CONSIDERING FOREST CHANGE IN EASTERN NORTH AMERICA FROM PERSPECTIVES OF FIRE, BIOGEOCHEMISTRY, AND ECOSYSTEM RESILIENCE

by

MELANIE KAY TAYLOR

(Under the Direction of NINA WURZBURGER)

ABSTRACT

Temperate forests of eastern North America have been transformed by centuries of disturbance. Before European Colonization, these oak- (*Quercus* spp.) and pine-dominated (*Pinus* spp.) forests were maintained by recurring fires, which have declined as forests recovered from clearing and logging. Today, forests are transitioning from oak dominance to increasing dominance by mesophytic species due to long-term fire exclusion—a hypothesized process termed “mesophication.” However, alternative explanations exist, and these focus on biogeochemical mechanisms. For instance, elevated atmospheric nitrogen deposition has been implicated in the increasing dominance of arbuscular mycorrhizal (AM) trees over ectomycorrhizal (ECM) trees. Additionally, exotic earthworm introductions appear to favor tree species that produce nutrient-rich, palatable litter over those that do not. As these hypotheses have been investigated independently, it is unclear whether fire exclusion and biogeochemical processes contribute to the same species transition. Further, it is unclear how the return of fire, either wildfire or prescribed, affects these forests under transition. Here, I sought to fill these knowledge gaps. First, I characterized wildfire effects, after a century of fire exclusion, on soil fauna communities and litter decomposition in a southern Appalachian forest undergoing mesophication. I found that wildfire altered fauna communities in litter, but not soil, and sped litter decomposition, and that detritivores were more abundant in mesophytic and AM-dominated forests. Second, I considered how forest change in the eastern United States might be due to both fire exclusion and biogeochemical changes. I found relationships between fire-adaptations and nutrient conservation across tree species and across forests of the region. I proposed a framework that expands the mesophication hypothesis to consider soil biogeochemical processes, which together reinforce forest change and resist a return to the former state. Third, I analyzed data from a 20-year, forest management experiment in the southern Appalachians in which three strategies were compared to untreated controls, to determine which may return forests to oak dominance. I found that basal area reduction through combined mechanical felling and repeated prescribed fires increased sapling-stage oak abundance. Together, this work integrates multiple frameworks of forest change towards the ultimate goal of understanding how to best manage these ecosystems.

INDEX WORDS: alternative stable states, biogeochemistry, ecosystem state change, fire exclusion, forest management, invasive earthworms, mechanical felling, mesophication, mycorrhizal fungi, prescribed fire, wildfire

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by

MELANIE KAY TAYLOR

BS, Concord University, 2012

MS, University of Georgia, 2015

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MELANIE KAY TAYLOR

Major Professor:	Nina Wurzburger
Committee:	Mac A. Callaham Jr. Ricardo Holdo Joseph J. O'Brien Kai Zhu

Electronic Version Approved:

Ron Walcott
Vice Provost for Graduate Education and Dean of the Graduate School
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TABLE OF CONTENTS

Page

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Temperate forests of eastern North America (eastern forests) have undergone considerable change over the last few centuries. Prior to European Colonization, recurring fires maintained most forests as vast, partly-open canopies of fire-adapted trees, with fire-sensitive species largely restricted to moist coves and riparian landscapes where fires were unable to spread (McEwan et al., 2007; Brose et al., 2014; Lafon et al., 2017; Hutchinson et al., 2019; Marschall et al., 2019; Stambaugh et al., 2020). Fire exclusion during the last century, has been posited as a trigger of forest change, as fire-sensitive species have increased in abundance while fire-adapted species have declined (Nowacki and Abrams, 2008; Hanberry et al., 2020). However, other post-Colonial human disturbances have also been implicated (Averill et al., 2018; Frelich et al., 2019), making it unclear which mechanisms are responsible for changing the composition of eastern forests. Understanding the drivers of this ongoing forest transition is imperative for determining if these alterations can be halted or reversed.

Eastern forests have an extensive history of human disturbance. Before the large-scale arrival of Europeans, forests were mostly dominated by oaks (*Quercus* spp.), mixed with pines (*Pinus* spp.), hickories (*Carya* spp.), and American chestnut (*Castanea dentata* (Marshall) Borkh.; Hanberry and Nowacki, 2016; Abrams and Nowacki, 2019). These forests were maintained through the influence of recurring fires, which were largely aided by Native peoples and early Euro-American settlers (Lafon et al., 2017; Stambaugh et al., 2018; Abrams and Nowacki, 2019; Stambaugh et al., 2020; Abrams et al., 2021). Since European Colonization, much of forested land was cleared for agriculture and nearly all forests were logged extensively, which may have contributed to changes in forest composition (Ayres and Ashe, 1905; Dyer, 2006; Thompson et al., 2023; Wurzburger et al., 2023). Invasive species introductions have further altered eastern forests. In the early 20th century, the regionally abundant American chestnut was functionally lost due to blight caused by invasive fungi (Ellison et al., 2005; Elliott and Swank, 2008). Exotic earthworm introductions, first from Europe, then from Asia, have altered forest floors, soil biogeochemistry, and plant communities (Craven et al., 2017; Ferlian et al., 2020; Mathieu et al., 2024). Further, climate change and elevated rates of atmospheric nitrogen (N) deposition in the region have resulted in altered communities of tree species (Thomas et al., 2010; Simkin et al., 2016; Fei et al., 2017; Knott et al., 2020). As a result of these disturbances, eastern forests today are different than they were a few centuries ago.

The widespread decline of oaks, pines, and hickories and increasing abundance of mesophytic species like maples (*Acer* spp.) have the potential to negatively impact ecosystem services, raising interest in the mechanisms behind this forest transition (Fei and Steiner, 2007; Fei et al., 2011; McShea et al., 2007; Caldwell et al., 2016; Jo et al., 2019; Knott et al., 2019; Zarri et al., 2020). The mesophication hypothesis posits that fire exclusion has led to the encroachment of fire-sensitive species and ecosystems that increasingly resist fire (Nowacki and Abrams, 2008). Separate from the mesophication hypothesis, researchers have found that tree species that associate with arbuscular mycorrhizal (AM) fungi are increasing in dominance, while those than associate with ectomycorrhizal (ECM) fungi are declining, a pattern widely attributed to elevated atmospheric N deposition (Averill et al., 2018). Once AM tree species establish, they can maintain N-rich soil conditions due to their N-rich litter (Phillips et al., 2013; Jo et al., 2019). As such, increases in mesophytic tree species and AM tree species have both been suggested to represent transitions in alternative stable states (Nowacki and Abrams, 2008; Averill et al., 2022). Independent of these hypotheses, earthworm introductions have also been posited as contributors to forest change, as they become established under trees that produce palatable litter and negatively impact oak regeneration (Szlavecz et al. 2011; Schelfhout et al., 2017; Frelich et al., 2019; Bethke and Midgley, 2020). As a result, it is unclear which mechanisms of forest change are at play in eastern forests.

Further complicating the issue, wildfire activity has increased in eastern forests (Donovan et al., 2023). This pattern is counterintuitive since the mesophication hypothesis predicts that forests become increasingly resistant to fire (Nowacki and Abrams, 2008). However, climate change has resulted in greater extremes in dry and wet periods, while annual precipitation has remained unchanged (Singh et al., 2013). During prolonged dry periods, there are sufficient receptive fuelbeds for fires, even in forests dominated by mesophytes. The long-term absence of fire has also created novel fuels—deep organic horizons (termed “duff”), which accumulate in forests dominated by fire-adapted trees. During recent wildfires in the southern Appalachians, the combustion of duff, and the roots that grew within it, led to decline for fire-adapted species, including oaks, suggesting that wildfire after long-term exclusion can increase mesophication (Carpenter et al., 2021; Robbins et al., 2022). These findings highlight the complex nature of interacting disturbances and the urgency of finding solutions to maintain oak-dominated forests and the ecosystem services they provide.

In this dissertation, I investigated the effects of fire on forest ecosystems transitioning in species composition in the eastern United States through multiple lenses. In Chapter 2, I characterized the impacts of a wildfire on soil fauna communities and leaf litter decomposition across southern Appalachian forests transitioning from ECM to AM tree dominance. As soil macrofauna are key contributors to biogeochemical cycling, it is crucial to understand how increasing wildfires might impact these communities. In Chapter 3, I took a broader view of forests in the eastern United States to examine how soil biogeochemistry and fire together might explain composition changes in forests. Given that hypotheses on forest change related to fire and soil biogeochemistry have been independently investigated, understanding how they may be linked could be key to advancing strategies for halting or reversing forest change. In Chapter 4, I investigated which management actions, including prescribed fire, might transition forests back towards oak dominance using a long-term dataset from the southern Appalachians.

The goal of this work was to integrate multiple frameworks of forest change to increase our understanding of how eastern forests function to ultimately shed light on how humans can best manage these important ecosystems. An examination of history demonstrates that humans have been intimately involved in shaping the composition of eastern forests. Intentionally, or not, human actions today will shape eastern forests for future generations. A holistic understanding of forest change incorporating multiple perspectives may point our actions towards a desired outcome.

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CHAPTER 2

WILDFIRE AFTER LONG-TERM FIRE EXCLUSION ALTERS LITTER-DWELLING FAUNA COMMUNITIES AND ACCELERATES LEAF LITTER DECOMPOSITION[1]

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[1] Taylor, M.K., Carpenter, D.O., Payne, I.C., Callaham Jr., M.A., O'Brien, J.J., and N. Wurzburger. To be submitted to a peer-reviewed journal.

Abstract

In fire-dependent forests, fire exclusion can alter biodiversity and ecosystem function, but it is unclear how the return of fire through wildfire impacts these novel ecosystems. After a century of fire exclusion, forests in eastern North America are transitioning from dominance by oak and hickory, which associate with ectomycorrhizal (ECM) fungi, to dominance by red maple and tulip poplar, which associate with arbuscular mycorrhizal (AM) fungi. Now, as wildfire activity is increasing, it is unclear how forest communities and processes might respond. To address this knowledge gap, we measured soil macrofauna community compositions and leaf litter decomposition across an AM-ECM forest gradient in burned and unburned areas around the Rock Mountain wildfire in the southern Appalachian Mountains. We found that in response to wildfire, litter-dwelling fauna communities were altered such that abundances of adult beetles (Coleoptera) decreased, and millipedes (Diplopoda) increased. In contrast, communities of soil-dwelling fauna did not respond to fire but did shift along an AM-ECM forest gradient, such that earthworms and millipedes (detritivores) were less abundant with increasing ECM tree dominance. Further, we found that leaf litter decomposition was faster in burned plots than unburned plots, and for AM litter compared to ECM litter. Our findings suggest that wildfires affect fauna communities and decomposition, but these effects are limited to the leaf litter layer. Further, our finding that soil-dwelling detritivores become less abundant with increasing ECM dominance suggests that soil food webs are shifting due to the continued expansion of AM trees in eastern North American forests.

Introduction

Fire has been a driving force in many terrestrial ecosystems for millennia (He et al., 2019), and thus, the exclusion of fire can disrupt communities and alter ecosystem processes (Bowman et al., 2012; Larson et al., 2013; Ritger et al., 2023). For instance, in eastern North American forests (hereafter eastern forests), the exclusion of fire has led to widespread changes in tree species composition (Nowacki and Abrams, 2008; Jo et al., 2019), with cascading consequences for forest-dwelling organisms and the ecosystem processes they mediate (Caldwell et al., 2016; McShea et al., 2007; Zarri et al., 2020). After roughly a century of fire exclusion, wildfire activity is increasing in eastern forests (Donovan et al., 2023), but it is unclear how the reintroduction of fire through wildfire impacts forest communities and processes.

Changes in eastern forests have largely been characterized by a loss of oaks (*Quercus* spp., L.) and hickories (*Carya* spp., Nutt.), which are increasingly replaced by maples (*Acer* spp., L.) and other mesophytic species (Knott et al., 2019), in a process widely termed mesophication (Nowacki and Abrams, 2008). This change in tree species has been recognized as a shift in the dominant mycorrhizal association type, from trees that associate with ectomycorrhizal (ECM) fungi, to those that associate with arbuscular mycorrhizal (AM) fungi (Jo et al., 2019). These mycorrhizal association types have distinct biogeochemical syndromes, which are hypothesized to result from interactions among plant litter, mycorrhizal fungi, and soil microbes (Phillips et al., 2013; Averill and Hawkes, 2016; Lu and Hedin, 2019). Trees that form AM associations tend to produce leaf litter that is readily decomposed by saprotrophic microbes (Averill et al., 2019; Keller and Phillips, 2019), which promotes the mineralization of nutrients that AM fungi can effectively scavenge. In contrast, ECM trees generally produce leaf litter that is chemically resistant to decomposition, and some ECM fungi can extract nutrients directly from soil organic matter (SOM) by promoting oxidative reactions (Op De Beeck et al., 2018; Nicolás et al., 2019). The mining of nutrients by ECM fungi is hypothesized to induce nutrient limitation on saprotrophic microbes, which suppresses rates of decomposition (Fernandez and Kennedy, 2016). As a result, ECM-dominated forests tend to exhibit slower rates of decomposition, soils with thicker organic horizons, higher ratios of carbon (C) to nitrogen (N), and a greater proportion of particulate SOM compared to AM-dominated forests (Zhu et al., 2018; Cotrufo et al., 2019; Wu et al., 2022; but see Hicks Pries et al., 2022).

A limitation in our understanding of the AM vs. ECM dichotomy in biogeochemistry is the paucity of studies that consider fire. In the eastern USA, where much of the work on mycorrhizal patterns in decomposition and biogeochemistry has been conducted (e.g. Averill and Hawkes, 2016; Craig et al., 2018; Hicks Pries et al., 2022; Zhu et al., 2018), several ECM tree species are adapted to fire (Carpenter et al., 2021), likely due to the coordination of traits for nutrient conservation and fire adaptation (Pellegrini et al., 2021). For the last century, however, fire has been excluded from many ECM-dominated forests, suggesting the possibility that some biogeochemical patterns along mycorrhizal gradients could be a product of the fire exclusion era. For example, the deep organic horizons that characterize many ECM-dominated stands may not accumulate under a frequent fire regime (Waldrop et al., 2016). Frequent fire not only consumes leaf litter, which slows the formation of organic horizons, but it may also speed leaf litter decomposition rates in two ways. First, leaf litter combusts to ash with a high concentration of non-volatized essential nutrients such as phosphorus and potassium (Scharenbroch et al., 2012). Second, ash can increase soil pH, which favors microbial transformations of N, leading to greater N availability (Martin et al., 2022). Both mechanisms have the potential to alleviate nutrient limitation on saprotrophic microbes and increase leaf litter decomposition rates. These positive effects of fire on decomposition should be greatest in ECM-dominated stands, which have deeper organic horizons (i.e. more fuels; Carpenter et al., 2021), and particularly those where fire has been reintroduced after a long period of exclusion. Fire effects on decomposition, however, may also depend on the faunal community and how it responds to the reintroduction of fire.

Fire effects on soil fauna depend largely on the life history traits of the group and the severity of the fire. For instance, fast-moving organisms and those capable of flight are more likely to escape oncoming flames. Soil-dwelling organisms, and those capable of burrowing into soil, are less likely to be affected by fire than litter-dwellers (Coyle et al., 2017). Litter-dwelling macrofauna (e.g. millipedes [Diplopoda] and epigeic earthworms [Lumbricina]) abundances are usually negatively impacted by fire in the short-term (Certini et al., 2021 and references therein), though results suggest no long-term impacts on macrofauna communities (Gongalsky et al., 2021). A meta-analysis revealed that fire generally has no effect on abundances of mesofauna (e.g. springtails [Collembola] and mites [Acari]), but it can negatively affect diversity (Pressler et al., 2019). Further, fires that are patchy (i.e. contain unburned areas within burned areas) and close to unburned areas recover faunal abundances more quickly than those that are uniform, because fauna from neighboring areas can quickly recolonize burned areas (Gongalsky and Persson, 2013).

Soil and litter dwelling fauna have largely been excluded from prior research on mycorrhizal patterns in biogeochemistry. These organisms occupy multiple trophic niches within soil food webs (e.g. herbivores, microbivores, detritivores, omnivores, predators), and are collectively responsible for fragmenting litter, creating pores and aggregates, and redistributing organic matter and microbes throughout the soil profile (Griffiths et al., 2021). As a result, fauna are critical drivers of litter decomposition, nutrient cycling, and SOM transformations (Frouz, 2018). Although poorly studied in direct context of mycorrhizal associations, prior work can provide a basis for how soil fauna communities may change along AM-ECM forest gradients. For example, soils and litter with low C:N promote large detritivores, such as earthworms and millipedes whereas those with high C:N are dominated by smaller invertebrates, such as springtails, mites, and their predators (Hedĕnec et al., 2022, Peng et al., 2022a). Further, there is evidence that the abundance and biomass of some taxa, particularly earthworms, increase with increasing soil pH (Petersen and Luxton, 1982). Because soil and litter C:N tend to be lower and soil pH tends to be higher in AM-dominated forests (Lin et al., 2022), it suggests that those forests could favor millipedes and earthworms, whereas ECM-dominated forests could favor springtails, mites, and their predators. However, it is an open question as to how soil fauna and their contributions to ecosystem processes might shift along an AM-ECM forest gradient.

Here, we consider soil fauna and fire in the context of forest mycorrhizal associations. Specifically, the aim of our study was to determine the effects of wildfire, after long-term fire exclusion, on soil fauna community compositions and leaf litter decomposition rates in the context of AM-ECM forest gradients. To that end, we identified a gradient of ECM dominance in burned and unburned forests following a wildfire in the southern Appalachians, USA—a region that had not experienced fire for at least seventy years, but likely burned at a regular interval prior to European Colonization (Lafon et al., 2017). Across this mycorrhizal gradient, we measured abundances of macro- and meso-fauna, soil chemistry, and mass loss of AM and ECM leaf litters. First, we hypothesized that fire would alter fauna communities in litter, which is often consumed by fire, but it would have minimal impact on communities in the mineral soil due to its insulating properties. Second, we hypothesized that with increasing ECM dominance, we would encounter fewer large detritivores (earthworms and millipedes), and more mesofauna (mites and springtails) and predators (centipedes [Chilopoda], spiders [Araneae], diplurans [Diplura]) in the soil faunal community. Third, we hypothesized that leaf litter decomposition would be slower with increasing ECM dominance, but the return of fire would remove this pattern, making decomposition rates more similar across forests.

Materials and Methods

Site description and experimental design

In 2016, the Rock Mountain wildfire burned 9,624 hectares in the Chattahoochee and Nantahala National Forests of northeast Georgia and southwest North Carolina over 25 days, after several months of unusually warm and dry conditions. The dry period allowed much of the organic horizon (duff) to become available as fuel (Carpenter et al., 2021). Fire had likely not been a factor in the area since the turn of the twentieth century (Lafon et al., 2017).

Dominant tree species of these forests are oaks (*Quercus* spp.), hickories (*Carya* spp.), maples (*Acer* spp.) and tulip poplar (*Liriodendron tulipifera* L.). Mean annual precipitation in the nearby Coweeta Hydrologic Laboratory is 190 cm and the mean monthly temperatures range from 20°C in June through August and 5°C in December and January (Knoepp et al., 2008). Soils across the area are Inceptisols or Ultisols, weathered from igneous or metamorphic parent material with soil textures characterized variously as loamy, fine-loamy, clayey, and loamy-skeletal (Soil Survey Staff, 2019).

For this study, we used 20 plots (12 m radius) in burned and unburned areas (10 burned/10 unburned), that were distributed across four topographic positions and four spatial blocks. These plots were part of a larger study (with 32 plots) investigating tree decline and organic horizons after the Rock Mountain wildfire (Carpenter et al., 2021). Topographic positions included low elevation, two midslopes (one north-facing, one south-facing), and ridge, as we expected these positions to influence vegetation and fire behavior. Within each plot, we tagged and identified all living trees or shrubs with a stem diameter at breast height (DBH) greater than 10 cm. Trees were categorized by their mycorrhizal association type observed in field conditions (Brundrett and Tedersoo, 2019). We calculated the relative abundance of ECM trees by percent basal area. Trees or large shrubs with the ericoid (ERM) mycorrhizal association, including *Oxydendrum arboretum* (L.) DC. and *Rhododendron maximum* L., were grouped with ECM trees due to ERM fungal traits being more like those of ECM fungi than AM fungi (Read and Perez-Moreno 2003). These accounted for, on average, 8.6 % of total basal area in our plots (range 0-22.8 %)

Data collection

To quantify leaf litter decomposition, we placed 24 litterbags (3 mm mesh) with 3.5 g of air-dried AM or ECM leaf litter (collected using elevated traps in fall 2017) onto the soil surface of each plot in the winter of 2017. The AM leaf litter contained *Acer* species and *L. tulipifera* at a ratio of 1.8:1, while the ECM litter contained *Quercus* species and *Carya* species litter combined at a ratio of 1.8:1, reflecting the relative contribution of these species to forest basal area in our plots. Six replicate litterbags (3 AM and 3 ECM) were retrieved on average 92 (range 78-101), 183 (range 169-204), 283 (range 266-302), and 1,105 (range 1,015-1,131) days after being placed in plots. We presented data from the third collection (266-302 days), from unburned plots only, in Carpenter et al. (2021). Thirty-five of the original 480 litterbags were either not found or were damaged and were excluded from analyses. For remaining bags, litter was soaked for 12 minutes in water to remove adhering soil, washed over a 2 mm sieve, and then oven dried (60° C for 72 h) before weighing.

To measure the effects of fire and mycorrhizal context on nitrogen availability, we extracted dissolved inorganic nitrogen (DIN) from three soil samples homogenized by depth (Oea horizon, 0-10 cm, and 10-20 cm) in each plot in the spring, summer, and fall of 2018. Immediately after sampling (i.e. in the field), we sieved soil (2 mm) and combined soil (~10 g dry weight equivalent) with 75 mL 2M KCl, and we vigorously shook bottles for 30 seconds, every 15 minutes, for 2 hrs. Solutions were filtered (Whatman 41) and frozen until analysis of NO_3^- and NH_4^+ using microsegmented flow analysis via colorimetry on a continuous flow analyzer (Astoria 2, Astoria-Pacific, Clackamas, Oregon).

To identify patterns in macrofauna communities, we sampled litter and soil in the spring, summer, and fall of 2018. To sample litter-dwelling macrofauna, we used a 2 m radius subplot on the outside edge of each plot and searched the litter layer for 30-person-minutes, collecting all encountered invertebrates (Schmidt, 2001; Snyder et al., 2006). To sample soil-dwelling macrofauna, we selected a location on the outside edge of the litter subplot and extracted soil volumes (30 x 30 x 30 cm) using a shovel, searching the entire volume twice by hand, to collect all encountered invertebrates. Invertebrates were preserved in 70% ethanol and identified into broad groups (class or order) using a dissecting microscope (10-20 x) and the group descriptions in Dindal (1990) and Tripplehorn and Johnson (2005). Abundances of each group (individuals per m^2) were summed across seasons for analyses. To further characterize earthworm communities, we identified all adult and subadult earthworms to family using the descriptions in Dindal (1990).

To quantify the effects of fire and mycorrhizal context on mesofauna, we extracted them from the first collection of litter bags (78-101 days in field) using the Berlese Tullgren method. Mesofauna were extracted from litter bags for 48 h and stored in 70% ethanol. We quantified abundances (per litter bag) of broad groups using a dissecting microscope (10–40 x) and the descriptions in Dindal (1990).

Statistical analyses

To analyze the community compositions of macrofauna, we used redundancy analysis (RDA), constrained by the effects of burn status (burned/unburned), layer (litter/soil), percentage of ECM basal area, and total plot basal area (to account for potential effects of tree abundance and size; all analyses conducted using R version 4.3.2; R Core Team, 2023). We allowed all constraining factors to interact, and we included block and topographic position as conditional factors (rda function in vegan package; Oksanen et al., 2022). We Hellinger-transformed abundances of each faunal group prior to analysis and used permutation tests to assess the significance of the RDA model, biplot axes, and non-conditional model terms (permutations = 5,000; Borcard et al., 2018).

To further understand effects of fire and mycorrhizal dominance on individual groups of macrofauna, we analyzed abundances (in litter and soil layers independently to facilitate convergence) using a generalized linear mixed effects model with a Poisson distribution (glmer function in lme4 package; Bates et al., 2015). We assigned taxonomic group, burn status, total plot basal area, and percentage of ECM basal area as fixed effects, while block and topographic position were random intercepts. We allowed taxonomic group to interact with each of the other variables. We added an additional random intercept of observation number to these models to account for overdispersion as needed (Harrison, 2014). We similarly analyzed abundances of earthworm families and mesofauna in leaf litter.

To quantify leaf litter decomposition rates, we compared fits of five decomposition models using AIC values, using the R package litterfitter (Cornwell and Weedon, 2014), and found the Weibull residence time model was the best performing. We used the parameter estimates from the model fit to each plot/litter type combination to calculate litter mean residence time (MRT) and half-life (Cornwell and Weedon, 2014). To analyze litter MRT and half-life, we constructed linear mixed effects models, where burn status, litter type (AM/ECM), and percentage of ECM basal area were interacting fixed effects, total plot basal area was an additional fixed effect, and block and topographic position were random intercepts (lmer function in lme4 package).

To analyze DIN concentrations, we used a linear mixed effects model that included depth, burn status, season, total plot basal area, and ECM dominance as fixed effects and block, topographic position, and individual plot (to account for variance attributable to plot) as random intercepts (lmer function). We allowed depth to interact with each of the other fixed effects in this model.

For all described mixed models, we assessed significance using the Wald chi-square test (Anova function in car package; Fox and Weisberg, 2019), and we removed non-significant interactions and terms. We performed *post-hoc* pairwise comparisons of group means using estimated marginal means with the Tukey adjustment for multiple comparisons (emmeans or emtrends function in emmeans package; Lenth, 2022).

Results

We sampled more than 1,800 individual specimens of macrofauna distributed across 21 groups (Appendix A: Table A1). Immature beetles (Coleoptera) were the most abundant group, followed (in order) by millipedes, diplurans, centipedes, and earthworms. We also commonly encountered colony-forming insects (ants [Formicidae] and termites [Termitoidae]) in our samples, but due to the difficulty of quantitatively collecting these from a discrete volume of litter and soil, we excluded these from our analyses. In our assessment of macroinvertebrate community compositions with RDA (adjusted *pseudo*-R^2: 52.4), the first two axes explained 46.1% and 5.7% of constrained variance, respectively. The dissimilarity of communities along RDA axis 1 was largely driven by layer (soil/litter; Figure 2.1a-b). We found that macrofauna community composition differed between burned and unburned plots in litter samples but not soil samples (burn status by layer interaction: *pseudo*-$F_{(1, 28)} = 2.81$, $P = 0.04$; Figure 2.1a), supporting our hypothesis. We found a near-significant relationship between ECM dominance and macrofauna community composition only in the soil-dwelling macrofauna (ECM by layer interaction: *pseudo*-$F_{(1, 28)} = 2.37$, $P = 0.06$; Figure 2.1b). Individual groups were distributed across the two RDA axes, showing relationships with soil layer, burn status, and ECM dominance (Figure 2.1c).

In our analysis of macrofauna abundances by taxonomic group, we encountered differing results in the two soil layers. In samples from leaf litter, we found that the effect of burn status differed by group (burn status x group interaction: $\chi^2 = 24.7$, *d.f.* = 15, $P = 0.05$), where adult beetles were less abundant in burned plots, but millipedes were more abundant (Figure 2.2). We did not find evidence of a relationship between leaf litter fauna abundances and ECM dominance, but we found a positive relationship between litter fauna abundance and total plot basal area ($\chi^2 = 6.3$, *d.f.* = 1, $P = 0.01$). In samples from soil, we found that the relationship of macrofauna abundance with ECM dominance depended upon taxonomic group (ECM x group interaction: $\chi^2 = 39.5$, *d.f.* = 11, $P < 0.0001$). Large detritivores (earthworms and millipedes) decreased in abundance with increasing ECM dominance (Figure 2.3), supporting our hypothesis. Cockroaches (Blattodea), immature lepidopterans (Lepidoptera), and snails (shelled Gastropoda) also had significant relationships with ECM dominance, but these were driven by only a few non-zero observations (Appendix A: Figure A1). We did not find evidence of a relationship between soil fauna groups and burn status, but we found a positive relationship between soil fauna abundance and total plot basal area ($\chi^2 = 5.9$, *d.f.* = 1, $P = 0.02$). Contrary to our hypothesis, predators (centipedes, diplurans, spiders) showed no relationship with ECM dominance in soil or litter samples.

We collected 117 earthworms, of which 81 were adults or subadults that could be further identified to family. Earthworms were dominated by the family Acanthodrilidae, which were predominantly found in soil (layer x family interaction: $\chi^2 = 111.4$, *d.f.* = 2, $P < 0.001$; Appendix A: Figure A2). Specimens from Lumbricidae and Megascolecidae were less commonly encountered, and we did not find support for an interaction of family with either ECM dominance or burn status.

In our analysis of mesofauna extracted from litterbags, we found that samples contained springtails and mites almost exclusively (Appendix A: Table A1), and thus we analyzed only these two groups. Abundances of both springtails and mites were unaffected by ECM dominance, total plot basal area, and litter type. Both groups were strongly influenced by burn status (springtails: $\chi^2 = 4.9$, *d.f.* = 1, $P = 0.03$; mites: $\chi^2 = 4.9$, *d.f.* = 1, $P = 0.03$) and were nearly three times more abundant in litterbags sampled from burned plots compared to those from unburned plots (Figure 2.4).

Over the four sampling times, the percentage of leaf litter mass remaining declined rapidly and was on average 70.4, 38.4, 36.5 and 5.4%, respectively (Figure 2.5a,c). We found that MRT was higher for ECM than AM litter ($\chi^2 = 13.8$, *d.f.* = 1, $P = 0.0002$), where the MRT of ECM leaf litter was 58.4 days longer than AM leaf litter on average (Figure 2.5b). Similarly, MRT was higher in unburned than in burned plots ($\chi^2 = 12.7$, *d.f.* = 1, $P = 0.0004$), such that MRT in unburned plots was 49.6 days longer on average than in burned plots (Figure 2.5d). While we hypothesized an ECM gradient effect on leaf litter decomposition, after accounting for differences in plot basal area, it was not significant, suggesting that tree density or size, not ECM dominance, were related to slower decomposition rates (Appendix A: Figure A3-A4). Our Weibull model estimates also allowed us to calculate leaf litter half-life, where ECM litter had a longer half-life than AM litter by an average of 76.7 days ($\chi^2 = 257.6$, *d.f.* = 1, $P < 0.001$; Appendix A: Figure A5). Like the results for MRT, leaf litter half-life increased with increasing plot basal area ($\chi^2 = 8.8$, *d.f.* = 1, $P = 0.003$). We found no evidence for effects of burn status or ECM dominance on leaf litter half-life.

