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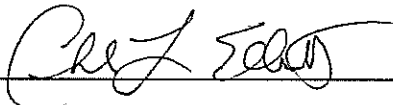
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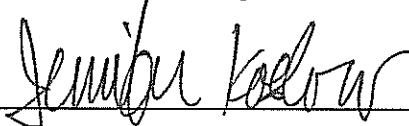
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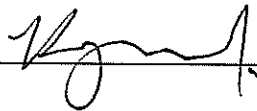
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THE DEVELOPMENT OF OLD-GROWTH STRUCTURAL CHARACTERISTICS IN

SECOND-GROWTH FORESTS OF THE CUMBERLAND PLATEAU, KENTUCKY, U.S.A.

By

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MASTER OF SCIENCE
December, 2012

DEDICATION

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

And

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

ACKNOWLEDGEMENTS

ABSTRACT

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

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1. INTRODUCTION

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

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

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

1.1 DEFINING OLD-GROWTH FOREST

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

Climax Old-Growth

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

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

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

Sub-Climax or Seral Old-Growth

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

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

Primary Forest

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

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

Secondary Old-Growth

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

1.2 STRUCTURAL CHARACTERISTICS

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

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

Canopy Age

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

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

Large Diameter Trees

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

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

Coarse Woody Debris

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

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

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

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

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

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

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

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

Large-Diameter Snags

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

past partial harvests or the cumulative basal area of smaller snags in the younger forests (McComb and Muller 1983; Goodburn and Lorimer 1999; Hale et al. 1999).

Cavity Trees

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

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

Uneven Age Distribution

Trees in old-growth forests often follow a multi-age distribution, with recruitment either continuous or occurring through multiple recruitment events, or both, depending on the spatial scale under consideration. An uneven-aged distribution results when stand development proceeds in the absence of major

disturbance, with tree mortality occurring individually or in small groups (Oliver and Larson 1996; Frelich 2002).

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

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

Multi-layered Canopy

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

Large Overstory Basal Area

The basal area (BA) of a stand is the sum of cross-sectional areas of all trees at 1.3 m, or breast-height, over a given area and expressed in m^2/ha (or ft2/ac in American forestry). Basal area tends to increase with stand maturity and inversely with stand density, and can vary considerably by forest type with drier or more disturbance-prone forests having lower basal areas than more productive and

sheltered forests. Martin (1992) provided a lower threshold for old-growth forests of 25 m²/ha based on values from Lilley Cornett Woods, where BA values ranged from 20.6 to 42.4 m²/ha across all communities. However, total forest BA for mature, and even young, second-growth forests sometimes falls within this same range (Goebel and Hix 1996; Hale et al. 1999).

Overstory Density

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

Herbaceous Diversity

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

Pit and Mound Topography

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

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

Canopy Gaps

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

1.3 REGION 8 GUIDANCE ON OLD-GROWTH

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

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

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

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

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

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

3) **Minimum Basal Area:** The minimum basal area set for both old-growth mixed mesophytic and dry-mesic oak communities is about 10 m²/ha (40 ft2/ac). This value is much lower than that found in the literature for these forest types, and is explained by stating that the value "is a conservative estimate to ensure that stands are not excluded due to the variety of ecological conditions which exist."

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

1.4 STAND DEVELOPMENT

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

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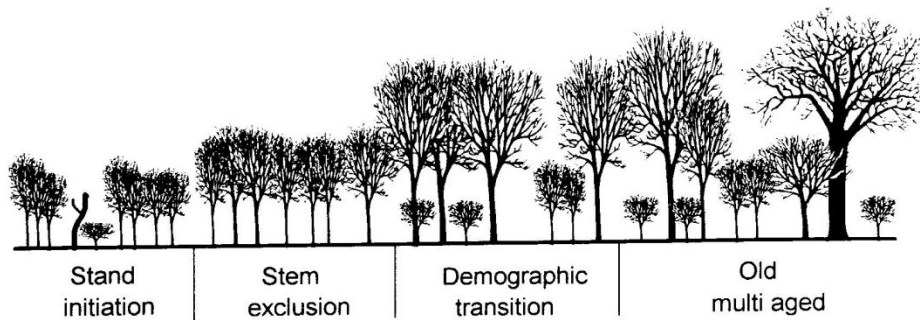
Figure 1: Sequence of structural phases in stand development.

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

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

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

Stage 2. Stem Exclusion: During this second stage, the young trees form a
dense, codominant canopy with a unimodal diameter distribution. Inter-tree,
density-dependent competition drives self-thinning in the stand, while
remaining trees rapidly fill in gaps through lateral growth. Tree density

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decreases while tree diameters, stand basal area, and crown height increase. Light exclusion inhibits growth of seedlings and saplings.

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

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

1.5 NATURAL DISTURBANCE

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

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

Wind

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

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

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

Gap Dynamics

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

Small gaps close rapidly through lateral growth of edge trees and effectively return the forest patch to a closed canopy condition in a few years. Gaps of sufficient

size, however, close more slowly through vertical growth of released understory trees or development of a new cohort from advance regeneration or seed bank. Further, Runkle (1998) found increased rates of mortality among edge trees in larger gaps, leading to further enlargement of the gap environment and longer persistence.

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

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

Ice

Ice storms are a periodic disturbance of intermediate severity in forests of the Cumberland Plateau. Glazing of ice on limbs can lead to limb breakage, stem snapping, and uprooting of trees (Lafon 2006). Ice damage can have a differential effect across species, thereby affecting species distributions in forests. Oak species, including *Quercus alba*, *Q. montana*, and *Q. rubra*, along with many *Pinus* species

(except *P. strobus*) are generally more resistant to ice damage than *Acer* species, which are, in turn, more resistant than basswood (*Tilia americana*), elm (*Ulumus americana*), black cherry (*Prunus serotina*), and other light-wooded trees.

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

Large Herbivores

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

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

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

Drought

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

1.6 ANTHROPOGENIC DISTURBANCE

Anthropogenic disturbance to forest ecosystems in Kentucky and the Central Appalachians has been occurring for at least 11,000 years (Pollock 2008). While the direct effects of human habitation and use for much of the Holocene may have been localized, the cumulative effects of anthropogenic fire, horticulture, and hunting

over millennia likely had major ramifications on forest and other community structure and function at the landscape scale. However, in the modern era, human activities have radically altered the forest landscape (Abernathy et al. 2010).

Fire

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

Fire is hypothesized to be an important driver of species dynamics in eastern forests — particularly as relates to the issue of oak dominance (Abrams 1992; McEwan et al. 2007). Throughout oak-dominated forests of the eastern U.S. there has been an observed pattern of poor oak establishment or success in the understory, countered by a concomitant, and marked, increase in maple abundance (particularly red maple, *Acer rubrum*)(Lorimer 1984). The "fire and oak hypothesis" suggests that this apparent shift in species dominance is a direct result of fire

suppression beginning ca. 1930 (Abrams 1992). While there is some evidence supporting this hypothesis, a review of the literature suggests that the observed oak-maple dynamics may reflect a more complicated suite of ecological drivers, including changes in herbivore populations, loss of the American chestnut (*Castanea dentata*), climate patterns, and other factors (McEwan et al. 2010).

