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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.

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