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Ericaceous shrub expansion and its relation to fire history in temperate pine-oak (*Pinus-Quercus*) forests of the eastern U.S.A.

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Abstract Shrub expansion is widespread in forests, but unlike the case for grasslands, contributing factors such as fire suppression have not been widely explored. In this dendroecological study, we investigate the role of fire suppression in the expansion of mountain laurel (*Kalmia latifolia*) shrubs in xerophytic pine-oak (*Pinus-Quercus*) stands of the Appalachian Mountains. The shrubs apparently were uncommon until two to four decades following the onset of fire suppression, after which they expanded to form thickets that are extensive today. Shrub expansion likely benefitted from chestnut blight [*Cryphonectria parasitica* (Murrill) Barr] and acid deposition, which coincided with shrub establishment in the mid-1900s. However, shrub establishment was not synchronous among study sites as would be expected if these region-scale factors controlled it. We conclude that fire suppression was the predominant factor enabling shrub establishment. Prescribed fire may therefore help control shrub cover, but only in landscapes that can be burned frequently.

Keywords Ericaceous shrubs · Fire history · *Kalmia latifolia* · Mesophication · *Pinus pungens* · Shrub expansion

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Introduction

Changes in disturbance regimes appear to have triggered shrub expansion in many forests worldwide and to have contributed to understory thickets that inhibit tree recruitment, potentially inducing a physiognomic shift toward shrub dominance (Mallik 2003; Royo and Carson 2006). Fire suppression is an especially widespread change among temperate forests (e.g., Nowacki and Abrams 2008), where reduced fire frequency has likely enhanced shrub density in stands that historically had an open, fire-maintained understory (Royo and Carson 2006; Brose and Waldrop 2010). However, the link between shrubs and fire suppression has not been explored widely in forests, in contrast to grasslands (e.g., Wilcox et al. 2018).

Because shrub expansion unfolds over many decades, its causes can be clarified by exploring the ecological history of shrub-encroached forests. The xerophytic pine-oak (*Pinus-Quercus*) forests in the Appalachian Mountains of the eastern U.S.A. are a good place to investigate shrub expansion because the history of fire and tree species establishment are well known from dendroecological records spanning the last few centuries (e.g., Aldrich et al. 2010, 2014; Stambaugh et al. 2018). The forests commonly harbor a dense understory of mountain laurel (*Kalmia latifolia*), an evergreen ericaceous shrub that can live ≥ 75 years and reach heights of about 2 m (Fig. 1; Nowacki and Abrams 2008; Brose and Waldrop 2010; Brose 2016; USDA, NRCS 2021). These shrubs are highly flammable (Nowacki and Abrams 2008) and readily top-killed by fire. They recover through basal sprouting (Hooper 1969; Hagan et al. 2015), but the sprouts are vulnerable to fires and may not have survived historically under frequent burning. Frequent burning would have also curtailed the expansion of the species through branch layering and seedling establishment, both of which are relatively slow means of spread—branch layering because of contiguity with existing plants and seedling establishment because seeds fall near the parent (Wilson and O'Keefe 1983; Brose 2017). Given the damage to mountain laurel from fire, it seems probable that the thickets observed today did not develop until fire suppression was initiated and had been practiced long enough for shrubs to fill the stands.

Other factors could have also contributed to the thickets. Brose (2016) identified four alternate hypotheses proposed by various researchers: (1) release from allelopathic litter of American chestnut (*Castanea dentata*) following chestnut blight (*Cryphonectria parasitica* (Murrill) Barr); (2) facilitation by soil acidification through acid deposition; (3) facilitation by deer browsing on competing species; and (4)

Fig. 1 Photograph of a pine-dominated stand with dense understory of mountain laurel, Reddish Knob study site

the thickets were present historically, as early writers described mountain laurel thickets before fire suppression (Brose 2016). However, these writings may describe topographically restricted heaths, e.g., on infrequently burned rocky summits (Whittaker 1956; Barden and Costa 2020).