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

Logging

Other than the complete removal of forests through agricultural conversion, surface mining, or development, logging has provided the most intensive, and certainly widespread, impacts to forests in the Eastern Deciduous Forest during the modern era. Logging historically has taken many forms resulting in a wide range of secondary forest conditions. In many cases, the practice of selective cutting of the most valuable trees, particularly over multiple entries, resulted in a shift in species composition while leaving trees that, from a timber perspective, are of poor form, quality, or health (Roach and Gingrich 1968, Kentucky Division of Forestry 2010). Modern forestry, beginning in the mid-20th century, emphasized even-aged methods of forest management, including clearcutting, seed-tree, and shelterwood methods with an emphasis on the regeneration of commercial species and high-value timber (Roach and Gingrich 1968; Wenger 1984), though uneven-aged

approaches have also been applied (Smith 1980; Wenger 1984) . More recently, selective approaches have been designed to enhance or better mimic old-growth forest conditions (Runkle 1991; Lorimer and Frelich 1994; Keeton 2006; Bauhus et al. 2009). However, most forest land in Kentucky is privately owned, with logging practices essentially unregulated and often carried out in the absence of a certified forester or management plan (Kentucky Division of Forestry 2010).

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

1.7 AMERICAN CHESTNUT (*CASTANEA DENTATA*)

Any discussion of the current structure and function of Appalachian forests would be remiss to omit addressing the loss of the American chestnut (*Castanea dentata*). While its prevalence was variable, American chestnut was a dominant species in many forests throughout the Appalachian region and Cumberland Plateau (Braun 1950). Prized for its rot-resistant timber and abundant, nutritious nuts, American chestnut was effectively extirpated as the result of the introduction of the Asian fungus *Cryphonectria parasitica*. First identified in New York in 1904 (Griffin 2000), the blight reached Kentucky by 1930 and quickly spread throughout the state. The fungus attacks the trees' vascular tissue, effectively girdling the tree and choking off the flow of nutrients and water. However, the rootstock can survive and send up new stems, which are frequently observed in Appalachian forests, though

rarely larger than saplings. Several efforts to develop and deploy resistant strains of American chestnut show promise (Griffin 2000; Jacobs 2007). American chestnut was able to survive a wide range of edaphic conditions, and replacement in the canopy following blight appears to have been strongly related to whichever species were both present at a given site at the time of decline and physiologically capable of exerting dominance (Elliot and Swank 2008). While an occasional chestnut stump can still be found, because of the > 70 years since chestnut decline in Kentucky, no direct, American chestnut-related structural impacts, such as gaps, down logs, etc, are common in present-day forests.

1.8 STATUS OF OLD-GROWTH FORESTS IN KENTUCKY

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

Lilley Cornett Woods

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

study as a benchmark for comparing structural characteristics of second-growth and old-growth forests.

Blanton Forest

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

Rock Creek Research Natural Area

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

Mammoth Cave Big Woods

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

logging and other activities in the past (Neil Pederson, Lamont-Doherty Earth Observatory, personal communication 2012).

Tight Hollow

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

Beaver Creek Wilderness

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

Other Old-Growth Forests

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

2. STUDY AREA

2.1 ECOLOGICAL SETTING

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

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

The landscape is predominantly a dissected plateau of hilly to mountainous terrain, including steep ravines, narrow stream channels, rolling hills, and more than 5,000 km of cliffline on national forest system lands alone (USDA FS 2004). Bedrock is a mix of sandstone, shale, siltstone, and limestone, and soils are generally acidic and of moderate to low fertility (USDA FS 2004). Average precipitation ranges from about 116 to 132 cm annually, generally increasing from north to south (Abernathy et al. 2010). By age, approximately 68,800 hectares (24%) is over 100 years old and 1,630 hectares (0.6%) over 140 years old. Of the latter, only an estimated 308 hectares is hardwoods, with the remainder mostly hemlock forests (USDA FS 2009).
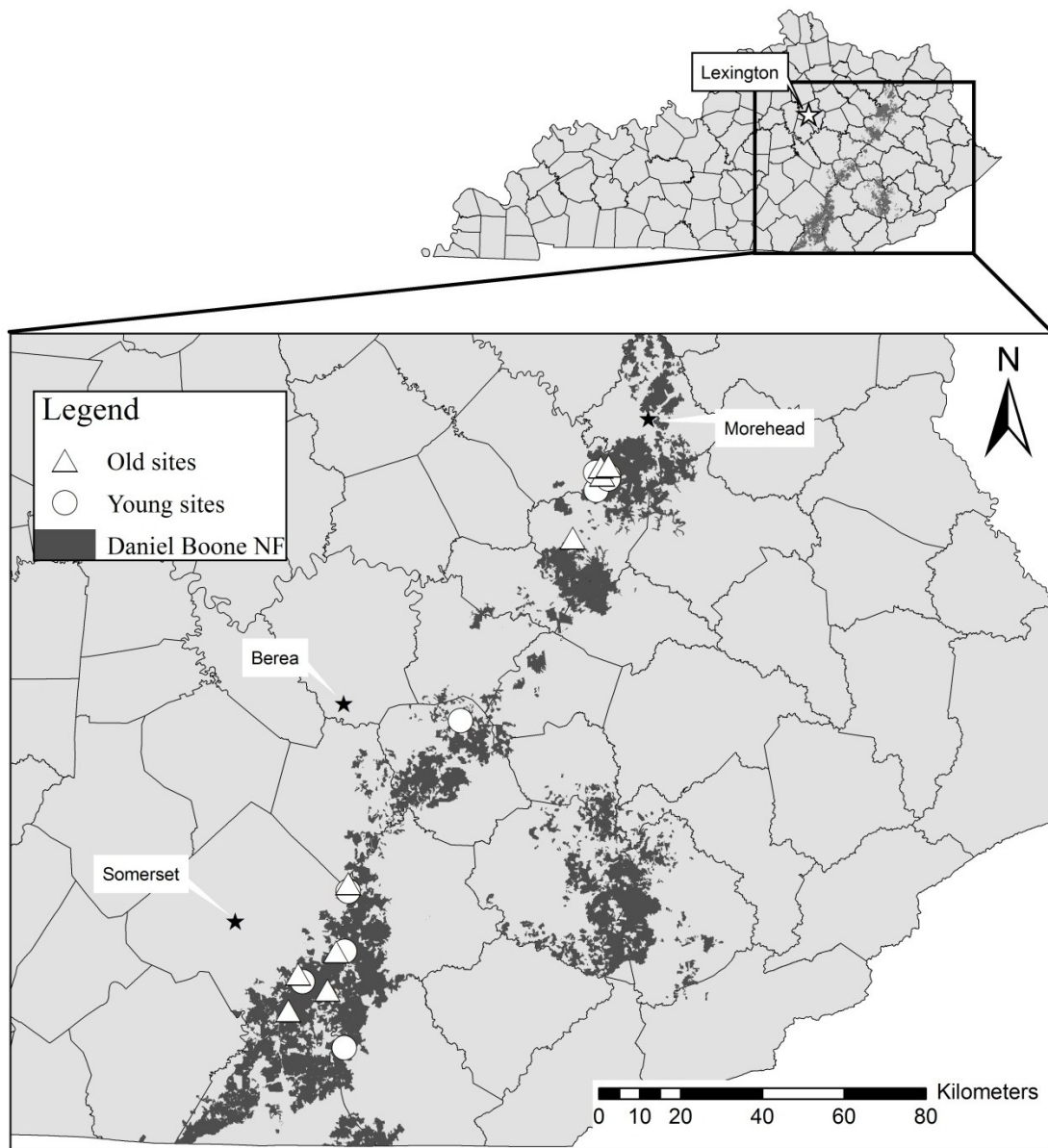
Figure 2: Map depicting study sites in the Daniel Boone National Forest, Kentucky. Circles indicate young study sites (70-90 years old); triangles indicate old study sites (140-160 years old).

