Abstract

1. Plant-soil feedback (PSF) is known to influence plant community composition, and recent work suggests that these effects may be regulated by traits related to mycorrhizal associations and phylogenetic relationships. However, there is a critical need to test the usefulness of these traits in predicting PSF outcomes in natural plant communities.
2. To test for evidence of mycorrhizal and phylogenetic controls over PSF at both the species and community level, we examined the spatial relationship between adult and juvenile trees in stem-mapped hardwood forest plots using point pattern analyses and linear mixed-effect models.
3. We found that spatial patterns of adult and juvenile trees, as well as overall adult tree recruitment, was significantly affected by the dominant mycorrhizal type of our forested communities, but was not influenced by the phylogenetic relationship between adult and juvenile trees. Additionally, PSF experienced by individual species was dependent on the mycorrhizal dominance of the surrounding community.
4. Spatial patterns in communities dominated by arbuscular mycorrhizal trees reflected overdispersion between adult and juvenile trees (suggestive of negative PSF), while communities dominated by ectomycorrhizal trees reflected clustering (suggestive of positive PSF).
5. Our findings indicate that PSFs are driven by the mycorrhizal associations of dominant trees, with effects of dominant community member traits on soil microorganisms and biogeochemistry "spilling over" onto less abundant individuals in the community. Our research supports the use of whole-community, mycorrhizal-based frameworks for studying PSF in plant communities where multiple mycorrhizal

types are present.

Keywords: Arbuscular mycorrhiza, community phylogeny, ectomycorrhiza, plant community structure, plant-soil feedback, point pattern analysis, spillover effects, temperate hardwood forest

Introduction

Plant-soil feedback (PSF) is thought to be a key driver of plant population size (Hovatter *et al*. 2013), community diversity (LaManna *et al*. 2016, Teste *et al*. 2017) and ecosystem function (Kulmatiski *et al*. 2012, Lange *et al*. 2015). Negative PSF effects are attributed to the growth of a plant resulting in buildup of plant pathogens that subsequently reduce the growth of conspecific plants grown in the same soil (Packer & Clay 2000, Bever *et al.* 2015). Negative PSF can increase plant diversity by preventing common species from competitively excluding rarer species (Connell 1971, van der Putten *et al*. 1993), increasing fecundity in rare species through compensatory responses (Bradley *et al*. 2008), and increasing plant productivity through the promotion of niche complementarity (Petermann *et al.* 2008, Schnitzer *et al*. 2011). Conversely, positive PSF can have the opposite effect on plant communities by creating favorable conditions for dominant species, ultimately reducing plant community diversity (Connell & Lowman 1989, Teste *et al*. 2017). These positive PSF effects result from plants creating unique soil conditions that select for their own specific resource acquisition strategies (Wurzburger & Hendrick 2009) or beneficial microbial species (Mangan *et al*. 2010). Since both positive and negative PSF are influenced by plant-microbe interactions, changes in microbial community composition caused by differences in plant functional traits (e.g., root and leaf tissue chemistry) should influence the strength and direction of PSF in a plant community (Wardle *et al*. 1999). However, a convenient framework for summarizing traits associated with the drivers of PSF remains elusive despite the ecological significance of these interactions (van der Putten *et al.* 2016).

Recently, the type of mycorrhizal association engaged in by a plant has been recognized as a potential indicator for a suite of integrated leaf and root traits that influence soil nutrient cycling (Cornelissen *et al*. 2001, Phillips *et al*. 2013), thus providing a predictive framework for soil biogeochemistry and microbial community composition that may also be important for PSF. Ectomycorrhizal (ECM) and ericoid mycorrhizal (ERM) plants typically have recalcitrant leaf litter that decomposes more slowly than the leaf litter of arbuscular mycorrhizal (AM) plants, thereby reducing decomposition rates in communities dominated by ECM and ERM plants (Wurzburger & Hendrick 2009, Averill & Hawkes 2016). Furthermore, some ECM and ERM fungi can directly decompose recalcitrant, senesced tissues and take up organic forms of nutrients, leading to competition with the larger saprotrophic microbial community, reducing rates of soil nutrient mineralization, and lowering soil pH (Gadgil & Gadgil 1971, Read & Perez-Moreno 2003, Averill *et al*. 2014, Tedersoo *et al.* 2020). The different nutrient acquisition strategies and microbial communities associated with AM versus ECM trees suggest that AM-associating species promote greater growth of non-mycorrhizal saprotrophic fungi, many of which may also be capable of facultative plant pathogen activity (Smith *et al.* 2017, Chen *et al.* 2019, Bahram *et al.* 2020). Because negative PSF is often associated with fungal pathogens (Bagchi *et al.* 2010, Liu *et al.* 2012, Liang *et al.* 2016), it seems likely that AM associations promote a microbial community that is more conducive to development of negative PSF. Indeed, Bennett *et al.* (2017) recently performed greenhouse experiments to measure feedback and observed that AM tree species largely experience negative PSF and ECM species largely experience positive PSF. However, signs of different mycorrhizal-associated PSF effects still need to be investigated in natural, established plant communities.

If the propensity for positive or negative PSF is influenced by mycorrhizal effects on soil biogeochemistry and the microbial community, there is the potential for effects of dominant plant species to “spill over” in natural settings and influence PSF mechanisms across the entire community. More abundant or larger community members have a greater effect on soil microbial communities and biogeochemical cycles than less abundant or smaller community members, as demonstrated by the strong influence of dominant mycorrhizal type (AM or ECM) on soil biogeochemical processes (Phillips *et al*. 2013). Thus, dominant community members may influence the direction and strength of PSF in less common community members. However, few studies have considered aggregated effects of entire plant communities when studying PSF (but see Eppinga *et al*. 2018), and only a handful of studies have explicitly considered species’ mycorrhizal types as a primary driver of PSF processes within entire plant communities (Johnson *et al.* 2018, Chen *et al.* 2019, Tedersoo *et al.* 2020). Given the differences in litter chemistry, microbial communities, and species level PSF based on the different mycorrhizal associations described above, we predict that negative PSF effects should become stronger with increasing AM dominance in a forested community. For example, even though an individual ECM tree might tend to experience positive feedback because of coupling between its ECM fungi and recalcitrant leaf litter, we reason this positive feedback would be lessened or nullified by dominant nearby AM trees having an overriding effect on the surrounding soil microbial community and biogeochemistry.

