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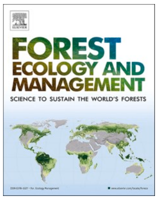

Impacts of disturbances on Table Mountain pine (*Pinus pungens*) and associated species in forests of the Eastern United States

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ABSTRACT

This study examines the structural and compositional changes in Table Mountain pine (*Pinus pungens* Lamb.) associated forest ecosystems over a two-decade period (1997–2017) and assesses the species' status across disturbed and undisturbed sites in the Appalachian Mountains of the United States. We analyzed data from 86 plots containing Table Mountain pine in the USDA Forest Service's Forest Inventory and Analysis (FIA) database. FIA plots consist of four subplots, each measuring 168.1 m^2, for a total of 672.4 m^2. Study objectives were to investigate forest stand characteristics, such as mortality, basal area, stems per hectare, mean height, and aboveground dry biomass, across life stages (tree, sapling, and seedling), evaluate species richness and diversity under forest disturbances, and identify density and dominance trends of Table Mountain pine and associated tree species. Some disturbances, including insect infestations and weather events, led to tree mortality across all species. The tree mortality was significantly higher in disturbance plots. Although tree mortality rates were similar between the first decade (midyear 2002) and the second decade (midyear 2012), sapling mortality increased substantially, particularly in the no-disturbance plots. Table Mountain pine density declined across all size categories; however, regeneration potential was evident from numerous saplings in disturbance plots. Table Mountain pine's Importance Value Percent also declined across all plots, though the decline was less pronounced in disturbance sites. There were no significant changes in sapling density among all plots and across the two decades. The findings underscore the role of disturbances in shaping forest ecosystems containing Table Mountain pine. A management approach incorporating disturbance—particularly prescribed fire—may enhance Table Mountain pine regeneration and sustain populations.

1. Introduction

Climate change is altering temperature and precipitation patterns across the eastern United States, reshaping the distribution, regeneration dynamics, and competitive interactions of many tree species (Iverson et al., 2019; Matthews et al., 2011). Over the past century, these climatic shifts have interacted with major changes in disturbance regimes, particularly fire frequency, insect outbreaks, and pathogen pressures (Dale et al., 2001). Historically, much of the Appalachian region experienced recurrent low- to moderate-intensity fires that maintained open-canopy pine–oak forests, promoted regeneration of fire-adapted species, and limited encroachment by shade-tolerant hardwoods (Brose et al., 2014; Flatley et al., 2013; Lafon et al., 2017). However, widespread fire suppression beginning in the early 20th century dramatically reduced disturbance frequency, resulting in denser forest structures, altered species composition, increased fuel accumulation, and heightened vulnerability to climate-related stressors (Nowacki and Abrams, 2008; Aldrich et al., 2010). These interacting changes have had pronounced effects on species in genera such as *Pinus*, *Ulmus*, *Magnolia*, and *Fagus*, many of which exhibit sensitivity to shifts in moisture availability, thermal stress, or alterations in disturbance (Clark et al., 2011; Clark et al., 2014; Pederson et al., 2015). Within this context, the Table Mountain pine (*Pinus pungens* Lamb.), a species closely tied to periodic fire and restricted to high-elevation habitats, may be particularly at risk. This study examines how structural and compositional characteristics of both tree communities associated with *P. pungens* are responding to these evolving climatic and disturbance conditions. The decline of Table Mountain pine populations has raised

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concerns among forest resource managers due to the species' ecological value for wildlife habitat and biodiversity (Aldrich, 2012).

Table Mountain pine is a tree species endemic to the Appalachian Mountains (Armbrister, 2002). It typically occurs as scattered individuals or in small groups (Potter et al., 2023), primarily located in South Central Pennsylvania, western Virginia, eastern West Virginia, East Tennessee, Western North Carolina, and northeastern Georgia. It is a pioneer species that establishes itself following canopy-opening disturbances such as fire, windthrow, ice storms, and timber harvesting. Over time, however, it has been replaced by more shade-tolerant species, including oaks (*Quercus* spp.), maples (*Acer* spp.), and black gum (*Nyssa sylvatica* Marsh., Brose, 2017).

The cones of Table Mountain pine have sharply pointed scales to help protect the seeds from predators—hence the scientific epithet *pungens*—and are serotinous, with seeds that remain viable for up to a decade. Seed release occurs primarily after exposure to heat, particularly from fire, although on dry, south-facing slopes, cones may also open soon after maturity (Coder, 2017). Serotinous cones enhance regeneration success by synchronizing seed dispersal with favorable post-fire conditions.

Table Mountain pine typically occupies xeric, fire-prone ridge systems where it forms mixed-conifer and mixed-oak communities with a characteristic suite of associates (Zobel, 1969; Williams, 1998). Across its range, the species is commonly found with pitch pine (*Pinus rigida* Mill.), Virginia pine (*P. virginiana* Mill.), and shortleaf pine (*P. echinata* Mill.), along with hardwoods such as chestnut oak (*Quercus montana* Willd.), scarlet oak (*Quercus coccinea* Meunchh.), and red maple (*Acer rubrum* L.) (Smith and Nicholas, 2000; Welch et al., 2002). These stands often support ericaceous shrubs, including mountain laurel (*Kalmia latifolia* L.) and huckleberry species (*Gaylussacia* spp.), which vary in abundance regionally (Clinton et al., 1993; Elliott and Vose, 2011). However, the relative dominance of associated species differs across the Appalachians, reflecting regional gradients in soil depth, climate, and disturbance history (Nowacki and Abrams, 1992; Stephenson, 2013). Documenting this variation in community composition is essential for understanding the ecological context in which Table Mountain pine persists under shifting disturbance regimes and competitive pressures.

Historically, Table Mountain pine was maintained by relatively frequent, high-intensity disturbances, especially crown fires, which removed competing canopy trees, exposed mineral soil, and triggered cone opening (Williams, 1998). However, widespread and prolonged fire suppression policies have dramatically altered disturbance regimes across much of its range (Brose and Waldrop, 2006). This shift has also facilitated the expansion of fire-intolerant species such as red maple, eastern white pine (*Pinus strobus* L.), and mountain laurel (Welch and Waldrop, 2001). Additional stressors, including changes in wind and ice disturbance frequency, insect outbreaks, and deer browsing, have further reduced the success of Table Mountain pine regeneration in some areas. As a result, formerly pine-dominated ridges and slopes have transitioned to mixed hardwood or white pine–dominated forests, with Table Mountain pine persisting mainly as aging, scattered individuals (Brose, 2017). For example, Barden (2000) reported a 92 % decrease in the number of Table Mountain pines under nine years of age between 1976 and 1996 in the Pisgah National Forest, North Carolina.