2.2 DISTURBANCE REGIMES

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

2.3 LAND USE HISTORY

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

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

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

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

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

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

*Eu*r*o-American Settlement*

From the late 1600s into the early and mid-1700s, Kentucky is considered to have been largely depopulated (Henderson et al. 1986; Aron 1996). While it has been suggested that this apparent low in resident population was a result of Iroquois attacks on the Shawnee in order to lay claim to game-lands in Kentucky and along the middle Ohio river valley (Aron 1996), it is probable that depopulation was driven more by pandemics and attendant social reordering (Henderson et al. 1986). The relationship between depopulation and evidence of extreme drought around 1660 (Haasis 1923) has not been explored. Regardless of why, eastern Kentucky seems to have remained sparsely populated throughout the eighteenth century, with Shawnee, Cherokee, and other peoples gradually moving back into the area as a seasonal hunting ground (Aron 1996). However, while the French and English had long travelled the Ohio river corridor, it wasn't until the late eighteenth century that Anglo-American long hunters, including Daniel Boone, began pressing

into Appalachian Kentucky in search of both game for the fur trade and land interests. Despite ongoing conflicts with Native American groups, by the late 1770s the first mass-migrations of white settlers through the Cumberland Gap and into Kentucky via the Wilderness Road began (Aron 1996). While the first migrants into Kentucky settled in the Bluegrass Region in central Kentucky, it was not until the first quarter of the nineteenth century that immigrants settled the more rugged lands of the Cumberland Plateau (Pudup 1990).

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

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

National Forest Establishment

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

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

3. METHODS

3.1 SITE SELECTION

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

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

growth characteristics in these particular stands somewhat moot and limit the applicability of this study's findings for future management decisions.

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

Plot Location

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

Sampling

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

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

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

Source: Modified from Jennings, S.B., N.D. Brown, and D. Sheil. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover, and other measures. Forestry 72(1): 59-73.
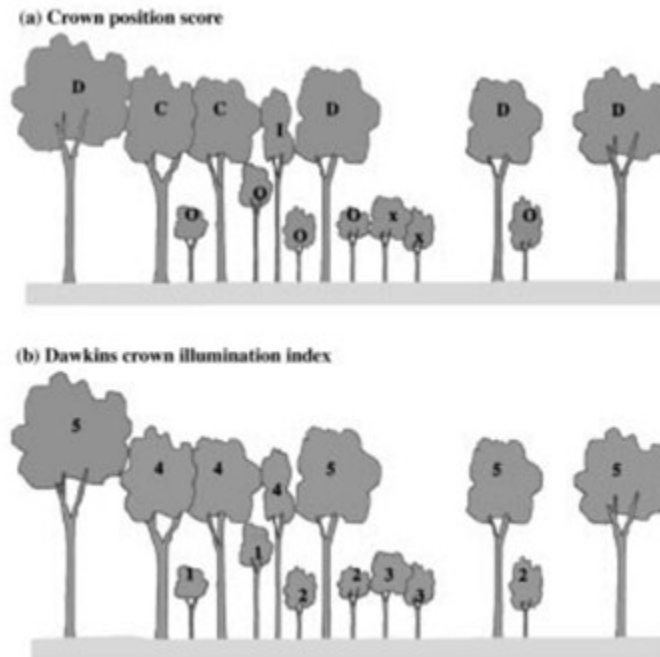
Figure 3: Diagram showing crown position (a) and illumination index (b) scores used to assess canopy structure in forests in the Daniel Boone National Forest, Kentucky.

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

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

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

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

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

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

3.2 ANALYSIS

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

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

Tree ages where cores were oblique to, but < 3 cm from the pith were estimated by fitting a circle of known radius to the curvature of existing rings and estimating the missing rings by applying the average number of rings in the last evident centimeter to the missing distance to the pith. Where trees were hollow and

cores oriented toward the pith, or oblique and > 3 cm from the pith, no age estimate was made. Unlike other metrics in this study, tree age data are provided as counts rather than means.

