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Tree compositional change in upland hardwood forests aligns with mycorrhizal type

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ABSTRACT

Long-term monitoring in the eastern United States has documented widespread declines in fire-adapted oaks (*Quercus* spp.) and concurrent increases in mesophytic species such as red maple (*Acer rubrum*). While these changes are typically attributed to fire exclusion and shifting light and moisture regimes, belowground functional traits—particularly mycorrhizal association—may play a central role in reinforcing mesophication and altering forest resilience. To gain insight into this process, we analyzed nearly five decades of demographic data from upland oak–hickory forests on the Cumberland Plateau in southeastern USA to quantify shifts in species composition, aboveground biomass, size-class structure, and functional traits. We found that fire tolerance varied significantly by mycorrhizal type, with arbuscular mycorrhizal (AM) species more often classified as fire intolerant than ectomycorrhizal (EM) species, whereas shade tolerance was unrelated to mycorrhizal type and was instead higher in fire-intolerant than fire-tolerant species. Over time, AM and ericoid (ErM) species gained importance value (calculated by combining relative density, frequency, and aboveground total biomass) through increases in frequency and stem density, while EM species declined in importance value despite continued biomass accumulation. Fire-tolerant and intermediate shade-tolerant species exhibited similar declines, indicating a regeneration bottleneck in historically dominant EM fire-adapted trees. In contrast, AM-associated species, including broadly tolerant generalists, now dominate small stems and regeneration strata. Although total aboveground biomass increased across all functional groups, regeneration failure among EM species suggests a structural transition masked by demographic inertia of long-lived canopy individuals. These results provide evidence that shifts in mycorrhizal dominance and fire-related traits reinforce mesophication trajectories, constraining oak regeneration and reshaping belowground mycorrhizal dynamics. Integrating mycorrhizal strategies and disturbance-related traits into management frameworks may be critical for sustaining oak ecosystems and restoring fire-adapted forest structure in the eastern United States.

1. Introduction

Forests of the eastern United States have undergone major shifts in structure and composition since the late nineteenth century, shaped by land-use legacies, altered disturbance regimes, and climate variability (Dale et al., 2001; Foster et al., 2003; McEwan et al., 2011; Canham, 2020). In upland forests of the Cumberland Plateau in the southeastern USA, long-term monitoring has revealed declining dominance of fire-adapted oaks (*Quercus* spp.) alongside expansion of shade-tolerant mesophytes, including red maple (*Acer rubrum*) (Reid et al., 2008; Evans et al., 2019). This transition threatens long-term persistence of oak-dominated forests and is likely to reshape canopy composition as existing cohorts senesce (Abrams, 1996; Knott et al., 2019).

This regional change is widely attributed to mesophication—the transition from open, fire-maintained forests to closed, mesic systems dominated by shade-tolerant species (Nowacki and Abrams, 2008; Alexander et al., 2021). Several interacting mechanisms contribute to this shift, including roughly a century of fire suppression. Historically, frequent low-intensity fires created the light and soil conditions necessary for oak recruitment (Abrams, 1992; McEwan et al., 2011). Fire exclusion, in contrast, led to stand densification, reduced understory light, and increased mesophyte establishment (Brose et al., 2001;

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McEwan et al., 2011). These processes operate within a self-reinforcing feedback in which fire exclusion enables mesophyte expansion, and denser canopies create cooler, wetter understories with litter characteristics that further suppress fire (Nowacki and Abrams, 2008; Alexander et al., 2021). As a result, mesophyte dominance stabilizes while oak regeneration is inhibited, often resisting reversal through fire reintroduction alone (Arthur et al., 2015; Culbert et al., 2025). Although fire historically structured these forests, emerging evidence suggests that interactions between fire and belowground processes, including soil microbial composition, mycorrhizal dominance, and nutrient cycling, may help shape long-term compositional trajectories in this drought-prone, nutrient-limited landscape (Alexander et al., 2021; Legge et al., 2025).

Oaks (*Quercus* spp.) are among the most ecologically and economically important trees in the eastern United States. They comprise the greatest number of native tree species and the highest biomass of any genus in North America (Cavender-Bares, 2016), and historically made up 40–70% of tree composition across much of the region (Hanberry and Nowacki, 2016). Their ecological importance is reflected in high carbon sequestration (Balaganesh et al., 2022), prolific acorn production supporting wildlife (Van Dersal, 1940), and extensive interactions with insect herbivores and pollinators (Tallamy and Shropshire, 2009; Traylor et al., 2023), while their economic importance makes them among the most valuable hardwoods in the U.S. timber industry (Luppold et al., 2022). As a foundation genus in eastern forests (Hanberry and Nowacki, 2016), oaks also shape fire, hydrologic, and light environments: thick bark and coarse, lignin-rich litter promote flammability and reinforce low-intensity fire regimes (MacMillan, 1988; Kreye et al., 2013; Babl et al., 2020), while open crowns increase throughfall, reduce stemflow and maintain brighter, drier understories (Alexander and Arthur, 2010; Caldwell et al., 2016; Siegert et al., 2019) that help sustain oak–hickory forests.

Although aboveground drivers of mesophication are well established, belowground mechanisms remain less integrated into explanations of long-term compositional change. Fire exclusion alters soil hydrology, organic matter accumulation, nutrient cycling, and microbial community composition, thereby reshaping the balance of mutualists and pathogens in ways that may further inhibit oak recruitment (Alexander et al., 2021; Legge et al., 2025). These changes intensify negative plant–soil feedback (PSF), particularly in shaded, moist environments where shade-intolerant seedlings experience high pathogen pressure (McCarthy-Neumann and Kobe, 2008; McCarthy-Neumann and Ibáñez, 2013; Wood et al., 2023). Reduced carbon availability under low light further increases the burden of maintaining mycorrhizal symbioses, shifting interactions toward parasitism (Ibáñez and McCarthy-Neumann, 2014, 2016; Konvalinková and Jansa, 2016). Conversely, under the historically bright and drier conditions maintained by periodic fire, greater carbon supply supported high mycorrhizal colonization and enhanced disease resistance (Borowicz, 2001; Pozo and Azcón-Aguilar, 2007; Zamioudis and Pieterse, 2012; Laliberté et al., 2015). When light is limited, seedlings may experience the worst-case scenario: elevated pathogen pressure coupled with insufficient carbon to sustain mutualists and defense responses, leading to higher mortality (Wood et al., 2023).

Together, these interactions form a coupled plant–soil–fire feedback that integrates above- and belowground processes (Legge et al., 2025). In this framework, fire exclusion reshapes both community composition and soil function through changes in hydrology, nutrient availability, free-living microbes, and root-associated fungi, including mycorrhizal fungi. Building on this idea, we focus on how canopy compositional change may reinforce mesophication through shifts in mycorrhizal dominance and their consequences for juvenile recruitment. Demographic studies show that maple seedlings establish readily near oaks, whereas oak seedlings rarely persist under maple or cherry canopies (Allen et al., 2018). These asymmetries may reflect contrasting belowground environments associated with arbuscular-mycorrhizal (AM) and ectomycorrhizal (EM) trees. AM seedlings often experience stronger negative density dependence (Brown et al., 2020; Jiang et al., 2020) and negative PSF (Bennett et al., 2017; Refsland et al., 2023; McCarthy-Neumann et al., 2026), such that successful recruitment occurs away from conspecific adults. By contrast, EM trees can create facilitative recruitment "hotspots": EM fungal networks can enhance nutrient and water acquisition (Simard et al., 2012; Liang et al., 2020), EM-associated soils often have lower pathogen pressure (Bennett et al., 2017), and adult EM trees can facilitate survival of both EM and AM juveniles nearby (Mao et al., 2024). In contrast, AM trees may favor heterospecific AM juveniles (Delavaux et al., 2023) but often inhibit EM seedlings (McCarthy-Neumann et al., 2026).