We found that extractable soil ammonium was ten times higher on average in the O-horizon than in the mineral soil layers (Appendix A: Figure A6). Ammonium concentrations were higher in the summer than in the spring or fall in the O-horizon only (depth x season interaction: $\chi^2 = 36.5$, *d.f.* = 4, $P < 0.001$). Our model results indicated that ammonium concentrations were higher in unburned than in burned plots in the O-horizon only (depth x burn status interaction: $\chi^2 = 23.1$, *d.f.* = 2, $P < 0.001$), but we lack confidence in this result since only one plot within the burned area had an O-horizon that was available for sampling. We did not find evidence for a relationship of extractable soil ammonium with ECM dominance or total plot basal area. Nitrate concentrations in these soils were only detectable from 5% of samples, thus were excluded from our analysis.

Discussion

Fire exclusion has altered community composition and ecosystem processes in eastern forests (Nowacki and Abrams, 2008; Jo et al., 2019). Now, as wildfire activity increases (Donovan et al., 2023), it is unclear how the return of fire through wildfire impacts these ecosystems. Our findings demonstrate that in a fire-excluded, southern Appalachian forest, wildfire altered the composition of litter-dwelling faunal communities and accelerated leaf litter decomposition. We also found evidence that soil macrofauna shifted along an AM-ECM forest gradient, suggesting that changes to soil food webs may coincide with changes to tree communities, and contribute to altered patterns in biogeochemistry.

We found that wildfire altered macrofauna community compositions in the litter but not in the soil (Figure 2.1a). This finding supports our hypothesis that mineral soil insulated soil-dwelling fauna from fire (Coyle et al., 2017). Fire effects on litter macrofauna may be through direct mortality, or through the indirect effects of altered habitat and resources (Certini et al., 2021). We saw changes in two groups of litter macrofauna in response to fire. Adult litter-dwelling beetles were less abundant in burned compared to unburned plots (Figure 2.2a), possibly due to the mortality of immature beetles (grubs) that were dwelling in the O-horizon, which was largely consumed by the wildfire (Carpenter et al., 2021). Grubs are less mobile than adult beetles and may have been unable escape the fire, leading to fewer adult beetles at the time of our sampling. In contrast, we found that litter-dwelling millipedes were more abundant in burned than in unburned plots (Figure 2.2b). Though abundance increases in arthropods after fire are not unheard of (Bess et al., 2002; Kral et al., 2017), it does seem to be the exception (Certini et al., 2021), and to our knowledge, this is the first report of millipedes increasing in abundance after fire. Gongalsky et al. (2021) found no effects of fire on soil food webs five years post-fire, suggesting the patterns we observed may be ephemeral if fire continues to be excluded. However, if fires continue to occur in this area, invertebrate assemblages may reach new equilibria (Brennan et al., 2009).

We found that soil-dwelling macrofauna community composition changed along an AM-ECM forest gradient (Figure 2.1b). Specifically, we found that large detritivores (earthworms and millipedes) were less abundant with increasing ECM dominance (Figure 2.4), possibly reflecting declines in litter palatability and soil pH (Lin et al., 2022; Peng et al., 2022a, b). This finding suggests that complex soil food webs, not just interactions with decomposer microbes, may contribute to the observed mycorrhizal patterns in biogeochemistry. Contrary to our hypotheses, we found no relationship between mesofauna or predator abundances and ECM dominance. Other studies have found increasing mesofauna or predator abundances with increasing litter and soil C:N (Heděnec et al., 2022; Peng et al., 2022a), suggesting patterns may be site- or scale-dependent. Further work is required to untangle invertebrate contributions to mycorrhizal patterns broadly, but our findings support the growing call for the inclusion of invertebrates in the study of ecosystem processes (Griffiths et al., 2021).

Our results showed that earthworm abundance declined with increasing ECM dominance (Figure 2.3a). Importantly, earthworms contribute to soil bioturbation and may catalyze the formation of microbial necromass (Angst et al., 2022), which is an important precursor of persistent mineral-associated SOM (Cotrufo et al., 2013). If earthworms are generally more abundant in AM-dominated forests, they may contribute to the larger pools of mineral-associated SOM there relative to ECM-dominated forests (Cotrufo et al., 2019). Indeed, the link between earthworm communities and SOM stabilization has been noted previously (Prescott and Vesterdal, 2021) and highlights a critical area for future study in the context of mycorrhizal associations. In our study, one earthworm family, Acanthodrilidae, was most abundant, and it was largely represented by the native genus *Diplocardia* (Garmon). Although rare in our samples, we encountered some earthworms in the family Megascolecidae, represented entirely by the invasive genus *Amynthas* (Kinberg), only in AM-dominated plots. Prior work suggests that AM-dominated forests are more vulnerable to plant invasions, likely due to heightened nutrient availability (Jo et al., 2018). Because invasive earthworms tend to be facilitated by, and are themselves prone to increasing, soil nutrient availability (Ferlian et al., 2020), increasing AM dominance may mediate the co-invasion of both plants and earthworms (Bethke and Midgley, 2020).

We found that abundances of mites and springtails extracted from litterbags were higher in burned plots than in unburned plots (Figure 2.4). Similar to our results for millipedes, this increase in abundance in response to fire was unexpected and its cause is unclear. Prior studies have found a neutral or negative effect of fire on soil mesofauna (Zaitsev et al., 2014; Saifutdinov et al., 2018; Pressler et al., 2019). It is possible that this result was an artifact of our sampling method. We extracted mesofauna from litterbags, which may have represented refugia for mesofauna in burned plots. Most of the organic matter was consumed during the fire in burned plots, and even though the litterbags were deployed more than a year after the fire, litter inside the bags may have represented a valuable resource in litter-depauperate stands.

Our results show that leaf litter residence time was shorter (i.e. faster decomposition) in burned plots than in unburned plots. One possibility for the acceleration of litter decomposition in burned plots is that fire heightened nutrient availability (Scharenbroch et al., 2012; Martin et al., 2022), either directly from ash inputs, or indirectly through an increase in soil pH, thereby alleviating nutrient limitation on decomposers, though we did not find support for this with our soil extractable ammonium results. Another potential explanation stems from our observation that fire increased the density of mesofauna in leaf litter (Figure 2.4). Mesofauna generally increase rates of litter decomposition (Kampichler and Bruckner, 2009), so the increased mesofauna abundance we measured in litterbags from burned plots may explain the faster decomposition we observed there. Importantly, these mechanisms could co-occur, highlighting the relationships between tree species composition, soil food webs, fuels, and fire. An additional caveat with our litter decomposition results is that litterbags are imperfect at measuring litter decomposition (Kampichler and Bruckner, 2009 and references therein) as they exclude the largest soil fauna (e.g. large earthworms, millipedes, very large spiders). Though we encountered fauna inside some litterbags (e.g. beetles, diplurans, earthworms, millipedes) during processing (MKT, personal observation), we cannot exclude the possibility that decomposition proceeded more slowly inside of our litterbags due to the exclusion of large fauna.

In our study, we did not find support for our hypothesis that the residence time of leaf litter would increase with increasing ECM dominance. Rather, we found that the ECM dominance effect that was apparent from our data in unburned plots (Appendix A: Figure A4) became non-significant once we considered total plot basal area in our model (Appendix A: Figure A3). In a previous study, we presented data from unburned plots for the third litterbag collection and noted decreasing litter decomposition rates with increasing ECM dominance (Carpenter et al., 2021). Now, after considering the influence of total plot basal area on the larger set of data, we recognize that the effect of ECM dominance on litter decomposition that we reported in Carpenter et al. (2021) may not be significant after accounting for total plot basal area. Basal area could affect decomposition by impacting rates of nutrient cycling (Bueis et al., 2018) or through the effects of canopy cover on soil microclimate conditions (de Godoy

Fernandes et al., 2021). Future studies investigating the effects of forest mycorrhizal gradients should consider the effects of total plot basal area in their experimental design.

Conclusion

Our study demonstrates that wildfire after long-term fire exclusion altered the community composition of litter-dwelling fauna communities and accelerated leaf litter decomposition. Given that the legacies of prior fire regimes influence fire severity and impacts (Roberts et al., 2019), the future occurrence of fire in such fire-excluded forests will determine trajectories of forest-dwelling populations and their effects on ecosystem processes. Further, our study provides evidence that soil invertebrate communities shift along forest gradients from AM to ECM dominance, complementing prior work documenting changes in microbial communities and nutrient cycling (Cheeke et al., 2017), and SOM fractions (Craig et al., 2018). Disentangling the mechanisms that underpin mycorrhizal patterns is critical for predicting future carbon and nutrient cycles (Braghiere et al., 2021), as well as predicting future fire behavior and forest structure.

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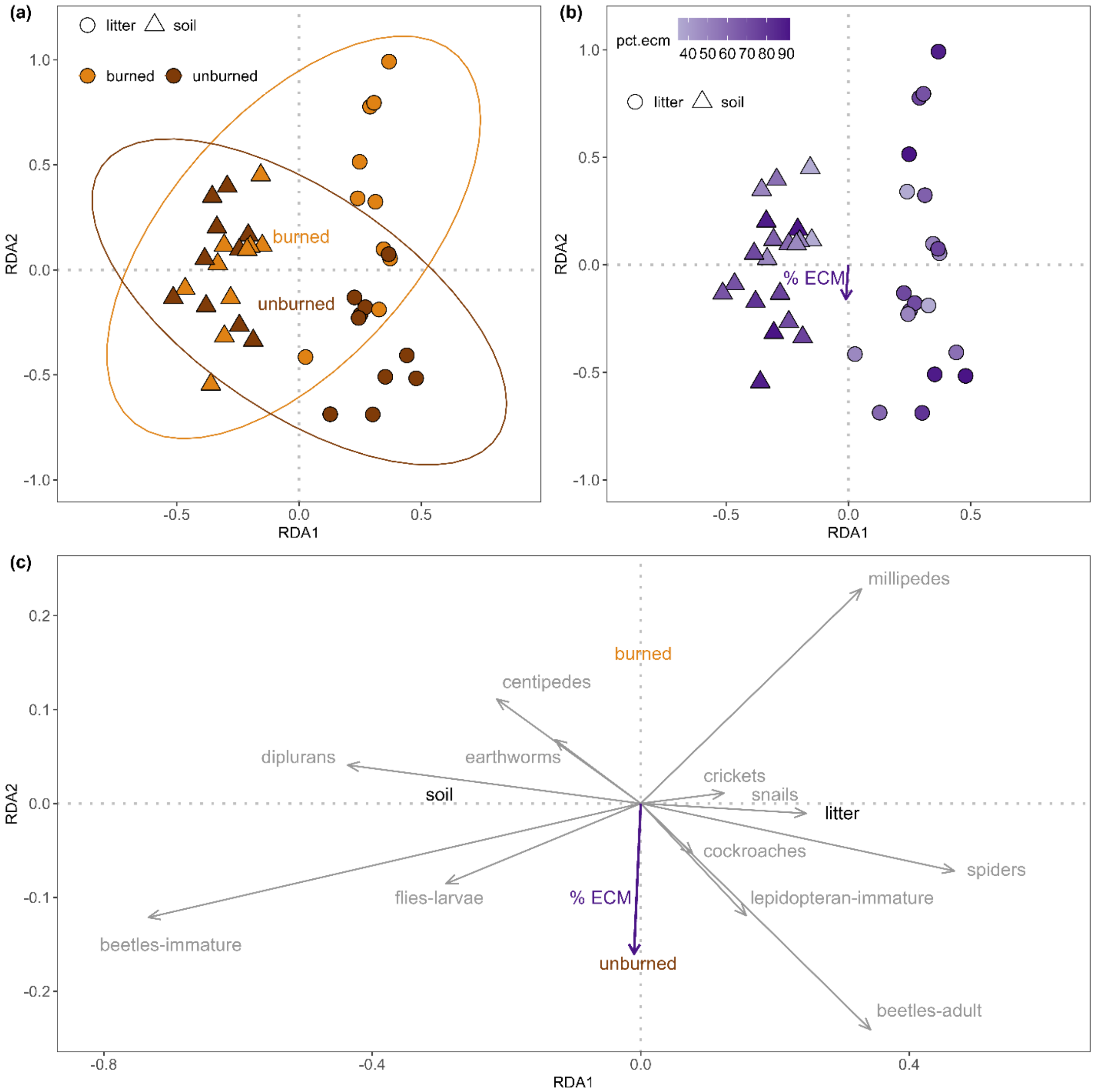

Figure 2.1. Soil macrofauna community composition from the area of the Rock Mountain wildfire, showing relationships with (a) soil layer (shape) and burn status (color), (b) mycorrhizal dominance (% ECM basal area; color gradient), and (c) patterns of individual taxa as related to soil layer, burn status, and % ECM basal area. Results are from redundancy analysis (RDA) ordination, where ellipses are 95% confidence intervals with factor centroids, and with RDA-

derived vectors of % ECM basal area (panel b) and 12 taxonomic groups (panel c). Seven taxonomic groups clustered around the origin were excluded from panel c to aid visualization.

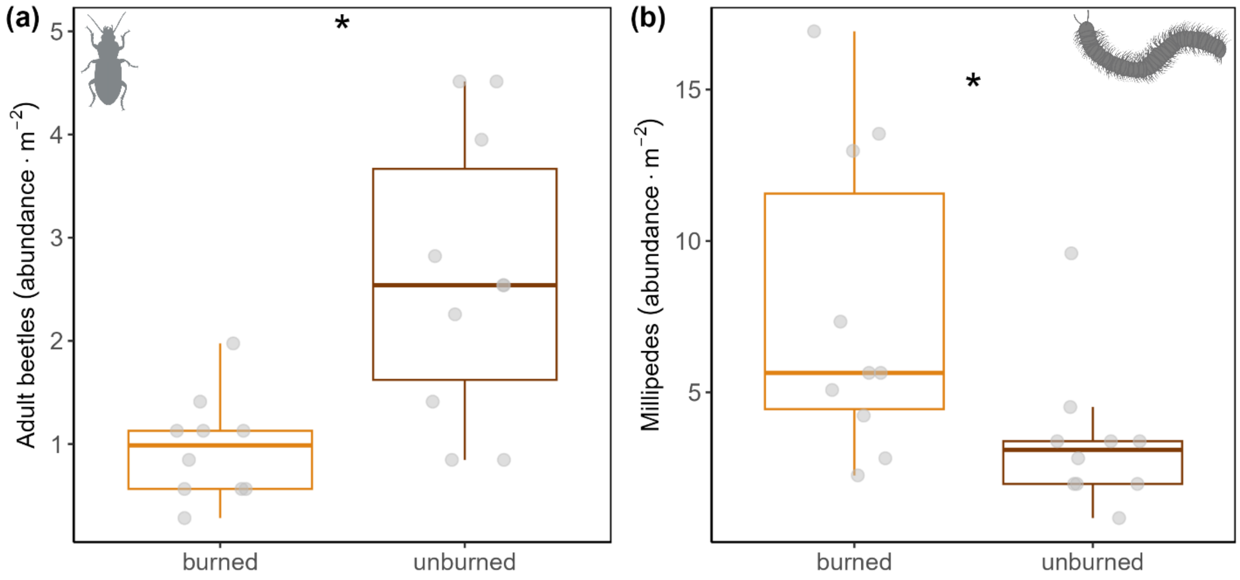

Figure 2.2. Abundances of litter-dwelling macrofauna that responded to fire from the area of the Rock Mountain wildfire, including (a) adult beetles (Coleoptera) and (b) millipedes (Diplopoda). Boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Points represent abundances from each plot summed across three seasons. Image modified with Biorender.com.

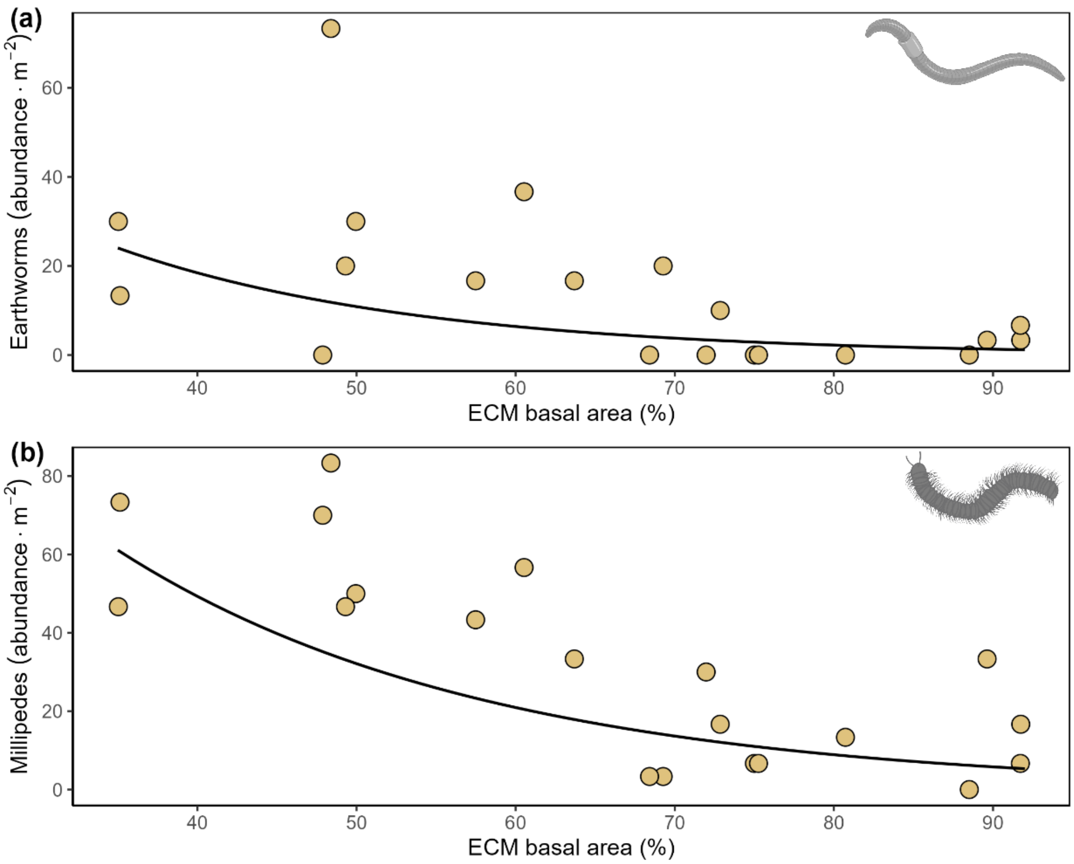

Figure 2.3. Abundances of soil-dwelling macrofauna that changed across a gradient of ECM basal area from the area of the Rock Mountain wildfire, including (a) earthworms (Lumbicina) and (b) millipedes (Diplopoda). Points represent abundances from each plot summed across three seasons and lines are model predictions with significant ($P \leq 0.05$) slopes. Image modified with Biorender.com.

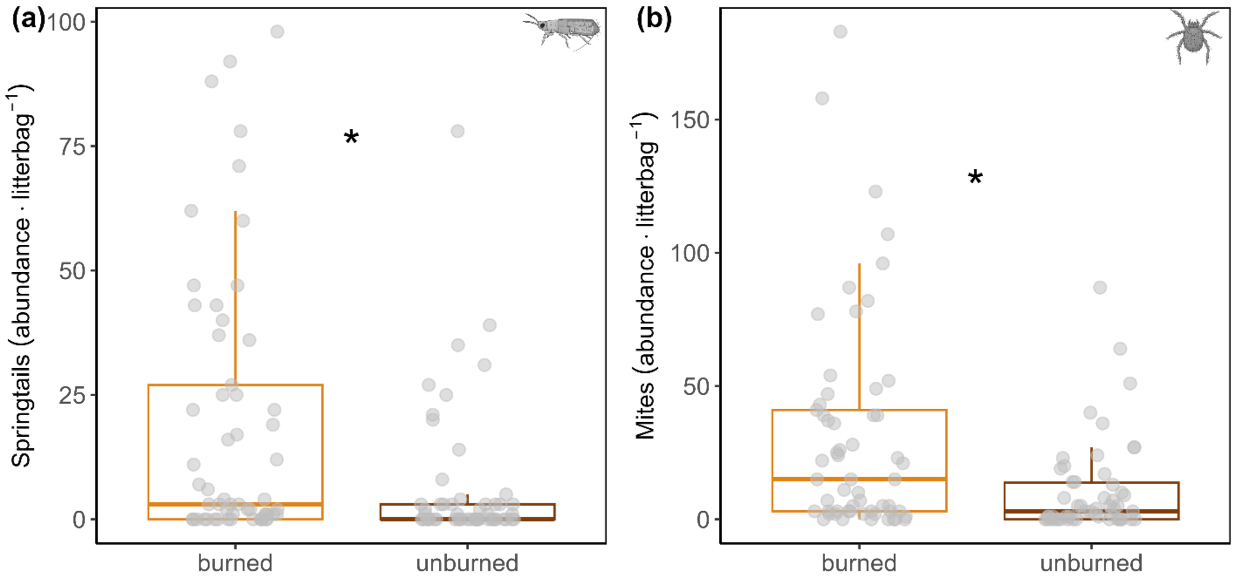

Figure 2.4. Abundances of mesofauna from litterbags in burned and unburned plots from the area of the Rock Mountain wildfire, including (a) springtails (Collembola) and (b) mites (Acari). Boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Points are abundances from individual litter bags. Significant effect (*P* < 0.05) of burn status denoted by asterisk.

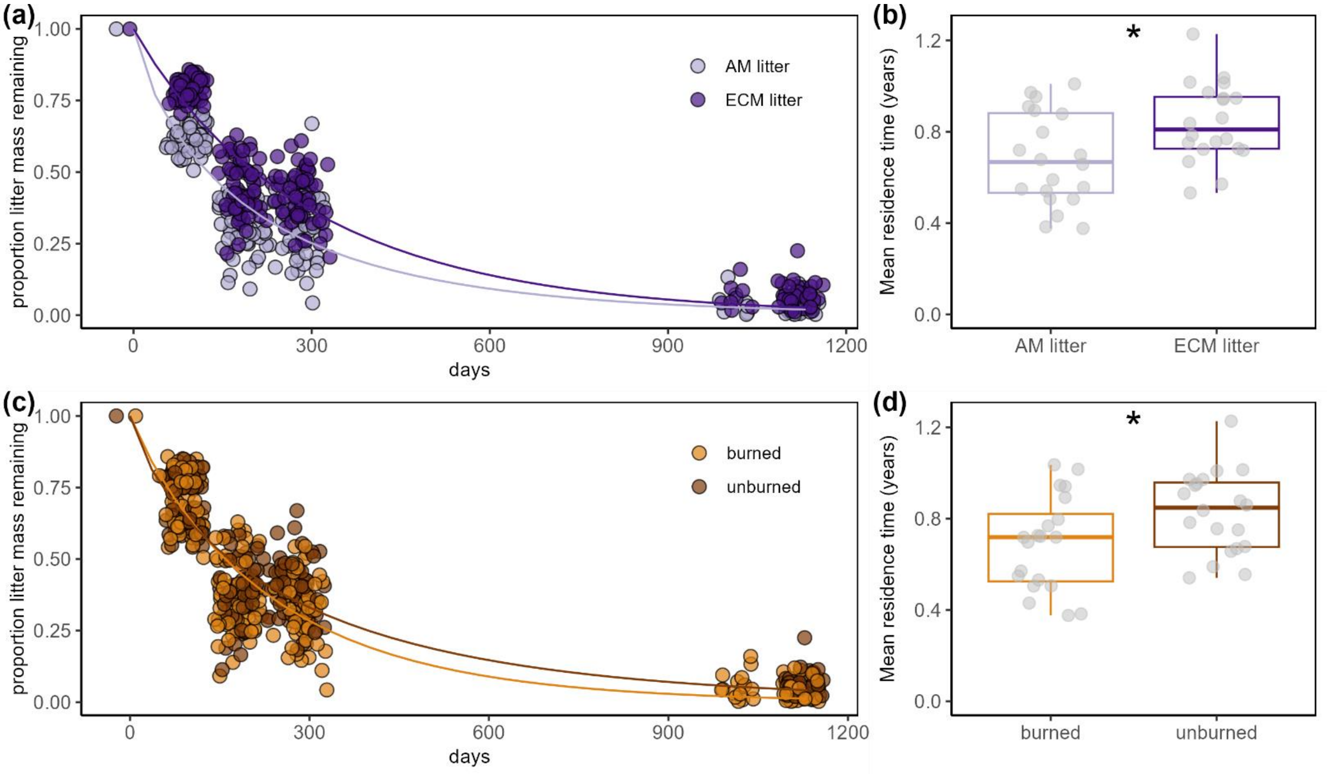

Figure 2.5. Leaf litter mass from the area of the Rock Mountain Fire, including the proportion of litter mass remaining over the duration of the study for (a) AM and ECM leaf litter and (c) in burned and unburned plots, and leaf litter mean residence times (MRT) for (b) litter types and (d) burn status. Lines are Weibull residence model predictions for each litter type (a) and burn status (c), and Weibull parameter estimates from each plot and litter type combination were used to calculate mean residence time (MRT) (b) and (d). For (b) and (d), boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Significant differences ($P < 0.05$) denoted by asterisk. For (a) and (c), points are jittered along x axis to aid visualization.

CHAPTER 3

MERGING FRAMEWORKS OF SOIL BIOGEOCHEMISTRY AND FIRE TO EXPLAIN CHANGES TO FORESTS OF THE EASTERN UNITED STATES[2]

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[2] Taylor, M.K., Steelman, J., Callaham Jr., M.A., Loudermilk, E.L., O'Brien, J.J., and N. Wurzburger. To be submitted to a peer-reviewed journal.

Abstract

Temperate forests in the eastern United States (U.S.) are transitioning to an increasingly mesophytic tree species composition. A widely accepted explanation for this change, the mesophication hypothesis, posits that fire exclusion has led to an increasing dominance of fire-intolerant trees which further resists fire. However, returning fire to forests does not always reverse mesophication. In the original conception of the mesophication hypothesis, authors acknowledged the likely role of soil nutrients, though few studies have investigated how biogeochemistry contributes to the positive and negative feedbacks implicated in the hypothesis. Soil biota are central to forest biogeochemistry and two groups in particular, mycorrhizal fungi and earthworms, are intimately involved in forest nutrient cycling. Independent of the mesophication hypothesis, other researchers have suggested that: 1) elevated atmospheric nitrogen (N) deposition has promoted the dominance of tree species that associate with arbuscular mycorrhizal (AM) fungi over those that associate with ectomycorrhizal (ECM) fungi, and 2) invasive earthworm introductions favor trees that produce palatable litter, to the detriment of those that produce unpalatable litter. Here, we ask if these biogeochemical mechanisms explaining forest change are related to the mesophication hypothesis. To investigate this question we: 1) conducted a bibliometric analysis on the forest change literature, 2) compared the dichotomies of AM/ECM with fire-adapted/fire-intolerant among abundant tree species, 3) compared tree traits for fire adaptation with litter decomposability/palatability among common tree species, 4) compared prevalences of fire-adapted and ECM tree species across the region using spatially robust forest inventory data, and 5) compared the spatial extent of forest change with fire exclusion, atmospheric N deposition, and invasive earthworm records. From our bibliometric analysis, we found that co-cited papers fall largely within clusters of academic disciplines, suggesting a lack of consideration of biogeochemistry in the fire literature and vice versa. Among the most abundant tree species of the region, AM species are generally considered fire-intolerant, while ECM trees are considered fire-adapted, and fire-intolerant species have faster litter decomposition rates than those that are fire-adapted. Analysis of traits for litter decomposition and fire adaptation revealed that both the AM and ECM guilds have tree species distributed across axes of decomposability and fire adaptations; however, only the ECM guild has tree species that fall within the trait space of high flammability, thick bark, high litter C:N and slow decomposition. Regarding species prevalences across the region, forest basal area of ECM trees and fire-adapted trees are correlated, particularly in the southern provinces of the region, indicating that dominant ECM tree species are also fire-adapted. We found that fire exclusion was spatially linked to increases in AM tree dominance, but we did not detect a relationship between forest change and N deposition or invasive earthworm records. Taken together, our findings suggest the possibility that three human disturbances: fire exclusion, atmospheric N deposition, and invasive earthworm introductions, may reinforce the shift in eastern U.S. forest composition. We propose an expansion of the mesophication framework to consider the role of soil biogeochemistry in the context of this ecosystem state change.

Introduction

Temperate forests of the eastern United States (U.S.) are transitioning from being dominated by oaks (*Quercus* spp.), pines (*Pinus* spp.), and hickories (*Carya* spp.), to being increasingly composed of maples (*Acer* spp.) and other mesophytic species (Jo et al., 2019). This alteration to forest composition is widespread across the region and has coincided with several post-Colonial human disturbances, notably fire exclusion (McEwan et al., 2011; Knott et al., 2019; Hanberry et al., 2020). The mesophication hypothesis has emerged as a widely accepted mechanism, where the exclusion of fire continually improves conditions for shade-tolerant and fire-sensitive tree species (mesophytes), while simultaneously deteriorating conditions for fire-adapted species (pyrophytes; Nowacki and Abrams, 2008; Alexander et al., 2021). As mesophytes increase in dominance, fuelbeds become increasingly moist and fire resistant and the likelihood of fire continues to diminish (Kane et al., 2021; Kreye et al., 2013; Varner et al., 2021). According to the mesophication hypothesis, reestablishing a frequent fire regime should slow or reverse this forest transition. However, fire alone often fails to produce this outcome (Brose et al., 2013; Keyser et al., 2017).

If re-establishing a regular fire regime does not return forests to their pyrophytic state, it suggests other forces are preventing this transition. In their formalization of the mesophication hypothesis, Nowacki and Abrams (2008) implicated soil nutrients as part of the transition in tree species, acknowledging that mesophytic hardwoods tend to produce more nutrient-rich litter that decays faster in comparison to pyrophytes, and they predicted that mesophication would proceed more quickly in nutrient-rich sites. Indeed, studies have found that rates of leaf litter decomposition and soil nitrogen (N) cycling are higher for mesophytic maples than for pyrophytic oaks (Alexander and Arthur, 2010; 2014). However, relatively few studies have investigated the biogeochemical processes that contribute to the positive and negative feedbacks associated with the mesophication hypothesis. Because nutrient cycling is mediated by soil organisms, it is impossible to consider these dynamics without extending direct consideration to the soil biota involved.

