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Changing fire regimes and old-growth forest succession along a topographic gradient in the Great Smoky Mountains

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ABSTRACT

Patterns of past fire disturbance may be an important contributor to contemporary vegetation composition and structure in old-growth forests of the southern Appalachian Mountains. However, due to a lack of information on pre-suppression fire regimes, vegetation pattern in the region has been primarily attributed to variability in soils and climate. To assess the pre-suppression fire regime's role in shaping vegetation pattern, we characterized temporal patterns of tree establishment in an old-growth forest that experienced two centuries of frequent fire, followed by a century of fire exclusion. Forest plots were inventoried and cored to characterize age structure and composition in yellow pine, chestnut oak, white pine-oak, and cove forest communities on the south-facing slope of an old-growth watershed in Great Smoky Mountains National Park, Tennessee USA. We compared the timing and composition of tree establishment from the following disturbance periods: (1) frequent fire 1700–1909; (2) post fire 1910–1949; and (3) mesophication 1950–2000. Non-metric multidimensional scaling characterized successional change between the three age classes. Multivariate dispersion, species richness, and beta diversity were calculated for establishment in each disturbance period. We found distinct peaks in tree establishment in the yellow pine, chestnut oak, and white pine-oak stand types that occurred soon (<40 years) after fire cessation at the site. Xerophytic fire-tolerant species dominated establishment during the period of frequent fire; a mixture of xerophytic and mesophytic species established during the period immediately following the last major fire; and mesophytic, fire-intolerant species dominated establishment during the recent period of mesophication. Cohort recruitment was less clearly linked to fire suppression in the mesic cove stands; however "fire protected" cove stands exhibited different age structure and composition compared to cove stands adjacent to the frequently burned south-facing slope. Mean plot level species richness was greatest in the tree cohort that established soon after the last major fire; while beta diversity and multivariate dispersion were highest in the trees that had established during the frequent fire period. Tree establishment has generally shifted from shade-intolerant, drought-tolerant species to shade-tolerant, drought-intolerant species along the entire south-facing slope. Successional trajectory indicates a loss of yellow pine and chestnut oak communities as the xeric and sub-xeric sites convert to white pine and cove forest communities, which were formerly restricted to sub-mesic and mesic positions. Declines in beta diversity and multivariate dispersion within younger age classes indicate that in the absence of fire disturbance, community differentiation is declining along the topographic moisture gradient.

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1. Introduction

Vegetation structure and composition reflect the controlling influences of climate and soil, as evident in global-scale biome distributions (Woodward et al., 2004) as well as local variations along topographic gradients of soil moisture and fertility (Whittaker, 1956). Yet underlying climatic and topographic gradients fail to account for certain vegetation patterns. Much attention has been

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focused, for example, on the ability of both savanna and forest to exist as stable vegetation states under identical climate and soil (e.g., Bond and Keeley, 2005; Murphy and Bowman, 2012), in which case the vegetation at a particular location appears to be determined largely by the fire regime under which the community developed. Numerous other vegetation patterns—from shrub versus tree dominance in Mediterranean climates to the distribution and species composition of midlatitude grasslands and forests—also suggest that fire can modify or override climatic influences (Abrams, 1992; Anderson, 2006; Odion et al., 2010). It is often difficult, however, to demonstrate that fire, rather than climate or another factor, is responsible for particular vegetation features.

One potentially clarifying pattern is seen in temperate forests, where xerophytic tree species such as oaks (*Quercus* L.) and pines (*Pinus* L.) dominate many stands even in humid climates. These stands commonly show a mismatch in species composition between older trees and younger trees (Harrod et al., 1998; McCarthy et al., 2001; Shumway et al., 2001; McEwan and Muller, 2006), with the older age classes dominated by oak or pine, whereas the younger age classes are composed of maples (*Acer* L.), beeches (*Fagus* L.), and other mesophytic trees that might be expected to thrive in a humid environment. One explanation for this mismatch, the fire–oak hypothesis, proposes that prior to fire exclusion in the early to mid-twentieth century, much of the landscape experienced frequent surface fires that inhibited the establishment of competitive, fire-sensitive species and thereby facilitated the establishment of the more fire-tolerant oaks (Lorimer, 1984; Abrams, 1992; Brose et al., 2001). Oaks and other xerophytic trees commonly have thick bark or other traits that favor persistence under periodic burning, and some produce flammable litter that facilitates fire and therefore indirectly thwarts the establishment of fire-sensitive competitors (Kane et al., 2008; Nowacki and Abrams, 2008; Kreye et al., 2013). According to the fire–oak hypothesis, fire-protection policies implemented during the early 20th century initiated a successional shift, termed "mesophication," by enabling fire-intolerant mesophytic species to colonize the understory of xerophytic forests that previously had been maintained by fire (Nowacki and Abrams, 2008, 2015). The increase in stand density associated with mesophication apparently has reduced available resources and decreased species diversity by impeding the recruitment of shade-intolerant species such as oaks and pines. The fire–oak hypothesis implies that frequent burning in the past had confined mesophytic forests to fire-protected landforms such as valley bottoms along streams, and had promoted xerophytic forests on other sites, thereby contributing to the well-known topographic zonation of forests.

Critics of the fire–oak hypothesis have argued that fire may not have played an important role in the past and that climatic fluctuations or non-fire disturbances could explain the ongoing successional changes (McEwan et al., 2011; Hart and Buchanan, 2012; Matlack, 2013). Increased precipitation over the past century, for example, may have enabled mesophytic trees to establish in forests that previously had been too dry for their survival (Pederson et al., 2014). It should be possible to distinguish the influence of fire suppression by ascertaining whether the onset of successional changes coincided with fire cessation at any particular site. Coupled data on fire and vegetation history are uncommon, however. A few dendroecological studies combining fire history and tree age structure (Hoss et al., 2008; Hutchinson et al., 2008; Aldrich et al., 2010; Hessl et al., 2011; McEwan et al., 2014) have demonstrated that fire cessation coincided with tree establishment pulses, consistent with the fire–oak hypothesis, but these studies were restricted to dry topographic positions and/or to second-growth forests in which the effects of past timber-cutting may obscure the effects of fire.

