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Plant-soil feedbacks affect hardwood regeneration in mountain laurel (*Kalmia latifolia*) thickets

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ABSTRACT

Ericaceous thickets inhibit hardwood regeneration, particularly of ectomycorrhizal tree species, yet mechanisms underlying effects of the ericaceous shrub *Kalmia latifolia* remain unclear. We explored these effects using spatial analyses of a forest stand and two greenhouse experiments testing plant-soil feedbacks (PSFs), their biotic basis, and light dependence. Spatial analyses confirmed that seedling abundance for most species was negatively correlated with *K. latifolia* basal area. Oaks (*Quercus* spp.) recruiting to the sapling stage occurred in areas with less *K. latifolia* than those where arbuscular or ericoid mycorrhiza-associated saplings established. Greenhouse Experiment 1 showed *Quercus alba* emergence was greater in conspecific than *K. latifolia*-conditioned soils under sterile conditions, indicating a negative abiotic effect of *K. latifolia* soil on oak emergence. In nonsterile treatments, soil microbes partially offset this effect and enhanced *Q. alba* emergence relative to sterilized *K. latifolia* soil. Seedling growth was greater in conspecific soil under low light, reflecting a positive, biotically mediated, light-dependent PSF. Seedlings of another ericaceous species, *Oxydendrum arboreum,* had greater survival and growth in *K. latifolia* soil than conspecific soil, but negative PSFs were not consistently biotically mediated or stronger in low light. Greenhouse Experiment 2 showed *Q. alba* emergence was lower in soils conditioned by *Vaccinium* spp., *O. arboreum*, and *K. latifolia* at 6 weeks, but not at 12 weeks, suggesting delayed emergence may characterize ericoid-conditioned soils. Collectively, results indicate that ericaceous shrubs constrain oak regeneration through stage-specific PSFs that interact with light and microbes, with implications for managing oak recruitment in mixed hardwood forests.

1. Introduction

Despite their historical dominance, many *Quercus* species are failing to regenerate, leading to widespread oak forest decline across eastern North America (Taylor and Lorimer, 2003; Fei et al., 2011; Knott et al., 2019). This regeneration failure likely reflects interacting biotic and abiotic factors across multiple life stages (McEwan et al., 2011; Jerome et al., 2017). One contributor may be the expansion of mountain laurel (*Kalmia latifolia*) thickets, which have proliferated in oak-hickory forests over the past century (Clinton et al., 1994; League, 2005; Brose, 2016). Expansion of ericaceous thickets, including *K.* latifolia, has been linked to fire suppression, logging, and increased canopy gaps from overstory decline (Pipkin, 2012; Brose, 2016; Woodbridge and Dovciak, 2022). The colonization of canopy gaps by *K. latifolia* and the closely related shrub, *Rhododendron maximum*, along with the subsequent suppression of hardwood regeneration, is well documented (Waterman et al., 1995; Van Lear et al., 2002; Brose, 2016).

Reduced *Quercus* sapling recruitment beneath *K. latifolia* thickets may reflect plant-soil feedbacks (PSFs), in which plants alter physical, chemical, or biotic soil conditions that subsequently influence seedling performance (Bever, 2003; Bennett and Klironomos, 2019). PSFs are often species-specific and generate spatial recruitment patterns such as conspecific distance- or density-dependent recruitment (Koga et al., 2020; Hülsmann et al., 2021). Negative PSFs occur when seedlings perform worse in soils conditioned by conspecifics than in soils conditioned by heterospecifics, promoting coexistence (Bever et al., 1997, 2015), whereas positive PSFs enhance conspecific recruitment and may foster monodominance (Dickie et al., 2014; Bennett et al., 2017). Accordingly, PSFs are commonly evaluated by comparing seedling performance in conspecific vs. heterospecific soils (Brinkman et al., 2010). Soil microbial communities play a central role in these processes, as plant roots shape the balance of mutualists and pathogens,

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many of which exhibit host preference (Van der Putten et al., 2013).

Light availability is substantially reduced within *K. latifolia* thickets, and although shading alone does not fully explain poor oak regeneration (Clinton, James, 1996; Lei et al., 2006; Elliott and Miniat, 2018), it may interact with other mechanisms. Light can modulate PSFs by altering soil microbial communities directly or by modifying plant-microbe interactions (Reinhart et al., 2010; Liu and He, 2019). Survival-based negative PSFs are often strongest under low light (McCarthy-Neumann and Ibáñez, 2013; McCarthy-Neumann and Kobe, 2010; McCarthy-Neumann et al., 2026b), potentially due to increased pathogen abundance (Reinhart et al., 2010; Hersh et al., 2012), parasitism by mycorrhizal fungi (Ibáñez and McCarthy-Neumann, 2016) reduced physical or chemical defenses (Ichihara, Yamaji. 2009; Wood et al., 2023a), and limited stress recovery under low light (Myers and Kitajima, 2007; Kobe et al., 2010; Wood et al., 2023b). Conversely, biomass-based PSFs may be strengthened under high light, where mutualistic mycorrhizal colonization can increase (Xi et al., 2023). Because *K. latifolia* thickets substantially reduce understory light, we explicitly test how light interacts with PSFs to shape hardwood seedling performance.

Although *K. latifolia* is the dominant ericaceous shrub at our field site, we included other ericoid mycorrhiza-associated species to test whether soil-mediated effects on hardwood regeneration extend beyond *K. latifolia*. *Oxydendrum arboreum*, an ericaceous tree common in upland hardwood forests, provides a useful contrast because it shares ericoid mycorrhizal associations with *K. latifolia* but differs in growth form and canopy structure. Including *O. arboreum* as both a response species and a soil-conditioning species allowed us to test whether feedbacks associated with *K. latifolia* reflect shrub-specific effects or broader ericaceous soil processes. Similarly, *Vaccinium* spp. provides an additional test of whether delayed oak emergence or reduced oak performance occurs across soils conditioned by plant species associated with ericoid mycorrhiza rather than only beneath *K. latifolia*.

Hereafter, we distinguish between mycorrhizal fungi and the plant species that typically associate with them: ericoid, ectomycorrhizal, and arbuscular mycorrhizal fungi are referred to as ERF, EMF, and AMF, respectively, whereas associated plant guilds are referred to as ERM, ECM, and AM. *K. latifolia* may affect soil microbial communities through both its leaf litter and its symbiotic relationship with ERF. Because direct studies on *K. latifolia*'s influence on soil microbiota are limited, evidence from related ERM species provides useful context. ERF appear to play a key role in ericaceous dominance, enhancing ericaceous seedling performance in soils cultured by both ERM and ECM trees in mesocosm and field experiments (Pfennigwerth et al., 2017; Lee et al., 2023). Although plant species are often categorized by their dominant mycorrhizal association, some taxa can form dual associations, particularly during early seedling stages, including AMF colonization in *Quercus* spp. (Teste et al., 2020). Notably, ERF have also been detected on *Quercus* root tips and in soils of *Quercus*-dominated stands lacking nearby ericaceous shrubs (Bergero et al., 2001, 2003). These observations suggest that oak roots may encounter non-EMF associates even in stands dominated by ECM trees, although whether ERF colonization directly inhibits EMF formation or alters oak recruitment remains unresolved. Ericoid shrubs often recruit into canopy gaps formed by the mortality of ECM trees such as *Tsuga canadensis* and *Castanea dentata* (Brose et al., 2002; Pfennigwerth et al., 2017), potentially placing ERM plants and their fungal associates in direct contact with regenerating hardwood seedlings. Indirect evidence for such interactions comes from studies showing that ericaceous shrubs suppress EMF formation (Kohout et al., 2011), and that shrub removal can reduce ERF abundance while increasing tree seedling establishment (Beckage et al., 2000; Osburn et al., 2021). Together, these findings indicate that ericaceous shrubs may inhibit hardwood regeneration through biotically-mediated, ERM-associated PSFs. Although this study focuses primarily on *Quercus* species, we extend field analyses to all tree species to assess whether responses to *K. latifolia* differ systematically by mycorrhizal association.

