability to create diverse food resources and cover in the same stand, and their application could positively impact grouse populations. Potential benefits of irregular shelterwood over shelterwood include greater stem density (Elliott and Knoepp 2005) and retention of mature mast-producing trees throughout the rotation.

Home Range and Landscape Characteristics

Ruffed grouse home range size has been reported across the species' range. Earlier studies used minimum convex polygon methods (MCP; Mohr 1947) to estimate utilization distributions (Table 4.17; White and Dimmick 1978, Kurzejeski and Root 1989, Thompson and Fritzell 1989, McDonald et al. 1998), and differences in methodology make comparisons across studies difficult (Lawson and Rodgers 1997). Use of 75% kernel methods allowed comparisons between this study and Appalachian Cooperative Research Project (ACGRP) results pooled across 9 study areas in Kentucky, Maryland, Pennsylvania, Rhode Island, Virginia, and West Virginia (Whitaker 2003). Female home ranges in fall, winter, and spring (Table 4.6) were similar to pooled estimates from other ACGRP sites (Table 4.17). Males had larger mean home ranges compared to ACGRP during all seasons. For fall-winter, mean home range size for males pooled across ACGRP sites was 17 ha, compared with 47 ha and 23 ha in fall and winter, respectively in this study. Mean spring-summer home range size for males on ACGRP sites was 10 ha compared with 22 ha reported here for spring only. Some differences in home range size may have resulted from comparisons of fall-winter, and spring-summer seasons used by ACGRP, with individual fall, winter, and spring estimates reported here. Greater number of locations collected during pooled seasons may have resulted in condensed 75% kernel contours and smaller home range areas on ACGRP sites.

Mean home range sizes were 2 times greater on WOC and WSP watersheds compared to CSP. Season, sex, and age were not predictors of home range size; therefore, structure and composition of available habitat were examined to explain differences among the 3 areas. Use of timber harvest to sustain a proportion of early seral stages is one of the most important aspects of grouse management (Gullion 1984*b*). Fifty percent coverage in the 5–15-year age class has been recommended in aspen communities (Gullion 1972). For mixed oak, prescriptions range from 12% (Stoll et al. 1999) to 20% (Storm et al. 2003). In this study, CSP had slightly less proportional coverage in SUBXER2 (7%) than WOC (9%) and WSP (9%); however, these differences were small and likely negligible in their effect on home range size. In the Appalachians, Endrulat (2003) found no relationship of home range size to habitat quality based on proportion of early successional habitats alone.

Size, dispersion, juxtaposition, and interspersion of habitats also must be considered. Mean size of SUBXER2 stands on CSP was 4.16 ha (0.8 SE). Gullion (1972) cited 4.2 ha as the optimal management unit for ruffed grouse habitat. Patches of SUBXER2 on WOC (7.81 ± 1.0 ha SE) and WSC (5.71 ± 1.0 ha SE) were larger than CSP, and slightly greater than the 0.5–5.0 ha range recommended for the Appalachians by Fearer and Stauffer (2003); however, they were within the 2–8 ha range suggested by Stoll et al. (1999) on mixed-oak sites in Ohio.

Mean nearest neighbor, MPI, and IJI revealed SUBXER2 patches were in closer proximity to each other and had greater interspersion and juxtaposition with other habitats on CSP. The combination of size, dispersion, juxtaposition, and interspersion of SUBXER2 likely influenced home range size. Dispersion of early successional forest stands on CSP allowed grouse to minimize movements between patches of cover while interspersion with uncut stands provided additional food sources in close proximity. In Ohio’s mixed mesophytic forests, Stoll et al. (1980) found that in addition to suitable cover, early successional stands ranked highest in production of preferred grouse foods.

Mature, uncut stands also provide important foods in the form of hard mast and herbaceous plants (Stoll et al. 1980, Servello and Kirkpatrick 1987). Interspersion of these forest types on CSP may have created relatively greater habitat quality, resulting in smaller home ranges.

Forest roads can be an important habitat for grouse in the Appalachians, providing an herbaceous food source especially important during winter and early spring and in years of low mast production (Whitaker 2003). Forest roads initially planted with a mix of clover and annual grasses, then mowed annually, also produce arthropods important to grouse chicks (Harper et al. 2001). In this study, ROAD was a preferred habitat for all sex and age classes during all seasons. Gated forest roads intersected most SUBXER2 patches on CSP, but not on the other watersheds. The intersection of SUBXER2 with ROAD decreased patch size and increased interspersion and juxtaposition. Similar to the relationship of SUBXER2 with mature forest, ROAD juxtaposed to SUBXER2 presented food and cover in immediate proximity.

Amount of edge in a landscape and its impact on grouse has been debated. Males tend to use drumming sites near edges (Kubisiak et al. 1980), where they can attract females while remaining near the safety of dense cover (Bergerud and Gratson 1988). Attesting to potential edge benefits to grouse, Fearer and Stauffer (2003) found high contrast edge had an inverse relationship with home range size. Conversely, Gullion (1984) suggested apparent edge use by grouse was a function of preference for interspersed habitats and extensive use indicated poor habitat quality. McCaffery et al. (1996) found that grouse abandoned edges in uncut forest when early successional habitats were made available. In this study, edge density was similar across watersheds despite greater intersperion of patch types on CSP. The presence of high contrast edge, such as along roads and clearcuts, did not appear to influence home range size; however, edge relationships with other aspects of population ecology, including nest success and survival, deserve further investigation (Donovan et al. 1997).

Amount of edge on a landscape is influenced by patch shape. Some studies propose regularly shaped cuts to provide habitat for ruffed grouse (Gullion 1984*b*, Fearer and Stauffer 2003, Storm et al. 2003). On some sites, topography, aspect, moisture, tract size, forest type, and stand age distribution are the most important considerations in prescribing management unit shape (Kubisiak 1985, Whitaker 2003). In this study, mean shape index (MSI) was used to quantify patch form. For MSI calculations in FRAGSTATS, regularly shaped features (circles or squares) are assigned a value of 1, and MSI increases without limit as shape becomes more irregular (McGarigal and Marks 1995). Mean shape index of SUBXER2 stands was <1.9 across watersheds, indicating regularly shaped patches. Based on similarity among watersheds, patch shape did not appear to affect home range size. In the central and southern Appalachians, where steep ridges are intersected by ephemeral and permanent drainages and paralleled by mesic lower slopes, landform and forest characteristics should influence patch shape. The ability to intersperse early successional stands according to site-specific features is the most important determinant of patch shape.

MANAGEMENT IMPLICATIONS

Provision of early successional forest habitat is a cornerstone of ruffed grouse management. To maximize benefits of silvicultural practices, land managers in the

Appalachians require information on size, shape, dispersion, interspersion, and juxtaposition of management units. Home range size can serve as an indicator of habitat quality and may be related to survival (Thompson and Fritzell 1989, Clark 2000). Insight was provided through description of landscape-scale features of available habitats associated with reduced home range size. The area with smallest home ranges had the following landscape characteristics when compared to 2 other areas with larger home ranges: (1) less distance between stands of mixed oak forest in the 6–20 year age class; (2) more patches of early successional forest within the mean daily movement distance of grouse; and (3) greater interspersion and juxtaposition of early successional habitats with gated forest roads and other forest types.

Topography of the southern Blue Ridge creates diverse vegetation communities defined by changes in soil type, thickness, and moisture (Whittaker 1959). Often, various communities and associated ecotones occur in close proximity. The diverse features of southern Appalachian forests offer a unique opportunity to provide a mosaic of habitat types preferred by ruffed grouse.

Management prescriptions should be based on interspersion and juxtaposition of early successional habitats to other preferred types. On this study site, in addition to 6–20-year-old mixed oak, important habitats included gated forest roads, 40–80-year old mixed oak, 80–130-year-old mixed oak, and 40–80-year-old mesic-mixed hardwood. Regarding patch size, early successional habitat created by several smaller cuts can increase interspersion compared to a single, larger cut, provided the smaller units are placed in close proximity to each other and to other important habitats. Based on home range differences across watersheds, ideal patch size was 4 ha (mean SUBXER2 patch size on CSP), though the range of 0.5–8.0 ha should be acceptable.

Results from this study support the contention that habitat management for ruffed grouse should include a diversity of forest types, age classes, and openings that provide food and cover in close proximity. In the Appalachians, leaves of herbaceous plants, soft mast, and hard mast are important food items. Herbaceous plants can be provided on forest roads and in mature stands, especially on mesic and subxeric sites. Soft fruits such as greenbriar (*Smilax* spp.), blackberry, raspberry (*Rubus* spp.), and hawthorn (*Crataegus* spp.) are found along roads, in forest openings, and in stands 0–5-years-old, whereas more shade tolerant fruit producers, including flowering dogwood, blueberry, and huckleberry occur under closed or partial canopies. Substantial hard mast production from oaks and beech requires trees ≥30 years old. These trees can be in mature tracts or as residuals in shelterwood and 2-aged stands. The main focus is to recognize ruffed grouse food sources (or potential food sources), and use silviculture to augment and intersperse these areas with early successional habitats.

The traditional approach to creating early successional cover for grouse relies on clearcutting. Currently, public land managers find litigation a difficult barrier limiting forest management options. Given their ability to produce food and cover and their utility as an esthetic alternative to clearcutting, alternative regeneration techniques (i.e., shelterwood, irregular shelterwood, and group selection) can be important tools in forest management for Appalachian ruffed grouse. Whether through traditional even-aged or alternative regeneration methods, creation of early successional habitat should occur on mid-slope subxeric sites to join mesic lower slopes with xeric uplands. Conditions also could be improved through timber harvest on upland and mesic sites. Placement of harvest units according to landform will allow site-specific flexibility and interspersion of habitat types across vegetation communities and moisture gradients.

Habitat could be improved further through a minimal maintenance approach to forest roads (Healy and Nenno 1983). By seeding a mixture of an annual grain such as winter wheat (*Triticum aestivum*) with clover (*Trifolium* spp.), roads can be stabilized to prevent erosion while providing food sources for grouse and other wildlife. Over time, forbs germinating from the seed bank should maintain vegetation on the site and further enhance habitat quality (Harper et al. 2001, Long et al. 2004). Opening the forest canopy along roads (i.e., daylighting) could be used to stimulate herbaceous plant growth and create adjacent midstory stem cover.

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APPENDIX

Table 4.1. Forest stand associations, understory characteristics, and corresponding USDA Forest Service (USFS) and Society of American Foresters (SAF) codes for land classifications used to define ruffed grouse habitats on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina 1999–2004. Adapted from McNab and Browning (1993).