These recruitment dynamics are reinforced by differences in litter and nutrient cycling. AM trees produce rapidly decomposing litter (McClaugherty et al., 1985) that enriches soils with labile nutrients (Lovett et al., 2002), but they also tend to support more pathogen-prone microbial communities and faster pathogen accumulation (Bennett et al., 2017; Chen et al., 2019; Eagar et al., 2023). EM trees, by contrast, produce more recalcitrant litter and rely on mycorrhizal access to organic nutrient pools (Phillips et al., 2013; Lindahl and Tunlid, 2015; Lu and Hedin, 2019), while also promoting EMF colonization and reducing pathogen infection in EM seedlings (Bennett et al., 2017). Collectively, these differences suggest that oak decline may reflect not only altered light and fire regimes, but also recruitment failure associated with a shift from EM- to AM-dominated soils (Alexander et al., 2021; Legge et al., 2025). Recent large-scale work further suggests that fire suppression is associated with declining EM dominance across eastern U.S. forests, supporting the idea that mycorrhizal shifts may be linked to broader changes in disturbance-adapted functional composition (Jo et al., 2019).

Taken together, these patterns imply that mycorrhizal association, fire tolerance, and shade tolerance form a coordinated functional spectrum rather than independent trait axes. Yet the extent to which these traits covary across species, and whether such covariance predicts long-term compositional change, has rarely been quantified. Here, we analyze nearly five decades of demographic data from two upland forest sites on the Cumberland Plateau to quantify changes in biomass, size-class structure, and species composition. Specifically, we assess whether biomass has increased while being redistributed among functional groups, evaluate associations among mycorrhizal type, fire tolerance, and shade tolerance, quantify shifts in size-class distributions across these trait categories, and track changes in frequency, density, aboveground biomass, and importance value. We first predicted that mycorrhizal type would covary with fire tolerance and shade tolerance, and that shade tolerance would differ among fire-tolerance classes. More specifically, we expected EM-associated species to be more fire-tolerant and shade-intolerant, whereas AM-associated species would be more fire-intolerant and shade-tolerant. We then hypothesize that shade-tolerant, fire-intolerant, AM-associated species have increased in dominance over time, while shade-intolerant, fire-tolerant, EM-associated species have declined, with the strongest shifts occurring in regeneration and small size classes rather than in total biomass due to persistence of mature canopy trees.

2. Materials and methods

2.1. Site description

We analyzed long-term demographic data from two forested watersheds on the Cumberland Plateau: Cross Creek (35°4'N, 85°51'W; Franklin State Forest, Marion County, Tennessee, USA) and Camp Branch (35°38'N, 85°18'W; Fall Creek Falls State Park, Bledsoe County, Tennessee, USA; see Appendix Fig. A). Cross Creek covers 36 ha and ranges in elevation from 495 to 574 m (Ramseur and Kelly, 1981), while Camp Branch covers 94 ha and ranges from 518 to 598 m (Kelly, 1979). The region has a temperate continental climate, with evenly distributed annual precipitation averaging 616 mm and a mean annual temperature of 14.5°C (National Oceanic and Atmospheric Administration, 2026). At both sites, dominant soils are sandy alfisols, inceptisols, and ultisols that are nutrient-poor, well-drained, leached, and acidic (pH 4.6–4.8) (Kelly, 1979; Kelly and Beauchamp, 1987). The canopy is dominated by white oak (*Quercus alba*), chestnut oak (*Quercus montana*), black oak (*Quercus velutina*), and hickory (*Carya* spp.), with mid- and understory species including red maple (*Acer rubrum*), tulip tree (*Liriodendron tulipifera*), sassafras (*Sassafras albidum*), and sourwood (*Oxydendrum arboreum*) (Braun, 1950; Ramseur and Kelly, 1981; Mays et al., 1991). Both watersheds were acquired by the state of Tennessee in the mid-1930s following a history of intensive timber cutting and frequent fires; subsequent management emphasized protection and natural regrowth, with no harvests since 1970 and fire suppression in place since 1942 (Cowan, 1970).

2.2. Plot establishment and census

Permanent plots were established as part of a Tennessee Valley Authority (TVA) community study (Ramseur, 1977). At Camp Branch, four 1-ha (100 × 100 m) plots were censused in 1976, with three re-censused in 2016 and all four in 2024. At Cross Creek, four 1-ha plots were censused in 1977 three were re-censused in 1998 and 2005, and all four in 2015 and 2023. Each hectare was subdivided into 100 subplots (10 × 10 m). Within each subplot, all woody stems ≥ 1.4 m tall were identified, measured for stem diameter, and mapped; measurement precision varied among censuses and is described below. For analyses comparing early and recent censuses, diameter data were harmonized to the coarser historical precision where necessary. Hickories (*Carya* spp.) were treated as a single group due to lack of species-level identification in the earliest survey.

2.3. Functional trait classification

We classified all tree species according to three functional trait categories: mycorrhizal association, shade tolerance, and fire tolerance. Species were assigned into their predominant mycorrhizal association—arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (EMF), or ericoid fungi (ErMF) (Phillips et al., 2013; Brundrett and Tedersoo, 2019, 2020)—while recognizing that some taxa may form dual mycorrhizal associations, especially during early seedling stages (Teste et al., 2020). Shade tolerance was assigned following Niinemets and Valladares (2006) and Knott et al. (2019). Niinemets and Valladares (2006) provide continuous tolerance scores ranging from 1 (shade intolerant) to 5 (shade tolerant), which we collapsed into three categories based on both published thresholds and consistency with Knott et al. (2019): *intolerant* (score < 2.5; categories 1–2; typically require >25% full sunlight), *intermediate* (score > 2.5 and < 3.5; category 3; ~10–25% full sunlight), and *tolerant* (score ≥ 3.5; categories 4–5; able to persist at <10% full sunlight). This approach merges "very intolerant" and "intolerant" into a single class, retains *intermediate* as a distinct category, and combines "tolerant" and "very tolerant" into a single class. Fire tolerance was assigned from published sources (Burns and Honkala, 1990; USDA NRCS, 2017; Knott et al., 2019). Species reported as "none" or "low" were combined into an *intolerant* category, those listed as "medium" as *intermediate*, and those described as "high" as *tolerant*. A complete list of species and their assigned functional trait classifications is provided in Appendix Table A. Functional group sizes varied across classifications (Appendix Table B), with AM-associated species representing the largest mycorrhizal group and fire-intolerant species comprising the largest fire-tolerance category.

2.4. Statistical analyses

2.4.1. Trait comparisons

We examined associations among functional traits by treating mycorrhizal type (AM, ErM, EM) and fire tolerance (intolerant, intermediate, tolerant) as ordinal factors, and shade tolerance as a continuous score (1–5). Although shade tolerance was categorized for group-level analyses, we retained continuous values here to capture finer variation among species. To test whether fire tolerance differed among mycorrhizal types, we fit a proportional-odds cumulative link model (logit) with fire tolerance as the ordered response and mycorrhizal type as the predictor. Model fit was evaluated with a likelihood-ratio test against a null model, and the proportional-odds assumption was confirmed. We summarized model coefficients as odds ratios with Wald 95% confidence intervals, using EM-associated species as the reference category. Differences in shade tolerance among mycorrhizal types and among fire-tolerance classes were assessed using Welch's ANOVA and HC3 robust Type II tests with Tukey-adjusted pairwise contrasts.

