

# Mycorrhizal type influences plant density dependence and species richness across 15 temperate forests

FENG JIANG,<sup>1,2</sup> JAMES A. LUTZ <sup>3</sup> QINGXI GUO,<sup>1,4</sup> ZHANQING HAO,<sup>5</sup> XUGAO WANG,<sup>5</sup> GREGORY S. GILBERT,<sup>6</sup>  
 ZIKUN MAO,<sup>5,7</sup> DAVID A. ORWIG <sup>8</sup> GEOFFREY G. PARKER,<sup>9</sup> WEIGUO SANG <sup>10</sup> YANKUN LIU,<sup>11,12</sup>  
 SONGYAN TIAN,<sup>11,13</sup> MARC W. CADOTTE <sup>2,14</sup> AND GUANGZE JIN <sup>1,4,15</sup>

<sup>1</sup>Center for Ecological Research, Northeast Forestry University, Harbin 150040 China

<sup>2</sup>Department of Biological Sciences, University of Toronto Scarborough, Toronto, Ontario M1C 1A4 Canada

<sup>3</sup>Wildland Resources Department, Utah State University, Logan, Utah UT 84322 USA

<sup>4</sup>Key Laboratory of Sustainable Forest Ecosystem Management-Ministry of Education, Northeast Forestry University, Harbin 150040 China

<sup>5</sup>CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164 China

<sup>6</sup>Environmental Studies Department, University of California, 1156 High Street, Santa Cruz, California 95064 USA

<sup>7</sup>University of Chinese Academy of Sciences, Beijing 100049 China

<sup>8</sup>Harvard Forest, Harvard University, Petersham, Massachusetts MA 01366 USA

<sup>9</sup>Forest Ecology Group, Smithsonian Environmental Research Center, Edgewater, Maryland MD 21037 USA

<sup>10</sup>Institute of Botany, Chinese Academy of Sciences, Beijing 100093 China

<sup>11</sup>Heilongjiang Forestry Engineering and Environment Institute, Harbin 150040 China

<sup>12</sup>Key Laboratory of Forest Ecology and Forestry Ecological Engineering of Heilongjiang Province, Harbin, Heilongjiang 150040 China

<sup>13</sup>National Positioning observation Station of Mudanjiang Forest Ecosystem in Heilongjiang Province, Mudanjiang, Muling 157500 China

<sup>14</sup>Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario M5S 1A1 Canada

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**Abstract.** Recent studies suggest that the mycorrhizal type associated with tree species is an important trait influencing ecological processes such as response to environmental conditions and conspecific negative density dependence (CNDD). However, we lack a general understanding of how tree mycorrhizal type influences CNDD strength and the resulting patterns of species abundance and richness at larger spatial scales. We assessed 305 species across 15 large, stem-mapped, temperate forest dynamics plots in Northeastern China and North America to explore the relationships between tree mycorrhizal type and CNDD, species abundance, and species richness at a regional scale. Tree species associated with arbuscular mycorrhizal (AM) fungi showed a stronger CNDD and a more positive relationship with species abundance than did tree species associated with ectomycorrhizal (ECM) fungi. For each plot, both basal area and stem abundance of AM tree species was lower than that of ECM tree species, suggesting that AM tree species were rarer than ECM tree species. Finally, ECM tree dominance showed a negative effect on plant richness across plots. These results provide evidence that tree mycorrhizal type plays an important role in influencing CNDD and species richness, highlighting this trait as an important factor in structuring plant communities in temperate forests.

**Key words:** forest dynamics plot; Janzen-Connell hypothesis; mycorrhizal association; sapling recruitment; species abundance; species richness.

## INTRODUCTION

Determining the mechanisms underlying the patterns of species richness is an important and central question in ecology. Ecological, evolutionary, and historical processes all influence local species richness (Brown 2014). One important ecological process, conspecific negative

density dependence (CNDD), was described by Janzen (1970) and Connell (1971) to explain the coexistence and extraordinarily high diversity of tree species in tropical forests. The Janzen-Connell hypothesis suggests that plant performance (e.g., recruitment, growth, and survival) will decline when surrounded by a greater number of conspecific rather than heterospecific individuals, due to greater impacts of species-specific enemies and pathogens, as well as intense competition with conspecific adults (Packer and Clay 2000, Mangan et al. 2010, Bagchi et al. 2014). The CNDD effect results in the thinning of conspecific individuals near parent individuals and

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<sup>15</sup>E-mail: taxus@126.com

thus provides heterospecific species with a local competitive advantage and thus greater access to limited resources. Numerous studies have observed CNDD effects in both tropical and temperate forests (Augspurger 1983, 1984, Webb and Peart 1999, Harms et al. 2000), and more recently these CNDD effects have been linked to increases in species richness at local and regional scales (Harms et al. 2000, Johnson et al. 2012, LaManna et al. 2016, 2017). Thus, differences in the mechanisms influencing CNDD strength among forests should be reflected in differences in the richness of coexisting species, and we would expect stronger overall CNDD in species-rich forests than in low-diversity forests (Harms et al. 2000, Johnson et al. 2012). Here we ask how geographic patterns in tree mycorrhizal association might influence the strength of CNDD and species richness at a broad scale.

Plant functional traits are increasingly employed by ecologists to explain variation in CNDD strength among species with the hypothesis that species with more resource-conservative traits should be less sensitive to the impacts of enemies cultivated by conspecific individuals. Empirical studies conducted in tropical forests have found that shade tolerance (Kobe and Vriesendorp 2011), seed mass (Lebrija-Trejos et al. 2016), and growth rates (e.g., reflecting life-history traits; Zhu et al. 2018) of trees are related to variation in CNDD strength among species. However, these studies are focused on data from single plots at small spatial scales in tropical forests and do not relate these traits that covary with CNDD strength to broader species richness patterns, which should be the ultimate manifestation of CNDD. Besides traits, CNDD strength also differs between common and rare species, with strong CNDD being a potential cause of species rarity in tropical forests (Comita et al. 2010, Mangan et al. 2010, Chen et al. 2018). Conversely, recent studies find that common species show a similar or stronger CNDD than rare species in temperate forests (Zhu et al. 2015, LaManna et al. 2017). Therefore, clarifying the drivers underlying the different CNDD-abundance relationships across forest ecosystems is important to understand how the CNDD effect determines species abundances (Comita et al. 2010).

Recent experimental studies find that the strength of plant–soil feedbacks, which influences CNDD, is affected by plant mycorrhizal type (Liang et al. 2015, Cortois et al. 2016, Bennett et al. 2017). Mycorrhizal associations are expected to reduce CNDD because plant mycorrhizal fungi can help plants take up soil nutrients and water, making them less sensitive to the indirect effects of competition, as well as directly providing protection from pathogens (Sikes et al. 2009, van der Heijden and Horton 2009, Delavaux et al. 2017). Tree species in temperate regions mostly form associations with either arbuscular mycorrhizal (AM) fungi or ectomycorrhizal (ECM) fungi (Read 1991). While colonization by either AM or ECM fungi can decrease the strength of CNDD (Liang et al. 2015, Cortois et al.