In addition to specific traits such as mycorrhizal type, evolutionary relationships can have a strong influence over ecological interactions, and thus may serve as an additional factor structuring PSF (Liu *et al.* 2012, Anacker *et al*. 2014, Parker *et al*. 2015). According to Darwin’s naturalization hypothesis, closely related species may occupy similar ecological niches and share similar natural enemies due to an overlap in traits associated with resource acquisition and defense (Cavender-Bares *et al*. 2009, Cadotte *et al.* 2017). Traits that are shared between closely related plant species may be similarly exploitable by generalist pathogens or mutualists, causing the effects of PSF to expand from conspecific individuals to nearby, closely related plant species (Parker & Gilbert 2004, Metz *et al.* 2010, Zambrano *et al*. 2017). If the drivers of PSF operate beyond the conspecific level, PSF between closely related species should be stronger than PSF between distantly related species (Liu *et al.* 2012). Despite this potential, evidence of phylogenetic structure in PSF remains mixed. For example, Liu *et al.* (2012) and Gilbert *et al.* (2015) found that pairs of closely related plant species experience stronger negative PSF compared to pairs of distant relatives, while Anacker and Strauss (2016) demonstrated that closely related plant species experience weaker negative PSF compared to distant relatives. Furthermore, other studies have concluded that phylogenetic relationships have no influence on PSF at all (Mehrabi & Tuck 2015, Fitzpatrick *et al*. 2017). These conflicting results require further investigation to determine if phylogenetically structured PSF effects are occurring in natural plant communities.

Point pattern analyses are powerful analytical tools that can compare the observed spatial patterns of plants against models of spatial randomness to identify if plants are growing closer to, or further away from, one another than expected (e.g., He & Duncan 2000, Calabrese *et al*. 2010, Johnson *et al*. 2018). For example, these analyses have identified interactions between shrub species in relation to patterns of fire-driven mortality (Biganzoli *et al*. 2009) and patterns in survival related to inter and intraspecific competition in an old-growth forest (He & Duncan 2000). Additionally, these analyses can detect signs of PSF in the fine-scale spatial structure found between plant community members (Brown *et al*. 2016). If PSF is an important driver of plant community dynamics, negative PSF should result in patterns of overdispersion between adult plants and their progeny, driven by the presence of pathogens near established adult individuals, while positive PSF should result in patterns of clustering due to advantageous conditions being found near conspecific plants (Martínez *et al.* 2013). Furthermore, if PSF is affected by the soil microbial community and biogeochemical environment, then traits of dominant tree species should dictate the strength and direction of PSF that spills over onto less common community members found nearby. Due to the distribution of mycorrhizal types and diverse assemblage of species in temperate hardwood forests (Steidinger *et al.* 2019), these communities are ideal for testing for spatial patterns consistent with PSF spillover effects based on community mycorrhizal types and phylogenetic relationships.

In this study, we explored the spatial structure of a temperate hardwood forest community with varying mycorrhizal dominance using stem-mapped plots and point pattern analyses. Our goal was to identify spatial patterns consistent with our overarching hypothesis that the strength of PSF is affected by factors extending beyond the presence of conspecifics, including spillover effects of dominant community members. We tested tree communities of varying mycorrhizal dominance for spatial patterns consistent with the following, specific hypotheses: **(H1)** Under a "mycorrhizal spillover" hypothesis, PSF between juvenile and adult trees is expected to be affected by the mycorrhizal associations of dominant community members, becoming more positive in ECM dominated communities and more negative in AM communities. This hypothesis leads to the prediction that adult trees in ECM-dominant communities will have more juvenile trees and more conspecific trees in close proximity than will adult trees in AM-dominant communities, regardless of individual tree species identity. **(H2)** Under an "individual species mycorrhizal type" hypothesis, dominant community members are less important, and PSF is affected by each individual species mycorrhizal type, with AM species experiencing negative

PSF and ECM species experiencing positive PSF regardless of surrounding community composition (Bennett *et al.* 2017; Johnson *et al.* 2018). According to this hypothesis, we expect that ECM adult trees will have more juvenile trees and more conspecific trees in close proximity than will AM adult trees, with these patterns being found irrespective of the mycorrhizal associations of the surrounding community. In addition, we tested **(H3)** that PSF is affected by the phylogenetic relationships between adult and juvenile individuals within a community, with more closely related individuals experiencing stronger PSF than distantly related individuals. These three hypotheses are not mutually exclusive, and effects may be additive. For example, if PSF is structured by both phylogenetic and mycorrhizal effects, we expect to find that ECM species or ECM-dominant communities will have more closely related juvenile trees in close proximity to adult trees, while AM species or AM-dominant communities will have more distantly related juvenile trees in close proximity to adult trees. In addition to point-pattern analyses, we examined how soil abiotic properties, adult and juvenile abundances, and species diversity change with community mycorrhizal dominance. Demographic information, such as adult recruitment and mortality over an 8-year time period, was also explored based on community mycorrhizal dominance.

Materials and Methods

Study site

Jennings Woods is a 30-hectare temperate hardwood forest owned by Kent State University in Northeastern Ohio, USA (41°10.4’ N, 81°12.1’ W). It contains 29 tree species (14 AM and 15 ECM), with sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), shagbark hickory (*Carya ovata*), American elm (*Ulmus americana*), red oak (*Quercus rubra*), and American hornbeam (musclewood; *Carpinus caroliniana*) accounting for >75% of the total abundance of all adult trees in the forest (Blackwood *et al*. 2013). It has remained undisturbed since 1973 and experienced selective harvesting prior to that, resulting in dominant, naturally regenerated canopy tree ages between 60 to 100 years old. Ninety-five circular plots 30 m in diameter (706.5 m^2) were established in 2008 when an initial survey of adult trees ≥ 10 cm diameter at breast height (DBH) and soil properties (percent C, percent N, total extractable P, percent moisture, and pH) was conducted (Fig. 1, Blackwood *et al.* 2013). These plots are an appropriate size to test for spatial patterns associated with PSF in local tree neighborhoods because these distance-dependent processes are known to act at local scales < 30 m (Hubbell *et al*. 2001, Wang *et al*. 2015).

Adult and juvenile tree inventory and mapping

In May-August 2016, individual trees above 1.4 m in height across 28 plots were identified to species and their locations were mapped from the center of each plot using a range finder (Sonin Multi-Measure Combo Pro 10300, Sonin, Inc., Charlotte, NC) and compass (Silva Lensatic 360; Johnson Outdoors Gear, Inc., Racine, WI). Trees with a DBH ≥ 5 cm were recorded as adult trees, while trees with a smaller DBH were recorded as juvenile trees. This resulted in a total of 1025 adult and 2254 juvenile trees across all plots. Tree mycorrhizal associations were assigned based on Brundrett (2009) and Maherali *et al*. (2016). Adult tree basal area (m^2) was calculated using the formula $\pi(DBH/2)^2 \times 10^{-4}$. Species and mycorrhizal type basal areas were calculated by summing the basal areas of individuals in each plot. The relative basal areas of AM and ECM trees were obtained for each plot by dividing a summed mycorrhizal type basal area by the total summed basal area of the plot. Thus, the AM relative basal area across our plots ranged from 92.1% (i.e., dominated by AM trees) to 7.9% (i.e., dominated by

ECM trees). In addition to this spatial survey, we resurveyed all original 95 plots for growth, recruitment, and mortality of adult trees.

