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RESEARCH ARTICLE

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Tree mycorrhizal type mediates the strength of negative density dependence in temperate forests

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Abstract

1. Recent plant–soil feedback experiments suggest that arbuscular mycorrhizal (AM) tree species experience stronger conspecific negative density dependence (CNDD) than ectomycorrhizal (EM) tree species. Yet, how these findings inform our understanding of natural systems is limited because the roles of local soil conditions, light availability and tree species abundances in influencing CNDD for AM and EM species are not clear.
2. Here we examined seedling and sapling survival in two temperate old-growth forests (broad-leaved pine and spruce-fir forests) in Northeast China, to evaluate the effects of both conspecific and heterospecific neighbour density, as well as the soil and light environments, on the survival of AM- and EM-dependent trees at early life stages.
3. While light availability increased the survival of EM seedlings, soil organic resources increased EM sapling survival in the spruce-fir plot. AM tree species suffered stronger CNDD than did EM tree species in both plots. In the spruce-fir plot, soil factors and light availability mediated species CNDD but their effects differed between AM and EM species, and also between seedlings and saplings. For seedlings in both plots, we found that AM species exhibited a positive relationship between species abundance and CNDD strength, whereas this relationship was negative for EM species.
4. *Synthesis*. Our results provide one of the few tests of how fungal symbioses determine species responses to intraspecific and interspecific interactions and the direct effects of local environmental conditions on seedling and sapling survival. We show that mycorrhizal type mediates the strength of CNDD and its relationship with species abundance. These results suggest that tree mycorrhizal association can determine the strength of CNDD effect on both rare and common species, and these CNDD differences are likely to influence the community composition of temperate forests.

KEYWORDS

arbuscular mycorrhizal (AM) tree species, conspecific negative density dependence (CNDD), ectomycorrhizal (EM) tree species, life stage, light availability, plant survival, soil environment, species abundance

1 | INTRODUCTION

There are a plethora of mechanistic processes and hypotheses that allow community ecologists to explain species coexistence and diversity in plant communities (Chesson, 2000; Wright, 2002). Two mechanisms in particular, conspecific negative density dependence (CNDD) and abiotic filtering, have been widely demonstrated to influence plant survival and community structure (Bagchi et al., 2011; Comita et al., 2014; Johnson, Condit, Hubbell, & Comita, 2017; LaManna et al., 2017), and thus form the basis for many theories explaining plant diversity. Specifically, CNDD predicts that plant performance and survival will decline when surrounded by a greater number of conspecific neighbours, and this negative effect can arise from intraspecific competition or pressure from shared host-specific enemies (Connell, 1971; Janzen, 1970; Klironomos, 2002; Mangan et al., 2010). Plant survival can also be influenced by other types of biotic interactions, the influence of local environmental conditions and species traits (Laughlin, Strahan, Adler, & Moore, 2018). However, few studies have considered these biotic and abiotic factors, specifically examining how plant functional traits and plant–microbe associations influence plant performance simultaneously (but see Fortunel et al., 2018 and Luo et al., 2016). Specifically, there is compelling evidence that tree species mycorrhizal type (reflecting root structure that can have a symbiosis with arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi) and their interactions with environmental factors and neighbouring trees can influence tree survival in temperate forests.

Results from previous studies show that the strength of CNDD varies among species that possess different traits, suggesting the different susceptibilities of species to the increasing density of conspecific neighbours (Kobe & Vriesendorp, 2011; Lebrija-Trejos, Reich, Hernandez, & Wright, 2016). Soil-borne pathogens are regarded as an important pressure that can drive CNDD in the early life stages of plants (Laliberte, Lambers, Burgess, & Wright, 2015; Liu, Fang, Chesson, & He, 2015), and consequently, below-ground traits and interactions should strongly influence interaction with and susceptibility to these pathogens. The type of mycorrhizae associated with plant hosts is an important root functional trait that can affect plant nutrient uptake and pathogen defence (Smith & Read, 2008), and should influence species CNDD strength (Dickie, Koele, Blum, Gleason, & McGlone, 2014). Temperate tree species almost always have a symbiosis with AM or EM fungi (hereafter we call these tree species as AM species and EM species, respectively; Brundrett, 2009; Wang & Qiu, 2006). AM fungi can penetrate the cortical cells of AM host plant roots to form arbuscules, but EM fungi do not penetrate the cortical cells and instead form a mantle covering root tip and a Hartig net (a hyphae network between cortical cells).