2.4.2. Size class distribution

To evaluate changes in size structure, individuals were grouped into 5-cm dbh classes beginning with stems ≥ 3 cm DBH. Because stems in the 3–5 cm range were recorded to the nearest 1 cm in the 1970s censuses, but to the nearest 0.1 cm in recent censuses, the first class included stems 3–5 cm in the 1970s and 3.0–5.4 cm in recent censuses. Larger stems were measured to the nearest 0.1 cm across census periods, and all subsequent classes were grouped in 5-cm increments. For each site (Camp Branch: 1976, 2024; Cross Creek: 1977, 2023), adult stem density (stems ha^{-1}) was calculated by size class and plot.

To test differences in size–class distributions among functional trait groups and census years, we modeled log-transformed density [log (Density + 1)] using linear models (*lm*) with size class (continuous), census year, and trait category (shade, fire, or mycorrhizal type) and their interactions as fixed effects. Plot identity was initially included as a random effect in a mixed-effects model but was removed after comparison indicated no improvement in model fit (non-significant variance component). Type III sums of squares were used to assess significance of fixed effects. Model predictions are presented on the log scale with 95% confidence intervals, and differences among groups were evaluated through pairwise slope comparisons of Size Class × Trait interactions across years.

2.4.3. Community composition metrics

To quantify temporal changes in community composition and dominance, we calculated four responses for each species in each 1-ha plot and census year: frequency (percentage of 10 × 10 m subplots with adult presence), stem density (stems ha^{-1}), aboveground biomass (AGB, Mg ha^{-1}), and importance value (IV,%). AGB was estimated using national-scale allometric equations from Chojnacky et al. (2014), which classify woody plants by wood density and growth rate. For species not assigned to a specific taxonomic group, we applied the mixed hardwood equations of Jenkins et al. (2003). Biomass values from these equations are expressed in kilograms per individual and were aggregated to the stand level as megagrams per hectare (Mg ha^{-1}). IV was calculated as the average of relative frequency, relative density, and relative AGB, multiplied by 100. Species-level values were then aggregated by functional trait categories (mycorrhizal association, shade tolerance, or fire tolerance). We also summarized current stems 1–2.9 cm DBH as a small-diameter stem layer. Because comparable data were not available from the initial census, these stems were analyzed separately using only current frequency and density by functional trait category and were not included in temporal change analyses.

We calculated cumulative plot-level responses (i.e., the sum across species within a trait category per plot) to quantify the net effect on community composition. Trait categories were compared using general linear models with HC3 robust standard errors. Estimated marginal means and pairwise contrasts were obtained using *emmeans*, with Tukey adjustment for multiple comparisons. Results are presented as mean (±95% CI) changes in frequency, density, AGB, or IV between the initial and most recent censuses, summarized by trait categories.

Species-level changes in frequency, density, AGB, and IV were analyzed using mixed-effects models with Site and Plot as candidate random effects. Random structures were simplified by likelihood-ratio tests, and when retained, F- and p-values were based on Satterthwaite's approximation. Estimated marginal means were tested against zero with Holm-adjusted p-values to identify significant increases or decreases. All statistical analyses were conducted in R v4.5.1 (R Core Team, 2025).

3. Results

Fire-tolerance categories varied by mycorrhizal type (LR $\chi^2(2) = 10.40$, $p = 0.006$). Relative to EM taxa, AM species had ~11.8 × higher odds of being classified as less fire-tolerant, whereas ErM did not differ from EM (Fig. 1). In contrast, shade tolerance did not vary by mycorrhizal association (Welch $F_2 = 0.27$, $p = 0.77$; Fig. 2A). Shade tolerance was, however, associated with fire tolerance (Welch $F_2 = 7.25$, $p = 0.004$; Fig. 2B), with fire-intolerant species exhibiting greater shade-tolerance scores than fire-tolerant species (MD = 1.14 on a 1–5 point scale, $t_{38} = 3.12$, $p = 0.01$).

Size–class distributions varied among mycorrhizal types across census years, as indicated by a significant Myco × Year × Size Class interactions, $F_{2,804} = 46.07$, $p < 0.0001$; Fig. 3A; Appendix Table C). In 1977, EM species had the highest densities across the full-size range, whereas by 2023 AM species dominated small size classes, and differences among mycorrhizal types diminished at larger classes. Slopes also differed among mycorrhizal types within years, except AM vs. ErM in 1977. At the community level, cumulative changes in IV, relative frequency, relative density, and relative AGB differed by mycorrhizal type (Fig. 4; Appendix Table D). AM (+15.7%) and ErM (+4.4%) taxa gained IV while EM declined (–19.3%), with all three mycorrhizal types differing significantly from one another, indicating a clear redistribution of community dominance from EM toward AM and, to a lesser extent, ErM taxa (Fig. 4A). These IV shifts were driven largely by frequency and density. AM (+15.7%) and ErM (+4.4%) increased in frequency, while EM declined (–19.3%; Fig. 4B); only EM showed a density loss (–621 stems ha^{-1}; Fig. 4C). All groups gained biomass, though EM exhibited the largest absolute increase (+32.8 Mg ha^{-1}), followed by AM (+19.0 Mg ha^{-1}) and ErM (+10.0 Mg ha^{-1}; Fig. 4D). Thus, EM declines in IV reflected widespread frequency and density losses despite biomass accumulation, whereas AM and ErM gained IV through broader frequency and stable densities.

Size–class distributions also differed by fire tolerance (Fire × Year × Size Class, $F_{2,804} = 32.26$, $p < 0.0001$; Fig. 3B; Appendix Table E). In 1977, tolerant species had the highest densities across all size classes, but by 2023 they declined sharply in small stems and remained dominant only among large trees, whereas intolerant species increased in small stems. Slopes differed among all categories except intolerant vs. intermediate in 1977 and in 2023 tolerant vs. intermediate species were only marginally different. IV declined in tolerant species (–16.5%) but increased in intolerant taxa (+12.2%), differing from tolerant and intermediate groups (Fig. 5A; Appendix Table F). Frequency and density both declined in tolerant species (–16.3%, –537 stems ha^{-1}), whereas intolerant taxa increased in frequency (16.7%) but not density (Fig. 5B-C; Appendix Table F). In contrast, biomass rose across all fire classes—greatest in tolerant species (+33.4 Mg ha^{-1}), followed by intolerant (+21.0 Mg ha^{-1}) and intermediate taxa (+7.5 Mg ha^{-1}); however, biomass did not differ among the fire tolerance categories (Fig. 5D; Appendix Table F). Collectively, tolerant species lost frequency and density dominance even as biomass continued to accrue, reflecting growth of surviving large stems rather than recruitment of new individuals.

Shade tolerance exhibited a similar pattern (Shade × Year × Size Class, $F_{2,804} = 26.08$, $p < 0.0001$; Fig. 3C; Appendix Table G). Between 1977 and 2023, shade-tolerant species increased strongly in small stems and now dominate regeneration, while intermediate and intolerant species declined. IV increased in tolerant species (+10.7%) but declined in intermediate (–8.7%) and intolerant (–5.0%) taxa, with tolerant species higher than both (Fig. 6A; Appendix Table F). Frequency increased among tolerant species (+12.6%) while declining in the other groups (–6.3%, –5.6%; Fig. 6B; Appendix Table H), and density decreased in intermediate (–493 stems ha^{-1}) and intolerant (–216 stems ha^{-1}) taxa but remained stable among tolerant species (Fig. 6C; Appendix Table H). All shade classes gained biomass, though intermediate taxa showed the largest increase (+47.9 Mg ha^{-1}), exceeding both tolerant and intolerant species (Fig. 6D; Appendix Table H). Overall, tolerant species gained IV through expanded plot frequency, whereas intermediate and intolerant taxa lost IV due to density declines despite continued biomass accumulation.