This study aimed to analyze structural and compositional changes in forest communities with Table Mountain and co-occurring tree species between 1997 and 2017 and to evaluate the status of the species across disturbance and no-disturbance sites. Specific objectives included assessing changes in species composition, dominance, mortality, and stand structure during the study period, and assessing how some of these changes were related to disturbances.

2. Materials and methods

2.1. Study area

The study area was selected based on stands that met the forest land criteria ($\geq$10 % canopy cover of live trees of any species) within the range of the Table Mountain pine. This area encompasses the Blue Ridge and Valley and Ridge physiographic provinces of the Appalachian Mountains, which include portions of Georgia, Tennessee, North Carolina, and Virginia (Fig. 1). The terrain of the southern Ridge and Valley section is mountainous, with elevations ranging from 1000 to 2000 m and an average slope of 40 %. The region is characterized by folded sandstone and limestone formations of valleys and ridges (McNab et al., 2007). The climate is temperate, characterized by distinct seasonal variations, with mild winters and cool summers. Average annual temperatures range from 10°C in the Valley and Ridge and Blue Ridge provinces to 14°C in the Piedmont Province. Recorded extremes range from −34 °C to over 38°C (Nelms et al., 1997). Annual precipitation ranges from 1000 to 2000 mm and is distributed relatively evenly throughout the year, although elevation has a considerable influence on variability. The region experiences occasional winter ice storms and intense summer rain events. Soils are typically deep, well-drained, acidic (pH $<$ 5.5), and composed of sandy or gravelly loams with high organic content at higher elevations (McNab et al., 2007).

Oak-hickory and oak-pine forest types dominate the vegetation. Table Mountain pine occurs with other pines such as shortleaf pine, Virginia pine, eastern white pine, loblolly pine (*Pinus taeda* L.), and pitch pine, and several species of oaks (Della-Bianca, 1990). The midstory primarily comprises hardwood species such as oaks, black gum, red maple, and sourwood (*Oxydendrum arboreum* L.) (Brose and Waldrop, 2006).

Forest community composition within the study area reflects the transitional nature of xeric Appalachian ridge systems. FIA plots containing Table Mountain pine included a diverse assemblage of co-occurring species, characteristic of these dry ridgetop forests (Potter et al., 2023). In the southern portion of the range, the plots were more commonly dominated by shortleaf pine, Virginia pine, and chestnut oak, with frequent presence of pitch pine and red maple (Williams, 1998; Elliott and Vose, 1995). Northern plots exhibited comparatively greater hardwood dominance, particularly scarlet oak, red maple, and hickory species, consistent with broader biogeographic patterns in Appalachian ridge communities (Nowacki and Abrams, 1992; Zobel and McNab, 2014). Shrub layers were typically composed of mountain laurel and huckleberry, although their relative abundance also varied across geographic regions (Clinton et al., 1993; Elliott and Vose, 2011). Including these compositional patterns provides important ecological context for interpreting the stand structure and regenerative dynamics of Table Mountain pine across its range.

2.2. Data acquisition, study design, and plot classification

Data were obtained from plots of the USDA Forest Service's Forest Inventory and Analysis (FIA) database, available at the FIA Data-Mart (https://apps.fs.usda.gov/fia/datamart/). The age distribution of Table Mountain pine is typically bimodal, indicating the presence of two distinct age clusters: trees and saplings (Williams and Johnson, 1990). Due to the bimodal age distribution of Table Mountain pine populations, we conducted our analyses across three major life stages: tree, sapling, and seedling. Life stage classification followed size-based FIA standards (Burrill et al., 2024): trees (diameter at breast height, 1.37 m above the ground, DBH $\geq$ 12.7 cm), saplings (DBH 2.5–12.6 cm), and seedlings (DBH $<$ 2.5 cm and height $\geq$ 30.5 cm). Biomass data were also retrieved from the FIA Database. Methods for biomass calculation are described in the FIA Database User Guide (Burrill et al., 2024).

FIA plots consist of four subplots with a radius of 7.3 m. One is centrally located, and the others are positioned 36.6 m apart in a