Research spanning a full topographic gradient across unlogged forests is necessary if the influence of fire is to be clarified, but the history of extensive forest clearance in temperate landscapes has impeded the development of long-term dendroecological datasets on past fire occurrence and coinciding patterns of forest establishment. For this study, we investigated tree establishment in an unlogged watershed of the southern Appalachian Mountains in the southeastern USA. The watershed had experienced frequent fire prior to the implementation of fire protection in the 1920s, as revealed by a fire history reconstruction that extends back to the 1700s (for further details on site fire history see Flatley et al., 2013). We hypothesized that (1) Xerophytic trees dominated establishment on dry ridges and slopes during the period of frequent fire, but mesophytic trees dominated establishment during the recent period of fire exclusion across the entire topographic gradient. (2) The timing of changes in tree establishment corresponds with fire exclusion. We expect a rapid response to fire cessation, as trees likely took advantage of the relatively open stands that had developed during previous centuries of frequent fire. (3) Species richness is lower among trees established during the latter stages of fire exclusion compared to trees established prior to or soon after fire exclusion. This hypothesis reflects the expectation that declining light availability has inhibited the establishment of some species. (4) Topographic zonation of species composition is lower among trees that established during the fire-exclusion period than among trees that established during the frequent-fire period. If frequent fire helped maintain the xerophytic-to-mesophytic zonation pattern in the past by confining mesophytic species to fire-sheltered landforms, topographic variations in species composition should be less pronounced among trees that established under fire exclusion.

2. Materials and methods

2.1. Study area

Licklog Ridge (35°33′N, 83°50′W) is located in Great Smoky Mountains National Park (GSMNP), Tennessee (Fig. 1), which was formally dedicated in 1940. The Great Smoky Mountains are part of the southern Appalachian Mountains, and lie within a humid temperate ecoregion (Bailey, 1998). Average annual precipitation is 1480 mm at Gatlinburg, Tennessee (443 m elevation), 29 km northeast of Licklog Ridge (NCDC, 2002). Mean January and July temperatures are 2.4 °C and 22.9 °C, respectively. Southern Appalachian forests were formerly classified broadly as oak-chestnut (Braun, 1950), but the chestnut blight fungus (*Endothia parasitica*) arrived ca. 1925 and killed nearly all the American chestnuts (*Castenea dentata* Marsh. Borkh.) (Woods and Shanks, 1959; McCormick and Platt, 1980). Appalachian forests are classified today as forming an oak-hickory (*Carya* Nutt.) association (Stephens et al., 1993).

At the local scale, plant cover varies strongly across topographic gradients, as seen at Licklog Ridge. Yellow pine (*Pinus*, subgenus *Diploxylon* Koehne)-dominated stands occupy dry ridgetops and southeast- to southwest-facing slopes; chestnut oak (*Quercus montana* Willd.)-dominated stands cover west- and east-facing slopes; white pine (*Pinus strobus* L.)-oak stands cover south-facing toeslopes; and mesophytic hardwood-eastern hemlock [*Tsuga canadensis* (L.) Carrière] forests occupy the coves along valley bottoms (Fig. 1). Licklog Ridge was not subjected to large-scale logging or agricultural clearance (Pyle, 1988), but fires occurred frequently before fire protection (Flatley et al., 2013). It is not possible to determine the ignition source for these past fires. However, fires currently result from both lightning and human ignitions, with the latter predominating (Flatley et al., 2011). It is probable that

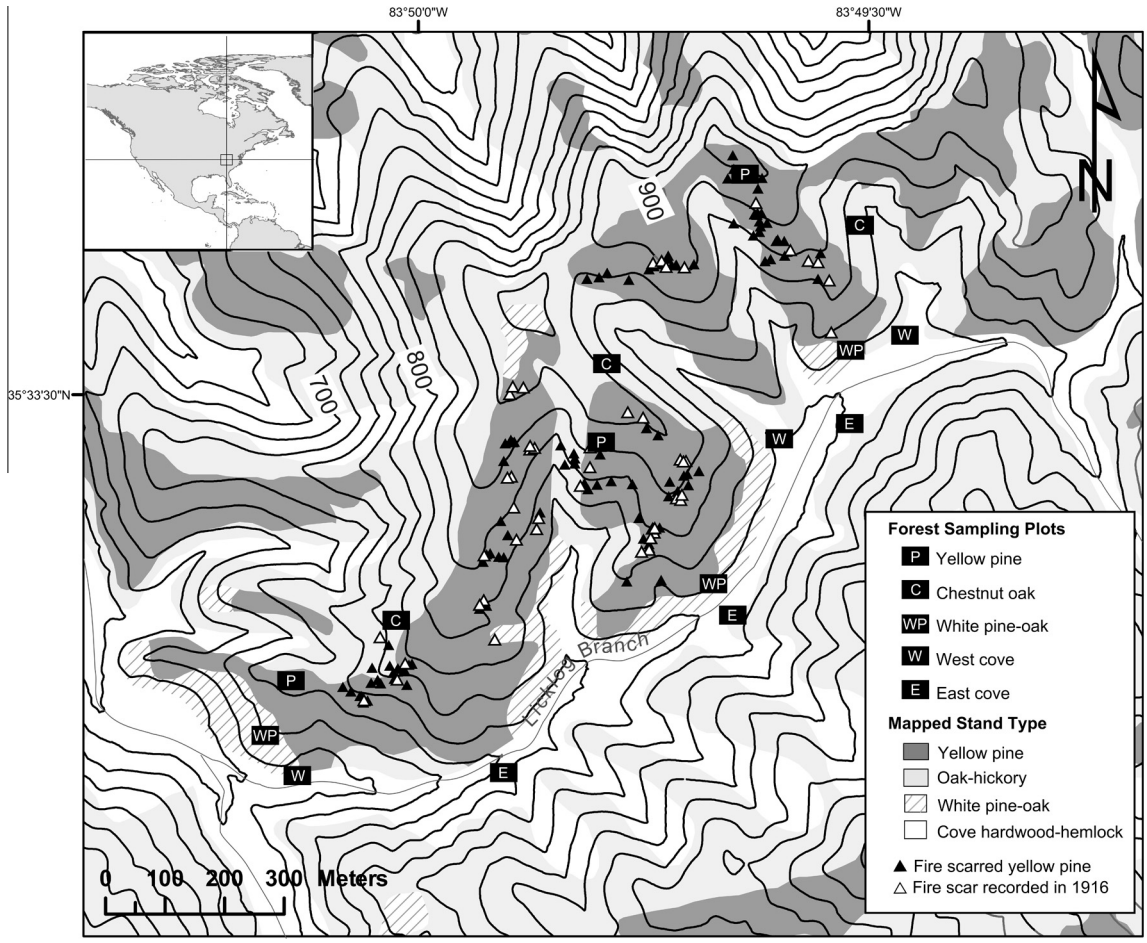

Fig. 1. Licklog Ridge study area, Great Smoky Mountains National Park, Tennessee USA. Rectangles are locations of sampled vegetation plots. Black triangles are the locations of fire-scarred yellow pine specimens; hollow triangles are specimens that recorded the last major fire in 1916.

humans were also the primary source of ignitions in the past. According to fire-scarred pines that we collected from across the south-facing slope of Licklog Ridge (Fig. 1), the composite mean fire interval was 2.2 years during 1773–1920. Our fire history study also showed that "area-wide fires," which burned across the entire slope, occurred at 6.5 year intervals. The last major fire (>25% of samples scarred) was recorded in 1916.