2016, Bennett et al. 2017), ECM tree species are expected to experience a weaker CNDD than AM tree species because the root tissues of ECM trees can be physically protected by the encasing mantle of fungus (Marx 1972, Bennett et al. 2017). Some studies also provide evidence that ECM, but not AM fungi, produce antibiotic compounds that deter some pathogens (Marx 1972, Lambers et al. 2017). In addition, ECM trees can experience a greater benefit from extensive mycorrhizal fungal networks than do AM trees (van der Heijden and Horton 2009). Finally, ECM fungi usually exhibit greater host specificity than AM fungi, which can provide ECM tree species with a larger advantage for conspecific over competing heterospecific individuals, alleviating CNDD more for ECM than AM tree species (Schroeder et al. 2020). The expected stronger CNDD for AM tree species reinforces recent findings that belowground soil-borne pathogens can be more important causes of the CNDD effect compared to other natural enemies such as insect herbivores, mammals, and foliar pathogens (Packer and Clay 2000, Mangan et al. 2010, Bagchi et al. 2014). Our recent study conducted in the Liangshui plot found that AM tree species suffered a stronger CNDD and a more positive CNDD–abundance relationship than ECM tree species (Jiang et al. 2020). However, whether these results are general across temperate forests remains to be tested.

Given that strong CNDD can decrease local species abundance (Comita et al. 2010), the abundance of AM tree species should be lower than ECM tree species if AM tree species experience a stronger CNDD. On the other hand, weaker CNDD and higher mean species abundance for ECM tree species will allow fewer species to coexist and then result in lower plant richness in ECM tree-dominated communities. Alternatively, ECM tree-dominated forests can cause the accumulation of organic nutrients (usually accessible for ECM tree species), which can exclude many AM tree species and thus decrease plant richness (Soudzilovskaia et al. 2019, Tedersoo et al. 2020). However, we lack an understanding about the effect of mycorrhizal type on species abundance and plant richness at a broad scale.

In this study, we examine data from 305 plant species in 15 temperate forest dynamics plots across northeastern China, western USA, and the eastern USA, to explore whether the tree mycorrhizal type influences CNDD strength. We hypothesize that ECM tree species experience a weaker CNDD effect than AM tree species because of the better root tissue protection from pathogens for ECM tree species (Fig. 1). Second, we ask whether the tree mycorrhizal type mediates the relationship between CNDD strength and plant species abundance. We predict that ECM tree species show a less positive CNDD-abundance relationship, as found in temperate forests, compared to AM tree species, as found in tropical forests (Fig. 1; LaManna et al. 2017, Jiang et al. 2020). Third, we compare the species abundance distributions of AM and ECM tree species. We

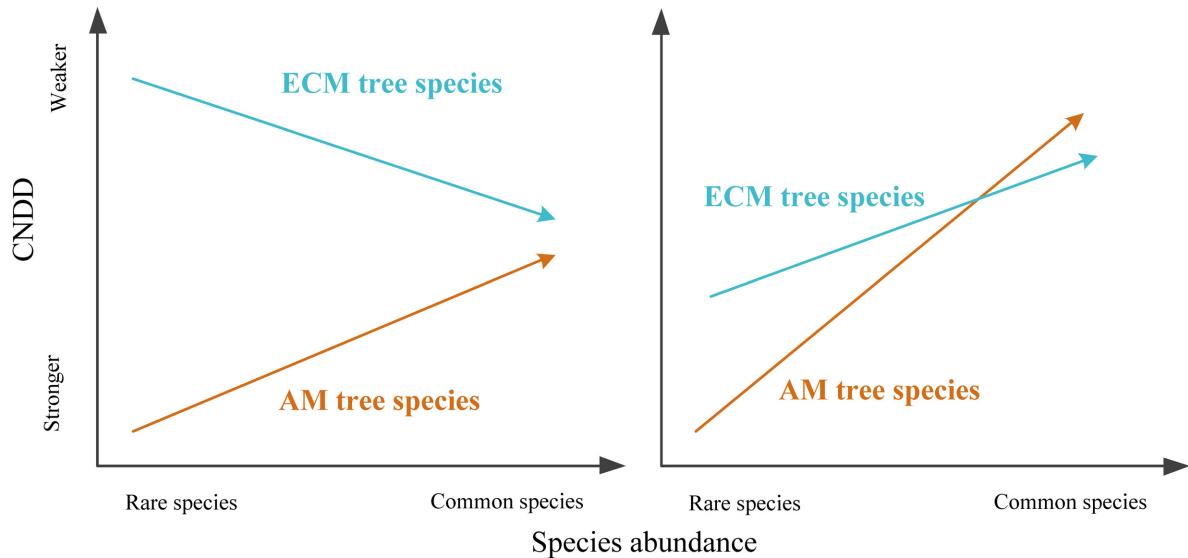


FIG. 1. Illustrations of expected differences of conspecific negative density dependence (CNDD) strength and CNDD–abundance relationships between AM and ECM tree species. Two panels show the generally stronger CNDD (i.e., lower CNDD estimate) of AM compared to ECM tree species. AM tree species are expected to show a more positive CNDD–abundance relationship than ECM tree species, which are expected to show a negative (left panel) or less positive relationship (right panel).

hypothesize that the mean abundance of AM tree species is lower than ECM tree species because of the stronger CNDD effect of AM tree species (Jiang et al. 2020). Finally, we compare how climate factors and ECM tree dominance explain species richness in temperate forests. We predict that communities with lower richness will show a higher ECM tree dominance, lower mean annual temperature and precipitation.

## MATERIALS AND METHODS

### Study sites

We used data from 305 plant species across 15 temperate forest dynamics plots from the CTFS-ForestGEO network and the CForBio network (Table 1). These plots were established following the standardized field methods of Condit (1998), which call for every free-standing woody stem  $\geq 1$  cm diameter at breast height (dbh) to be identified, tagged, measured, and mapped. These plots are located in three geographical regions (Appendix S1: Fig. S1): western USA (three plots), eastern USA (three plots), and northeastern China (nine plots). Plot sizes ranged from 6 ha (Santa Cruz, USA) to 35 ha (Harvard Forest, USA). Plot latitudes were between  $37.01^\circ$  N (Santa Cruz, USA) and  $49.48^\circ$  N (Shengshan, China), and mean elevations ranged from 8 m (Smithsonian Environmental Research Center, USA) to 3,104 m (Utah, USA). These plots exhibited a large range of elevation and evolutionary history reflected in their differences in species composition and richness. Two locations in northeastern China, Liangshui and Changbaishan, include more than one plot; different plots at each

location belong to forests with contrasting successional stages or vegetation types, which show different species compositions. Mantel tests for CNDD strength, CNDD–abundance slope, richness, and ECM tree dominance did not show strong spatial autocorrelations, so we treated these 15 plots as independent sites.