Dendroecological studies from the Blue Ridge Mountains of North Carolina suggested that mountain laurel and the mesophytic ericad rhododendron (*Rhododendron* spp.) began to establish in hardwood forests around the onset of fire suppression (McGee and Smith 1967; Monk et al. 1985). These studies were limited in extent, but a recent, more extensive study in Pennsylvania oak forests (Brose 2016) showed that mountain laurel establishment began in the 1920s–1940s and peaked in the 1970s–1980s across three study sites in the Allegheny Plateau, Ridge and Valley, and Pocono Plateau provinces. As these sites did not appear to encompass fire-prone habitats, shrub expansion was attributed to chestnut blight, acid deposition, and/or deer browsing. In contrast, findings from xerophytic pine-oak stands in the southern Blue Ridge Mountains of Georgia, South Carolina, and Tennessee suggested that fire suppression fostered mountain laurel expansion (Brose and Waldrop 2010), prompting a conceptual model where pine and oak were historically maintained through frequent fire and periodic canopy disturbance, and where shrub cover remained sparse until fire suppression was implemented.

In this study, we evaluate Brose and Waldrop's (2010) prediction that mountain laurel thickets appeared under fire suppression in montane pine-oak stands. Our study sites are suited for this purpose because their fire histories are known from detailed fire-scar records (Aldrich et al. 2010, 2014; Lafon et al. 2021), which reveal a natural experiment: fire suppression began at different times among sites, so shrub establishment should correspond with the onset of suppression at each site. If shrub thickets resulted from another factor, however, establishment dates should reflect that factor.

Materials and methods

The study sites lie within the George Washington and Jefferson National Forests (GWJNF), Virginia—six sites in the Ridge and Valley physiographic province, and one in the northern Blue Ridge. The landscapes are largely covered by oak forests, but pine-dominated stands form small patches on xeric, west-facing mountain slopes with thin, infertile, acidic soils, mostly Typic and Lithic Dystrudepts with low pH buffering capacity (Williams 1998; SoilWeb at https://casoilresource.lawr.ucdavis.edu/gmap). Multiple pine stands are encompassed within the 0.2–1.7 km^2 area of each study site. They are dominated by Table Mountain pine (*Pinus pungens*), which composes 52% of total basal area, on average (Aldrich et al. 2010; Aldrich 2011; Lafon et al. 2021). Some stands contain other pines, primarily pitch pine (*Pinus rigida*). They also include a substantial oak component, with chestnut oak (*Quercus montana*) averaging 24% of basal area. Nomenclature follows Kartesz and Kartesz (1980).

We collected dendroecological field data on fire history and tree/shrub ages during 2003–2005. The fire history and tree-age results, published elsewhere (Aldrich et al. 2010, 2014; Lafon et al. 2021), show that burning historically recurred at intervals of approximately 3–11 years but largely ceased by the 1910s–1930s. With fire suppression came a shift in forest composition. Dendroecological age-structure data, collected from a 20 × 50 m quadrat in each of three pine stands at each site, reveal that the pine-oak stands are changing toward a diverse assemblage containing more fire-sensitive tree species such as white pine (*Pinus strobus*), black gum (*Nyssa sylvatica*), and red maple (*Acer rubrum*).

To investigate mountain laurel establishment, we cut cross-sections from the base of 20 shrubs in each stand where trees were cored. We targeted the largest (presumably oldest) individuals in and around the quadrats to estimate when shrub establishment began. The cross-sections were air-dried and sanded to 400 grit using progressively finer sandpaper (Orvis and Grissino-Mayer 2002), then the rings were dated. We assigned each shrub to a decadal establishment bin and tallied the number of shrubs per bin to create establishment-decade histograms. To synthesize shrub establishment among the seven study sites, which had different onset dates for fire suppression, we stacked the decadal establishment bins to align them relative to the last major fire. The last major fire was defined as the last fire of the pre-suppression era scarring ≥ 25% of sampled trees. For each site, the decade containing the last major fire was designated as decade 0. Additionally, we compiled tree-age data from all the quadrats to place shrub establishment into the context of forest change. Tree-age histograms were generated for three groups: yellow pine, oak, and miscellaneous species. The last group contains various species that differ in fire-tolerance but probably did not compose a significant component of the pre-suppression pine stands (Williams 1998; Lafon et al. 2021). These tree-age graphs summarize age-structure patterns detailed elsewhere (Aldrich et al. 2010; Aldrich 2011; Lafon et al. 2021).