One such group of soil biota, mycorrhizal fungi, has emerged as a key driver of forest biogeochemistry. Mycorrhizal fungi acquire carbon from host plants in exchange for enhanced nutrient access, thereby mediating the connection between plants and soils. Trees generally form one of two mycorrhizal associations—arbuscular mycorrhizas (AM) or ectomycorrhizas (ECM)—which create distinct biogeochemical syndromes. Trees that associate with ECM fungi tend to produce litter that is chemically resistant to decomposition, resulting in low nutrient availability (Averill et al., 2019; Keller and Phillips, 2019). While considered a carbon-costly strategy, some ECM fungi can extract nutrients directly from soil organic matter (i.e. "mining" *sensu* Phillips et al., 2013), allowing ECM hosts to persist in nutrient-poor conditions (Op De Beeck et al., 2018; Lu and Hedin, 2019; Nicolás et al., 2019). In contrast, trees that associate with AM fungi tend to produce litter that is readily decomposed, thereby promoting the mineralization of nutrients, which favors the less carbon-costly strategy used by AM fungi to scavenge available nutrients. These two mycorrhizal associations appear to represent alternative stable states in the eastern U.S. (Lu and Hedin, 2019; Averill et al., 2022), but the dominant mycorrhizal type has the potential to shift under changing nutrient regimes. For example, elevated atmospheric N deposition has been implicated in recent changes to forest mycorrhizal dominance—forests have become less ECM-dominated and more AM-dominated (Jo et al., 2019), as patterns of N deposition are positively related to the growth and recruitment of AM (but not ECM) tree species (Averill et al., 2018). Further, the N-rich soil conditions initiated by atmospheric N deposition are perpetuated in its absence (i.e. "nitrogen acceleration," Jo et al., 2019), due to the positive feedbacks instituted by AM trees (Lin et al., 2017).

A second group of soil biota, earthworms, is also central to forest biogeochemistry. Earthworms are intimately involved in nutrient cycling through their burrowing and mixing activities and their transformations of plant litter. Most earthworm communities in the eastern U.S. are dominated by exotic species, which raise soil pH, rates of litter decomposition, and N fluxes in mineral soil where they become established (Szlavecz et al. 2011; Ferlian et al., 2020; Mathieu et al., 2024). Higher leaf litter chemical quality is known to positively influence earthworm abundance, suggesting that invasive earthworms become preferentially established in forests dominated by labile litter producing tree species (Reich et al, 2005; Schelfhout et al., 2017; Bethke and Midgley, 2020). Further, invasive earthworms have been demonstrated to have negative effects on the growth of oak, but not maple seedlings (Szlavecz et al. 2011; Bethke and Midgley, 2020), inviting the possibility that invasive earthworms promote changes in tree species composition through their effect on soil biogeochemistry. Indeed, invasive earthworms have been posited as a major driver of forest community change (Craven et al., 2017), including the ongoing tree species transition in eastern U.S. forests (Frelich et al., 2019).

While not explicitly considered in the context of the mesophication hypothesis, mycorrhizal associations and earthworms have inspired separate explanations for the recent changes in eastern forests, both rooted in a biogeochemical perspective. Taken together, three disturbance-response relationships have been proposed as mechanisms of forest change—fire exclusion promoting mesophytic trees to the exclusion of pyrophytes, atmospheric N deposition promoting AM trees to the exclusion of ECM trees, and invasive earthworm introductions promoting trees with labile litter to the exclusion of those with decay-resistant litter. In each case, positive feedbacks have been proposed to propagate forest change, while negative feedbacks simultaneously resist a return to the former state. Yet, each of these disturbances has largely been considered by distinct academic disciplines (i.e. forest ecology, biogeochemistry, invasion biology) in isolation from the others, despite disturbances co-occurring across the landscape. As a result, it remains unclear whether and how these three hypotheses relate to one another. Merging perspectives of forest change may yield a more holistic understanding of the mechanisms that facilitate forest change, and those that allow forests to resist a return to their prior composition.

In this paper, we asked whether these biogeochemical mechanisms explaining forest change are related to the mesophication hypothesis. First, we evaluated the contribution of these three perspectives to the conceptual structure of studies investigating forest change using a bibliometric analysis. We hypothesized that literature was largely siloed amongst the three disciplines investigating forest change. Second, we tested the hypothesis that the AM/ECM dichotomy largely corresponds with the fire-intolerant/fire-adapted tree dichotomy in the eastern U.S. We expected to find that fire-intolerant species were largely AM, and fire-adapted species were ECM. Third, we explored species traits for bark thickness, leaf litter chemical quality, decomposability, and flammability. We hypothesized that traits for fire-adaptation would be collinear with traits for decomposability such that species with high flammability and thicker bark had high C:N and low decomposition rates. Fourth, we explored the spatial prevalence of tree species that have traits for fire adaptation and nutrient conservation (ECM mycorrhizal association) using spatially robust forest inventory data. We hypothesized a positive relationship exists amongst ECM and fire-adapted basal areas across the region. Finally, we compared the spatial extent of the change in forest species composition and the proposed change drivers. We hypothesized that fire exclusion, N deposition, and invasive earthworm establishment were all related to the transition in forest composition.

Materials and methods

Bibliometric analysis

To investigate the relationships of published literature on forest composition change focusing on fire, N deposition, and invasive earthworms, we performed a bibliometric analysis of literature. First, we searched Web of Science for papers published within the last 30 years with topics of interest using the following advanced search query in September 2024:

((PY = 1993-2024) AND ((TS="tree species" OR TS="forest composition" OR TS="tree mycorrhiza*" OR TS="tree assemblage" OR TS="plant communit*" OR TS="mycorrhiza* dominance" OR TS="dominan* mycorrhiza*" OR TS=mesophication) AND (TS=shift OR TS=alter OR TS=chang*) AND (TS="North America*" OR TS="United States" OR TS=US OR TS=Canad*)) AND (TS=fire OR TS="nitrogen deposition" OR TS="N deposition" OR TS="invasive earthworm*" OR TS="introduced earthworm*" OR TS="exotic earthworm*")) NOT (TI=boreal OR TI=arctic OR TI=prairie OR TI="bog" OR TI=grassland* OR TI="western North America*" OR TI="southwestern USA" OR TI="western United States" OR TI="western US" OR TI="western Canad*" OR TI=Alaska* OR TI="Pacific Northwest*" OR TI=paleo* OR TI="Europe" OR TI="China" OR TI="desert" OR TI="fossil")

Publication year is indicated by "PY", and title is indicated by "TI." Topic is indicated by "TS" and includes publication title, abstract, and keywords. This query returned 869 results. We first excluded titles not in English, leaving 865 results. We examined the titles and abstracts of each remaining result and excluded: 1) those outside of eastern North American temperate, subtropical, or mixed forests (434 results); 2) those not considering changes in plant communities or plant mycorrhizal dominance linked to fire, N deposition, or invasive earthworms (e.g. studies measuring only bird abundance among differing forest compositions;

174 results); and 3) those not considering forest changes within the last century (e.g. palaeoecological studies; 46 results). This filtering returned a final list of 211 results.

We explored patterns in the results using the R package bibliometrix and its associated web interface, biblioshiny (Aria and Cuccurullo, 2017). We conducted a co-word analysis of terms (bigrams) extracted from the abstracts of the results (Appendix B: Table B1). We then conducted a co-citation analysis of the references cited in each of those results. For both analyses, we used biblioshiny to create a bibliographic network (nodes = 75) and apply k-means clustering to identify shared terms and citations.

Data collection

We obtained tree inventory data from forested plots in the 26 states in the eastern United States (Alabama, Connecticut, Delaware, Florida, Georgia, Illinois, Indiana, Kentucky, Maine, Maryland, Massachusetts, Michigan, Mississippi, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, South Carolina, Tennessee, Vermont, Virginia, West Virginia, Wisconsin) from the USDA Forest Service Forest Inventory and Analysis (FIA) program (USDA Forest Service, 2024). The FIA program uses a nation-wide grid of permanent plots (approximately one plot every 2428 ha) composed of four subplots (7.3 m radius) arranged in a triangular grid. In each subplot, trees ≥ 12.7 cm diameter are measured. Nested within each subplot, there is a microplot (2.1 m radius) on which trees < 12.7 cm diameter are measured. This standard plot design was adopted by FIA in the mid-1990s, and prior periodic inventories used a variety of designs (Burrill et al., 2024). For our analyses, we excluded dead trees and timber production land.

To compare AM/ECM with fire-intolerant/fire-adapted among common tree species, we first determined the most abundant 75 tree species (in basal area) in the eastern US using FIA tree inventory data for 2015-2022. We assigned mycorrhizal status to each species based on classifications previously reported (Phillips et al., 2013; Brundrett and Tedersoo, 2019; Brundrett and Tedersoo 2020). We excluded two species that were not strictly AM or ECM: (*Oxydendrum arboreum* (L.) DC. (ericoid (ERM)) and *Salix nigra* Marshall (dual AM-ECM). The remaining 73 species accounted for 95.9% of the total basal area on FIA plots. We classified each species as fire-adapted or fire-intolerant based on classifications previously reported (Nowacki and Abrams, 2015), or from information in the Fire Effects Information System (FEIS, 2023; Appendix B: Table B2).

To compare leaf litter chemical quality and decomposition rate among AM/ECM and fire-intolerant/fire-adapted, we sought out literature values for leaf litter C:N and decomposition rate (*k* constant of negative exponential model of decay) for the most abundant tree species we identified previously. We found these data for 29 species (Appendix B: Table B3). We excluded *O. arboreum* from analyses since it forms ERM.

To compare traits for fire adaptation and decomposability/palatability amongst AM/ECM species and fire-adapted/intolerant species, we compiled traits from literature for the most abundant tree species we identified previously for leaf litter flammability (flame height, flame duration, percent consumed, smolder duration) and bark thickness to complement our compiled data on leaf litter C:N and leaf litter *k*. Since bark thickness changes with tree diameter (Jackson et al., 1999), we used the ratio of bark thickness and tree diameter. We found all these variables for 29 tree species (Appendix B: Table B3), which accounted for 71.3% of the total basal area on FIA plots in the eastern United States.

To compare spatial prevalences of ECM and fire-adapted basal area, we used our previously constructed list of 73 of the most abundant tree species classified as AM/ECM and fire-intolerant/fire-adapted and FIA tree inventory data for 2015-2022. We calculated the percentage of fire-adapted and ECM basal area on FIA plots for each county by first averaging observations for each plot (if a plot was visited multiple times), and then averaging the values across plots for each county. To account for ecological province-specific relationships, we assigned each county to one of twelve ecological provinces, which we mapped using a publicly available raster file (USDA Forest Service ECOMAP Team, 2017) and ArcGIS Pro (ESRI, 2024).

To quantify forest change, we calculated the change in mycorrhizal dominance over time. We compared FIA tree inventory data for each county from 1980-1998 (T1; 79,689 plots) to data from 2015-2022 (T2; 53,279 plots). For each tree species represented in those data, we classified each as AM, ECM, AM-ECM, ERM, or non-mycorrhizal based on classifications previously reported (Akhmetzhanova et al., 2012; Brundrett and Tedersoo, 2019; Brundrett and Tedersoo 2020; Phillips et al., 2013), or unknown if the classification could not be verified. Tree species that were classified as ERM, non-mycorrhizal, or unknown made up approximately 1% of total basal area for both time periods and were excluded from analyses. For tree species that form dual AM-ECM associations, we counted half of their basal area as AM and half as ECM. To calculate the change in AM basal area over time for each county, we started by summing the basal areas of AM and ECM trees, respectively, at each observation of a plot for the periods during T1 and T2. To find the mean AM proportion for each plot, we averaged those values and divided that average by the sum of AM and ECM basal areas. To calculate the AM proportion for each county, we took the average of the proportions from each plot within the county. Then, we subtracted the T1 AM proportion from the T2 AM proportion to find the change in AM proportion for each county (i.e. possible values range from -1 to 1 where positive values represent an increase in the proportion of AM basal area, negative values represent a decrease, and zero represents no change).

To quantify the effects of fire frequency on mycorrhizal dominance change, we extracted fire disturbance codes from FIA during the period 1999- 2022. Since 1999, FIA has collected condition data each time that a plot is visited. Those conditions include disturbance codes indicating fire damage (DSTRBCD1-3 = 30, 31, or 32), which are recorded when the area affected is at least 0.41 ha in size and damage is observed on at least 25% of trees (Burrill et al., 2024). We calculated fire observations per plot by dividing the number of times that a fire disturbance code was reported in a county by the number of distinct FIA plots in that county.

To assess the effects of atmospheric N deposition on mycorrhizal dominance change, we collected data on N deposition between 1980 and 2022 from the National Atmospheric Deposition Program's National Trends Network (NADP, 2022). We excluded sites and years with missing data, as well as "years" with less than 180 days duration. The timespan of each measurement was multiplied by the proportion of days with valid measurements to find daily deposition. That value was then multiplied by 365 to find an annualized value for each year. Once an average yearly value was found for each site, we used ArcGIS Pro's inverse distance weighted interpolation (IDW) to create a raster (ESRI, 2024). Each county was assigned a mean annual nitrogen deposition in kg/ha/year based on that raster.

To account for the effects of climate changes on mycorrhizal dominance change, we collected data on climate from Oregon State University's PRISM program (PRISM Climate Group, 2024). We calculated changes in mean annual temperature (MAT) and mean annual precipitation (MAP) based on PRISM's Recent Years rasters. We downloaded one raster for each year from 1980-1998 (T1), as well as each year from 2015-2022 (T2). We used ArcGIS Pro's raster calculator tool to make one raster with the average values for all the years in T1 and another with the average values for all the years in T2. Then, we subtracted the average T1 values from the average T2 values to get a change in MAT and MAP per county.

To assess the effects of invasive earthworm spread on mycorrhizal dominance change, we compiled invasive earthworm species occurrence and location data from three sources: Chang et al., 2021, Phillips et al., 2021, and Drake et al., 2024. Using the location data, we were able to assign each county as having had invasive earthworms recorded or not. In addition, we classified each species according to its ecological group based on feeding/burrowing behavior (anecic, endogeic, epigeic, or epi-endogeic; Phillips et al., 2021) and used the location data to map counties where each group had been recorded or not.

Statistical analyses

To compare AM/ECM with fire-intolerant/fire-adapted among 73 of the most abundant tree species, we classified fire-adapted as a score of one and fire-intolerant as a score of zero and conducted a logistic regression (all analyses conducted in R version 4.4.1; R Core Team, 2024) in which mycorrhizal association type was the sole fixed effect. We assessed significance using the Wald χ^2 test (Anova function in the car package; Fox and Weisberg, 2019).

To compare leaf litter C:N and *k* amongst AM/ECM and fire-intolerant/fire-adapted tree species, we used 28 species for which we had compiled data. We compared leaf litter C:N to fire adaptation classification and AM/ECM using a linear model in which we allowed the two effects to interact. Then, we compared leaf litter *k* to fire adaptation and AM/ECM using a similarly constructed linear model. We assessed significance in both models using analysis of variance (Anova function in the car package; Fox and Weisberg, 2019).

To explore patterns in traits for fire adaptation and decomposability/palatability amongst AM/ECM species and fire-adapted/intolerant species, we performed a principal components analysis (PCA) on our compiled literature values for 29 abundant tree species (prcomp function in the stats package; R Core Team, 2024). First, we conducted a PCA on only the four litter flammability metrics. We used the primary principal component (PC1) from that analysis as "flammability" in the subsequent PCA that included the other trait variables (Appendix B: Figure B1).

To determine the relationship between fire-adapted basal area and ECM basal area, we used two generalized additive models (GAM) using the mgcv package (Wood, 2011). For both models, we included a smooth over the latitude and longitude of the centroid for each county to account for spatial dependence in our data (Wood, 2017). Our first GAM compared the percentage of fire-adapted basal area as a function of ECM basal area (as a linear term) to understand the overall effect. Our second GAM compared fire-adapted basal area as a function of the linear interaction of ecological province and the percentage of ECM basal area to understand province-specific relationships. Significance was assessed using the Wald test (anova.gam function in the mgcv package). We performed *post-hoc* comparisons using estimated marginal means (emtrends and emmeans functions in the emmeans package; Lenth, 2024).

To understand the effects of hypothesized drivers of forest change on our county-level data, we constructed a GAM using the mgcv package (Wood, 2011) with a smooth over the latitude and longitude of the centroid for each county to account for spatial dependence in our data (Wood, 2017). We included the difference in AM dominance (T2-T1) as the response variable and the following linear predictors: fires per plot, mean N deposition, the presence of invasive earthworms, ecological province, and changes in MAP and MAT. We assessed the significance of each predictor using the Wald test (anova.gam function in the mgcv package). For the final version of this model used to plot predictions, we removed predictor variables that were non-significant at $P \leq 0.1$. We performed post-hoc comparisons among province estimates using estimated marginal means (emmeans function in the emmeans package; Lenth, 2024). We similarly constructed four additional GAMs, including the predictors described here, with linear terms of the presence of the four ecological groups of earthworms, rather than the presence of invasive earthworms overall, to determine patterns of individual ecological groups.

Results

For our bibliometric analysis, we performed a co-word and co-citation analysis on 211 papers resulting from our literature search. In our co-word analysis of the abstract texts from papers on forest change, we found three clusters in the conceptual structure indicated by Bibliometrix. The strongest linkages between the three clusters were to "species composition" and to a lesser degree, "plant community," (Figure 3.1a). The three clusters indicated distinct conceptual groupings: 1) fire regime-fire management-pine-southeast-coastal plain, 2) fire exclusion-hardwood-oak-maple, and 3) plant community-forest understory-seedling-invasive earthworm-N deposition-northeast. Our co-citation analysis of the bibliographies of those papers also yielded three main clusters: 1) papers on fire, 2) papers on earthworm invasion, and 3) papers on N deposition, though Bibliometrix detected two minor clusters linking those (Figure 3.1b).

For our logistic regression of fire adaptation given AM or ECM mycorrhizal association for 73 of the most abundant tree species in FIA plots, we found that the probability of fire-adaptation was higher for ECM than AM tree species ($\chi^2 = 16.7$, $d.f. = 1$, $P < 0.001$). Our model predicted the probability of fire adaptation to be 0.07 for AM species and 0.65 for ECM species (Figure 3.2).

In our comparison of leaf litter C:N and k for fire-adapted/intolerant and AM/ECM among 28 tree species, we found no relationship between leaf litter C:N and fire classification or mycorrhizal association ($P > 0.1$; Figure 3.3a). We found a relationship between leaf litter k and fire classification such that the mean k value for fire intolerant species was 2.4x greater (i.e. faster decomposition) than the mean value for fire-adapted species ($F = 6.3$, $d.f. = 1$, $P = 0.02$), but we found no relationship between leaf litter k and mycorrhizal association (Figure 3.3b).

In our PCA of tree species traits for 29 species, we found that the first three principal component axes accounted for 36.8%, 27.9% and 22.0% of the explained variance, respectively (Figure 3.3c; Appendix B: Figure B2). Within the plane of the first two principal components, two notable dimensions of trait variation stand out. Variation along PC1 was largely associated with decomposition rate (k) and leaf litter C:N, in opposing directions. Variation along PC2 was associated with litter flammability and bark thickness:diameter, which were collinear. In this trait space, we did not encounter collinearity amongst decomposability and flammability or bark thickness. We found that within the trait space of high C:N, high flammability, slow decomposition and thick bark was occupied by only ECM species. Further, AM tree species are tightly clumped, while ECM species encompass and extend beyond the trait space occupied by AM species. Among ECM species, there is a slight separation of fire-adapted and fire intolerant species. We compiled trait data for only one fire-adapted AM species (*Sassafras albidum* (Nutt.)

Nees) and one ERM species (*O. arboretum*), preventing us from assessing fire classification patterns in those groups.

In our analysis of fire-adapted vs. ECM basal area for each county, we found an overall positive relationship of the percentages of ECM and fire-adapted basal area ($F = 3{,}300.0$, $d.f. = 1$, $P < 0.001$), but the slope estimate of 0.81 fell below the 1:1 line (Figure 3.4a). When we included an interaction of ecological province (Figure 3.4b), we found that the relationship differed by province (province x % ECM: $F = 5.6$, $d.f. = 11$, $P < 0.001$), such that the estimated slope varied from 0.37 for Adirondack-New England to 1.03 for Everglades (Figure 3.4c).

In our county level analysis of hypothesized change drivers (Figure 3.5), we found a negative relationship between AM dominance change and fire frequency ($F = 6.8$, $d.f. = 1$, $P = 0.01$), such that without fire, the predicted change was 0.1 (i.e. a 10% increase in AM basal area over time) and the predicted change diminished to zero with increasing fire frequency (Figure 3.6). We found that precipitation change had a near-significant positive relationship with AM dominance change ($F = 2.8$, $d.f. = 1$, $P = 0.1$), such that counties had higher AM dominance over time where precipitation had increased more (Appendix B: Figure B3). Even after accounting for spatial dependence among counties, ecological province had a significant effect on AM dominance change ($F = 2.1$, $d.f. = 11$, $P = 0.02$), such that positive model estimates differed from zero for all regions except Everglades and Lower Mississippi (Appendix B: Figure B4). We found no detectable relationship between AM dominance change and N deposition, invasive earthworm presence, or MAT changes ($P > 0.1$; Figure 3.5c-d). Additionally, we found no detectable effect of the presence of different ecological groups of earthworms on AM dominance change ($P > 0.1$; Appendix B: Figure B5).

Discussion

In the original conception of the mesophication hypothesis, authors acknowledged the likely role of soil nutrients. However, few studies have explicitly tested how biogeochemistry is related to increasing forest species transitions. Instead, forest biogeochemical alterations have been investigated through the lenses of other disturbances— atmospheric N deposition leading to AM tree expansion, and invasive earthworm introductions leading to palatable-litter-producing tree encroachment. We explored evidence for how these transitions may be linked. Overall, our results suggest that forest compositional changes in the eastern U.S. are towards fire-intolerant, AM-associating, fast-decaying-litter-producing tree species, which are largely the same tree species. This suggests that each human disturbance (i.e. fire exclusion, N deposition, and invasive earthworm introductions) may reinforce the shift towards an increasingly mesophytic species composition in eastern U.S. forests.

In our bibliometric co-word analysis, we did not find the expected clusters indicating three perspectives of inquiry (i.e. forest ecology, biogeochemistry, and invasion biology), but rather we found clustering related to geography and focus. The terms, “coastal plain”, “pine *Pinus*”, “fire regime”, “southeastern”, and “prescribed fire” were clustered together while “northeastern north,” “northern hardwood,” “nitrogen deposition,” “invasive earthworms, and “forest understory,” made up another cluster (Figure 3.1a). These indicate that, of the papers examining forest transition, those exploring forest management using prescribed fire tend to be in southeastern or coastal plain pine-dominated forests. This is consistent with the area’s overwhelming representation in fire occurrences (Figure 3.6b) and long history of using prescribed fire in forest management (Mitchell et al., 2014). Papers focused on invasive earthworms and N deposition tended to be in the northern part of the region, and particularly in the northeast. This clustering may be due to higher rates of N deposition in the northern areas (Figure 3.6c) and the fact that the region has no native earthworm fauna (Mathieu et al., 2024). The N deposition/earthworm cluster is also linked to “forest understory,” “plant community,” and “seedling establishment,” suggesting these papers tend to focus on understory plants and tree seedlings rather than dominant overstory trees. The terms, “oak, “maple,” “mesophytic species,” and “fire exclusion,” were represented in one cluster, suggesting the shift among those two genera tend to be linked to the explanatory cause of fire exclusion. Though we did not see the expected pattern among academic disciplines, the clustering highlights that fire is generally not considered in studies on effects from N deposition and invasive earthworms and that biogeochemical changes are seldom considered in studies on fire exclusion or fire management.

In our bibliometric co-citation analysis, we found that co-cited papers tended to largely be within clusters indicating the perspectives of inquiry: 1) forest (fire) ecology (green cluster in Figure 3.1b), 2) N deposition effects (yellow cluster), and 3) invasive earthworm effects (blue cluster). While the clustering is unsurprising given the search criteria, the dominance of linkages within clusters, rather than among them, shows that most co-citations are within the same perspective (e.g. two papers about fire are cited together more than two papers where one is about N deposition and one is about fire), partially confirming our hypothesis that studies rarely consider multiple drivers of forest change. A couple of notable exceptions stand out: two papers on mammals (Pournelle and Barrington, 1953; Côté et al., 2004) are co-cited with papers in both the fire and earthworm clusters, likely due to recent investigations of links between rodents/deer and invasive earthworms on plant communities (e.g. Jonsson et al., 2023; Reed et al., 2023). Likewise, a study on N deposition effects on tree C storage (Thomas et al., 2010) is co-cited with papers in both the N deposition and fire clusters.

Among the most abundant tree species in the eastern U.S., we found that AM species are largely classified as fire-intolerant, whereas ECM trees are generally classified as fire-adapted (Figure 3.2), mostly supporting our hypothesis. However, there are some common fire-intolerant ECM species (e.g. *Fagus*), and a couple fire-adapted AM species (e.g. *Sassafras*). These results suggest that studies of eastern U.S. forests investigating mesophication, and those investigating increases in AM dominance, may very well be considering the same tree species under a different name, although rarely framed as such.

Among the 28 ECM/AM tree species we compiled traits for, we found no relationship among fire-adapted/fire intolerant or ECM/AM on leaf litter C:N (Figure 3.3a). The lack of an ECM/AM effect on leaf litter C:N contrasts with previous work showing differences in litter stoichiometries among ECM/AM tree species (Averill et al., 2019), suggesting data on more species may reveal a relationship. However, we did find higher leaf litter decomposition rates for fire-intolerant species than for fire-adapted species (Figure 3.3b). This finding extends the pattern of faster decomposition in maple versus oak litter (Alexander and Arthur, 2014) to the guilds of fire-intolerant versus fire-adapted tree species.

While we were able to classify trees as fire-adapted or fire-intolerant based on prior literature, it is important to point out that tree species exhibit many traits for fire-adaptation (e.g. thick bark, flammable litter, epicormic buds) that fall along gradients. This suggests that a simple dichotomy of fire-adapted/fire-intolerant is tenuous, unlike the mostly discrete AM/ECM categorization. For this reason, we found it important to quantitatively evaluate patterns among species within that trait space using PCA. When we explored patterns in these data, we did not find that flammability was collinear with decomposition rate, in contrast with our hypothesis. In fact, the two vectors were at right angles, showing they were completely uncorrelated (Figure

3.3c). However, species occupying the trait space of slow decomposition rate, high litter C:N, high flammability and thick bark (lower left quadrant in Figure 3.3c) are all ECM-associated, fire-adapted oak and pine, suggesting that these traits correspond in some tree species. Tree species occupying the trait space of high decomposition rate and high flammability (e.g. *Liriodendron* and *Nyssa*) call into question the ecological relevance of flammability metrics for fast-decaying species. That is, even if a species produces highly flammable litter, if it decays rapidly, it has a narrow temporal window to promote fire. There are a couple of caveats with these compiled trait data on 29 species. First, while ECM species represented 57% of the most abundant species in the eastern U.S. (Appendix B: Table B2), they account for 66% of the species in our trait data, largely driven by higher proportions of data for *Pinus* and *Quercus* than other genera (Appendix B: Table B3). Second, for ease of interpretation, we used the primary principal component from a PCA on literature values for four flammability metrics to describe flammability's variance with other traits, but this technique is imperfect at fully capturing the litter flammability of a given species.

Using data on the 1,564 counties in the eastern U.S., we compared the relationship of fire-adapted basal area and ECM basal area, expecting to find a strong positive relationship. We found a positive relationship (slope of 0.81), with many counties on the ECM side of the 1:1 line (i.e. more ECM than fire-adapted; Figure 3.4a). This is consistent with our other findings demonstrating that some abundant ECM species are fire-intolerant (Figure 3.2; Figure 3.3c). Interestingly, the slope of the regression differed by ecological province such that most slopes in the southern part of the region did not significantly differ from one, while more northern provinces did (i.e. increasing ECM basal area did not increase fire-adapted basal area; Figure 3.4b-c). Incorporating prevalences of fire-adapted and ECM tree basal area highlights an important nuance in our consideration of how these traits are distributed. Our findings suggest that, how synonymous "ECM" is with "fire-adapted" largely depends on the location of consideration. Further, it is worth noting that provinces with slopes closest to one are those where fire is most frequent on the landscape (Figure 3.5b), and/or where fire has historically been frequent (Guyette et al., 2006; Lafon et al., 2017), suggesting that frequent fire regimes may have restricted ECM-fire-intolerant species to more northern latitudes.

In our analysis of the spatial extent of forest change, we found that most counties in the eastern U.S. have increased in AM tree basal area in recent decades (Figure 3.5a; Appendix B: Figure B6). We found that fire frequency was negatively associated with AM expansion (Figure 3.5b; Figure 3.6), partially confirming our hypothesis. However, in contrast with our hypothesis, we were unable to detect relationships between AM expansion and atmospheric N deposition or invasive earthworm records (Figures 3.5c-d). While acknowledging that our hypothesis may be incorrect, there are limitations with these data that may explain why we were unable to detect such a relationship. The inventory data used to calculate forest change and fire frequency (USDA Forest Service, 2024) are spatially robust, and were both collected on FIA plots. In contrast, atmospheric N deposition is less robust, requiring some interpolation, and was collected in locations removed from forest change measurements. Similarly, earthworm presence was measured separately from forest change, and we were unable to standardize earthworm biomass or density from our data sources due to differing collection methods. Therefore, we could only verify if invasive earthworms were recorded in each county, and they overwhelmingly were (Figure 3.5d). We did find a significant relationship between forest change and ecological province, which was somewhat surprising given our explicit modeling of the spatial dependence within the dataset (Appendix B: Figure B4).

We present an integrated framework that considers both fire and soil biogeochemistry in the context of changing eastern US forests. In the original mesophication hypothesis, fire exclusion has promoted the rise of fire-intolerant tree species and an ecosystem that increasingly suppresses fire, largely due to modification of litter fuel beds (Nowacki and Abrams 2008; Alexander et al., 2021; Figure 3.7a). A second view of forest change implicates atmospheric nitrogen (N) deposition for promoting conditions that favor AM tree species over ECM tree species, which then further promote rapid decomposition and N cycling in the ecosystem (Lin et al., 2017; Averill et al., 2018; Jo et al., 2019; Figure 3.7b). A third view is that invasive earthworms have favored tree species that produce fast-decaying litter, while suppressing those that produce slow-decaying litter (Szlavecz et al. 2011; Frelich et al., 2019; Bethke and Midgley, 2020; Figure 3.7c). In each of these cases, the tree traits favored by disturbance are largely shared among species (Figure 3.7d). That is, fire-adapted tree species tend to associate with ECM fungi and produce nutrient-poor, slow-decaying litter that is unpalatable to invasive earthworms. Thus, by considering multiple dimensions of tree functional traits, three apparent transitions can be distilled into one.

One possibility raised here is that the reinforcement of fire and soil biogeochemistry (Figure 3.7d) means that multiple disturbances help promote the ecosystem state transition. For example, when fire exclusion favors the expansion of fire-intolerant tree species, it may also favor the nutrient acquisition strategies of AM tree species, even in the absence of elevated atmospheric N deposition. Similarly, earthworm invasion increases soil pH, thereby possibly promoting N transformations that most benefit AM tree species (Ferlian et al., 2020; Lin et al., 2022). We speculate that fire-biogeochemical relationships could also provide an explanation for why forests seem to resist a return to the former species composition. For example, fire alone may not promote pyrophytes if atmospheric N deposition or invasive earthworm establishment has entrenched N-rich soil conditions. This possibility aligns with the prediction of Nowacki and Abrams (2008) that mesophication would proceed most slowly in nutrient-poor sites, and these biogeochemical mechanisms may explain why. Empirical studies evaluating biogeochemical alterations through each disturbance are required to further investigate this possibility and studies on the ability of management actions to eliminate nutrient-rich conditions may point toward a path forward.