### Species mycorrhizal types

We determined mycorrhizal associations for each tree species using the FungalRoot data set (Soudzilovskaia et al. 2020). A total of 291 (94%) species were classified as AM or ECM tree species. We excluded the 14 ericoid mycorrhizae tree species from the analyses of CNDD strength but included them for calculating species richness. Because we hypothesized that ECM fungi can suppress soil-borne pathogens or protect root tissue against antagonists, directly, we regarded the six species that are known to be associated with both AM and ECM fungi as ECM tree species (Bennett et al. 2017). We also used the genus-level (74 tree species) and family-level (the mycorrhizal type most genera belong to, 8 tree species) mycorrhizal types provided by Soudzilovskaia et al. (2020) for those species with no available data. Finally, there are four tree species (*Acer mono*, *A. ukurunduense*, *Ulmus davidiana* var. *japonica*, and *U. laciniata*) that were identified as ECM tree species because at least two separate studies have found them to be colonized by ECM fungi (Guo et al. 2008, Shi et al. 2008, Sun et al. 2018), which were not consistent with the genus-level list of FungalRoot (Soudzilovskaia et al. 2020). However, identifying them as AM tree species did not change our results (Appendix S2). Information about species mycorrhizal

TABLE 1. Summary information for the 15 temperate forest dynamics plots in our study listed by increasing latitude.

Plot	Abbreviation	Latitude	Longitude	Elevation (m)	Size (ha)	Region	Citation
Santa Cruz	UCSC	37.01° N	122.08° W	323.0	6	western United States	Gilbert et al. (2010)
Utah	UT	37.66° N	112.85° W	3104.0	13.64	western United States	
Smithsonian Environmental Research Center	SERC	38.89° N	76.56° W	8.0	16	eastern United States	McMahon and Parker (2015)
Smithsonian Conservation Biology Institutes	SCBI	38.89° N	78.15° W	305.5	25.6	eastern United States	Bourg et al. (2013)
Donglingshan	DLS	39.96° N	115.43° E	1399.7	20	China	Liu et al. (2011)
Changbaishan-PB	CBSPB	42.37° N	128.00° E	794.5	24	China	Yuan et al. (2016)
Changbaishan-BK	CBSBK	42.38° N	128.08° E	800.7	25	China	Yuan et al. (2016)
Harvard Forest	HF	42.54° N	72.18° W	354.0	35	eastern United States	
Muling	ML	43.95° N	130.07° E	719.5	25	China	
Wind River	WR	45.82° N	121.96° W	368.6	25.6	western United States	Lutz et al. (2013)
Liangshui-BK	LSBK	47.18° N	128.88° E	466.5	9	China	Piao et al. (2013)
Liangshui-BK 2	LSBK2	47.22° N	128.87° E	418.0	10.4	China	
Liangshui-SP	LSSP	47.20° N	128.85° E	350.0	9.12	China	Pu et al. (2017)
Fenglin	FL	48.08° N	129.12° E	419.0	30	China	Liu et al. (2018)
Shengshan	SS	49.48° N	126.78° E	552.0	10.4	China	

Note: BK, broad-leaved Korean pine forest; PB, poplar–birch forest; SP, spruce–fir valley forest.

type and the number of plots in which each species is presented are shown in Appendix S1: Table S1.

### Statistical analysis

In our study, we calculated CNDD and the CNDD–abundance relationship following the methods of LaManna et al. (2017, 2018), except for some particular cases that we will describe. Because certain methods used in LaManna et al. (2017) have been questioned recently (Chisholm and Fung 2018, Hulsmann and Hartig 2018), we instead used the improved methods of LaManna et al. (2018). We quantified the effects of CNDD on sapling presence for each species in each plot within square quadrats using the Ricker model (Ricker 1954, LaManna et al. 2017). Because LaManna et al. (2017) found that the CNDD effect measured by the Ricker model was similar for  $10 \times 10$  m and  $20 \times 20$  m quadrats, we performed the analyses using  $10 \times 10$  m quadrats. The Ricker model with negative binomial error takes the following form:

$$S_i = A_i \exp(r + \text{CNDD} \times A_i + \text{HNDD}_{\text{adult}} \times a_i + \text{HNDD}_{\text{sap}} \times S_i)$$

$$S_i \sim \text{Negative binomial}(S_i, \gamma)$$

where  $S_i$  is the expected number of saplings for the focal species in quadrat  $i$ ;  $A_i$  is the observed number of conspecific adults for the focal species in quadrat  $i$  (see the detailed description of conspecific adults number below);  $r$  is the per capita recruitment rate for the focal species at low conspecific adult densities;  $a_i$  is the observed number of heterospecific adults in quadrat  $i$ ; and  $s_i$  is the observed number of heterospecific saplings

in quadrat  $i$  (LaManna et al. 2017). Thus, CNDD is the per capita effect of conspecific adult density on sapling presence for the focal species;  $\text{HNDD}_{\text{adult}}$  is the per capita effect of heterospecific adult density on sapling presence of the focal species;  $\text{HNDD}_{\text{sap}}$  is the per capita effect of heterospecific sapling density on sapling presence of the focal species, and  $\gamma$  is the negative binomial overdispersion parameter for the focal species (LaManna et al. 2017). For the original measurement of the CNDD effect, LaManna et al. (2017) used the raw number of conspecific adults and an offset to include the quadrats that had saplings but no adults. We instead used the distance-weighted abundance of adults to perform the Ricker model to avoid the probable bias from including those quadrats (LaManna et al. 2018). In addition, the adults in neighboring quadrats might also influence sapling recruitment in focal quadrats. Thus, the distance-weighted adult abundance was generated by weighting the conspecific adult number and incorporating that in neighboring quadrats (LaManna et al. 2018). This adapted method should reduce the bias caused by adding an offset for those quadrats that only had saplings. Specifically, we used Clark's 2dT dispersal kernel to represent the probability of sapling survival in one quadrat from the adult in another quadrat (Clark et al. 1999, Muller-Landau et al. 2008). We followed LaManna et al. (2018) and used the dispersal distance of 30 m as in the 2dT kernel, based on the average of more than 60 species observations in previous studies (Clark et al. 1999, Muller-Landau et al. 2008). Thus this distance-weighted approach could generate non-zero adult abundance and a larger weight for adults nearby. This method should make our results robust when accounting for other

factors, such as habitat specificity and adult/sapling ratio (LaManna et al. 2018).

The classification of life stages (saplings and adults) followed the methods of LaManna et al. (2017; Appendix S1: Table S2). Saplings were generally defined as individuals with a dbh < 10 cm. If this division resulted in fewer than 20% of individuals of a given species being classified as adults, then the threshold was lowered to 5 cm dbh for those species. Similarly, if a 5-cm dbh threshold for adults resulted in fewer than 20% of individuals of a given species being classified as adults, then the threshold was lowered to 2 cm dbh for those species. Such species were considered to represent small-stature understory species (e.g., shrubs and understory trees) that never or rarely reach 10 or 5 cm dbh, respectively (LaManna et al. 2017). Although there are other alternatives to define the ontogenetic stages (Lasky et al. 2015), this method makes our results comparable to those of LaManna et al. (2017, 2018).

We estimated the relationship between the strength of CNDD and tree species abundance using a linear model. Species abundance was calculated as the number of species per hectare and as species basal area divided by plot area ( $\text{m}^2/\text{ha}$ ). We used the log-transformed species abundance in the analyses and the CNDD strength of species was weighted by the inverse of the standard error of the estimate (i.e., weight =  $1/\text{SE}$  in the linear model; LaManna et al. 2018). We estimated the difference of mean and median CNDD effects for AM and ECM tree species across plots using the paired  $t$  test. Because there was only one AM tree species that had a CNDD estimate in the Utah plot, we exclude this plot from this analysis. We used a paired  $t$  test to test for different slopes of the relationships between number- and basal-area-based species abundance with the CNDD effects of AM and ECM tree species across plots. In this analysis, we only included the nine plots that had more than five AM and ECM tree species respectively, to reduce the statistical bias from low samples. While the method to estimate CNDD by LaManna et al. (2017) has been questioned recently (Damgaard 2019, Detto et al. 2019), the paired difference of CNDD and its relationship with abundance between groups of AM and ECM tree species cannot be largely biased by the method we used.