2.2. Data collection and preparation

During 2008–2010, we established vegetation sampling plots to characterize age structure and species composition on or adjacent to the south-facing slope of Licklog Ridge, where fire history material had been collected. Three 50 × 20 m plots were placed in each of the four stand types (yellow pine, chestnut oak, white pine-oak, and cove hardwood–hemlock), as depicted by the national park vegetation map (Madden et al., 2004). In the cove hardwood–hemlock stand type, however, we established six plots, with three on the west side of Licklog Branch adjacent to the south-facing slope, where widespread burning was evident in the form of the fire-scarred pines that were collected for fire-history reconstruction (Flatley et al., 2013), and by fire-scarred hardwoods and hemlocks growing downslope to the streamside. For comparison, we set up three additional cove plots on the east side of the stream, where fire would have been less likely to spread because of its position between the stream and the adjacent north-facing slope. Harmon et al. (1984) found that northeast-facing lower slopes exhibited the least evidence of fire disturbance in lower elevation forests of GSMNP. Because we report data from the west and east cove plots separately below, we refer to them as two stand types, and describe our entire sample as comprising five stand types.

In each plot, we recorded the species identification and stem diameter at breast height (DBH) for each living tree (DBH ⩾ 5 cm), and extracted two increment cores from opposite sides at the tree base. Saplings (<5 cm DBH, ⩾50 cm height) were recorded by species. We recorded seedlings (>50 cm height) by species within five 2 × 20 m subplots evenly spaced within the plot.

Increment cores were dried, mounted on wooden core mounts, and sanded (Orvis and Grissino-Mayer, 2002). After processing, a stereo-zoom microscope was used to determine establishment dates for each of the cores. For cores that did not intersect the pith, we estimated the establishment date from the width and curvature of the earliest rings (Applequist, 1958). Broken and rotten cores, for which a pith date could not be estimated, were removed (88 of 1565 trees). For analysis, we assigned each tree to a decadal establishment bin.

2.3. Data analysis

To assess hypothesis 1, concerning general establishment patterns under differing fire regimes, we classified each species broadly as either xerophytic or mesophytic (Table 1) according to Whittaker's distributional groupings for tree species in the Great

Table 1
Xerophytic and mesophytic tree species groups. Species are further divided into eight subgroups used in age structure diagrams.

Xerophytic tree species	Mesophytic tree species
Yellow pines	Maples
Pinus pungens Lamb.	*Acer rubrum* L.
Pinus rigida Mill.	*Acer saccharum* Marshall
	Acer pensylvanicum L.
White oaks	
Quercus montana Willd.	Mesic hardwoods
Quercus alba L.	*Aesculus octandra* Marshall
	Betula lenta L.
Xeric red oaks	*Carya glabra* (Mill.) Sweet
Quercus coccinea Münchh.	*Carya ovata* (Mill.) K. Koch
Quercus velutina Lam.	*Carya alba* (L.) Nutt. ex Elliott
	Fraxinus americana L.
Xeric hardwoods	*Halesia carolina* L.
Nyssa sylvatica Marshall	*Quercus rubra* L.
Oxydendrum arboreum L. DC.	*Liriodendron tulipifera* L.
Sassafras albidum (Nutt.) Nees	*Tilia heterophylla* Vent.
	Ilex opaca Aiton
White pine	*Magnolia fraseri* Walter
Pinus strobus L.	
	Hemlock
	Tsuga canadensis (L.) Carrière

Smoky Mountains (Whittaker, 1956). We aggregated establishment dates into three broad disturbance periods representing different fire regimes and stand conditions: First, the frequent-fire period consists of all decades before the 1910–1919 decade, which contains the last major fire recorded on at least 25% of recording samples (Flatley et al., 2013; Swetnam and Baisan, 1996). Second, the post-fire period comprises the four decades from 1910 to 1949, when stands probably were fairly open following centuries of frequent fire. Third, the mesophication period includes the decades after 1949, when canopy closure and increased stand density likely reduced understory light availability and initiated a shift in species establishment from shade-intolerant xerophytic species to shade-tolerant mesophytic species, as proposed by Nowacki and Abrams (2008). In defining the mesophication period as beginning about 35 years after the last major fire, we approximate the time to canopy closure suggested by dendroecological and forest plot data (Harrod et al., 2000; Aldrich et al., 2010). We performed a chi-square test for each of the five stand types to look for differences in the frequency of xerophytic versus mesophytic establishment across the three periods (Zar, 1999).

To portray the timing of tree species establishment relative to fire cessation (hypothesis 2), we first broke the broad xerophytic and mesophytic tree groups into eight subgroups (Table 1). Then we created a decadal age-class histogram for each subgroup, for a total of 40 histograms (8 subgroups × 5 stand types).

To examine hypothesis 3, regarding differences in tree species richness, we calculated the number of species per plot for each disturbance period. We then performed a Kruskal–Wallis test (Zar, 1999) to look for differences in richness among the three periods, for each stand type. The Dunn post hoc test (Zar, 1999) was used to make pair-wise comparisons between the periods.

To evaluate hypothesis 4, which addresses species compositional change along the topographic gradient under different fire regimes, we examined the species makeup through a non-metric multidimensional scaling (NMDS) ordination. The ordination included 45 sample points, i.e., 15 plots × 3 disturbance periods (the frequent-fire, post-fire, and mesophication periods noted above). Species counts—the number of individuals of a species that established in a specific plot during a particular disturbance period—were standardized according to sample point totals and Sørensen distance was used as the dissimilarity measure. The stability criterion was 0.0001, with a maximum number of 200 iterations, and a random starting configuration. We completed multiple runs of NMDS ($n = 40$) and performed a Monte Carlo test ($n = 40$) to determine the minimum number of dimensions that produced the lowest stress. All ordination procedures were carried out in PC-ORD version 4.14 (McCune and Mefford, 2011).