Previous work on AM and ECM trees, the two dominant mycorrhizal guilds in temperate forests, demonstrates consistent differences in PSF direction and strength, as well as in associated patterns of conspecific density-dependence (Bennett et al., 2017). In contrast, the role of ERF in shaping PSFs remains poorly understood. Specifically, it is unclear whether ERM species generate feedbacks that differ systematically depending on the mycorrhizal type of neighboring tree species, or whether their effects are broadly suppressive across guilds.

Studies examining the effects of *K. latifolia* on *Quercus* seedlings consistently report reduced growth, yet the mechanism behind this phenomenon remains unresolved (Waterman et al., 1995; Beier et al., 2005; Eppard et al., 2005). Known ericaceous effects on soil conditions suggest that biotically-mediated PSFs may contribute to this suppression. Ericaceous species and ERF produce polyphenols and melanin that slow decomposition and favor microbial communities capable of degrading these compounds (Wurzburger and Hendrick, 2009; Clemmensen et al., 2015; Ward et al., 2022). Soils from within *K. latifolia* thickets exhibit higher relative saprotroph abundance but lower saprotroph richness, reduced decomposition rates, diminished EMF abundance, and representation of two ERF lineages (Serendipitaceae and Leotiomycetes) compared to soils outside thickets (Ward et al., 2022; Polussa et al., 2024). Reduced EMF abundance, together with lower EMF colonization near ericaceous plants, supports the hypothesis that biotically mediated PSFs inhibit oak regeneration within *K. latifolia* thickets (Kohout et al., 2011). In contrast, AM tree species may benefit from increased saprotroph dominance in *K. latifolia* soils, as AMF have limited decomposer capacity and rely on saprotrophs to mineralize nutrients (Whiteside et al., 2012). Together, these patterns raise the possibility that ericaceous shrubs disproportionately suppress ECM seedling performance through alterations to soil microbial communities.

The objective of this study was to test whether *K. latifolia* shrubs inhibit non-ericaceous seedling performance through spatially structured PSFs. The Field Study examined density-dependent effects of *K. latifolia* by relating seedling and sapling recruitment, and adult tree growth to *K. latifolia* basal area, density, and tree mycorrhizal associations. We predicted:

1. Seedling abundance declines with increasing *K. latifolia* basal area.
2. Sapling distributions vary by mycorrhizal type, with ECM species less frequent in high *K. latifolia* areas than AM or ERM tree species.
3. Adult tree growth declines with *K. latifolia* basal area, especially for ECM trees.

Greenhouse Experiment 1 tested the causal roles of biotically mediated PSFs and light. We grew *Quercus alba* and *O. arboreum* in soils conditioned by conspecific or *K. latifolia* adults, under sterile vs. nonsterile and high vs. low light conditions. We predicted:

4. Q. alba performance (emergence, survival, and/or growth) is enhanced in conspecific soils (i.e., positive PSF), whereas O. arboreum seedling performance is reduced (i.e., negative PSF) relative to K. latifolia soils.
5. PSFs are biotically mediated (i.e., only present in nonsterile soil).
6. PSFs strengthen under low light.

Greenhouse Experiment 2 assessed whether reduced Q. alba performance is a general response to ERM-conditioned soils by comparing seedlings grown in conspecific soils versus soils conditioned by *K. latifolia*, *O. arboreum*, and *Vaccinium* spp. We predicted:

7. *Q. alba* performance is inhibited in all ERM-conditioned soils (i.e., positive PSF).

Our study integrates spatial field patterns with controlled greenhouse experiments to test whether landscape-level regeneration failure can be explained by experimentally demonstrable PSFs.

2. Materials and methods

To assess the effect of *K. latifolia* on hardwood seedling recruitment, we analyzed spatial patterns of seedlings and saplings and adult growth with species categorized by their mycorrhizal association. We then used two greenhouse experiments to test whether PSFs contribute to seedling regeneration failure in *K. latifolia* thickets. Greenhouse Experiment 1 assessed emergence, survivorship, and biomass of *Q. alba* and *O. arboreum* seedlings in conspecific and *K. latifolia*-conditioned soils under sterilization and light treatments. Greenhouse Experiment 2 tested whether effects on *Q. alba* extend across ericaceous-conditioned soils by comparing conspecific soil with soils conditioned by *K. latifolia*, *O. arboreum*, and *Vaccinium* spp.

2.1. Field study: hardwood recruitment in and outside of K. latifolia thickets

2.1.1. Site Description

Fieldwork was conducted in the Cross Creek watershed, Franklin State Forest, Marion County, Tennessee, USA (35°04'N, 85°51'W). The 36-ha watershed spans elevations from 495 to 574 m (Ramseur and Kelly, 1981) with mean annual precipitation of 670 mm and mean temperature of 13.1°C (National Oceanic and Atmospheric Administration, 2025). Soils include nutrient-poor, and acidic alfisols, inceptisols, and ultisols (Kelly, 1979) with more fertile, seasonally saturated swale soils in valley bottoms (Ramseur and Kelly, 1981). Vegetation is dominated by *Q. alba*, *Acer rubrum*, and *Quercus montana* in the canopy and *A. rubrum*, *K. latifolia*, and *Sassafras albidum* in the understory (McCarthy-Neumann et al., 2026a). There is a creek running longitudinally through the plot, with steep slopes on either side.

2.1.2. Spatial data collection

We surveyed a 1-ha (100 ×100 m) permanent plot established in 1976 (Ramseur, 1977). The plot was divided into 100 subplots (100 m^2 each), which were further subdivided into 25-m^2 units. In summer 2015, all woody stems > 1.4 m in height were mapped, identified to species (with *Vaccinium* to genus), and measured for diameter at breast height (DBH). In summer 2023, we extended this methodology to include mapping and identifying to species all individuals > 50 cm in height, and all data were recorded using ArcGIS Field Maps (ESRI, 2024) with positional accuracy < 50 cm. Seedling abundance was scored in ordinal bins (0, 1, 2–7, 8–25, and >25 seedlings per 100 m^2) to standardize rapid field estimation across subplots in 2023. *Quercus* seedlings were re-surveyed in summer 2024 following a mast event.