Even though previous studies have found that both AM fungi and EM fungi can mitigate the negative effects of conspecific interactions (Newbery, Alexander, & Rother, 2000; Teste et al., 2009, 2017; van der Heijden & Horton, 2009), EM fungi are believed to reduce CNDD more than AM fungi (Bennett et al., 2017; Lambers et al., 2017). These differences might arise through three different mechanisms. First, the mantle and Hartig net formed by EM fungi can provide physical barriers around root tissues, which might reduce pathogen access to root tissue (Bennett et al., 2017; Marx, 1972). Second, EM fungi produce specific antibiotic compounds (e.g. diatretyne amide and diatretyne 3) that protect root tissue, and which AM fungi do not produce (Lambers et al., 2017; Marx, 1972). Third, EM species can better benefit from mycorrhizal fungal networks than AM species because AM fungi form aseptate cells that cannot easily grow from one root to another (van der Heijden & Horton, 2009).

Abiotic factors such as soil and light environments can also influence plant demography (Johnson et al., 2017) and the direct effect of environmental factors might be mediated by AM- and EM-associated tree species. For example, AM trees mostly require soil inorganic nutrients but EM trees show a competitive advantage in accessing and absorbing organic nutrients (Corrales, Mangan, Turner, & Dalling, 2016; Liu et al., 2018). On the other hand, environmental factors can also influence the strength of CNDD at local and regional scales (Johnson, Beaulieu, Bever, & Clay, 2012; Lin, Comita, Zheng, & Cao, 2012). Soil pH and moisture are considered as important factors in driving the abundance and distribution of microbial biota (Fierer & Jackson, 2006), which then can influence the strength of plant–microbe interactions, further varying the strength of CNDD along environmental gradients (Comita et al., 2014; LaManna, Walton, Turner, & Myers, 2016). In addition, lower light availability can increase the likelihood of lethal leaf damage by herbivores and pathogen-induced death (Augspurger, 1984; Norghauer, Malcolm, & Zimmerman, 2008), and also results in reduced benefits for fungal mutualists because of the reduced photosynthetic rates and resource supply to mutualists. Furthermore, light availability should be the most important limiting resource that influences plant survival at early life stages (Comita et al., 2009). As seedlings grow into saplings, a taller stature will decrease the effect of light limitation, and so the limiting resources could shift to the availability of soil nutrients and water (Niinemets, 2010). Therefore, we expect that the soil environmental conditions will be more important for saplings than seedlings, while light serves as a greater factor for seedlings.

There is an increasing interest in how the strength of CNDD is differentially experienced by common and rare species (Comita, Muller-Landau, Aguilar, & Hubbell, 2010; Johnson et al., 2012). Stronger CNDD can prevent the domination of a local community by a single species but can also provide recruitment and survival advantages under low density. It is expected then that abundant species will be weakly affected by CNDD, while rare species are subject to strong CNDD. This expectation is supported by recent findings showing that rare species experience stronger CNDD than common species in tropical forests (Comita et al., 2010; LaManna et al., 2017; Mangan et al., 2010). However, some studies in temperate forests observed stronger CNDD for common species than rare species (LaManna et al., 2017; Zhu, Woodall, Monteiro, & Clark, 2015). While there are a number of well-understood factors that drive the variation of CNDD strength among species, there are few studies demonstrating why there are different relationships between species abundance and CNDD strength across forests. Given that temperate and tropical forests differ in the mycorrhizal associations of tree species (Read, 1991), we question whether AM and EM species differentially influence the relationship between species abundance and CNDD strength.

Here we explore whether seedling and sapling survival are influenced by the density and identity of tree neighbours, soil factors and light availability using tree demography data in two large old-growth temperate forest dynamics plots. Then we estimated whether CNDD strength was influenced by species mycorrhizal type and environmental factors. We asked three questions with three predictions: (a) *Do soil resource and light availability influence plant survival, and are the environmental effects different for AM and EM species and for seedlings and saplings?* We predict that light availability will increase plant survival, and soil organic nutrients (e.g. nitrogen) will increase the survival of EM species; while seedling survival should be influenced by light availability, the sapling survival will be mainly influenced by soil environment. (b) *Does the strength of CNDD depend on species mycorrhizal type, soil environment and light availability?* We predict that AM species have a relatively stronger CNDD than EM species; the CNDD strength varies with soil environmental gradients and decreases with increasing light availability. (c) *How does the strength of CNDD vary with species abundance for AM and EM species?* We predict that AM species will show a more positive relationship between species abundance and CNDD strength than does EM species.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study was conducted in the Heilongjiang Liangshui National Natural Reserve (47°10′50″N, 128°53′20″E), Northeast China. The mean annual temperature is −0.3°C, and the mean annual precipitation is 676 mm (Piao, Comita, Jin, & Kim, 2013). In Northeast China, the mixed broad-leaved Korean pine *Pinus koraiensis* forest is the main type of old-growth forest, where accommodates many broad-leaved species such as tree *Acer mono* and shrub *Corylus mandshurica*. In some regions, the spruce-fir valley forest (spruce-fir), as an alternative old-growth forest, is formed in a special habitat created by the moist micro-climate of streams and temperate inversion phenomena in valleys. The spruce-fir is dominated by three EM species: *Picea koraiensis*, *Abies nephrolepis* and *Larix gmelinii*; the dominated AM species are *Acer tsegmentosum* and *Prunus padus*. In 2005 and 2006, we established a 9 ha (300 m × 300 m) forest dynamics plot in the broad-leaved pine forest and a 9.12 ha (380 m × 240 m) forest dynamics plot in the spruce-fir forest (Pu & Jin, 2018). The broad-leaved pine plot shows a more rugged terrain than the spruce-fir plot, the elevation range is 83 m in the broad-leaved pine plot but only 5 m in the spruce-fir plot. Even though these two old-growth forests are located few kilometres away in the Liangshui Reserve, the species composition, abundance and diversity vary greatly (Figure S1).