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Data and code availability

Forest inventory and fire data are available at https://apps.fs.usda.gov/fia/datamart/datamart.html. Nitrogen deposition data are available at https://nadp.slh.wisc.edu. Climate data are available at https://prism.oregonstate.edu/. Data on earthworm reports are available at https://doi.org/10.1038/s41597-021-00912-z, https://doi.org/10.1007/s10530-021-02598-1, and https://figshare.com/s/3a5b2cba8d6475eff7e7.

Code for extracting and compiling these data are available at https://github.com/JasonSteelmanCoder/east_us_mycorrhizal_changes.

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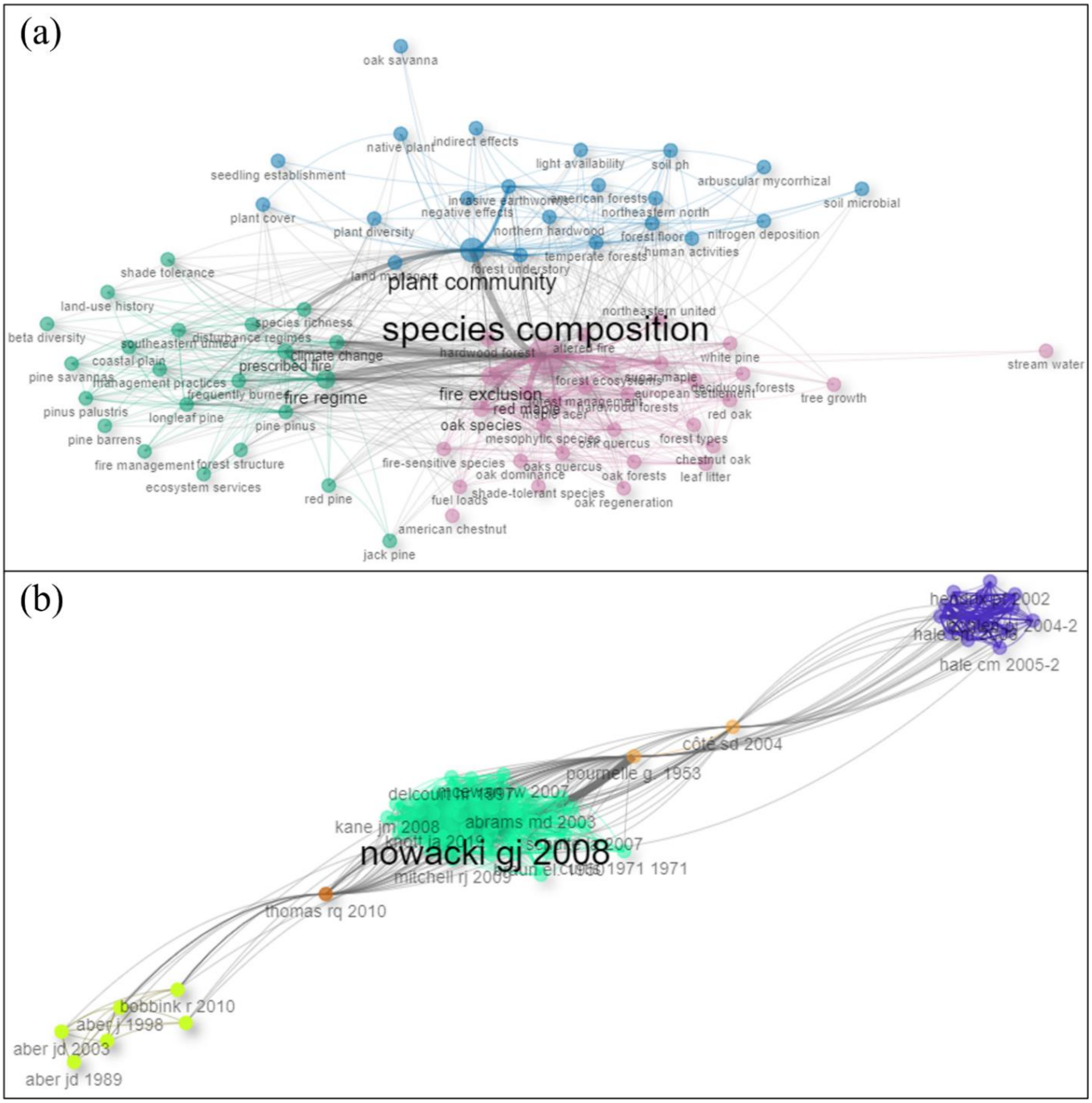

Figure 3.1. Bibliometric analysis of 211 papers on forest change in eastern North America. (a) Co-word network of text extracted from abstracts detected three distinct clusters (shown in different colors). Linked concepts appear in the same paper, with thicker links indicating more shared papers. (b) Co-citation network of bibliographies extracted from each paper detected three main clusters, with two minor clusters linking them (shown in different colors). Co-cited papers are indicated by links. Image created with Bibliometrix.

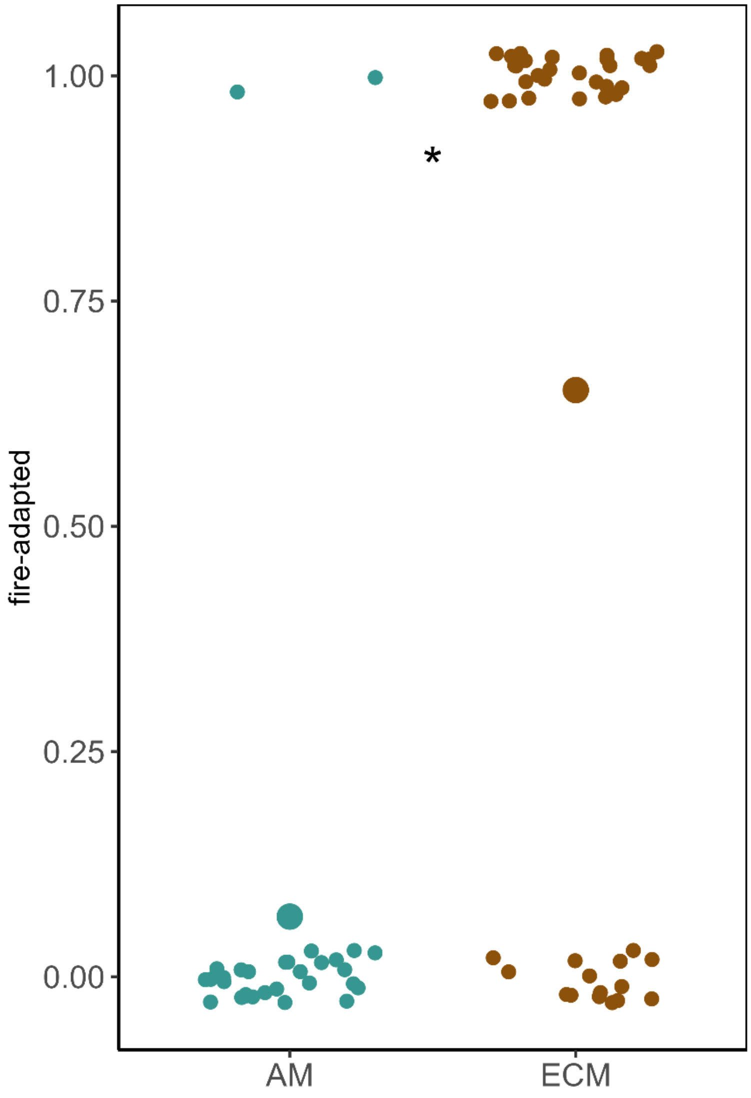

Figure 3.2. Logistic regression results for 73 of the most abundant tree species in the eastern United States. Fire adaptation is classified as zero for fire-intolerant species and one for fire-adapted species. Larger points represent model predictions. The asterisk indicates statistical significance ($P \leq 0.05$). Species represented in this figure account for 95.9% of basal area on forest inventory plots in the eastern United States.

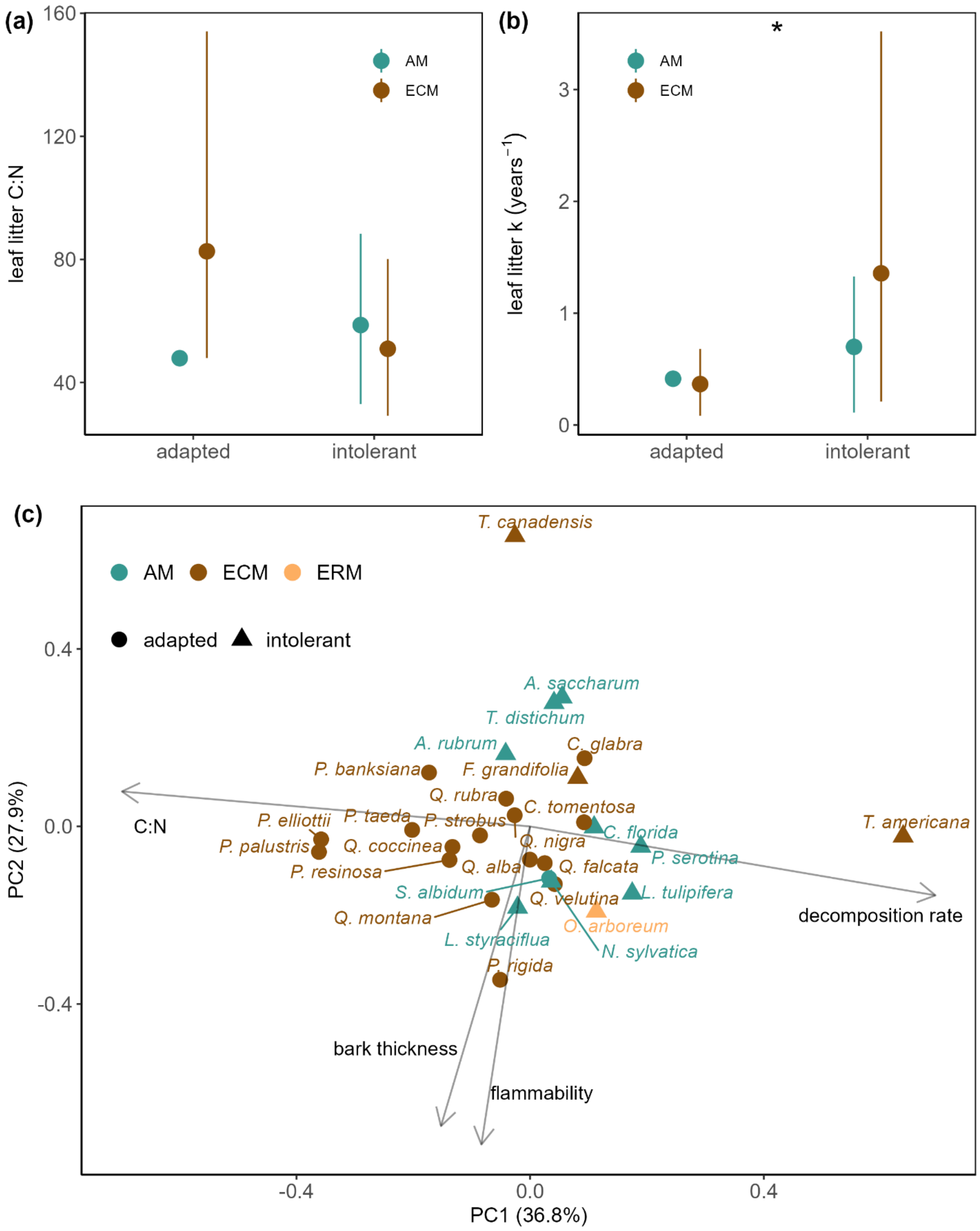
(a)
leaf litter C:N
160
120
80
40
AM
ECM
adapted
intolerant
(b)
*
leaf litter k (years^{-1})
3
2
1
0
AM
ECM
adapted
intolerant
(c)
AM
ECM
ERM
adapted
intolerant
T. canadensis
A. saccharum
T. distichum
A. rubrum
C. glabra
P. banksiana
F. grandifolia
Q. rubra
C. tomentosa
P. elliottii
P. taeda
P. strobus
C. florida
T. americana
P. palustris
Q. coccinea
Q. nigra
P. serotina
P. resinosa
Q. alba
Q. falcata
S. albidum
L. tulipifera
Q. velutina
Q. montana
O. arboreum
L. styraciflua
N. sylvatica
P. rigida
C:N
decomposition rate
bark thickness
flammability
PC2 (27.9%)
0.4
0.0
-0.4
PC1 (36.8%)
-0.4
0.0
0.4

Figure 3.3. Species traits categorized by fire adaptation and mycorrhizal association. (a) Leaf litter C:N, (b) decomposition rate (*k*), for 28 tree species categorized as arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM), and fire-adapted or fire-intolerant. (c) Principal components analysis ordination across traits for fire adaptation and litter decomposability/palatability for 29 common tree species. Colors indicate mycorrhizal association while shapes indicate fire adaptation classification. Abbreviated species names are in italics. Arrows indicate direction and weighting of vectors representing the four traits considered. In (a) and (b), points indicate mean values, lines indicate the range, and asterisks indicate statistical significance ($P \leq 0.05$). In (c), flammability is the resulting primary principal component from a principal components analysis of four litter flammability traits. Bark thickness is the ratio of bark thickness to tree diameter.

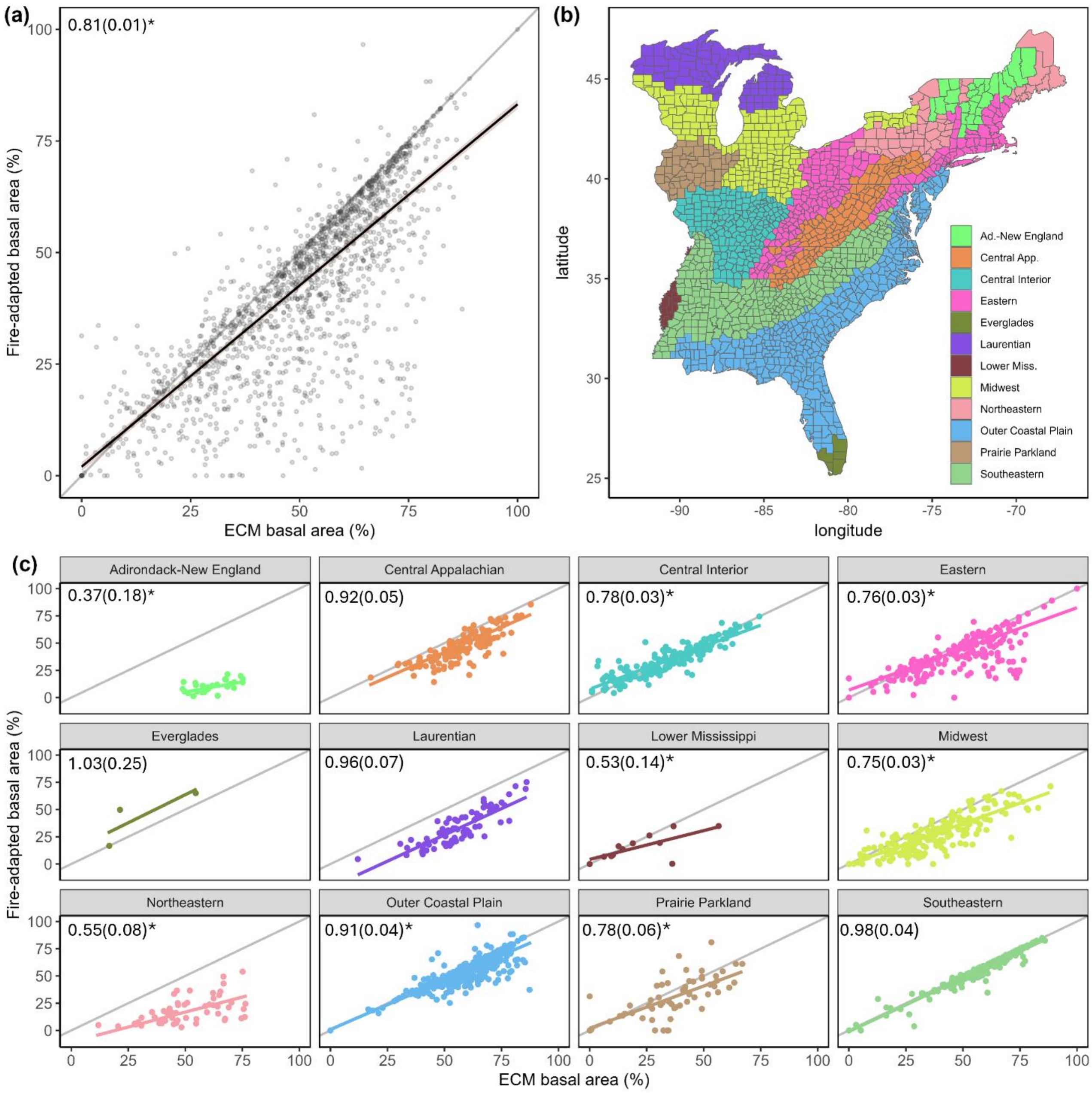

Figure 3.4. A county-level comparison of the percentages of fire-adapted and ectomycorrhizal (ECM) species basal area in the eastern United States. (a) The overall pattern, (b) A map of the 12 ecological provinces of the region, (c) Individual province relationships. Basal area calculations used forest inventory data. In (a) and (c), each point represents a county, the gray

line is 1:1, and the other line represents model predictions. Values in the upper left are estimated slopes (standard error) and asterisks indicate slopes statistically different than one ($P \leq 0.05$).

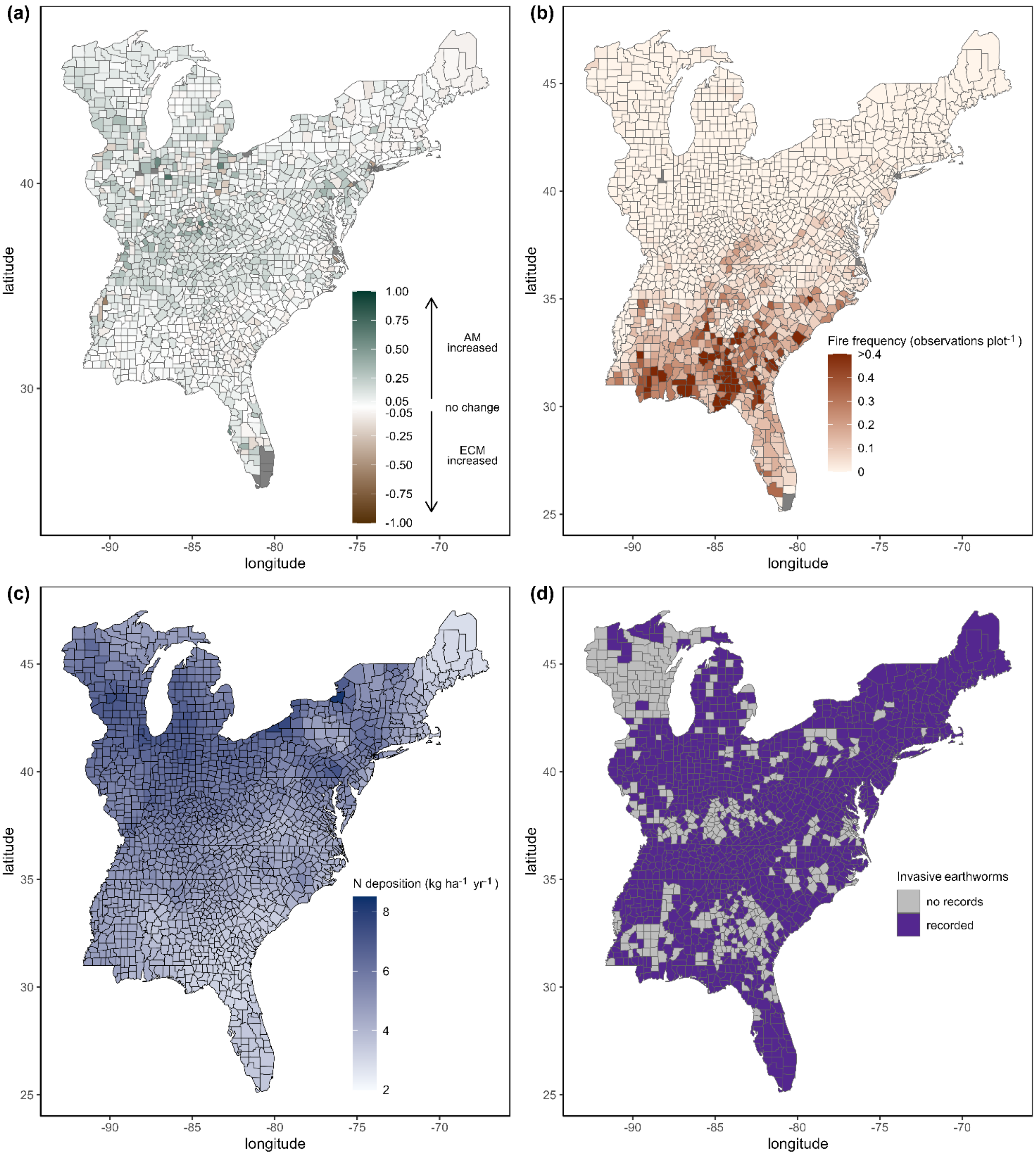

Figure 3.5. County-level maps of the eastern United States indicating forest change and the predicted change drivers. (a) The difference in the proportion of arbuscular mycorrhizal (AM) species basal area between T2 (2015-2022) and T1 (1980-1998), calculated from forest inventory data. ECM = ectomycorrhizal. Colors indicate the direction and magnitude of change. Gray indicates missing data. (b) Fire observations in forest inventory plots per the number of plots (1999-2022). (c) Mean atmospheric nitrogen deposition (1980-2022). (d) The presence of records of invasive earthworm occurrence.

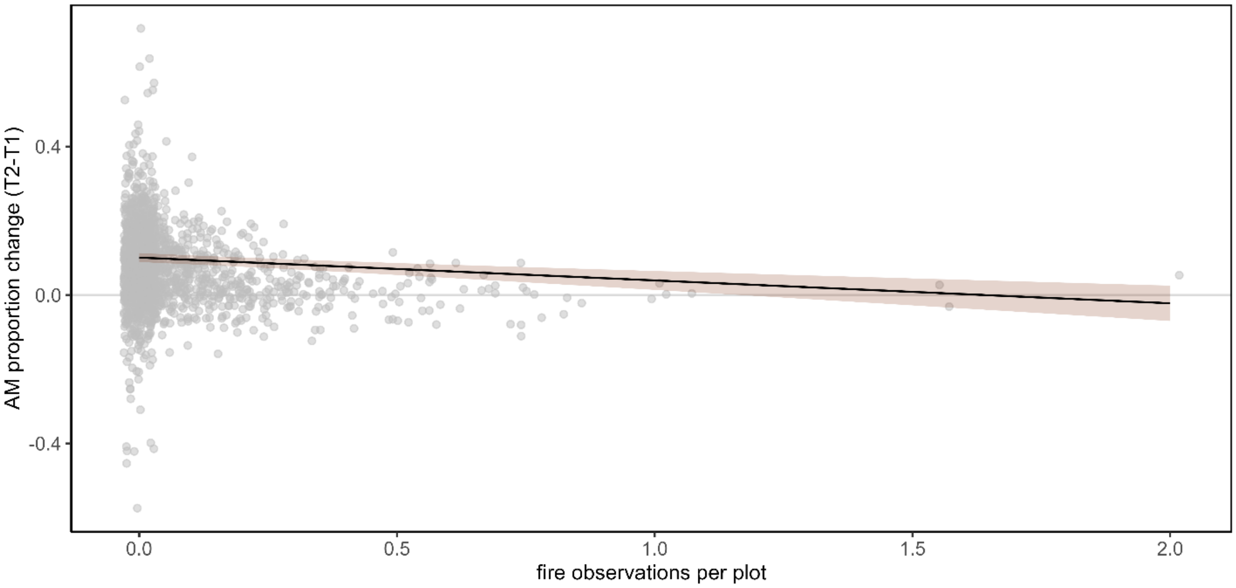

Figure 3.6. Basal area proportion changes of arbuscular mycorrhizal (AM) tree species compared to fire frequency from forest inventory data. Each point represents a county. The gray line indicates no change (zero). The black line is the model prediction shaded by its estimated standard error.

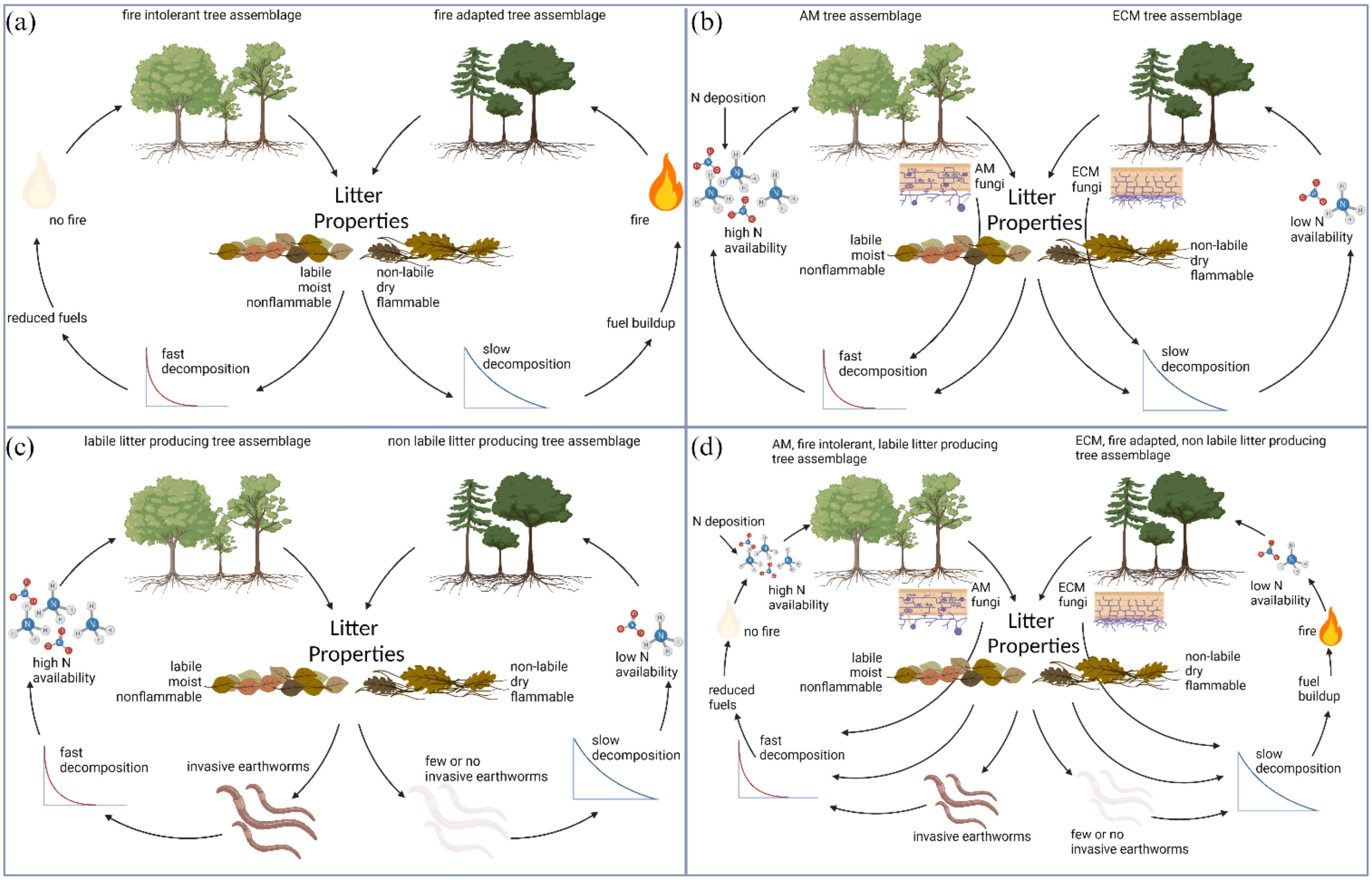

Figure 3.7. Hypothesized drivers of ecosystem state change in eastern North American forests. Positive and negative feedbacks reinforce the change in the context of three human disturbances (a-c). These changes largely involve the same tree species, suggesting that they should be considered together (d). (a) Fire exclusion promotes fire-intolerant tree species, which tend to produce labile, moist, and nonflammable litter. This litter decomposes quickly and is therefore unavailable for fires, further reducing fire and excluding fire-adapted tree species. (b) Atmospheric nitrogen (N) deposition causes high N availability in soils, which benefits tree species that associate with arbuscular mycorrhizal (AM) fungi. AM trees produce labile litter that decomposes quickly, contributing to a higher availability of N. This further excludes tree species that associate with ectomycorrhizal (ECM) fungi, which mine N from organic matter; (c)

Invasive earthworms increase rates of litter decomposition, which leads to higher nutrient availability, which favors tree species that produce labile litter, the preferred food source of invasive earthworms. This effect of earthworms on nutrient dynamics further excludes tree species that form nonlabile litter. (d) These three models of ecosystem state change can be unified into one. Many fire-adapted tree species associate with ECM fungi and produce non-labile litter. All models of alternative stable states hinge on litter decay, which has direct effects on nutrient dynamics. Image created with Biorender.com.

CHAPTER 4

PAYING DOWN RESILIENCE DEBT: MECHANICAL FELLING AND REPEATED PRESCRIBED FIRE MAY SUSTAIN EASTERN OAK FORESTS[3]

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[3] Taylor, M.K., Hagan, D., Coates, T.A., DeFeo, J., Callaham Jr., M.A., Mohr, H., Waldrop, T., and N. Wurzburger. Submitted to *Ecological Applications* 4/3/2024.

Abstract

Tree species assemblages of eastern North American forests have shifted to become less oak-dominated and increasingly composed of mesophytic species such as maples. The replacement of oaks is widespread, threatening the ecosystem services these forests provide. Researchers have sought to understand whether forest management actions can halt or reverse this change. One large scale study of forest management practices was the national Fire and Fire Surrogate (FFS) study. The Green River FFS site in western North Carolina was initiated in 2001 and has continued to have treatments applied, offering the opportunity to understand how management actions affect forest composition. The Green River FFS site implemented three experimental treatments replicated across three spatial blocks: mechanical felling of saplings and ericaceous shrubs (Mech), prescribed fire (Fire), and a combination (Mech + Fire), which were compared to untreated controls (Control). Here, we used this long-running experiment to evaluate changes in overstory basal area, forest composition, and duff depth 17 years after its initiation. We found that basal area increased in the Control and Mech treatments, was unchanged in the Fire treatment, and decreased in the Mech + Fire treatment. Duff depth decreased in the two prescribed fire treatments but was only related to overstory mortality in the Mech + Fire treatment. Oak sapling abundances increased with increasing loss of basal area; a pattern not found with their major mesophytic competitor, maples. This suggests that oaks are well positioned to outcompete maples at the Green River FFS site in plots where basal area has decreased due to overstory mortality, which are mostly in the Mech + Fire treatment. These results indicate that the Mech + Fire treatment created conditions where oak saplings were competitive, but doing so required the mortality of overstory trees, including oaks. Taken

together, our findings suggest that the misalignment of past and current fire regimes has led to resilience debt in oak forests, which may be “paid” through the death of overstory trees when management actions simulate a severe disturbance. Combined with repeated prescribed fires, such a payment may promote sustained oak dominance in the future.