2.2. Greenhouse experiment 1: PSFs in K. latifolia Soils

2.2.1. Experimental design

To test whether *K. latifolia* inhibits hardwood recruitment via PSFs, we conducted a fully factorial experiment with two species (*Q. alba*, ECM tree; *O. arboreum*, ERM tree), two soil sources (conspecific vs. *K. latifolia*), two soil treatments (nonsterile vs. sterile), and two light levels (~ 2% vs. 8% full sun). Each of the 16 treatment combinations was replicated 20 times (N = 320).

2.2.2. Soil collection and preparation

Soils were collected between Dec 2022 - Jan 2023 from the upper 15 cm within 1 m of the bole of four randomly selected adult trees in the top DBH quartile of each species (*Q. alba*, *O. arboreum*, and *K. latifolia*). To reduce potential mycorrhizal contamination from surrounding vegetation, focal trees were spaced at least two crown diameters from heterospecifics of different mycorrhizal types. Soils were sieved; roots were cut into 2.5 cm fragments. Half of each replicate was sterilized by two autoclave cycles for 30 min at 121°C, 24 h apart. Soil from each adult was kept as separate replicates (Rinella et al., (2018).

2.2.3. Seed collection and planting

Q. alba acorns were locally sourced (< 10 miles from the study site) and *O. arboreum* seeds were purchased from Sheffield's Seed Company (Locke, NY, USA). To minimize non-experimental soil pathogens, seeds were surface sterilized for 3 min with 0.6% NaOCl before stratification and germination. Prior to planting, *Q. alba* acorns with emerged radicles were weighed; *O. arboreum* seedlings were measured for height as they had germinated one week prior. Due to staggered germination, planting occurred Feb-March into 6.4 cm diameter × 25 cm deep pots with a 1:2 mixture of sterilized field soil and commercial peat moss (Premier Pro-Mix BX; Premier Tech Growers and Consumers; Rivière-du-Loup, QC, Canada).

2.2.4. Growth conditions and harvest

Seedlings were grown under two understory light levels: 8.2% of full sun (simulated open understory), and 1.8% of full sun (simulated *K. latifolia* thickets). Light treatments were created by covering greenhouse benches with black shade cloth and an outer layer of reflective poly-aluminum shade cloth (BFG Supply, Burton, OH, USA). Photosynthetically active radiation (PAR) was verified with a LI-COR 205 A quantum sensor (LI-COR, Lincoln, NE, USA), consistent with understory conditions in *R. maximum* thickets (Lei et al., 2006). Seedlings were watered with 25 ml deionized water and monitored for emergence and survival three times per week; *Bacillus thuringiensis* was added to the water approximately once per week to control fungus gnats. Seedlings were monitored immediately after planting; deaths during the first week were attributed to transplant shock, excluded from analyses, and pots were replanted. After 12 weeks, all seedlings with root biomass were considered alive and harvested; a subsample of each seedling's roots were collected and frozen for future mycorrhizal analyses, tissues were oven-dried at 70°C, and total biomass (mg) was measured. Roots reserved for mycorrhizal measurements from *Q. alba* seedlings were corrected for dry mass using fresh:dry ratios. For small *O. arboreum* seedlings, root biomass was estimated from regression equations.

2.3. Greenhouse experiment 2: Q. alba in ericaceous-conditioned soils

We tested whether *K. latifolia* effects on *Q. alba* are generalizable across ERM plants by growing *Q. alba* seedlings in soils conditioned by *O. arboreum*, *K. latifolia*, and *Vaccinium* spp. vs. conspecific soil. Ten seedlings per soil source (N = 40) were planted in January 2024 into nonsterile soils collected in December 2023 from Cross Creek beneath adult *Q. alba*, *O. arboreum*, *K. latifolia*, and *Vaccinium* spp., using the same soil collection and planting protocols as Greenhouse Experiment 1. Seedlings were grown under ~3% full sun for 125 days, watered with 25 ml deionized water and censused for emergence and survival three times per week, and harvested for biomass following the same procedures as Greenhouse Experiment 1.

2.4. Statistical analysis

All statistical analyses were conducted in R 4.5.2 (R Core Team, 2025). We used the "coin" package for permutation-based tests of Spearman's rank correlations with tied ordinal data (Hothorn et al., 2006), "emmeans" for estimated marginal means (Lenth, 2025), "infer" for bootstrap resampling of log-response ratios (Couch et al., 2021), "AICcmodavg" for biomass model selection in Greenhouse Experiment 1 (Mazerolle, 2023), and "pwr" and "effectsize" for post-hoc power analysis of the Greenhouse Experiment 2 biomass ANOVA (Champely, 2023; Ben-Shachar et al., 2020). Bayesian survival and emergence models were fit using the RStan interface to Stan (Stan Development Team, 2025) and used the packages "rstanarm" (Goodrich et al., 2025), "survival" (Therneau, 2024), "coda" (Plummer et al., 2006), "tidyverse" (Wickham et al., 2019), "parallel", and "doparallel" (Weston, 2022). Spatial models were conducted using "spdep" (Bivand and Wong, 2018), "sf" (Pebesma Bivand, 2023), "spatialreg"

(Bivand et al., 2013), and “lmtest” (Zeileis and Hothorn, 2002).

2.4.1. Field study

We tested the relationship between *K. latifolia* basal area and seedling abundance using Spearman’s rank correlation (Rho; $n = 100$; prediction 1) and assessed statistical significance using a permutation-based p-value ($n = 9999$ resamples) due to tied ranks in the ordinal seedling data. We performed sensitivity analysis using the low, middle, and high points of each ordinal bin to ensure robustness. Sapling distributions across mycorrhizal types were compared with a one-way ANOVA by cumulative *K. latifolia* basal area within 5 m (prediction 2). Adult tree growth (change in basal area 2015–2023) was analyzed with linear regression against proximate summed *K. latifolia* basal area (within 5 m), calculated from root collar diameter due to *K. latifolia’s* multi-stemmed form (prediction 3).

Because subplots were spatially contiguous within a single 1-ha plot, we tested for spatial autocorrelation in *K. latifolia* basal area and seedling abundance using Moran’s I. We then fit spatial lag models (SAR) for all species using a queen contiguity weights matrix to evaluate whether relationships between *K. latifolia* basal area and seedling abundance remained after accounting for spatial structure. Spatial autocorrelation in sapling ANOVA residuals was tested using Moran's I with a distance-based weights matrix ($d = 1$ m), and a spatial lag model was fit using the same weights matrix to evaluate whether differences in proximate *K. latifolia* basal area among mycorrhizal types were robust to spatial non-independence. The 1 m threshold represented the most conservative distance tested and was selected to minimize neighbor counts given the high stem density of the mapped community. Spatial autocorrelation in adult growth regression residuals was also tested using Moran’s I and fit with a spatial lag model. Spatial terms were included to account for non-independence among neighboring individuals and subplots. These analyses were used as sensitivity tests for the Spearman correlations, one-way ANOVA, and multiple linear regressions, respectively.