Statistical approach and packages

To test our specific hypotheses, we conducted a series of analyses to examine spatial patterns in juvenile trees. First, point pattern analyses were performed to examine overall densities, heterospecific/conspecific ratios, and phylogenetic structure of juveniles at differing distances from adult trees. Results were then aggregated in two ways. First, plots were divided into two groups, one with >50% relative AM basal area and one with <50% relative AM basal area, and results were aggregated across plots within each group. Second, results were aggregated across species within each mycorrhizal type. We then performed similar analyses separately for several common species. We also used linear mixed models to explicitly test for differences in juvenile density and heterospecific/conspecific ratios driven by plot mycorrhizal type. Finally, we tested for effects of dominant mycorrhizal types on tree community demographics and soil characteristics. Considering these analyses together provides a detailed examination of the spatial structure between adult and juvenile trees to determine the consistency of observed patterns with predicted PSF outcomes.

All point pattern analyses were conducted in Programita (Wiegand & Moloney 2004, 2013) using circular windows to account for the shape of our plots (Wiegand *et al*. 2006). Generalized linear mixed-effect models (GLMMs) were performed in R version 3.3.0 (R Development Core Team 2017) using the packages nlme (Pinheiro *et al.* 2017) and lme4 (Bates *et al.* 2014). R^2 values for significant GLMMs were obtained using the MuMIn package from Barton (2009).

Within-plot point pattern functions aggregated by community or species mycorrhizal type

Point pattern analyses involve assessment of a response variable (in this case, based on characteristics of juvenile trees) at different distance intervals from focal points (adult trees). The observed response variable is then compared to results of a simulation under an appropriate null model of spatial randomness. Edge effects will occur when part of a distance interval around an individual focal point falls outside the plot where data was collected, resulting in undercounts of surrounding points. To correct for edge effects, we used the Wiegand-Moloney edge correction method, which applies a weighted correction to each calculation based on the area analyzed for each focal point at a given distance interval, with the maximum distance interval less than half the diameter of a plot (Wiegand & Moloney 2004, 2013). For example, for a given adult tree near the edge of a plot, the number of surrounding juvenile trees is divided by the proportion of the area sampled to obtain an estimate of total juvenile trees surrounding this adult point within and outside of the plot.

To test for spatial patterns consistent with PSF, we first examined the distribution of juvenile trees relative to adult trees considering only adult tree mycorrhizal type and not species identity. Tests of spatial randomness were used to determine if juvenile trees were distributed randomly around adult trees, or if juveniles were clustered or overdispersed around adults. We used the neighborhood density function (i.e., bivariate O-ring statistic), which measures the probabilistic density of points surrounding a focal point at a given distance class (Wiegand & Moloney 2004), to determine the spatial distribution of juvenile trees surrounding adult trees. For each plot, the observed location of juvenile trees relative to adults was compared to a random distribution obtained under the null model of spatial randomness generated by 199 Monte Carlo simulations randomizing the spatial location of juvenile trees in each plot. Values above the null model simulation envelopes indicate significantly higher densities of juvenile trees surrounding adult trees (i.e., clustering with adult trees, suggesting positive PSF), while values below these envelopes indicate significantly lower densities than expected (i.e., overdispersion from adult trees, suggesting negative PSF). Values within these envelopes indicate conformity with spatially random models and signify no patterns of clustering or overdispersion occur between adult and juvenile individuals.

To test **H1** (PSF is influenced by the dominant mycorrhizal type of the surrounding community), individual plot neighborhood density statistics were aggregated by community-dominant mycorrhizal type (binning plots according to > 50% and < 50% AM relative basal area) to obtain an average observed statistic and null model distribution. To test **H2** (PSF is influenced by species' mycorrhizal types regardless of surrounding community mycorrhizal associations), the neighborhood density point pattern analysis was repeated at the plot level with only tree species of a single mycorrhizal type included. These species-specific results were then aggregated by mycorrhizal type across all plots. This procedure resulted in an average statistic and null model distribution for AM and ECM tree species and their juvenile communities irrespective of the dominant mycorrhizal type of our plots. The use of spatial randomness as a null hypothesis assumes that the intensity of points (i.e., mean number of points per unit area) is homogeneous across the study area (Wiegand & Moloney 2013). Inhomogeneous intensities caused by environmental gradients or geographic features can create false observations of clustering or overdispersion if unaccounted for. To test for homogeneous intensities in our plots, we used the homtest() function in the R packages Spatstat and Spatstat.local from Baddeley & Turner (2004). Of our 28 plots, 24 demonstrated homogeneity in their pattern intensity. Including four plots with inhomogeneous intensities had no qualitative influence on the outcome of our aggregated results, and so we present analysis of the full dataset.

We also examined the ratio of heterospecific-to-conspecific juveniles surrounding adults without varying the spatial position of juvenile points, with larger than expected ratios nearby adults suggesting negative PSF, and smaller ratios suggesting positive. To test for patterns in the distribution of conspecific individuals consistent with PSF, we used the mark correlation function (Illian *et al*. 2008) to calculate the ratio of heterospecific-to-conspecific juvenile trees surrounding adult trees. Mark correlation functions were calculated for each species in each plot, with these results being aggregated by dominant plot mycorrhizal type (**H1**) or by species' mycorrhizal type (**H2**). Random labelling of juvenile points was used to construct null model envelopes from 199 Monte Carlo simulations in which the heterospecific/conspecific labeling of juvenile individuals was randomly shuffled (Illian *et al*. 2008, Jacquemyn *et al*. 2010). Observed values above this simulation envelope indicate significantly higher proportions of heterospecific juveniles surrounding adult trees (a pattern consistent with negative PSF), while values below the simulation envelope indicate significantly higher proportions of conspecific juveniles (a pattern consistent with positive PSF).

To test for spatial patterns consistent with phylogenetically structured PSF between adult and juvenile trees (**H3**), the phylogenetic mark correlation function was calculated for each species in each plot (Shen *et al*. 2013, Wiegand & Moloney 2013). For this function, a similar analytical approach to the mark correlation function was taken using a phylogenetic distance matrix constructed in Phylocom (Webb *et al*. 2008) using Phylomatic (Webb & Donoghue 2005) and data from Zanne *et al*. (2014) (see Appendix S1 for detailed methods).

In order to further explore PSF effects on individual species, we conducted three additional point pattern analyses on the seven most abundant adult tree species in our forest, comprising >75% relative abundance. This included three AM species (*A. saccharum*, *A. rubrum*, and *U. americana*) and four ECM species (*F. grandifolia*, *C. ovata*, *C. caroliniana*, and *Q. rubra*). We used the neighborhood density and mark correlation functions to examine the density of conspecific juveniles and heterospecific juveniles surrounding adult focal trees of each species, following the same spatially random modeling approach mentioned above for the neighborhood density function and random labelling modeling approach for the mark correlation function. These species-level results were aggregated by plot mycorrhizal dominance to see if patterns observed in these analyses are consistent within a species across plots of different mycorrhizal types.