As a further assessment of hypothesis 4, we calculated beta diversity for each of the three disturbance periods using Whittaker's beta (Whittaker, 1960), which indicates the degree to which species composition varies among stands. For an additional characterization of beta diversity, we calculated the ordination distance from each observation to the centroid for that age class according to the Sørensen dissimilarity measure (Anderson, 2004). Difference in the mean distance to centroid provides an additional assessment of beta diversity, based on compositional similarity among plots in each age class. The mean distance to centroid for each age class was compared using ANOVA. Pair-wise *a posteriori* tests were performed to identify which age classes differed significantly.

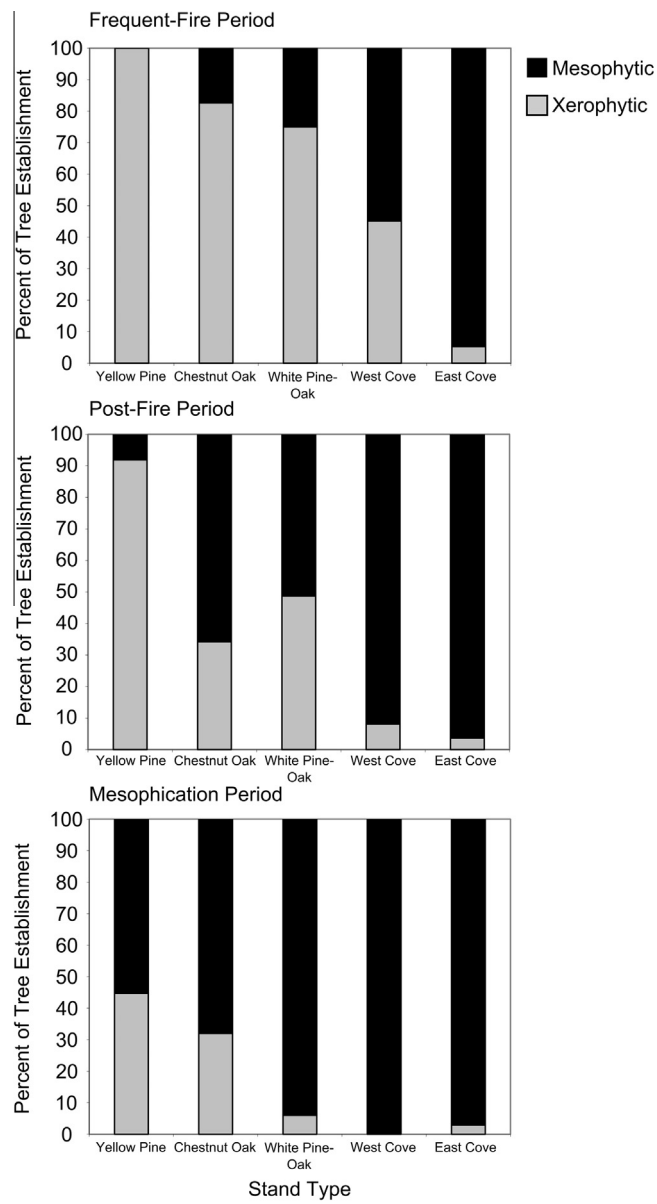

Fig. 2. Percent of tree establishment representing xerophytic and mesophytic species in each stand type during the disturbance periods at Licklog Ridge study site.

3. Results

The frequency of xerophytic versus mesophytic trees (Fig. 2) differs across the three disturbance periods in all except the east cove stands (chi-square tests for pine stands: $\chi^2(2, N = 400) = 102.0$, $p < 0.001$; chestnut oak stands: $\chi^2(2, N = 301) = 21.7$, $p < 0.001$; white pine-oak stands: $\chi^2(2, N = 366) = 71.0$, $p < 0.001$; west cove stands: $\chi^2(2, N = 272) = 21.6$, $p < 0.001$: east cove stands: $\chi^2(2, N = 138) = 0.1$, $p = 0.48$). Consistent with hypothesis 1, xerophytic species account for the majority of trees established during the frequent-fire period in the yellow pine, chestnut oak, and white pine-oak stands, and nearly half of those in the west cove stands. This trend was reversed following fire cessation, with mesophytic species prevailing, especially during the mesophication period. As a consequence of these temporal variations in tree establishment, a mixture of xerophytic and mesophytic species inhabits the landscape today (i.e., at the time of sampling), as seen in the detailed compositional summaries presented in Appendices A and B. Xerophytic trees such as Table Mountain pine (*Pinus pungens* Lamb.) and chestnut oak remain dominant in terms of basal area in the yellow pine and chestnut oak stands, but mesophytic species, especially red maple (*Acer rubrum* L.), are abundant among the saplings and seedlings.

All the stand types contain trees dating to the eighteenth or nineteenth century (Fig. 3), but the majority of stems (1057 out of the total of 1477 trees) established during the four decades following fire cessation. This pattern agrees with hypothesis 2: distinct cohorts of tree establishment align with the post-fire period. These cohorts represent several of the eight tree subgroups, with the specific mix of subgroups depending on the stand type. The more recent mesophication period, in contrast, has seen the recruitment of fewer trees.

Concerning hypothesis 3, species richness differs among the three disturbance periods for the yellow pine stands (Kruskal–Wallis test, $\chi^2(2, N = 9) = 7.261$, $p = 0.03$), the chestnut oak stands ($\chi^2(2, N = 9) = 6.826$, $p = 0.03$), and the white pine-oak stands ($\chi^2(2, N = 9) = 7.784$, $p = 0.02$). The results partially conform to the hypothesized pattern: in the white pine-oak stands, richness is lower among the trees that established under mesophication than among the post-fire trees (Fig. 4). Contrary to the hypothesis, however, yellow pine and chestnut oak stands have low richness values among the trees established during the frequent-fire period. The pattern that most resembles the hypothesized one emerges in the west cove stands ($\chi^2(2, N = 9) = 5.658$, $p = 0.06$). In the east cove stands, richness values do not vary across the three age classes ($\chi^2(2, N = 9) = 0.881$, $p = 0.64$).