2.4.2. Greenhouse Experiment 1

To test whether *K. latifolia* inhibits hardwood seedling performance through biotically mediated PSFs and whether these effects vary with light availability, we analyzed emergence, survival, and biomass responses of *Q. alba* and *O. arboreum* under factorial combinations of soil source, soil treatment, and light. Specifically, these analyses tested whether PSF direction differed between species (prediction 4), whether PSFs were biotically mediated via soil microbes (prediction 5), and whether PSF strength varied across light levels (prediction 6).

Q. alba emergence was modeled with a binary logistic regression that included soil source (conspecific vs. *K. latifolia*), soil treatment (nonsterile vs. sterile), light level (low vs. high), and their interactions. Model structure was selected by AICc. Emergence was not analyzed for *O. arboreum* since they were planted one-week post-germination.

O. arboreum survival was analyzed using an individual-based Cox proportional hazards model (Andersen and Gill, 1982; McCarthy-Neumann and Ibáñez, 2012). Survival data were structured as time-to-event observations, with each seedling contributing a single mortality event or being right-censored at the conclusion of the experiment (84 days). Mortality events were modeled as a Poisson counting process, with the expected event rate defined as:

$$dN_{i,\ t} \sim \text{Poisson}(\lambda_{i,t})$$

and the process as:

$$\lambda_{i,t} = \exp(\text{risk}_i) * dL_0[t]$$

where $dL_0(t)$ represents a time-specific baseline hazard and the risk term captures treatment-related effects on mortality.

Risk was modeled as a function of soil source (conspecific vs. *K. latifolia*), soil treatment (nonsterile vs. sterile), light availability (high vs. low), and initial seedling height, such that:

$$\text{risk}_i = \alpha_{\text{soil}[i],\text{treatment}[i],\text{light}[i]} + \beta * \text{InitialHeight}_i$$

.

Treatment effects were included as categorical fixed effects, and initial seedling height was included as a continuous covariate; parameter estimates from this model are presented in Appendix Table A.

Models were fit within a Bayesian framework to propagate uncertainty in parameter estimates and predicted survival (Clark, 2007). Baseline hazards were assigned weakly informative gamma priors, and regression coefficients were assigned weakly informative normal priors. Model convergence was assessed through inspection of trace plots and effective sample sizes.

As differences in survival are ecologically more interpretable than model coefficients, predicted survival was estimated from the posterior samples of the hazard and risk functions. Predicted survival time to time t was calculated as:

$$\widehat{S}(t) = \exp\left(-\int_0^t dL_0\right)^{\exp(risk)}$$

.

PSFs were calculated as the difference in predicted survival between conspecific and *K. latifolia* soils at each light level. The biotic effects of soil microbes were quantified as differences in survival between nonsterile and sterilized soils for each soil source and light treatment. Differences whose 95% credible intervals did not overlap zero were considered statistically significant.

Models were run for 10,000 iterations followed by an additional 50,000 iterations to estimate posterior distributions of model parameters and predicted survival. *Q. alba* survival was not modeled because no seedlings died following emergence. Full model code is provided in Appendix Code A.

Biomass responses were analyzed with multiple linear regressions with factors of soil source, soil treatment, and light level and with initial acorn mass (*Q. alba*) or seedling height (*O. arboreum*) as covariates (prediction 4–6). For *Q. alba*, biomass included the dry mass of leaves, stems, roots, and cotyledons. For *O. arboreum*, biomass included dry mass of leaves and stems plus fresh root mass, as seedlings were small and their entire root systems were removed for future mycorrhizal measurements. Models were selected using AICc (Burnham and Anderson, 2002; Appendix Code B). PSFs were calculated as log-response ratios (lnRR) of biomass in conspecific vs. *K. latifolia* soils, with uncertainty estimated by 10,000 bootstrap resamples (Brinkman et al., 2010; Bates et al., 2020). To assess biotic effects within each soil type, we compared biomass in nonsterile versus sterile conspecific or *K. latifolia* soils using the same lnRR and bootstrapping approach.

2.4.3. Greenhouse Experiment 2

Emergence timing across soil types was analyzed with a Cox proportional hazards model using the same Bayesian time-to-event framework described for *O. arboreum* survival in Greenhouse Experiment 1; parameter estimates are presented in Appendix Table B. This approach was not used for *Q. alba* emergence in Greenhouse Experiment 1 because treatments affected whether emergence occurred, not the timing. Emergence estimates were evaluated at 6 weeks, when early-emerging seedlings had significantly greater biomass than late-emerging ones. Total biomass was compared across soil sources using a one-way ANOVA, and PSFs were calculated as lnRR of conspecific vs. ERM heterospecific soils with bootstrapping confidence intervals. Due to lower replication than in Greenhouse Experiment 1, we conducted a post-hoc power analysis for the biomass ANOVA. All Greenhouse Experiment 2 analyses test prediction 7.

3. Results

3.1. Field study: hardwood recruitment in- and outside of Kalmia latifolia thickets

Seedling abundance is negatively correlated with *K. latifolia* basal area for all ECM species and most AM species (prediction 1) - *K. latifolia* basal area was significantly negatively correlated with the abundance of oak seedlings – *Q. alba*, *Q. coccinea*, *Q. montana*, and *Q. velutina* (Rho = −0.35 to −0.56; Appendix Table C). This pattern did not change following a regional mast event (Appendix Table D). Among AM species, *A. rubrum*, *D. virginiana* and *S. albidum* also exhibited significant negative correlations and *L. tulipifera* exhibited a marginally significant negative correlation ($p = 0.058$) with *K. latifolia* cumulative basal area, although the magnitude of the correlation was smaller than that of the oaks (Rho = −0.19 to −0.34). *Nyssa sylvatica* was the only species exhibiting a positive correlation with *K. latifolia* (Rho = 0.35). Of the two ERM species evaluated, *O. arboreum* showed no significant correlation with *K. latifolia* stem density or basal area, but *Vaccinium* spp. displayed the strongest negative correlation of any species in the analysis (Rho = −0.63; Fig. 1). Sensitivity analyses using the low, midpoint, and high values of each ordinal seedling bin did not change the overall interpretation: species with significant negative or positive relationships in the ordinal-bin analysis showed the same directional patterns under alternative bin-value assumptions. Moran's I analysis on OLS residuals revealed significant spatial autocorrelation for 9 of 11 species (I = 0.10–0.41, $p < 0.05$; Appendix Table E), but spatial lag (SAR) models confirmed that the results of the Spearman rank correlation were robust to spatial non-independence (Appendix Table F).