Land class	Moisture	Forest associations	Understory	USFS	SAF
Xeric	Xeric	Scarlet oak	>75% ericaceous	59	NA
	.	Pitch pine-oak	>75% ericaceous	15	45
	.	Chestnut oak-scarlet oak	50-75% ericaceous	60	NA
	Subxeric	Chestnut oak	50-75% ericaceous	52	44
Subxeric	Subxeric	Chestnut oak	25-50% ericaceous	52	44
	.	White oak-red oak-hickory	25-50% ericaceous	55	52
	.	Northern red oak	Herbaceous	53	55
	Submesic	Yellow poplar-white oak-red oak	Herbaceous	56	59
Mesic	Submesic	Yellow poplar	Herbaceous	50	57
	.	Sugar maple-beech-yellow birch	Herbaceous	81	25
	.	Basswood-yellow buckeye	Herbaceous	41	26
	Mesic	Hemlock	>75% rhododendron	8	23

Table 4.2. Land class, stand age (years), resultant ruffed grouse habitat delineations, number of stands, mean stand size (ha) and study area coverage (%) of Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Land class	Age	Habitat	*n*	Mean ± SE	Coverage
Mesic	40-80	MESIC4	23	21 ± 5.3	9.7
Mesic	>80	MESIC5	12	37 ± 8.7	9.1
Mesic	NA	RHODO	18	53 ± 20.3	19.6
Subxeric	0-5	SUBXER1	30	2 ± 0.4	0.8
Subxeric	6-20	SUBXER2	40	10 ± 0.6	8.1
Subxeric	21-39	SUBXER3	7	11 ± 1.7	1.6
Subxeric	40-80	SUBXER4	8	16 ± 3.9	2.7
Subxeric	>80	SUBXER5	43	36 ± 4.3	31.5
Xeric	6-20	XERIC2	4	15 ± 4.4	1.2
Xeric	40-80	XERIC4	6	20 ± 3.4	2.4
Xeric	>80	XERIC5	15	39 ± 11.2	11.9
Roads	NA	ROAD	NA	NA	1.1
Openings	NA	WLO	24	0.5 ± 0.1	0.2

Table 4.3. Metrics used to quantify landscape-scale habitat variables for ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Metric	Scale	Description
Total area	Landscape	Landscape area (ha)
Shannon's diversity index	Landscape	Measure of diversity by richness
Shannon's evenness index	Landscape	Measure of diversity by evenness
Largest patch index	Landscape	Proportion of the landscape occupied by the largest patch (%)
Mean patch size	Landscape, patch	Mean size (ha) of habitat patches
Mean shape index	Landscape, patch	Shape complexity of habitat patches
Total core area index	Landscape, patch	Proportion of core area within patches
Contrast weighted edge density	Landscape, patch	Total edge, weighted by contrast values, per unit area
Interspersion-juxtaposition index	Landscape, patch	Distribution of patch adjacencies
Proportions	Class	Proportion of landscape covered by each patch type
Mean nearest neighbor	Patch	Degree of isolation of habitat patches
Mean proximity index	Patch	Degree of isolation and fragmentation of habitat patches

* See McGarigal and Marks (1995) for formulas and detailed descriptions of habitat metrics.

Table 4.4. Edge weights used in evaluating ruffed grouse habitat at the landscape scale on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Habitat 1	Habitat 2	Edge Weight
MesCov4	MesCov5	0.00
Subxer4	Subxer5	0.00
Subxer2	Xeric2	0.00
Xeric4	Xeric5	0.00
Subxer4	MesCov4	0.25
Subxer5	MesCov4	0.25
Subxer4	MesCov5	0.25
Subxer5	MesCov5	0.25
Subxer3	MesCov4	0.50
Subxer3	MesCov5	0.50
Subxer3	Subxer4	0.50
Subxer3	Subxer5	0.50
Rhodo	Xeric4	0.50
Subxer3	Xeric4	0.50
Subxer4	Xeric4	0.50
Rhodo	Xeric5	0.50
Subxer4	Xeric5	0.50
Subxer5	Xeric5	0.50
MesCov4	Xeric4	0.75
MesCov5	Xeric4	0.75
Subxer5	Xeric4	0.75
MesCov4	Xeric5	0.75
MesCov5	Xeric5	0.75

Table 4.4. continued.

Habitat 1	Habitat 2	Edge Weight
Subxer1	Rhodo	1.00
Subxer2	Rhodo	1.00
Subxer3	Rhodo	1.00
Subxer4	Rhodo	1.00
Subxer5	Rhodo	1.00
MesCov4	Road	1.00
MesCov5	Road	1.00
Rhodo	Road	1.00
Subxer1	Road	1.00
Subxer2	Road	1.00
Subxer3	Road	1.00
Subxer4	Road	1.00
Subxer5	Road	1.00
Subxer1	Subxer2	1.00
Subxer1	Subxer3	1.00
Subxer2	Subxer3	1.00
Subxer1	Subxer4	1.00
Subxer2	Subxer4	1.00
Subxer1	Subxer5	1.00
Subxer2	Subxer5	1.00
MesCov4	WLO	1.00
MesCov5	WLO	1.00
Rhodo	WLO	1.00
Road	WLO	1.00
Subxer1	WLO	1.00
Subxer2	WLO	1.00
Subxer3	WLO	1.00
Subxer4	WLO	1.00
Subxer5	WLO	1.00
Xeric2	WLO	1.00
Xeric4	WLO	1.00

Table 4.4. continued.

Habitat 1	Habitat 2	Edge Weight
Xeric5	WLO	1.00
MesCov4	Xeric2	1.00
MesCov5	Xeric2	1.00
Rhodo	Xeric2	1.00
Road	Xeric2	1.00
Subxer1	Xeric2	1.00
Subxer3	Xeric2	1.00
Subxer4	Xeric2	1.00
Subxer5	Xeric2	1.00
Road	Xeric4	1.00
Subxer1	Xeric4	1.00
Subxer2	Xeric4	1.00
Xeric2	Xeric4	1.00
Road	Xeric5	1.00
Subxer1	Xeric5	1.00
Subxer2	Xeric5	1.00
Xeric2	Xeric5	1.00

Table 4.5. A-*priori* candidate models used to evaluate variation in home range size of ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model structure	Model definition
HR(age)	HR differs by age
HR(sex)	HR differs by sex
HR(season)	HR differs among seasons
HR(watershed)	HR differs among watersheds
HR(sex*age)	HR differs by sex and age
HR(sex*age*season)	HR differs by sex and age among seasons
HR(sex*season)	HR differs by sex among seasons
HR(age*season)	HR differs by age among seasons
HR(age*watershed)	HR differs by age among watersheds
HR(sex*watershed)	HR differs by sex among watersheds
HR(season*watershed)	HR differs by season among watersheds
HR(sex*age*watershed)	HR differs by sex and age among watersheds
HR(spring≠[fall=winter])	HR in breeding season differs from non-breeding seasons
HR(sex*age*spring≠[fall=winter])	HR differs by sex and age and by breeding or non-breeding seasons
HR(watershed*sex*age*season)	Global model used to assess overdispersion

Table 4.6. Mean home range size (ha), sample size, standard error (SE), and 95% confidence intervals for ruffed grouse by sex, age and season on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Season	Sexage[a]	*n*	Mean	SE	LCL	UCL
Fall	AF	17	28.3	7.4	12.7	43.9
	JF	9	41.2	9.5	19.3	63.0
	AM	27	35.2	10.4	13.7	56.7
	JM	8	59.1	27.4	5.6	123.8
Winter	AF	11	22.1	5.1	10.7	33.4
	JF	12	28.1	6.1	14.7	41.6
	AM	21	24.5	4.3	15.5	33.5
	JM	6	21.5	6.9	3.8	39.2
Spring	AF	13	31.6	4.3	22.2	41.1
	JF	16	30.9	4.9	20.4	41.4
	AM	18	15.0	3.7	7.3	22.7
	JM	14	28.2	6.6	13.9	42.4

[a] Sex and age classes
AF = adult female
JF = juvenile female
AM = adult male
JM = juvenile male

Table 4.7. Comparison of number of parameters estimated (K), Akaike's Information Criterion (AIC_c), differences in AIC_c, and model weights (w_i) for ruffed grouse home range size models based on sex, age, season and location (watershed) on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model	K	AICc	ΔAICc	*w*i
HR(watershed)	4	1729.03	0.00	0.999999
HR(age)	3	1764.01	34.98	0.000001
HR(sex)	3	1765.07	36.04	0.000000
HR(spring≠[fall=winter])	3	1768.51	39.48	0.000000
HR(season)	4	1769.99	40.96	0.000000
HR(sex*age*spring≠[fall=winter])	6	1770.84	41.81	0.000000
HR(sex*watershed)	9	1771.25	42.22	0.000000
HR(age*watershed)	9	1772.11	43.08	0.000000
HR(sex*age)	5	1772.49	43.46	0.000000
HR(sex*season)	9	1772.62	43.59	0.000000
HR(age*season)	9	1776.85	47.83	0.000000
HR(season*watershed)	13	1779.33	50.30	0.000000
HR(sex*age*watershed)	13	1789.97	60.94	0.000000
HR(sex*age*season)	17	1790.26	61.23	0.000000

Table 4.8. Mean home range size (ha), sample size, standard error (SE), and 95% confidence intervals for ruffed grouse on 3 watersheds on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Watershed	*n*	Mean	SE	LCL	UCL
Cold Spring	40	14.6	2.8	9.0	20.2
White Oak	43	29.3	5.9	17.4	41.3
Wine Spring	89	36.2	3.6	29.0	43.4

Table 4.9. FRAGSTATS landscape indices calculated for habitats available to ruffed grouse on 3 locations (watersheds) on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Metric	Units	Watershed		
		Cold Spring	White Oak	Wine Spring
Total landscape area	ha	841.85	1,399.10	987.31
Shannon's diversity index	none	2.05	1.82	1.75
Shannon's evenness index	none	0.86	0.76	0.73
Mean patch size	ha	10.79	16.86	10.18
Largest patch index	%	7.88	15.45	16.18
Mean shape index	none	2.26	2.15	2.32
Total core area index	%	91.51	93.07	91.56
Contrast weighted edge density	m/ha	96.33	79.34	105.01
Interspersion juxtaposition index	%	83.86	72.82	76.47

Table 4.10. FRAGSTATS patch and class indices calculated for habitats available to ruffed grouse on 3 locations (watersheds) on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Habitat type[a]	Metric	Units	Watershed Cold Spring	 White Oak	 Wine Spring
SUBXER2	Proportion of habitat type	%	7.30	8.70	8.60
SUBXER2	Mean patch size	ha	4.16	7.81	5.71
SUBXER2	Largest patch index	%	1.42	1.00	1.21
SUBXER2	Mean shape index	none	1.73	1.67	1.83
SUBXER2	Total core area index	%	88.99	92.01	90.21
SUBXER2	Contrast weighted edge density	m/ha	25.59	21.09	27.89
SUBXER2	Mean nearest neighbor	m	30.52	99.84	102.83
SUBXER2	Mean proximity index	none	2,375.60	1,670.20	1,200.40
SUBXER2	Interspersion juxtaposition index	%	75.97	54.99	60.16
ROAD	Proportion of habitat type	%	1.40	0.70	1.50
ROAD	Mean patch size	ha	NA	NA	NA
ROAD	Largest patch index	%	NA	NA	NA
ROAD	Mean shape index	none	NA	NA	NA
ROAD	Total core area index	%	NA	NA	NA
ROAD	Contrast weighted edge density	m/ha	39.18	24.29	40.61
ROAD	Mean nearest neighbor	m	NA	NA	NA
ROAD	Mean proximity index	none	NA	NA	NA
ROAD	Interspersion juxtaposition index	%	85.20	76.02	77.56

[a] SUBXER2 = mixed oak stands in the 6–20-year age class
ROAD = gated forest roads

Table 4.11. Ranks of habitats used versus availability at the study area scale for female ruffed grouse in fall on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it with corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at $\alpha = 0.05$.