Effects of dominant community mycorrhizal type on average point pattern statistics

The aggregation approach of our point pattern analyses described above resulted in a qualitative comparison of the significant spatial patterns in communities dominated (>50%) by AM or ECM trees. To directly explore how community mycorrhizal dominance changed plot-level spatial patterns, we used generalized linear mixed-effect models (GLMMs). We used the plot-level neighborhood density statistic or mark correlation function at each distance class as the response variable, with "plot" included as a random effect to account for non-independence of different distances within each plot. Percent AM basal area (7.9% to 92.1% AM), distance, and an interaction term (mycorrhizal type × distance) were supplied as fixed effects. After detection of a significant "mycorrhizal type × distance" interaction, this analysis was also repeated for the neighborhood density statistic after separating plots into four groups based on mycorrhizal dominance: 0 – 25%, 25 – 50%, 50 – 75%, and 75 – 100% relative AM basal area plots. These four models were analyzed with distance as the only fixed effect.

Effects of dominant mycorrhizal types on tree community and soil characteristics

GLMMs were also used to test for responses in plot-level community characteristics to the continuous mycorrhizal type gradient (7.9% to 92.1% relative AM basal area) and the discrete, majority mycorrhizal type of each plot (AM or ECM). Response variables included data from the 2016 juvenile and adult inventory for 28 plots (number of adults, number of juveniles, rarified species diversity) as well as demographic variables calculated by comparison of the 2008 and 2016 adult inventories for 95 plots (adult growth rates, recruitment of new adult trees ≥ 10 cm DBH, and percent mortality of adult trees). The number of adult and juvenile individuals, in addition to the recruitment data, were analyzed using a Poisson error distribution, while percent mortality data were analyzed using a binomial distribution with a logistic model. We used additional GLMMs to test for an effect of the mycorrhizal gradient and majority mycorrhizal type on soil percent C, percent N, total extractable P, percent moisture, and pH (see Blackwood *et al*. 2013 for description of soil measurements).

Results

Within-plot point pattern functions aggregated by community or species mycorrhizal type

The average distance between adult and juvenile trees was 2.7 (±1.5) m in AM plots and 2.1 (±0.7) m in ECM plots. Across all plots surveyed, the neighborhood density function indicated that densities of juvenile trees surrounding adult individuals were greater than expected according to the null model for all distances ≥ 2 m ($P < 0.05$; Fig. 2A). Aggregating plots by dominant mycorrhizal type (to test **H1**) resulted in a notable change to this pattern, consistent with our prediction of patterns suggesting more positive PSF in ECM-dominant communities and more negative PSF in AM-dominant communities. Juvenile tree densities in AM-dominant communities shifted towards a more random pattern and were less dense than expected ~ 2 m from adult trees. Juvenile densities were greater than expected only for distances ≥ 8 m in AM-dominant communities ($P < 0.05$; Fig. 2B). Meanwhile, juvenile densities in ECM-dominant communities were greater than expected for most distances ≥ 2 m ($P < 0.05$; Fig. 2C). To test for effects of mycorrhizal type of individual trees regardless of community mycorrhizal dominance (**H2**), the neighborhood density function was aggregated according to tree species' mycorrhizal associations. This test revealed no deviations from the null model envelope in juvenile distribution between either AM- or ECM-associating adult tree species ($P > 0.05$; Fig. 2D and E).

Across all plots, the mark correlation function (i.e., the heterospecific/conspecific ratio of juvenile trees surrounding adult trees) revealed fewer heterospecific juvenile individuals surrounding adult trees than expected under the null model for most distances ≤ 6 m ($P < 0.05$; Fig. 3A). When plots were aggregated by dominant mycorrhizal type (**H1**), patterns were again consistent with our predictions. The heterospecific/conspecific ratio in AM-dominant communities shifted towards a more random pattern and only deviated from the null model envelope at 11 m ($P < 0.05$; Fig. 3B). Conversely, ECM-dominant communities had more conspecific juvenile trees than expected under the null model for most distances ≤ 6 m ($P < 0.05$; Fig. 3C). However, when aggregating the mark correlation function by species mycorrhizal type (**H2**), results were similar for both AM and ECM species, with fewer heterospecific juveniles found at distances ≤ 1 m from adult trees ($P < 0.05$; Fig. 3D & E).

The phylogenetic mark correlation function, which was used to test for a phylogenetic signal in the spatial pattern of adult and juvenile trees (**H3**), did not deviate from the random null model across all distances when aggregated across all plots ($P > 0.05$). This pattern did not change when plots were aggregated by their dominant mycorrhizal type ($P > 0.05$) or when individual adult tree species were aggregated by their mycorrhizal associations ($P > 0.05$).

Results of the point pattern analyses conducted for individual tree species

We found that individual species often exhibited different results in AM and ECM-dominated plots, but there is a consistent trend of patterns being more indicative of negative feedback in AM plots and positive feedback in ECM plots. For AM-associated species, the neighborhood density function revealed that both *A. saccharum* and *U. americana* exhibited no spatial structure of conspecific juveniles in AM plots, but had higher densities of conspecific juveniles in ECM plots at short distances (1 – 4m) (Appendix S1: Fig. S1). *A. rubrum* conspecific juveniles did not deviate from random spatial models in ECM plots, but in AM plots there were too few conspecific juvenile individuals to analyze. However, since *A. rubrum* adults were often present in AM plots, this could be indicative of negative feedback. Additionally, there were higher densities of heterospecific juveniles around *A. saccharum* at short distance intervals, but only in ECM plots (Appendix S1: Fig. S1). The ratio of heterospecific to conspecific juveniles around adult trees for all three species did not deviate from models of random labeling in AM plots, while both *A. rubrum* and *U. americana* exhibited lower ratios at short distances between adult and juvenile trees in ECM plots (Appendix S1: Fig. S3).

Trends were similar for ECM-associated species, with more signs of negative feedback in AM plots and positive feedback in ECM plots. The neighborhood density function indicated that *F. grandifolia* had higher densities of conspecific juvenile trees at moderate distances (5 – 7 m) between adult and juvenile trees in ECM plots, and lower densities around 6m in AM plots. *F. grandifolia* also appeared to have a negative effect on heterospecific juveniles at short distances in both plot types, with lower densities of heterospecific juvenile trees than expected under the null model of spatial randomness (Appendix S1: Fig. S2). *F. grandifolia* adults had lower ratios of heterospecific to conspecific juveniles at ~1m, but only in ECM plots (Appendix S1: Fig. S4). In ECM plots, *Q. rubra* showed higher densities of conspecific juveniles surrounding adults at short distances (Appendix S1: Fig. S2). There were too few of *Q. rubra* or *C. ovata* juveniles in AM plots to analyze their structure, again indicative of negative feedback. All other combinations of species and plots did not deviate from the simulated models of spatial randomness (Appendix S1: Fig. S1 – S4).

Effects of dominant community mycorrhizal type on average point pattern statistics

Across all 95 plots, linear modeling indicated that the neighborhood density function was affected by a significant interaction between distance and percent AM basal area ($P < 0.001$; $R^2 = 0.07$), but the main effects of the mycorrhizal gradient and distance were not significant. Furthermore, when distance from adult tree was tested as a predictor for plots separated into different AM dominance categories, the effect of distance from adult trees on juvenile densities notably shifted from a positive relationship in plots with a majority AM basal area to a negative relationship in plots with a majority ECM basal area (Fig. 4). This result suggests that as ECM dominance increases, juvenile densities shift from being farther away from adult trees to closer to them, consistent with **H1**.