ECM saplings occur in areas with lower K. latifolia basal area than saplings of other mycorrhizal types (prediction 2) – Nearby *K. latifolia* basal area varied among saplings of different mycorrhizal types, with ECM saplings occurring in areas with the lowest *K. latifolia* basal area (48.5 cm^2), followed by ERM saplings (91.7 cm^2) and AM saplings (113.1 cm^2) (Fig. 2; Appendix Table G). This corresponded to 47% lower *K. latifolia* basal area around ECM than ERM saplings, 57% lower around ECM than AM saplings, and 18.9% lower around ERM than AM saplings. Moran's I analysis revealed significant spatial autocorrelation in OLS residuals (Moran's I = 0.82, $p < 0.0001$), but the direction and significance of mycorrhizal type effects in spatial lag models remained consistent, showing robustness to spatial non-independence (Appendix Table H).

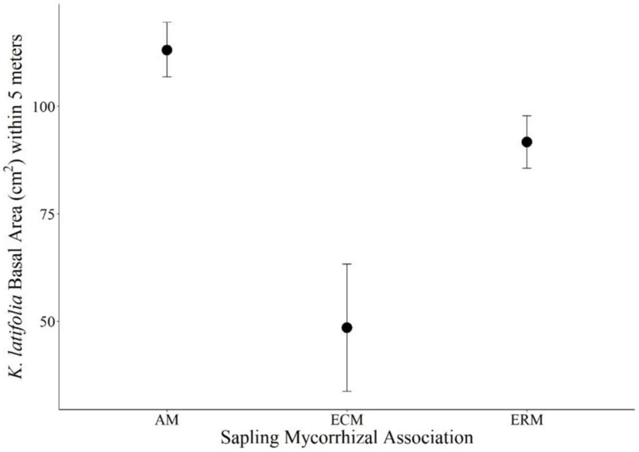

Fig. 2. *Kalmia latifolia* basal area within 5 m of focal saplings by mycorrhizal association. All groups differ significantly (one-way ANOVA with Tukey HSD post-hoc test, $p < 0.001$).

Adult tree growth was greater in K. latifolia thickets, but only for AM trees (prediction 3) - Tree growth was positively correlated with proximate *K. latifolia* basal area for AM species ($p = 0.03$, $\beta = 0.05$), but not for ECM or ERM species ($p = 0.7$ and $p = 0.3$, respectively). The linear model was significant ($F(5, 332) = 28.41$, $p < 0.001$), explaining 29% of the variation in growth (Fig. 3; Appendix Table I). These results did not change when the outlier was removed. Moran's I indicated weak but significant spatial autocorrelation in regression residuals (I = 0.073, $p = 0.011$). A spatial lag model confirmed that the spatial term was not significant ($\rho = 0.119$; Appendix Table J), and all regression coefficients were robust to spatial correction with negligible change in model fit (AIC: 4768.5 vs. 4769.8).

3.2. Greenhouse Experiment 1: PSFs in K. latifolia conditioned soil

***Q. alba* seedling growth is inhibited, whereas *O. arboreum* seedling survival and growth are enhanced in *K. latifolia*-conditioned soils, but results are not consistently biotically mediated or stronger in low light (prediction 4–6) -** In sterile treatments, *Q. alba* emergence was higher in conspecific than in *K. latifolia*-conditioned soil, indicating reduced emergence in *K. latifolia* soil under sterile conditions ($\chi^2(4) = 15.25$,

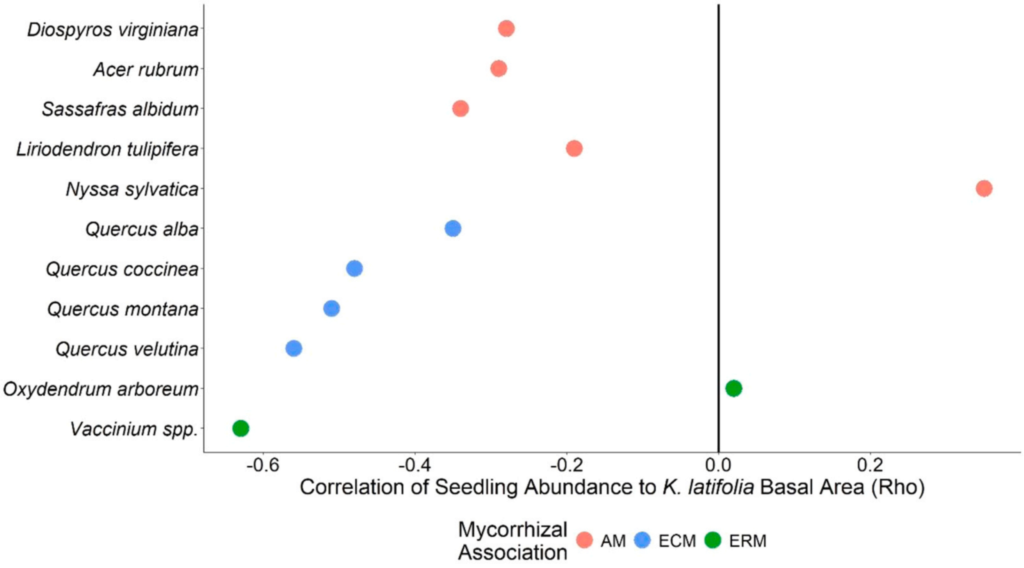

Fig. 1. Correlation of seedling abundance to *Kalmia latifolia* basal area by mycorrhizal type.

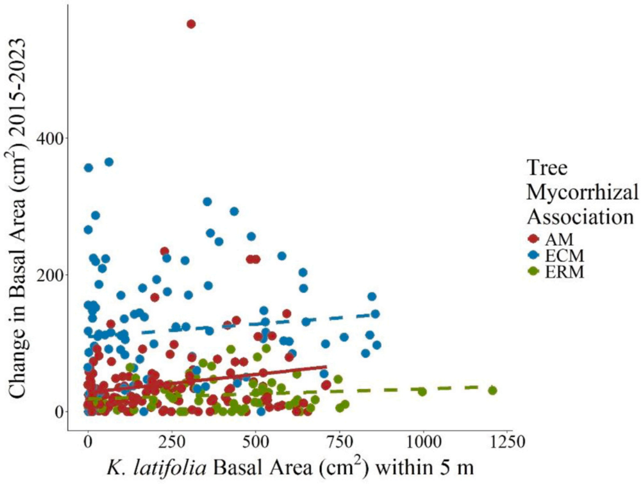

Fig. 3. Correlation of growth and proximate *K. latifolia* basal area by mycorrhizal type (AM – arbuscular mycorrhiza, ECM – ectomycorrhiza, ERM – ericoid mycorrhiza). Dashed lines indicate non-significant correlations.

p = 0.004; Fig. 4A; Appendix Table K). In contrast, emergence did not differ between conspecific and *K. latifolia*-conditioned soils in the nonsterile treatment (Fig. 4A). No post-emergence mortality occurred across treatments. However, in the nonsterile treatment, *Q. alba* seedling growth was significantly greater in conspecific soil than in *K. latifolia*-conditioned soil under low light conditions, revealing a light-dependent, biotically-mediated positive PSF ($F(4, 147) = 21.56$, adjusted $R^2 = 0.35$, $p = 0.001$; Fig. 4B; Appendix Fig. A and B; Appendix Table L). These results suggest that *Q. alba* experiences a neutral PSF for emergence and survival, but a positive PSF for growth in low light, partially supporting predictions 4–6. *Q. alba* emergence was 28% higher in nonsterile compared to sterile *K. latifolia* soil, indicating a net benefit of soil microbes in heterospecific soils (Appendix Table K). Growth, however, did not differ significantly between sterile and nonsterile treatments (Fig. 4B).