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

4. RESULTS

Age Distributions

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

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

Coarse Woody Debris

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

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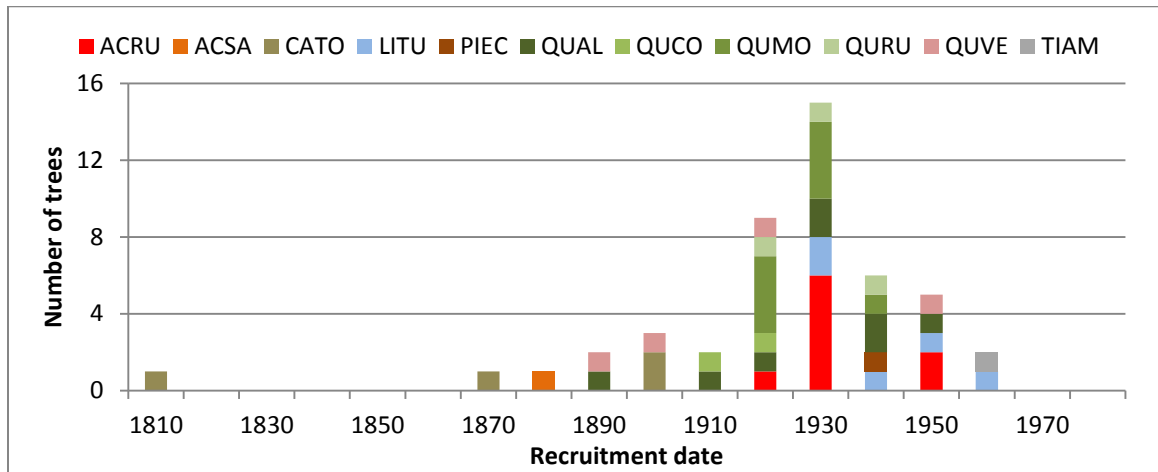
b.
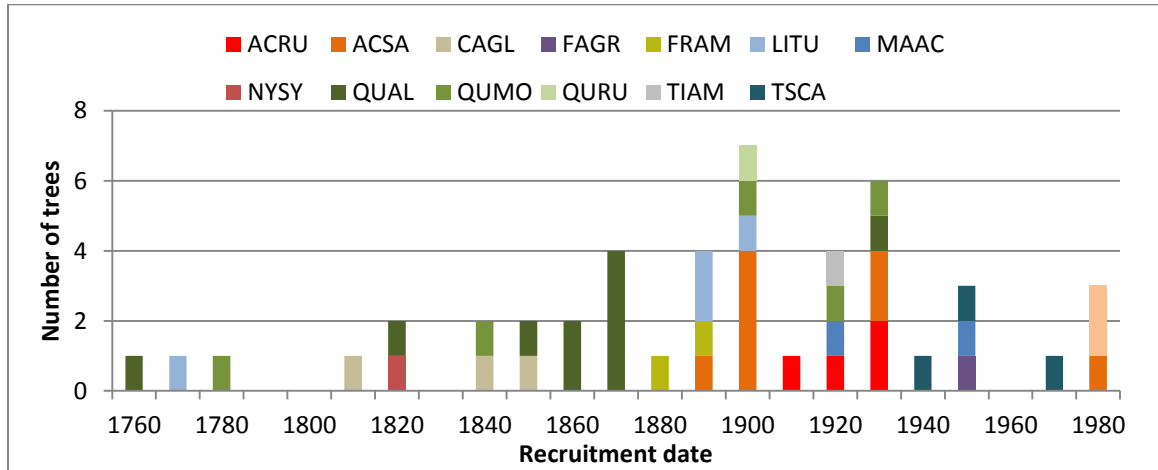
Figure 4: Age distribution of trees in young (a) and old (b) forest. Abbreviations as follows: ACRU = red maple (*Acer rubrum*); ACSA = sugar maple (*Acer saccharum*); CATO = mockernut hickory (*Carya tomentosa*); FAGR = American beech (*Fagus grandifolia*); FRAM = white ash (*Fraxinus* americana); LITU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

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

Source: Old-growth value from Muller, R.N. and Y. Liu. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Canadian Journal of Forest Research 21(11): 1567-1572).
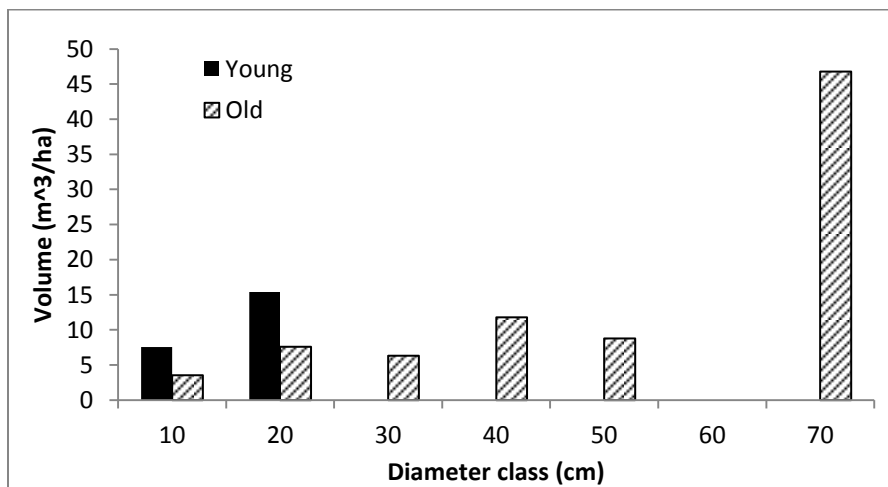
Figure 6: Coarse woody debris volume by diameter class in young (70-90 years old) and old (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

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

Snags

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

Crown Position

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

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

Illumination Index

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

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

Figure 8: Snag density by diameter class in young (70-90 years old) and old (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.
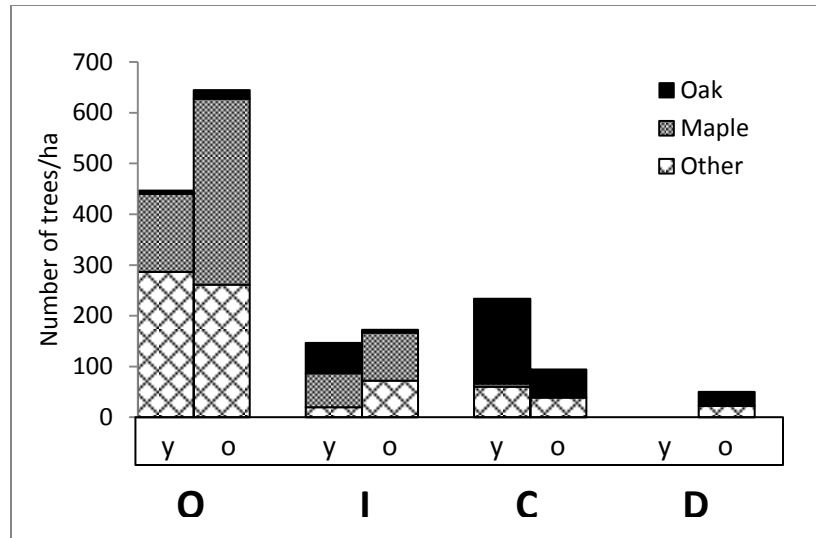
Figure 9: Crown position in young (y) (70-90 years old) and old (o) (140-160 years old) forest in the Daniel Boone National Forest, Kentucky. Categories are overtopped (O), intermediate (I), codominant (C), and dominant (D).