Habitat	Subxer2	Road	Rhodo	Subxer1	Mesic4	Subxer5	Xeric2	Xeric5	Subxer3	Subxer4	Mesic5	Xeric4	Rank
Subxer2		+	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	1
Road			+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	2
Rhodo				+	+	+	+ + +	+	+ + +	+ + +	+ + +	+ + +	3
Subxer1					+	+	+	+	+	+ + +	+ + +	+ + +	4
Mesic4						+	+	+	+	+ + +	+ + +	+ + +	5
Subxer5							+	+	+	+ + +	+ + +	+ + +	6
Xeric2								+	+	+ + +	+	+ + +	7
Xeric5									+	+	+	+	8
Subxer3										+	+	+ + +	9
Subxer4											+	+	10
Mesic5												+	11
Xeric4													12

Table 4.12. Ranks of habitats used versus availability at the study area scale for adult male ruffed grouse in fall on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it with corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Subxer2	Road	Subxer1	Rhodo	Mesic4	Subxer5	Xeric2	Subxer3	Xeric5	Xeric4	Subxer4	Mesic5	Rank
Subxer2	▨	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	1
Road		▨	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	2
Subxer1			▨	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	3
Rhodo				▨	+	+	+	+ + +	+	+ + +	+ + +	+ + +	4
Mesic4					▨	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	5
Subxer5						▨	+	+ + +	+	+ + +	+ + +	+ + +	6
Xeric2							▨	+	+	+ + +	+ + +	+ + +	7
Subxer3								▨	+	+	+	+	8
Xeric5									▨	+	+	+	9
Xeric4										▨	+	+	10
Subxer4											▨	+	11
Mesic5												▨	12

Table 4.13. Ranks of habitats used versus availability at the study area scale for female ruffed grouse in winter on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it to corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at $\alpha = 0.05$.

Habitat	Road	Rhodo	Subxer2	Subxer1	Subxer5	Xeric5	Mesic4	Subxer3	Xeric2	Subxer4	Xeric4	Mesic5	Rank
Road		+	+	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	1
Rhodo			+	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	2
Subxer2				+	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	3
Subxer1					+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	4
Subxer5						+	+	+	+ + +	+ + +	+ + +	+ + +	5
Xeric5							+	+	+	+	+ + +	+	6
Mesic4								+	+	+	+	+ + +	7
Subxer3									+	+	+ + +	+ + +	8
Xeric2										+	+	+ + +	9
Subxer4											+	+	10
Xeric4												+	11
Mesic5													12

Table 4.14. Ranks of habitats used versus availability at the study area scale for male ruffed grouse in winter on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it WITH corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Subxer2	Road	Rhodo	Subxer1	Mesic4	Subxer5	Xeric2	Subxer3	Subxer4	Xeric5	Xeric4	Mesic5	Rank
Subxer2		+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	1
Road			+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	2
Rhodo				+	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	3
Subxer1					+	+	+	+	+ + +	+ + +	+ + +	+ + +	4
Mesic4						+	+	+	+ + +	+ + +	+ + +	+ + +	5
Subxer5							+	+	+ + +	+	+ + +	+ + +	6
Xeric2								+	+ + +	+ + +	+ + +	+ + +	7
Subxer3									+ + +	+	+ + +	+ + +	8
Subxer4										+	+	+	9
Xeric5											+	+	10
Xeric4												+	11
Mesic5													12

Table 4.15. Ranks of habitats used versus availability at the study area scale for female ruffed grouse in spring on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it with corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Road	Rhodo	Subxer1	Subxer2	Mesic4	Subxer5	Subxer3	Xeric2	Xeric5	Mesic5	Subxer4	Xeric4	Rank
Road		+	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	1
Rhodo			+	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	2
Subxer1				+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	3
Subxer2					+	+	+ + +	+ + +	+	+ + +	+ + +	+ + +	4
Mesic4						+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	5
Subxer5							+	+ + +	+	+	+ + +	+ + +	6
Subxer3								+	+	+	+	+ + +	7
Xeric2									+	+	+	+ + +	8
Xeric5										+	+	+	9
Mesic5											+	+	10
Subxer4												+	11
Xeric4													12

Table 4.16. Ranks of habitats used versus availability at the study area scale for male ruffed grouse in spring on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it to corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Road	Subxer1	Subxer2	Subxer5	Rhodo	Mesic4	Subxer3	Xeric2	Mesic5	Xeric4	Subxer4	Xeric5	Rank
Road	▨	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	1
Subxer1		▨	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	2
Subxer2			▨	+	+	+	+	+	+ + +	+ + +	+ + +	+ + +	3
Subxer5				▨	+	+	+	+ + +	+ + +	+ + +	+ + +	+ + +	4
Rhodo					▨	+	+	+	+ + +	+ + +	+ + +	+ + +	5
Mesic4						▨	+	+	+	+ + +	+ + +	+ + +	6
Subxer3							▨	+	+	+ + +	+ + +	+ + +	7
Xeric2								▨	+	+ + +	+ + +	+ + +	8
Mesic5									▨	+	+	+	9
Xeric4										▨	+	+	10
Subxer4											▨	+	11
Xeric5												▨	12

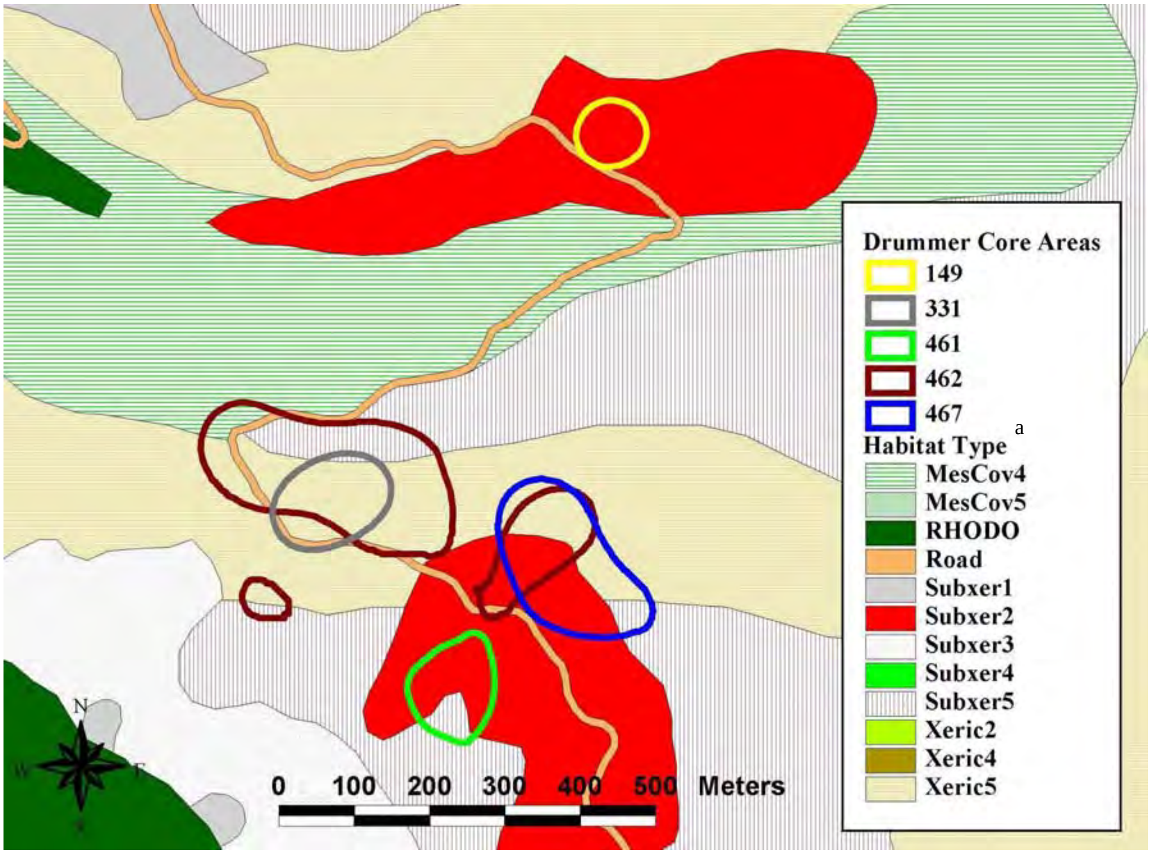

Figure 4.1. Example of core areas (50% kernel) of male ruffed grouse positioned near gated forest roads on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004. Apparent overlap resulted from projecting core areas across years.