O. arboreum exhibited significantly lower survival in conspecific soil relative to *K. latifolia*-conditioned soil, indicating a negative PSF for survival (Fig. 5A) and supporting prediction 4. This effect was observed across soil treatments under high light, but only in sterile soil under low light, indicating that the negative survival PSF was not consistently biotically mediated nor stronger in low light (Fig. 5A; predictions 5–6). Growth of *O. arboreum* was also lower in conspecific soil, but only in nonsterile soils under low light, suggesting a negative PSF for growth that is both biotically mediated and light-dependent ($F(8, 111) = 27.95$, $R^2 = 0.644$, $p < 0.001$; Fig. 5B, Appendix Fig. C, Appendix Table M).

Soil microbes from conspecific soils reduced *O. arboreum* survival by 0.75%, while those from *K. latifolia* soils enhanced survival by 7.5%, but only under low light conditions (predictions 5–6; Fig. 6A; Appendix Table N). However, seedling growth was 35% greater in nonsterile *K. latifolia* soil under high light, suggesting a net microbial benefit under heterospecific conditions when light is not limiting (prediction 6; Fig. 6B).

3.3. *Greenhouse Experiment 2: performance of Q. alba seedlings in ericaceous-conditioned soils*

Q. alba emergence is reduced in all ERM-conditioned soils, consistent with positive PSFs (prediction 7) - *Q. alba* seedlings had significantly lower estimated emergence in all three ERM-conditioned soils (*Vaccinium spp.*, *O. arboreum*, and *K. latifolia*) compared to conspecific soil at six weeks (Appendix Fig. D). Conspecific soil consistently supported the highest emergence rates throughout the duration of the experiment (Appendix Fig. E). Seedling growth did not differ significantly among soil sources ($F(3, 22) = 0.80$, $p = 0.51$). However, post-hoc power analysis indicated that the biomass ANOVA was underpowered (power = 0.12, f = 0.18), so biomass results should be considered preliminary.

4. Discussion

Understanding the mechanisms underlying seedling recruitment dynamics is critical for predicting long-term shifts in forest composition, especially given persistent regeneration failures among dominant canopy species (Knott et al., 2019). This study provides field and experimental evidence that *K. latifolia*, a dominant ericaceous shrub in eastern U.S. forests, contributes to hardwood regeneration failure through context-dependent PSFs that include both biotic and abiotic mediated soil effects. Seedling abundance for most ECM and several AM species was negatively correlated with *K. latifolia* basal area. ECM saplings were found in areas with significantly lower *K. latifolia* basal area than AM or ERM saplings. Greenhouse experiments revealed that the ECM tree *Q. alba* was suppressed in *K. latifolia*-conditioned soils through a combination of likely abiotic effects on emergence and biotically mediated, light-dependent effects on growth, whereas the ERM tree *O. arboreum* benefited from heterospecific soils. Together, these results provide a

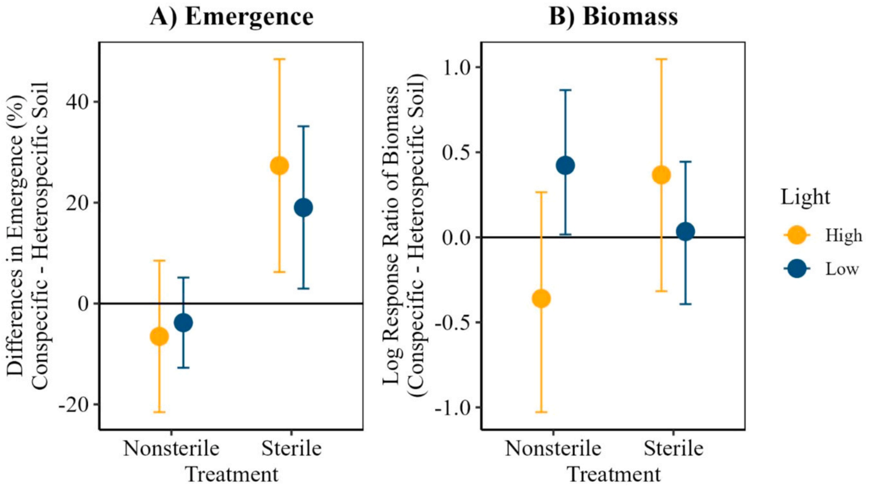

Fig. 4. Contrasts of *Quercus alba* seedling performance after 12 weeks in conspecific versus heterospecific soils. (A) Difference in seedling emergence (%). (B) Difference in dry biomass, expressed as the log response ratio, for seedlings surviving to the end of the experiment. Points are mean contrasts with 95% prediction intervals; intervals excluding zero indicate significant contrasts.

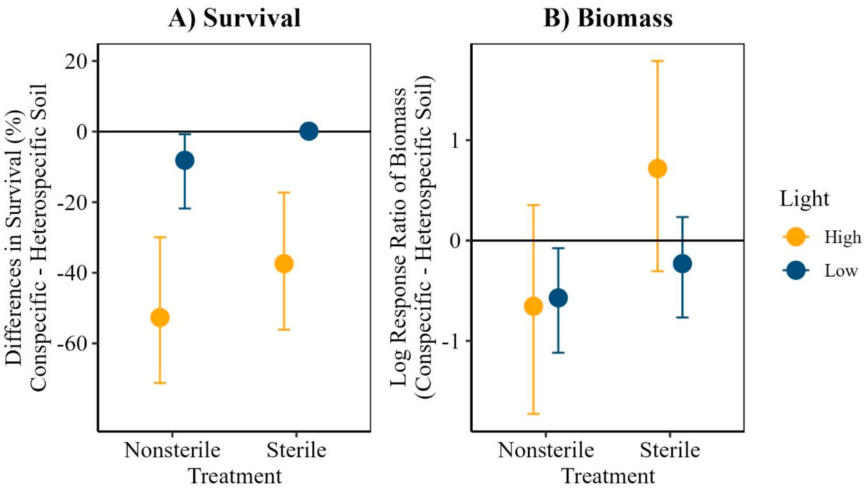

Fig. 5. Contrasts of *Oxydendrum arboreum* seedling performance after 12 weeks in conspecific versus heterospecific soils. (A) Differences in seedling survival (%). (B) Difference in dry biomass, expressed as the log response ratio, for seedlings surviving to the end of the experiment. Points are mean contrasts with 95% prediction intervals; intervals excluding zero indicate significant contrasts.