The mark correlation function was significantly affected by the distance between adult and juvenile trees ($P < 0.001$; $R^2 = 0.03$), but not by the mycorrhizal gradient or the interaction between the mycorrhizal gradient and distance. While this suggests that overall average values of the mark correlation function are similar in AM- and ECM-dominant plots, the previous comparison to spatial null models found that AM- and ECM-dominant plots do differ in the spatial arrangement of conspecific juvenile trees when constrained by each plot's neighborhood density (Fig. 3).

Effects of dominant mycorrhizal types on tree community and soil characteristics

Recruitment of new adult trees between 2008 and 2016 significantly decreased with increasing AM dominance along the mycorrhizal gradient ($P < 0.05$; $R^2 = 0.05$; Appendix S1: Fig. S5). Additionally, recruitment of new adult trees between 2008 and 2016 was significantly higher in ECM-dominant plots, nearly double that of adult recruitment in AM-dominant plots ($P < 0.05$; Appendix S1: Table S1). GLMMs indicated that mycorrhizal type had no effects on other demographic or community parameters (adult and juvenile abundances, species richness, adult growth rates, and adult mortality) or abiotic soil variables (percent C, Percent N, C:N ratio, total P, percent moisture, and pH) (Appendix S1: Table S1).

Discussion

Our analyses indicate that dominant community mycorrhizal associations influence the local structure of tree recruitment in forest communities, with ECM-dominant and AM-dominant communities exhibiting different spatial relationships between adult and juvenile individuals. These patterns are consistent with our hypothesis that the mycorrhizal type of dominant community members can result in PSF effects that spill over onto less common individuals and affect the entire tree community (**H1**). ECM-dominant communities had greater densities of juvenile trees (Fig. 2) and more conspecific individuals (Fig. 3) near adult trees than expected, in contrast to AM-dominant communities, which also exhibited lower recruitment of adult trees generally (Appendix S1: Fig. S5, Table S1). These spatial patterns support the idea that soils of varying mycorrhizal dominance reflect important differences in the way arbuscular and ectomycorrhizas cycle soil nutrients and interact with soil microbial communities (Phillips *et al.*

2013, Averill *et al*. 2014, Lin *et al.* 2017), thereby influencing the recruitment of juvenile trees near established adults at the community level. ECM fungal activity can suppress saprotrophs through competition, reduce soil mineral nutrient availability, and increase acidity in ECM soil (Phillips *et al*. 2013, Averill *et al.* 2014, Averill & Hawkes 2016, Tedersoo *et al.* 2020), which may reduce pathogen activity (LaManna *et al.* 2016, Smith *et al.* 2017) and create soil conditions conducive for positive PSF in ECM-dominant communities. This mechanism has recently been supported at the species level by Chen *et al.* (2019), who found that tree species that experience stronger negative density dependence also more rapidly accumulate pathogenic soil fungi, while trees that experience weaker negative density dependence more rapidly accumulate ECM fungi. Our findings expand on these mechanisms by documenting their influence across entire forest communities.

Collectively, our analyses show no differences between spatial patterns of AM and ECM species when considered independent from their surrounding community mycorrhizal associations (**H2**). This lack of influence of individual species' mycorrhizal associations on adult and juvenile spatial structure, in contrast to the effect from the dominant mycorrhizal type of the community, indicates that spillover effects from dominant community mycorrhizal associations may be the overriding factor influencing PSF in other individuals found nearby. Recent work by Bennett *et al.* (2017) demonstrated that the mycorrhizal associations of different species can result in different feedback outcomes, with ECM species largely experiencing positive feedback and AM species largely experiencing negative feedback when grown on soil conditioned by conspecific individuals. However, we found that community-level context, explored here as dominant mycorrhizal type, is also a key driver of feedback patterns. For example, we found no pattern in both *A. saccharum* and *U. americana* in AM plots, but clustering of conspecific juveniles and lower heterospecific/conspecific ratios nearby adults in ECM plots. This positive feedback signal in ECM plots for *A. saccharum* was unexpected, since Bennett *et al.* (2017) indicated that *A. saccharum* experiences little feedback in either direction. For *A. rubrum*, the presence of conspecific juveniles in ECM plots and lack of conspecific juveniles in AM plots implies that the negative feedback identified in Bennett *et al.* 2017 is only strong in AM plots. Of our ECM species, *F. grandifolia* and *Q. rubra* showed patterns of positive feedback consistent with Bennett *et al.* (2017) only in ECM plots. *Q. rubra* juveniles in AM plots were nearly absent, pointing to potential negative feedback for *Q. rubra* when the dominant community members are AM trees. Because tree species grow at different rates, future analyses could be improved by tracking individual juveniles over time or reconsidering the general size cutoff between adult and juvenile individuals of each species (Detto *et al.* 2019). However, taken holistically, the results of our analyses at the community and species levels support our overarching hypothesis that dominant community members have a dramatic influence on the local environment based on their mycorrhizal associations, resulting in PSF effects spilling over onto less common individuals in the community.

PSF is just one of several explanations that has been put forward for explaining the spatial distribution of plants in a community (Tilman 1988, Jones *et al*. 2008), but it is difficult to explain the patterns we have observed using alternative mechanisms. For example, strong intraspecific and interspecific competition can lead to non-random patterns of mortality, with surviving plant species being regularly spaced throughout a community (He & Duncan 2000). Specifically, competition for soil resources can create uniform or overdispersed spatial patterns between individual trees when resource availabilities are low (Getzin *et al*. 2006). ECM tree communities have been shown to induce lower inorganic nutrient availabilities (Read & Perez-

Moreno 2003, Averill *et al*. 2014), which should lead to stronger competitive interactions between trees within these communities. However, our results show a pattern that is opposite to expectations from increased competition for soil nutrients in ECM communities, with all juvenile trees clustering around adults instead of being overdispersed in ECM plots (Fig. 2C). This suggests that ECM associations can reduce the negative effects of competition and low inorganic nutrient availability through positive PSF between tree community members, likely driven by the ability of ECM fungi to obtain organic nutrients from host plant leaf litter (Read & Perez-Moreno 2003, Wurzburger & Hendrick 2009). Additionally, some saprotrophs may function as facultative biotrophic or necrotrophic pathogens (Olson *et al.* 2012, Smith *et al.* 2017). Under conditions of low mineral nutrient availability, pathogen populations may be suppressed by competition for organic resources from ECM fungi (Averill & Hawkes 2016). Conversely, weaker effects of competition between trees might be expected in AM communities because mineral nutrient availability is frequently higher under AM trees (Lin *et al*. 2017, Lin *et al*. 2018). Again, we observed the opposite pattern, with overdispersion at short distances between adult and juvenile trees in our AM communities, as well as lower overall recruitment rates. Larger pathogen populations may be a consequence of greater soil mineral nutrient availability (LaManna *et al*. 2016), which can lead to stronger pathogen-driven negative PSF and override the benefits of greater soil nutrient availability in AM communities. Therefore, the contrasting PSF outcomes of different mycorrhizal communities observed in our study are likely contingent on the ability of ECM communities to overcome the negative effects of reduced mineral nutrient availability and to suppress the growth of saprotrophs/facultative pathogens. We did not find any differences between abiotic soil properties of different mycorrhizal types, although the variables we measured may not represent the specific mineral and organic forms of nutrients expected to differ between soil of different mycorrhizal types (Phillips *et al.* 2013, Averill *et al*. 2014, Lin *et al*. 2017).