In the current 1–2.9 cm DBH small-diameter stem layer, AM species occurred in 60.4% of plots, significantly more than ErM (29.4%) and EM species (10.2%; all $p \leq 0.002$; Appendix Fig. Ba). AM species also had higher density than EM species (1020 vs. 99 stems ha^{-1}; $p = 0.0002$; Appendix Fig. Bb), with no other density comparisons significant. Fire-intolerant species were more frequent than intermediate and tolerant species (+32.9% and +56.8%, respectively; both $p < 0.0001$; Appendix Fig. Bc) and had higher density than fire-tolerant species (+1110 stems ha^{-1}; $p < 0.0001$; Appendix Fig. Bd). Shade-tolerant species were more frequent than intermediate and intolerant species (45.4% vs. 23.6% and 30.7%, respectively; $p \leq 0.03$; Appendix Fig. Be), though density did not differ among shade-tolerance groups (Appendix Fig. Bf).

At the species level, models confirmed strong heterogeneity in IV trajectories (overall $F_{43,224} = 4.60$, $p < 0.0001$; Fig. 7A; Appendix Table I). In terms of total IV change, *A. rubrum*, *Nyssa sylvatica*, and *L. tulipifera* showed increases, while declines were strongest in *Q. alba*, *Cornus florida*, *Q. velutina*, *Carya*, and *Q. stellata*. Frequency changes mirrored these patterns (overall $F_{43,224} = 8.78$, $p < 0.0001$; Fig. 7B; Appendix Table J). *A. rubrum*, *N. sylvatica*, *L. tulipifera*, *O. arboreum*, and *Ilex opaca* all increased in frequency, whereas *C. florida*, *Q. velutina*, *Q. falcata*, *Carya*, *Q. stellata*, and *Q. coccinea*. Species-level differences in stem density were also detected ($F_{43,163.7} = 2.69$, $p < 0.0001$; Fig. 7C; Appendix Table K), although site-level variation was small ($\sigma^2_{site} = 35.5$). *Kalmia latifolia* increased in density, while *Q. alba*, *C. florida*, and *Q. velutina*, all declined sharply. Changes in AGB, by contrast, were overwhelmingly positive (overall $F_{43,218.4} = 3.76$, $p < 0.0001$; Fig. 7D; Appendix Table L), with little variation attributable to site ($\sigma^2_{site} = 2.1$). Gains occurred in *Q. alba*, *Q. montana*, and *A. rubrum*. Collectively, these species-level responses reveal compositional reorganization dominated by *A. rubrum*, *N. sylvatica*, and *L. tulipifera* expansion and concurrent losses in multiple *Quercus* and *Carya* species along with

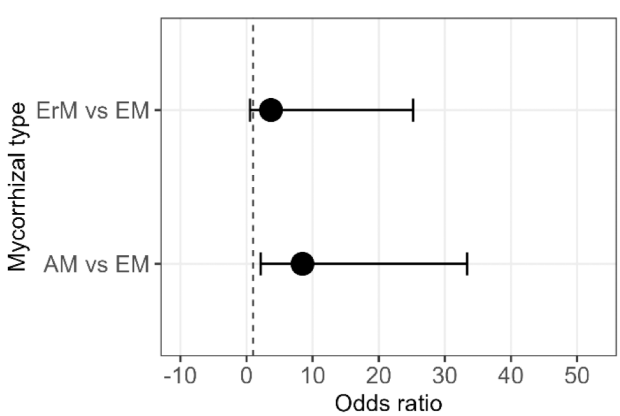

Fig. 1. Differences in fire tolerance among mycorrhizal types of tree species on the Cumberland Plateau. Points show odds ratios from a proportional-odds model comparing fire-tolerance category relative to ectomycorrhizal (EM) species. Values greater than 1 indicate higher odds of belonging to less fire-tolerant categories than EM species. Error bars show 95% confidence intervals; intervals not overlapping 1 denote significant differences.

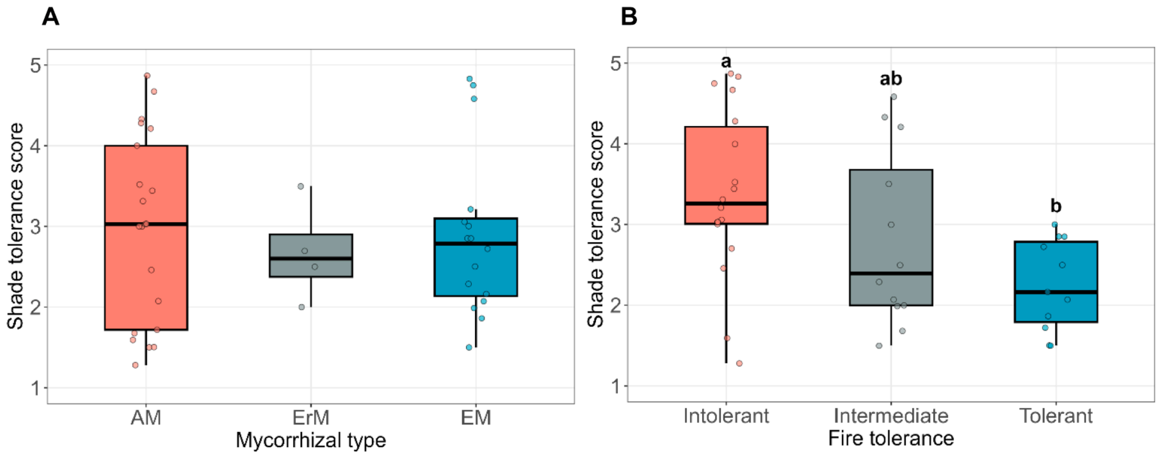

Fig. 2. Relationships between shade tolerance and (A) mycorrhizal type and (B) fire tolerance of tree species on the Cumberland Plateau. Shade tolerance scores range from 1 to 5, with higher values indicating greater shade tolerance. Different letters denote significant differences among groups (Tukey HSD, $p < 0.05$).