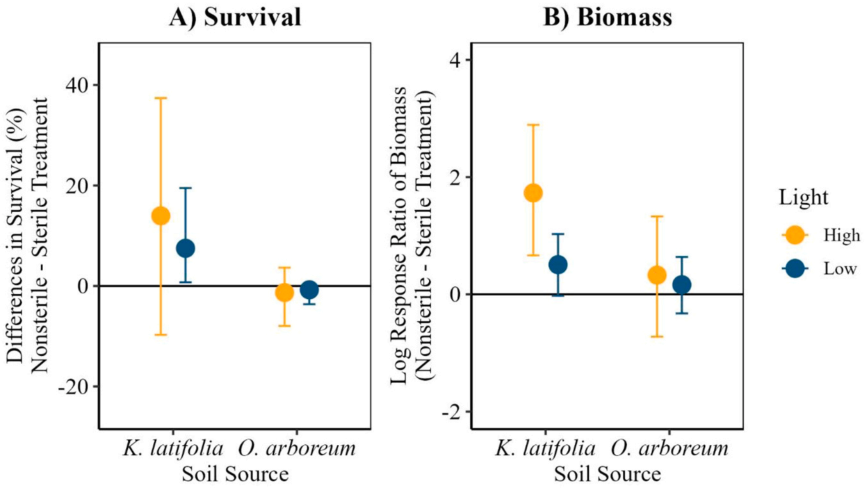

Fig. 6. Contrasts of *Oxydendrum arboreum* seedling performance after 12 weeks in soils subjected to sterile versus nonsterile treatments. (A) Differences in seedling survival (%). (B) Difference in dry biomass, expressed as the log response ratio, for seedlings surviving to the end of the experiment. Points are mean contrasts with 95% prediction intervals; intervals excluding zero indicate significant contrasts.

mechanistic explanation for long-observed pattern of oak regeneration failure beneath *K. latifolia* thickets and suggest potential long-term shifts in forest composition.

The strong and consistent negative relationship between *K. latifolia* basal area and hardwood seedling abundance (such as *Quercus* spp., *A, rubrum*, and *L. tulipifera*) supports decades of field observations (Eppard et al., 2005; Brose, 2016). This pattern was especially pronounced for ECM species, which exhibited the strongest negative correlations in both pre- and post-mast periods, indicating that seedling suppression is not simply a function of seed availability. Indeed, seed rain is unlikely to explain these patterns, because most of the canopy in the Cross Creek permanent plot is composed of ECM trees, both inside and outside of *K. latifolia* thickets, and AM canopy trees are also distributed throughout the hectare (Appendix Fig. F). Although AM species were less negatively affected than ECM species, several AM species still showed negative relationships between seedling abundance and *K. latifolia* basal area, indicating that they did not completely escape inhibitory effects. However, AM saplings occurred in areas with higher *K. latifolia* basal area than ECM or ERM saplings, suggesting that AM species may be more tolerant of *K. latifolia* thicket conditions once they establish. Waterman et al. (1995) similarly found that *Q. coccinea* seedlings had greater growth and survival following *K. latifolia* removal, whereas *A. rubrum* performance remained unchanged between treatments, further supporting the differential sensitivity of ECM versus AM species. The weaker regeneration inhibition observed for AM species may reflect their greater average shade tolerance relative to ECM species (McCarthy-Neumann et al., 2026a). However, a biotic mechanism cannot be ruled out, given the substantial research gap regarding the effects of ericaceous shrubs on AMF and AM plants. ERM species showed inconsistent patterns: *O. arboreum* seedling abundance was not significantly correlated with *K. latifolia* basal area, whereas *Vaccinium* spp. exhibited the strongest negative correlation among all the species tested. Given that both *Vaccinium* spp. and *K. latifolia* associate with at least one common ERM taxa (Helotiales), this spatial pattern likely reflects the preference of wild *Vaccinium* spp. for habitats with greater light availability than what is found in *K. latifolia* thickets (Wurzburger et al., 2012; Khan, 2014; Morvan et al., 2020).

Adult AM trees exhibited greater growth in areas with higher *K. latifolia* basal area, contradicting prediction 3. This contrasts with our findings that AM juveniles are negatively associated with *K. latifolia* basal area and suggests that responses to *K. latifolia* vary across ontogenetic stages. Such stage-specific responses may arise from shifts in the balance between pathogen pressure and mycorrhizal benefits as trees mature (Kardol et al., 2013). AM adults may experience increased growth due to reduced pathogen pressure, as *K. latifolia* has less saprotroph richness beneath AM canopy trees (Polussa et al., 2024). Although these are different lifestyles, there are fungal species known to live as either saprotrophs or root endophytes, and root endophytes can act as mutualists or parasites depending on environmental conditions (Johnson et al., 1997; Weiß et al. 2016). This interpretation is consistent with Clinton et al. (1993) and Waterman et al. (1995), who showed that once trees escape the shaded understory, *K. latifolia* no longer limits growth and may even enhance growth by reducing overstory density and competition for resources. In contrast, adult growth of ECM and ERM tree species showed no significant relationship with *K. latifolia*, indicating that inhibitory effects for these groups may be limited to early life stages —a pattern consistent with other studies showing that processes shaping forest community composition often operate most strongly during recruitment (Green et al., 2014; Yao et al., 2020).

Results from the greenhouse experiments clarified how belowground mechanisms contributed to these field patterns, while also showing that not all effects of *K. latifolia*-conditioned soil were directly biotically mediated. Greenhouse Experiment 2 confirmed that *Q. alba* emergence was lower in nonsterile *K. latifolia* soil than in nonsterile conspecific soil six weeks after planting, although both greenhouse experiments showed no significant emergence difference between nonsterile soil sources by 12 weeks. In contrast, Greenhouse Experiment 1 revealed significantly lower *Q. alba* emergence in sterile *K. latifolia* soil than in sterile conspecific soil at 12 weeks. Taken together, these results indicate an abiotic constraint on early emergence in *K. latifolia* soil that is partially alleviated by a positive biotic effect. One plausible mechanism is reduced nutrient availability — sites dominated by *K. latifolia* consistently exhibit lower inorganic nitrogen availability than nearby sites without thickets (Knoepp et al., 2000; Polussa et al., 2024), and oak emergence is lower in nutrient-poor soils (Leverkus et al., 2026). Under natural conditions, delayed emergence may reduce seedling survival by shortening the growing period needed to accumulate sufficient biomass before winter dormancy (Urbieta et al., 2008). In contrast, reduced *Q. alba* growth in nonsterile *K. latifolia* soil under low light provides stronger evidence for a biotically mediated PSF, while *O. arboreum* responses suggest that *K. latifolia* soil effects vary by species, light environment, and sterilization treatment.

Q. alba seedling growth was reduced in *K. latifolia* soil, but only in the nonsterile low-light treatment in Greenhouse Experiment 1. This pattern indicates a light-dependent, biotically mediated soil effect in which oak seedlings performed better in conspecific soil than in *K. latifolia* soil, potentially contributing to poor oak regeneration beneath *K. latifolia*. These results align with broader PSF literature showing that *Quercus* species and ECM species frequently exhibit positive PSFs (Bennett et al., 2017). However, the emergence of positive PSFs only under low light was unexpected. Although mycorrhizal fungi can shift from mutualistic to parasitic under low carbon availability (Ibáñez and McCarthy-Neumann, 2016), positive PSFs have also been documented in shaded conditions (McCarthy-Neumann et al., 2026b; McCarthy-Neumann et al., 2026c). In Greenhouse Experiment 2, biomass did not differ among ERM-conditioned soil sources, although this result should be interpreted cautiously because the biomass ANOVA had low statistical power.