Dispersal strategies can also dictate where plants grow relative to one another (Howe & Smallwood 1982). Individuals of a species that exhibits limited dispersal capabilities are typically found clustered together, while species that can disperse greater distances are more randomly distributed throughout a community (Jacquemyn & Hermy 2001). If seed dispersal alone controlled the spatial distribution of trees in our sites, we would expect random distributions between adult and juvenile individuals throughout our community due to the size of our plots (30 m diameter) and the high likelihood of dispersal at these scales (Nathan & Muller-Landau 2000). Thus, post-dispersal filters, both abiotic and biotic, ultimately influence where plants establish within a community and therefore play a larger role than dispersal in influencing plant community structure at this spatial scale (Leck *et al*. 2008, Wang *et al*. 2015). Furthermore, we are unaware of any trait-based link between mycorrhizal associations and dispersal that can explain the community-wide, mycorrhizal-associated spatial patterns observed at the scale in our study, though dispersal colimitation of plants and mycorrhizal fungi may be an important consideration (Tedersoo *et al.* 2020).

For evolutionary relationships to play a role in driving PSF, trait dissimilarity and evolutionary distance need to be positively correlated so that closely related species overlap in traits that drive PSF (**H3**; Anacker *et al*. 2014, Parker *et al*. 2015, Cadotte *et al.* 2017). The random phylogenetic spatial structure observed in our analysis of both AM- and ECM-associating tree communities do not suggest this level of phylogenetic conservatism of traits that are associated with PSF. While our results agree with several other published studies that suggest phylogenetic relatedness is a poor predictor of PSF strength and direction (e.g., Mehrabi *et al.*

2015, Fitzpatrick *et al*. 2017), our study only considers aggregate phylogenetic distances between species with no consideration for specific traits. Furthermore, although Jennings Woods includes several pairs of congeneric species and five species of *Quercus*, greater species sampling may be necessary to detect a subtle phylogenetic signal in PSF (e.g., Liu *et al.* 2012). Additional work is needed to identify and evaluate more plant traits associated with PSF that are related to species' mycorrhizal types and how these relationships have shaped plant evolutionary history. Mycorrhizal fungi are thought to have played a significant role in plant niche differentiation (Gerz *et al*. 2018) and, while the evolution of mycorrhizas has been well studied across many plant clades (Brundrett 2002, Valverde-Barrantes *et al*. 2016, Brundrett & Tedersoo 2018), the implications of these symbiotic relationships for speciation rates and the evolution of traits connected to PSF are still poorly understood. Gaining a better understanding of these relationships, such as identifying differences in the defensive benefits conferred by AM vs. ECM fungal structures, should yield important insights into the evolutionary consequences of PSF and the mechanisms that shape these relationships through time.

Although additional studies are needed to fully establish the mechanisms behind the patterns observed here, our results indicate that community-level mycorrhizal dominance is an important factor that structures spatial patterns and demography in natural forests. The patterns we identified are consistent with mycorrhizal type differences in leaf litter and root traits driving variation in PSF by influencing the abundance of pathogenic microbial functional groups and soil mineral nutrient availability. Our research highlights the prominent role of mycorrhizas in structuring community-level interactions through spillover PSF effects from dominant community members. We recommend more PSF work adopt a holistic, community-level approach in order to expand from the perspective of species-specific interactions in communities where multiple mycorrhizal types are present.

References

Anacker, B. L., Klironomos, J. N., Maherali, H., Reinhart, K. O., & Strauss, S. Y. (2014). Phylogenetic conservatism in plant-soil feedback and its implications for plant abundance. *Ecology Letters*, *17*(12), 1613-1621.

Anacker, B. L., & Strauss, S. Y. (2016). Ecological similarity is related to phylogenetic distance between species in a cross-niche field transplant experiment. *Ecology*, *97*(7), 1807-1818.

Averill, C., Turner, B. L., & Finzi, A. C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature*, *505*(7484), 543.

Averill, C., & Hawkes, C. V. (2016). Ectomycorrhizal fungi slow soil carbon cycling. *Ecology Letters*, *19*(8), 937-947.

Baddeley, A.J. and Turner, R., 2004. Spatstat: An R package for analyzing spatial point pattens.

Bagchi, R., Swinfield, T., Gallery, R.E., Lewis, O.T., Gripenberg, S., Narayan, L. and Freckleton, R.P., 2010. Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters*, *13*(10), 1262-1269.

Bahram, M., Netherway, T., Hildebrand, F., Pritsch, K., Drenkhan, R., Loit, K., Anslan, S., Bork, P. and Tedersoo, L., 2020. Plant nutrient-acquisition strategies drive topsoil microbiome structure and function. *New Phytologist*.

Barton, K. (2009). MuMIn: multi-model inference, R package version 0.12. 0. *http://r-forge. r-project. org/projects/mumin/*.

Bates, D., Mächler, M., Bolker, B. and Walker, S., 2014. Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.

Bennett, J. A., Maherali, H., Reinhart, K. O., Lekberg, Y., Hart, M. M., & Klironomos, J. (2017). Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science*, *355*(6321), 181-184.

Bever, J. D., Platt, T. G., & Morton, E. R. (2012). Microbial population and community dynamics on plant roots and their feedbacks on plant communities. *Annual Review of Microbiology*, *66*, 265-283.

Bever, J.D., Mangan, S.A. and Alexander, H.M., 2015. Maintenance of plant species diversity by pathogens. *Annual review of ecology, evolution, and systematics*, *46*, 305-325.

Biganzoli, F., Wiegand, T. and Batista, W.B., 2009. Fire-mediated interactions between shrubs in a South American temperate savannah. *Oikos*, *118*(9), 1383-1395.

Blackwood, C. B., Smemo, K. A., Kershner, M. W., Feinstein, L. M., & Valverde-Barrantes, O. J. (2013). Decay of ecosystem differences and decoupling of tree community–soil environment relationships at ecotones. *Ecological Monographs*, *83*(3), 403-417.

Bradley, D. J., Gilbert, G. S., & Martiny, J. B. (2008). Pathogens promote plant diversity through a compensatory response. *Ecology Letters*, *11*(5), 461-469.

Brown, C., Illian, J. B., & Burslem, D. F. (2016). Success of spatial statistics in determining underlying process in simulated plant communities. *Journal of Ecology*, *104*(1), 160-172.