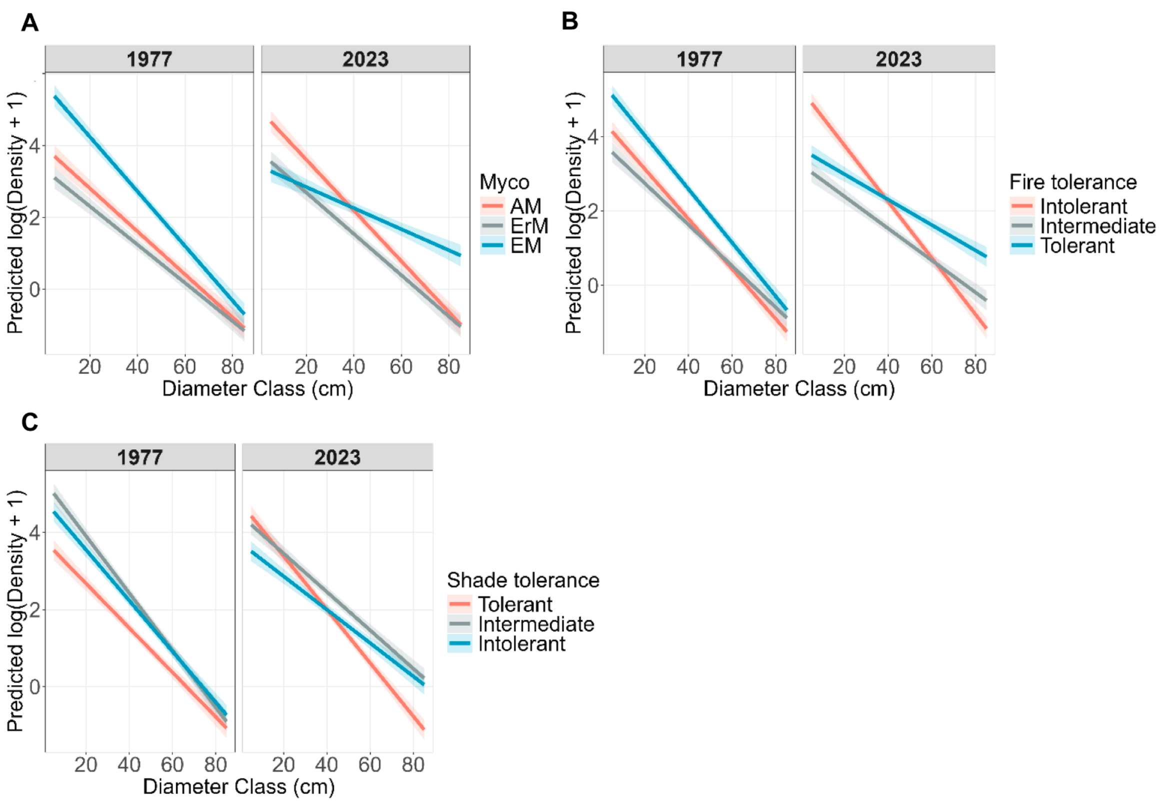

Fig. 3. Predicted changes in stem density across diameter classes (20–80 cm dbh) by (A) mycorrhizal association, (B) fire-tolerance class, and (C) shade-tolerance class in 1977 and 2023. Lines represent predicted values of log-transformed stem density (stems ha^{-1}) from mixed-effects models; shaded ribbons denote 95% confidence intervals. Non-overlapping intervals indicate significant differences among groups within each census year.

C. florida—consistent with community-level declines in EM-associated taxa, fire-tolerant and intermediate shade-tolerant groups.

4. Discussion

Our long-term resurvey of upland oak–hickory forests reveals substantial functional reorganization in tree community composition over nearly five decades, including a pronounced shift in mycorrhizal dominance. Across size classes, AM- and ErM-associated species increased in importance value, while EM-associated species declined sharply, with the largest percent decrease among functional groups. These changes align with trait associations observed in our dataset: fire tolerance was associated with both mycorrhizal type and shade tolerance. AM species had higher odds of being classified as less fire-tolerant than EM species, and fire-intolerant species had greater shade-tolerance scores than fire-tolerant species. In contrast, mycorrhizal type and shade tolerance were not significantly correlated. Suggesting that fire tolerance may be the more direct functional axis linking mycorrhizal gradients to community reorganization.

Consistent with declining EM dominance, fire-tolerant species declined while fire-intolerant taxa increased, indicating that functional change is tightly linked to disturbance-adapted traits. Shade-tolerant species increased and intermediately tolerant species declined, while shade-intolerant species showed little change, suggesting weaker effects

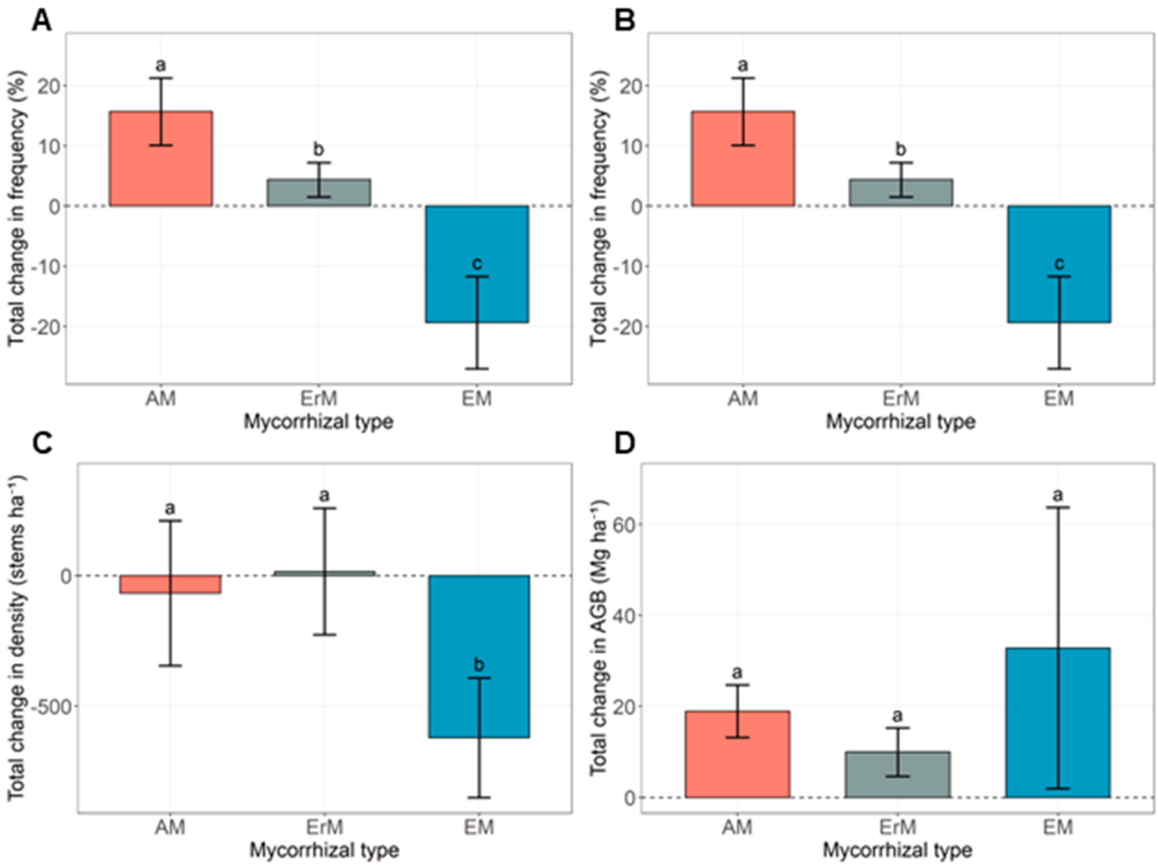

Fig. 4. Cumulative plot-level changes in community composition by mycorrhizal association. Panels show total changes (mean ± 95% CI) in (A) importance value (IV,%), (B) frequency (%), (C) stem density (stems ha^{-1}), and (D) aboveground biomass (AGB, Mg ha^{-1}) between 1977 and 2023. Cumulative responses were calculated as the sum of species-level changes within each mycorrhizal type per plot. Within a mycorrhizal type, means whose 95% CIs do not overlap zero indicate significant temporal change; different letters denote significant differences among mycorrhizal types (Tukey HSD, $p < 0.05$).

along the shade-tolerance axis. The decline in intermediate shade–tolerant species may reflect a contraction of suitable light environments as forest canopies often densify under mesophication (Hanberry et al., 2020), reducing moderate-light conditions where intermediate species are competitive and shifting conditions toward shade-tolerant taxa (Canham et al., 1994). Together, these patterns are consistent with mesophication trajectories reported across eastern North American forests (Knott et al., 2019; Alexander et al., 2021), while also identifying a parallel shift in which AM-associated species increased as EM-associated species declined.

These results further align with emerging mycorrhizal–fire feedback frameworks that describe reciprocal interactions among mycorrhizal strategies, fuel characteristics, and disturbance regimes (Legge et al., 2025). Previous work in Cumberland Plateau uplands showed that canopy composition can remain relatively stable because long-lived canopy trees persist and many species retain vegetative regeneration via basal sprouting and root suckering (Evans et al., 2019). This apparent stability can mask substantial change in regeneration and functional composition until recruitment failure is expressed in the canopy. Thus, aboveground inertia reflects continued dominance of large EM canopy trees even as recruitment and replacement decline in smaller size classes. Here, declining EM-associated recruitment coupled with increased AM dominance suggests that mycorrhizal shifts may reinforce mesophication even where canopy turnover remains slow.