Introduction

Forests of eastern North America have been characterized over the past century by extensive changes in tree species composition. Mounting evidence demonstrates the change from forests composed primarily of oaks (*Quercus* spp. L.) to forests increasingly dominated by maples (*Acer* spp. L.) and other mesophytic species (Fei et al., 2011; Jo et al., 2019; Knott et al., 2019), a process widely termed “mesophication” (Nowacki and Abrams, 2008). Implications of this change are potentially massive and widespread, touching on declining necessities for wildlife populations (McShea et al., 2007) and human water needs (Caldwell et al., 2016). Although the need for solutions is clear, the problem has been a slow-moving one as tree populations turn over gradually, and as such, science has yet to answer questions regarding which management actions may be necessary to halt or reverse this change.

The current composition of eastern North American forests (hereafter eastern forests) has been shaped by centuries of disturbances. Oaks dominated most eastern forests prior to European Colonization (Hanberry and Nowacki, 2016), which resulted in widespread logging and the clearing of forested land for agriculture (Ayres and Ashe, 1905; Thompson et al., 2013). During the last century, many lands have been reforested while concurrently, atmospheric nitrogen (N) deposition has increased (Boerner et al., 2008; Averill et al., 2018) and most of eastern North

America has fallen under widespread fire exclusion (Nowacki and Abrams, 2008). Fire exclusion has led to the expansion of ericaceous shrubs in some forests (Lafon et al., 2022), including great rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifoli*a L.), which have reduced light availability to young trees and suppressed oak regeneration (Brose, 2016). As a result of these disturbances and the resulting patterns of forest successional trajectories that have favored mesophytes (Wurzburger et al., 2023), eastern forests today are less oak-dominated than they were a few centuries earlier.

Researchers and land managers have sought solutions to halt the trajectory of oak decline. Recognizing that young oaks failed to compete with mesophytic tree species, particularly red maple (*Acer rubrum*, L.) and yellow-poplar (*Liriodendron tulipifera*, L.), for canopy positions (i.e. regeneration failure; Lorimer, 1993) in forests that were increasingly denser, shadier, and less flammable (Nowacki and Abrams, 2008; Alexander et al., 2021; Woodall and Weiskittel, 2021), studies focused primarily on the use of prescribed fire and thinning to encourage oak regeneration. Early results from these studies suggested that neither prescribed fire nor thinning alone is sufficient to halt the encroachment of mesophytes into areas previously dominated by oaks (Arthur et al., 2015; Hutchinson et al., 2005; Hutchinson et al., 2012; Keyser et al., 2017; Schweitzer and Dey, 2011). The combination of prescribed fire and thinning seems promising, given the dual necessities of minimizing fire-intolerant competitors and providing young oaks with sufficient light to reach overstory positions. Indeed, early results from such studies have shown an increase in oak reproduction, but with continued strong mesophytic competition (Iverson et al., 2008, 2017; Schweitzer et al., 2019; Waldrop et al., 2016, but see Albrecht and McCarthy, 2006). Given the slow turnover of tree populations, continued treatments and monitoring from such studies will provide valuable guidance for researchers and land managers.

The reintroduction of fire after long-term exclusion poses an unexpected and counterintuitive risk to oak-dominated forests. Recent evidence from the southern Appalachians suggests that long-term fire exclusion led to an accumulation of soil Oe and Oa horizons, or duff, which when burned, makes fire-adapted trees, including oaks, more vulnerable to post-fire mortality (Carpenter et al., 2021). Tree roots readily colonize nutrient-rich duff, which when sufficiently dry, can act as fuel for fire. When duff, and roots therein, are consumed during fire, it can lead to high rates of tree mortality (Varner et al., 2005; O'Brien et al., 2010). Thus, the return of fire to fire-adapted but long-unburned oak forests can lead to oak decline and may represent an example of resilience debt (sensu Johnstone et al., 2016). That is, the misalignment of past and current fire regimes led to a loss of resilience, or debt, in oak forests, which is "paid" through increased mortality when fire is returned. As such, future wildfires may continue to contribute to oak decline (Robbins et al., 2022), highlighting the need to understand how fire can be reintroduced to long-unburned forests without furthering the demise of oaks. Multiple prescribed fires over time may prove useful for minimizing the buildup of duff, but it remains unclear if prescribed fire can successfully diminish existing duff layers without leading to increased tree mortality.

Successful oak regeneration begins when sufficient light is available to oak seedlings on the forest floor (Lorimer, 1993 and references therein). These seedlings can grow to saplings when competition from mesophytes or evergreen ericaceous shrubs is minimized, and ultimately may recruit to the overstory (Dey, 2014). This opportunity usually occurs when overstory trees die, leaving canopy gaps where sufficient light reaches smaller trees. Indeed, a combination of canopy gaps and multiple prescribed fires that limit mesophyte competition can increase oak regeneration and advancement (Izbicki et al., 2020). One way in which canopy gaps (and/or removals of ericaceous shrubs) are created is through severe fires that lead to overstory mortality. Such fires are generally the product of high fuel loadings (i.e. duff, tree litter, or dead vegetation; Waldrop et al., 2016), but can also be related to site moisture. For example, repeated prescribed fires in Ohio led to increased overstory mortality and oak regeneration in drier sites relative to moist ones (Iverson et al., 2008; Iverson et al., 2017; Hutchinson et al., 2024). Taken together, these findings invite the possibility that in the current ambient conditions of eastern forests, heightened overstory mortality is a necessary sacrifice for the advancement of young oaks. That is, the payment of resilience debt through the death of overstory trees, combined with a return to the fire regime in which they evolved, may result in the return of oak dominance if sufficient ecological memory (e.g. acorns and oak seedlings) is held in the system (Johnstone et al., 2016; Webster et al., 2018). If this is the case, understanding the interaction of management actions with resilience debt and ecological memory will be vital to our ability to promote and sustain oak forests moving forward.

One large scale study of forest management practices was the national Fire and Fire-Surrogate (FFS) study (McIver et al., 2012). In the FFS study, three forest treatments: mechanical thinning or felling (Mech), prescribed fire (Fire), or a combination (Mech + Fire) were experimentally applied and compared to untreated controls (Control). One location of the FFS study, the Green River site in western North Carolina, used mechanical felling of saplings and ericaceous shrubs as the Mech treatment. The Green River FFS site has continued to have experimental treatments applied after the FFS study ended, allowing the opportunity for the continued monitoring of treatment effects on forest trajectories. In an earlier summary of findings from the Green River FFS site, Waldrop et al. (2016) reported that after 12 years, basal area was lower in the two prescribed fire treatments than the Control treatment, but that the

Mech treatment did not differ from the Control treatment. They further reported that oak reproduction was higher in all treatments than in the Control treatment. Since then, another prescribed fire has been applied and forest composition has continued to be monitored, offering the opportunity for more insight into the success of management strategies and the mechanisms that may help reestablish oak dominance.

Here, we evaluated changes in overstory basal area 17 years after the initiation of the Green River FFS site, and how these changes relate to tree mortality, recruitment, and growth. We specifically sought to examine whether reductions of duff depth in the prescribed fire treatments were associated with tree mortality, providing evidence of the payment of resilience debt. Additionally, we investigated forest composition of overstory trees, saplings, and seedlings and their relationships with treatments. We first hypothesized that changes in overstory basal area would be positive in all treatments except the Fire and the Mech + Fire treatments, where we expected tree mortality to lead to reductions in basal area. Second, we hypothesized that tree mortality would be associated with reductions in duff depth, suggesting that prescribed fires can cause tree mortality through the consumption of fine roots in duff. Third, we hypothesized that oak seedling and sapling abundance would be greatest in the Fire and Mech + Fire treatments, which we expected to have the greatest reductions in overstory basal area, thereby increasing light levels for lower strata.

Materials and Methods

Study Location and Design

The Green River site covers 5,841 mountainous hectares (ha) in Polk County, North Carolina (35.287633, -82.327276), with elevations of 300-800 m above sea level. When the study was initiated in 2001, overstory trees averaged 80 to 120 years old and consisted primarily of mixed-xeric or mesic upland oak and pine (*Pinus* spp. Mill) species depending on topographic position. Canopy cover was near 100%. Ericaceous shrubs, like mountain laurel and great rhododendron, made up a dense midstory throughout the study area, with the former more prevalent in xeric sites and the latter more prevalent in mesic sites. Mesophytic tree species such as red maple and yellow-poplar were abundant in the midstory. Understory communities were composed of many species of broadleaved forbs, ferns, graminoids, shrubs, and tree seedlings. Soils are deep and well-drained, primarily in the Evard and Cliffield soil series (fine-loamy, oxidic, mesic, Typic Hapludults), with inclusions of the Ashe series (coarse-loamy, mixed, active, mesic Typic Dystrudepts) found throughout. The region has a humid-subtropical climate, with hot/humid summers and cool/mild winters. Mean annual rainfall is 139 cm, with no distinct dry season.

The Green River site used a randomized complete block design (Appendix C: Figure C1), with four treatment units in each of three replicate blocks for a total of 12 treatment units. Each treatment unit covered an average of 12 ha, each surrounded by a treated, but unsampled 4 ha buffer. Within the replicate blocks, each of the four treatment units were randomly assigned to one treatment. Treatment units were of sufficient size to include all prevailing combinations of elevation, aspect, slope, and landscape position.

The Fire treatment was applied in February-March of 2003, 2006, 2012, and 2015. Funding constraints prevented burning in 2009. All fires were burned with a spot fire technique; the first was done by helicopter ignition and the others were done by hand ignition. Fire intensity was generally low, with flame lengths typically ≤ 1 m, and fire severity (defined as the consumption of soil organic horizons) was also low. However, some spots burned with higher intensity (flame lengths approximately 10 m), particularly during the 2003 and 2006 fires. The Mech treatment was applied in the winters of 2001-2002 and 2011-2012 and included cutting of all woody vegetation >1.4 m tall and <10.2 cm in diameter at breast height (DBH) with a chainsaw. The Mech + Fire treatment had the first mechanical cutting in 2001-2002, and was treated with the prescribed fire in 2003, 2006, 2012 and 2015. A second mechanical cutting was not required in the Mech + Fire treatment. Localized areas of higher fire intensity (flame lengths >2 m) were occasionally observed in the Mech + Fire treatment, presumably due to higher fuel loading created by that treatment. Visual estimates indicated near 100% burn coverage in both the Fire and Mech + Fire treatments during each fire. Further details on fire patterns are available in Waldrop et al. (2016).

Sampling

A permanently marked, 50 m × 50 m grid was established in each treatment unit. Modified Whitaker plots, 20 m x 50 m in size (Waldrop et al. 2016), were established at ten randomly selected grid points within each treatment unit. Each plot consisted of ten, 10 m x 10 m subplots. For vegetation sampling within each plot, the forest was divided into 3 strata: overstory, sapling, and understory. Overstory and sapling data were collected in 5 subplots down one side of the plot, and seedling data were collected in two, 1 m x 1 m quadrats in opposite corners of each subplot (Appendix C: Figure C1). The overstory was defined as all woody vegetation, excluding mountain laurel and rhododendron, greater than 10 cm DBH. In 2001, overstory trees were marked with numbered tags, identified to species, and DBH was measured to the nearest 0.1 cm. Trees were re-measured in subsequent years, recorded as alive or dead, and any trees newly recruited into the overstory size class were identified and tagged. Saplings were defined as trees in the midstory taller than 137 cm, but less than 10 cm DBH. Seedlings were defined as all woody stems less than 137 cm in height. All strata were identified to species and grouped into genera for analyses.

Vegetation data were collected in the pre-treatment year (2001), and in the growing seasons following each treatment (2003, 2005, 2006, 2008, 2011, 2012, 2013, 2014, 2015 and 2016). Overstory data were also collected in 2018. To calculate relative growth rate (RGR) over the course of the study, we used the formula: $RGR = (\ln DBH_{2018} - \ln DBH_{2001})/ (2018 - 2001)$. To sample duff depth, we used a modified version (Coates et al., 2020) of Brown's Planar Intercept method to assess duff (Oe + Oa horizons) depth. Duff depth was measured in 2001 and 2014. Changes (Δ) in basal area and duff depth were calculated by subtracting the latest values from the 2001 (pretreatment) values.

Statistical analyses

We analyzed Δ basal area with a linear mixed-effects model (all analyses conducted using R version 4.3.2; R Core Team, 2023), with treatment as a fixed effect and block and treatment unit as nested random intercepts (lmer function in lme4 package; Bates et al., 2015). We analyzed the mortality of overstory trees with a logistic regression using two models that both included block, treatment unit, and plot as nested random intercepts (glmer function in lme4 package). The first, to identify treatment effects, included treatment and genus as interacting fixed effects. The second, to identify interactions with Δ duff depth, included genus and an interaction of treatment and Δ duff depth as fixed effects. Similarly, we analyzed Δ duff depth with a linear mixed-effects model with treatment as a fixed effect and block and treatment unit as nested random intercepts. We analyzed RGR using a linear mixed-effects model with treatment and genus as interacting fixed effects and block, treatment unit, and plot as nested random intercepts.

Count data (overstory recruits, saplings, and seedlings) were analyzed with a generalized linear mixed-effects model with a *Poisson* distribution, with treatment and genus as interacting fixed effects and block, treatment unit, and plot as nested random intercepts. To compare saplings and seedlings to Δ basal area, we constructed two generalized linear mixed-effects models, for saplings and seedlings, respectively. The first analyzed total sapling/seedling abundance with Δ basal area as a fixed effect and block, treatment unit, and plot as nested random intercepts. The second analyzed sapling/seedling abundance with Δ basal area and genus as interacting fixed effects and block, treatment unit, and plot as nested random intercepts. An additional observation-level random intercept was added to models of count data to correct overdispersion as needed (Harrison, 2014).

For each described model, significance was assessed using the Wald χ^2 test (Anova function in car package; Fox and Weisberg, 2019) and non-significant ($P > 0.05$) interactions were removed from final versions of the models. *Post-hoc* comparisons were conducted using estimated marginal means (emmeans or emtrends function in emmeans package; Lenth, 2023). To facilitate model convergence where genus was a variable, we included the top seven genera (*Acer, Carya, Liriodendron, Nyssa, Oxydendrum, Pinus,* and *Quercus*) which represented 96.7% of overstory trees, 79.9 % of saplings, and 86.2 % of seedlings (Appendix C: Table C1).

Results

We found that Δ basal area differed by treatment, where it was higher in the Control and Mech treatments relative to the Mech + Fire treatment ($\chi^2 = 51.11$, *d.f.* = 3, $P < 0.01$; Figure 4.1). In contrast with our hypothesis, however, Δ basal area was not negative in both the fire treatments. Instead, Δ basal area was only negative in the Mech + Fire treatment and did not differ from zero in the Fire treatment. In the Control and Mech treatments, Δ basal area was positive. Thus, only the Mech + Fire treatment was sufficient to reduce basal area over the last 17 years.

From 2001 to 2018, 211 trees were recruited to the overstory, over half of which were in the Control treatment. Indeed, we found that overstory recruitment was highest in the Control treatment relative to the others ($\chi^2 = 63.34$, *d.f.* = 3, $P < 0.01$; Figure 4.2a), though we did not find support for an interaction of treatment and genus ($P > 0.05$). Overstory recruitment varied by genus, where *Oxydendrum* had greater recruitment than *Pinus*, *Carya*, *Nyssa*, and *Liriodendron* and *Acer* had greater recruitment than *Carya* and *Liriodendron* ($\chi^2 = 49.92$, *d.f.* = 6, $P < 0.01$; Appendix C: Figure C2). When we evaluated relative growth rate (RGR), we did not find support for an interaction of treatment and genus or any treatment differences. However, RGR differed by genus, where it was higher in *Quercus* relative to *Carya* and *Oxydendrum* ($\chi^2 = 25.17$, *d.f.* = 6, $P < 0.01$; Appendix C: Figure C3).

Over the course of the study, 303 overstory trees died, a third of which were in the Mech + Fire treatment. Accordingly, we found that the probability of overstory tree mortality was highest in the Mech + Fire treatment relative to the other treatments ($\chi^2 = 32.30$, *d.f.* = 3, $P < 0.01$; Figure 4.2b). Though we did not find support for an interaction of treatment and genus, we found the probability of overstory tree mortality to vary by genus ($\chi^2 = 58.64$, *d.f.* = 6, $P < 0.01$), where it was higher for *Pinus* relative to the other genera, and higher for *Quercus* relative to *Acer* (Appendix C: Figure C4). Collectively, these findings indicate that recruitment explained the positive basal area gains in the Control treatment, while mortality was responsible for reductions in basal area in the Mech + Fire treatment.

We found that Δ duff depth differed by treatment, where it was lower in the two prescribed fire treatments than in the Control treatment, and lower in the Mech + Fire treatment than in the Control and Mech treatments ($\chi^2 = 41.98$, *d.f.* = 3, $P < 0.01$; Figure 4.3a). In contrast with our hypothesis, we found that the probability of overstory mortality increased sharply with decreasing duff depth in the Mech + Fire treatment, but not other treatments ($\chi^2 = 20.9$, *d.f.* = 3, $P < 0.01$; Figure 4.3b). Thus, duff depth decreased in the two prescribed fire treatments, but this decrease was only linked to overstory mortality in the Mech + Fire treatment.

In the lower strata, we found that treatment effects on both sapling and seedling abundances were dependent upon genus (saplings: $\chi^2 = 174.34$, *d.f.* = 18, $P < 0.01$; seedlings: $\chi^2 = 75.21$, *d.f.* = 18, $P < 0.01$; Appendix C: Tables C2-C3). In contrast with our hypothesis, *Quercus* sapling abundance was not higher in the two prescribed fire treatments relative to the other treatments, but rather was higher in the Mech + Fire treatment relative to the Mech and the Fire treatments and was higher in the Control treatment relative to the Fire treatment. Comparing the two most abundant genera of saplings, *Acer* and *Quercus*, we found no significant differences in their abundances in any treatment with the exception of the Fire treatment, where *Acer* saplings were more abundant (Appendix C: Table C2). For *Quercus* seedling abundances, we did not find support for treatment differences ($P > 0.05$). Comparing the two most abundant genera of seedlings, *Acer* and *Quercus*, we found no significant differences in their abundances in any treatment (Appendix C: Table C3).

Although total sapling abundance increased with larger decreases in basal area (indicated by more negative Δ basal area values; Figure 4.4a), we found that the relationship was dependent upon genus ($\chi^2 = 2331.03$, *d.f.* = 6, $P < 0.01$). Confirming our hypothesis, *Quercus* sapling abundance increased with larger decreases in basal area, as did all genera except *Acer* (Figure 4.4b; Appendix C: Figure C5). Total seedling abundance had no relationship with Δ basal area ($P > 0.05$), but we found that the relationship differed by genus ($\chi^2 = 549.46$, *d.f.* = 6, $P < 0.01$). In contrast with our hypothesis, we found no relationship between *Quercus* seedling abundance and Δ basal area, though *Acer* seedling abundance increased with larger increases in basal area, and *Liriodendron*, *Nyssa*, *Oxydendrum*, and *Pinus* seedling abundances decreased with larger increases in basal area (Appendix C: Figure C6).

Discussion

Eastern forests have become denser, shadier, and less oak-dominated over the past several decades (Fei et al., 2011; Jo et al., 2019; Knott et al., 2019), threatening the ecosystem services these forests provide. Understanding if management actions can halt or reverse this trend is critical to the development of effective forest management strategies. Our findings from the Green River FFS site demonstrate that over time, some continuously applied forest management treatments can halt or reverse the ongoing accretion of forest basal area. Over the 17-year observation period, in the Control treatment, we observed an increase in basal area (Figure 4.1) largely due to overstory recruitment (Figure 4.2a). This increase in basal area was unabated by the Mech treatment, showing that two mechanical felling treatments over the study period were insufficient to halt these increases. In contrast, the Fire treatment halted the accretion of forest basal area, suggesting that periodic prescribed fire applied repeatedly over time may dampen or cease forest basal area increases. However, the only treatment to reduce basal area over the course of the study was the Mech + Fire treatment, suggesting that the synergistic effects of mechanical felling and multiple prescribed fires can reverse the trend of basal area accretion. Reductions in basal area in the Mech + Fire treatment over the course of the study were largely due to overstory tree mortality (Figure 4.2b).

Accumulated duff can pose a threat to trees in the event of wildfire, but it is unclear if multiple prescribed fires over time can diminish existing duff without also leading to heightened tree mortality. In our study, duff depth was diminished in the two prescribed fire treatments, while remaining essentially unchanged in the Control and Mech treatments (Figure 4.3a). Interestingly, losses of duff were not systematically linked to overstory tree mortality in our study (Figure 4.3b). For example, there was no significant relationship between mortality and Δ duff depth in the Fire treatment. This suggests that multiple prescribed fires can diminish existing duff layers without causing overstory tree mortality. Given the danger to fire-adapted trees in long-unburned forests with accumulated duff during wildfire (Capenter et al., 2021), and the increase in wildfire activity in eastern forests (Donovan et al., 2023), these findings point toward repeated prescribed fire as a vital management tool for minimizing wildfire risk to overstory trees surrounded by accumulated duff. This finding is particularly useful for land managers wishing to apply prescribed fire in long-unburned eastern forests where duff has accumulated, similar to the forests of the Green River FFS site.

Interestingly, we found that the probability of overstory tree mortality was only linked to declines in duff depth in the Mech + Fire treatment (Figure 4.3b). The mechanical treatment used in this study cut saplings and shrubs, which remained on the forest floor, thereby increasing fuel loadings which were largely consumed during subsequent prescribed fires in the Mech + Fire treatment (Waldrop et al., 2010, 2016). Given the linkage of fuel loading to fire intensity (Mitchell et al., 2009), the likely explanation for this pattern is that higher fire intensity led to an increasing probability of overstory mortality, as reported by Waldrop et al. (2010, 2016). It could be the case that these more intense fires combusted more accumulated duff, leading to the death of roots within that duff, and therefore, an increased probability of mortality with increasing loss of duff in the Mech + Fire treatment. However, given the low probability of mortality in the Fire treatment at extreme values of duff loss (Figure 4.3b), it seems more likely that high fire intensity driven by high fuel loadings led to increased top kill of trees and also high duff consumption. This suggests that the relationship between duff depth loss and overstory tree mortality we found in the Mech + Fire treatment is one of correlation and not causation.

Ultimately, the future composition of eastern forests will depend upon the current composition of younger trees and how they are impacted by management actions. At the Green River FFS site, we found that treatment effects on these lower strata were dependent upon genus (Appendix C: Tables C2-C3). Half of inventoried saplings and over 75% of seedlings were in the genera *Acer* and *Quercus* (Appendix C: Table C1), suggesting that at the Green River FFS site, maples are the major mesophytic competitor with young oaks. We found that total sapling abundance increased with increasing loss of basal area (Figure 4.4a), a pattern likely driven by heightened light availability with decreasing plot basal area. However, we observed contrasting relationships among oaks and maples, where oak sapling abundance increased with increasing losses of basal area, whereas maple sapling abundance had no such relationship. These contrasting responses are likely due to differing shade tolerances among the two genera, as oaks are generally considered less shade tolerant than maples (Honkala and Burns, 1990). This finding suggests that oaks are well-positioned to compete with maples in plots where basal area has decreased, especially if prescribed fire treatments continue.

It is well established that in the current ambient conditions of eastern forests, oaks are poor competitors with mesophytic trees (Fei et al., 2011; Knott et al., 2019). The crux of the problem is one of regeneration, i.e. moribund overstory oaks cannot be replaced by oak saplings that are outcompeted in dense, shady, nutrient-rich forests (Lorimer, 1993; Jo et al., 2019). As such, low levels of oak regeneration have been found to be the key co-morbidity to oak recovery across several canopy-opening disturbances (Vickers et al., 2023). Our results suggest that young oaks are well-positioned to outcompete their major competitor (maples) at the Green River FFS site in plots that have had basal area reduced through overstory mortality (Figure 4.4b), most of which are in the Mech + Fire treatment. These findings suggest that management actions (e.g. mechanical felling and repeated prescribed fires) can make young oaks more successful in competition with maples, but that this success comes with the cost of overstory mortality, which in these oak-dominated forests, is largely represented by the death of older, established oaks. Collectively, these findings represent the intersection of forest management actions with resilience debt and ecological memory (Jõgiste et al., 2017). That is, the misalignment of past and current fire regimes led to oak forests incurring resilience debt, which is paid through the death of overstory oaks when management actions (in this case the Mech + Fire treatment) mimic a severe disturbance. Ecological memory is held in this system by the life-history traits of oak seedlings, and then saplings, which when presented the fire regime in which they evolved, become abundant in the high light availability offered through the demise of their ancestors. Further, in forests like the Green River FFS site that have dense ericaceous midstories due to fire exclusion (Lafon et al., 2022), paying this resilience debt may also depend on the felling of these shrubs, thereby increasing fuel loadings for subsequent prescribed fires, as was accomplished in the Mech + Fire treatment. Although it seems that young oaks are positioned to outcompete maples in plots where forest basal area decreased at the Green River FFS site, a test of this hypothesis will only be possible once this cohort of saplings recruits to the overstory.

There are limitations and caveats with our study. A limitation of this study is that it consists of only one site in the southern Appalachians and may not be representative of all eastern forests. For example, at another FFS site in Ohio where treatments have continued, basal area accretion was dampened by the Mech treatment (Hutchinson et al., 2024), in contrast with our results. The Ohio FFS site differs from the Green River FFS site in two apparent ways that may explain this difference. First, the Ohio FFS site used an overstory thinning method for the mechanical treatments, rather than the sapling/shrub felling used at the Green River FFS site. Second, the Ohio FFS site lacked much of the evergreen ericaceous shrub component found at Green River. These shrubs present novel understory dynamics and fuel conditions that may differ from some eastern forests (Elliott and Miniat, 2021). A caveat with our study is that we grouped species by genera to identify broad taxonomic patterns in our data, but some genera contain many species, which may differ in their life history traits. In particular, *Quercus* contains many species which differ somewhat in their shade tolerance, fire sensitivity, litter flammability, and germination phenology (Honkala and Burns, 1990; Varner et al., 2016; Oakman et al., 2019). At the Green River FFS, oak species included (high-low overstory abundances): *Quercus montana* Willd., *Quercus coccinea* Muenchh., *Quercus alba* L., *Quercus velutina* Lam., *Quercus rubra* L., *Quercus stellata* Wangenh., and *Quercus marilandica* Muenchh. An interesting follow-up study may investigate the relationship with treatments and changes in overstory basal area among oak species.

Tree assemblages change slowly, challenging researchers to make recommendations to land managers with limited data that likely represent pieces of a multigenerational puzzle. Here, we used a long-term (in the human sense) study of forest management applications to show forest changes due to repeated applications of prescribed fire and mechanical felling. We found that a combination of prescribed fire and mechanical felling is the best treatment of those tested for oak regeneration, though it comes with the cost of overstory tree mortality. Further, we found that repeated prescribed fires over time diminish existing duff layers, likely protecting trees surrounded by deep duff from wildfire. Such studies are invaluable to researchers and land managers alike hoping to manage forests today such that subsequent generations can benefit from oak-dominated forests and the ecosystem services they provide.

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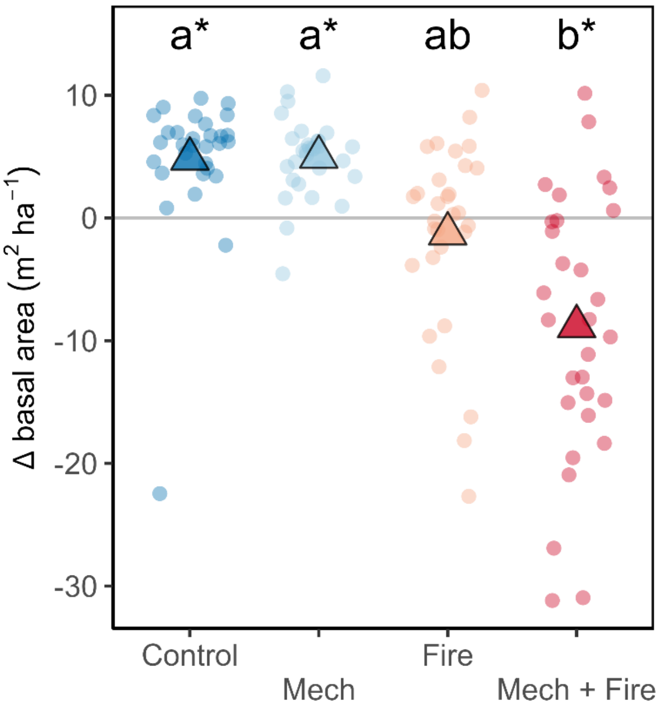

Figure 4.1. Changes (Δ) to overstory basal area at the Green River Fire and Fire Surrogate Study site 2001-2018. Each point represents one plot in each of the four treatments. Triangles represent model predictions for each treatment. Absence of the same letter signifies treatment differences ($P \leq 0.05$) and asterisks signify model predictions that differ from zero.