[a] MESIC4 = mesic forest in 40–80-year age class
MESIC5 = mesic forest in >80-year age class
RHODO = forest with >75% midstory coverage in rhododendron
ROAD = gated forest roads
SUBXER1 = subxeric forest in 0–5-year age class
SUBXER2 = subxeric forest in 6–20-year age class
SUBXER3 = subxeric forest in 21–39-year age class
SUBXER4 = subxeric forest in 40–80-year age class
SUBXER5 = subxeric forest in >80-year age class
XERIC2 = xeric uplands in 6–20-year age class
XERIC4 = xeric uplands in 40–80-year age class
XERIC5 = xeric uplands in >80-year age class
WLO = wildlife openings

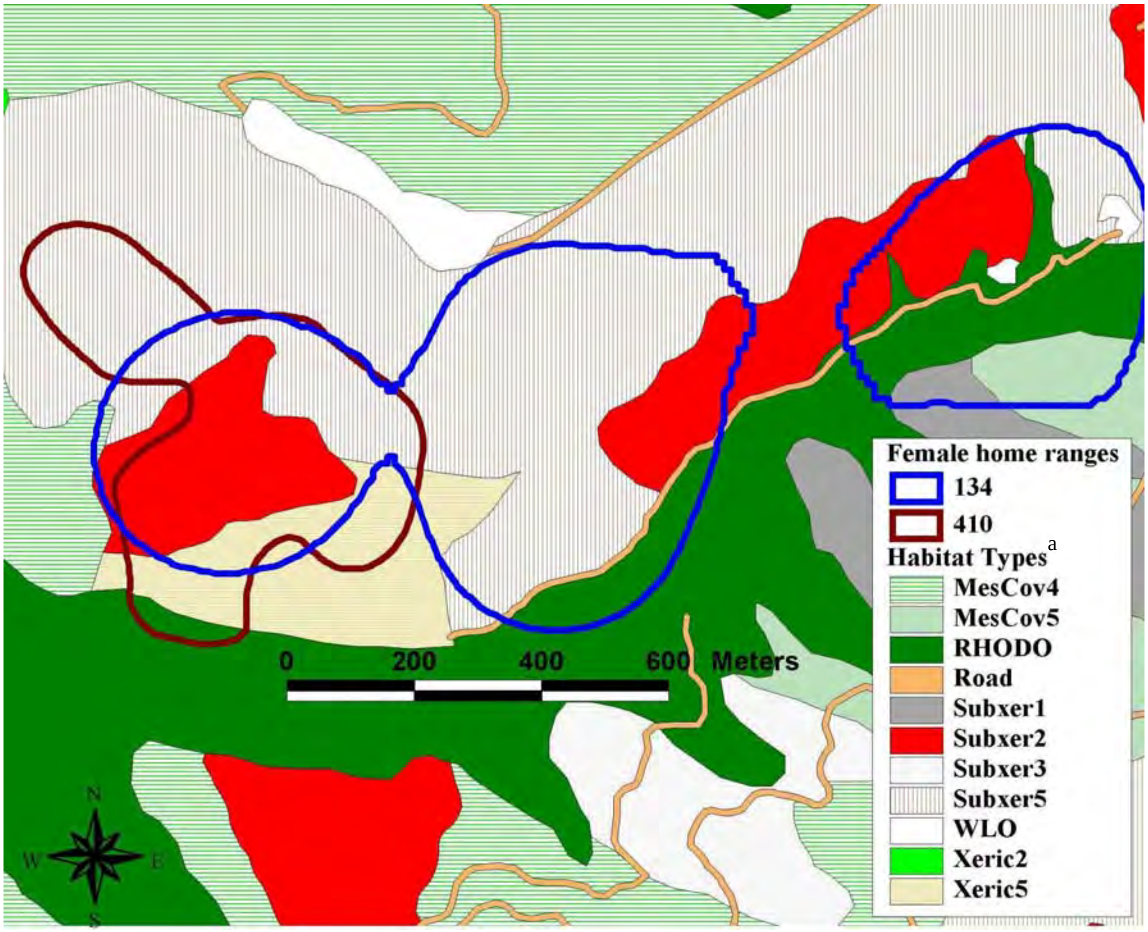

Figure 4.2. Example of female ruffed grouse use (75% kernel home range) of mature forest juxtaposed to early successional stands in winter on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

[a] MESIC4 = mesic forest in 40–80-year age class
MESIC5 = mesic forest in >80-year age class
RHODO = forest with >75% midstory coverage in rhododendron
ROAD = gated forest roads
SUBXER1 = subxeric forest in 0–5-year age class
SUBXER2 = subxeric forest in 6–20-year age class
SUBXER3 = subxeric forest in 21–39-year age class
SUBXER4 = subxeric forest in 40–80-year age class
SUBXER5 = subxeric forest in >80-year age class
XERIC2 = xeric uplands in 6–20-year age class
XERIC4 = xeric uplands in 40–80-year age class
XERIC5 = xeric uplands in >80-year age class
WLO = wildlife openings

Table 4.17. Comparison of mean ruffed grouse home range size (ha) reported by season, sex, and estimation method from ruffed grouse studies outside the range of aspen.

Study area[a]	Season	Sex	Method	Mean
ACGRP	fall-winter	male	75% kernel	17
ACGRP	spring-summer	male	75% kernel	10
ACGRP	fall-winter	female	75% kernel	25
ACGRP	spring-summer	female	75% kernel	25
PA	spring	male	MCP	5
MO	spring	male	MCP	43
MO	spring	male	MCP	230
MO	spring	female	MCP	202
MO	fall-winter	male	MCP	507
MO	fall-winter	female	MCP	505
TN	fall	male and female	MCP	133

[a] ACGRP=Appalachina Cooperative Grouse Research Project, mean of Kentucky, Maryland, Pennsylvania, Rhode Island, Virginia, and West Virginia, Whitaker (2003).
PA=Pennsylvania, McDonald et al. (1998)
MO1=Missouri, Thompson and Fritzell (1989)
MO2=Missouri, Kurzejeski and Root (1989)
TN=Tennessee, White and Dimmick (1978)

CHAPTER V.

RUFFED GROUSE SURVIVAL AND POPULATION STRUCTURE IN WESTERN NORTH CAROLINA

ABSTRACT

Sound management of ruffed grouse (Bonasa umbellus) populations requires an understanding of survival and cause-specific mortality; however, these parameters have not been investigated at the southern extent of the species' range. Ruffed grouse were studied in the mountains of western North Carolina. Grouse (n = 276) were radiotagged and monitored ≥3 times/week. Mean annual survival was 0.39 (± 0.052 SE) and did not differ between sex and age classes. Seasonal survival was greatest in summer (0.87, 95% CI = 0.81–0.91), followed by fall (0.77, 95% CI = 0.73–0.80), winter (0.76, 95% CI = 0.72–0.80), and spring (0.74, 95% CI = 0.68–0.79). The most parsimonious survival model included a year*season interaction as the only explanatory variable (AIC_c = 1964.7, ω_i = 0.9999). Of 155 mortalities, the greatest proportion was attributed to mammalian predators (42.6%), followed by avian (26.5%), unknown predation (12.9%), hunter harvest (11.0%), and other (7.0%). Scavenging prior to transmitter recovery may have positively biased mammalian predation rates. Mean hunter harvest rates based on band returns was 0.06 (± 0.005 SE). Population densities were 5.9–11.4 grouse/100 ha and were not negatively associated with hunter harvest. The most viable option for increasing grouse abundance is through creation and maintenance of habitat.

Key words: Appalachians, *Bonasa umbellus*, hunting, mortality, population, ruffed grouse, survival.

INTRODUCTION

Survival and cause-specific mortality are important population parameters relevant to setting hunting seasons and bag limits for upland gamebirds.

For ruffed grouse, difficulties in setting harvest are further complicated by 10-year population cycles across northern parts of the species' range (Dorny and Kabat 1960). Most ruffed grouse survival studies have been conducted to determine acceptable harvest rates from hunter-submitted wings, tails, and band returns (Fischer and Keith 1974, Kubisiak 1984, Rusch et al. 1984, DeStefano and Rusch 1986). Although these methods provide valuable information, they reveal little about seasonal and cause-specific mortality. Alternatively, radiotelemetry studies can provide comprehensive information by monitoring individuals across time periods and ascertaining mortality from all sources, not just hunting (Heisey and Fuller 1985).

Most ruffed grouse survival studies have been conducted in northern states. Differences in population ecology, including lower population abundance (Johnsgard 1973), lower reproductive output (Devers 2005), different fall age structure (Davis and Stoll 1973), extended hunting seasons (Stoll et al 1995), and apparent lack of a 10-year population cycle preclude application of northern harvest recommendations to southern portions of ruffed grouse range.

In recent years, survival was estimated via radiotelemetry in the central and southern Appalachians as part of the Appalachian Cooperative Grouse Research Project (ACGRP; Devers 2005). Compared with telemetry studies in northern states, survival estimates for Appalachian ruffed grouse were greater. Across ACGRP sites, mean annual survival was 42% (Devers 2005). Also in the Appalachians, survival was 62% in Kentucky (Triquet 1989) and 39% in Ohio (Swanson et al. 2003). By comparison, survival was 25% in Wisconsin (Small et al. 1991), 11% in Minnesota (Gutierrez 2003), and 25–37% in Michigan (Clark 2000).

Partial data from this study (2 of 5 years) were included in ACGRP results (Devers 2005). More detailed results from the complete data set are presented here. Further, the North Carolina study site was the most southerly of ACGRP studies, and no other studies have examined ruffed grouse survival and cause-specific mortality at the southern tip of the species' range.

Objectives were to (1) identify temporal patterns in ruffed grouse survival; (2) investigate sex and age-specific survival; (3) identify mortality causes; and (4) compare population structure at the southern extent of ruffed grouse range to other areas.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (WSC, 3230 ha), within Nantahala National Forest in western Macon County, North Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1,644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges that connect upper elevations to narrow valley floors (Whittaker 1956). Mean annual temperature was 10.4° C, and mean annual precipitation was 160 cm. The area was predominantly forested. Forest types included, mixed oak >40 years-old (34.2%), rhododendron (*Rhododendron maximum*) dominated midstory (19.6%), mixed mesophytic and northern hardwood >40 years-old (18.8%), xeric upper elevation oak >40 years-old (14.3%), regenerating mixed oak 6–20 years-old (9.3%), pole-stage mixed oak 21–39 years-old

(1.6%), regenerating mixed oak 0–5 years-old (0.8%), and maintained herbaceousclearings (0.2%). There were 52.6 km of gated forest roads (1.1%).

Capture and Telemetry

Grouse were captured using intercept traps (Gullion 1965) during late August – early November, and 1 March–8 April, 1999–2003. Gender and age (juvenile or adult) were assessed by feather characteristics and molt patterns (Kalla and Dimmick 1995). Grouse tagged as juveniles in fall graduated to the adult age class at the end of the following summer. Grouse were weighed, leg-banded, fitted with 12-g necklace-style radiotransmitters with a 3-hour mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA), and released at capture sites after processing. Notification of a $25 reward and contact information were printed on transmitters for hunter return. The proportion of bands returned by hunters (i.e., crude return rates) was calculated for comparison to other studies.