One explanation of *Q. alba*'s negative growth response to *K. latifolia* under low light, nonsterile conditions may involve increased soil pathogen pressure under shaded conditions (Reinhart et al., 2010; Liu and He, 2019). These effects may be reduced in conspecific soils, where EMF can suppress pathogens through nutrient competition and physical protection of root tips (Zak, 1964; Eagar et al., 2025). Additionally, *Q. alba* has also been shown to accumulate higher phenolic concentrations in conspecific soils, compounds known to serve as chemical defenses against soil-borne pathogens (Ichihara, Yamaji. 2009; Wood et al., 2023a). Together, these mechanisms suggest that *Q. alba*'s response to shading differs between conspecific and heterospecific soils due to microbial communities, although further investigation is needed to confirm the exact mechanisms affecting seedlings.

Our field and experimental results differ from previous work reporting no relationship between *K. latifolia* basal area and *Quercus* spp. seedling survival or growth. This discrepancy likely reflects differences in experimental design: Beier et al. (2005) transplanted 16-week old seedlings into ericaceous thickets, whereas our study exposed seedlings to ericaceous soil and light conditions immediately after germination, more closely simulating natural field conditions. In contrast, our findings align with Eppard et al. (2005), who found that *Pinus rigida*, an ECM tree species, exhibited reduced root biomass when grown in substrates from *K. latifolia*-dominated sites.

While no apparent effect of *K. latifolia* soil on *Q. alba* survival was observed in the greenhouse experiments, this likely reflects the short experimental duration. Oaks can rely on cotyledon reserves during their first year (Garcia-Cebrian et al., 2003), and many harvested seedlings retained cotyledons, potentially buffering early mortality. In the field, however, oak survival is markedly lower under *K. latifolia* thickets: at our study site, 68% of plots in the highest quartile of *K. latifolia* basal area contained *Q. alba* seedlings, yet none supported saplings (McCarthy-Neumann, (2023). This pattern suggests delayed mortality or chronic suppression that prevents transition into the sapling stage. Given that *Q. rubra* seedlings typically survive only 3–4 years and are vulnerable to winter mortality (Cleavitt et al., 2024), future work on *Q. alba* should span multiple seasons and incorporate environmental stressors to capture long-term dynamics.

The performance of *O. arboreum* provides insight into the role of ericoid-associated soil biota in *K. latifolia*'s soil effects. In Greenhouse Experiment 1, *O. arboreum* exhibited higher survival and growth in *K. latifolia* soil than in conspecific soil, indicating a negative PSF. This pattern suggests that conspecific soil may accumulate host-specific pathogens or other antagonistic soil biota that reduce *O. arboreum* performance. In contrast, *K. latifolia*-conditioned soil may provide compatible ericoid mycorrhizal inoculum, as both species associate with at least one common ericoid mycorrhizal fungus, *Hymenoscyphus ericae* (Gorman, Mark, 2003), while avoiding some of the negative effects associated with conspecific soil. These greenhouse results may help explain why *O. arboreum* seedling abundance was not negatively associated with *K. latifolia* basal area in the field, unlike most ECM and several AM tree species. Given the regional importance of *O. arboreum* as a subcanopy species in southern Appalachian forests, future research should investigate whether it experiences similar feedbacks in ECM- or AM- conditioned soils.

Most AM tree species had lower juvenile abundance near *K. latifolia*, but these patterns were weaker than those observed for ECM species. Although AM seedlings exhibited weaker negative correlations with *K. latifolia* basal area than ECM tree species, several AM species were still negatively associated with *K. latifolia*, indicating that they did not fully escape inhibitory effects. However, AM saplings were found in areas with significantly higher *K. latifolia* basal area than ECM or ERM saplings, suggesting greater tolerance of thicket conditions. 1 AM tree species, *N. sylvatica*, exhibited a positive correlation between seedling abundance and *K. latifolia* basal area. This pattern is unlikely to be driven by seed availability, as adult trees occur both within and outside of the thickets (McCarthy-Neumann, 2023) and warrants further research. Although AM species were not included in greenhouse PSF trials, future work should investigate whether they experience similar microbial and light-mediated effects.

This study provides experimental evidence that *K. latifolia*, long associated with hardwood regeneration failure, directly inhibits oak recruitment through biotically mediated PSFs. Although previous work has implicated *R. maximum* in similar dynamics (Clinton, James, 1996; Wurzburger and Hendrick, 2009; Dharmadi et al., 2019), the ecological role of *K. latifolia* has remained largely unresolved. By integrating field observations with greenhouse experiments, this study demonstrates that suppression of *Q. alba* establishment is driven not only by abiotic factors such as reduced light availability, but also by belowground biotic interactions operating early in seedling development. The interactive effects of light and microbial communities further underscore the context dependency of these belowground processes.

Because ECM and ERM species responded differently to *K. latifolia*-conditioned soils, with some ERM species potentially benefiting, current regeneration trajectories could lead to shifts in forest composition. The canopy of the Cross Creek Watershed permanent plot —dominated by ECM trees with some AM species — likely predates widespread *K. latifolia* expansion into thickets (Brose, 2016). Despite ongoing seed production, regeneration to sapling and subcanopy stages is rare beneath thickets. Similar patterns have been documented for *R. maximum*, which colonizes gaps left by ECM trees (Pfennigwerth et al., 2017) and may function as a foundational species as overstory trees die (Dudley et al., 2020).

We note two limitations - *Q. alba* seedling survival in greenhouse experiments may have been buffered by cotyledon reserves, masking early-stage mortality that is likely to occur in the field. Longer-term experiments incorporating seasonal stressors would better capture survival dynamics. Second, AM species were not included in greenhouse PSF trials, limiting inference about their responses to soil feedbacks from *K. latifolia*.

Overall, this study bridges decades of observational evidence with experimental tests and expands the PSF framework to include ericaceous shrubs. This study experimentally demonstrates that *K. latifolia*—long associated with hardwood regeneration failure—can reduce oak seedling performance through both biotically and abiotically mediated PSFs. That *K. latifolia* suppresses ECM regeneration while facilitating ERM species suggests it may function as an ecosystem engineer (Hastings et al., 2007) in temperate forests of eastern North America, with the capacity to reshape forest trajectories through persistent effects on soil conditions, microbial communities and seedling recruitment.

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CRediT authorship contribution statement

Sarah McCarthy-Neumann: Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Schutte Maria:** Writing – original draft, Investigation, Formal analysis, Conceptualization. **Jon Evans:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124083.

Data availability

Data upon which this study is based are available through the Dryad Digital Repository: doi:10.5061/dryad.1jwstqkb0.

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