2.2 | Focal individuals and the mycorrhizal type of species

In the first census in 2005 and 2006, all woody stems with a diameter at breast height (DBH) ≥2 cm in these two plots were mapped, measured, tagged and identified to the species level (Pu & Jin, 2018). Then, for the later censuses since 2010 and 2011, we included all woody stems whose DBH ≥ 1 cm (Condit, 1998). We established 900 seedling quadrats (2 m × 2 m) in 2006 in the broad-leaved pine plot and 912 seedling quadrats (2 m × 2 m) in 2007 in the spruce-fir plot, and these quadrats were located at the corners of 10 m × 10 m grids in these two plots. In each quadrat, all woody seedlings with a DBH <1 cm and a height ≥10 cm were tagged, identified and measured for height (Pu & Jin, 2018). Because there were some missing DBH measurements for some large individuals in our previous censuses, here we defined the seedlings as individuals with 10 cm ≤ height ≤ 1.6 m. In this study, we used the survival data from 2012 to 2016 for seedlings and from 2010 to 2015 for saplings in the broad-leaved pine plot, and survival data from 2011 to 2015 for seedlings and from 2011 to 2016 for saplings in the spruce-fir plot (Pu & Jin, 2018). That is, there is only one survival observation for each seedling or sapling from the start to the end year in our analyses. Previous studies have found that the CNDD is often stronger for plants in early life stages (LaManna et al., 2016; Zhu, Comita, Hubbell, Ma, & Shefferson, 2015; Zhu et al., 2018); and correspondingly we performed our analyses focusing on seedlings and saplings. We defined our sapling stage class according to LaManna et al. (2016), with saplings as the individuals with 1 cm ≤ DBH < 10 cm for overstory tree species defined in Pu and Jin (2018). For the understorey tree species and shrubs, we defined the saplings as the individuals with DBH < 5 and 2 cm (LaManna et al., 2016). The adults were defined as individuals with DBH larger than those of saplings. The numbers of species and individuals for each mycorrhizal type, life stage and plot are shown in Table S1. The mycorrhizal type of species in these two plots was compiled from the published literature (Akhmetzhanova et al., 2012; Iversen et al., 2017; Wang & Qiu, 2006). If the mycorrhizal type of any species has not been reported, we determined by examining the root anatomical structure using methods in Li, Liu, McCormack, Ma, and Guo (2017). Mycorrhizal types for all species are shown in Table S2.

2.3 | Neighbour density index

For each focal individual, we divided its surrounding neighbours into two groups and calculated the corresponding indices: the conspecific neighbour's index (CI) and the heterospecific neighbour's index (HI). These neighbour indices account for both the neighbour basal area and its distance to the focal individual (Chen et al., 2016; Pu & Jin, 2018). For simplicity, we only showed the formula of CI (cm^2/m):

$$\text{CI} = \sum_{i}^{N} \frac{\text{BA}_i}{\text{Distance}_i},$$

where N is the number of conspecific neighbours within 10 m, which was selected because a previous study in our plot found that neighbour interactions were negligible beyond a 10-m distance (Piao et al., 2013). We excluded all focal seedlings and saplings closer than 10 m to the edge of these two plots because the neighbours of these focal individuals within 10-m distance might be located outside of the plot used in analyses. BA_i is the basal area and Distance_i is the distance of the ith individual to the focal individual. HI (cm^2/m) can be calculated by replacing conspecific neighbours with the heterospecific neighbours. All neighbours for seedlings and sapling were individuals with DBH ≥ 1 cm in these two plots.