Grouse were checked for survival 3–5 times/week during routine telemetry. When a mortality signal was emitted, the transmitter was located and cause of death ascertained from evidence at the site. Transmitters were located within a few hours (i.e., the length of time it took to traverse terrain and home on the signal) after detection of a mortality signal. At mortality sites, predator sign (i.e., tracks, scat, whitewash), presence of cache, evidence of feeding on remains, and various site characteristics were recorded. For example, chewed bones cached under a log indicated mammalian predation. Picked bones and whitewash indicated avian. If conflicting sign was present, the mortality was classified as unknown predation. Additional causes of mortality included hunter harvest, and “other” (disease, crippling loss, vehicle/tree collision). Date of death was recorded as the midpoint between the last known alive date and detection of mortality (Pollack et al. 1989).

Population Estimates

Grouse caught per unit effort (grouse/100 trap-days) was calculated as an index to population density from fall capture data. These data should provide an index to population density as trapping methods and effort were similar across years.

Population density estimates also were obtained from spring drumming counts. For drumming counts, observers walked designated routes (i.e., gated forest roads) on 2 consecutive mornings beginning 30 minutes before sunrise and ending three hours after sunrise. The starting point on the second morning was the endpoint from the first morning. Routes were selected such that approximately 20% of the area was sampled. Effective sampling area was defined by 400 m buffers around each route (i.e., 200m on each side, see Chapter I). Drumming counts were cancelled when winds were >13 km/h because of reduced ability to hear drumming. Observers listened for drumming while walking selected routes. When a drumming male was heard, distance to drummer, time, and an azimuth to the bird were recorded. An approximate location for each drumming grouse was plotted on a geographic information system (GIS) created for the study area. Locations of drumming males were buffered by 150 m because grouse may use alternate drumming sites (Lovallo et al. 2000). If two locations from consecutive days fell within the same 150 m buffer, they were considered the same bird. Population estimates (grouse/100 ha) were calculated by doubling number of drumming males to account for females under the assumption of a 1:1 breeding season sex ratio (Bump et al. 1947, Gullion and Marshall 1968, Rusch and Keith 1971).

Fall sex and age ratios were calculated from fall capture data as a recruitment index. Although capture data may be biased due to greater vulnerability of juveniles to trapping (Destefano and Rusch 1982), capture data should provide an index for comparison to other studies.

Data Analysis

Survival was analyzed using the known fates procedure in Program MARK (White and Burnham 1999). Known fates uses a staggered entry (Pollack et al. 1989) modification of the product limit estimator (Kaplan and Meier 1958). A 30-day time step was used. A bird was "at risk" during an encounter occasion if it was captured during the first 15 days of the interval. If it was captured from day 16-30 in an interval, it was entered in the next encounter occasion. If contact was lost when a bird left the study area or a transmitter failed, it was right-censored (Pollack et al. 1989). Right censoring indicated contact was lost without specifying fate. Juvenile grouse that survived through the year were right-censored 14 August following capture and re-entered as an adult on 15 August. Cause-specific mortality is defined as losses to a given mortality source in the absence of all other sources, or competing risks (Heisey and Fuller 1985:670); therefore, cause-specific estimates were calculated in MARK by retaining the mortality source of interest while right-censoring all other mortalities. Grouse were entered in survival analysis after a 7-day period to exclude mortalities potentially caused by capture stress.

Annual survival was calculated from 15 September–14 September. Each year was further delineated into 4, 91-day seasons defined by plant phenology and grouse biology. Fall (15 September–14 December) was a period of food abundance and dispersal among juveniles. Winter (15 December–15 March) was defined by minimal food resources and physiological stress. Spring (16 March–14 June) coincided with vegetation green-up and breeding activity. Summer (15 June–14 September) was a period of low stress with maximum cover and food availability.

Ridges surrounding Wine Spring Creek, White Oak Creek, and Cold Spring Creek watersheds naturally divided the study area into 3 distinct sections. Grouse tended to remain within their watershed of capture; therefore, in survival analysis, each watershed was treated as a separate area and used as an explanatory variable to examine effects of available habitat on survival. Radiotagged grouse that occupied >1 watershed (n = 3) were not included in analysis.

An information-theoretic approach (Burnham and Anderson 1998) was used to evaluate sources of variation in survival. A set of a-*priori* candidate models was created using combinations of sex, age, year, season, and watershed. Models were assessed in program MARK using a bias-corrected version of Akaike's Information Criterion (AIC_c), and weight of evidence (w_i) to rank and select the model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). Bootstrapping was used to analyze goodness of fit and overdispersion (Cooch and White 2001). Relationships between fall population density and annual survival were investigated using multiple regression (Proc REG) in SAS (SAS Institute Inc., Cary, North Carolina, USA).

RESULTS

Two hundred seventy-six grouse were radiotagged over 5 years (Table 5.1; tables are located in the Appendix). The overall percentage of juveniles in fall captures was 59.6%, ranging from 46.2–66.7% Twenty-two grouse died during the initial 7-day period after capture. Of these, 11/22 were juveniles captured in fall 2000; therefore, survival estimates may have been biased low due to capture-induced stress during that year. Contact was lost during the initial 7-day period for an additional 7 grouse. Recapture of censored birds suggested faulty transmitters were most likely to fail within a few days following capture; therefore, these censors may have been due to transmitter failure rather than unrecovered mortalities.

Two hundred-thirty two grouse were available for survival analysis. Of these, 155 mortalities were observed. Across years, the greatest proportion was attributed to mammalian predators (42.6%), followed by avian (26.5%), unknown predation (12.9%), hunter harvest (11.0%), and other (7.0%). Mean annual hunter harvest (i.e., proportion of annual mortalities due to hunting) based on band returns was 6% (± 0.5 SE). The “other” category included 9 unknown causes, 1 vehicle collision, and 1 death from *Aspergillosis* (Schumacher 2002). Mean annual cause-specific rates (i.e., risk of death to individual mortality sources) followed the same pattern as raw proportions, with mammalian predation being most common (0.31 ± 0.074 SE) followed by avian (0.22 ± 0.044 SE), unknown predation (0.13 ± 0.044 SE), hunter harvest (0.10 ± 0.028 SE), and other (0.07 ± 0.033 SE). The seasonal risk of mammalian predation was lowest in summer (0.07), and relatively constant across fall (0.11), winter (0.10), and spring (0.11). Risk of avian predation was greatest in spring (0.09) compared with fall (0.06), winter (0.06), and summer (0.05).

Mean annual survival was 0.39 (± 0.052 SE), ranging from 0.26–0.56. Seasonal survival was greatest in summer (0.87, 95% CI = 0.81–0.91), followed by fall (0.77, 95% CI = 0.73–0.80), winter (0.76, 95% CI = 0.72–0.80) and spring (0.74, 95% CI = 0.68–

0.79). Overlapping confidence intervals suggest similar survival rates among fall, winter, and spring. By sex and age classes, mean annual survival was 0.39 (95% CI = 0.28–0.51) for adult males, 0.42 (95% CI = 0.31–0.52) for juvenile males, 0.32 (95% CI = 0.13–0.50) for adult females, and 0.40 (95% CI = 0.36–0.43) for juvenile females.

The most parsimonious model contained a YEAR*SEASON interaction (AIC_c = 1964.7, ω_i = 0.9999), indicating seasonal survival differed among years (Table 5.2, 5.3). Bootstrapping revealed data were not overdispersed ($\hat{c}$ = 1.11). There was no support for models with combinations of sex, age, or watershed as explanatory variables (ω_i < 0.0001).

Annual survival showed an inverse relationship with the population index calculated from fall trapping data ($r^2 = 0.76$, $P = 0.054$, Figure 5.1). Spring population density, estimated from drumming counts, ranged from 5.88 grouse/100 ha in 2004 (the year of greatest survival) to 11.4 grouse/100ha in 2000 (the year of lowest survival).

DISCUSSION

Survival and Cause-Specific Mortality

Compared with other radiotelemetry studies, annual survival (39%) was greater than reports from northern areas, and within the range of estimates for the Appalachians. Devers (2005) estimated 42% survival with a range of 17%–57% across the central and southern Appalachians. Of 11 ACGRP study areas, mean annual survival on WSC was similar to KY1 (40%), greater than MD1 (35%), OH2 (17%), PA1 (29%), RI1 (30%), and VA3 (33%), and less than OH1 (55%), VA1 (56%), VA2 (49%), WV1 (47%), and WV2 (57%, see Devers 2005 for study locations and acronymns). By comparison, annual survival rates were 11% in Minnesota (Gutierrez et al. 2003), and 25–37% in Michigan (Clark 2000). In Wisconsin, annual survival was 25% for adults and 7% for juveniles (Small et al. 1991).

The trend for greater survival in the Appalachians may be partially explained by differences in predator communities. In the core of ruffed grouse range, species such as the northern goshawk (*Accipiter gentiles*) have adapted to prey specifically on grouse. The presence of these efficient predators can lead to greater mortality (Bergerud and Gratson 1988). Survival may be enhanced in the Appalachians because specialists are largely replaced by generalist predators that prey on grouse opportunistically (Bumann and Stauffer 2004).

Even though goshawks are not a frequent threat in the Appalachians, avian predators, including red-tailed hawks (*Buteo jamaicensis*), red-shouldered hawks (*Buteo lineatus*) broad-winged hawks (*Buteo platypterus*), Cooper's hawks (*Accipiter cooperii*), and great horned owls (*Bubo virginianus*) are important mortality sources (Bumann and Stauffer 2004). Avian predation is frequently cited as a leading cause of ruffed grouse mortality. As determined from evidence at mortality sites, mammalian rather than avian predation accounted for the greatest proportion of losses on WSC. Bumann and Stauffer (2002) found mammals scavenged >65% of placed carcasses and warned of potential for overestimating mammalian predation of ruffed grouse. The narrow margin between mammalian and avian predation on WSC may have resulted from such bias.

Survival estimates did not differ between juveniles and adults, as the most parsimonious survival model did not include an age effect. Similar results were reported in Minnesota (Gutierrez et al. 2003) and across ACGRP study sites (Devers 2005). An age effect was apparent in Wisconsin (Small et al. 1991) and other non-telemetry studies in New York (Bump et al. 1947) and Alberta (Rusch and Keith 1971). These authors proposed greater juvenile mortality was a function of dispersal. A combination of factors, including exposure to predators during extended movements, increased energetic demand, and traversing unfamiliar space may lead to increased risk for dispersing juveniles (Small and Holzwart 1993, Yoder et al. 2004). There may be several reasons age-specific differences in survival were not observed. First, there actually may not have been a difference in survival between juveniles and adults. Second, trapping efforts were conducted in fall, concurrent with dispersal. Juveniles may have completed or nearly completed dispersal at their time of capture. Juveniles radiotagged during a dispersal movement may have been passing through the study area, and were subsequently right-censored when contact was lost. As a result, only those grouse that completed dispersal movements were monitored, hence obscuring survival differences for dispersing juveniles.