We compared the abundance distribution of AM and ECM tree species separately using the density plots (i.e., the kernel density estimate of the histogram on species abundance distribution; Wickham et al. 2019). Besides the visualization evaluation, we also compared the difference of the mean abundance for AM and ECM tree species across 15 plots using a paired  $t$  test.

We estimated the effects of mean annual temperature, mean annual precipitation, and ECM tree dominance on species richness across plots using linear mixed effect models using the lme4 package in R 3.5.0 (R Core Team 2018). Species richness was rarified for each plot based on the 8,234 individuals in Santa Cruz (lowest abundance of these 15 plots; LaManna et al. 2018). We

generated the ECM tree dominance of each plot using the proportion of ECM tree species number, individual number, and basal area. Climate data were generated from the WorldClim version 2.1 (Fick and Hijmans 2017). We also estimated the effects of temperature and precipitation on the proportion of ECM tree species using mixed effect models with a beta distribution using the glmmTMB package (Averill et al. 2018, Jo et al. 2019). In these mixed models of species richness and ECM tree dominance, we included regions (northeastern China, eastern United States, and western United States) as a random effect.

## RESULTS

AM tree species experienced a stronger CNDD effect than did ECM tree species for median estimates across plots (paired  $t$  test, mean difference of  $-0.151$ ,  $P = 0.047$ ; Fig. 2a), whereas the mean values showed no significant difference in CNDD between AM and ECM tree species (mean difference of  $-0.028$ ,  $P = 0.205$ ; Fig. 2b). The CNDD strength of AM tree species showed a larger variation than ECM tree species across plots (Fig. 2). AM tree species had a more positive relationship between CNDD and species abundance compared to ECM tree species, whether measured as a function of the individual number (paired  $t$  test, mean difference of  $0.047$ ,  $P = 0.007$ ; Fig. 2c) or basal area (mean difference of  $0.060$ ,  $P = 0.002$ , Fig. 2d).

For all 15 plots, species basal area distributions showed a clear separation between AM and ECM tree species (Fig. 3), which indicated that AM tree species were relatively rarer than ECM tree species. ECM tree species showed a mean basal area of  $1.951 \text{ m}^2/\text{ha}$  per species more compared to AM tree species across the 15 plots (paired  $t$  test,  $P < 0.001$ ; Appendix S1: Table S3). Individual stem number also showed a difference between AM and ECM tree species, but this difference was less pronounced than that of basal area (Appendix S1: Fig. S2). ECM tree species showed a mean stem number of 68.5 stems/ha more compared with AM tree species (paired  $t$ -test,  $P < 0.001$ ; Appendix S1: Table S3).

As we predicted, ECM tree dominance, measured as species number, individual number, or basal area, showed significant negative effects on total species richness (Table 2 and Fig. 4). The effects of climate on richness depended on the variables we used to calculate ECM tree dominance. Mean annual precipitation only showed a negative effect on richness in the ECM dominance model with species number (Model 1 in Table 2), and mean annual temperature only showed a positive effect on richness in the ECM dominance model using stem counts (Model 2 in Table 2). Finally, in the ECM dominance model using basal area, we found no effects of climate on richness (Model 3 in Table 2). ECM tree dominance was influenced by climate (Appendix S1: Table S4). The proportion of ECM tree species number

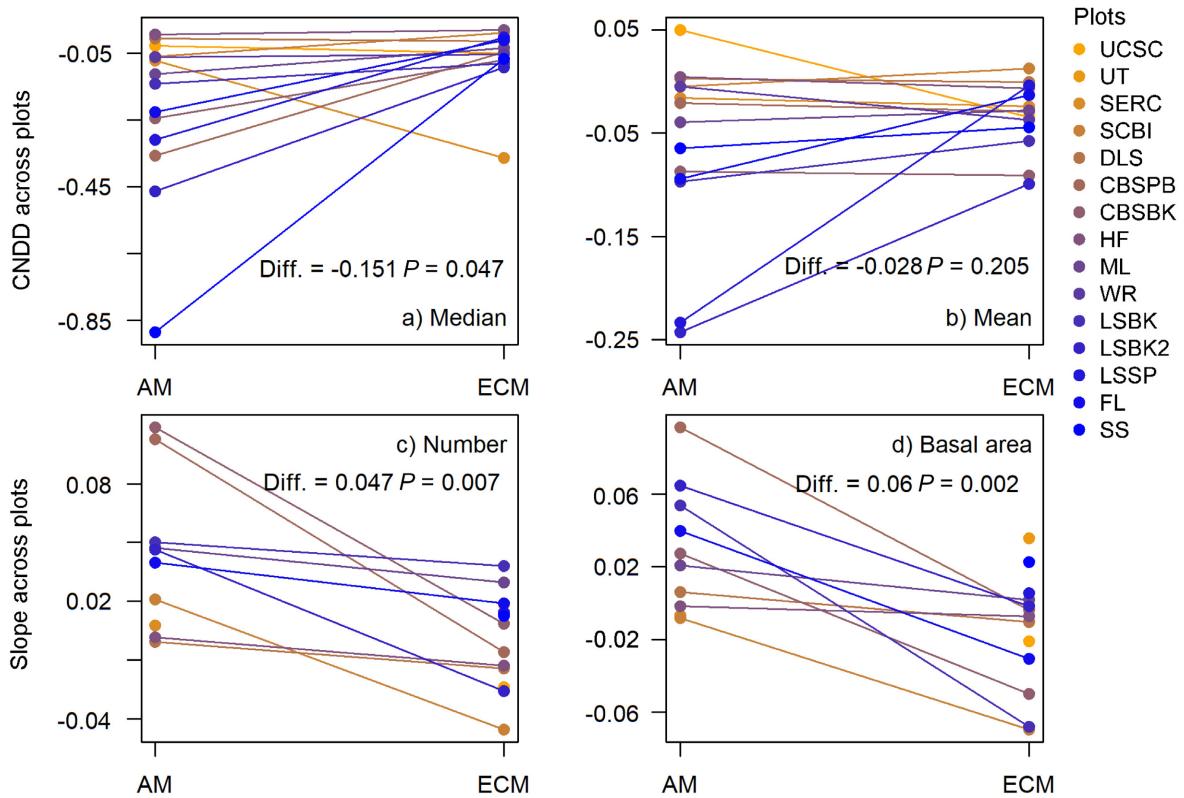


FIG. 2. The conspecific negative density dependence (CNDD) effect based on (a) median and (b) mean values and the slopes of relationships between (c) stem number-weighted, and (d) basal-area-weighted species abundance and CNDD strength in each plot. These results indicate that AM tree species experience stronger CNDD and more positive CNDD-abundance relationships than ECM tree species. The mean difference (Diff.) between AM and ECM tree species and  $P$  values from the paired  $t$  test are shown. Colors indicate increased latitude from orange to blue. The full name of plots can be found in Table 1.

was lower at high mean annual temperature and precipitation plots, and the proportion of ECM tree basal area was lower at high mean annual temperature. The proportion of ECM tree individuals was not affected by climates.