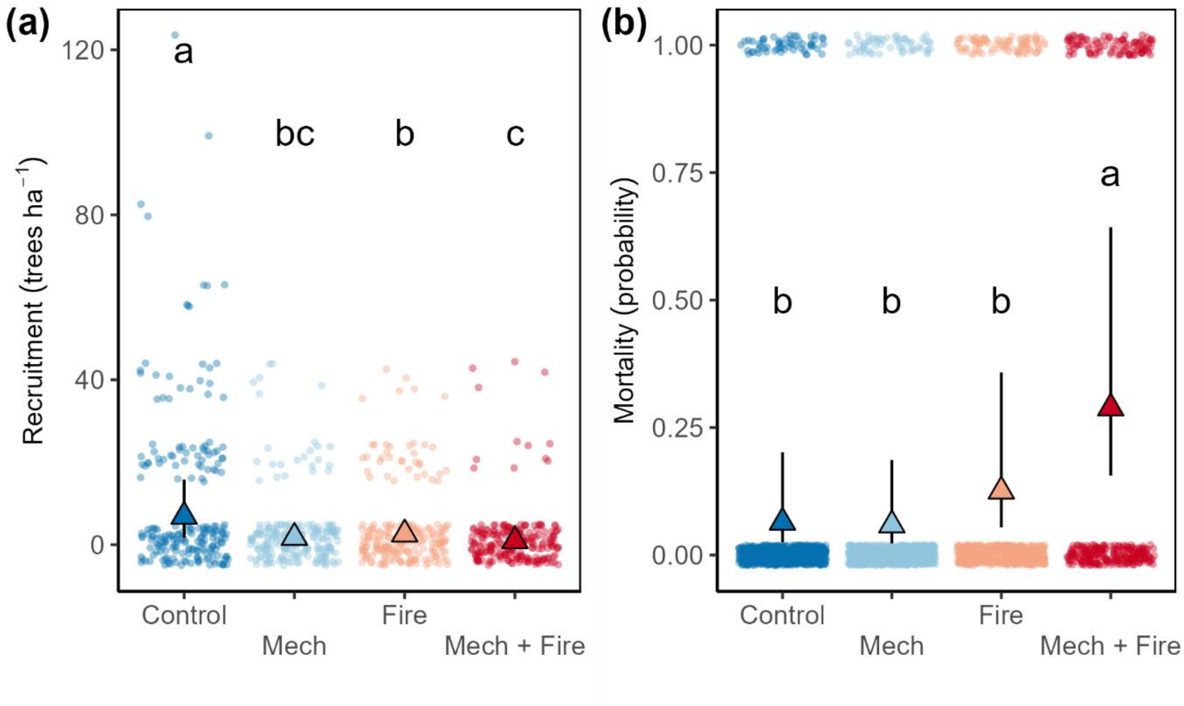

Figure 4.2. Overstory tree recruitment and mortality at the Green River Fire and Fire Surrogate Study site 2001-2018. (a) Recruitment of overstory trees in each of the treatments. Points represent each of seven tree genera in each plot (30 per treatment). (b) Mortality probability of overstory trees in each of the treatments. Points represent trees that lived (0) and died (1) by 2018. In both (a) and (b), triangles represent model predictions for each treatment and lines represent the range of model predictions across genera. Absence of the same letter signifies treatment differences ($P \leq 0.05$).

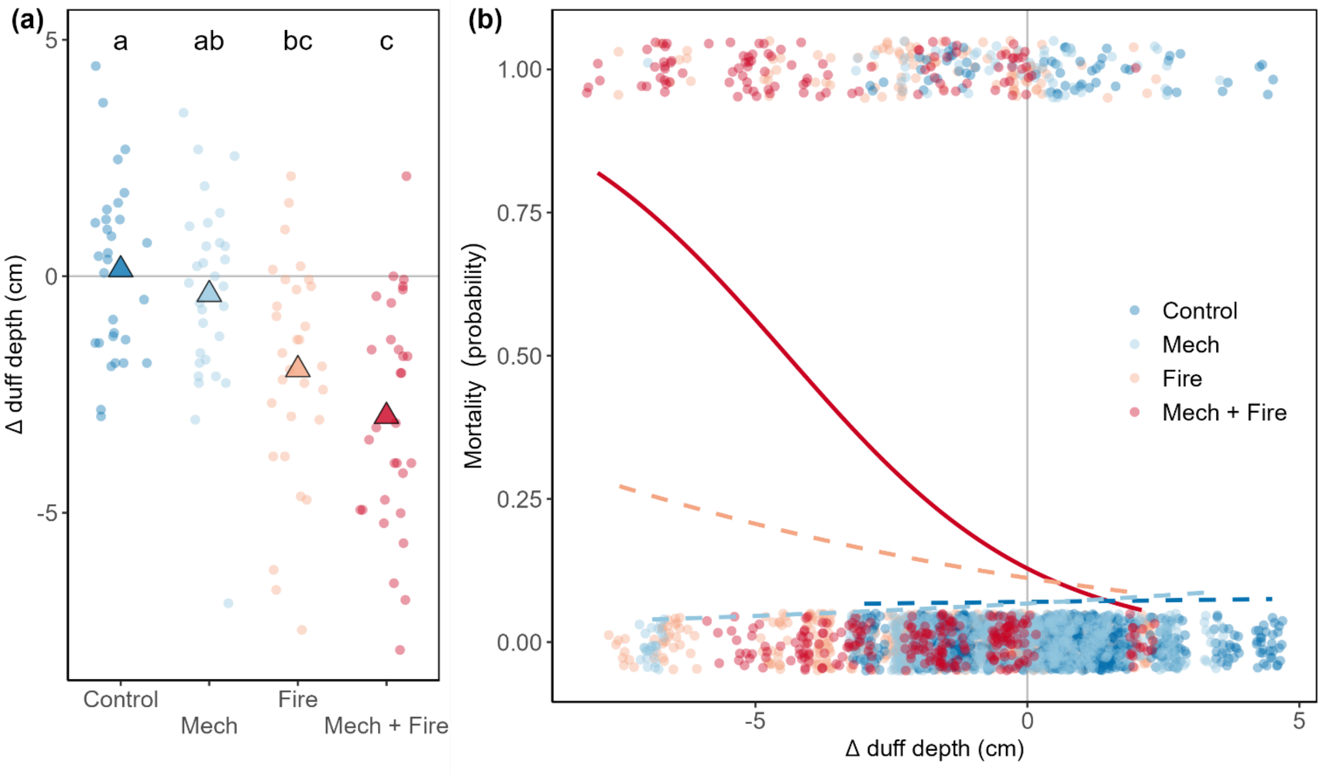

Figure 4.3. Changes (Δ) to duff depth and associated overstory tree mortality at the Green River Fire and Fire Surrogate Study site 2001-2018. (a) Duff depth changes in each treatment. Each point represents one plot. Triangles represent model predictions and absence of the same letter signifies treatment differences ($P \leq 0.05$). (b) Probability of overstory tree mortality compared to changes in duff depth in each of four treatments, represented by different colors. Lines are model predictions for *Quercus*; solid denotes estimated slope difference from zero. Model predictions for the Mech + Fire treatment differ from other treatments except the Fire treatment ($P = 0.06$). Model predictions for the Control, Mech, and Fire treatments do not differ from each other.

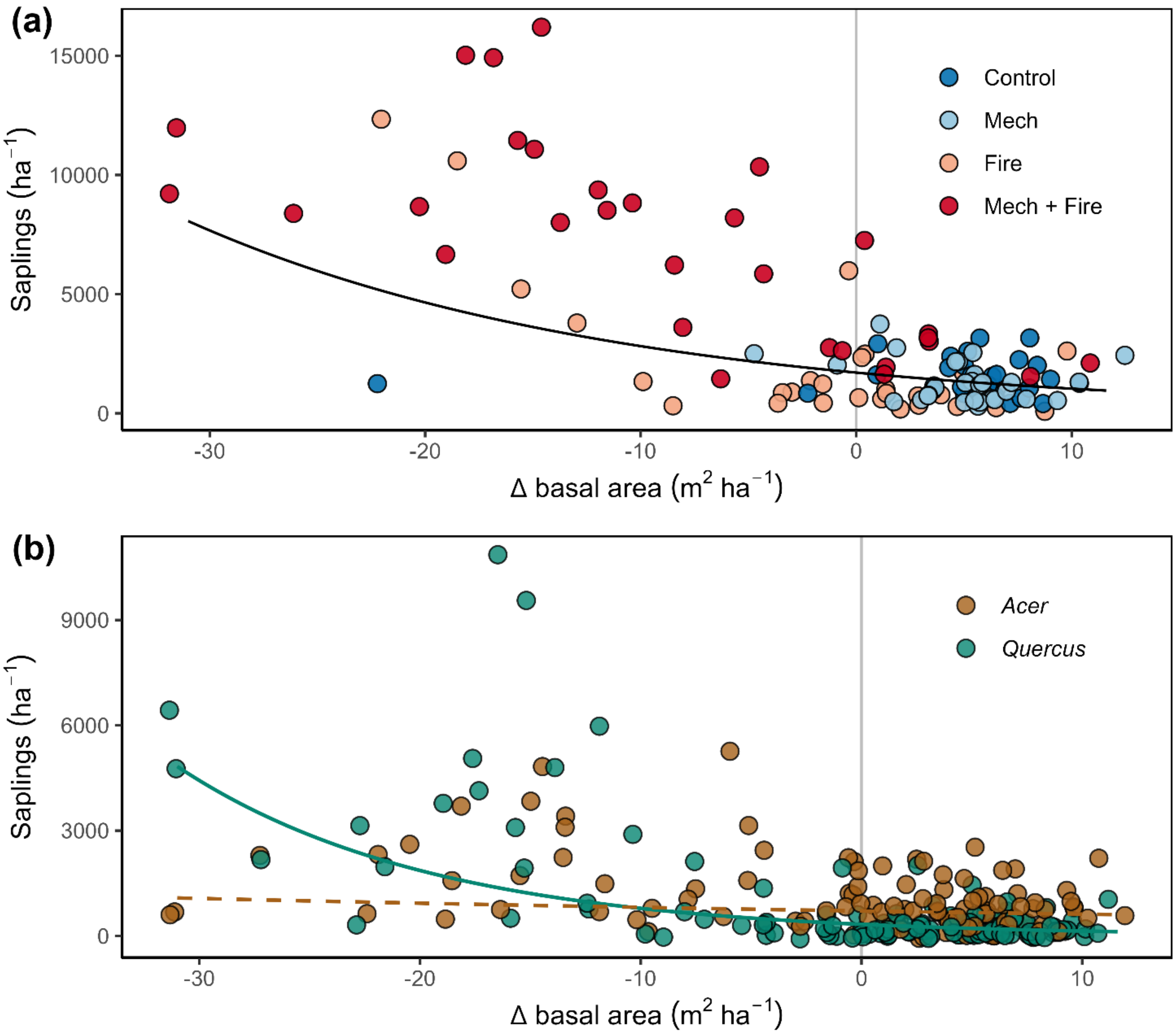

Figure 4.4. Saplings in 2018 compared to changes (Δ) in basal area over 17 years of treatments at the Green River Fire and Fire Surrogate Study site. (a) Total saplings. The treatment which each point represents is provided for reference. (b) Saplings of the two most abundant genera. Points in both figures are jittered slightly to aid visualization. Lines are model predictions, and solid denotes the estimated slope differs ($P \leq 0.05$) from zero. Slopes of lines in (b) differ from each other.

CHAPTER 5

CONCLUSIONS

Temperate forests of eastern North America (eastern forests) are transitioning from pyrophytic and oak-dominated to mesophytic and maple-dominated. The mesophication hypothesis posits that fire exclusion has led to an increase in fire-sensitive tree species and fuelbeds that increasingly resist fire (Nowacki and Abrams, 2008; Alexander et al., 2021). Simultaneously, biogeochemical alterations to the forest floor have been proposed as driving forest change towards increasing composition of tree species that associate with arbuscular mycorrhizal (AM) fungi and produce palatable leaf litter and decreasing composition of tree species that associate with ectomycorrhizal (ECM) fungi and produce unpalatable litter (Szlavecz et al., 2011; Averill et al., 2018; Frelich et al., 2019; Jo et al., 2019; Bethke and Midgley, 2020). Currently, it is unclear how these multiple hypothesized drivers may influence forest composition. Further, it is unclear how the return of fire, either as wildfire or as prescribed fire, might affect transitioning forests, hindering society’s ability to manage oak-dominated forests for future generations. This dissertation addressed these knowledge gaps using multiple approaches.

In Chapter 2, I determined soil macrofauna community compositions and leaf litter decomposition across an AM-ECM forest gradient in burned and unburned areas around the Rock Mountain wildfire in the southern Appalachian Mountains. The area studied had not burned for nearly a century. I found that in response to wildfire, litter-dwelling fauna communities were altered such that abundances of adult beetles decreased, and millipedes increased. In contrast, communities of soil-dwelling fauna did not respond to fire but did shift along an AM-ECM forest gradient, such that earthworms and millipedes (detritivores) were less abundant with increasing ECM tree dominance. Further, I found that leaf litter decomposition was faster in burned plots than unburned plots, and for AM litter compared to ECM litter.

These findings suggest that wildfires affect fauna communities and decomposition, but these effects are limited to the leaf litter layer, which may mean that effects are temporally limited until leaf litter accumulates. Further, my finding that soil-dwelling detritivores become less abundant with increasing ECM dominance suggests that soil food webs may be shifting due to the continued expansion of AM trees in eastern forests. Results from this study may mean that detritivores are more abundant in AM-dominated forests, likely due to higher litter palatability in AM stands, which directly ties these organisms to the mechanisms posited in hypotheses of mesophication and AM tree expansion (Nowacki and Abrams, 2008; Averill et al., 2018). Soil macrofauna have not been explicitly considered in the context of mesophication or AM tree expansion, despite their essential roles in litter decomposition and biogeochemical cycling (Griffiths et al., 2021; Zeng et al, 2024).

In Chapter 3, I considered how soil biogeochemical mechanisms might be related to the mesophication hypothesis. I used multiple approaches, including a bibliometric analysis of published literature, a comparison of literature values and classifications of species, and an analysis of expansive datasets on forest inventories and change drivers. From the bibliometric analysis, I found that co-cited papers fall largely within clusters of academic disciplines, suggesting a lack of consideration of biogeochemistry in the fire literature, and vice versa. I found that among the most abundant tree species of eastern forests, AM species are generally considered fire-intolerant, while ECM trees are considered fire-adapted, and that fire-intolerant species have faster litter decomposition rates than those that are fire-adapted. However, when I looked across multiple traits, I found both AM and ECM tree species distributed across traits for decomposability/palatability and fire adaptation, though only ECM trees fell within the trait space of high flammability, thick bark, high litter C:N, and slow decomposition. When I analyzed species prevalences across the region, I found that forest basal area of ECM trees and fire-adapted trees were correlated, particularly in the southern provinces of the region, indicating that dominant ECM tree species are also fire-adapted. Using forest inventory data and literature classifications and values, I found that fire exclusion was spatially linked to increases in AM tree dominance, but I did not detect a relationship between forest change and N deposition or invasive earthworm records.

Broadly, these findings suggest that in eastern forests, traits for fire-adaptation, nutrient conservation, and litter palatability are shared among species, further suggesting the possibility that three human disturbances: fire exclusion, atmospheric N deposition, and invasive earthworm introductions, may reinforce the shift in eastern U.S. forest composition. I proposed an expansion of the mesophication framework to consider the role of soil biogeochemistry in the context of transitioning forest composition and how fire exclusion and soil biogeochemical changes may reinforce the same ecosystem state change. This proposed framework may generate new hypotheses about how forest transitions towards mesophyte- and AM-dominance can be limited and how returns to prior compositions can be promoted.

In Chapter 4, I used a long-term forest management experiment in the southern Appalachians to find which (if any) forest management treatment (prescribed fire, mechanical felling, or a combination) might be sufficient to restore oak dominance to eastern forests. I looked at compositions of overstory trees, and the younger sapling-sized cohort since it will make up future overstory composition. I found that the combination of mechanical felling of saplings and ericaceous shrubs combined with repeated prescribed fires over decades was the only treatment to reduce overstory basal area. In contrast, basal area increased in the control and mechanical felling treatment, as forests gained more mesophytic trees. Basal area reductions in the combination treatment were largely due to mortality of overstory trees, which in these oak-dominated forests, were mostly oaks. Saplings were most abundant in the combination treatment and were dominated by oak and maple. Though abundances of the two genera did not differ in the combination treatment, they exhibited contrasting responses to decreases in overstory basal area. I found that oak sapling abundances increased with increasing loss of basal area; a pattern not found with maples, suggesting that young oaks are well positioned to outcompete maples where basal area decreased due to overstory oak mortality.

Together, these findings suggest that overstory oak mortality may be a necessary sacrifice to promote oak dominance in future forest overstories. The misalignment of past and current disturbance regimes has been suggested to lead to a loss of ecosystem resilience, termed "resilience debt," which is only realized after ecosystems experience further disturbance (Johnstone et al., 2016; Webster et al, 2018). I suggest that this may be the case with eastern forests. That is, the misalignment of past and current fire regimes has led to resilience debt in oak forests, which is "paid" through the death of overstory trees when management actions simulate a severe disturbance. Combined with repeated prescribed fires, such a payment may promote oak dominance in the future. Further, this work ties ecosystem resilience to forest management, a perspective that may be necessary as managers seek ways to increase forest resilience to multiple stressors (Jõgiste et al., 2017).

The unifying theme of this dissertation is the integration of multiple perspectives of forest change towards the ultimate goal of a more holistic understanding of how these ecosystems function and change. Such an understanding will be required to shed light on how humans can best mange these ecosystems. In Chapter 2, I integrated perspectives of fire and biogeochemistry to better understand the effects of wildfire on long-unburned forests. In Chapter 3, I proposed a new framework merging models of ecosystem state change from perspectives of fire and biogeochemistry and described ways multiple transitions may reinforce an ecosystem state change. In Chapter 4, I incorporated ecosystem resilience into the perspective of fire and forest management, and demonstrated how doing so can illuminate paths towards desired outcomes. Taken together, my findings clarify how eastern forests have transitioned amid multifaceted cooccurring disturbances and what actions may reverse this transition. Further, this work demonstrates how human actions are intimately connected to driving eastern forest change. Human actions created conditions that led to the current state of eastern forests and my work suggests that human actions can create conditions that lead to different outcomes for eastern forests for future generations.

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APPENDIX A

SUPPLEMENTARY INFORMATION: CHAPTER 2

Table A1. Macro- and meso-fauna observed in this study with taxonomic classification and trophic guild assignment (based on Potapov et al., 2022). Macrofauna were collected from litter and soil by hand. Mesofauna were extracted from litterbags recovered from forest plots.

Macrofauna	**Taxonomic classification**	**Trophic guild(s)**
Ants	Formicidae	predators, omnivores
Beetles-adult	Coleoptera (adult)	herbivores, fungivores, predators, omnivores, saprophages
Beetles-larvae	Coleoptera (immature)	coprophages, herbivores, necrophages, predators, omnivores, saprophages,
Booklice	Psocodea	likely microbivores
Centipedes	Chilopoda	predators
Crickets	Orthoptera	herbivores, omnivores
Cockroaches	Blattodea	detritivores, omnivores
Diplurans	Diplura (Japygidae)	predators
Earthworms	Lumbricina	detritivores, geophages
Flies-adult	Diptera (adult)	detritivores, herbivores, predators, saprophages
Flies-larvae	Diptera (immature)	detritivores, fungivores, microbivores, omnivores, predators, saprophages
Lepidopteran-larvae	Lepidoptera (immature)	likely herbivores

Millipedes	Diplopoda	detritivores, microbivores
Pseudoscorpions	Pseudoscorpiones	predators
Slugs	Gastropoda (unshelled)	detritivores, herbivores, microbivores
Snails	Gastropoda (shelled)	detritivores, herbivores, microbivores
Spiders	Araneae	predators
Termites	Termitoidae	detritivores
Ticks	Ixodida	parasites
Hemiptera	Hemiptera	likely herbivores
Wasps	Hymenoptera	omnivores
Mesofauna	**Taxonomic classification**	**Trophic guild(s)**
Springtails	Collembola	detritivores, fungivores, microbivores
Mites	Acari	herbivores, detritivores, fungivores, microbivores, omnivores, parasites, predators

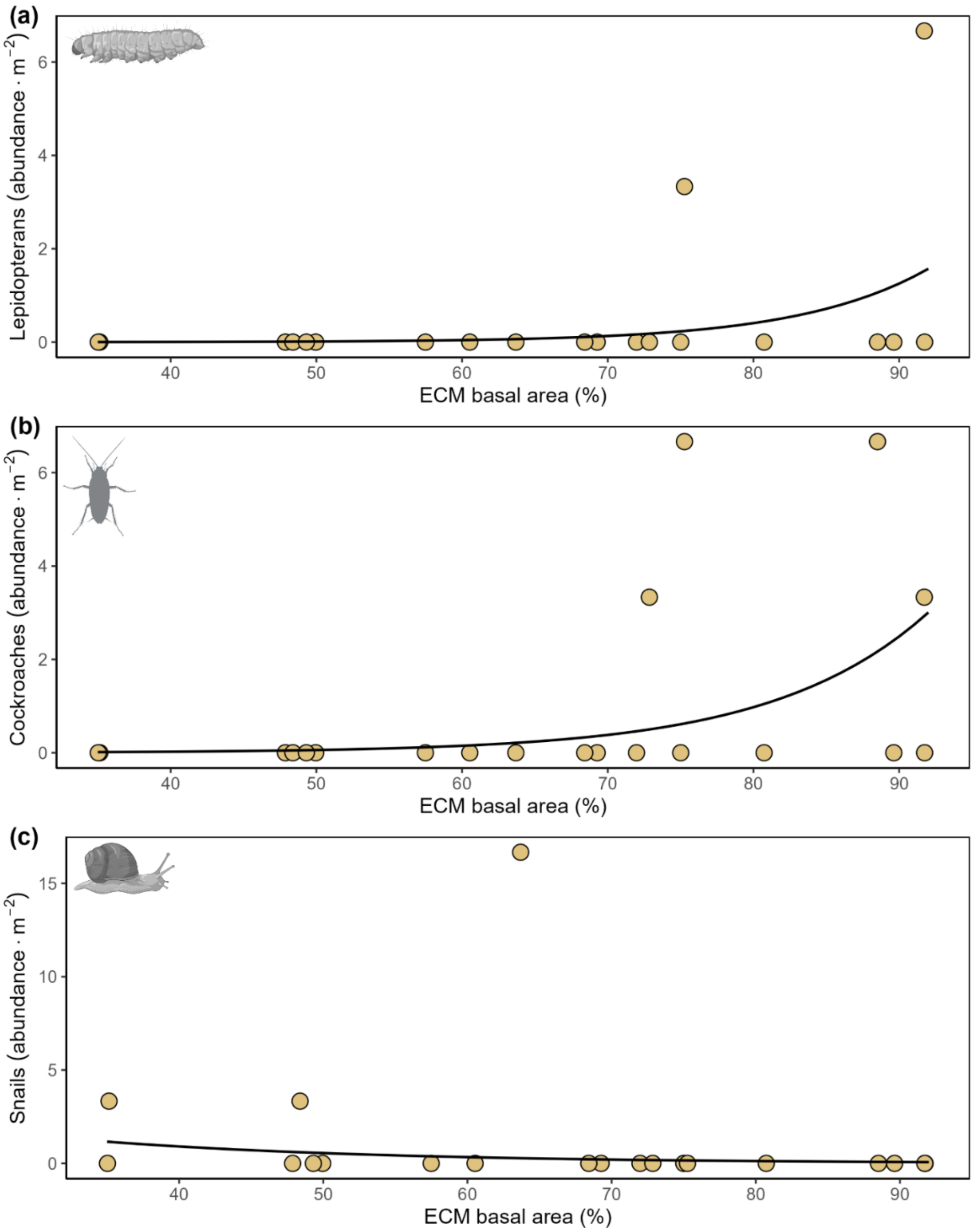


Figure A1. Abundances of soil-dwelling fauna across a gradient of ECM dominance from the area of the Rock Mountain wildfire. Abundances are summed across three seasons. (a) Immature lepidopterans (Lepidoptera); (b) Cockroaches (Blattoidae); (c) Snails (shelled Gastropoda). Lines represent model predictions. Each line is significantly different from zero ($P \leq 0.05$), but relationships are driven by 2-4 non-zero observations. Image modified with Biorender.com.

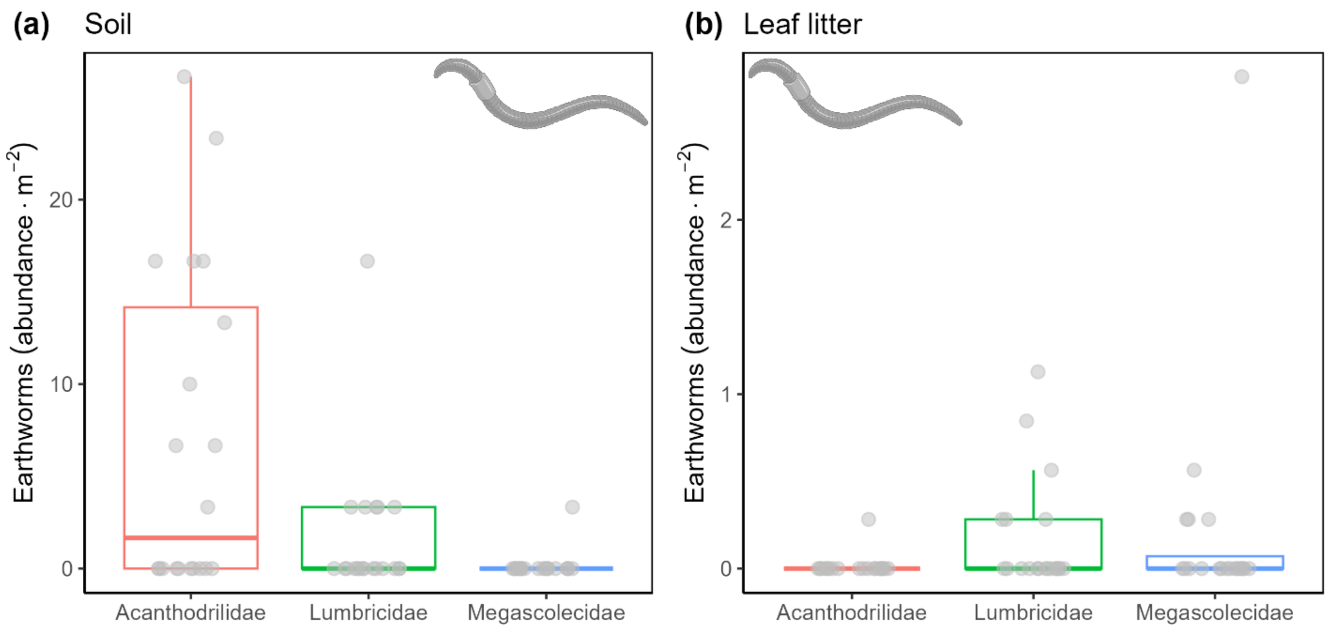


Figure A2. Adult and sub-adult earthworms collected from the area of the Rock Mountain wildfire. Abundances are summed across three seasons. (a) Soil (b) Leaf litter. Colors and labels indicate family taxonomy. Boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Individual points are overlaid. Note the y-axis change from (a) to (b). Image modified with Biorender.com.

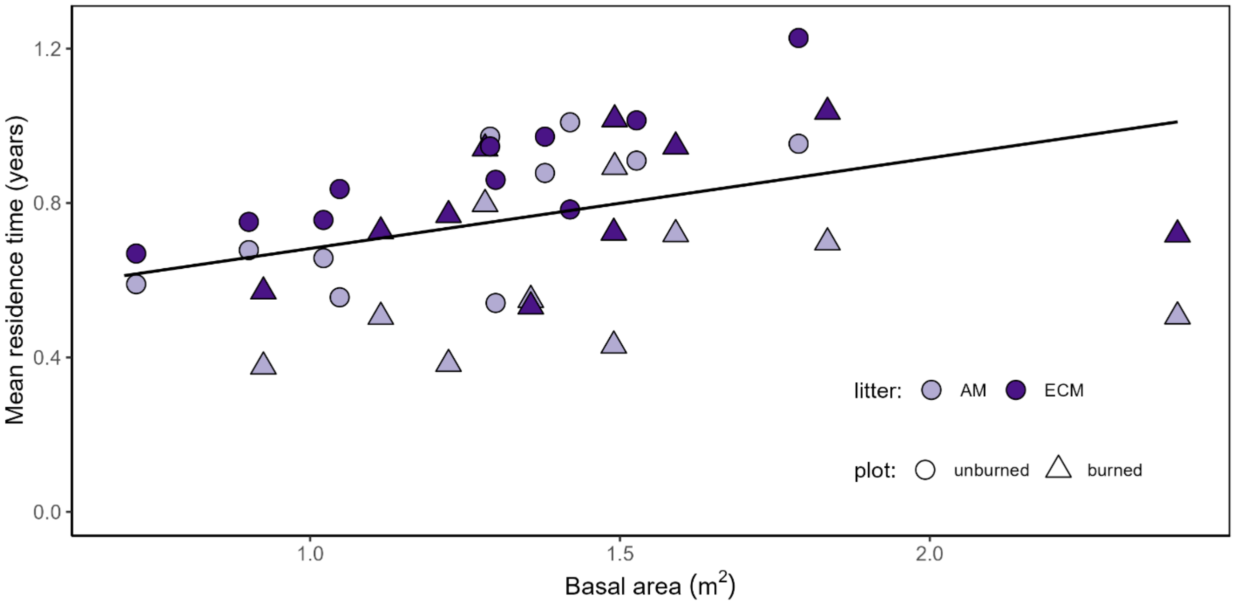


Figure A3. Leaf litter mean residence time compared to total plot basal area for the area of the Rock Mountain wildfire. Shapes indicate plot burn status while colors indicate the mycorrhizal identity of the leaf litter inside the litterbag. The line represents model predictions and the estimated slope differs from zero ($P \leq 0.05$).

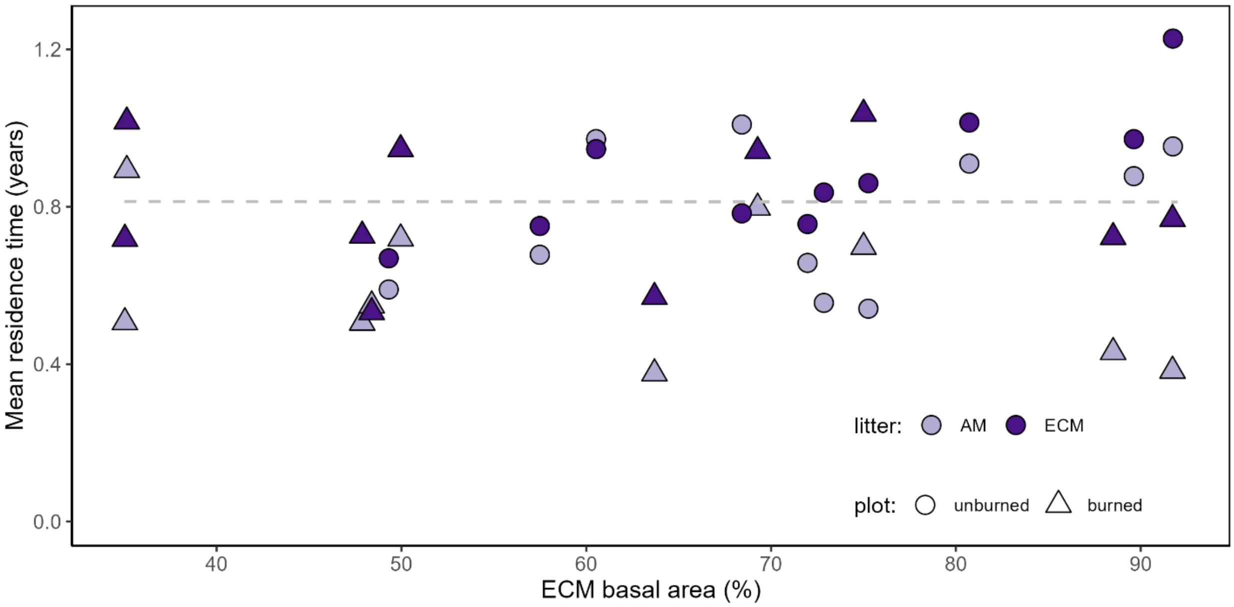


Figure A4. Leaf litter mean residence time across a gradient of ECM dominance for the area of the Rock Mountain wildfire. Shapes indicate plot burn status while colors indicate the mycorrhizal identity of the leaf litter inside the litterbag. The line represents model predictions and the estimated slope does not differ from zero (*P* > 0.05).