With respect to hypothesis 4, the NMDS ordination indicates a two-dimensional solution (Fig. 5) with a final stress of 18.0 (mean stress = 21.4, $p = 0.02$). The ordination reveals a pattern consistent with the hypothesized differences in topographic zonation. For trees established during the frequent-fire period, plots are widely dispersed in ordination space, and grouped by stand type (Fig. 5a). For the mesophication period, in contrast, plots are more clustered in the center and lower portion of ordination space, indicating less compositional difference among the stand types (Fig. 5c). That is, forest zonation is less pronounced among the younger trees than the older ones.

Beta diversity declines across the three age classes, with a Whittaker's beta of 3.9 for trees established during the frequent-fire period, 2.4 for the post-fire period, and 1.6 for the mesophication period. Furthermore, the permutational test of multivariate dispersion indicates that the mean distance from the centroid differs significantly for the different disturbance periods ($F(2,42) = 4.79$, $p = 0.02$). Pair-wise *a posteriori* comparisons show that mean distance from centroid is significantly smaller for the mesophication period compared to the frequent-fire period ($t(2) = 2.74$, $p = 0.01$). The decline in beta diversity by tree age is consistent with hypothesis 4, as it indicates a lower degree of compositional distinction among the trees established following fire cessation than the trees established during the frequent fire period.

4. Discussion

4.1. Xerophytic and mesophytic tree establishment

The patterns of tree establishment at Licklog watershed support the argument that fire promoted xerophytic vegetation and shaped the topographic zonation of the forest. The stand conditions associated with frequent fire enabled pines, oaks, and other xerophytic species to establish on dry topographic positions. This result agrees with hypothesis 1 and with the fire–oak hypothesis. The high light availability within the open, fire-maintained stands probably would have benefited mesophytic species, too, but those trees evidently could not withstand the short fire intervals of the frequent-fire period. Fire acted as a filter that precluded their establishment (McEwan et al., 2014). When this constraint was relaxed at the beginning of the post-fire period, however, mesophytic species encroached over the entire topographic gradient.

Eastern hemlock did not show this rapid response to fire exclusion on dry sites. In the yellow pine and chestnut oak stands, hemlock was more abundant among the stems recruited during the mesophication period than the post-fire period. The delayed response of hemlock suggests that mesophication may have facilitated hemlock establishment on sites that previously were too dry for it. Similar successional changes have been noted in other dendroecological assessments of recruitment in old-growth oak stands (Abrams and Copenheaver, 1999; McEwan and Muller, 2006). Such an outcome is consistent with the mesophication process as described by Nowacki and Abrams (2008), who proposed that cooler, damper stands would lead to the accumulation of fire-resistant litter and further recruitment of mesophytic species. The accumulation of coarse woody debris, which previously would have been consumed by surface fires, may also have played a role in providing micro-sites for hemlock regeneration during the recent mesophication period (Marx and Walters, 2008; Witt and Webster, 2010).

4.2. The timing of tree establishment with respect to fire cessation

With the exception of hemlock, most tree species established within 40 years of fire cessation. Xerophytic and mesophytic species alike established in distinct cohorts initiated during the post-fire period, as also seen in pine and oak stands at other sites in the eastern US (Shumway et al., 2001; Hutchinson et al., 2008; Aldrich et al., 2010). Rapid recruitment following the last major fire is consistent with hypothesis 2. It indicates that fire had previously exerted strong control over vegetation composition, and that the recent changes in tree establishment are a consequence of fire exclusion, not primarily of climate or other factors (McEwan et al., 2011; Pederson et al., 2014). In fact, most of the trees became established during the relatively dry decades of the 1910s–1940s (cf. NOAA, 2014), not during the wetter 1960s and 1970s. The tree-age distribution at the Licklog watershed, therefore, contradicts the argument that mesophytic species recruitment is a response to a long-term increase in precipitation. Rather, compositional change coincides with fire cessation. The results that we obtained from this particular location match the vegetation changes that are hypothesized to have occurred across the eastern