#### DISCUSSION

Our analyses from 15 temperate forest plots showed that tree mycorrhizal type can influence the strength of conspecific negative density dependence (CNDD), species abundance, and richness at a regional scale. CNDD was weaker for ECM than AM tree species, and ECM tree species exhibited a less positive relationship between CNDD strength and species abundance. Consequently, mean species abundance was higher for ECM than AM tree species. ECM tree dominance showed a stronger effect on species richness than climate variables across these plots. These findings suggest that tree mycorrhizal association is an important mediator of ecological processes and community structure in temperate forests.

#### *Different CNDD strength between AM and ECM tree species*

As predicted, AM tree species showed a stronger CNDD effect than did ECM tree species across these temperate forests. This result is partly in line with a recent plant–soil feedback experiment that finds ECM tree species show positive feedback and AM tree species negative feedback (Bennett et al. 2017), and the findings from natural forests that CNDD of AM tree species is stronger than ECM tree species (Chen et al. 2019, Jiang et al. 2020, Liang et al. 2020). However, our study provided evidence that this pattern might be generalizable across temperate forests at a broad spatial scale. Although the colonization of AM fungi can diminish the CNDD on tree performance (Liang et al. 2015), the positive effect is more prominent for ECM compared to AM fungi. Supporting this hypothesis, recent studies found that using fungicide and removing fungal hyphae showed a stronger negative influence on the growth and survival of ECM than AM tree species (Jia et al. 2020,

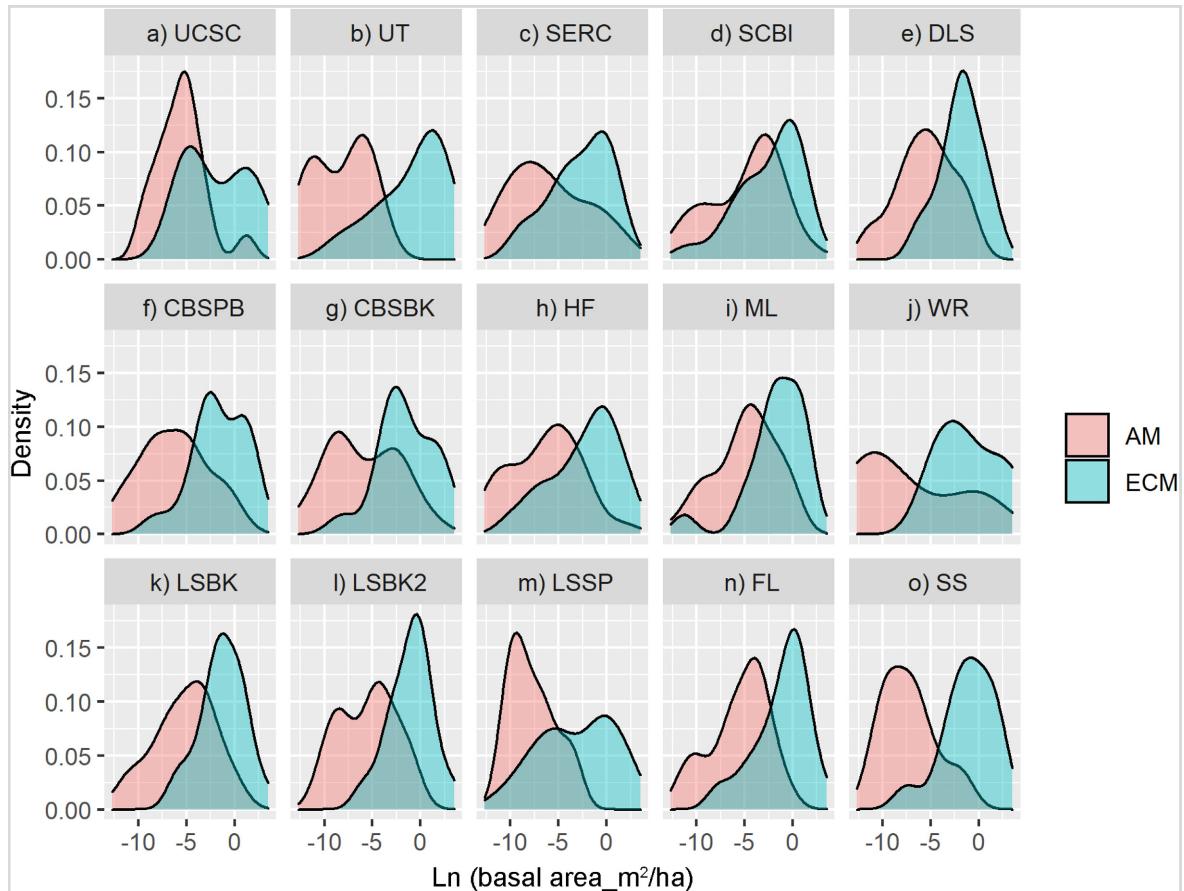


FIG. 3. Density plots of AM and ECM tree species for 15 forest dynamics plots, which indicate the basal area-based species abundance distributions. The density plots show distinct abundance distributions between tree mycorrhizal type groups, where AM tree species are generally rarer than ECM tree species. The species' basal-area-based abundance is ln-transformed. The full name of plots can be found in Table 1.

Liang et al. 2020). Multiple factors can contribute to the weaker CNDD of ECM tree species. For example, Bennett et al. (2017) suggested that the fungal mantle around root tissues of ECM tree species could protect them physically from the soil-borne antagonists, especially pathogens. Chen et al. (2019) found the pathogen accumulation rate around ECM tree species was lower than that observed for AM tree species. Other studies also used the ectomycorrhizal nitrogen economy (Corrales et al. 2016), positive plant–soil feedback (Laliberte et al. 2015), and the benefit of mycorrhizal networks for ECM plants (van der Heijden and Horton 2009, Simard et al. 2012) to explain the assembly of the predominantly ECM stands in tropical forests (Connell and Lowman 1989). While our results were consistent with the prediction that CNDD strength varied between AM and EM tree species, we acknowledge that the method of estimating CNDD based on single-census data using the Ricker model could bias our results and overestimate CNDD strength by not accounting for dispersal processes (but see LaManna et al. 2020). Our results point to the need for further studies that include demographic and

temporal data to generate a clearer understanding of the relationship between mycorrhizal type and CNDD (Jiang et al. 2020). Finally, given that many functional traits (e.g., leaf nitrogen content) might be related to tree mycorrhizal type (Averill et al. 2019), including these potentially important traits (e.g., defense traits) will be very valuable in determining the relative importance of different functional traits influencing the CNDD strength.