Seasonally, survival was greatest in summer (87%) and similar among fall, winter, and spring (74–77%). Slightly lower survival in spring may have been a function of reproductive activities (i.e., nesting and drumming) coinciding with raptor migrations. Further, mortality risk to avian predators was greatest during spring. Relatively high survival in summer might be expected considering it is a period of maximum vegetation cover and food availability. Similarly, Swanson et al. (2003) reported survival of Ohio ruffed grouse was greatest in summer, and lowest in spring and fall. Other studies also showed greatest survival in summer (Small et al. 1991, Devers 2005), though these reports indicated seasonal rates were lowest in winter. Winter survival on WSC (76%)

was similar to other ACGRP sites (72%, Devers 2005) and greater than in Wisconsin (55–57%, Small et al. 1991). Greater survival of Appalachian grouse in winter compared with northern areas may have been influenced by less severe winters in southern portions of ruffed grouse range.

Hunter Harvest

Concern has been raised regarding potential additive mortality effects of hunting seasons that extend through the winter (DeStefano and Rusch 1982, Bergerud 1985, Stoll and Culbertson 1995). On WSC, mean harvest rate based on band recoveries (6%) was considerably lower than harvest rates of 17–49% in Wisconsin (Kubisiak 1984, Rusch et al. 1984) and 13–20% in New York (Bump et al. 1947). Harvest recommendations in northern latitudes were 20–23%, with sustained harvests ≥23% viewed as potentially additive and detrimental to populations (Kubisiak 1984, Rusch et al. 1984).

Appalachian harvest rates were somewhat lower compared to northern areas with a range of 4–13% on ACGRP sites (Devers 2005) and 4–20% in Ohio (Stoll and Culbertson 1995). Devers (2005) conducted a compensatory mortality experiment by comparing survival between areas open and closed to hunting. He found no increase in survival in the absence of hunting and suggested conservative harvest rates <20% would be compensatory in the Appalachians. Using flush counts to index population density, Monschein (1974) determined grouse density was not affected by varying levels of hunting pressure in northwestern North Carolina.

Harvest rates on WSC were among the lowest reported. Although hunting seasons extended through the end of February, 65% of harvests occurred during the first 9 weeks of the season (October–December). Given relatively high annual survival and low harvest, there appeared to be no evidence that hunting was detrimental to the WSC grouse population. Further, spring population density was at its highest level (11.4 grouse/100 ha) following the year of greatest hunter harvest (7%), indicating hunting mortality may have been compensatory.

Population Structure

Spring population density estimated from drumming counts was 5.88–11.4 grouse/100 ha, with a decreasing trend observed throughout the study. As density decreased, an increase in survival was observed (Figure 5.1). The inverse relationship between survival and population density may have been caused in part by habitat availability. As density increased, some grouse may have used marginal habitats, thus decreasing survival by increasing efficiency of generalist predators. Predators switching from other prey as grouse became more abundant may have compounded this effect (Bergerud 1988). Survival of juveniles and adults may exert the greatest influence on population density in the central and southern Appalachians, compared with other population parameters (Tirpak 2005). Increasing survival observed over time on WSC could have increased density; however, this effect may not have been realized in the absence of sufficient suitable habitat.

Recruitment, the addition of individuals to a population through reproduction and immigration (Krebs 1994), is an important aspect of population ecology. As a recruitment index, ruffed grouse studies have used hunter-submitted wings and tails to estimate proportion of juveniles in fall populations (Davis and Stoll 1973, Destefano and Rusch 1982, Norman et al. 1997). On WSC, hunter band returns were limited to radiotagged grouse; therefore, proportion of juveniles in fall captures provided the only recruitment index. Although this index may have been biased because juveniles are more susceptible to capture than adults (Destefano and Rusch 1986), it serves as a basis for comparison with other studies. Despite potential positive bias, proportion of juveniles in fall on WSC (47–67%) was less than means of 76% in Alberta ((Rusch and Keith 1971) and 78% in Wisconsin (Dorney 1963). Means from harvest data in Ohio (42–56%, Davis and Stoll 1973) and Virginia (22–59%, Norman et al. 1997) also were lower than reports from Wisconsin and Alberta. In the Appalachians, lower recruitment may be influenced by habitats with nutritionally inadequate foods that cause physiological stress and decreased reproductive output (Servello and Kirkpatrick 1987). Although nest success was relatively high on WSC (see Chapter II), the recruitment index suggested other aspects (i.e., chick survival and immigration) might have been limiting. Because chicks were not radiotagged on WSC, reliable estimates of chick survival (Larson et al. 2001) were not available.

In addition to reproduction, immigration and emigration influence recruitment. During dispersal in early fall, juvenile grouse move 1– 6 km from their natal ranges (Bump et al. 1947, Chambers and Sharp 1958, Godfrey and Marshall 1969, Small and Rusch 1989). During this time, 50% of juveniles may emigrate from an area (Chambers and Sharp 1958), with a greater proportion dispersing when habitat was limiting (Bump et al. 1947). Recruitment and resultant population density on WSC may have been affected by losses to emigration that were not balanced by equal immigration. The landscape within a 5-km radius surrounding WSC contained 5% coverage in 6–20-year-old mixed oak forest (a preferred habitat type, see Chapter IV). At such low levels, interspersion of age classes is probably limited andmay fall below a minimum threshold for ruffed grouse. Relatively poor habitat in the surrounding area may have resulted in WSC acting as a source population that contributed birds, surrounded by a sink that did not replace these losses.

MANAGEMENT IMPLICATIONS

In the core of ruffed grouse range, densities may exceed 50 grouse/100 ha on areas under intensive aspen management (Kubisiak 1985, Gullion 1990). Increasing the proportion of landscapes in the 0–25-year age class has been shown to increase grouse density on these areas. In Wisconsin, grouse density increased from 14 to 32 grouse/100 ha as proportion of early successional forest increased from 13% to 55% (Kubisiak 1985). Forest management and interspersion of aspen age classes also increased grouse density on the Stone Lake Area in Wisconsin (McCaffrey et al. 1996).

Although population responses following management are well documented in aspen forests, similar grouse densities in Pennsylvania mixed oak forest were achieved by interspersing age classes and maintaining 20% coverage in the 0–20-year age class (Storm et al. 2003). In mixed mesophytic and mixed oak forests in Ohio, grouse abundance increased 50–100% following creation of early successional habitat on 12% of the study area (Stoll et al. 1999).

Approximately 9% of WSC was in the 6–20-year age class. As discussed, habitat availability may have influenced the inverse relationship between survival and population density. With habitat improvement (i.e., creation of early successional forest interspersed with other habitat types), grouse density may increase as it has done on other mixed oak-dominated areas. In the absence of forest management, the proportion of forest in the 6–

20-year age class on WSC will be reduced to 2% by 2010, potentially causing further population decline. Potential for unbalanced emigration and immigration stresses the need to manage whole landscapes as opposed to creating habitat islands surrounded by an otherwise unsuitable matrix.

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APPENDIX

Table 5.1. Capture period, capture effort (trap-days), number of grouse tagged, capture rate (grouse/100 trap-days), and sex and age of grouse captured during ruffed grouse research on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Period	Trap-days	Captured	Rate	Ad fem[a]	Juv fem	Ad male	Juv male
Fall							
1999	6,770	65	0.96	14 (22)[b]	24 (37)	21 (32)	6 (9)
2000	9,040	63	0.70	5 (8)	29 (46)	16 (25)	13 (21)
2001	10,350	70	0.68	8 (11)	22 (31)	17 (24)	23 (33)
2002	9,576	46	0.48	7 (15)	17 (37)	10 (22)	12 (26)
2003	8,560	16	0.19	2 (13)	4 (25)	5(31)	5 (31)
Spring							
2000	94	4	4.26	0	0	4 (100)	0
2001	938	6	0.64	2 (33)	0	4 (67)	0
2002	96	1	1.04	1 (100)	0	0	0
2003	114	5	4.39	1 (20)	1(20)	2 (40)	1 (20)
Total	39,538	276	0.70	40 (14)	97 (35)	79 (29)	60 (22)

[a] Ad fem = adult female
Juv fem = juvenile female
Ad male = adult male
Juv male = juvenile male

[b] Values in parentheses are percentage of total capture during the period.

Table 5.2. Comparison of Akaike's Information Criterion (AIC_c), differences in AIC_c, and model weights (w_i) for ruffed grouse survival models based on year, season, area, sex, and age on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model[a]	K	AICc	ΔAICc	*w*i
{Year*season}	20	1964.7	0.0	0.9999
{Year}	5	2001.7	37.0	<0.0001
{Season}	4	2003.2	38.6	0.0000
{Area*season}	12	2004.8	40.1	0.0000
{Season*sex}	8	2008.6	43.9	0.0000
{Season*age}	8	2008.8	44.2	0.0000
{Area}	3	2009.5	44.8	0.0000
{Age}	2	2011.5	46.9	0.0000
{Sex}	2	2012.0	47.4	0.0000
{Sex*age}	4	2013.6	48.9	0.0000
{Season*sex*age}	16	2018.8	54.1	0.0000
{Area*year*season}	60	2018.8	54.1	0.0000
{Global}	236	2221.5	256.9	0.0000

[a] Year = annual period from September 15–September 14.
Season = fall (15 September–14 December)
winter (15 December–15 March)
spring (16 March–14 June)
summer (15 June–14 September)
Sex = male, female
Age = juvenile, adult
Area = watershed

Table 5.3. Survival rates of ruffed grouse by year and season on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Annual survival for all years was calculated as an across year average. Seasonal survival for all years was calculated with years pooled.