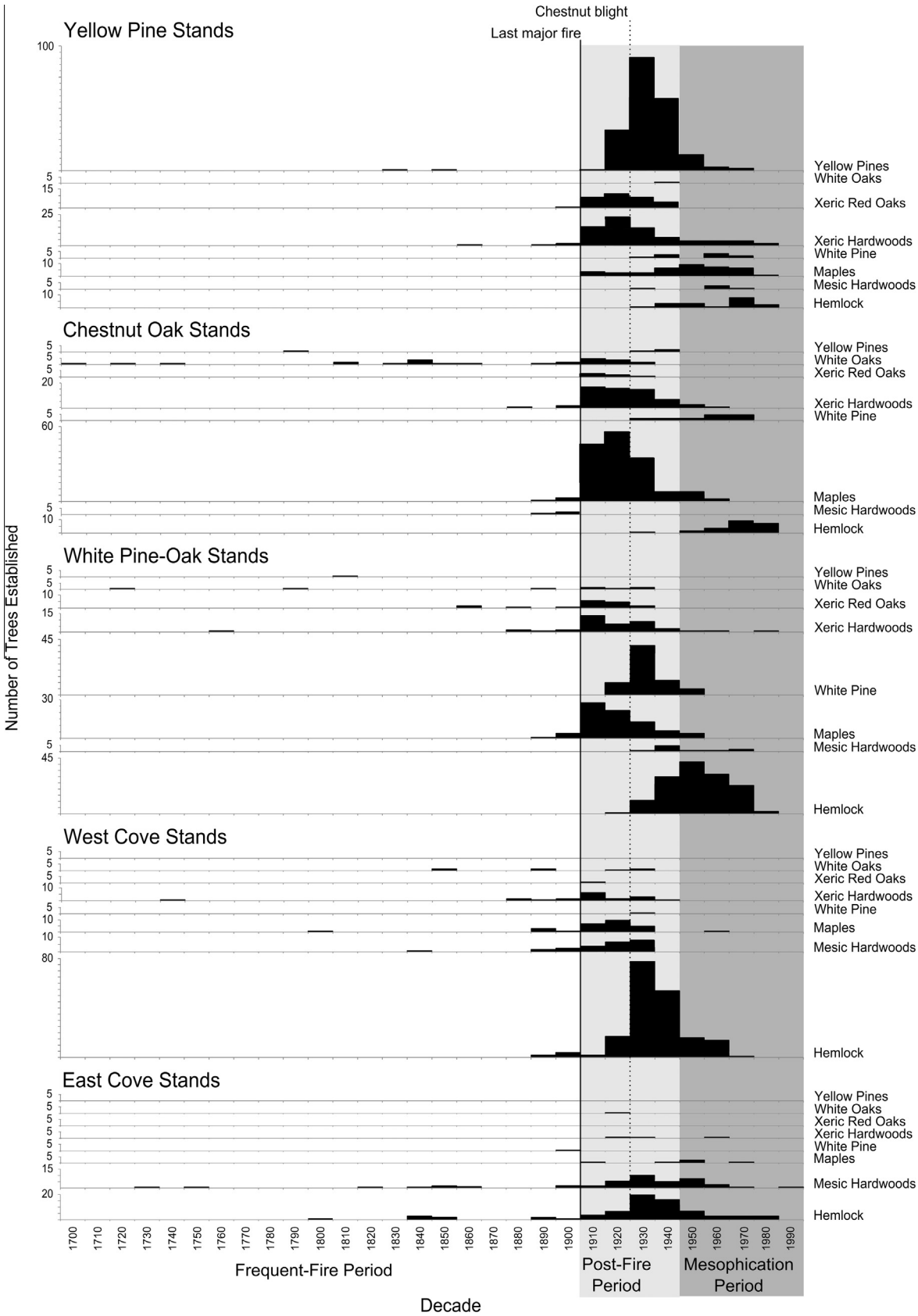

Fig. 3. Temporal patterns of species establishment in the different stand types at Licklog Ridge study site. Solid line indicates the decade of the last major fire at the site and the dotted line indicates the arrival of chestnut blight. Disturbance periods labeled on *x*-axis are the frequent-fire period prior to fire exclusion (1700–1909), the post-fire period when stands probably remained fairly open (1910–1949), and the mesophication period following four decades of post-fire successional change (1950–2000).

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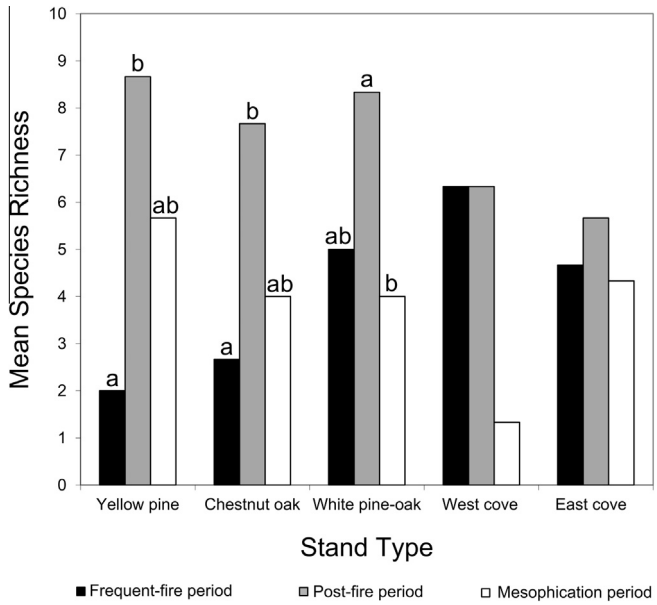

Fig. 4. Mean species richness values in the stand types during each of the disturbance periods at Licklog Ridge study site. Within stand types, richness values with the same letter are not significantly different according to Dunn post hoc test.

US (Nowacki and Abrams, 2008, 2015), and therefore they complement analyses conducted over a broader spatial scale but with less temporal precision.

The post-fire establishment pulse is particularly evident in the chestnut oak stands, where maples and xerophytic hardwoods responded strongly to the end of burning, but it is also evident across the entire south-facing slope, including the middle- to lower-slope sites covered by white pine-oak forest. These post-fire changes suggest that fire had previously constrained tree recruitment and shaped forest composition along the whole slope, and that the removal of fire effected a widespread change in tree recruitment among the stands that covered the ridge. Additionally, fires burning along the ridge must have spread downslope to the adjacent cove, at least on occasion, and encompassed the west cove stands. Although the west cove stands showed limited recruitment immediately following fire cessation, suggesting that fire had exerted less control over vegetation than on the drier slope, they show evidence of having been influenced by fire. Specifically, these west cove stands adjacent to the frequently burned south-facing slope differ in species composition and age structure from the east cove stands that inhabit virtually identical terrain across the stream, which likely protected the east side from fire. The west cove tree stratum includes oak species, which are absent or less abundant in the east cove stands, and the age structure graphs demonstrate that oaks and xeropytic hardwoods had been recruited regularly in the west cove stands during the frequent-fire period. The west cove also saw greater post-fire tree establishment than the east cove, suggesting that fires had maintained more open conditions that enabled tree recruitment after the burning had ceased.

The recruitment of white pine and hemlock cohorts in the white pine-oak and west cove stands during the 1930s may have been linked to the mortality of American chestnut following the arrival of chestnut blight. Previous research (Woods and Shanks, 1959; Vandermast and Van Lear, 2002) shows that chestnut was widely distributed in sub-mesic and mesic positions similar to these sites. Fire disturbance would help explain this distribution (Vandermast and Van Lear, 2002), because in the absence of fire, these stands probably would have been dominated by hemlock and mesophytic hardwoods all along. Dominance by these species would be consistent with previous studies of mesic-site vegetation (e.g. Leopold and Parker, 1985) and with the successional trends under fire exclusion that are implied by our age structure data. The strong hemlock recruitment pulse in the west cove stands, as compared with the east cove, is consistent with a greater presence of chestnut on the fire-exposed west side. In contrast to the west cove stands, the east cove stands contained old hemlocks and mesic hardwoods, providing further evidence that Licklog creek served as a fire break and enabled the persistence of fire-sensitive species in this more protected location.