4.1. Demographic bottlenecks and regeneration failure

Demographic patterns across functional groups support a structural reorganization driven in part by regeneration failure among EM-associated, fire-tolerant taxa. The steepest declines in these groups occurred in smaller adult size classes (< 20 cm DBH) despite persistence in the canopy, indicating a regeneration bottleneck in which established cohorts remain while replacement fails (Arthur et al., 2012). In contrast, AM- and ErM-associated species gained importance value primarily through increases in frequency and stable or increasing densities, reflecting successful recruitment and spread across plots. Although comparable historical data were unavailable for stems 1–2.9 cm DBH, the current small-diameter stem layer was also dominated by AM-associated and fire-intolerant taxa, while EM-associated and fire-tolerant species were poorly represented. This contemporary pattern supports the interpretation that long-term declines in EM and fire-tolerant species reflect weak replacement in the smallest measured stems, not simply losses from larger adult size classes.

Species-level analyses reinforced these demographic shifts, with significant increases in *A. rubrum*, *N. sylvatica*, and *L. tulipifera* and declines in multiple *Quercus* and *Carya* species—trends documented across the Eastern U.S. (Fei et al., 2011; Knott et al., 2019; Woodbridge et al., 2022). While these increases are consistent with mesophication, the growing dominance of *A. rubrum* and *N. sylvatica* may also reflect the success of broadly tolerant, AM-associated generalists rather than only the expansion of strictly mesic-site specialists. Despite declining recruitment, EM canopy adults continue to dominate biomass, generating demographic inertia that masks regeneration failure and maintains present-day forest structure. Long-lived EM species such as oaks can persist for centuries under unfavorable conditions, delaying visible canopy decline even as replacement fails (Oldfield et al., 2021; Radcliffe et al., 2021). This persistence maintains seed production and a seedling bank that could respond if disturbance or environmental conditions shift

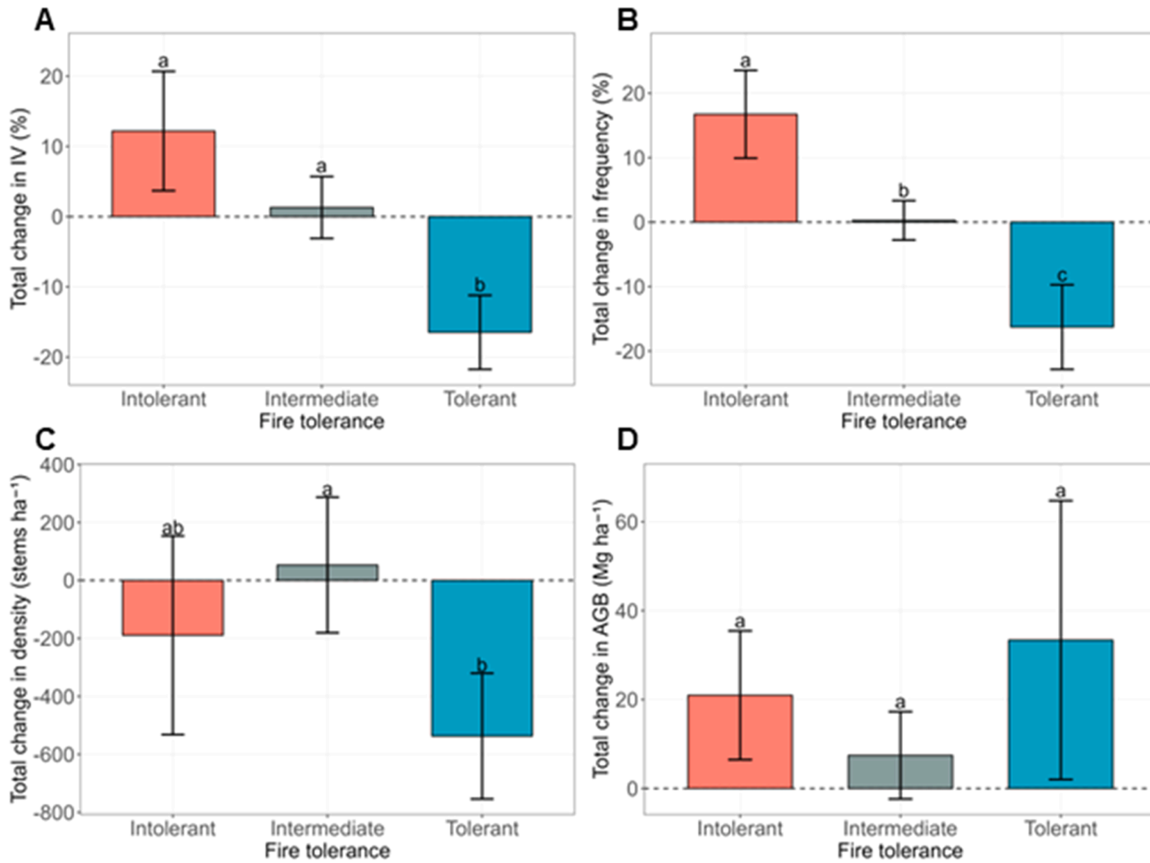

Fig. 5. Cumulative plot-level changes in community composition by fire tolerance group. Panels show total changes (mean ± 95% CI) in (A) importance value (IV, %), (B) frequency (%), (C) stem density (stems ha^{-1}), and (D) aboveground biomass (AGB, Mg ha^{-1}) between 1977 and 2023. Cumulative responses were calculated as the sum of species-level changes within each fire tolerance group per plot. Within a fire tolerance group, means whose 95% CIs do not overlap zero indicate significant temporal change; different letters denote significant differences among fire tolerance groups (Tukey HSD, $p < 0.05$).

(Warner and Chesson, 1985; Larsen and Johnson, 1998; Johnson et al., 2009; Vickers et al., 2023). At the same time, mesophication may also alter adult performance or reproductive output, although direct evidence for such fitness effects in mature *Quercus* and *Carya* trees remains limited. Yet, underlying demographic trends signal a long-term transition away from EM and fire-tolerant dominance toward AM and shade-tolerant assemblages.

4.2. Study limitations and inference scope

At the species level, our significance tests likely underestimate the number of taxa experiencing meaningful change. Because replication occurred at the plot level, species absent from some plots were assigned zero change, which reduces mean responses and can mask strong site-level losses. As a result, the relatively small number of species showing statistically significant trends should not be interpreted as demographic stability, but rather as a conservative outcome imposed by our sampling design and analytical framework. Importantly, the functional-group patterns we document—declines in EM and fire-tolerant taxa and increases in AM-associated mesophytes—remain robust to these constraints and are consistent with long-term regional trends.

4.3. Biomass inertia and structural instability

Despite pronounced composition reorganization, aboveground biomass increased across trait and species groups, consistent with studies showing that mature forests can maintain or increase biomass accumulation over time (Johnson and Abrams, 2009; Stephenson et al., 2014; Pontius et al., 2016). At our site, continued biomass accumulation likely reflects growth of persistent canopy adults rather than successful regeneration, such that structurally unstable forests may still appear productive. Compositional shifts toward fast-growing mesophytes may further sustain aboveground biomass, albeit within a functionally distinct forest type (Knott et al., 2019; Schedlbauer and Polohovich, 2020; Zenoble, 2021). Thus, increased biomass does not necessarily indicate ecosystem recovery; rather, it can mask declining regeneration, reduced structural heterogeneity, and weaker resilience to future disturbance.