			Season							
	Annual		Fall		Winter		Spring		Summer	
Year	Survival	95% CI	Survival	95% CI	Survival	95% CI	Survival	95% CI	Survival	95% CI
1999–2000	0.32	0.23–0.40	0.69	0.59–0.77	0.83	0.72–0.90	0.64	0.50–0.75	0.91	0.79–0.97
2000–2001	0.26	0.18–0.34	0.69	0.59–0.77	0.67	0.56–0.77	0.73	0.59–0.83	0.81	0.67–0.90
2001–2002	0.37	0.29–0.45	0.78	0.70–0.85	0.78	0.68–0.85	0.80	0.69–0.87	0.76	0.62–0.85
2002–2003	0.43	0.33–0.54	0.79	0.69–0.86	0.73	0.61–0.82	0.82	0.67–0.91	1.00	1.00–1.00
2003–2004	0.56	0.41–0.69	1.00	1.00–1.00	0.81	0.68–0.90	0.64	0.45–0.79	1.00	1.00–1.00
All years	0.39	0.29–0.49	0.77	0.73–0.80	0.76	0.72–0.80	0.74	0.68–0.79	0.87	0.81–0.91

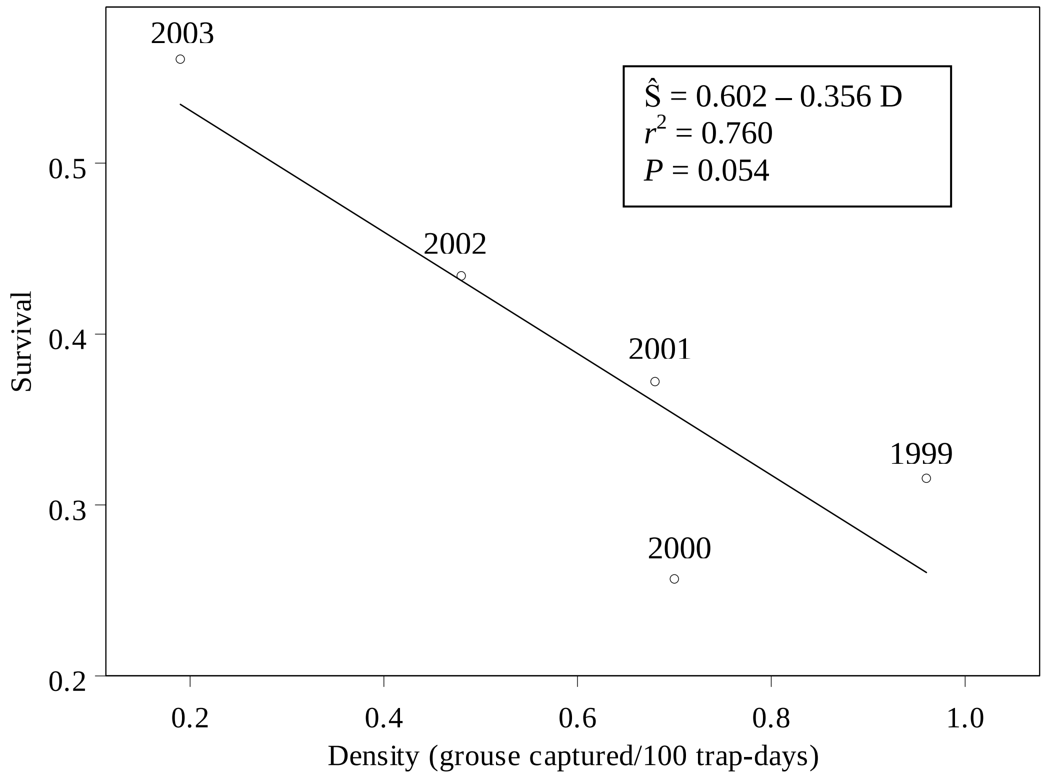

Figure 5.1. Relationship of ruffed grouse annual survival with a population density index calculated from fall trapping success on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

CHAPTER VI.

MANAGEMENT IMPLICATIONS OF RUFFED GROUSE RESEARCH ON WINE SPRING CREEK ECOSYSTEM MANAGEMENT AREA

INTRODUCTION

Ruffed grouse in the central and southern Appalachian Mountains have unique population structure and habitat needs that differ from the core of the species' range. In the mid-1990s, a regional research effort, the Appalachian Cooperative Grouse Research Projects (ACGRP), was undertaken to gain an understanding of ruffed grouse ecology in the region. The ACGRP was a partnership among state and federal agencies, universities, and private conservation groups on 12 study sites in 8 states.

Research conducted on Wine Spring Creek Ecosystem Management Area (WSC) in North Carolina was designed to contribute to this regional effort and address local topics of interest. The WSC study site was unique among ACGRP sites in that its location was at the southern extent of grouse range. Previously, no studies had undertaken such a comprehensive effort to identify grouse habitats and population structure at the southern end of the Blue Ridge Mountains.

During the 5-year study (1999–2004), 276 grouse were radiotagged, resulting in information on habitat use, reproduction, and survival. Management implications from WSC are relevant to mixed hardwood forests in western North Carolina (including over 200,000 ha of national forest) and similar forest types in northern Georgia and eastern Tennessee.

RECRUITMENT AND POPULATION STRUCTURE

Annual population density indexed using spring drumming counts and fall trapping success decreased from 1999–2004. Yet, during that period, annual survival increased (Chapter V). These observations may be an indication of low recruitment.

Indeed, proportion of juveniles in fall captures suggested recruitment on WSC was lower than in northern portions of grouse range (Chapter V). However, nesting rates and nest success were relatively high (Chapter II) and whole brood survival during the 5 weeks following hatch was moderate (Chapter III). It is possible that chick losses during summer may have resulted in low recruitment but a more reliable estimate of chick survival was not available as chicks could not be radiotagged and monitored through fall.

Low recruitment also may have been influenced by an imbalance between emigration and immigration. During dispersal in early fall, juvenile grouse move 1– 6 km from their natal ranges and during this time, >50% of juveniles may emigrate from an area. There was proportionally more forest in the 6–20-year age class (an important habitat component) on WSC compared with the surrounding landscape. WSC may have been a source population that contributed birds, surrounded by a sink that did not replace those losses. If so, managing habitat at a landscape scale, as opposed to creating habitat islands within a matrix of unsuitable habitat, may offset losses to emigration with additions from immigration.

The inverse relationship between population density and survival may have been caused in part by habitat availability on WSC. As density increased, some grouse may have used marginal habitats, thus decreasing survival. Increases in survival over time could exert a positive influence on the population; however, such an effect may not be realized as the proportion of early successional forest on WSC declines from 9% to 2% by 2010.

HABITAT PREFERENCE

Grouse on WSC used a variety of habitats as food and cover availability and life-history functions changed through the year (Chapters III, IV). In the absence of aspen (*Populus tremuloides, P. grandidentata*), grouse depended on a diversity of food sources, including hard mast, buds, soft mast, and herbaceous plants. In general, cover was provided by young forest stands in the 6–20-years age class. Mature stands presented an important food source in the form of acorns and beechnuts, and gated forest roads with forbs and legumes provided herbaceous forage. Grouse homeranges were smallest (an indicator of habitat quality) where these habitats were well interspersed. The greatest determinant of habitat quality was interspersion and juxtaposition of food with cover.

METHODS TO IMPROVE HABITAT

Alternative regeneration techniques including shelterwood, irregular shelterwood, and group selection can be used to create and improve grouse habitat (Chapter IV). Shelterwood and irregular shelterwood can maximize interspersion by providing food (i.e., hard mast) and cover (i.e., regenerating stems) in the same stand. Techniques that retain mature, mast-producing trees (i.e., 2-age systems) may have the greatest long-term benefits.

In managing landscapes for grouse, group selection can be used to increase interspersion by connecting otherwise disjunct habitat patches. Perhaps the greatest utility for group selection is in creating small canopy gaps used by broods during the first few weeks after hatch (Chapter III). Brood habitat also could be improved by converting perennial cool-season grass cover in wildlife openings to more desirable structure afforded by forbs and legumes. Broods used edges of wildlife openings, and thinning these areas could further enhance vegetation structure.

Timber stand improvement techniques increase sunlight to the forest floor, promoting herbaceous plant growth and hardwood regeneration. Habitat use by female ruffed grouse suggested thinnings on mesic sites resulted in desirable conditions on WSC (Chapter IV). Thinnings also could be used to connect group selection cuts, soften edges along harvest boundaries, and increase herbaceous cover on forest roads.

Gated forest roads were important habitats for grouse during all seasons. By seeding a mixture of an annual grain such as winter wheat (*Triticum aestivum*) with clover (*Trifolium* spp.), roads can be stabilized to prevent erosion while providing food sources for grouse and other wildlife. Over time, forbs germinating from the seed bank should maintain vegetation on the site and further enhance habitat quality (Chapter IV). Opening the forest canopy along roads (i.e., daylighting) could be used to stimulate herbaceous plant growth and create adjacent midstory stem cover.

SUMMARY

The grouse population on WSC declined through the study period. Habitat improvement on the study site and surrounding area is the most feasible approach to increasing ruffed grouse abundance. Prescriptions that maximize diversity of forest types and age classes should satisfy ruffed grouse habitat requirements that change seasonally with life-history functions. Because ruffed grouse are associated with ephemeral habitats, a long-term approach is necessary to retain habitat quality and quantity over time.

VITA

Benjamin Colter Jones was born in New Castle, Pennsylvania on March 9, 1975. He was raised in rural Pennsylvania where he attended high school at Mansfield Junior-Senior High. He graduated from Pennsylvania State University in 1998 with a B.S. in Wildlife and Fisheries Science (Forest Science minor). He completed M.S. research in Wildlife and Fisheries Science at Mississippi State University in 2001. His research interests include impacts of silvicultural prescriptions on wildlife and the use of forest management for improving wildlife habitat. Ben is currently the Wildlife Planning Biologist with the Pennsylvania Game Commission.

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.