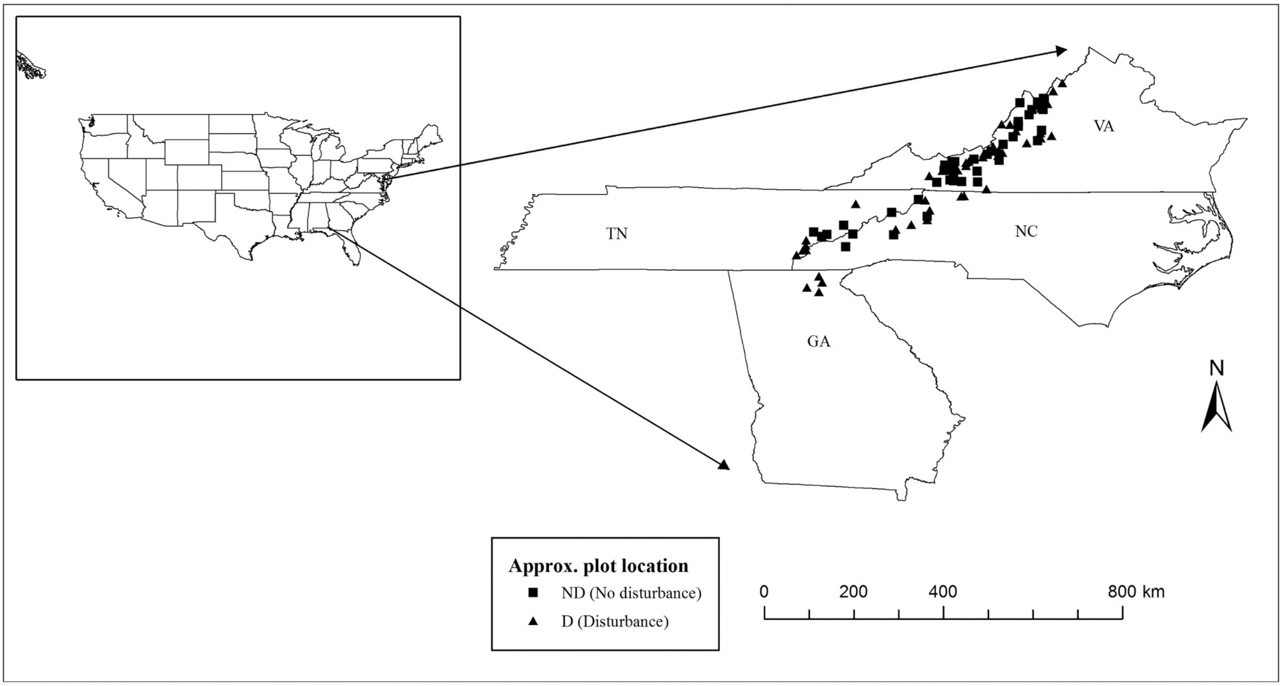

Fig. 1. Sample plots were located in Georgia, Tennessee, North Carolina, and Virginia.

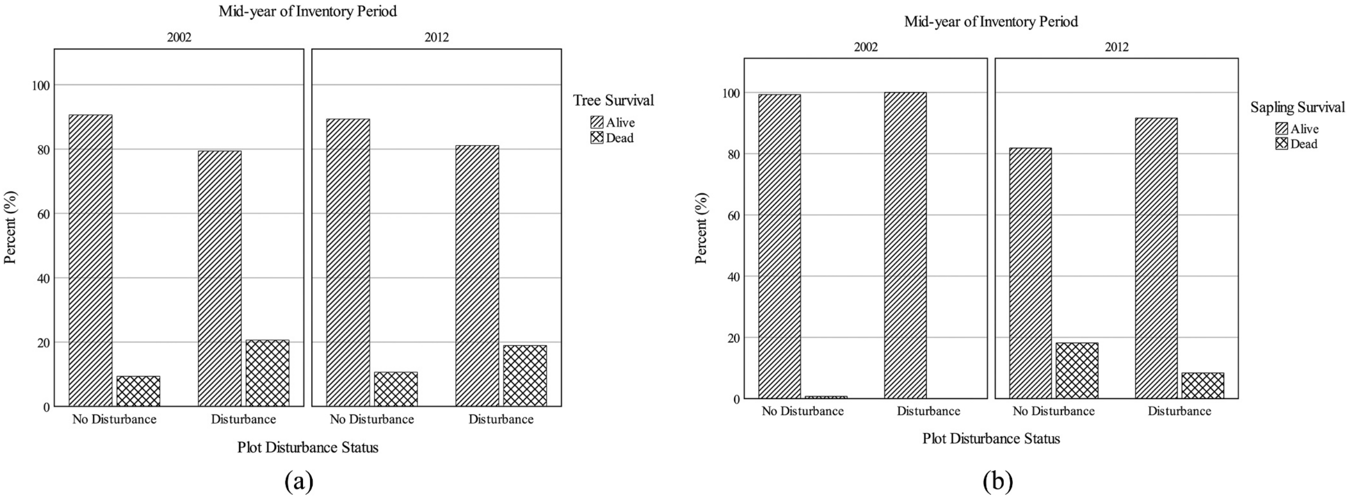

Fig. 2. Percent of alive and dead trees (A) and saplings (B) in no disturbance and disturbance plots by inventory periods.

triangular configuration. Each subplot includes a nested 2.07 m radius microplot for sampling saplings and seedlings. Detailed plot design and variable descriptions are available in the FIA Database User Guide (Burrill et al., 2024).

A total of 86 FIA plots containing Table Mountain pine of any size were selected. All plots met the FIA forest land criteria (≥10 % canopy cover of live trees of any species). Each plot was measured during two inventory intervals: 1997–2007 and 2008–2017. For clarity, these intervals (periods) are referred to by their midpoints as “2002” and “2012,” respectively. The FIA’s data collection schedule dictated these intervals. The 86 plots were not all measured at the same time, so the first measurements of these plots occurred between 1997 (when the new FIA fixed-plot design was implemented) and 2007. The second measurement of these same plots occurred during 2008–2017.

Plots were classified as either “no-disturbance’ or with “disturbance.” According to FIA protocol, a disturbance was recorded only if it affected at least 0.4 ha and killed or damaged more than 25 % of all trees, either since the previous measurement (for remeasured plots) or within the last five years (for new plots). Up to three different disturbances were recorded, from most important to least important. In total, 45 plots were identified as “no-disturbance plots” and 41 as “disturbance plots” (Fig. 1). Disturbance agents included both natural factors (insects, weather, fire) and anthropogenic factors (timber harvesting, prescribed fire, or other human-induced damage). Due to the small number of plots and the overlap in disturbance agents, classification by disturbance type was not feasible. Some of the damage from disturbances led to mortality, which was quantified at the time of measurement as the proportion of dead individuals by species and life stage per plot.

2.3. Analysis

Stand structure and composition were evaluated across tree, sapling, and seedling layers in 2002 and 2012 sampling periods. Species richness (number of species per plot) and Shannon’s diversity index (Shannon,