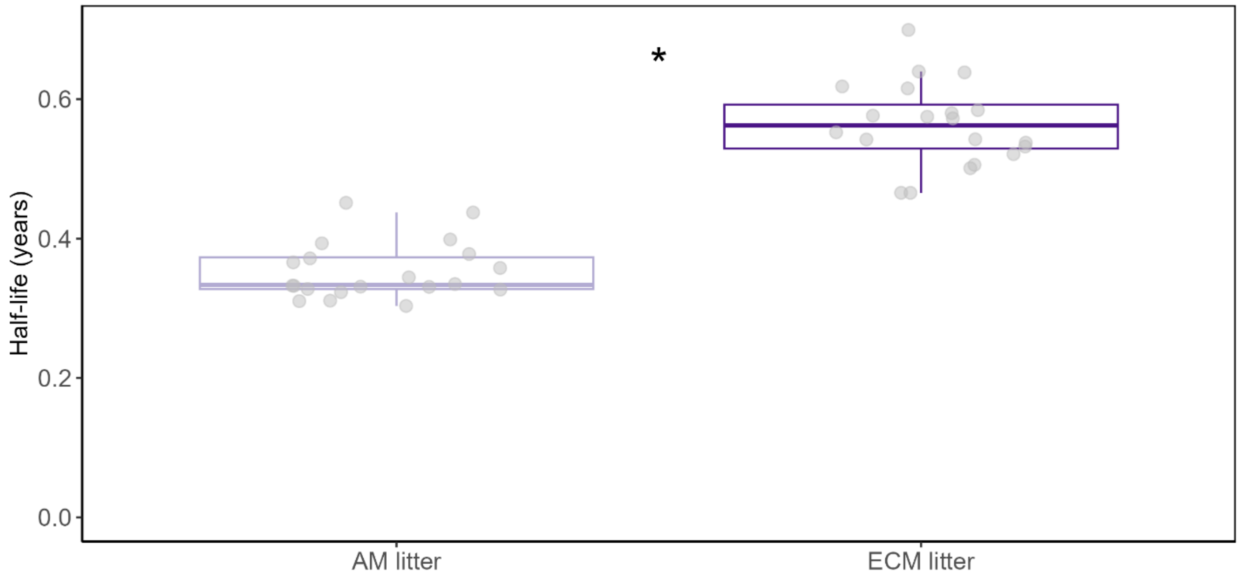
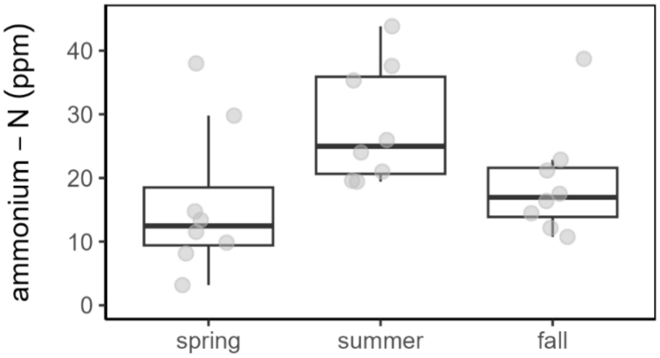
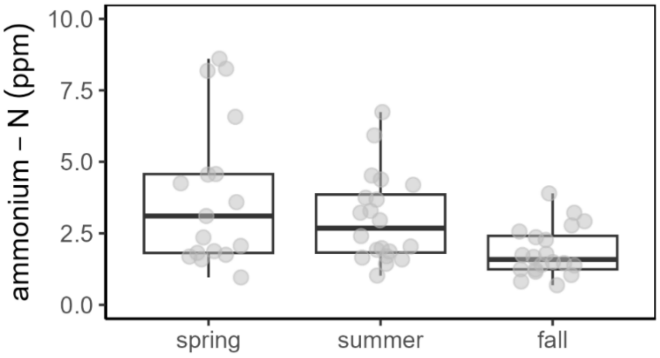


Figure A5. Leaf litter half-life differs for ECM litter (dark purple) and AM litter (light purple) decomposing in the area of the Rock Mountain wildfire. Boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Individual points are overlaid. Significant difference (*P* < 0.05) denoted by asterisk.

(a) O horizon



(b) 0-10 cm



(c) 10-20 cm

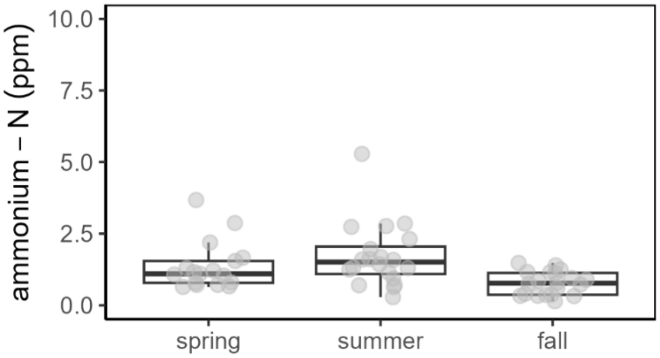


Figure A6. Concentrations of ammonium-N (NH_4^+-N) at three depths in three seasons in the area of the Rock Mountain wildfire. (a) Organic "O" horizon; (b) 0-10 cm depth; (c) 10-20 cm depth. Boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Individual points are overlaid. Note the y-axis change from the O-horizon to the two mineral soil layers. The O-horizon differs from the other depths ($P \leq 0.05$) and in the O-horizon, summer differs from the two other seasons.

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APPENDIX B

SUPPLEMENTARY INFORMATION: CHAPTER 3

Table B1. Bibliometric co-word analysis terms for removal and synonyms.

Terms removed
Forest inventory, forest dynamics, North America, North American, eastern north, eastern United, ha- yr-, diameter distributions
Terms indicated as synonyms
species composition, community composition, forest composition, tree species
plant community, plant communities, plant species
maple, acer, maples
quercus, oak, oaks
pine, pinus, pines
fire regime, fire regimes, fire frequency
prescribed fire, prescribed burning
invasive earthworms, earthworm invasion, earthworm biomass, earthworm abundance, earthworm invasions, earthworm species
frequently burned, frequent fire
forest understory, understory plant
forest ecosystems, forest landscape
red maple, acer rubrum
fire exclusion, fire suppression
oak species, quercus spp
sugar maple, acer saccharum
white pine, eastern white
oak dominance, oak-dominated forests

Table B2. The 75 most abundant tree species (in basal area) in the USDA Forest Service Forest Inventory and Analysis forested plots in the eastern United States with mycorrhizal association and fire adaptation classification and citation.

genus	species	fire classification	mycorrhizal association
Abies	*balsamea*	intolerant [a]	ECM [c]
Acer	*negundo*	intolerant [a]	AM [c]
Acer	*rubrum*	intolerant [a]	AM [c]
Acer	*saccharinum*	intolerant [a]	AM [c]
Acer	*saccharum*	intolerant [a]	AM [c]
Betula	*alleghaniensis*	intolerant [a]	ECM [c]
Betula	*lenta*	intolerant [a]	ECM [c]
Betula	*papyrifera*	adapted [a]	ECM [c]
Carya	*alba*	adapted [b]	ECM [c]
Carya	*cordiformis*	intolerant [a]	ECM [c]
Carya	*glabra*	adapted [a]	ECM [c]
Carya	*ovata*	adapted [a]	ECM [c]
Celtis	*laevigata*	intolerant [b]	AM [c]
Celtis	*occidentalis*	intolerant [a]	AM [c]
Fagus	*grandifolia*	intolerant [a]	ECM [c]
Fraxinus	*americana*	intolerant [a]	AM [c]
Fraxinus	*nigra*	intolerant [a]	AM [c]
Fraxinus	*pennsylvanica*	intolerant [a]	AM [c]
Ilex	*opaca*	intolerant [b]	AM [c]
Juglans	*nigra*	intolerant [a]	AM [c]
Juniperus	*virginiana*	intolerant [a]	AM [c]
Larix	*laricina*	intolerant [a]	ECM [c]
Liquidambar	*styraciflua*	intolerant [a]	AM [c]
Liriodendron	*tulipifera*	intolerant [a]	AM [c]
Magnolia	*acuminata*	intolerant [a]	AM [c]
Magnolia	*virginiana*	intolerant [b]	AM [c]
Nyssa	*aquatica*	intolerant [b]	AM [e]
Nyssa	*biflora*	intolerant [a]	AM [e]
Nyssa	*sylvatica*	intolerant [a]	AM [e]
Ostrya	*virginiana*	intolerant [a]	ECM [c]
Oxydendrum	*arboreum*	intolerant[b]	Ericoid [e]
Picea	*glauca*	intolerant [a]	ECM [c]
Picea	*mariana*	intolerant [a]	ECM [c]
Picea	*rubens*	intolerant [a]	ECM [c]
Pinus	*banksiana*	adapted [a]	ECM [c]
Pinus	*echinata*	adapted [a]	ECM [c]
Pinus	*elliottii*	adapted [a]	ECM [c]

genus	species	fire classification	mycorrhizal association
Pinus	*palustris*	adapted [a]	ECM [c]
Pinus	*resinosa*	adapted [a]	ECM [c]
Pinus	*rigida*	adapted [a]	ECM [c]
Pinus	*serotina*	adapted [b]	ECM [c]
Pinus	*strobus*	adapted[a]	ECM [c]
Pinus	*taeda*	adapted [a]	ECM [c]
Pinus	*virginiana*	adapted [a]	ECM [c]
Platanus	*occidentalis*	intolerant [a]	AM [c]
Populus	*deltoides*	intolerant [a]	ECM [c]
Populus	*grandidentata*	adapted [a]	ECM [c]
Populus	*tremuloides*	adapted [a]	ECM [c]
Prunus	*serotina*	intolerant [a]	AM [c]
Quercus	*alba*	adapted [a]	ECM [c]
Quercus	*coccinea*	adapted [a]	ECM [c]
Quercus	*ellipsoidalis*	adapted [a]	ECM [c]
Quercus	*falcata*	adapted [a]	ECM [c]
Quercus	*laurifolia*	intolerant [b]	ECM [c]
Quercus	*macrocarpa*	adapted [a]	ECM [c]
Quercus	*nigra*	adapted [a]	ECM [c]
Quercus	*pagoda*	adapted [b]	ECM [c]
Quercus	*phellos*	adapted [a]	ECM [c]
Quercus	*prinus*	adapted [a]	ECM [c]
Quercus	*rubra*	adapted [a]	ECM [c]
Quercus	*stellata*	adapted [a]	ECM [c]
Quercus	*velutina*	adapted [a]	ECM [c]
Quercus	*virginiana*	intolerant [b]	ECM [c]
Robinia	*pseudoacacia*	intolerant[a]	AM [c]
Sabal	*palmetto*	adapted [b]	AM [e]
Salix	*nigra*	intolerant [a]	AM-ECM [c]
Sassafras	*albidum*	adapted [a]	AM [e]
Taxodium	*ascendens*	intolerant [a]	AM [d]
Taxodium	*distichum*	intolerant [a]	AM [d]
Thuja	*occidentalis*	intolerant [a]	AM [c]
Tilia	*americana*	intolerant [a]	ECM [c]
Tsuga	*canadensis*	intolerant [a]	ECM [c]
Ulmus	*alata*	intolerant [a]	AM [c]
Ulmus	*americana*	intolerant [a]	AM [c]
Ulmus	*Rubra*	intolerant [a]	AM [c]

[a] Nowacki and Abrams, 2015 [b] FEIS [c] Brundrett and Tedersoo, 2020 [d] Phillips et al., 2013 [e] Brundrett and Tedersoo 2019

Table B3. Compiled trait data for 29 tree species with citations.

genus	species	flame height (cm)	flame duration (s)	% consumed	smolder duration (s)	k ($year^{-1}$)	C:N	bark thickness: diameter
Acer	*rubrum*	59.7[a]	47.1[a]	84.3[a]	248.6[a]	0.54[d]	88.3[pqr]	0.030[δ]
Acer	*saccharum*	65.0[a]	32.0[b]	82.0[b]	170.0[b]	0.48[d]	65.1[s]	0.013[β]
Carya	*glabra*	72.6[a]	31.1[a]	87.4[a]	152.3[a]	0.64[d]	56.1[t]	0.025[β]
Carya	*tomentosa*	70.7[a]	34.7[a]	85.7[a]	115.3[a]	0.68[e]	50.0[u]	0.048[εθ]
Cornus	*florida*	76.3[a]	54.2[a]	84.1[a]	188.0[a]	1.06[d]	62.9[r]	0.044[δ]
Fagus	*grandifolia*	81.0[a]	50.8[a]	85.6[a]	177.6[a]	0.34[d]	43.6[u]	0.029[δ]
Liquidambar	*styraciflua*	54.4[a]	48.2[a]	87.2[a]	288.6[a]	0.55[f]	65.3[q]	0.075[δ]
Liriodendron	*tulipifera*	84.6[a]	48.6[a]	89.0[a]	173.4[a]	0.94[d]	33.0[v]	0.057[δ]
Nyssa	*sylvatica*	58.6[a]	55.9[a]	87.9[a]	256.4[a]	0.59[d]	54.4[w]	0.066[δ]
Oxydendrum	*arboreum*	98.5[a]	37.3[a]	93.6[a]	136.5[a]	1.11[g]	57.0[g]	0.056[δ]
Pinus	*banksiana*	49.4[c]	149.4[c]	71.5[c]	258.8[c]	0.20[d]	103.0[d]	0.056[ι]
Pinus	*elliottii*	71.1[a]	85.9[a]	90.9[a]	277.3[a]	0.28[h]	154.1[i]	0.055[ι]
Pinus	*palustris*	86.8[a]	57.0[a]	92.4[a]	273.7[a]	0.11[i]	147.6[i]	0.050[δ]

genus	species	flame height (cm)	flame duration (s)	% consumed	smolder duration (s)	k (year^{-1})	C:N	bark thickness: diameter
Pinus	*resinosa*	65.0[c]	140.2[c]	88.4[c]	476.2[c]	0.28[d]	92.1[d]	0.055[ι]
Pinus	*rigida*	85.5[a]	89.0[a]	87.0[a]	153.0[a]	0.52[d]	64.4[x]	0.093[δ]
Pinus	*strobus*	64.2[a]	158.0[a]	73.9[a]	129.2[a]	0.38[dj]	80.1[dj]	0.072[δ]
Pinus	*taeda*	84.1[c]	72.0[c]	86.9[c]	261.1[c]	0.08[d]	104.1[q]	0.0456[ι]
Prunus	*serotina*	67.6[a]	58.6[a]	87.9[a]	295.6[a]	1.33[d]	52.0[v]	0.045[ɳ]
Quercus	*alba*	72.0[a]	54.0[a]	91.0[a]	249.0[a]	0.48[d]	62.9[u]	0.053[δ]
Quercus	*coccinea*	73.3[a]	32.1[a]	90.9[a]	290.9[a]	0.30[d]	93.3[p]	0.048[δ]
Quercus	*falcata*	75.0[a]	52.1[a]	87.0[a]	399.8[a]	0.38[k]	52.4[y]	0.047[θʉ]
Quercus	*montana*	64.0[a]	41.0[a]	90.1[a]	302.4[a]	0.40[d]	72.5[pr]	0.067[αφ]
Quercus	*nigra*	57.3[a]	77.1[a]	77.9[a]	268.8[a]	0.22[l]	60.9[z]	0.054[δ]
Quercus	*rubra*	67.7[a]	46.1[a]	91.1[a]	283.0[a]	0.46[d]	80.8[n]	0.035[δ]
Quercus	*velutina*	76.0[b]	61.0[b]	92.0[b]	205.0[b]	0.47[d]	47.9[α]	0.060[δ]
Sassafras	*albidum*	63.4[a]	52.4[a]	86.5[a]	253.1[a]	0.41[m]	47.9[β]	0.064[δ]
Taxodium	*distichum*	51.9[a]	74.4[a]	62.3[a]	230.0[a]	0.11[n]	48.4[j]	0.031[χ]

genus	species	flame height (cm)	flame duration (s)	% consumed	smolder duration (s)	k ($year^{-1}$)	C:N	bark thickness: diameter
Tilia	*americana*	50.9[a]	53.6[a]	81.0[a]	172.7[a]	3.52[n]	29.2[n]	0.044[δ]
Tsuga	*canadensis*	9.2[a]	63.8[a]	2.3[a]	23.8[a]	0.21[o]	80.1[γ]	0.040[δ]

If multiple values were compiled, the mean value is shown. Citations:

[a]Varner et al., 2021 [b]Kreye et al., 2023 [c]Varner et al., 2022 [d]Kattge et al., 2020 (TRY) [e]Babl-Plauche et al., 2022 [f]McArthur et al., 1994 [g]Andersen and Wurzburger, unpublished [h]Wienand and Stock, 1995 [i]Hendricks et al., 2002 [j]Zhang et al., 2022 [k] Reitl and Jackson, 2012 [l]McArthur et al., 1994 [m]Strojan, 1978 [n]Holdsworth et al., 2008 [o]Cobb, 2010 [p]Alexander and McArthur, 2014 [q]Finzi et al., 2001 [r]Blair, 1988 [s]King et al., 2001 [t]Midgely et al, 2015 [u]Taylor et al., 2016 [v]Adams and Angradi, 1996 [w]Shure et al., 1986 [x]Won et al., 2018 [y]Campbell et al., 2021 [z]Mehring et al., 2014 [α]Babl, 2018 [β]Ostrofsky, 1997 [γ]Ignace et al., 2018 [δ]Pellegrini et al., 2017 [ε]Shearman and Varner, 2021 [θ]Scavotto et al., 2024 [ι]Jackson et al., 1999 [η]Hengst and Dawson, 1994 [ʉ]Graves et al., 2014 [φ]Hammond et al., 2015 [χ]Lickey et al. 2002

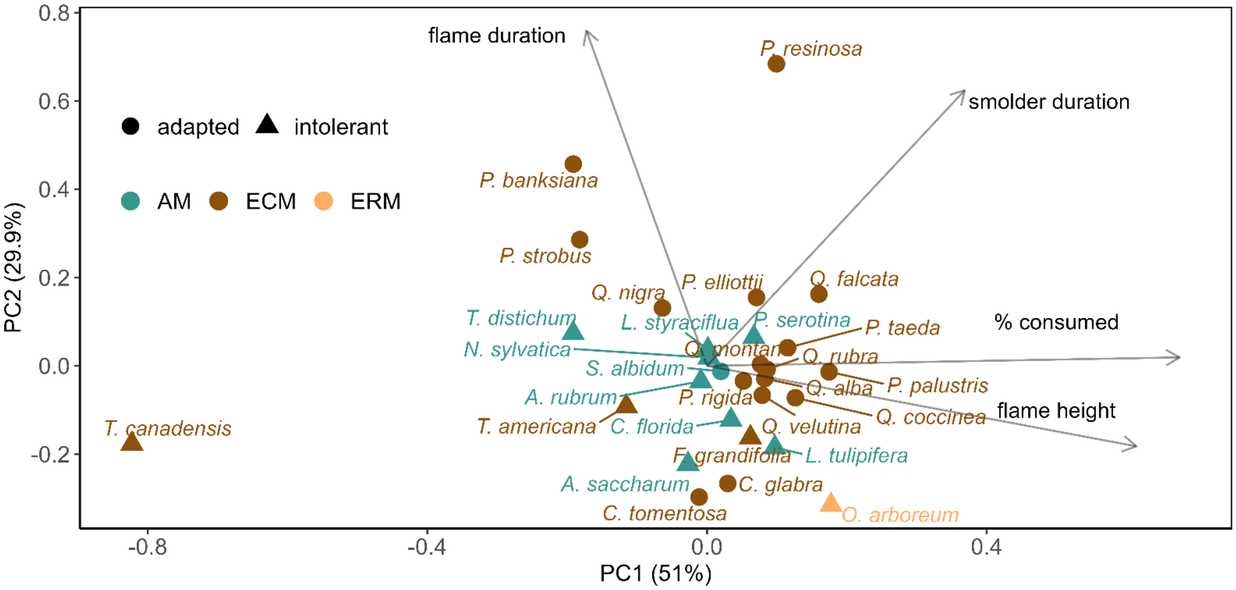

Figure B1. Principal components analysis ordination of leaf litter flammability traits for 29 common tree species.

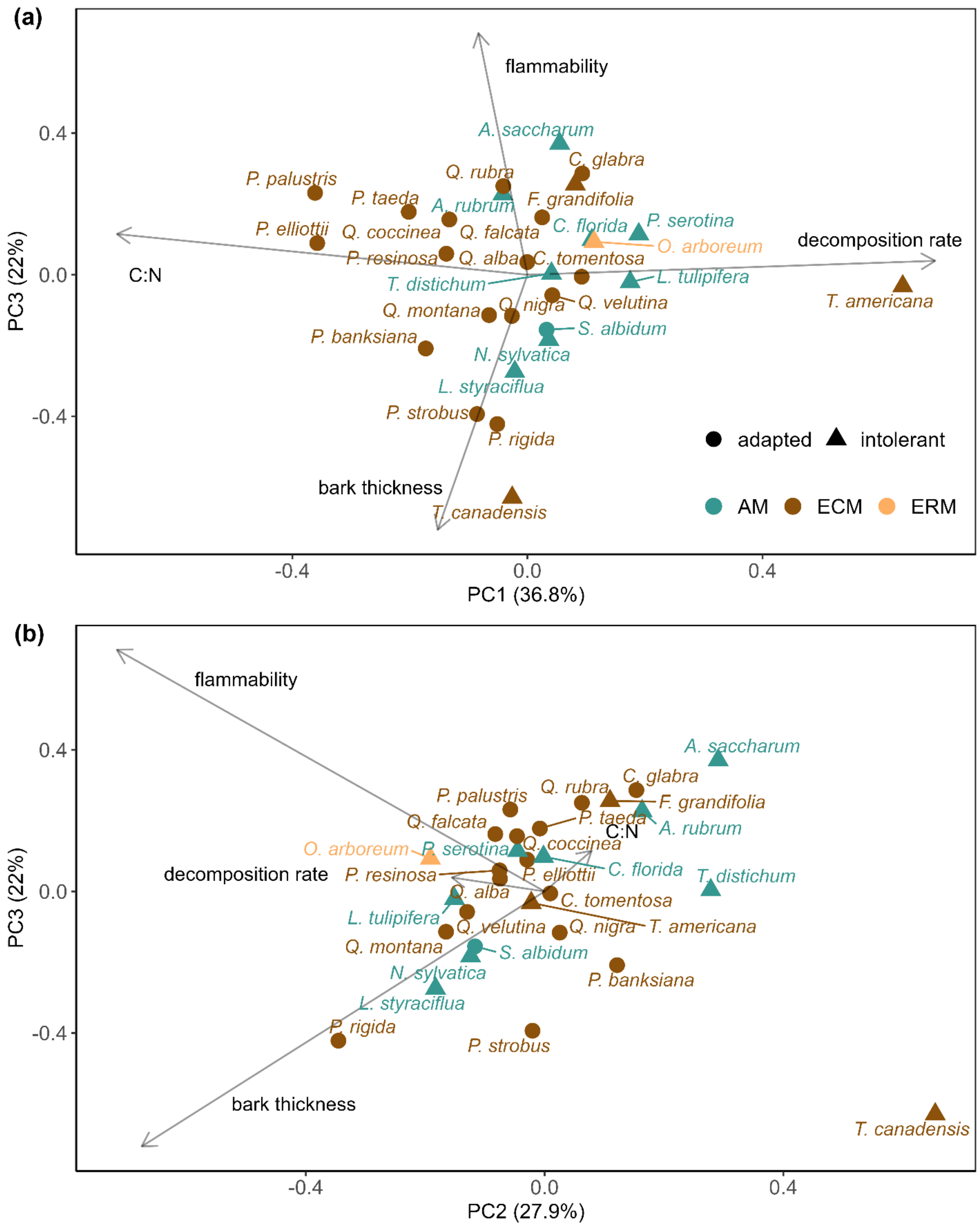

Figure B2. Principal components analysis ordinations for other combinations of principal components for 29 common tree species. Colors indicate mycorrhizal associations, shapes indicate fire-adapted or fire-intolerant.

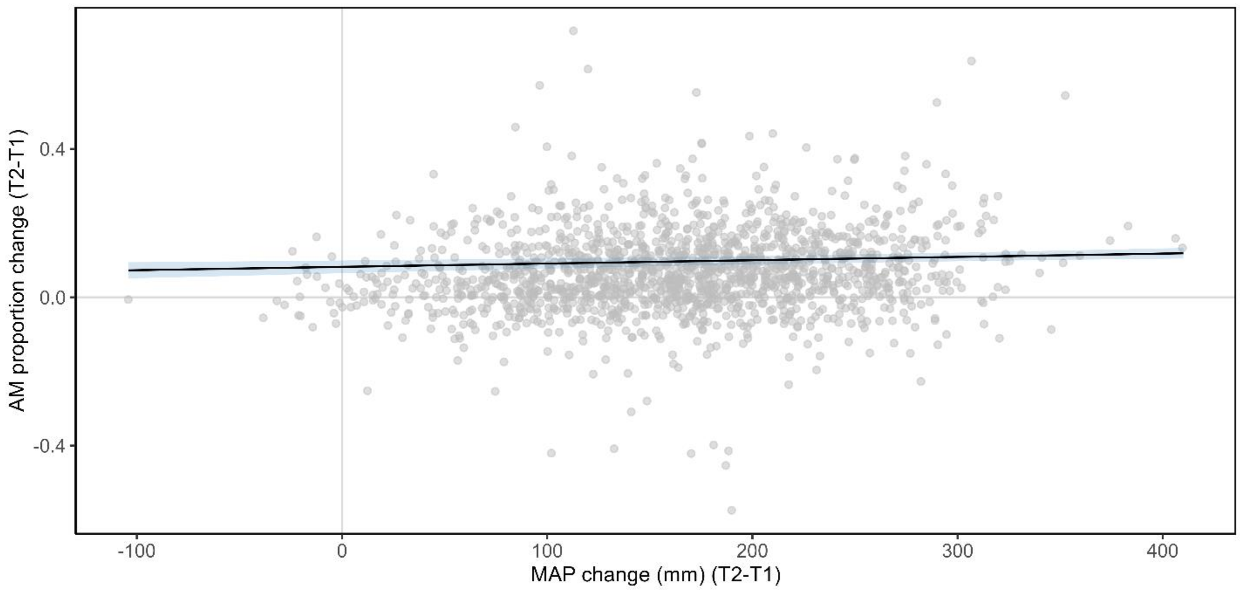

Figure B3. The proportion difference of arbuscular mycorrhizal (AM) species basal area compared to changes in mean annual precipitation (MAP). Each point is a county. The line indicates model predictions, shaded by standard error estimates.

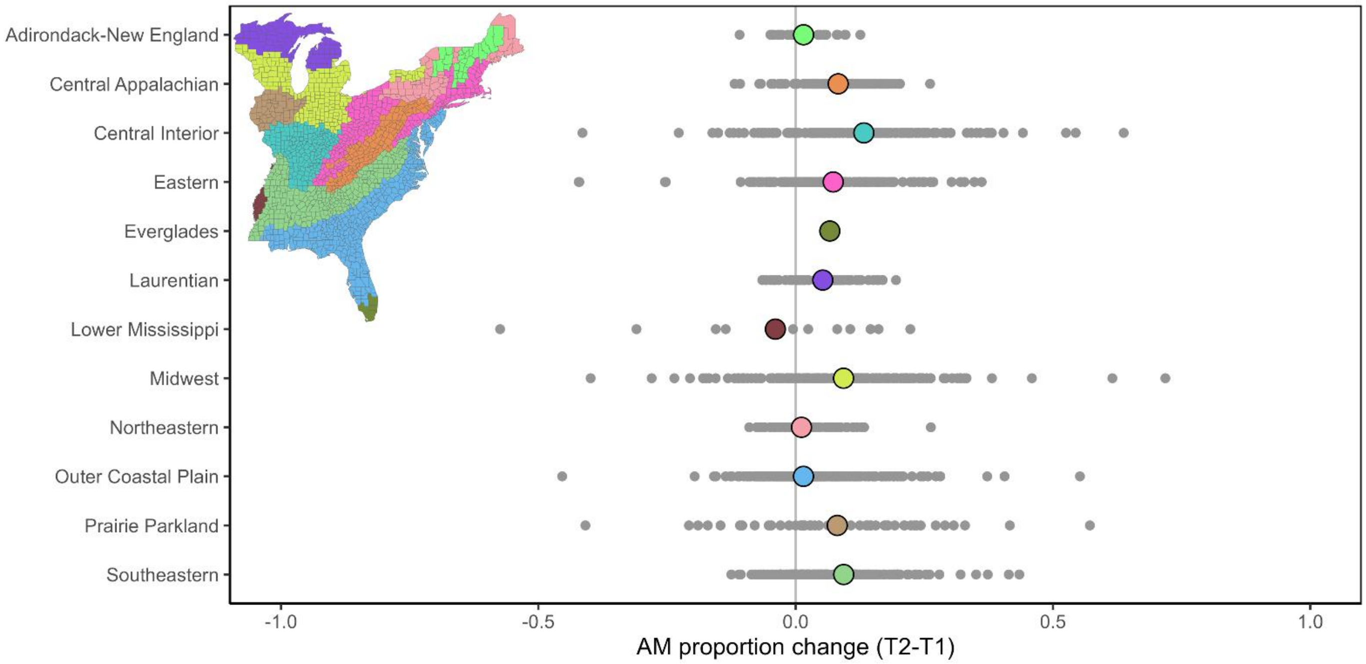

Figure B4. Predicted basal area proportion changes of arbuscular mycorrhizal (AM) trees for each ecological province. Each gray point indicates a county, and the colored points indicate province-specific model predictions, corresponding with inset map.