2.4 | Soil environment and light availability

We measured 10 soil factors to quantify the soil environmental gradient (e.g. soil nutrients and water availability), including bulk density, available N, available P, available K, organic C, total N, total P, pH, volumetric moisture and mass moisture (Jiang, Xun, Cai, & Jin, 2017; Shi, Gao, Cai, & Jin, 2015). Sampling methods followed John et al. (2007) where a 20 m × 20 m square grid was placed in the plot to create a total of 256 intersections (Figure S2). For bulk density and mass moisture, we only collected the soil samples from these 256 sample points. For the remaining soil factors, we also selected two additional soil samples based on the points (2, 5 or 8 m to each intersection) in a randomly assigned cardinal direction (Jiang et al., 2017). The measurement approaches for each soil factor could be found in Jiang et al. (2017). All soil samples were taken within 10 cm in depth. A total of 768 and 780 soil samples were collected in broad-leaved pine and spruce-fir plots, respectively. The soil environment of focal individuals was allocated using the values of the 10 m × 10 m quadrat soil factors they belonged to, which was generated by the ordinary kriging geostatistical technique (John et al., 2007). We used principal component analysis to reduce the dimensions of the soil environmental variables and to summarize the soil resource gradient (Table S3). We chose the PC1 axis of soil variables for both broad-leaved pine plot (variation explained: 43.3%; Figure S3) and spruce-fir plot (variation explained: 39.2%; Figure S3). The PC1 axis in broad-leaved pine plot indicated the higher available N, total N, available K, water availability, total P, organic C and lower bulk density. The PC1 axis in the spruce-fir plot described the higher water availability, total N, organic C, pH (the soil at this forest is slightly acid), available N and lower bulk density. These two PCs in both plots described a gradient of soil resource availability from relatively dry with low soil nutrient (e.g. N) content to moist with high soil nutrient content. Soil PC2 axes from both plots were not reported here because they did not show significant effects on CNDD strength in either plot.

We estimated the light availability in the understorey using hemispherical photographs (Nikon Coolpix 4500 digital camera with a 180° fish-eye lens; Liu, Chen, Jin, & Qi, 2015; Umana, Zhang, Cao, Lin, & Swenson, 2017). In the broad-leaved pine plot, pictures were taken at each seedling plot (1 m above-ground) in 2013 (Figure S2). In the spruce-fir plot, pictures were taken at a slightly coarse way in 2017 (Figure S2). We divided the plot into 10 m × 10 m grid subplots, where the pictures were taken at the centre of subplots. However, we only took the pictures for subplots which belonged to the odd rows and odd columns. Therefore, in the spruce-fir plot, the distance from each seedling plot to their nearest location of the picture was taken was 7 m (Figure S2). We generated the canopy openness index as the light availability using the Gap Light Analyser software (http://www.caryinstitute.org/science-program/our-scientists/dr-charles-d-canham/gap-light-analyzer-gla).

2.5 | Survival analysis

We examined the effects of conspecific and heterospecific neighbours, soil resource, light availability and their interactions with mycorrhizal type on the survival of seedlings and saplings using generalized linear mixed-effects models (GLMMs; Bolker et al., 2009) with binomial errors. The survival of plant individual i in quadrat q for species s (y_{iqs}) was modelled using GLMMs as follows (community-level analysis):

$$y_{iqs} \sim \text{Bernoulli}(\theta_{iqs})$$

$$\begin{aligned}\text{logit}(\theta_{iqs}) = {} & \beta_{0\text{s}} + \beta_1 \times \text{size}_{iqs} + \beta_{2\text{s}} \times \text{CI}_{iqs} + \beta_3 \times \text{HI}_{iqs} \\ & + \beta_{4\text{s}} \times \text{soil}_{iqs} + \beta_{5\text{s}} \times \text{light}_{iqs} + \beta_6 \times \text{CI}_{iqs} \times \text{soil}_{iqs} \\ & + \beta_7 \times \text{CI}_{iqs} \times \text{light}_{iqs} + \Phi_q. \end{aligned} \tag{1}$$

$\beta_{0\text{s}}$ (random effect) was the species-specific intercept (random effect) because species' baseline survival rates can vary widely (Zhu et al., 2018); β_1 (fixed effect) indicated the effect of plant initial size (height for seedling and DBH for sapling); $\beta_{2\text{s}}$, $\beta_{4\text{s}}$ and $\beta_{5\text{s}}$ represented, respectively, the effects of conspecific neighbours, soil resource and light availability (Question 1), where we included these as the random effects of species to allow their difference among species; β_3 (fixed effect) indicated the effect of heterospecific neighbours; β_6 and β_7 (fixed effect) represented the interactions of conspecific neighbours with soil resource and light availability to know how CNDD depends on them (Question 2). Φ_q indicated the random effect of quadrat to account for the spatial autocorrelation. All predictors were standardized using a z-score to have a mean of zero and a standard deviation of one, which allows us to compare the effect of different predictors directly. We did not include the species mycorrhizal type as a categorical predictor in the model; instead, we modelled the AM and EM species survival separately. These two approaches lead to identical modelling outcomes, but modelling AM and EM separately facilitated our interpretation of the results.