4.3. Species richness

Our results offer some evidence that the stand conditions that developed under mesophication have inhibited the recruitment of a diverse tree assemblage (Nowacki and Abrams, 2008; Hedl et al., 2010). The pattern is most evident in the white pine-oak stands, where species richness was significantly lower for the mesophication period than for the post-fire period that preceded

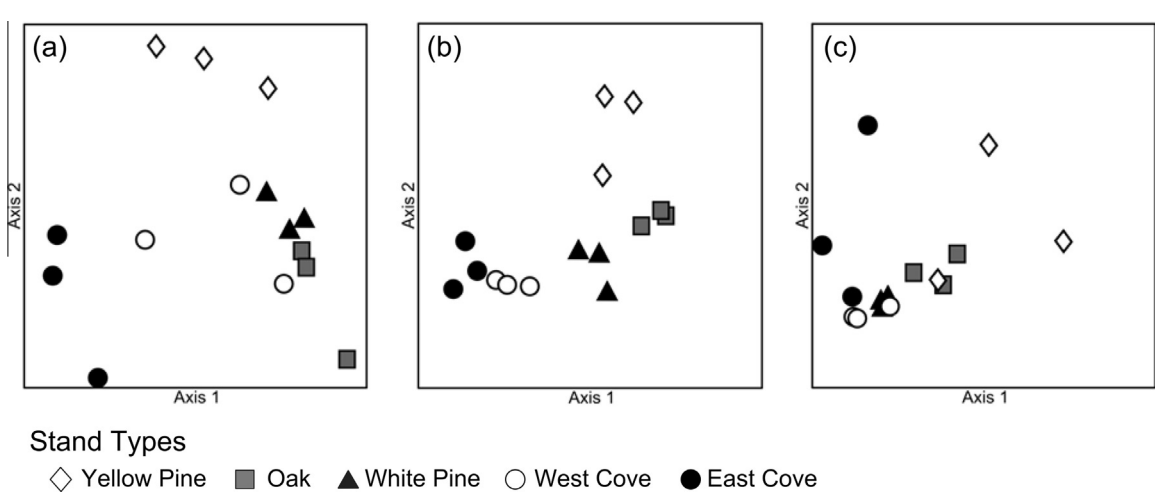

Fig. 5. Nonmetric multidimensional scaling (NMDS) ordination of vegetation plots at Licklog Ridge study site. Plots are separated according to disturbance periods: (a) frequent fire (1700–1909), (b) post-fire (1910–1949), and (c) mesophication (1950–2000). Although the ordination was performed on all 45 samples together, we graphed the three disturbance periods separately to more clearly illustrate temporal changes in species composition of the plots.

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it; and a similar tendency is observed across the entire south-facing slope and adjacent west cove stands. The shift toward lower species richness is consistent with a decline in the availability of light and perhaps other resources that would be expected to accompany canopy closure and maturation of the initial post-fire cohort (Grime, 1977).

If the post-fire period saw open stands and high light availability, the same must also have been the case during the frequent-fire period. Therefore, the low species richness observed in the yellow pine and chestnut oak stands for the frequent-fire period apparently reflects the filtering of the species pool by frequent fire, which precluded the establishment of fire-sensitive species. This pattern corresponds with predictions of biodiversity theory (Huston, 1994) that species richness should be low on stressful sites (e.g., dry ridges and slopes) that are disturbed frequently. Few species can tolerate such a rigorous environment. A reduction in disturbance frequency should permit additional species to establish and species richness to increase. Without disturbances, in fact, stressful sites should harbor relatively high richness, as observed in the Licklog yellow pine and chestnut oak stands under fire exclusion, because slow plant growth on these sites delays canopy closure and prevents one or a few species from exploiting most of the resources.

A contrasting pattern should emerge in more productive vegetation (Huston, 1994): frequent disturbances would maintain high species richness by periodically reducing the abundance of dominant competitors and availing other species of resources, thereby enabling them to persist in the community. Richness would be predicted to decline if disturbances became less frequent. Again, the Licklog patterns correspond to the predicted response, with low species richness developing in the semi-mesic and mesic sites (white pine-oak and west cove stands) under mesophication. In consequence of these spatial and temporal dynamics of tree establishment, tree richness shows opposing patterns by age class among the four stand types arrayed along the south-facing slope and west cove. The old, frequent-fire class increases in species richness over the xeric-to-mesic gradient, while the mesophication class sees a decline over the same gradient. This reversal in species richness over the topographic gradient is consistent with the theoretical expectations that plant diversity should rise toward the mesic end of a moisture gradient under frequent disturbances, but should decline along the gradient under infrequent disturbances (Smith and Huston, 1989; Huston, 1994). As for the east cove stands, where fire appears to have exerted little influence on stand development, tree establishment likely reflects a gap dynamics process where the periodic mortality of large overstory trees creates canopy openings of sufficient size to enable the establishment of a diverse suite of species and to maintain relatively high species richness over the long term (Lorimer, 1980; Busing, 1998).

4.4. Topographic zonation

Our results suggest that fire exerted a strong control on species distribution along the topographic gradient at Licklog watershed during the frequent-fire period, producing a landscape that had high beta diversity and that generally matched other old-growth forests in the southern Appalachian region (Whittaker, 1956; Golden, 1981; Callaway et al., 1987). Previous interpretations of vegetation pattern have largely attributed topographic zonation to differences in soil moisture alone (but see Harmon et al., 1984; Delcourt and Delcourt, 1998; Reilly et al., 2006). Our results suggest that community variation actually reflected both moisture and fire, with the combination of moisture stress and frequent fire thwarting mesophytic tree establishment on the dry slopes and ridges. Mesophytic trees were largely confined to the mesic valley sites, where greater soil moisture would have favored their survival and growth, and where fires probably were less frequent or severe (cf. Wimberly and Reilly, 2007). Streams and other fire breaks contributed to vegetation differences even within the mesic streamside zone itself, as evidenced by the contrasts between the east and west cove stands growing along Licklog Branch.

Fire exclusion has led to a reorganization of species along the topographic gradient and a decline in spatial zonation among the trees established during the post-fire and mesophication period, as illustrated by the contraction of the stand types within ordination space and by the decline in beta diversity during the post-fire and mesophication periods. Continued forest succession in the absence of fire likely will diminish or even eliminate the yellow pine and chestnut oak communities and will expand the mesophytic communities, albeit without hemlock, which is being killed by an invasive exotic insect, hemlock wooly adelgid (*Adelges tsugae* Annand). The changes in tree establishment under fire exclusion indicate that by suppressing fire, humans have removed an important factor that shaped forest diversity and influenced the spatial arrangement of species and communities. The "natural experiment" that resulted from altering the fire regime over a topographic gradient supports the conclusion that past fires limited the extent of mesophytic communities while promoting the wide distribution of xerophytic trees across a humid landscape.