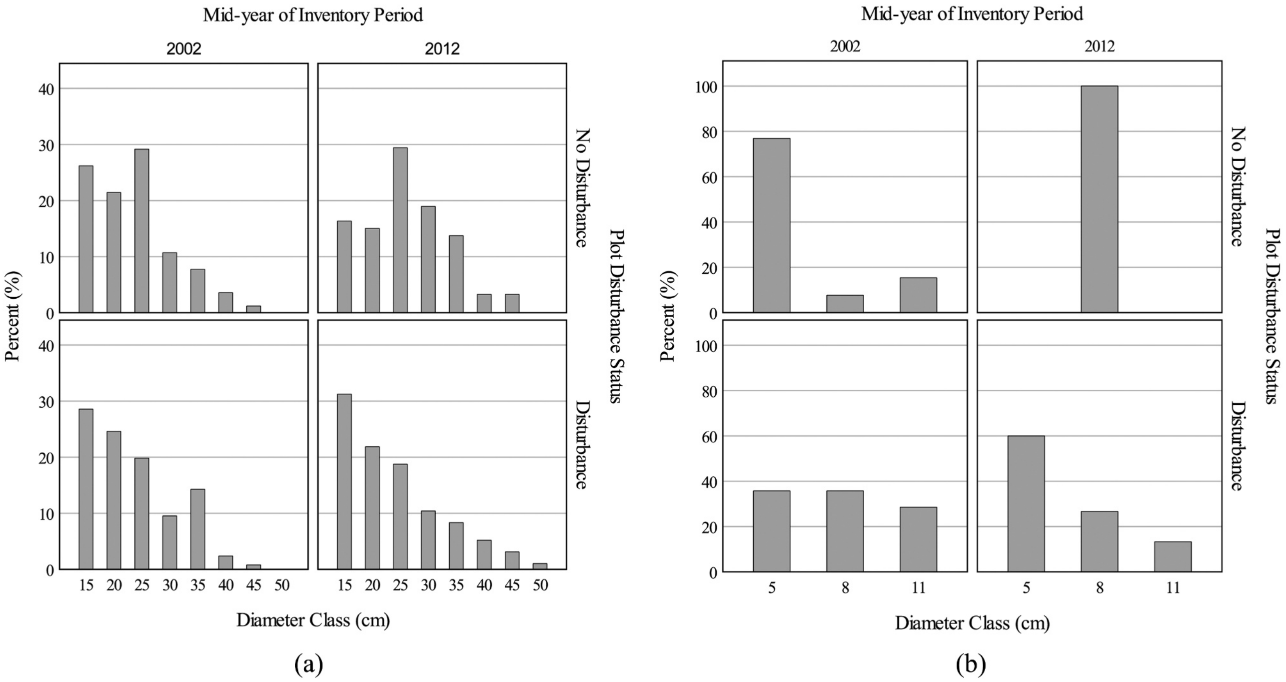

Fig. 3. Diameter distribution class of Table Mountain pine trees (A) and saplings (B) in no disturbance and disturbance plots by inventory periods.

1948) for trees, saplings, and seedlings were calculated. Importance Value Percent (IVP, Curtis and McIntosh, 1951) was computed for tree and sapling layers as the average of relative frequency, relative density, and relative dominance (based on basal area). IVP was based on relative frequency for seedlings because only count data were available.

Chi-square contingency tables based on observed counts were used to test the independence of mortality-related variables at $\alpha = 0.05$. Mortality percentages were calculated across all plots for descriptive purposes. To evaluate differences in stand attribute means between groups, Welch's *t*-tests (assuming unequal variances) were conducted at $\alpha = 0.05$. We used IBM SPSS Statistics version 31 (https://www.ibm.com/products/spss) for data management and statistical analysis, PC-ORD 7 (https://www.wildblueberrymedia.net) for vegetation structure and composition analysis, and ArcGIS Desktop 10.6.1 for the map of Fig. 1.

3. Results

3.1. Species composition, dominance, and geographic patterns

Across the 86 FIA plots containing Table Mountain pine, we identified 40 associated tree species, reflecting the species' occupation of a diverse set of xeric ridge communities (Bechtold and Patterson, 2005; Potter et al., 2023). Community composition differed geographically. Southern Appalachian plots exhibited higher basal area contributions from shortleaf pine, Virginia pine, and chestnut oak, with pitch pine present but less dominant (Elliott and Vose, 1995; Welch et al., 2002). In contrast, northern plots were characterized by greater hardwood dominance, particularly scarlet oak, red maple, and hickory species, patterns consistent with known gradients in Appalachian ridge-top forest structure (Nowacki and Abrams, 1992; Stephenson, 2013). Shrub composition also varied across the region, with mountain laurel more prevalent in the southern and central Appalachians and huckleberry species more common in northern sites (Clinton et al., 1993; Elliott and Vose, 2011). These composition patterns clarify the ecological context of Table Mountain pine distribution and regeneration. Shifts in dominance, stem density, and basal area varied by disturbance status and forest stratum. In the seedling layer of no-disturbance plots, the most dominant species in 2002 were sassafras, red maple, serviceberry, black gum, and chestnut oak. By 2012, eastern white pine became the most dominant species (IVP = 20.9 %), while Table Mountain pine's IVP increased only marginally (Fig. 4). In disturbance plots, Table Mountain pine exhibited greater IVP gains in the seedling layer, although red maple, serviceberry, scarlet oak, and sourwood showed larger increases.

In the sapling layer, Table Mountain pine experienced the most decline in density in no-disturbance plots, whereas sapling density increased slightly in disturbance plots. Sapling basal area declined across both disturbance classes but decreased more sharply in no-disturbance plots (Fig. 5). The IVP of Table Mountain pine saplings declined substantially in no-disturbance plots but decreased less in disturbance plots, where Virginia pine, pitch pine, and black locust exhibited the most gains.

In the tree layer, Table Mountain pine remained among the most dominant species in both disturbance classes but experienced declines in density and IVP between 2002 and 2012, particularly in disturbance plots (Fig. 6). Basal area declined in disturbance plots but increased slightly in no-disturbance plots.

3.2. Mortality and stand structure changes between inventory periods

No statistically significant differences in mortality were observed between 2002 and 2012 in trees (Fig. 2a) and saplings (Fig. 2b). In contrast, sapling mortality increased substantially between 2002 and 2012, with greater losses (from 0.7 % to 16.6 %) in no-disturbance plots ($\chi^2 = 48.76$, $p < 0.01$) than in disturbance plots (from 0.0 % to 8.8 %; $\chi^2 = 22.40$, $p < 0.01$).

Tree biomass and basal area increased significantly in no-disturbance plots between 2002 and 2012, while no significant change was observed in disturbance plots (Table 1). No significant changes in other tree attributes were observed between 2002 and 2012. Sapling height increased significantly in no-disturbance plots, whereas diameter increased significantly in disturbance plots during the same period. There were no significant changes in sapling density among all plots across the two inventory periods.