The functional implications of this pattern may be substantial. As forests shift toward mesophytic, AM-dominated assemblages, nutrient cycling may accelerate because AM-associated trees typically produce more rapidly decomposing litter and rely more heavily on inorganic nutrient pools, whereas EM-associated trees are linked to slower organic nutrient cycling (Phillips et al., 2013). Faster nutrient turnover may help sustain aboveground productivity in the short term, but it may also alter belowground carbon retention and long-term storage stability (Brzostek et al., 2014; Benson et al., 2025). Thus, even where aboveground biomass increased, shifts toward AM dominance may change the distribution and persistence of forest carbon storage.

4.4. Belowground feedbacks and interacting disturbances

More broadly, our results address a gap in mesophication research in which belowground drivers have often been discussed conceptually but remain less well integrated into explanations of long-term compositional change. The ecosystem-level consequences of these shifts include accelerated nutrient turnover, destabilization of soil carbon pools, and

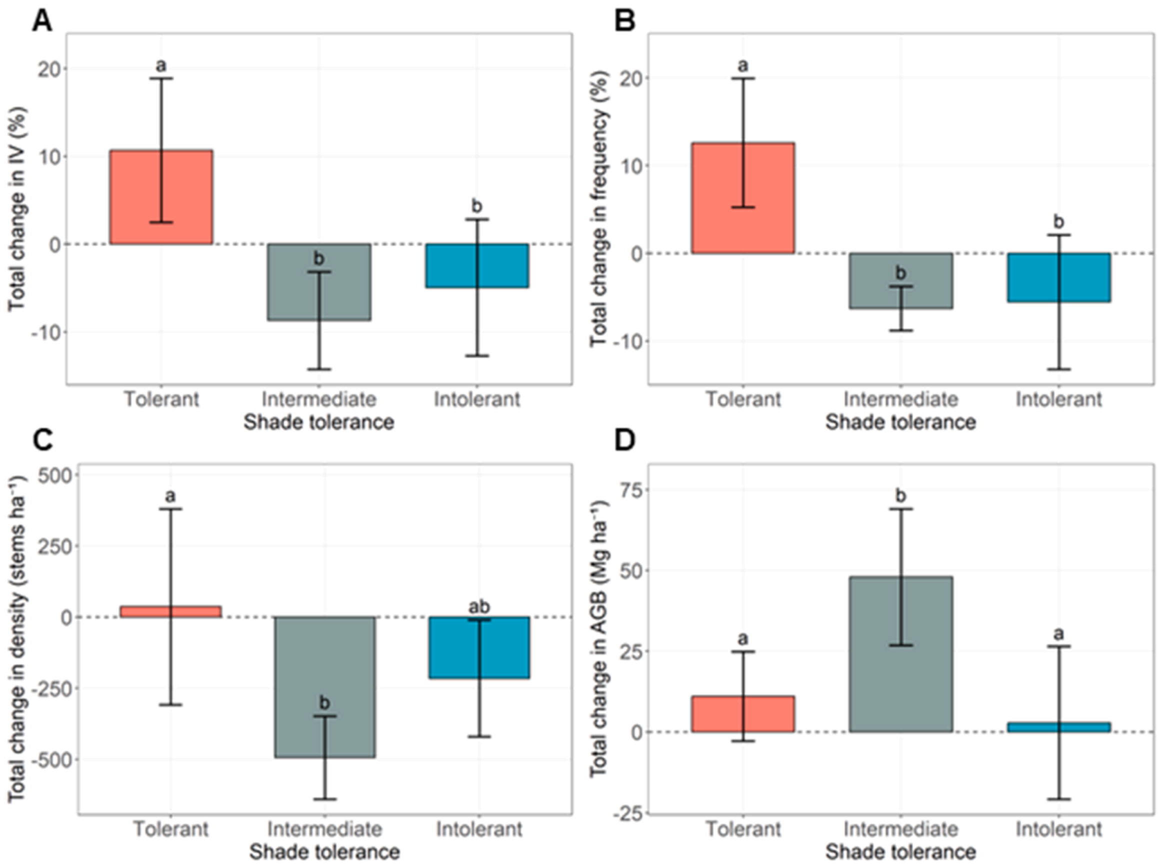

Fig. 6. Cumulative plot-level changes in community composition by shade tolerance group. Panels show total changes (mean ± 95% CI) in (A) importance value (IV, %), (B) frequency (%), (C) stem density (stems ha^{-1}), and (D) aboveground biomass (AGB, Mg ha^{-1}) between 1977 and 2023. Cumulative responses were calculated as the sum of species-level changes within each shade tolerance group per plot. Within a shade tolerance group, means whose 95% CIs do not overlap zero indicate significant temporal change; different letters denote significant differences among shade tolerance groups (Tukey HSD, $p < 0.05$).

restructuring of plant–microbe interactions. In the absence of fire, soil fertility and inorganic nitrogen can increase (Agbeshie et al., 2022), potentially contributing to AM tree dominance (Jo et al., 2019), because EM fungi are generally more efficient at acquiring nitrogen bound in organic matter than excess inorganic nitrogen (Brzostek et al., 2014; Cheeke et al., 2017; Jörgensen et al., 2025). AM trees may reinforce these conditions through low C:N, rapidly decomposing litter that elevates soil nitrogen availability (Phillips et al., 2013). Increasing importance of ErM-associated shrubs may further modify belowground processes by altering saprotrophic fungal communities (Polussa et al., 2024). Mycorrhizal type is also a major determinant of PSF directionality, with AM species predominantly experiencing negative PSF and EM species positive PSF (Bennett et al., 2017; Refsland et al., 2023), reflecting contrasting microbial interactions and nutrient cycling strategies (Eagar et al., 2024). Under increasing AM tree dominance, negative PSF may intensify through mycorrhizal spillover, as dominant mycorrhizal type alter soil biogeochemistry and microbial communities in ways that elevate pathogen loads and suppress EM seedling survival (Eagar et al., 2024). As AM trees increasingly dominate, EM seedlings may encounter reduced access to EM mutualists (Cortese and Horton, 2024) and increased pathogen pressure (Chen et al., 2019; Eagar et al., 2022, 2023), further inhibiting regeneration (McCarthy-Neumann, 2026). These interpretations are consistent with previously documented neighborhood asymmetries in which maple seedlings establish readily near oaks, whereas oak seedlings rarely persist beneath maple or cherry canopies (Allen et al., 2018), suggesting that AM- versus EM-dominated neighborhood conditions may help drive the recruitment patterns observed here.

These mechanisms align with our observed demographic patterns—declining EM recruitment concurrent with increasing AM juvenile dominance—and suggest feedbacks that may help reinforce mesophication. EM trees can facilitate nearby AM and EM juveniles through mycorrhizal networks that provide nutrient access and reduced pathogen pressure, generating coexistence “hotspots” (Mao et al., 2024), but these refugia may shrink as EM adults decline. Other biotic stressors, including regional decline of the AM-associated *C. florida* following pathogen introduction (Hiers and Evans, 1997) and expansion of ericoid *Kalmia latifolia* thickets that suppress hardwood regeneration (Schutte et al., in review), may further compound mesophication effects.