Across 15 temperate forest plots, CNDD strength based on either the median or mean values varied largely for AM tree species, whereas it was relatively consistent for ECM tree species. These results suggest that the CNDD strength of AM tree species is more strongly influenced by other external and variable factors compared to ECM tree species. The lack of a protective fungal mantle for AM tree species could make them more sensitive to the effects of conspecific neighbors, which, in the context of varying pathogen abundance, might lead to different CNDD strength than experienced by ECM tree species along with environment gradients. For example, Bennett and Klironomos (2018) found that

TABLE 2. Results of linear mixed effect models, where species richness is the response variable and ECM tree dominance, mean annual temperature (MAT), and mean annual precipitation (MAP) as predictors.

Variable	Estimate	<i>P</i>	$R^2_{\text{marginal}}$	$R^2_{\text{conditional}}$
<b>Model 1</b>				
Intercept	<b>41.62</b>	<b>0.017</b>	0.593	0.937
ECM tree dominance SP	<b>-10.02</b>	<b>&lt; 0.001</b>		
MAT	0.19	0.937		
MAP	<b>-6.98</b>	<b>0.002</b>		
<b>Model 2</b>				
Intercept	<b>36.58</b>	<b>0.041</b>	0.335	0.887
ECM tree dominance N	<b>-6.03</b>	<b>0.012</b>		
MAT	<b>5.52</b>	<b>0.043</b>		
MAP	-3.96	0.069		
<b>Model 3</b>				
Intercept	35.13	0.051	0.344	0.906
ECM tree dominance BA	<b>-6.64</b>	<b>0.035</b>		
MAT	4.56	0.148		
MAP	-1.10	0.558		

Notes: Dominance was estimated in three ways, by: species richness (SP); number of stems (N); and basal area (BA). MAT, mean annual temperature; MAP, mean annual precipitation. The bold fonts indicate significant relationships.

both seed mass and drought tolerance influenced the plant–soil feedback strength of both AM and ECM tree species, but that precipitation during the dry season only influenced the plant–soil feedback strength of AM tree species. Therefore, we expected that species with resource-acquisitive (e.g., higher leaf nitrogen and shorter lifespan) and less defense traits might experience stronger CNDD effects and that this CNDD strength

would be more sensitive to environmental change than for species with resource-conservative traits. However, this hypothesis needs to be tested further.

#### *Different CNDD–abundance relationships and abundance distributions between AM and ECM tree species*

Across all nine plots, AM tree species always showed a more positive relationship between CNDD and abundance than did ECM tree species, with abundance measured as either basal area or individual number. This result supported our recent findings by the demographic data in the Liangshui plot (Jiang et al. 2020). Therefore, the different proportions of tree mycorrhizal associations (i.e., AM vs. ECM) between tropical and temperate forests could partly explain why LaManna et al. (2017) found that the CNDD–abundance relationships changed from positive in tropical forests to neutral or negative in temperate forests. The different CNDD–abundance relationships also indicated that rare species (i.e., low local density) with AM associations experienced a stronger CNDD effect than did rare ECM tree species, and that common ECM tree species (i.e., high local density) might experience a similar or stronger CNDD effect than did common AM tree species (Fig. 1). This implies that the influence of CNDD on species abundance probably differed between tree mycorrhizal groups (Comita et al. 2010). The stronger CNDD and a more positive CNDD–abundance relationship for AM tree species result in a lower abundance of AM tree species than ECM tree species. Supporting this expectation, species abundance distributions (density plots in Fig. 3) for AM and ECM tree species were different, where AM tree species showed an overwhelming proportion of relatively rare species.

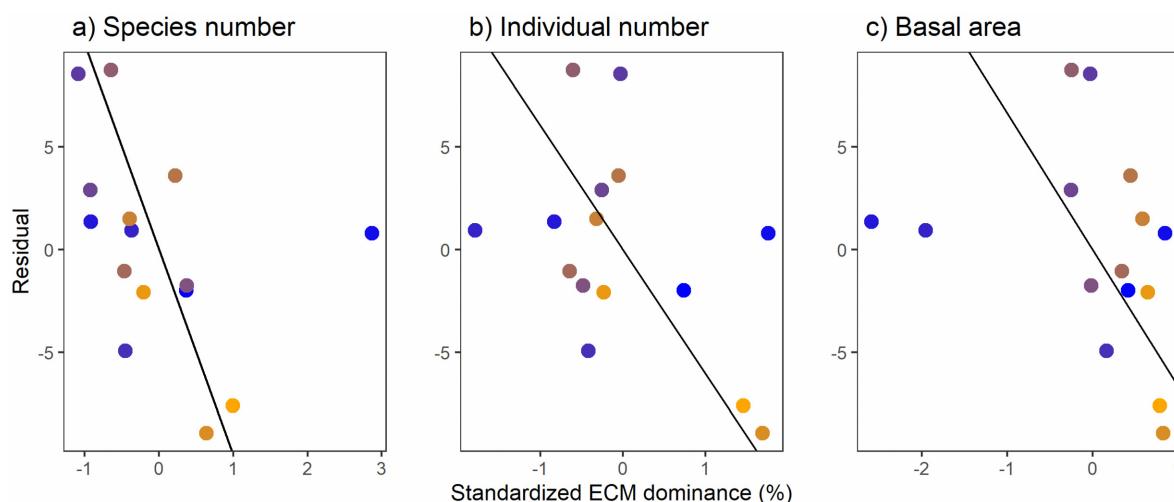


FIG. 4. The effects of ECM tree dominance on species richness (i.e., residuals after controlling the covariates of mean annual temperature, and mean annual precipitation). Species richness is decreased with increased ECM tree dominance. ECM tree dominance is calculated by species number, basal area, and individual stem number. Colors indicate increased latitude from orange to blue.

The different relationships between species abundance and CNDD strength for AM and ECM tree species also influenced our estimate of CNDD strength (Fig. 2a, b). The Ricker model used here excluded many rare species (mean 59.4% AM and 36.0% ECM tree species of species were excluded across all plots) to allow accurate CNDD estimates (LaManna et al. 2017). Therefore, the differential CNDD strength for rare AM and ECM tree species (Fig. 2c, d) should lead to different, but systematic influences on our estimate of CNDD strength by excluding many rare species in this analysis. For AM tree species, the mean and median values of CNDD strength should have been underestimated compared to the ECM tree species, because of the exclusion of rare species. Therefore, we would expect that in natural forests, the negative CNDD effect for AM tree species would be even stronger than for ECM tree species than shown in our results in Fig. 2a, b.

Finally, there are some limitations with our study that need to be recognized. The CNDD estimate in our study is a statistical one and species densities can be influenced by multiple processes and is likely biased by the method that uses snapshot data (Detto et al. 2019). However, the observed differences of CNDD strength and CNDD–abundance relationship between AM and ECM tree species cannot be caused by the general biases described by Detto et al. (2019) because the biases would influence the estimate of AM and ECM tree species similarly and thus should not influence CNDD differences between both groups. In addition, LaManna et al. (2020) recently re-evaluated (e.g., more iterations in labeling null models) the analyses of Detto et al. (2019) and found the Ricker model used here could provide a relatively reliable estimate of CNDD. Finally, the long-term tracking of individual recruitment, growth, and survival, as well as experiments, will be helpful to clarify these mechanisms underlying the patterns found in our study (e.g., Wang et al. 2020), and our analyses provide the first step to explore the role of mycorrhizal type on species abundance and community richness at the broad scale.