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

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

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

Canopy Species

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

Basal Area and Density

Total basal area was greater in old forest, with 31.5 m^2/ha in young forest and 41.0 m^2/ha in old forest (t(31) = 1.50, P = 0.072) (Figure 12). The density of trees > 10 cm DBH in young and old forest was 420 stems/ha and 378 stems/ha, respectively, with differences not significant (Mann-Whitney U = 145, n_1 = 18, n_2 = 15, $P > 0.2$, two-tailed). This compares to 536 stems/ha from the 2010 Lilley Cornett Woods data and the 250 stems/ha average reported for the same forest by Martin (1992) (Figure 13).
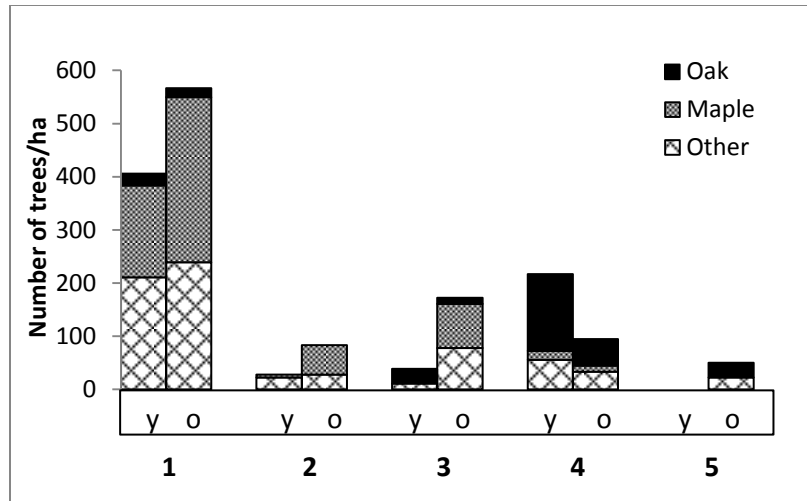
Figure 10: Illumination indices (1-5) for young (y) (70-90 years old) and old (o) (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

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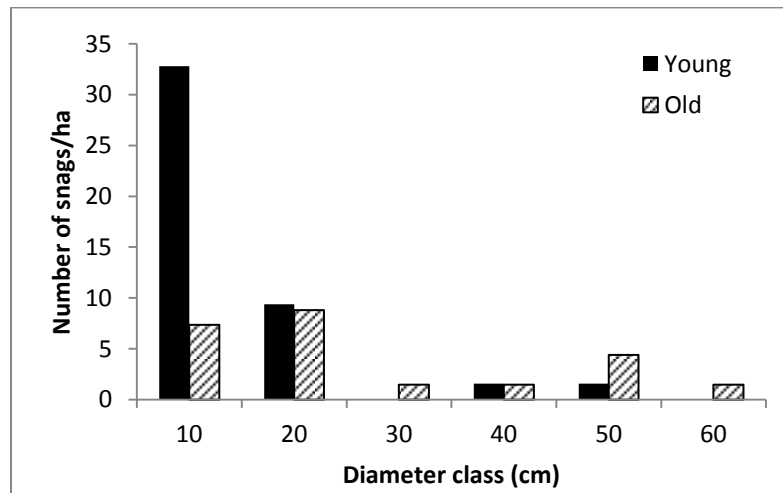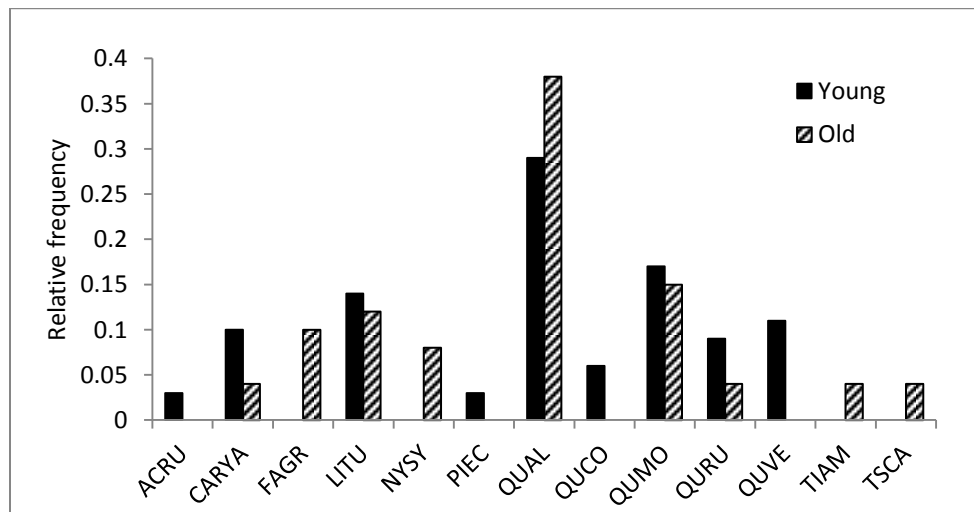

Figure 11: Canopy species in young and old forest, including codominant and dominant trees in young (70-90 years old) and old (140-160 years old) forest in the Daniel Boone National Forest, Kentucky.

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

Source: Old-growth value is calculated from McEwan, R.W. and S. Richter. 2010.
   Lilley Cornett Woods long-term data. Division of Natural Areas, Eastern
   Kentucky University, Richmond, KY.
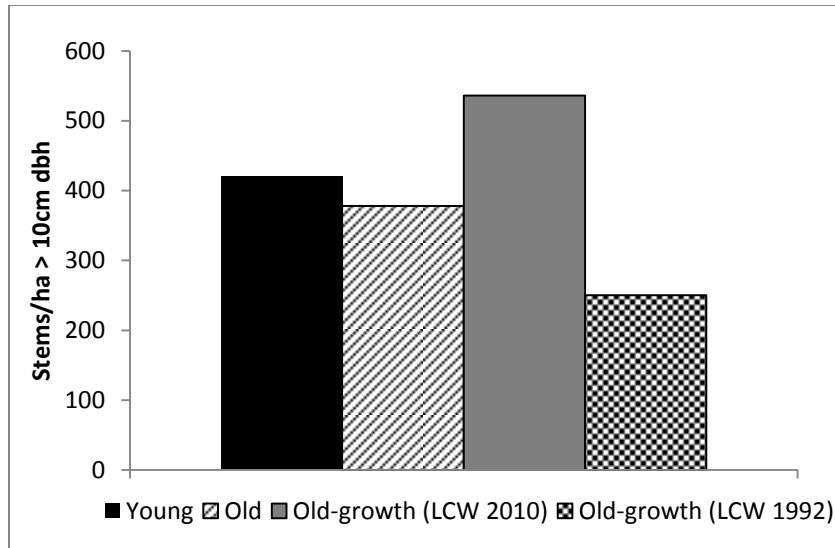
Figure 13: Density of trees > 10 cm DBH in young, old, and old-growth forests (Lilley Cornett Woods) in the Cumberland Plateau of Kentucky.