4.5. Management implications

The combined effects of biomass inertia, demographic bottlenecks, and feedback-mediated suppression of EM regeneration indicate that effective restoration of upland oak forests under mesophication will likely require approaches that address both above- and belowground constraints. Our results suggest that reliance on any single intervention, such as prescribed fire or silvicultural disturbance alone, may be insufficient once flammability has declined and microbial communities have reorganized (Arthur et al., 2015; Culbert et al., 2025), particularly where pathogen–mutualist dynamics constrain oak recruitment (McCarthy-Neumann et al., 2026). Instead, effective strategies may need to combine canopy gap creation (Tinya et al., 2025), reduction of AM-associated mesophytes (Rademacher et al., 2025), mitigation of deer browse (Horsley et al., 2003; Miller et al., 2023), restoration of fuel structure (Hutchinson et al., 2024), and protection of EM mycorrhizal networks (Bermúdez-Contreras et al., 2022). This interpretation is consistent with evidence that long-term fire exclusion can reduce fire

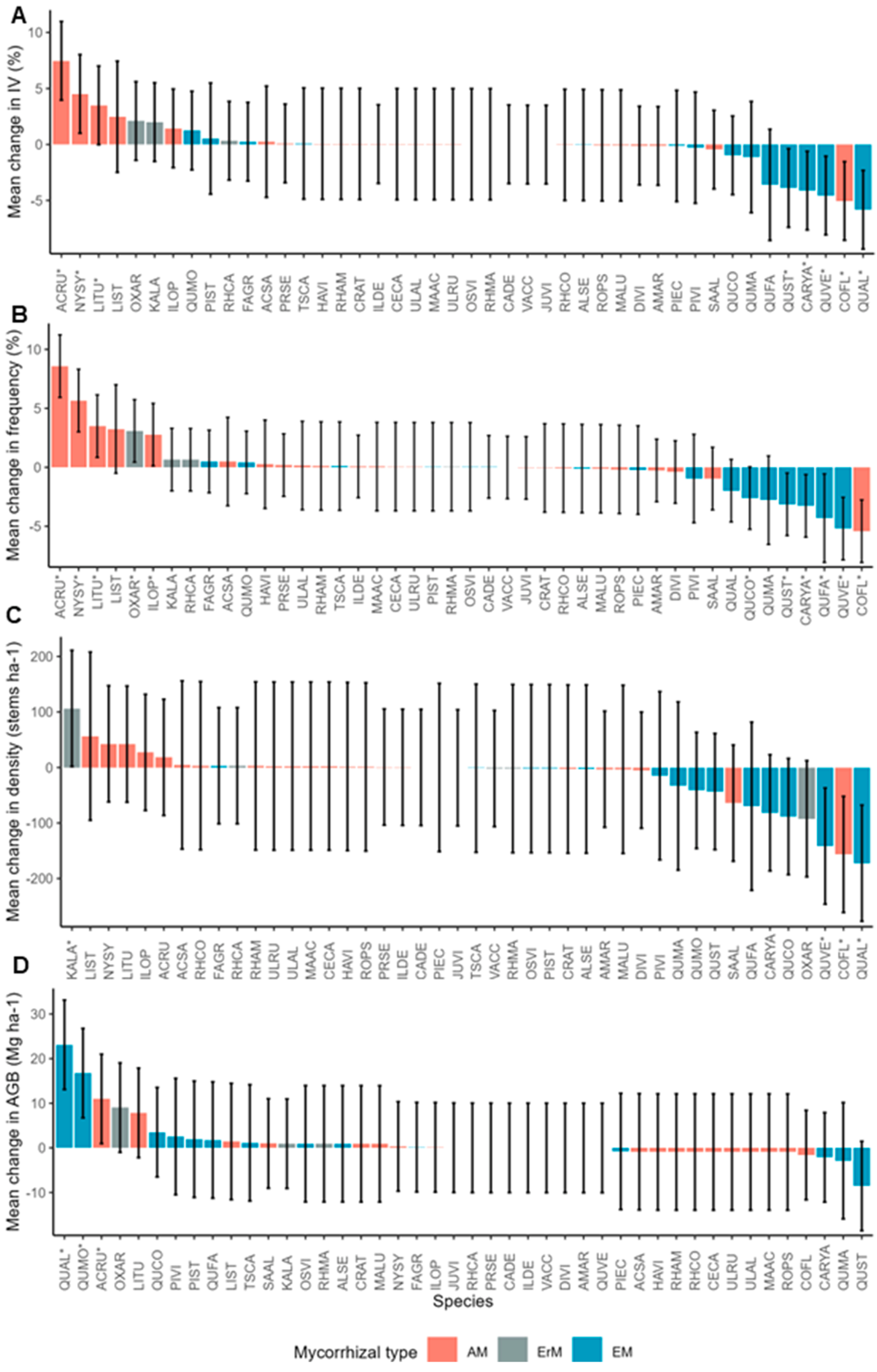

Fig. 7. Species-level changes in (A) importance value (IV,%), (B) frequency (%), (C) stem density (stems ha^{-1}), and (D) aboveground biomass (AGB, Mg ha^{-1}) between 1977 and 2023. Bars show estimated mean change (±95% CI) from mixed-effects models with species as fixed effects and Site/Plot as random effects where supported. Bar colors indicate mycorrhizal association (AM-, ErM-, or EM-associated species). Species codes correspond to full species names in Appendix Table A. Asterisks indicate species with significant differences from zero after Holm-adjusted $p < 0.05$.

resistance in historically EM-dominated forests by promoting deep organic horizons and fine-root accumulation, increasing vulnerability to belowground heating during subsequent burns (Carpenter et al., 2021). In addition, clear-cutting can favor AM-associated competitors (Elliott et al., 2019) by disrupting canopy carbon inputs, soil microclimate, and EM mycorrhizal networks (Simard et al., 2012; Cortese and Horton, 2024), while also benefiting strongly sprouting mesophytic species such as red maple (Nieves et al., 2022). At the same time, persistence of large EM canopy individuals (Evans et al., 2019; Oldfield et al., 2021; Radcliffe et al., 2021) suggests that natural gap dynamics may still create intermittent recruitment windows for oaks (Larsen and Johnson, 1998; Johnson and Abrams, 2009; Vickers et al., 2023), although their frequency and duration remain uncertain. More broadly, some upland oak forests may be approaching more stable AM-associated mesophytic state with faster nutrient turnover (Nowacki and Abrams, 2008; Alexander et al., 2021). Management may therefore be most effective when it targets reinforcing feedbacks that stabilize these forests, rather than focusing solely on restoring historical species composition.

5. Conclusions

Together, our results demonstrate that upland oak–hickory forests on the Cumberland Plateau are undergoing a profound functional transition driven by shifts in mycorrhizal dominance, fire-related traits, and regeneration dynamics rather than changes in productivity or biomass alone. By centering mycorrhizal associations as a key functional axis, this study underscores the critical role of belowground processes in shaping forest trajectories and highlights how plant–soil–fire feedbacks may help reinforce mesophication. The integration of nearly 5 decades of demographic data with functional trait and mycorrhizal perspectives provides novel evidence that mesophication may be maintained by interacting above- and belowground feedbacks that increasingly constrain EM regeneration and favor AM dominance. Understanding how these coupled feedbacks determine forest persistence, transformation, and resilience will be central to sustaining ecosystem function and guiding restoration in a rapidly changing climate.

Author contributions

Sarah McCarthy-Neumann and Jon Evans conceived and designed the study. All authors contributed to fieldwork, material preparation, and data collection. Sarah McCarthy-Neumann conducted statistical analyses and led manuscript writing, with all authors contributing to revisions. All authors read and approved of the final manuscript. Funding was secured by Sarah McCarthy-Neumann and Jon Evans.

CRediT authorship contribution statement

Jon Evans: Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Robert Phillips:** Writing – review & editing, Visualization, Investigation. **J.T. Michel:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Sarah McCarthy-Neumann:** Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Maria I. Schutte:** Writing – review & editing, Supervision, Methodology, Investigation, Data curation.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123960.

Data availability

Data upon which this study is based are available through the Dryad Digital Repository https://doi.org/10.5061/dryad.2ngf1vj3z (McCarthy-Neumann et al., 2026).

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