Results

The oldest shrubs were established during or after the last major fire at six study sites but preceded it at one (Fig. 2). The peak establishment decades are the 1950s–1970s, except the 1930s at Reddish Knob. The peak lags the last major fire by two to four decades (mean = three decades; Fig. 3a).

This pattern of shrub expansion contrasts with yellow pine and oak establishment, where many trees date to pre-suppression decades (Fig. 3b, c). It more closely resembles the miscellaneous tree species, which show limited pre-suppression establishment (Fig. 3d). However, the delayed establishment peak of mountain laurel contrasts with the immediate post-fire pulse of these miscellaneous tree species. Note that the tree and shrub histograms are not directly comparable because the tree histograms include all trees within the plots, whereas shrub histograms include only the largest shrubs and therefore do not include smaller, potentially younger individuals.

Discussion

Mountain laurel establishment dates are consistent with shrub expansion after the onset of fire suppression. Establishment dates vary among study sites and generally follow the beginning of fire suppression, with a multi-decade lag to the establishment peak. The lag probably indicates gradual expansion as shrubs filled the previously open understory. This sequence was disrupted at North Mountain by an anomalous, widespread fire in 1963 (Lafon et al. 2021) that undoubtedly top-killed many shrubs that had already become established. However, these

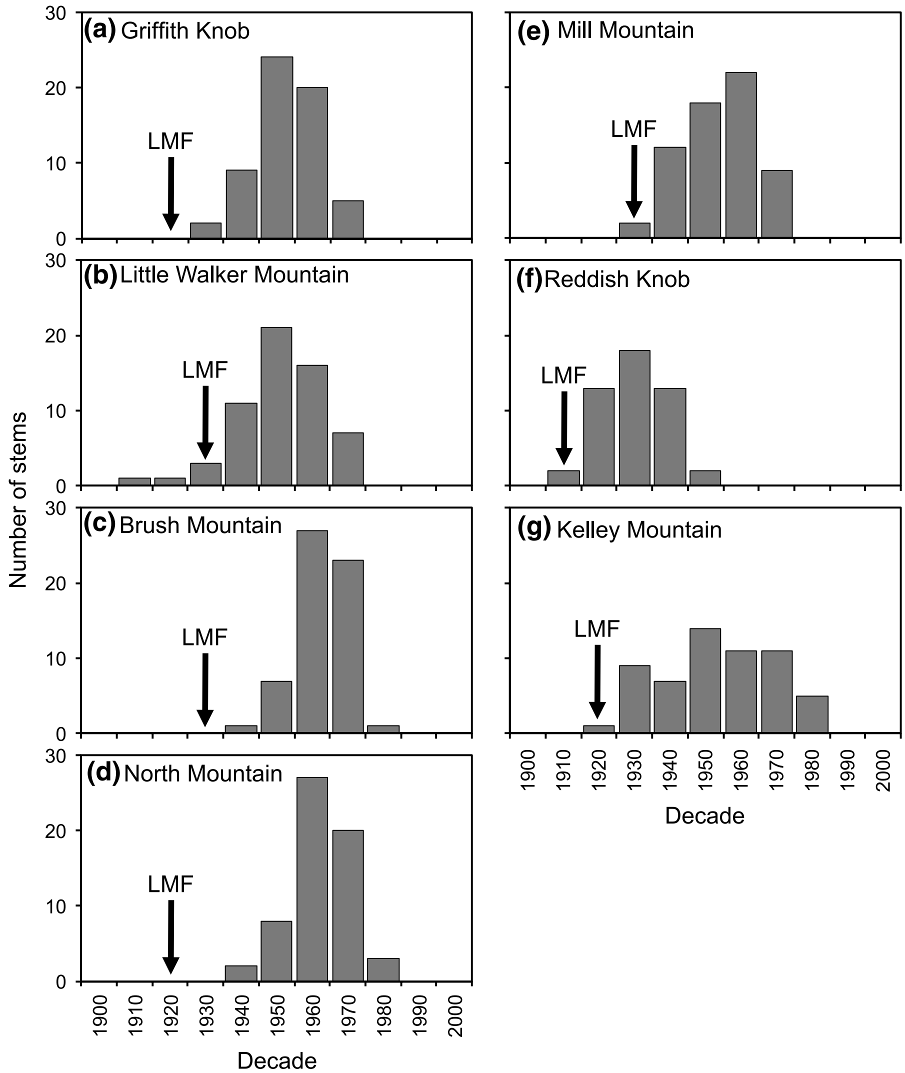