To explore the relationship between CNDD strength and species abundance for AM and EM species (Question 3), we extracted CNDD strength (i.e. $\beta_{2\text{s}}$) from (Equation 1) and performed a linear model using this CNDD strength as the dependent variable and species basal area-based abundance, species mycorrhizal type and their interaction as the independent variables (species-level analysis). Species abundance was z-score standardized in the linear model. Specifically, to account for the estimated uncertainty of CNDD strength, these regression models were weighted by the inverse of SE (LaManna et al., 2017; Zhu, Comita, et al., 2015). If the interaction term was significant, then that indicated there was a different relationship with abundance for AM and EM species. All statistical analyses were performed in R-3.5.0 (R Core Team, 2018). The GLMMs were performed using the LME4 package (Bates, Maechler, Bolker, & Walker, 2015).

3 | RESULTS

Not surprisingly, seedlings and saplings experienced greater survival with greater plant size and more heterospecific neighbours (Figure 1a,c; Table S4). In the broad-leaved pine plot, we did not find direct effects of soil variables and light availability on plant survival (Figure 1d,e). In the spruce-fir plot, we only found significant influences of the environmental variables on EM species, with EM seedling survival increasing with high light availability and sapling survival increasing with soil PC1 (Figure 1d,e).

At the community level, where we assessed the impact of neighbours on individual survival, GLMMs indicated that AM species experienced a slightly stronger CNDD than did EM species for seedlings in both plots (Figure 1b). At the species level, where we examined species abundance influences on CNDD, linear models indicated that AM species suffered a significantly stronger CNDD than EM species except for seedlings in the spruce-fir plot (Table 1; Figure 2). In the broad-leaved pine plot, the CNDD strength of

TABLE 1 Results of multiple linear regression models show the effects of species abundance, mycorrhizal type and their interaction on the strength of negative density dependence effect in two plots

	Abundance	Mycorrhizal type (EM)	Abundance × Mycorrhizal type (EM)
BKPF seedling	0.028	**0.732****	**−0.386*****
BKPF sapling	*0.050*	**0.153****	−0.041
SPVF seedling	**3.633****	0.955	**−3.750****
SPVF sapling	−0.021	**0.355*****	0.024

Abbreviations: BKPF, broad-leaved Korean pine forest; SPVF, spruce-fir valley forest.

Italics represent $p < 0.1$.

Bold values indicate $^{**}p < 0.01$; $^{***}p < 0.001$.