Brundrett, M. C. (2002). Coevolution of roots and mycorrhizas of land plants. *New Phytologist*, *154*(2), 275-304.

Brundrett, M. C. (2009). Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil*, *320*(1-2), 37-77.

Brundrett, M. C., & Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist*.

Cadotte, M.W., Davies, T.J. and Peres-Neto, P.R., 2017. Why phylogenies do not always predict ecological differences. *Ecological Monographs*, *87*(4), pp.535-551.

Calabrese, J. M., Vazquez, F., Lopez, C., San Miguel, M., & Grimm, V. (2010). The independent and interactive effects of tree-tree establishment competition and fire on savanna structure and dynamics. *The American Naturalist*, *175*(3), E44-E65.

Cavender-Bares, J., Kozak, K.H., Fine, P.V. and Kembel, S.W., (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*(7), 693-715.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations*.

Connell, J. H., & Lowman, M. D. (1989). Low-diversity tropical rain forests: some possible mechanisms for their existence. *The American Naturalist*, *134*(1), 88-119.

Cornelissen, J., Aerts, R., Cerabolini, B., Werger, M., & Van Der Heijden, M. (2001). Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*, *129*(4), 611-619.

Detto, M., Visser, M.D., Wright, S.J. and Pacala, S.W., 2019. Bias in the detection of negative density dependence in plant communities. *Ecology Letters*, 22(11), pp.1923-1939.

Eppinga, M. B., Baudena, M., Johnson, D. J., Jiang, J., Mack, K. M., Strand, A. E., & Bever, J. D. (2018). Frequency-dependent feedback constrains plant community coexistence. *Nature Ecology & Evolution*, *2*(9), 1403.

Fitzpatrick, C. R., Gehant, L., Kotanen, P. M., & Johnson, M. T. (2017). Phylogenetic relatedness, phenotypic similarity and plant–soil feedbacks. *Journal of Ecology*, *105*(3), 786-800.

Gadgil, R. L. & Gadgil, P. D. (1971). Mycorrhiza and litter decomposition. *Nature*, 233, 133.

Gerz, M., Guillermo Bueno, C., Ozinga, W. A., Zobel, M., & Moora, M. (2018). Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology*, *106*(1), 254-264.

Getzin, S., Dean, C., He, F., Trofymow, J. A., Wiegand, K., & Wiegand, T. (2006). Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography*, *29*(5), 671-682.

Gilbert, G. S., Briggs, H. M., & Magarey, R. (2015). The impact of plant enemies shows a phylogenetic signal. *PloS One*, *10*(4), e0123758.

He, F., & Duncan, R. P. (2000). Density-dependent effects on tree survival in an old-growth Douglas fir forest. *Journal of Ecology*, *88*(4), 676-688.

Hovatter, S., Blackwood, C. B., & Case, A. L. (2013). Conspecific plant–soil feedback scales with population size in Lobelia siphilitica (Lobeliaceae). *Oecologia*, *173*(4), 1295-1307.

Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*(1), 201-228.

Hubbell, S. P., Ahumada, J. A., Condit, R., & Foster, R. B. (2001). Local neighborhood effects on long-term survival of individual trees in a Neotropical forest. *Ecological Research*, *16*(5), 859-875.

Illian, J., Penttinen, A., Stoyan, H., & Stoyan, D. (2008). *Statistical analysis and modelling of spatial point patterns* (Vol. 70). John Wiley & Sons.

Jacquemyn, H., Butaye, J., & Hermy, M. (2001). Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. *Journal of Biogeography*, *28*(6), 801-812.

Johnson, D. J., Clay, K., & Phillips, R. P. (2018). Mycorrhizal associations and the spatial structure of an old-growth forest community. *Oecologia*, *186*(1), 195-204.

Jones, M. M., Tuomisto, H., Borcard, D., Legendre, P., Clark, D. B., & Olivas, P. C. (2008). Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. *Oecologia*, *155*(3), 593-604.

Kulmatiski, A., Beard, K. H., & Heavilin, J. (2012). Plant–soil feedbacks provide an additional explanation for diversity–productivity relationships. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20120285.

LaManna, J. A., Walton, M. L., Turner, B. L., & Myers, J. A. (2016). Negative density dependence is stronger in resource-rich environments and diversifies communities when stronger for common but not rare species. *Ecology Letters*, *19*(6), 657-667.

Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S. and Steinbeiss, S., 2015. Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications*, *6*.

Leck, M. A., Parker, V. T., & Simpson, R. L. (Eds.). (2008). *Seedling ecology and evolution*. Cambridge University Press.

Liang, M., Liu, X., Gilbert, G.S., Zheng, Y., Luo, S., Huang, F. and Yu, S., 2016. Adult trees cause density-dependent mortality in conspecific seedlings by regulating the frequency of pathogenic soil fungi. *Ecology Letters*, *19*(12), 1448-1456.

Lin, G., McCormack, M. L., Ma, C., & Guo, D. (2017). Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *New Phytologist*, *213*(3), 1440-1451.

Lin, G., Guo, D., Li, L., Ma, C., & Zeng, D. H. (2018). Contrasting effects of ectomycorrhizal and arbuscular mycorrhizal tropical tree species on soil nitrogen cycling: the potential mechanisms and corresponding adaptive strategies. *Oikos*, *127*(4), 518-530.

Liu X, Liang M, Etienne RS, Wang Y, Staehelin C, Yu S. 2012. Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest. Ecology Letters 15: 111-118.

Maherali, H., Oberle, B., Stevens, P. F., Cornwell, W. K., & McGlinn, D. J. (2016). Mutualism persistence and abandonment during the evolution of the mycorrhizal symbiosis. *The American Naturalist*, *188*(5), E113-E125.

Mangan, S. A., Herre, E. A., & Bever, J. D. (2010). Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant–soil feedback. *Ecology*, *91*(9), 2594-2603.

Martínez, I., Taboada, F.G., Wiegand, T. and Obeso, J.R., 2013. Spatial patterns of seedling-adult associations in a temperate forest community. *Forest Ecology and Management*, *296*, pp.74-80.

Mehrabi, Z., & Tuck, S. L. (2015). Relatedness is a poor predictor of negative plant–soil feedbacks. *New Phytologist*, *205*(3), 1071-1075.

Metz, M.R., Sousa, W.P. and Valencia, R., (2010). Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology*, *91*(12), 3675-3685.

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, *15*(7), 278-285.

Packer, A., & Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, *404*(6775), 278.

Parker, I. M., & Gilbert, G. S. (2004). The evolutionary ecology of novel plant-pathogen interactions. *Annu. Rev. Ecol. Evol. Syst.*, *35*, 675-700.

Parker, I. M., Saunders, M., Bontrager, M., Weitz, A. P., Hendricks, R., Magarey, R., ... & Gilbert, G. S. (2015). Phylogenetic structure and host abundance drive disease pressure in communities. *Nature*, *520*(7548), 542.

Petermann, J.S., Fergus, A.J., Turnbull, L.A. and Schmid, B., 2008. Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology*, *89*, 2399-2406.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package ‘nlme’. *Linear and Nonlinear Mixed Effects Models*, 3-1.