Fig. 2 Number of mountain laurel stems established by decade for each study site, with the decade of the last major fire (LMF) indicated by a labeled arrow. Study sites represented in the left column are on the Jefferson National Forest, and those in the right column are on the George Washington National Forest

top-killed shrubs recovered quickly through sprouting, as attested by the 1960s recruitment pulse.

There is no evidence that shrub thickets were present before fire suppression. The scarcity of establishment dates before the 1940s–1970s at most sites (only 30–60 years before our sampling) does not reflect the lifespan of mountain laurel. The species can live ≥ 75 years according to previous studies (Brose 2016), and up to 90 years as shown by the 1910s establishment dates at two of our study sites. If thickets had been present before fire suppression, all the sites would have contained numerous shrubs dating to the 1910s–1930s or earlier.

In contrast, many pine and oak trees were established in the open stands that were maintained under the historical fire regime. These taxa showed a recruitment pulse with the onset of fire suppression, when the seedlings and sprouts were no longer being thinned by fire (Brose and Waldrop 2006; Lafon et al. 2017). Even the miscellaneous tree species responded strongly to the post-fire environment, probably through sprouting and by seed dispersal from the surrounding landscape. In the case of mountain laurel, however, sprouting and seedling establishment were apparently limited because shrub cover was initially sparse in the pine stands and neighboring oak stands. Shrub thickets likely occupied fire-protected microenvironments such as rock outcrops from which mountain laurel slowly dispersed under fire suppression.