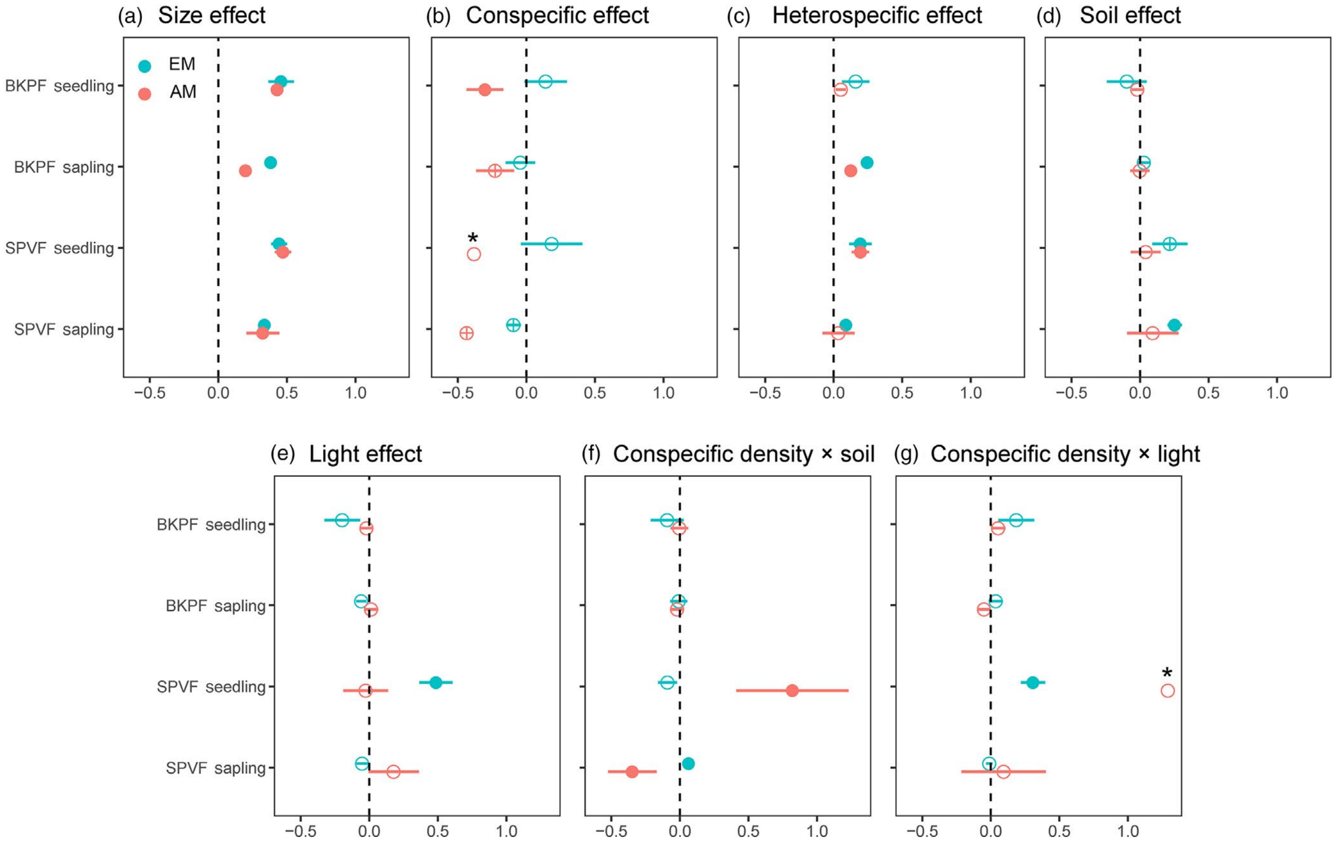

FIGURE 1 Coefficient estimates (±SE) of effects of the initial size (a), conspecific neighbours index (b), heterospecific neighbour index (c), soil resource gradient (d), light availability gradient (e) and their interactions (f and g) on seedling and sapling survival in the BKPF (broad-leaved Korean pine forest) and SPVF (spruce-fir valley forest) plots modelled using GLMMs. Open circle: not significant; open circle with inserted '+': marginally significant ($p < 0.1$); solid circle: significant ($p < 0.05$). '*' in panel (b) for SPVF AM seedling: estimate ± SE, −2.849 ± 3.408; $p = 0.403$. '*' in panel (g) for SPVF AM seedling: estimate ± SE, 1.292 ± 1.258; $p = 0.304$

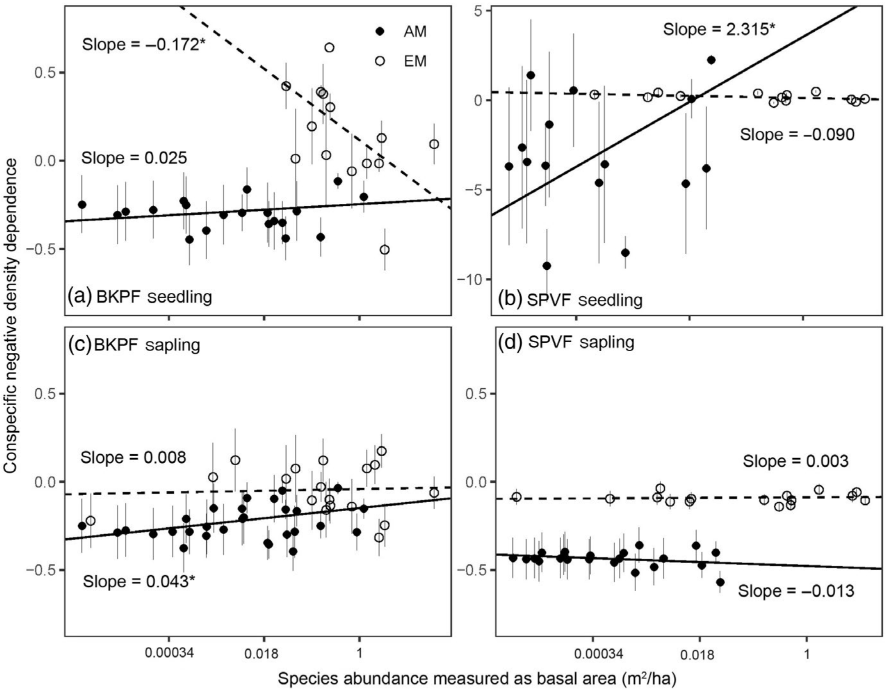

FIGURE 2 The relationships between species abundance and strength of negative density dependence (CNDD) effect are different between AM and EM species for (a) seedlings and (c) saplings in the BKPF (broad-leaved Korean pine forest) plot and (b) seedlings and (d) saplings in the SPVF (spruce-fir valley forest) plot. The slopes of linear models for each case are also shown. The CNDD for SPVF seedlings shows larger variation than others. $^*p < 0.05$

seedlings and saplings did not vary with changing soil environment and light availability (Figure 1f,g). In the spruce-fir plot, the CNDD strength of AM seedlings and EM saplings decreased with increasing soil PC1 but that of AM saplings became stronger with increasing soil PC1 (Figure 1f); the CNDD strength of only EM seedlings in the spruce-fir plot decreased with increasing light availability (Figure 1g).