#### *The factors driving species richness pattern across temperate forests*

Many studies have suggested that ECM tree association could be an important factor leading to low diversity monodominant tropical forests (Connell and Lowman 1989, Laliberte et al. 2015, Corrales et al. 2016). Our results provide evidence that species richness is, in fact, lower in ECM-dominated temperate forests, which is consistent with recent suggestions that ECM dominance can decrease plant richness (Mao et al. 2019, Tedersoo et al. 2020). The weaker CNDD of ECM tree species could result in a community with relatively few but abundant ECM tree species, which might explain the low diversity in ECM-dominated forests. The effect of ECM tree dominance on species richness is important for understanding changing forest dynamics. A recent

study found that the proportion of ECM tree basal area has declined by more than 15% in some regions in the eastern United States over the past three decades (Jo et al. 2019). Therefore, we should expect that species richness should increase in these regions. In our models, ECM tree dominance showed a stronger effect on richness than mean annual temperature and precipitation. This reflects the importance of biotic interactions (i.e., CNDD) on species richness, although it is important to note the non-independence between biotic and abiotic interactions (Cadotte and Tucker 2017), and specifically, increased ECM tree dominance should also strengthen abiotic pressure because of the accumulation of organic material (Tedersoo et al. 2020). ECM dominance increased with decreasing temperature and precipitation, and so climate appears to affect richness indirectly through these competitive interactions (Jo et al. 2019, Soudzilovskaia et al. 2019, Steidinger et al. 2019). Although our results indicated a strong effect of ECM tree dominance on plant richness in temperate forests, a global evaluation of the ECM tree dominance-plant diversity relationship is still needed.

#### CONCLUSIONS

Using tree inventory data of 15 forest dynamics plots across temperate regions in the United States and China, we explored the roles of the type of mycorrhizal association of tree species on CNDD strength, species abundance, and richness. Compared to ECM tree species, AM tree species generally showed a stronger CNDD effect and a more positive CNDD–abundance relationship. This was associated with a greater proportion of rare species for AM trees compared to relatively fewer, but dominant, ECM tree species in these forests. Our study highlights the important role of the tree mycorrhizal type on community structure and diversity in temperate forests.

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#### LITERATURE CITED

- Augsburger, C. K. 1983. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40:189.
- Augsburger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712.

- Averill, C., J. M. Bhatnagar, M. C. Dietze, W. D. Pearse, and S. N. Kivlin. 2019. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proceedings of the National Academy of Sciences USA* 116:23163–23168.
- Averill, C., M. C. Dietze, and J. M. Bhatnagar. 2018. Continental-scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. *Global Change Biology* 24:4544–4553.
- Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T. Lewis. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506:85–88.
- Bennett, J. A., and J. Klironomos. 2018. Climate, but not trait, effects on plant–soil feedback depend on mycorrhizal type in temperate forests. *Ecosphere* 9:e02132.
- Bennett, J. A., H. Maherali, K. O. Reinhart, Y. Lekberg, M. M. Hart, and J. Klironomos. 2017. Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* 355:181–184.
- Bourg, N. A., W. J. McShea, J. R. Thompson, J. C. McGarvey, and X. Shen. 2013. Initial census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large Forest Dynamics Plot. *Ecology* 94:2111–2112.
- Brown, J. H. 2014. Why are there so many species in the tropics? *Journal of Biogeography* 41:8–22.
- Cadotte, M. W., and C. M. Tucker. 2017. Should environmental filtering be abandoned? *Trends in Ecology & Evolution* 32:429–437.
- Chen, L., N. G. Swenson, N. Ji, X. Mi, H. Ren, L. Guo, and K. Ma. 2019. Differential soil fungus accumulation and density dependence of trees in a subtropical forest. *Science* 366:124–128.
- Chen, Y., P. Jia, M. W. Cadotte, P. Wang, X. Liu, Y. Qi, X. Jiang, Z. Wang, W. Shu, and P. Thrall. 2018. Rare and phylogenetically distinct plant species exhibit less diverse root-associated pathogen communities. *Journal of Ecology* 107:1226–1237.
- Chisholm, R. A., and T. Fung. 2018. Comment on “Plant diversity increases with the strength of negative density dependence at the global scale”. *Science* 360:eaar4685.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475–1494.
- Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:330–332.
- Condit, R. 1998. *Tropical forest census plots*. Springer, Berlin, Germany.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in P. J. den Boer and Gradwell, G. R., editors. *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Connell, J. H., and M. D. Lowman. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. *American Naturalist* 134:88–119.
- Corrales, A., S. A. Mangan, B. L. Turner, and J. W. Dalling. 2016. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. *Ecology Letters* 19:383–392.
- Cortois, R., T. Schröder-Georgi, A. Weigelt, W. H. van der Putten, G. B. De Deyn, and M. van der Heijden. 2016. Plant-soil feedbacks: role of plant functional group and plant traits. *Journal of Ecology* 104:1608–1617.
- Damgaard, C.. 2019. A critique of the space-for-time substitution practice in community ecology. *Trends in Ecology & Evolution* 34:416–421.
- Delavaux, C. S., L. M. Smith-Ramesh, and S. E. Kuebbing. 2017. Beyond nutrients: a meta-analysis of the diverse effects of arbuscular mycorrhizal fungi on plants and soils. *Ecology* 98:2111–2119.
- Detto, M., M. D. Visser, S. J. Wright, and S. W. Pacala. 2019. Bias in the detection of negative density dependence in plant communities. *Ecology Letters* 22:1923–1939.
- Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37:4302–4315.
- Gilbert, G. S., E. Howard, B. Ayala-Orozco, M. Bonilla-Moheno, J. Cummings, S. Langridge, I. M. Parker, J. Pasari, D. Schweizer, and S. Swope. 2010. Beyond the tropics: forest structure in a temperate forest mapped plot. *Journal of Vegetation Science* 21:388–405.
- Guo, D., M. Xia, X. Wei, W. Chang, Y. Liu, and Z. Wang. 2008. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. *New Phytologist* 180:673–683.
- Liu, Haifeng, Liang Li, and Weiguo Sang. 2011. Species composition and community structure of the Donglingshan forest dynamic plot in a warm temperate deciduous broad-leaved secondary forest, China. *Biodiversity Science* 19:232–242.
- Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495.
- Hulsmann, L., and F. Hartig. 2018. Comment on “Plant diversity increases with the strength of negative density dependence at the global scale”. *Science* 360:eaar2435.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Jia, S., X. Wang, Z. Yuan, F. Lin, J. Ye, G. Lin, Z. Hao, and R. Bagchi. 2020. Tree species traits affect which natural enemies drive the Janzen–Connell effect in a temperate forest. *Nature Communications* 11:286.
- Jiang, F., K. Zhu, M. W. Cadotte, and G. Jin. 2020. Tree mycorrhizal type mediates the strength of negative density dependence in temperate forests. *Journal of Ecology* 108:2601–2610.
- Jo, I., S. Fei, C. M. Oswalt, G. M. Domke, and R. P. Phillips. 2019. Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. *Science Advances* 5: eaav6358.
- Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. Conspecific negative density dependence and forest diversity. *Science* 336:904–907.
- Kobe, R. K., and C. F. Vriesendorp. 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecology Letters* 14:503–510.
- Laliberte, E., H. Lambers, T. I. Burgess, and S. J. Wright. 2015. Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist* 206:507–521.
- LaManna, J. A. et al 2017. Plant diversity increases with the strength of negative density dependence at the global scale. *Science* 356:1389–1392.
- LaManna, J. A. et al 2018. Response to Comment on "Plant diversity increases with the strength of negative density dependence at the global scale". *Science* 360:eaar5245.
- LaManna, J. A., S. A. Mangan, and J. A. Myers. 2020. Conspecific negative density dependence and why its study should not be abandoned. *bioRxiv*, In press. <https://www.biorxiv.org/content/10.1101/2020.05.11.089334v1>