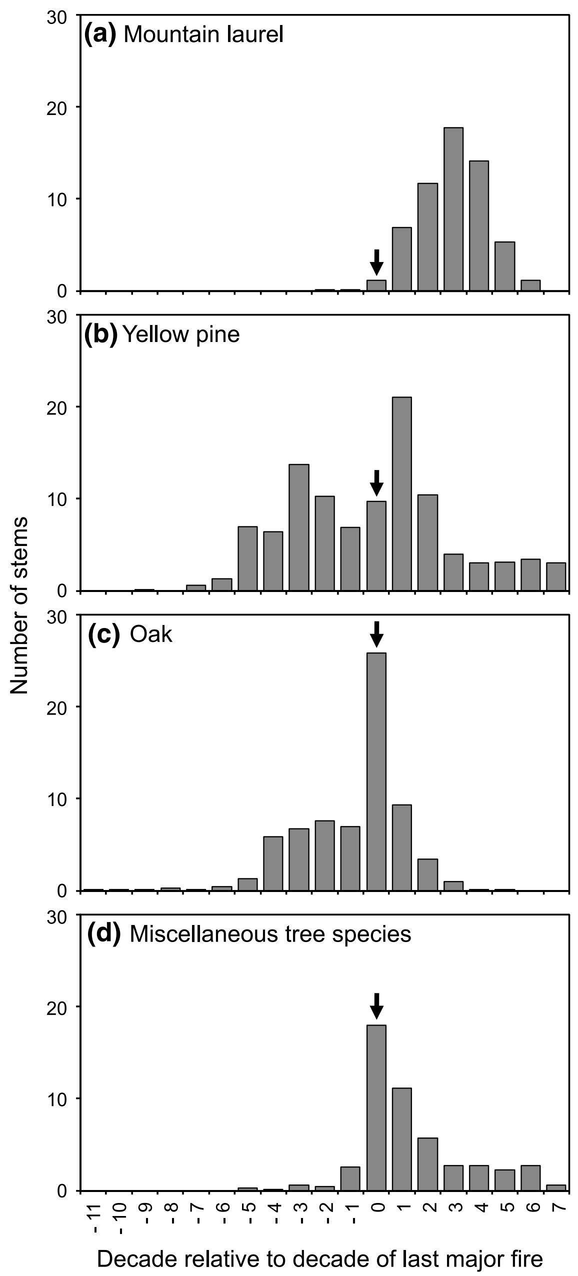

Fig. 3 Mean number of stems established per decade across all study sites, relative to the decade of the last major fire for each species group. Decade "0" refers to the decade in which the last major fire occurred, and is indicated with an arrow on each panel. Negative values indicate pre-suppression decades while positive values indicate suppression-era decades

Shrub expansion may have also been aided by chestnut blight, acid deposition, or deer browsing. The presence of chestnut sprouts in our sampling plots (Aldrich et al. 2010; Aldrich 2011; Lafon et al. 2021), indicates that chestnut trees grew at the study sites before the blight, which killed most chestnut trees in western Virginia by the 1930s (McCormick and Platt 1980). However, shrub establishment dates are not synchronous among the study sites, as would have been expected if the region-wide chestnut blight had been the primary factor in shrub expansion. Moreover, chestnut was less common in pine stands than oak stands (Whittaker 1956) so had weaker allelopathic effects than in the oak forests studied by Brose (2016). Although the chestnut blight probably favored mountain laurel establishment in pine stands, it did not control the occurrence and timing as strongly as fire suppression. Acid deposition was not the primary control, either. Acid deposition became widespread around 1950 and peaked in the 1970s (Cogbill 1976; Likens et al. 2021), so if this were the main factor, shrub colonization would have begun then, or subsequently if there was an establishment lag. But shrub establishment began earlier (1910s–1940s) and was too unsynchronized to implicate acid deposition. Therefore, while acid deposition undoubtedly benefited the shrubs, it was not required for their expansion on these naturally acidic soils. As for deer browsing, it can be ruled out because deer were nearly extirpated from western Virginia by the early 1900s and did not recover to high densities until the 1980s–1990s (VDGIF 2015). Deer remained at only one study site, Mill Mountain, according to a 1938 survey (VDGIF 2015), but shrubs did not establish earlier at Mill Mountain than elsewhere. Another site, Reddish Knob, had abundant mountain laurel establishment in the 1920s–1930s when deer were absent. Moreover, shrubs established in abundance at Little Walker Mountain and Brush Mountain during the 1950s–1960s, but few if any deer were present before 1970.

Conclusions

Our results are consistent with the model of mountain laurel expansion proposed by Brose and Waldrop (2010). Scattered shrubs likely occupied Appalachian pine stands under the historical fire regime, but thickets developed through gradual shrub expansion after the onset of fire suppression. Suppression was the primary factor in shrub expansion, but the process may have also benefited from chestnut blight and acid deposition. Deer browsing did not play an important role.

The presence of the shrub thickets seems to portend a successional shift toward greater shrub abundance or even dominance. Reversing this shift is an important management objective (Waldrop et al. 2016; Brose and Miller 2019), but it would be difficult to achieve, given the present density of mountain laurel and its sprouting capacity. To control mountain laurel would entail repeated burning combined with herbicides or mechanical thinning (Hagan et al. 2015; Waldrop et al. 2016; Brose and Miller 2019). However, treating thickets over the whole landscape would be impracticable. This means the thickets will endure in most places, burning occasionally during wildfires, but too infrequently to curtail shrub recovery. The disruption of the historical fire regime appears to have precipitated a major physiognomic change that will long endure. Resource managers may need to accept ericaceous shrub thickets as stable, spatially extensive ecological communities (Dudley et al. 2020).

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Declarations

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Research involving human and animal participants The authors have no relevant information to disclose.

Consent to participate The authors have no relevant information to disclose.

Consent to publish The authors have no relevant information to disclose.

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