We found a significant interaction effect between species abundance and mycorrhizal type on the strength of CNDD for seedlings in both plots (Table 1; Figure 2). AM species showed positive relationships between CNDD strength and species abundance, but EM species showed negative (or less positive) relationships (Figure 2a,c). For saplings in the spruce-fir plot, both AM and EM species had weak relationships between CNDD strength and species abundance (slope: −0.013 vs. 0.003, Figure 2d).

4 | DISCUSSION

In two old-growth temperate forests in Northeast China, we found that soil organic resources and light availability did not directly influence plant survival in the broad-leaved pine plot, but positively influenced EM species survival in the spruce-fir plot. AM species experienced stronger CNDD than EM species in both plots. In the spruce-fir plot, AM saplings suffered stronger CNDD along soil resource gradients, whereas CNDD strength decreased for AM seedlings and EM saplings. Surprisingly, for seedlings, there were different relationships between species abundance and CNDD strength for AM and EM species. These results provide novel insights about the influences of mycorrhizal type in driving the change of CNDD strength among species and the dependent nature of the relationship between species abundance and CNDD strength.

4.1 | Question 1: The influences of environmental resources and heterospecific neighbours on plant survival

We found that light availability strongly increased the survival of EM seedlings in the spruce-fir plot, which was consistent with previous studies that found light availability was an important factor promoting the recruitment of understorey plants in tropical forests (Augspurger, 1983; Comita et al., 2009; Hubbell, 1999). The fact that light availability did not appear to influence plant survival in the broad-leaved pine plot might result from the low amount of variation in light availability (Figure S4). Consistent with our predictions, EM saplings recruited better at locations with higher soil total N (mostly organic N) and organic C. These results support the hypothesis of the mycorrhizal-associated nutrient economy (Corrales et al., 2016; Phillips, Brzostek, & Midgley, 2013), which suggests that EM trees can use organic soil nutrients. EM species are inferior competitors at inorganic nutrient-rich locations compared to AM species because of the high absorption cost for soil nutrients via ectomycorrhizas (Raven, Lambers, Smith, & Westoby, 2018). Previous studies have found that light availability is an important factor for seedlings and that soil nutrients influence species distributions for plants at later life stages with DBH ≥ 1 cm (Comita et al., 2009; Condit, Engelbrecht, Pino, Perez, & Turner, 2013; John et al., 2007). We suggest that combining data across life stages can clarify how different mechanisms influence plant dynamics for different life stages.

We found the positive effect of heterospecific neighbours on plant survival, which was consistent with previous studies in tropical, subtropical and temperate forests (Chen et al., 2010; Comita et al., 2010; Johnson et al., 2014). The potential reason is that survival is greater in patches with rich resources that also contain a high density of heterospecific neighbours (Comita et al., 2009). In addition, the diversity and density of heterospecific neighbours can influence the prevalence, spread and impact of natural enemies (Keesing, Holt, & Ostfeld, 2006; Mitchell, Tilman, & Groth, 2002; Peters, 2003). Both processes (nutrient covariation and reduced enemies) might offset the negative effects of increasing shade or resource competition by increasing heterospecific neighbour density. These results suggest that this positive heterospecific effect on species coexistence can be a common feature of forest ecosystems.

4.2 | Question 2: Does the strength of CNDD vary between AM and EM species, and with soil resource and light availability change?

Our finding that CNDD was stronger for AM species than EM species was consistent with our prediction and recent findings of plant–soil feedback studies (Bennett et al., 2017; Dickie et al., 2014). These results were supported by the analyses at community (examining interspecific neighbour density) and species (correlating CNDD with conspecific abundance) levels (Table 1; Figure 1). However, EM species in these temperate forests did not always show a positive conspecific neighbour effect on CNDD as expected from previous studies (Connell & Lowman, 1989; Laliberte et al., 2015). Specifically, species-level analysis indicated that the difference of CNDD for AM and EM seedlings in the spruce-fir plot was not significant. In some plant–soil feedback experiments, AM and EM species have been observed to suffer similarly strong conspecific negative effects (Corrales et al., 2016). Therefore, whether this slightly stronger CNDD of AM species compared to EM species found in our study contributes to species richness variation among forests remains to be confirmed, but it is clear that multiple factors and context dependency are critical factors influencing CNDD for AM and EM species. Further studies at broad scales across different forests can help us to understand the generalization of our results (LaManna et al., 2017; Zhu, Comita, et al., 2015). Field experiments in natural conditions can also distinguish the effect of mycorrhizal type from other confounding factors.