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

Diameter Distributions

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

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

Seedlings and Saplings

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

There were more maple (*Acer*) seedlings in young forest than old forest (9,259 stems/ha and 3,810 stems/ha, respectively; Mann-Whitney $U = 177$, $n_1 = 18$, $n_2 = 15$, $P < 0.1$, one-tailed). Oak (*Quercus*) seedling densities were greater in young forest (14,519 stems/ha) than in old forest (2,037 stems/ha) (Mann-Whitney $U = 229.5$, $n_1 = 18$, $n_2 = 15$, $P < .01$, one-tailed). The large number of oak seedlings in the young forest was driven, in large part, by a single plot that had a very large number of very small chestnut oak (*Q. montana*) seedlings. Removing this plot resulted in a
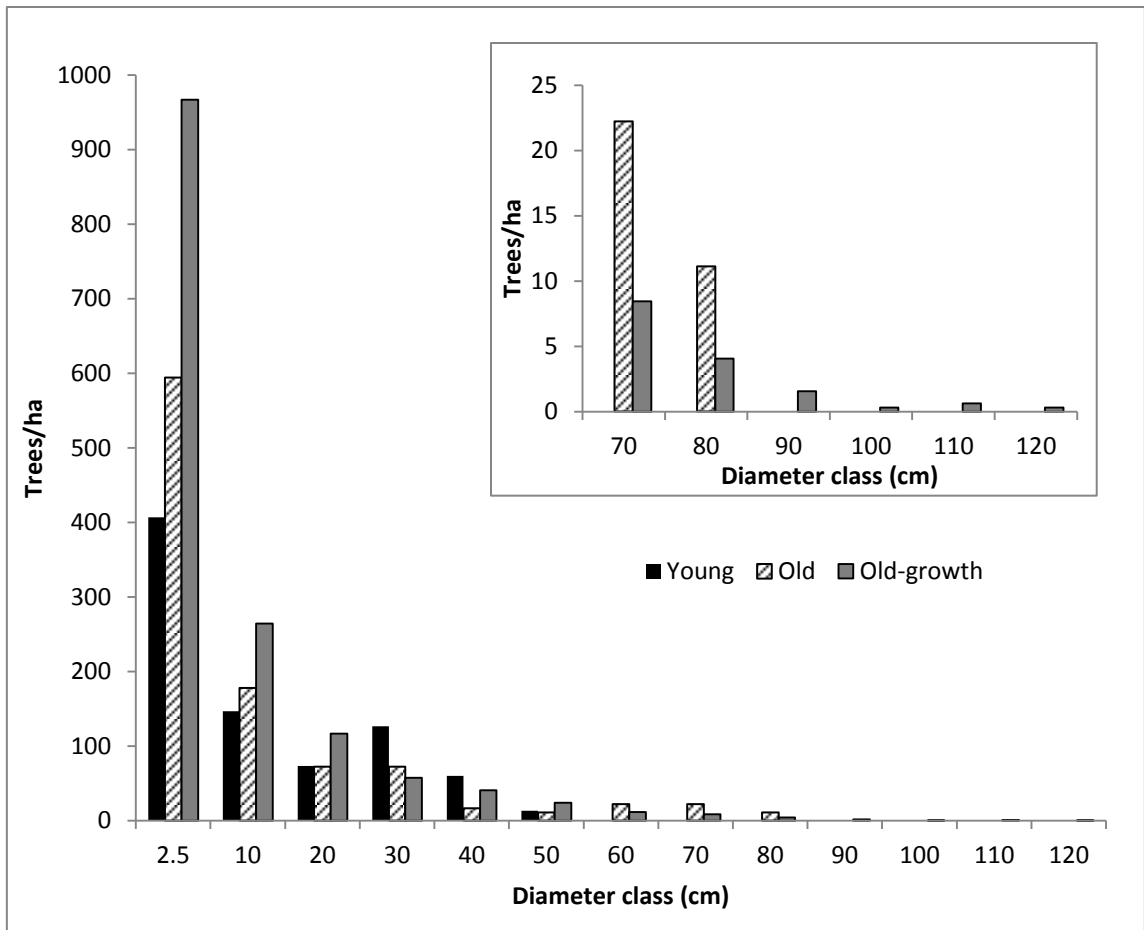
Figure 14: Diameter distributions of live trees in young (70-90 years old), old (140-160 years old), and old-growth forest (Lilley Cornett Woods) in the Cumberland Plateau of Kentucky.
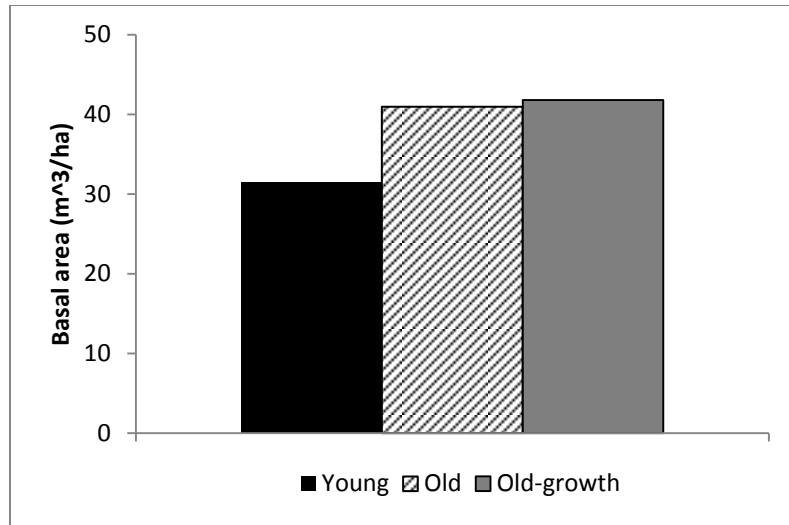
Note: Inset shows diameters >70 cm dbh.

Source: Old-growth values calculated from McEwan, R.W. and S. Richter. 2010. Lilley Cornett Woods long-term data. Division of Natural Areas, Eastern Kentucky University, Richmond, KY.
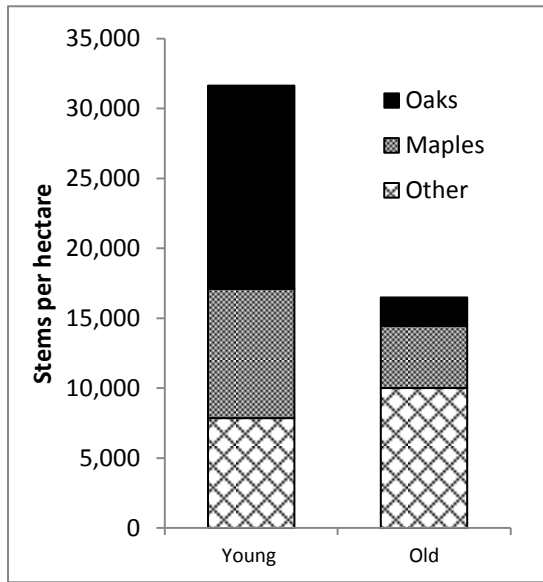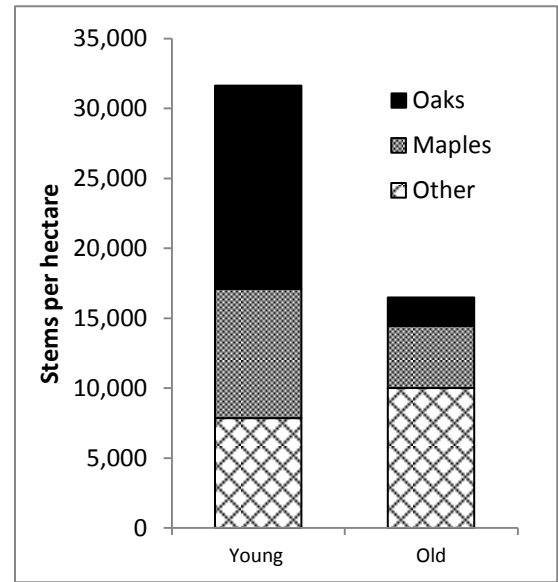
Figure 15: Density of seedlings (A) and saplings (B) in young (70-90 years old) and old (140-160 years old) forests in the Daniel Boone National Forest, Kentucky.