Phillips, R. P., Brzostek, E., & Midgley, M. G. (2013). The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist*, 199(1), 41-51.

R Development Core Team (2017). *R: A language and environment for statistical computing*, Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org/.

Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems–a journey towards relevance?. *New Phytologist*, *157*(3), 475-492.

Schnitzer, S. A., Klironomos, J. N., HilleRisLambers, J., Kinkel, L. L., Reich, P. B., Xiao, K., ... & Van Nes, E. H. (2011). Soil microbes drive the classic plant diversity–productivity pattern. *Ecology*, *92*(2), 296-303.

Shen, G., Wiegand, T., Mi, X., & He, F. (2013). Quantifying spatial phylogenetic structures of fully stem-mapped plant communities. *Methods in Ecology and Evolution*, *4*(12), 1132-1141.

Smith, S. E., & Read, D. J. (2008). *Mycorrhizal Symbiosis*. Academic press.

Smith, G.R., Finlay, R.D., Stenlid, J., Vasaitis, R. and Menkis, A., (2017). Growing evidence for facultative biotrophy in saprotrophic fungi: data from microcosm tests with 201 species of wood-decay basidiomycetes. *New Phytologist*, *215*(2), 747-755.

Steidinger, B.S., Crowther, T.W., Liang, J., Van Nuland, M.E., Werner, G.D., Reich, P.B., Nabuurs, G., de-Miguel, S., Zhou, M., Picard, N. and Herault, B., 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature*, *569*(7756), p.404.

Tedersoo, L., Bahram, M. and Zobel, M., 2020. How mycorrhizal associations drive plant population and community biology. *Science*, *367*.

Teste, F. P., Kardol, P., Turner, B. L., Wardle, D. A., Zemunik, G., Renton, M., & Laliberté, E. (2017). Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science*, *355*(6321), 173-176.

Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press.

Valverde-Barrantes, O. J., Horning, A. L., Smemo, K. A., & Blackwood, C. B. (2016). Phylogenetically structured traits in root systems influence arbuscular mycorrhizal colonization in woody angiosperms. *Plant and Soil*, *404*(1-2), 1-12.

van der Putten, W.H., Van Dijk, C. and Peters, B.A.M., 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature*, *362*(6415), 53.

van der Putten, W. H., Bradford, M. A., Pernilla Brinkman, E., van de Voorde, T. F., & Veen, G. F. (2016). Where, when and how plant–soil feedback matters in a changing world. *Functional Ecology*, *30*(7), 1109-1121.

Wang, X., Wiegand, T., Swenson, N. G., Wolf, A. T., Howe, R. W., Hao, Z., ... & Yuan, Z. (2015). Mechanisms underlying local functional and phylogenetic beta diversity in two temperate forests. *Ecology*, *96*(4), 1062-1073.

Wardle, D. A., Bonner, K. I., Barker, G. M., Yeates, G. W., Nicholson, K. S., Bardgett, R. D., ... & Ghani, A. (1999). Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs*, *69*(4), 535-568.

Webb, C. O., & Donoghue, M. J. (2005). Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes*, *5*(1), 181-183.

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, *24*(18).

Wiegand, T., & A Moloney, K. (2004). Rings, circles, and null-models for point pattern analysis in ecology. *Oikos*, *104*(2), 209-229.

Wiegand, T., Kissling, W. D., Cipriotti, P. A., & Aguiar, M. R. (2006). Extending point pattern analysis for objects of finite size and irregular shape. *Journal of Ecology*, *94*(4), 825-837.

Wiegand, T., & Moloney, K. A. (2013). *Handbook of spatial point-pattern analysis in ecology*. CRC Press.

Wurzburger, N., & Hendrick, R. L. (2009). Plant litter chemistry and mycorrhizal roots promote a nitrogen feedback in a temperate forest. *Journal of Ecology*, *97*(3), 528-536.

Zambrano, J., Iida, Y., Howe, R., Lin, L., Umana, M. N., Wolf, A., ... & Swenson, N. G. (2017). Neighbourhood defence gene similarity effects on tree performance: a community transcriptomic approach. *Journal of Ecology*, *105*(3), 616-626.

Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G. et al. (2014). Three keys to the radiation of angiosperms into freezing environments. Nature, 506, 89–92.

Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1 Supplemental methods for phylogenetic mark correlation analysis.

Table S1 Community properties and abiotic soil data by dominant community mycorrhizal type.

Figure S1 Neighborhood density function results for three AM-associated tree species across AM and ECM-dominated plots

Figure S2 Neighborhood density function results for four ECM-associated tree species across AM and ECM-dominate plots.

Figure S3 Mark correlation function results for three AM-associated tree species across AM and ECM-dominate plots.

Figure S4 Mark correlation function results for four ECM-associated tree species across AM and ECM-dominate plots.

Figure S5 Recruitment of new adult trees by plot mycorrhizal basal area.

Figures

Fig. 1 – Map of Jennings Woods. Colored points include the juvenile and adult trees that had their spatial locations mapped during our 2016 survey. Black squares represent the center of each plot included in our 2008 and 2016 demographic surveys. Comprehensive site information can be found in Blackwood *et al.* (2013).

Fig. 2 - Neighborhood density function showing the density of juvenile trees surrounding adult trees. Results are aggregated across all plots (A), by dominant community mycorrhizal type (B and C), or by individual species mycorrhizal type (D and E). Significant deviations in the observed neighborhood density function from the random null model envelope are indicated by hollow points.

Fig. 3 - Mark correlation function showing the heterospecific/conspecific ratio of juvenile trees surrounding adult trees. Results are aggregated across all plots (A), by dominant community mycorrhizal type (B and C), or by individual species mycorrhizal type (D and E). Values above the null model envelope indicate higher proportions of heterospecific juvenile trees, while values below the null model envelope indicate higher proportions of conspecific juvenile trees. Significant deviations in the mark correlation function from the random null model envelope are indicated by hollow points.

Fig. 4 - Generalized linear mixed-effect modeling results demonstrating the significant changes in juvenile density with distance from adult trees. Separate analyses were conducted for **A)** plots with a relative percent AM basal area between 75-100% (few ECM trees present; $P = 0.01$; $R^2 = 0.076$), **B)** plots with a relative percent AM basal area between 50-75% ($P = 0.001$; $R^2 = 0.125$), **C)** plots with a relative percent AM basal area between 25-50% ($P = 0.5748$), and

D) plots with a relative percent AM basal area between 0-25% (few AM trees but many ECM trees present; *P* = 0.002; $R^2 = 0.122$). Points indicate values for the neighborhood density function at a specific distance interval for each plot, while colors correspond to the relative AM/ECM basal area percent of a plot. Lines represent the predicted model values for each plot in our forest and highlight the shifts in spatial patterns occurring in the juvenile community along the mycorrhizal gradient. Plot was held as a random effect to account for non-independence of neighborhood densities within the same plot, resulting in different intercepts for each plot.