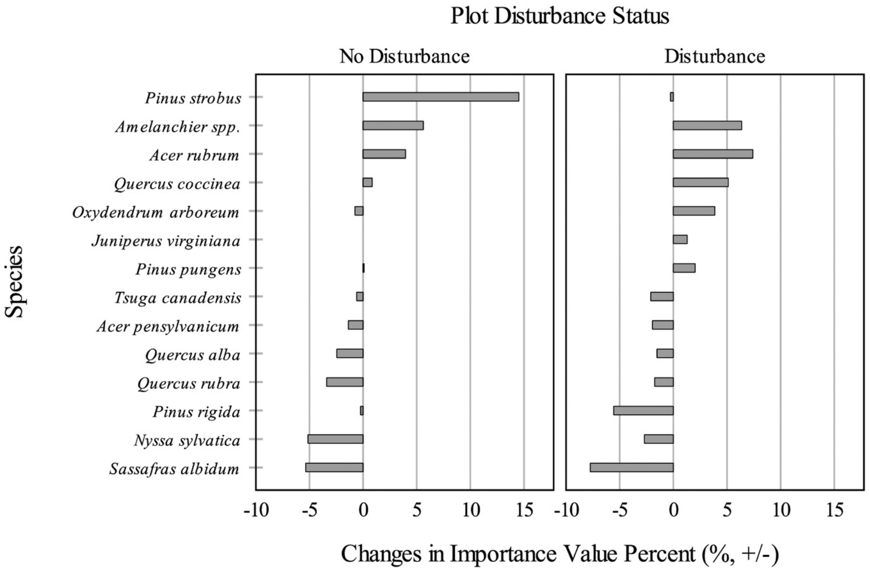

Fig. 4. Change of Importance Value Percent (IVP) of species in the seedling layer by plot disturbance status during the 2002–2012 period.

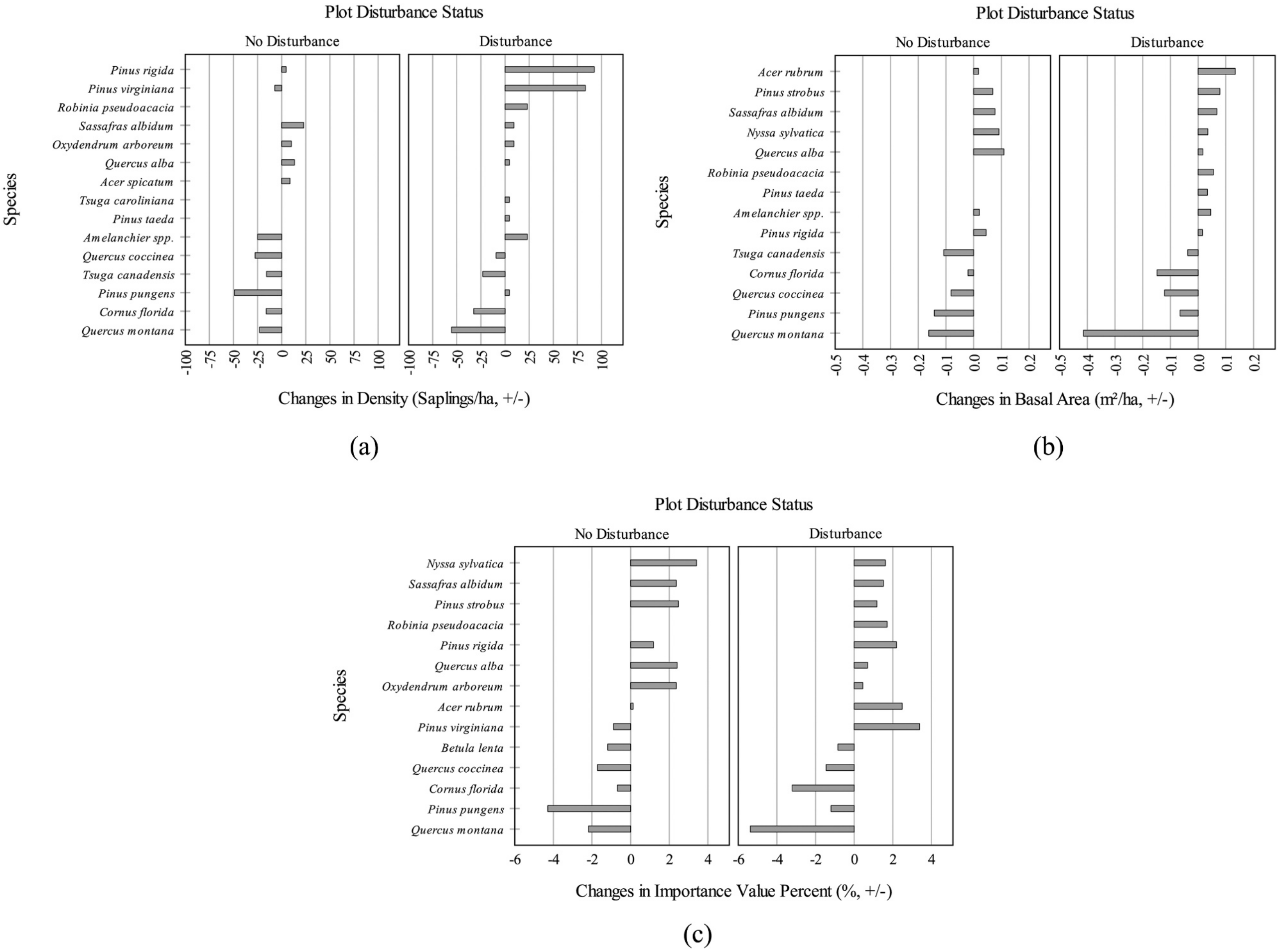

Fig. 5. Changes in stem density (A), basal area (B), and IVP (C) of species in the sapling layer by plot disturbance status during the 2002–2012 period.

3.3. *Mortality and stand structure differences by disturbance status*

Overall tree mortality in disturbance plots was 19.8 %, compared to 8.2 % in no-disturbance plots. This difference was statistically significant based on a Chi-square test ($\chi^2 = 115.8$, $p < 0.001$). By contrast, mortality of Table Mountain pine trees was 51.6 % in disturbance plots compared to 21.5 % in no-disturbance plots, a difference that was also significant ($\chi^2 = 85.9$, $p < 0.001$). The difference between the mortality of Table Mountain pine and other tree species was significant in both disturbance plots ($\chi^2 = 354.7$, $p < 0.001$) and no-disturbance plots ($\chi^2 =$