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

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

5. DISCUSSION

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

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

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

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

Source	Characteristic	Benchmark	Young forest	Old forest
Martin (1992) R8 Guidance	Large canopy trees	> 7 trees/ha > 75cm DBH Canopy trees > 50 cm DBH	No; (0/ha) Few (13.3/ha)	Yes (16.7/ha) Many (66.7/ha)
Martin (1992) R8 Guidance	Tree ages	Oldest trees > 200 years Canopy > 150 years	No No	Yes Yes
Martin (1992) Parker (1989)	Stem density	160-315 stems >10 cm DBH/ha 161-427 stems > 10 cm DBH/ha	No (420/ha) Yes	No (378/ha) Yes
Martin (1992) R8 Guidance	Total basal area	Total basal area > 25 m^2/ha Total basal area > 10 m^2/ha	Yes Yes	Yes Yes
Martin (1992)	Snag density	Ave. 10 snags > 30 cm DBH/ha	No (3/ha)	No (8.82/ha)
Muller & Liu (1991)	Coarse woody debris	More in old –growth; 50.4 m³/ha in LCW	23.0 m³/ha	84.9 m³/ha
Oliver and Larson (1996), Frelich (2002)	Age distribution	Uneven age distribution	No	Yes
Frelich (2002)	Canopy Structure	Vertical and horizontal structural complexity	Less	More

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

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

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

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

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

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

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

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

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

It is also notable that the oldest trees in the old forest were often not the largest (Figure 16), suggesting that larger old-growth trees were removed. It may also be that selectively removing the largest trees would have been extremely difficult this early in settlement, when major infrastructure to support large-scale
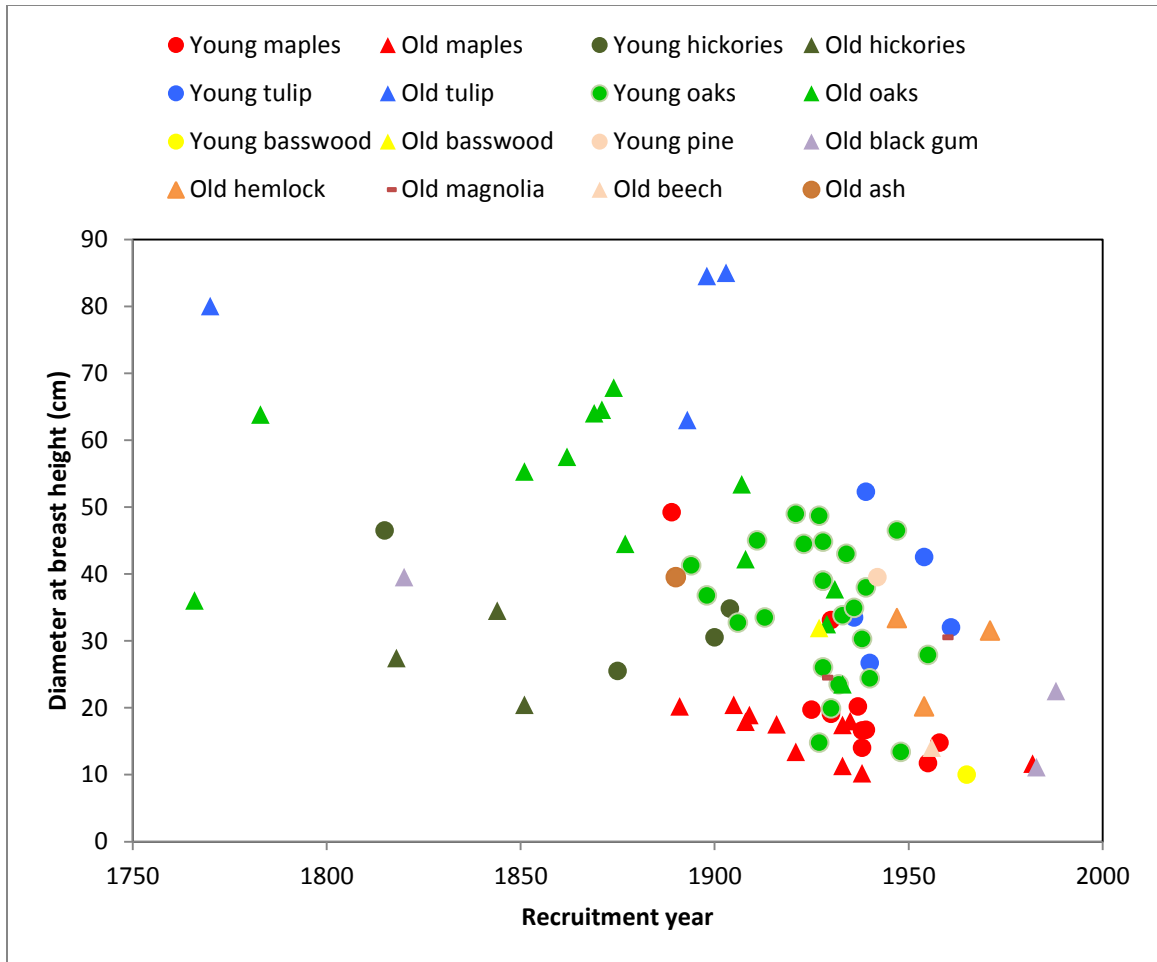
Figure 16: Size vs. age relationships for trees by species in young (70-90 years old)(triangle) and old (140-160 years old)(circle) forests in the Daniel Boone National Forest, Kentucky.

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

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

5.1 OLD-GROWTH CHARACTERISTICS

Age Distributions

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

whether recruitment from about 1840 to 1900 represents continuous recruitment in individual stands or instead reflects error in canopy age determination, ongoing recruitment after 1900 was common in old forest plots. This, along with the presence of several trees > 200 years old, lends legitimacy to the determination that the old forests in this study are indeed mixed-aged forests.