- LaManna, J. A., M. L. Walton, B. L. Turner, and J. A. Myers. 2016. Negative density dependence is stronger in resource-rich environments and diversifies communities when stronger for common but not rare species. *Ecology Letters* 19:657–667.
- Lambers, H., F. Albornoz, L. Kotula, E. Laliberté, K. Ranathunge, F. P. Teste, and G. Zemunik. 2017. How below-ground interactions contribute to the coexistence of mycorrhizal and non-mycorrhizal species in severely phosphorus-impooverished hyperdiverse ecosystems. *Plant and Soil* 424:11–33.
- Lasky, J. R., B. Bachelot, R. Muscarella, N. Schwartz, J. Forero-Montaña, C. J. Nyctch, N. G. Swenson, J. Thompson, J. K. Zimmerman, and M. Uriarte. 2015. Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology* 96:2157–2169.
- Lebrija-Trejos, E., P. B. Reich, A. Hernandez, and S. J. Wright. 2016. Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest. *Ecology Letters* 19:1071–1080.
- Liang, M., D. Johnson, D. F. R. P. Burslem, S. Yu, M. Fang, J. D. Taylor, A. F. S. Taylor, T. Helgason, and X. Liu. 2020. Soil fungal networks maintain local dominance of ectomycorrhizal trees. *Nature Communications* 11:2636.
- Liang, M., X. Liu, R. S. Etienne, F. Huang, Y. Wang, and S. Yu. 2015. Arbuscular mycorrhizal fungi counteract the Janzen-Connell effect of soil pathogens. *Ecology* 96:562–574.
- Liu, Q., L. Bi, G. Song, Q. Wang, and G. Jin. 2018. Species-habitat associations in an old-growth temperate forest in northeastern China. *BMC Ecology* 18:20.
- Lutz, J. A., A. J. Larson, J. A. Freund, M. E. Swanson, and K. J. Bible. 2013. The importance of large-diameter trees to forest structural heterogeneity. *PLoS ONE* 8:e82784.
- Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466:752–755.
- Mao, Z., A. Corrales, K. Zhu, Z. Yuan, F. Lin, J. Ye, Z. Hao, and X. Wang. 2019. Tree mycorrhizal associations mediate soil fertility effects on forest community structure in a temperate forest. *New Phytologist* 223:475–486.
- Marx, D. H. 1972. Ectomycorrhizae as biological deterrents to pathogenic root infections. *Annual Review of Phytopathology* 10:429–454.
- McMahon, S. M., and G. G. Parker. 2015. A general model of intra-annual tree growth using dendrometer bands. *Ecology and Evolution* 5:243–254.
- Muller-Landau, H. C., S. J. Wright, O. Calderón, R. Condit, and S. P. Hubbell. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology* 96:653–667.
- Packer, A., and K. Clay. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281.
- Piao, T., L. S. Comita, G. Jin, and J. H. Kim. 2013. Density dependence across multiple life stages in a temperate old-growth forest of northeast China. *Oecologia* 172:207–217.
- Pu, X., Y. Zhu, and G. Jin. 2017. Effects of local biotic neighbors and habitat heterogeneity on seedling survival in a spruce-fir valley forest, northeastern China. *Ecology and Evolution* 7:4582–4591.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Read, D. J. 1991. Mycorrhizas in ecosystems. *Experientia* 47:376–391.
- Ricker, W. E. 1954. Stock and Recruitment. *Journal of the Fisheries Research Board of Canada* 11:559–623.
- Schroeder, J. W., A. Dobson, S. A. Mangan, D. F. Petticord, and E. A. Herre. 2020. Mutualist and pathogen traits interact to affect plant community structure in a spatially explicit model. *Nature Communications* 11:2204.
- Shi, W., Z. Q. Wang, J. L. Liu, and G. U. Jia-Cun. 2008. Fine root morphology of twenty hardwood species in maershan natural secondary forest in northeastern china. *Journal of Plant Ecology* 32:1217–1226.
- Sikes, B. A., K. Cottenie, and J. N. Klironomos. 2009. Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. *Journal of Ecology* 97:1274–1280.
- Simard, S. W., K. J. Beiler, M. A. Bingham, J. R. Deslippe, L. J. Philip, and F. P. Teste. 2012. Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biology Reviews* 26:39–60.
- Soudzilovskaia, N. A., S. Vaessen, M. Barcelo, J. He, S. Rahimlou, K. Abarenkov, M. C. Brundrett, S. I. F. Gomes, V. Merckx, and L. Tedersoo. 2020. FungalRoot: global online database of plant mycorrhizal associations. *New Phytologist* 227:955–966.
- Soudzilovskaia, N. A., P. M. van Bodegom, C. Terrer, M. V. Zelfde, I. McCallum, M. Luke McCormack, J. B. Fisher, M. C. Brundrett, N. C. de Sa, and L. Tedersoo. 2019. Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nature Communications* 10:5077.
- Steidinger, B. S. et al 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* 569:404–408.
- Sun, T., S. E. Hobbie, B. Berg, H. Zhang, Q. Wang, Z. Wang, and S. Hattenschwiler. 2018. Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition. *Proceedings of the National Academy of Sciences USA* 115:10392–10397.
- Tedersoo, L., M. Bahram, and M. Zobel. 2020. How mycorrhizal associations drive plant population and community biology. *Science* 367:eaba1223.
- van der Heijden, M. G. A., and T. R. Horton. 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology* 97:1139–1150.
- Wang, Y., M. W. Cadotte, J. Chen, X. Mi, H. Ren, X. Liu, M. Yu, J. Zhang, and K. Ma. 2020. Neighborhood interactions on seedling survival were greatly altered following an extreme winter storm. *Forest Ecology and Management* 461:117940.
- Webb, C. O., and D. R. Peart. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80:2006–2017.
- Wickham, H. et al 2019. Welcome to the Tidyverse. *Journal of Open Source Software* 4:1686.
- Yuan, Z., S. Wang, A. Gazol, J. Mellard, F. Lin, J. Ye, Z. Hao, X. Wang, and M. Loreau. 2016. Multiple metrics of diversity have different effects on temperate forest functioning over succession. *Oecologia* 182:1175–1185.
- Zhu, K., C. W. Woodall, J. V. D. Monteiro, and J. S. Clark. 2015. Prevalence and strength of density-dependent tree recruitment. *Ecology* 96:2319–2327.
- Zhu, Y., S. A. Queenborough, R. Condit, S. P. Hubbell, K. P. Ma, and L. S. Comita. 2018. Density-dependent survival varies with species life-history strategy in a tropical forest. *Ecology Letters* 21:506–515.

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