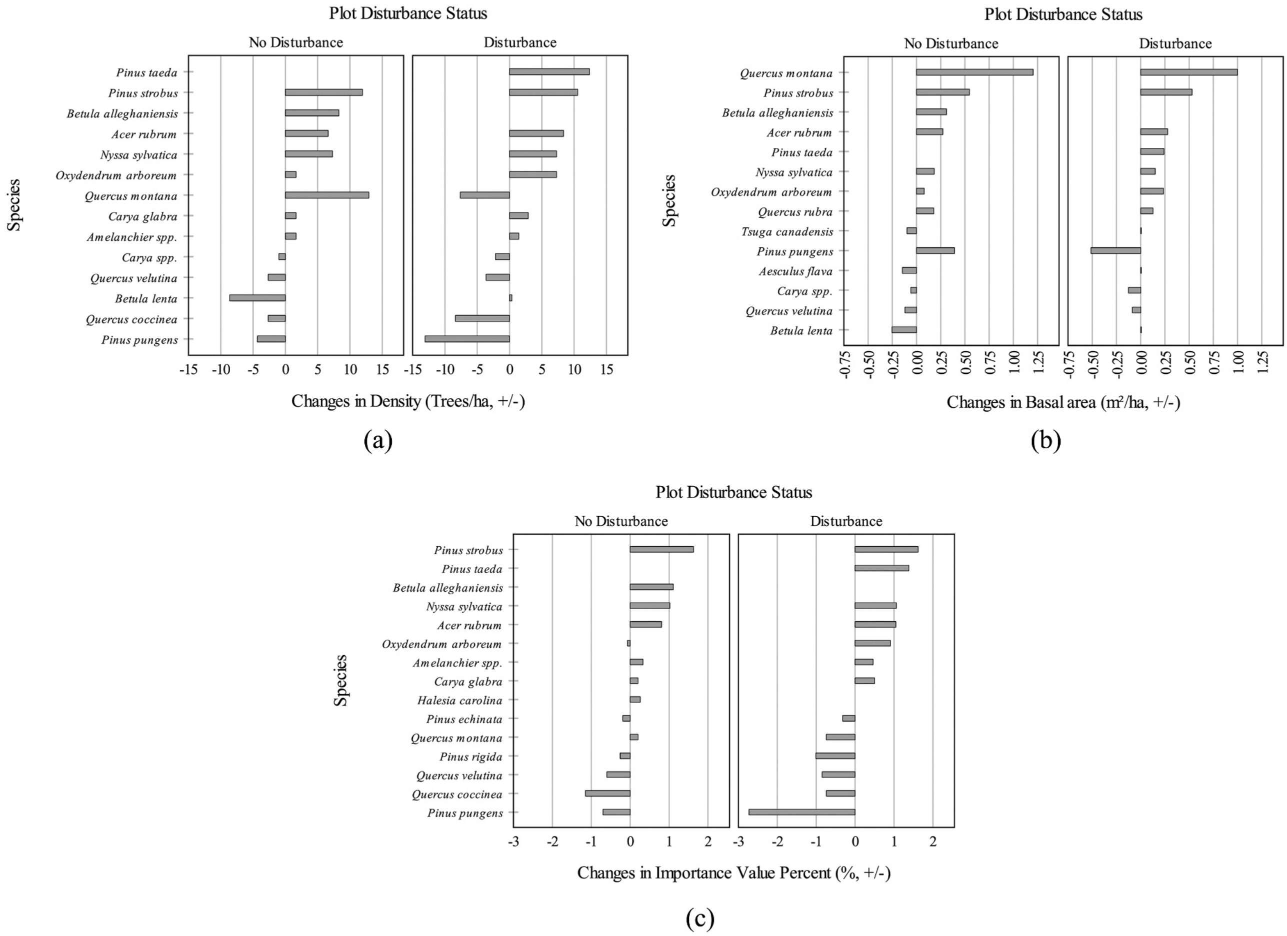

Fig. 6. Changes in stem density (A), basal area (B), and IVP (C) of species in the tree layer by plot disturbance status during the 2002–2012 period.

114.2, $p < 0.001$). Sapling mortality in disturbance plots averaged 4.7 %, compared to 9.9 % in no-disturbance plots. This difference was also significant ($\chi^2 = 8.91$, $p < 0.01$).

Besides mortality, disturbances caused the breakage of tree branches or stems and damage to leaves, bark, and wood tissues. Insect damage and weather events, such as windstorms and ice storms, were the primary disturbance agents, affecting 39 % and 12 % of plots in 2002 and 7 % and 2 % of plots in 2012, respectively. The higher incidence of disturbances in the earlier decade was associated with a sequence of ice storms and southern pine beetle (Dendroctonus frontalis) outbreaks during the 1998–2002 drought (Lafon and Kutac, 2003). Few plots recorded other disturbances: one was harvested, one experienced fire damage, and two were impacted by human-induced disturbances in 2002. Two plots were recorded as experiencing fire disturbance in 2012.

3.4. Species composition and diversity between inventory periods

Tree species richness and diversity, measured across tree, sapling, and seedling layers, did not differ significantly between 2002 and 2012 in either disturbance or no-disturbance plots ($\alpha = 0.05$; Table 2). Across all plots, species count in the seedling layer exceeded that of the tree and sapling layers and increased slightly over the study period in both disturbance classes (Table 3); however, these differences were not statistically significant. Species count in all three structural layers increased more in disturbance plots than in no-disturbance plots from 2002 to 2012, but these increases were also not statistically significant.

3.5. Diameter distribution of Table Mountain pine

In both 2002 and 2012, most of the Table Mountain pine trees occurred in the four smallest diameter classes (15–30 cm) across all plots, regardless of disturbance status (Fig. 3A). In 2002, saplings were distributed across several diameter classes in both disturbance groups; however, by 2012, only the 8 cm diameter class (6.6 cm $<$ DBH $<$ 9.5 cm) was represented in saplings within no-disturbance plots (Fig. 3B), indicating a decline in size diversity. These changes may reflect the gradual advancement of a pre-existing cohort of individuals into larger sapling diameter classes by 2012, resulting in reduced representation of smaller diameter classes.

4. Discussion

This study assessed changes in the species composition and structure of Table Mountain pine–associated stands over time, evaluated the effects of disturbances on species diversity and regeneration patterns, and examined how disturbances influence the survival of Table Mountain pine across seedling, sapling, and tree stages. Together, our findings emphasize that periodic disturbances remain critical for sustaining this fire-dependent species and limiting competitive displacement by more shade-tolerant associates.