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

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

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

modest size (< 20 cm DBH) at the time of disturbance. Therefore, in an absolute sense, the old forest had more old trees, but in a relative sense of forest development they are similar.

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

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

Succession

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

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

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

Coarse Woody Debris

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

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

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

Snags

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

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

stand-replacing cohort. If these trees are dying as a result of long-term suppression it could signify that young forest in this study is in a late stage of stem exclusion or transitional between stem exclusion and demographic transition.

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

Crown Position and Illumination Index

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

canopy as well as allow for increased species diversity through partitioning of a greater number of environmental microsites (Messier et al. 2009).

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

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

Basal Area and Density

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

The data here, however, do suggest that stand-level basal increases with age, with both old and old-growth forest basal areas greater than that found in young

forest. In this case, old forest appears to have reached approximately the same basal area as old-growth. The value of 41.0 m²/ha for old forest is nearly identical to the 41.8 m²/ha for Lilley Cornett Woods in 2010, and toward the upper range value of 42.4 m²/ha for Lilley Cornett Woods reported by Martin (1992), who provided a range of 20.6 m²/ha to 42.4 m²/ha across all community types in that forest. Alternatively, it may be that the differences in basal area in this study are an artifact of differences in site productivity. Despite having chosen sites to maximize similarity in community type, the species distribution of canopy trees does suggest the possibility that the pool of old sites may have skewed more mesic than mature sites, affecting overall values (Figure 11). However, even if this were partly true, the major differences here still suggest increasing BA, and therefore biomass, with time well into old-growth phases of forest development, an observation now frequently found globally (Luyssaert et al. 2008; Keeton et al. 2011).

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

Neither young nor old forest fits within Martin's (1992) reported values for Lilley Cornett Woods, though both fall within Parker's (1989) range for Midwestern old-growth forests. Notably, the 2010 Lilley Cornett data fits neither, with a density of 536 trees/ha > 10 cm DBH, and Hart et. al (2012a) similarly reported 620 stems/ha >10 cm DBH at Savage Gulf. Both Lilley Cornett Woods and Savage Gulf are old-growth forests on the Cumberland Plateau, yet both exhibit a density well

over that for both young and old second-growth forests in this study. Hart et. al (2012) suggested that the higher density in upland forests at Savage Gulf may be driven by lower site productivity, but this does not explain the results for Lilley Cornett Woods.

Diameter Distributions

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

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

By contrast, the diameter of young forest trees did not reach beyond 55.6 cm, which was less than half that of the old-growth forest, and exhibited a secondary peak around 30 cm DBH in an otherwise truncated, reverse-J distribution. This secondary peak suggests the initial, 70-90 year old stand-replacing cohort having

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

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

While the appearance of a trend in the 2.5 cm diameter cohort of increasing density with age proved statistically insignificant, the pattern may warrant further investigation. It could suggest a transition from the understory reinitiation or demographic transition phase into the multi-aged or old-growth phase of stand

development. While greater number of seedlings and saplings in the young forest noted previously implies a greater capacity for advance regeneration than in the old forest, an alternative hypothesis is that the increased understory light conditions observed in old forest are allowing more seedlings and saplings to advance into larger diameter cohorts, thus decreasing the bank of seedlings and saplings. While speculative, this would be a logical extrapolation from what is generally understood about forest development.

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

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

approached through the interplay of competition and species-specific growth characteristics, with absolute age and canopy turnover less important.

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

5.2 OAK AND MAPLE DYNAMICS

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

While the above implies an overall pattern of shifting recruitment and dominance with time, the dendrochronological analysis reveals more complex and nuanced patterns. Oak recruitment peaks with both age groups around the period of

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stand initiation, and continues in an episodic fashion in the old forest from 1900 through 1940 and through the 1950s in young forest. However, whether the post-regeneration, episodic recruitment of oaks is related to natural disturbance, selective logging, or is independent of disturbance is unclear from the data. Regardless of the initiator, the timing suggests that intense disturbance may be an important aspect of successful oak recruitment.

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

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

The oldest red maple in the young forest dates to 1924, aligning with passage of the Clarke-McNary Act, though the oldest red maples in the old forest date to 1916 and 1921, just prior to the recognized period of fire suppression. Cooper (2011) and Tackett (2012) show the period of red maple recruitment in various old and old-growth forests around the Cumberland Plateau predating the period of fire

suppression, with red maples initiating as early as the 1860s. It may be that the peak influx of red maple is attributable to something other than fire suppression.

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

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

Maples, and especially red maples, have been predicted to eventually attain canopy dominance (Lorimer 1984; Hart et al. 2012b). In this study, illumination indices show that maples are in a position to take advantage of increased light conditions in the understory in old forest stands (index ratings 2 and 3). Through the process known as 'disturbance-mediated accelerated succession,' the successional transition toward dominance of increasingly shade-tolerant species can proceed more rapidly in the presence of disturbance, whereby shade-tolerant trees are released and attain codominant or dominant status (Abrams and Scott 1989). Hart et al. (2012b) found that 61% of red maples in the canopy at Savage Gulf originated in gaps and reached the canopy without exhibiting periods of suppression. However, only 24% of red maples established in the understory and reached the canopy after one or more gap releases. For trees following this strategy,

the mean age of trees upon ascent to the canopy was 20 years, with the longest duration suppressed in the understory being 71 years. In my study, the two oldest red maples were a 92 year old, 17.5 cm DBH tree with an intermediate (I) crown position and illumination index of 2 (receiving some lateral light exposure) and an 89 year old, 13.4 cm DBH tree with an overtopped (O) crown position and illumination index of 1 (no direct light exposure), suggesting that red maple can stay in the lower strata of forests for nearly a century. It may be that small-scale, gap creating disturbances will produce the necessary conditions to release maples from their currently suppressed state and allow them to eventually attain canopy dominance. However, it is not clear how long red maples can persist in a suppressed state in the understory. Since many oaks can live for 300 to 500 years, in the absence of widespread disturbance, it might be that red maples will continue to be relegated to suppressed understory status and could eventually drop in importance as individuals decline due to insufficient resources.

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

Further, because of the association between dry climatological conditions and fire regimes (Lynch and Hessl 2010; Lafon and Quiring, 2012), it stands to

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

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

5.3 PROSPECTS FOR OLD-GROWTH RECOVERY

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

Daniel Boone National Forest

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

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

Kentucky State Nature Preserves and Natural Areas

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

Kentucky Natural Lands Trust

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

Bernheim Arboretum and Research Forest

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

Robinson Forest

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

Land Between the Lakes

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

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

Mammoth Cave National Park

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

Big South Fork National Recreation Area

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

5.4 SILVICULTURE FOR OLD-GROWTH CHARACTERISTICS

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

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

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

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

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

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

6. CONCLUSION

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

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

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