We found that the strength of CNDD for EM seedlings decreased with increasing light availability, which was consistent with that of previous studies (Comita et al., 2009; Hood, Swaine, & Mason, 2004; McCarthy-Neumann & Ibáñez, 2013). For example, Hood et al. (2004) found the negative effect of conspecific adults on seedling survival disappeared at high irradiance. In Puerto Rico, Comita et al. (2009) found decreased CNDD under forest gaps after a hurricane event. Potential reasons were that faster plant growth (e.g. leaf production) with high light availability could offset the tissue damage from herbivores and pathogens (Hood et al., 2004; Norghauer et al., 2008). In addition, plants at high light conditions might have a higher concentration of defence chemicals (Shure & Wilson, 1993). We also found that the CNDD strength of AM and EM species in the spruce-fir plot varied along the soil environmental gradient, which was consistent with previous studies that soil environments could influence CNDD strength (Givnish, 1999; LaManna et al., 2016). Consistent with our predictions AM seedlings and EM saplings showed weaker CNDD strength at locations with higher soil organic nutrients (Corrales et al., 2016). Stronger CNDD for AM saplings along soil PC1 axis indicated that AM saplings might be influenced by soil factors differently than for AM seedlings and EM saplings, and especially sensitive to increased soil pH and moisture. Previous studies have suggested that soil environmental factors, such as pH and moisture, can influence soil microbial communities (Fierer & Jackson, 2006; Givnish, 1999; Prober et al., 2015). Future studies should collect microbial data though genetic sequencing to assess the potential varying microbial–plant interactions strength along local soil gradients. Furthermore, the environment-dependent CNDD change found in this and previous studies might result from different rates of predation, species trait turnover along environmental gradients or both (Givnish, 1999), we call for future research to distinguish these mechanisms.

4.3 | Question 3: How did the strength of CNDD vary with abundance among AM and EM species?

We found different relationships between abundance and CNDD strength for AM and EM species in both plots. Previous studies have found that there is a positive or negative relationship between species abundance and the CNDD strength in temperate and tropical forests (Comita et al., 2010; Johnson et al., 2012; LaManna et al., 2016; Zhu, Woodall, et al., 2015). In a recent global analysis, LaManna et al. (2017) found a positive relationship between species abundance and CNDD strength for tropical forests while a neutral or negative relationship for temperate forests. In our study, the positive relationship between AM species abundance and CNDD strength was consistent with that in tropical forests, which are dominated by AM species (Read, 1991; Steidinger et al., 2019), while EM species are more commonly found in temperate forests. The mixture of AM and EM species in temperate forests might cause a less positive relationship between species abundance and CNDD strength (LaManna et al., 2016, 2017; Zhu, Woodall, et al., 2015). This difference in the effect of AM and EM species on CNDD indicates that the stronger CNDD for AM species should result in greater maintenance of rare species than for EM species. However, the explicit mechanisms underlying these different relationships between CNDD and abundance are not clear. A recent study in a tropical forest suggested that the variation in pathogen resistance gene diversity among species contributed to the relationship between CNDD and species abundance (Marden et al., 2017). Whether the different relationships between CNDD and abundance for AM and EM species are explained by pathogen resistance gene diversity needs to be verified in the future. A recent study also suggested that a relationship between CNDD and abundance could be caused when the predictor (neighbour index here) is an error-prone proxy (Detto, Visser, Wright, & Pacala, 2019). However, this bias cannot explain the different relationships between CNDD and abundance for AM and EM species found in our study. First, as suggested by Detto et al. (2019), conspecific effects will decrease to neutral for AM and EM tree species with increased abundance; however, our results (e.g. for EM species in BKPF shown in Figure 2a,c) showed a clear trend that CNDD can be positive to negative or negative to positive from rare to common species. Second, if the error-prone proxy showed an effect on our analyses, the strength of this effect should be similar for AM and EM species; however, our results showed that only one species group of AM and EM species had a significant relationship between CNDD and abundance. Therefore, the different relationships between CNDD and species abundance for AM and EM species likely reflect different mechanisms underlying them. Finally, this result can be clarified further using experiments such as plant–soil feedback as conducted by Mangan et al. (2010).

5 | CONCLUSIONS

By analysing the demographic data of two early life stages (seedlings and saplings) in two different old-growth temperate forests in Northeast China, we found stronger CNDD for AM species than EM species consistent with previous predictions. We also found different relationships between CNDD strength and abundance for AM and EM species at the seedling stage. These results suggested that mycorrhizal type might play a more important role than previously thought, in influencing community structure and species richness across temperate and tropical forests.

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AUTHORS' CONTRIBUTIONS

F.J. and G.J. conceived the idea; F.J. analysed the data; F.J. and G.J. wrote the first manuscript with substantial comments from K.Z. and M.W.C. All authors revised the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.s7h44j145 (Jiang, Zhu, Cadotte, & Jin, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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