4.1. Species composition and persistence of Table Mountain pine

Between 2002 and 2012, shifts in tree, sapling, and seedling species composition were evident across both disturbance and no-disturbance plots, though not statistically significant. However, increased seedling

Table 1
Stand attributes (mean ±SE) in tree, sapling, and seedling layers by plot disturbance status and inventory period. Only living stems were used in this analysis.

Plot disturbance Status	Inventory period	Trees						Saplings						Seedlings	
		No. of plots	Quadratic mean diameter (cm)	Stems/ ha	Basal area (m^2/ha)	Height (m)	Aboveground dry biomass (ton/ha)	No. of plots	Quadratic mean diameter (cm)	Stems/ha	Basal area (m^2/ha)	Height (m)	Aboveground dry biomass (ton/ha)	No. of plots	Stems/ha
No disturbance	2002	45	24.5 ± 0.7^{a}	444 ± 24.0^{a}	20.5 ± 1.0^{a}	15.0 ± 0.4^{a}	98.6 ± 6.2^{a}	45	6.4 ± 0.3^{a}	1128 ± 117.6^{a}	3.6 ± 0.4^{a}	6.2 ± 0.2^{a}	9.3 ± 1.1^{a}	41	1970 ± 219.2^{a}
	2012	45	25.3 ± 0.6^{a}	482 ± 22.9^{a}	23.5 ± 1.0^{b}	15.8 ± 0.4^{a}	118 ± 6.5^{b}	43	6.9 ± 0.3^{a}	892 ± 103.6^{a}	3.3 ± 0.3^{a}	7.1 ± 0.3^{b}	8.6 ± 1.0^{a}	40	2830 ± 459.9^{a}
Disturbance	2002	41	23.6 ± 0.6^{a}	446 ± 23.7^{a}	19.3 ± 1.1^{a}	15.3 ± 0.4^{a}	97.6 ± 7.2^{a}	40	7.0 ± 0.2^{a}	1181 ± 104.4^{a}	4.4 ± 0.4^{a}	7.0 ± 0.3^{a}	11.5 ± 1.1^{a}	35	2779 ± 675.6^{a}
	2012	41	24.6 ± 0.6^{a}	458 ± 22.9^{a}	21.7 ± 1.2^{a}	15.8 ± 0.4^{a}	113.4 ± 8.4^{a}	40	6.2 ± 0.3^{b}	1264 ± 210.8^{a}	3.7 ± 0.5^{a}	6.3 ± 0.2^{a}	8.7 ± 1.1^{a}	39	2565 ± 386.5^{a}

Means with the same letters are not significantly different at α= 0.05 (*t*-test for independent samples with variances assumed not equal). The analyses are separate for each plot disturbance status.

species richness in disturbance plots suggests that while disturbances may not immediately alter overstory composition, they can facilitate seedling establishment of both pioneer and shade-tolerant species, with potential long-term implications for forest structure and composition (Nowacki and Abrams, 2008; Hanberry, 2014).

Across forest strata, species composition strongly influenced Table Mountain pine regeneration. In no-disturbance plots, the seedling layer became increasingly dominated by eastern white pine, red maple, and serviceberry—species whose shade tolerance and rapid juvenile growth enable them to outcompete Table Mountain pine seedlings over time (Fig. 4). At the sapling stage, the sharp decline in Table Mountain pine density in no-disturbance plots (from 53.5 to 4.3 stems ha^{-1}), coupled with gains by sassafras, white oak, and sourwood, indicates that hardwood competitors increasingly shape stand development where disturbances are absent (Fig. 5A). In the tree layer, Table Mountain pine declined in both density and IVP across disturbance classes. At the same time, basal area increased slightly in no-disturbance plots, likely reflecting aging cohorts rather than successful recruitment. Collectively, these patterns reinforce the importance of disturbances for maintaining a multi-aged stand structure.

Higher sapling mortality in no-disturbance plots further suggests that Table Mountain pine is not regenerating successfully in the absence of disturbances. Across no-disturbance plots, sapling, tree densities, and IPVs of Table Mountain pine declined sharply, whereas disturbance plots retained higher sapling density and modest seedling recruitment. This pattern indicates that non-fire disturbances may contribute to Table Mountain pine persistence by reducing overstory shading, accelerating litter mineralization, and exposing mineral soil, conditions favorable for germination (Zobel, 1969). At the same time, the frequency and severity of disturbances affecting these plots highlight the species' vulnerability to specific agents. Ice storms disproportionately affect Table Mountain pine relative to co-occurring species (Whitney and Johnson, 1984; Lafon and Kutac, 2003), while southern pine beetle outbreaks have historically reduced populations in the southern portion of its range (Dodds et al., 2018). Under shifting climate regimes, these agents are expected to expand in frequency or geographic extent, potentially increasing pressure on northern populations as well (Lesk et al., 2017).

Fire disturbance was infrequently detected in the FIA plots, limiting direct assessment of its effects. Nevertheless, fire remains the most effective mechanism for promoting Table Mountain pine regeneration because its serotinous cones open in response to high temperatures (Barden, 1977; Brose and Waldrop, 2006). Fire reduces competition from shade-tolerant hardwoods and prepares seedbeds for germination, as observed in other fire-adapted eastern pine systems such as sand pine (Pinus clausa [Chapm. Ex Engelm.] Vasey ex Sarg.) and pitch pine (Parker et al., 2001; Lee et al., 2019). Extended fire-free intervals have been widely linked to regeneration failure and population declines across these species' ranges (Mitchell et al., 2014).

Alternative silvicultural treatments, including group selection, gap cutting, or small clearcuts, may partially mimic fire by increasing light availability and reducing competition (Patterson et al., 2022; Reddy et al., 2025). However, such treatments typically fail to expose mineral soil or stimulate serotinous cone opening. Evidence from other pine systems suggests that combined canopy removal and surface fire—such as shelterwood-burn or fell-and-burn approaches—may be most effective for cone opening and regeneration (Brose et al., 2014; Pile and Waldrop, 2016), particularly given the limited commercial value of Table Mountain pine (Della-Bianca, 1990). Wildfires following prolonged suppression often remove both hardwoods and pines, but hardwood sprouting dominates post-fire regeneration (Lafon and Kutac, 2003). In contrast, prescribed fire applied at appropriate frequencies and intensities can reduce hardwood competition while promoting pine regeneration (Waldrop et al., 2002).