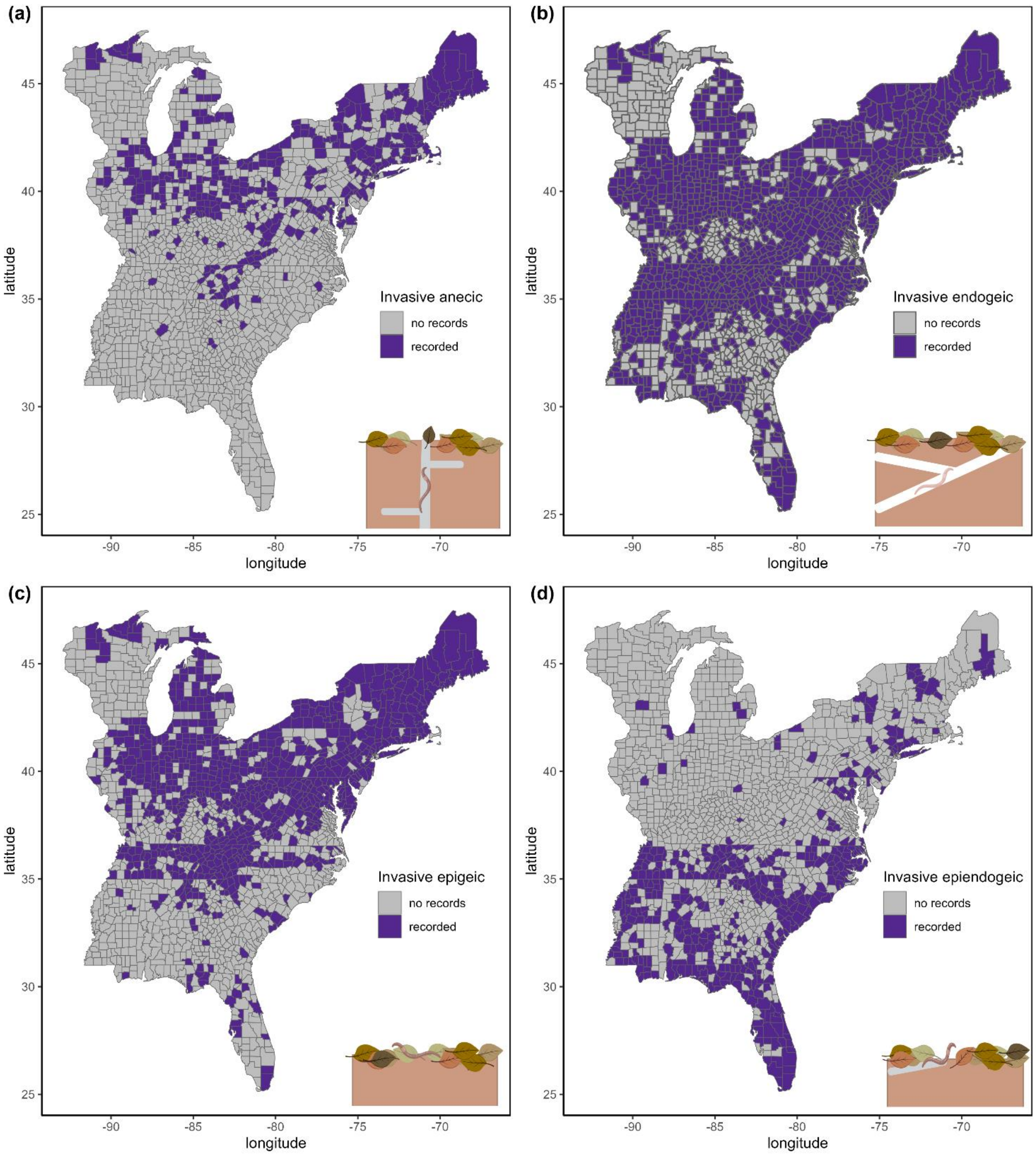

Figure B5. County-level maps showing the presence of records for invasive earthworms categorized by each ecological group.

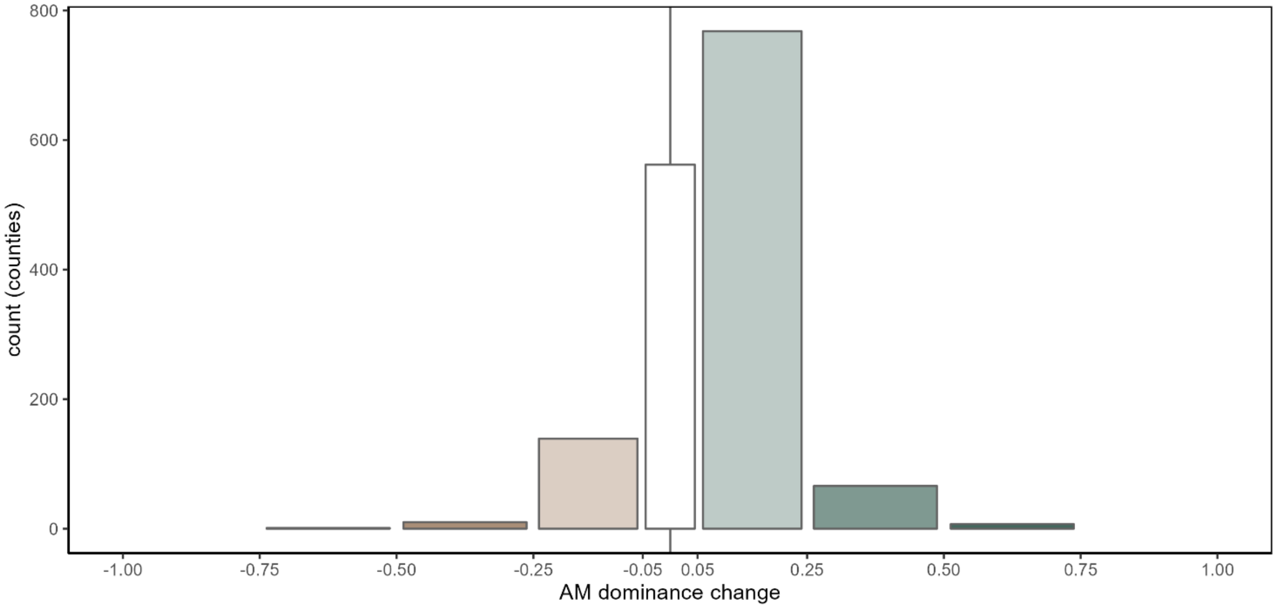

Figure B6. A histogram of arbuscular mycorrhizal (AM) dominance change among counties in the eastern United States.

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APPENDIX C

SUPPLEMENTARY INFORMATION: CHAPTER 4

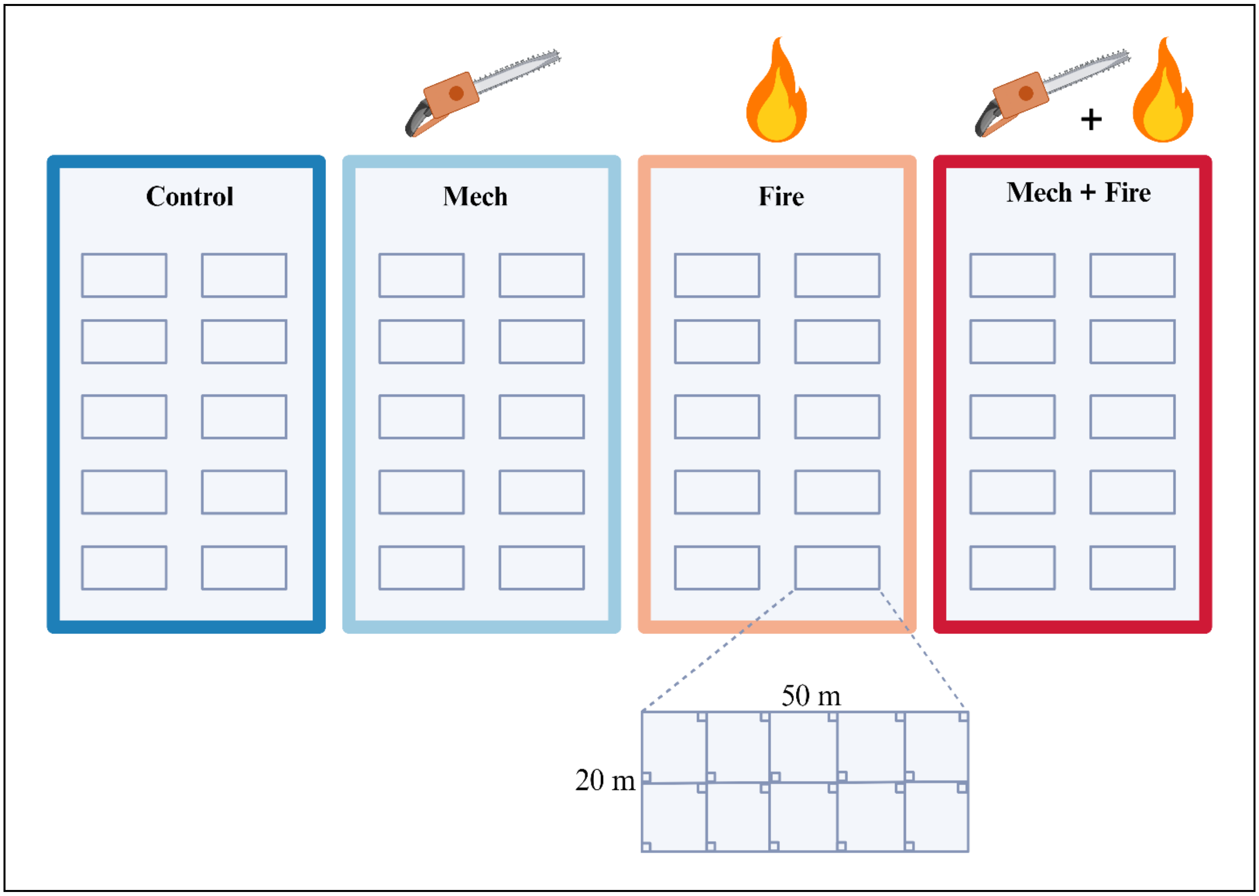

Figure C1. Experimental design of the Green River Fire and Fire Surrogates site. This schematic diagram represents one of the three replicated spatial blocks. Within each 12-hectare treatment unit, there are ten sampled plots (represented by rectangles). Mech = mechanical felling. Mechanical treatments have been applied twice in the Mech treatment and once in the Mech +

Fire treatment. Fire treatments have been applied four times. Each plot is further divided into ten subplots (callout). Each subplot contains two 1 m^2 quadrats. Image created with BioRender.com.

Table C1. Tree genera represented at the Green River Game Lands study in 2018. Each genus is listed with its percentage of the composition of the overstory, sapling, and seedling layers.

Genus	Overstory (%)	Sapling (%)	Seedling (%)
Acer	10.03	26.92	31.58
Amelanchier	0.00	0.06	0.44
Asimina	0.00	0.04	0.03
Betula	0.11	0.11	0.09
Carya	4.16	1.61	1.73
Castanea	0.00	0.64	0.19
Cercis	0.00	0.01	0.03
Chionanthus	0.00	0.00	0.00
Cornus	0.44	0.34	0.67
Diospyros	0.00	0.85	0.38
Fagus	0.00	0.00	0.02
Fraxinus	0.00	0.01	0.02
Halesia	0.07	2.46	0.49
Hamamelis	0.00	1.07	0.55
Ilex	0.00	0.01	0.02
Liriodendron	3.94	10.76	2.64
Magnolia	0.99	2.58	0.71
Nyssa	6.05	4.12	3.58
Oxydendrum	20.93	12.89	1.37
Pinus	5.18	0.91	0.96
Prunus	0.00	0.71	0.49
Quercus	46.43	22.64	44.36
Robinia	0.55	2.54	0.54
Sassafras	0.07	8.50	9.07
Tilia	0.00	0.00	0.00
Tsuga	1.06	0.20	0.03

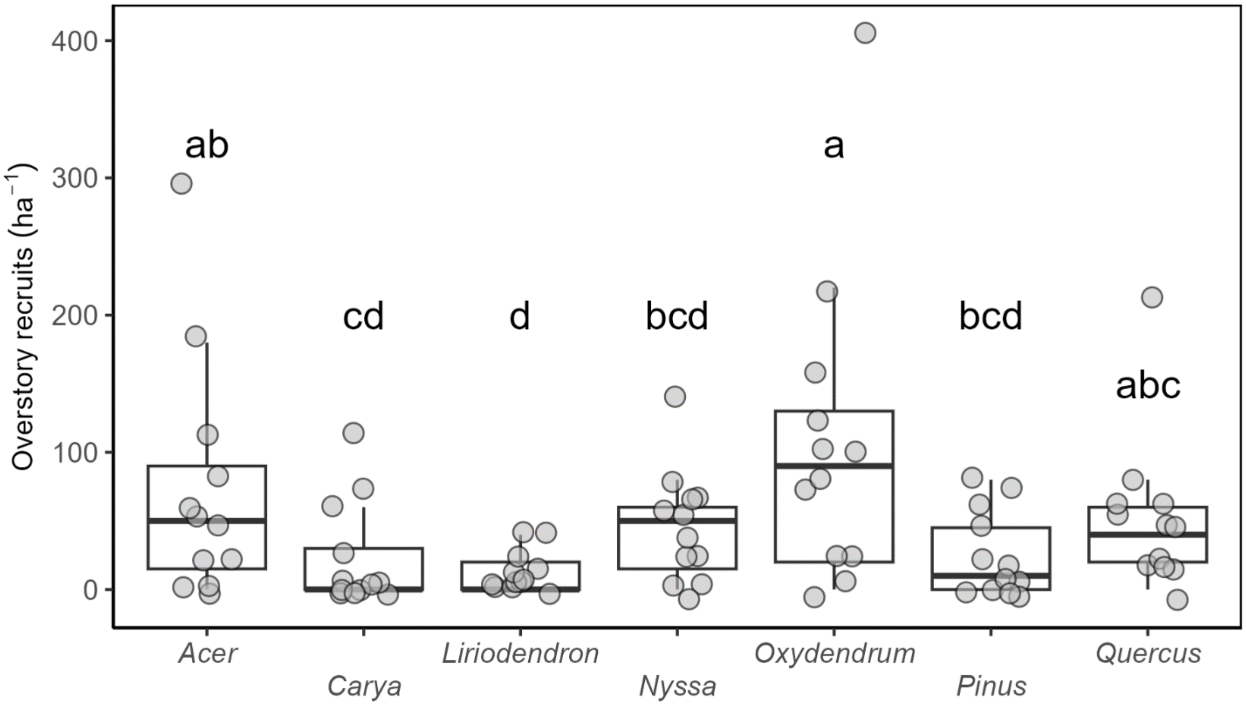

Figure C2. Overstory recruitment of the seven major genera during 2001-2018 at the Green River Fire and Fire Surrogates site. Recruits are summarized by treatment unit. Boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Individual points are overlaid. Absence of the same letter signifies differences ($P \leq 0.05$) amongst genera.

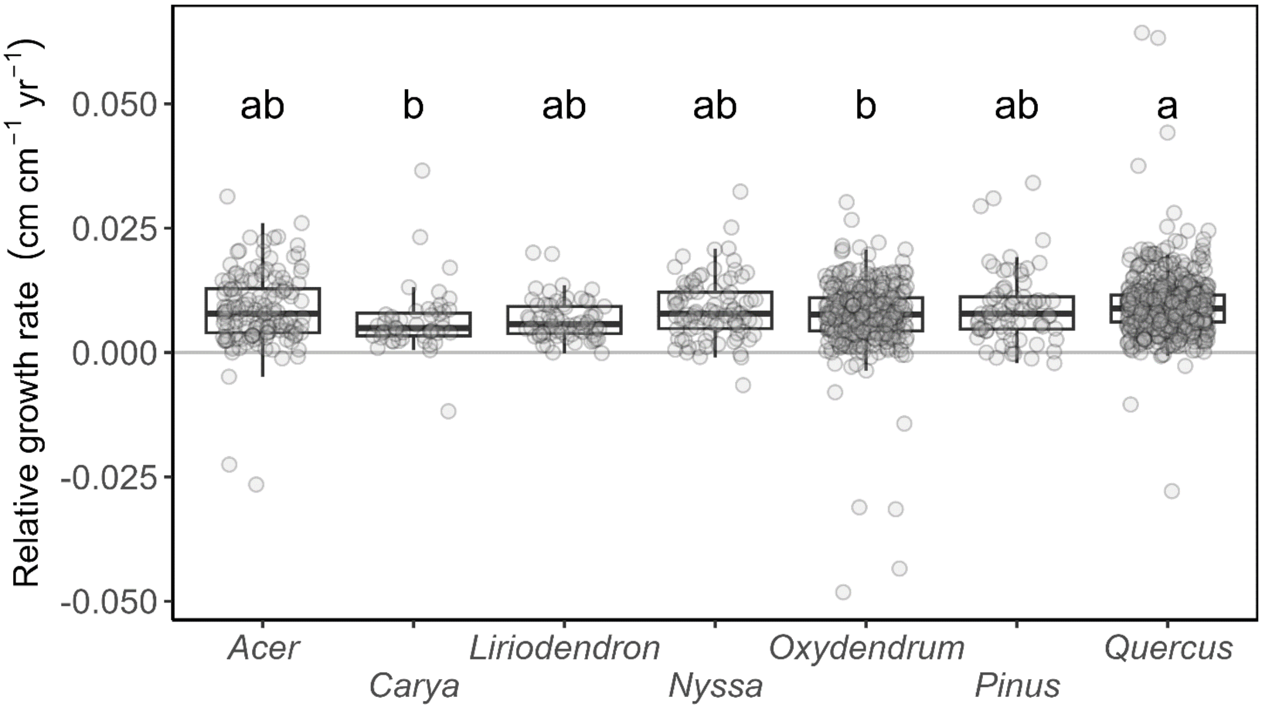

Figure C3. Relative growth rate of overstory trees of seven genera at the Green River Fire and Fire Surrogates Site during 2001-2018. Boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Individual points are overlaid. Absence of the same letter signifies differences ($P \leq 0.05$) amongst genera.

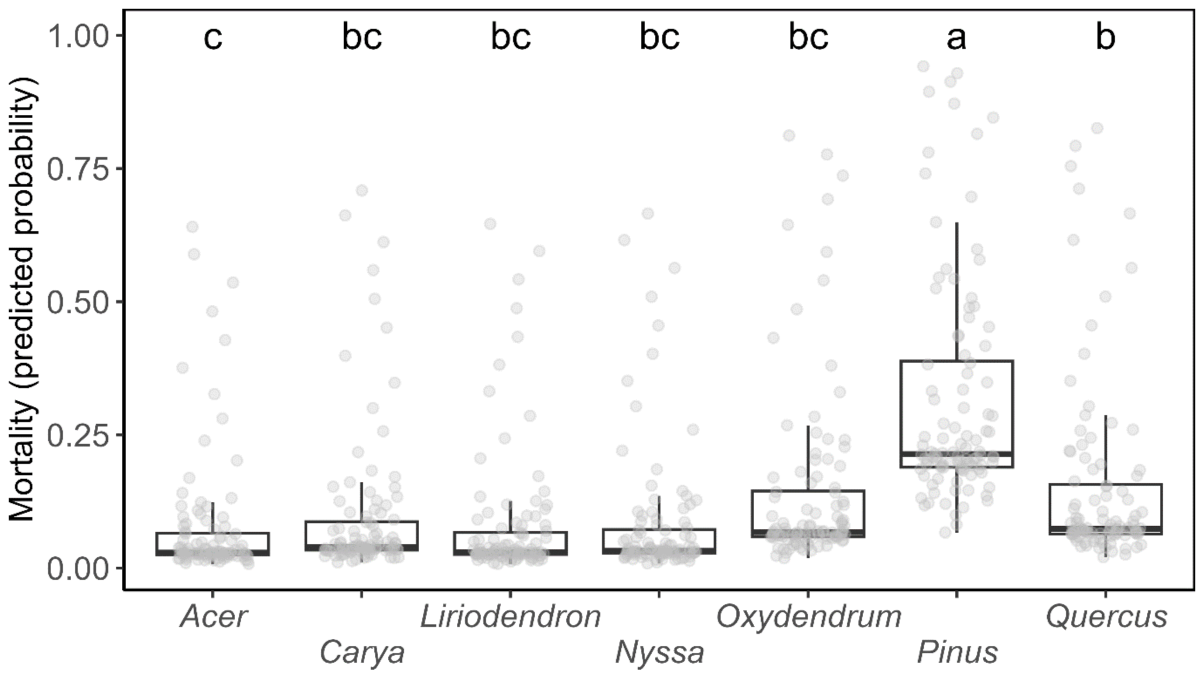

Figure C4. Predicted probabilities of mortality for overstory trees of the seven major genera during 2001-2018 at Green River Fire and Fire Surrogates site. Boxes represent the interquartile range (IQR), horizontal lines within boxes are median values, and whiskers represent points that fall within 1.5*IQR. Individual predictions are overlaid. Absence of the same letter signifies differences ($P \leq 0.05$) amongst genera.

Table C2. Estimated marginal means (SE) from our generalized linear mixed model of sapling abundances per hectare of the seven major genera in four treatments at the Green River Fire and Fire Surrogates study. Absence of the same lowercase letter signifies treatment differences (*P* ≤ 0.05) within a genus (horizontally across table). Absence of the same uppercase letter signifies differences amongst genera within a treatment (vertically across table).

	Control	**Mech**	**Fire**	**Mech + Fire**
Acer	540.5 (296.9) a A	383.7 (212.3) a A	294.0 (162.9) a A	1468.7 (810.1) a A
Carya	12.7 (7.3) a C	0.9 (0.6) b B	1.5 (0.9) b C	4.4 (2.6) ab D
Liriodendron	1.5 (0.9) b D	0.03 (0.02) c C	1.4 (0.9) b C	131.5 (74.1) a BC
Nyssa	29.3 (16.5) a BC	0.2 (0.1) b BC	13.4 (7.7) a B	21.7 (12.6) a CD
Oxydendrum	62.9 (35.2) b BC	113.2 (63.0) ab A	309.0 (284.7) ab A	513.19 (284.7) a AB
Pinus	14.1 (8.0) a C	1.5 (0.9) c B	0.1 (0.1) b D	0.21 (0.14) bc E
Quercus	182.6 (100.9) ab AB	65.8 (37.1) bc A	24.1 (13.8) c B	785.2 (435.0) a AB

Table C3. Estimated marginal means (SE) from our generalized linear mixed model of seedling abundances per hectare of the seven major genera in four treatments at the Green River Fire and Fire Surrogates study. Absence of the same lowercase letter signifies treatment differences (*P* ≤ 0.05) within a genus (horizontally across table). Absence of the same uppercase letter signifies differences amongst genera within a treatment (vertically across table).

	Control	**Mech**	**Fire**	**Mech + Fire**
Acer	2612.0 (1982.0) a A	5259.8 (4027.0) a A	25044.1 (19511.2) a A	1869.3 (1463.1) a A
Carya	13.8 (11.6) ab B	1.1 (1.1) b BC	72.1 (58.5) a B	67.5 (54.9) a BC
Liriodendron	0.3 (0.3) b C	0.3 (0.3) b C	163.9 (131.3) a B	26.1 (22.0) a C
Nyssa	53.4 (43.2) c B	40.5 (33.1) b B	255.2 (202.9) ab B	1222.5 (958.4) a AB
Oxydendrum	0.003 (0.003) c D	0.8 (0.8) b C	11.1 (9.5) ab B	34.7 (28.9) a C
Pinus	0.009 (0.008) c CD	0.2 (0.2) bc C	14.3 (12.2) a B	4.3 (3.9) ab C
Quercus	12533.3 (9692.9) a A	12904.1 (9992.1) a A	22867.9 (17772.4) a A	24123.8 (18722.3) a A

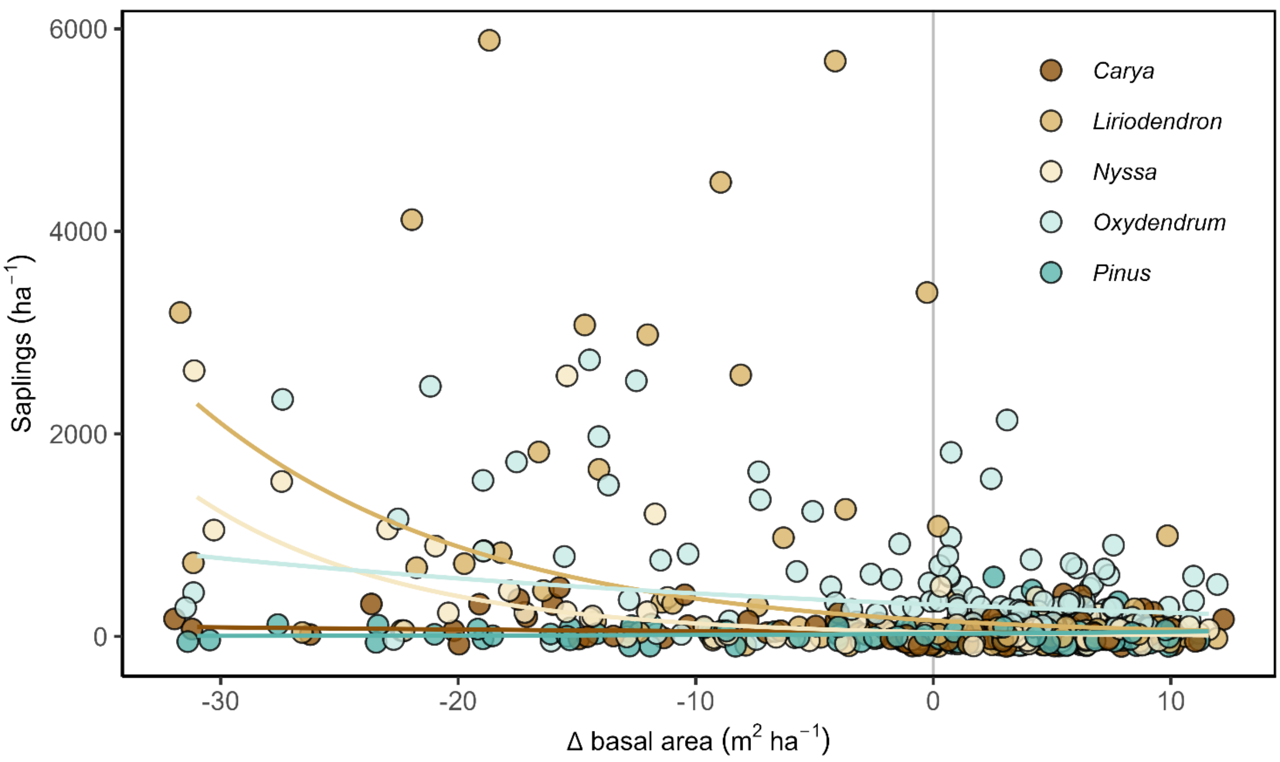

Figure C5. Sapling abundance compared to Δ basal area for less abundant genera at the Green River Fire and Fire Surrogates site. Lines are model predictions. Slope estimates for each line differ ($P \leq 0.05$) from zero. Slope estimates for each line differ from each other, apart from *Carya* and *Oxydendrum*.

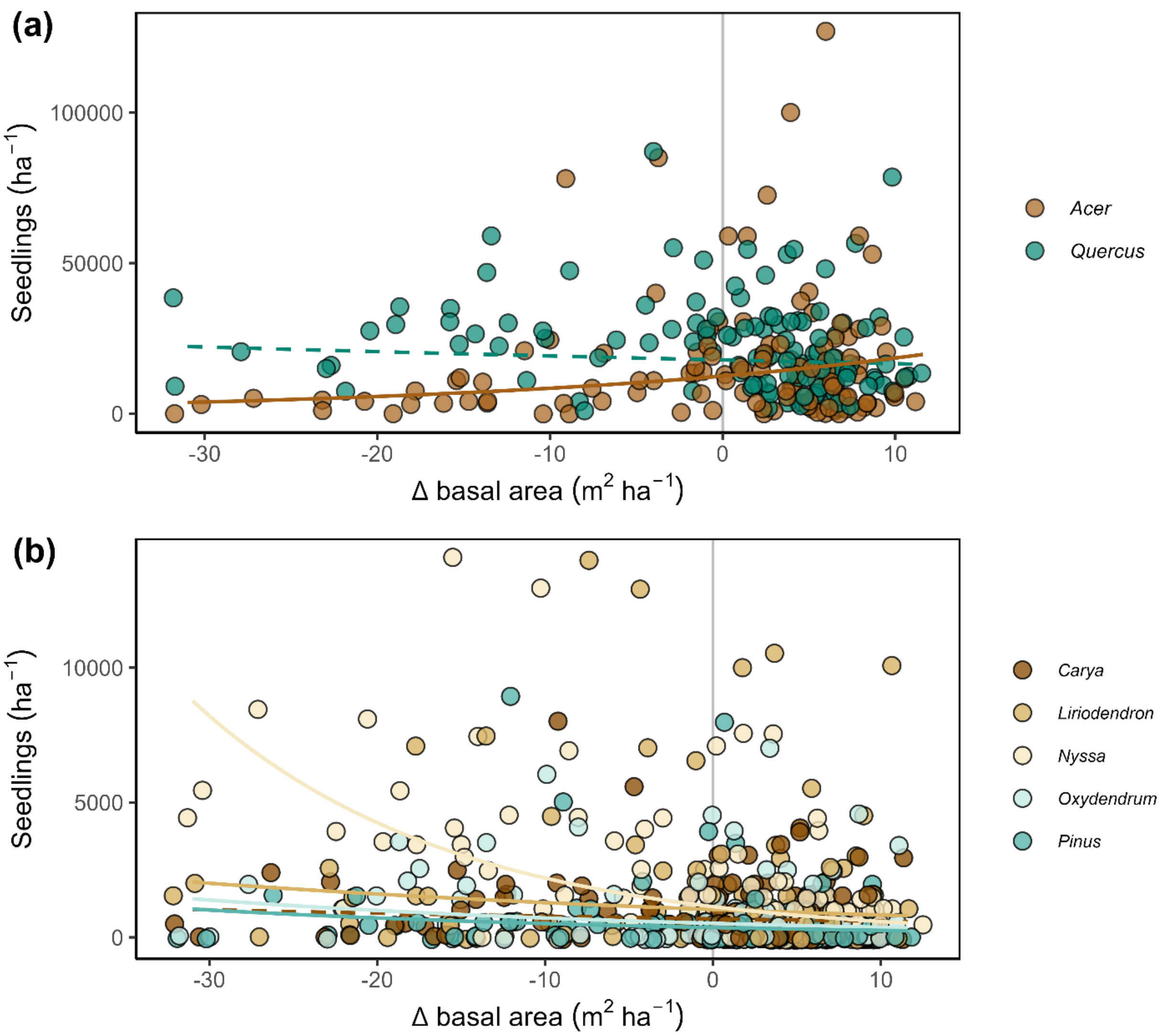

Figure C6. Seedling abundances compared to Δ basal area at the Green River Fire and Fire Surrogates site. (a) *Acer* and *Quercus*, (b) less abundant genera. Points are jittered slightly to aid visualization. Lines are model predictions, and solid denotes the estimated slope differs ($P \leq 0.05$) from zero. Slope estimates for each line differ from each other, apart from these combinations: *Carya* with *Liriodendron*, *Oxydendrum*, *Pinus*, and *Quercus*, *Liriodendron* with *Oxydendrum*, *Pinus*, and *Quercus*, and *Oxydendrum* with *Pinus*.