Go to full podcast

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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West Nile Virus

PA Game Commission Research Summary

WNV Overview

- **WNV is an arbovirus most commonly transmitted by mosquitoes.**
- **70-80% of infected people show no symptoms. 1 in 5 will show flu-like symptoms. <1% may develop serious neurological illness such as meningitis, which may be fatal.**
- **WNV is known from Europe, Africa and Asia. It was first detected in North America in 1999 (NY). Human and wildlife infections have been documented in all 48 contiguous states.**

Impacts of WNV on Wildlife

- **WNV has been detected in over 300 avian species in the United States. Populations of some species are not impacted. Some experience steep declines followed by population recovery. Others experience steep declines followed by continued population suppression.**
- **WNV has been shown to have dramatic impacts on sage grouse, reducing juvenile, yearling and adult survival.**

Historic Impacts of WNV on Ruffed Grouse

- **In 2000, NY DEC received nearly 150 grouse carcasses found on the landscape by residents. Eighteen percent of these tested positive for WNV using the tests available at the time.**
- **PA's largest grouse propagator (flock= 30 birds) lost 80% of his flock in a two week period in September 2003. WNV was confirmed as cause of death in the single carcass submitted for testing from this outbreak.**
- **The nation's largest grouse propagator (in Idaho) lost 25% of his ruffed grouse in 4 days in 2013 (n=10 of 40 grouse). WNV was not lab-confirmed, but since beginning an annual vaccination program losses have been minimal (n=3 deaths in 2014).**
- **118 hunter-harvested birds were tested for WNV antibodies during the National Grouse and Woodcock Hunt in MN in 2005. One bird was found to have antibodies to WNV (suggesting previous exposure). This study confirmed that grouse contract the disease and can survive. The low number of antibody-positive birds suggested *either* that WNV prevalence was low in MN in 2005 *or* that grouse mortality was high (i.e. birds were not living to time of harvest). Researchers called for a follow-up experimental study of grouse and WNV at that time, but resources were unavailable.**
- **Eastern/Mid-Atlantic states with Cooperator programs exhibited a multi-state grouse population decline in the years 2001-2005 (Figure 1). Population recovery has varied from state to state since that time. It is likely that the severity of WNV impacts will vary from state to state and year to year depending upon habitat quantity and quality, annual WNV prevalence, and individual- and population-level recovery.**
- **PA grouse populations (as indicated by hunter flush rates) showed steep declines in the initial years of the PA outbreak (2001-2005), followed by weak recovery (Figure 2). When WNV prevalence increased again in 2009-2014, grouse populations again showed steep declines. When corrected for hunter effort (harvest/100 days), grouse harvest declined 45% (2001-2005) and 28% (2009-2014).**

Current Impacts of WNV on Ruffed Grouse

- **The PA Game Commission (PGC) is working to better understand the impact of WNV. Colorado State University, Guelph University (Ontario), Ruffed Grouse Society and Woodcock Limited have been partners in this effort. We are fortunate to be working with some of the top WNV researchers in the country on this project.**
- **The two main early objectives of this research are 1) to determine the susceptibility of grouse to WNV, and 2) to measure statewide exposure to WNV in grouse.**
- **For Objective 1, PGC and collaborators used chicks hatched from wild-collected eggs to conduct an experimental infection trial in 2015. Results indicated that WNV affects multiple critical organs in grouse, including brain, heart, muscle, and kidneys. Some birds had rapidly fatal infections (within 8 days of infection) while others survived to the end of the 2-week trial, but had WNV-associated damage to heart and brain tissue. In all, 80% of the inoculated grouse died or had significant lesions due to WNV.**
- **PGC, with RGS support, tested hunter-harvested grouse for antibodies (exposure) to WNV in the 2015-16 season. This revealed that in every region of PA, some wild grouse are exposed to WNV and some proportion survive until the hunting season. Sampling will continue in the 2016-17 season.**

The Habitat Connection

- **WNV does not apply annual and steady pressure on grouse populations throughout their range. Rather, prevalence (and risk to grouse) rises and falls over time. In PA, dramatic WNV peaks occurred in 2001-2004 and 2012-2014. WNV peak years are most likely triggered by weather, so the timing of peak years will vary in other states, regions and time periods.**
- **PA's population monitoring (based on hunter flushes/hour) indicates that regions with <u>high-quality and abundant habitat</u> appear to show a <u>strong grouse population recovery</u> between peaks of WNV (i.e. grouse populations recover between WNV peaks) (Figure 3).**
- **PA's population monitoring also shows that in regions with lower-quality, less abundant and more fragmented habitat, grouse numbers show only an anemic recovery and continue to decline below long term average (i.e. populations do not recover between WNV peaks) (Figure 3).**
- **Preliminary results indicate that regions with high-quality and abundant habitat may also be producing more <u>individuals</u> that survive WNV than regions with poor habitat (i.e. individual birds exposed to WNV may have a higher rate of survival in high quality habitat than they do in low quality habitat). This could be due to better 'baseline' health, easier access to high-quality forage, better protective cover from predators or some other benefit associated with high-quality habitat.**
- **These are early observations and additional samples/results will help further support or refute these trends, and may reveal other factors involved in grouse population dynamics.**

WHAT CAN WE DO?

- **WNV is a Call to Action to create more high-quality habitat at a landscape scale. This has always been a priority for many of our conservation partners, but with the onset of this additional mortality factor and its potential role in grouse declines, urgent action is needed. PA's preliminary data suggests that habitat quality may affect the recovery of grouse populations.**

- **Until the protective mechanism of high-quality habitat is defined, managers should focus on creating areas with <u>diverse native food sources</u> and <u>thick protective cover</u> to support birds if and when they are exposed to WNV.**

Figure 1: State Hunter Flush Rates (flushes/hour) observed in states that maintain a Hunter Cooperator program.

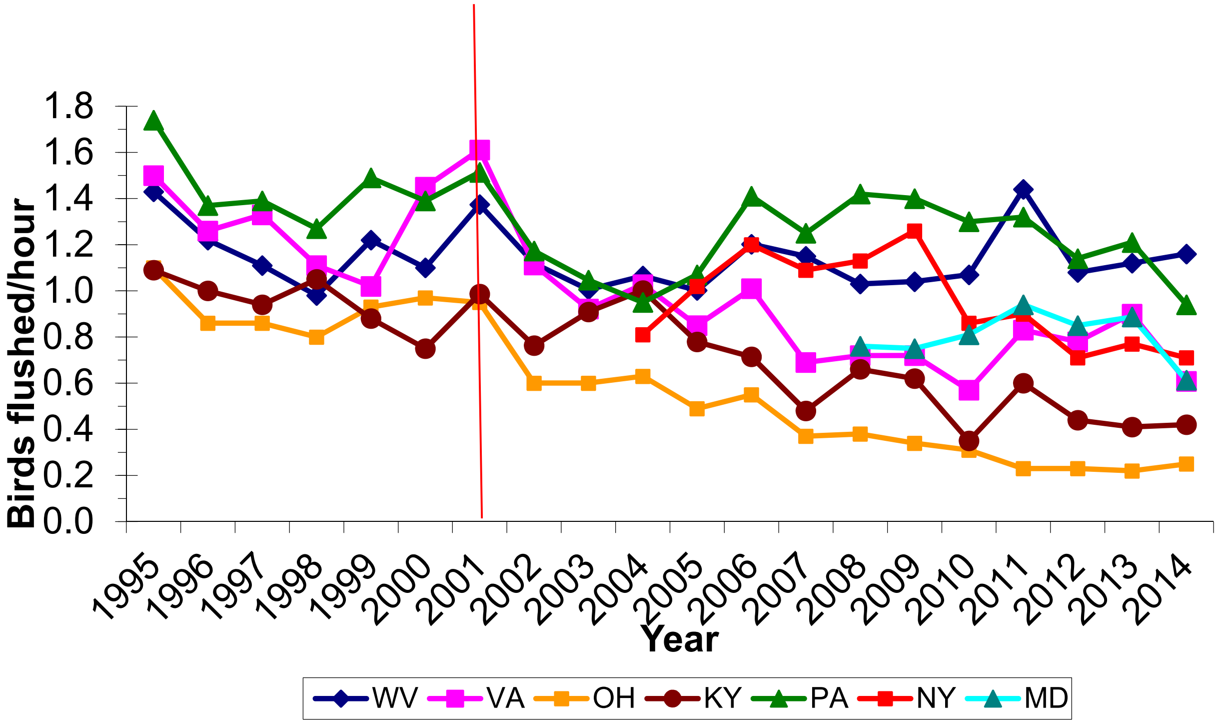

Figure 2: Long term grouse population trends, as reported by PA Grouse Cooperators, 1965 – 2015. WNV was found in PA in 2000 and occurred statewide by 2002.

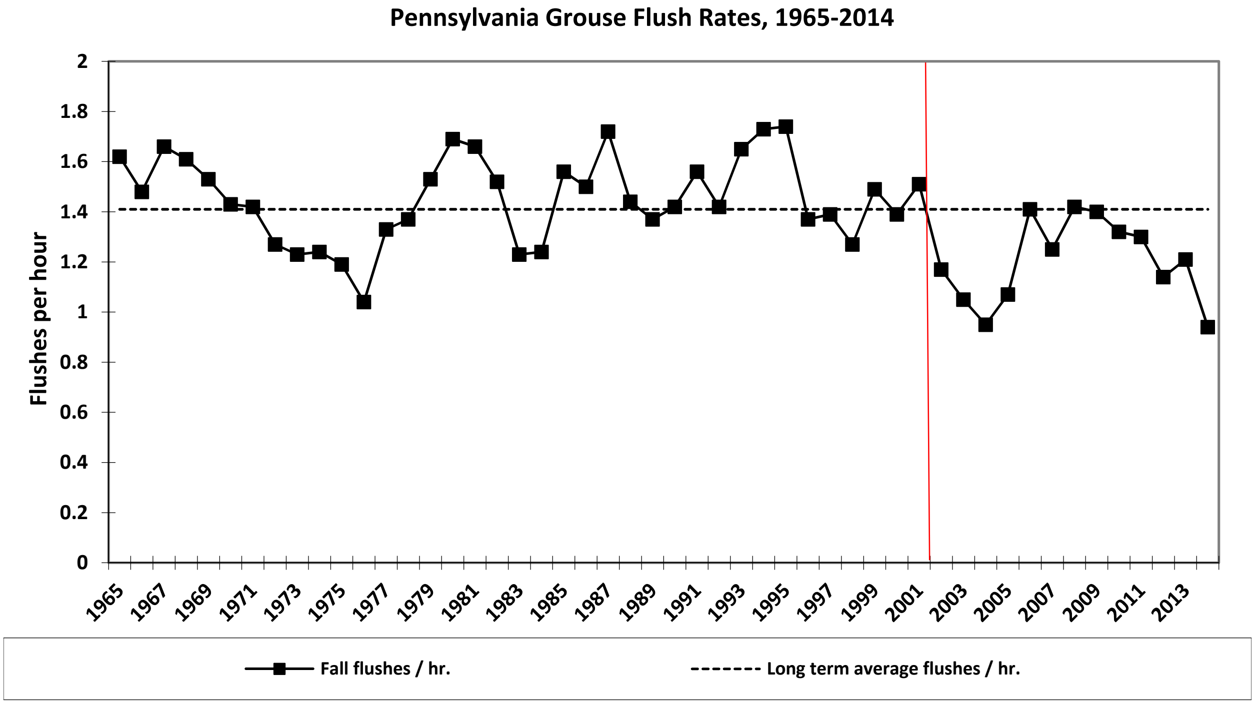

Figure 3: Grouse population trends in PA, showing robust recovery between WNV peaks in a region with high-quality and abundant habitat (represented by the NW region) and weak recovery in a region with less-abundant, fragmented habitat (represented by the SW region). Periods indicated in red represent peak WNV activity years, based on PA DEP surveillance data.