4.5. Management implications

To maintain yellow pine and oak communities and perpetuate the topographic zonation of forest types that typifies Appalachian vegetation (e.g. Whittaker, 1956), it will be necessary to reintroduce fire. These burns should occur frequently enough to control fire-intolerant mesophytic trees and maintain open understory conditions that would favor the persistence of shade-intolerant understory plants, including oaks and pines. Given that these species recruited successfully across multiple topographic positions under a pre-suppression fire interval of about 5–8 years (Flatley et al., 2013), it would seem prudent to burn at a similar interval where possible. Initially, mechanical thinning may be desirable in permitted locations to remove mesophytic hardwoods that have grown large enough to survive low intensity surface burns (Harmon, 1984; Blankenship and Arthur, 2006). Furthermore, prescribed fire should not necessarily be limited to xeric ridgetops, but can be allowed to burn down south-facing slopes to influence forest composition across the entire topographic gradient.

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Appendix A

Basal area and tree density for tree species in each stand type at Licklog Ridge study site.

	Pine stands		Chestnut oak stands		White pine-oak stands		West cove stands		East cove stands	
	Basal area (m^2 ha^{-1})	Tree density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Tree density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Tree density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Tree density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Tree density (stems ha^{-1})
Acer pensylvanicum						3.3				
Acer rubrum	1.3	146.5	6.0	569.4	5.9	296.4	9.0	109.9	2.1	3.3
Acer saccharum									3.2	26.6
Aesculus octandra							0.1	3.3	0.2	6.7
Amelanchier arborea		10.0	0.1	3.3		6.7	0.0			
Betula lenta					0.3	13.3	3.1	53.3	4.9	83.3
Carya glabra					0.2	3.3	1.9	16.7		
Carya ovate									0.6	13.3
Carya alba									0.1	3.3
Fraxinus americana								3.3		
Halesia carolina									0.3	6.7
Ilex opaca		3.3				3.3			0.4	16.7
Liriodendron tulipifera					0.3	3.3	3.1	6.7	4.6	20.0
Magnolia fraseri	0.3	13.3			0.1	16.7	0.4	3.3	0.2	6.7
Nyssa sylvatica	1.6	159.8	0.7	109.9	0.7	20.0	1.1	10.0	0.1	3.3
Oxydendrum arboreum	1.4	76.6	1.8	83.3	2.1	109.9	2.5	53.3	0.5	6.7
Pinus pungens	14.6	576.1								
Pinus rigida	2.9	126.5	0.7	16.7	0.5	3.3				
Pinus strobus	1.2	33.3	2.1	59.9	16.5	229.8	0.9	10.0	2.1	3.3
Quercus alba					0.1	3.3	0.3	6.7		
Quercus coccinea	4.4	126.5	1.7	23.3	5.4	59.9	0.3	3.3		
Quercus montana	0.1	3.3	17.0	113.2	3.0	26.6	1.9	16.7		3.3
Quercus rubra			0.2	10.0			2.9	20.0	0.9	3.3
Quercus velutina	0.1	3.3								
Sassafras albidum	0.2	53.3	0.1	20.0	0.1	3.3				
Tilia heterophylla									3.5	33.3
Tsuga canadensis	1.2	73.3	0.9	83.3	4.0	479.5	12.9	632.7	13.1	243.1
Total	29.3	1405.3	31.3	1092.2	39.3	1282.1	40.3	949.1	36.6	482.9

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Appendix B

Sapling density and seedling density for tree species in each stand type at Licklog Ridge study site.

	Pine stands		Chestnut oak stands		White pine-oak stands		West cove stand		East cove stand	
	Sapling density (saplings ha^{-1})	Seedling density (seedlings ha^{-1})	Sapling density (saplings ha^{-1})	Seedling density (seedlings ha^{-1})	Sapling density (saplings ha^{-1})	Seedling density (seedlings ha^{-1})	Sapling density (saplings ha^{-1})	Seedling density (seedlings ha^{-1})	Sapling density (saplings ha^{-1})	Seedling density (seedlings ha^{-1})
Acer pensylvanicum	6.7	20.0	3.3	23.3	10.0	20.0	86.6	103.2	6.6	6.6
Acer rubrum	969.0	1182.2	346.3	96.6	109.9	666.0	10.0	2314.4	3.3	2234.4
Acer saccharum							10.0	13.3	26.6	133.2
Aesculus octandra									46.6	29.97
Amelanchier arborea	26.6	43.3	3.3		3.3	10.0	6.7	20.0		
Betula lenta										159.8
Carya glabra			3.3				10.0			
Carya ovate									3.3	9.9
Castanea dentata			186.5	16.7	13.3					
Fraxinus americana							23.3	123.2	6.6	26.6
Halesia carolina									9.9	6.6
Ilex opaca	20.0	3.3	3.3	3.3	53.3	13.3	53.3	36.6	6.6	23.3
Liriodendron tulipifera							53.3	233.1	9.9	362.9
Magnolia fraseri	156.5	59.9	23.3	20.0	79.9	13.3	10.0	6.7	6.6	53.2
Nyssa sylvatica	189.8	156.5	359.6	96.6	20.0	13.3	20.0	176.5	3.3	43.2
Oxydendrum arboreum	279.7	50.0	103.2		93.2		3.3	26.6	3.3	3.3
Pinus pungens	36.6	6.7	3.3							
Pinus rigida	33.3	13.3								
Pinus strobus	233.1	116.6	50.0	6.7	20.0	6.7				
Prunus serotina								13.3		
Quercus alba	3.3	33.3								
Quercus coccinea	176.5	572.8	66.6	103.2	10.0	169.8		66.6		3.3
Quercus montana	13.3	13.3	16.7	1132.2		40.0		119.9	3.3	3.3
Quercus rubra	6.7	59.9	16.7	56.6		13.3	36.6	96.6		136.5
Quercus velutina	20.0	33.3	6.7	3.3				3.3		
Robinia pseudoacacia			6.7					3.3		
Sassafras albidum	1228.8	2174.5	233.1	196.5	13.3	10.0	3.3	30.0	23.3	13.3
Tilia heterophylla									16.6	
Tsuga canadensis	83.3	16.7	273.1	26.6	482.9	23.3	86.6	10.0	36.6	3.3
Total	3483.2	4555.4	1705.0	1781.6	909.1	999.0	412.9	3396.6	213.1	3253.4

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