Furthermore, fire intensity affects regeneration outcomes. Low-intensity fires may promote seedling establishment but fail to

Table 2
Variation (mean ±SE) in species richness and Shannon's diversity index in tree, sapling, and seedling layers by plot disturbance status and inventory period.

		Tree			Sapling			Seedling		
Plot disturbance status	Inventory period	No. of plots	Species richness	Shannon's diversity index	No. of plots	Species richness	Shannon's diversity index	No. of plots	Species richness	Shannon's diversity index
No-disturbance	2002	45	7.2 ± 0.2^{a}	1.4 ± 0.0^{a}	45	3.2 ± 0.2^{a}	0.9 ± 0.1^{a}	41	4.3 ± 0.4^{a}	1.1 ± 0.1^{a}
	2012	45	7.3 ± 0.3^{a}	1.5 ± 0.1^{a}	43	2.7 ± 0.3^{a}	0.6 ± 0.1^{a}	40	4.2 ± 0.4^{a}	1.0 ± 0.1^{a}
Disturbance	2002	41	7.1 ± 0.3^{a}	1.4 ± 0.1^{a}	40	3.4 ± 0.3^{a}	0.9 ± 0.1^{a}	35	4.3 ± 0.4^{a}	1.0 ± 0.1^{a}
	2012	41	7.4 ± 0.4^{a}	1.5 ± 0.1^{a}	40	2.8 ± 0.2^{a}	0.7 ± 0.1^{a}	39	4.5 ± 0.4^{a}	1.1 ± 0.1^{a}

Means with the same letters are not significantly different at $\alpha = 0.05$ (applied a *t*-test for independent samples with equal variances not assumed). Shannon's diversity index was calculated based on the trees and saplings' basal area and seedling counts. There was no significant difference. The analyses are separate for each plot disturbance status.

Table 3
Number of species counted in seedling, sapling, and tree layers by plot disturbance status and inventory period.

		Tree		Sapling		Seedling	
Plot disturbance Status	Inventory period	No. of plots	Total species count	Plots	Total species count	No. of plots	Total species count
No	2002	45	30	45	26	41	30
Disturbance	2012	45	30	43	25	40	33
	2002	41	31	40	28	35	35
Disturbance	2012	41	32	40	23	39	37

sufficiently reduce canopy cover, whereas high-intensity fires may reduce seed viability. Prescribed fires of moderate to moderately high intensity likely provide the most favorable balance between canopy removal and seed survival (Waldrop and Brose, 1999).

4.2. Ecological role and broader relevance of Table Mountain pine

Table Mountain pine occupies a narrow geographic range in the southern and central Appalachians and functions as a disturbance-dependent conifer within fire-adapted ridge-top ecosystems (Williams, 1998). Its decline reflects the broader degradation of these systems, which support diverse associated species, including rare plants and animals (Welch et al., 2000; Harper et al., 2016). Comparisons with other North American serotinous pines, including lodgepole pine (Pinus contorta Dougl. ex Loud.) and jack pine (Pinus banksiana Lamb.), highlight shared vulnerabilities to fire exclusion and climate change (Turner et al., 2007; Splawinski et al., 2015) and underscore the role of prescribed fire in restoring stand structure and biodiversity.

Although Table Mountain pine has limited commercial value, its ecological importance warrants targeted conservation attention. Prescribed fire—particularly at moderate to high intensities—can simultaneously reduce hardwood competition and promote cone opening, creating conditions favorable for regeneration and long-term ecosystem restoration (Waldrop and Brose, 1999; Flatley et al., 2015).

4.3. Research needs and future data priorities

Despite the insights gained in this study, considerable knowledge gaps remain. Greater understanding of spatial variability in serotiny, cone viability, and seed release across elevations and disturbance histories would improve predictions of regeneration success. While this study documents declining recruitment in no-disturbance plots, longer-term monitoring is needed to assess cohort survival under increasing climatic stress and competition.

Seedling establishment is closely tied to canopy openness and mineral soil exposure, yet these variables were not measured at fine spatial scales. Microhabitat-level data could clarify which disturbance types most consistently create favorable regeneration niches.

Table Mountain pine faces compounding pressures from fire exclusion, ice storms, insect outbreaks, and warming temperatures. Experimental and modeling studies are needed to quantify how these interacting disturbances influence regeneration outcomes and to refine management guidance on fire intensity thresholds, return intervals, and combined mechanical–fire treatments. Such work would directly inform restoration and conservation planning for this declining, disturbance-dependent species.

5. Conclusions

This study provides new insights into the dynamics of Table Mountain pine-associated stands in the southern Appalachian region by examining structural characteristics, species diversity, and regeneration patterns across different life stage classes and disturbance histories. We found that stand structure and composition varied across the three life stage classes, with older plots shifting toward hardwood dominance and younger or disturbance plots retaining a stronger pine component. At the same time, while species richness did not differ significantly between disturbance and no-disturbance plots overall, a trend toward higher seedling richness in disturbed areas suggests that disturbance events contribute to regeneration and structural diversity by opening growing space and reducing competition—an effect consistent with other studies (Taeroe et al., 2019; White et al., 2014). Table Mountain pine declined sharply in no-disturbance stands, particularly in the sapling and tree layers, highlighting its dependence on disturbance for its persistence and regeneration.

While natural disturbances such as windstorms, ice, or insect outbreaks are inherently uncontrollable, their ecological role in creating regeneration opportunities is critical. Managed disturbances, such as prescribed fire and strategic canopy reductions, may be used to promote suitable regeneration conditions for disturbance-dependent species, such as Table Mountain pine. However, a rigid focus on fire alone may overlook opportunities for other silviculture canopy-reducing treatments, such as expanding-gap shelterwood cuts, that can contribute to the restoration of Table Mountain pine.

Ultimately, understanding how different disturbance regimes influence structural development, species diversity, and the persistence of Table Mountain pine and other rare pines is key to maintaining the ecological integrity of these declining forest types. Continued monitoring and comparative studies are essential to guide restoration and conservation efforts in Appalachian pine–oak systems and beyond.

CRediT authorship contribution statement

Santosh K. Ojha: Writing – original draft, Software, Methodology,

Formal analysis, Conceptualization. **Kozma Naka:** Writing – review & editing, Writing – original draft, Supervision, Software, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Luben D. Dimov:** Writing – review & editing, Methodology.

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Declaration of Competing Interest

We have nothing to declare.

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Data availability

Data will be made available on request.

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