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ARTICLE

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Experimental and observational evidence of negative conspecific density dependence in temperate ectomycorrhizal trees

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Abstract

Conspecific negative density dependence (CNDD) promotes tree species diversity by reducing recruitment near conspecific adults due to biotic feedbacks from herbivores, pathogens, or competitors. While this process is well-described in tropical forests, tests of temperate tree species range from strong positive to strong negative density dependence. To explain this, several studies have suggested that tree species traits may help predict the strength and direction of density dependence: for example, ectomycorrhizal-associated tree species typically exhibit either positive or weaker negative conspecific density dependence. More generally, the strength of density dependence may be predictably related to other species-specific ecological attributes such as shade tolerance, or the relative local abundance of a species. To test the strength of density dependence and whether it affects seedling community diversity in a temperate forest, we tracked the survival of seedlings of three ectomycorrhizal-associated species experimentally planted beneath conspecific and heterospecific adults on the Prospect Hill tract of the Harvard Forest, in Massachusetts, USA. Experimental seedling survival was always lower under conspecific adults, which increased seedling community diversity in one of six treatments. We compared these results to evidence of CNDD from observed sapling survival patterns of 28 species over approximately 8 years in an adjacent 35-ha forest plot. We tested whether species-specific estimates of CNDD were associated with mycorrhizal association, shade tolerance, and local abundance. We found evidence of significant, negative conspecific density dependence (CNDD) in 23 of 28 species, and positive conspecific

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density dependence in two species. Contrary to our expectations, ectomycorrhizal-associated species generally exhibited stronger (e.g., more negative) CNDD than arbuscular mycorrhizal-associated species. CNDD was also stronger in more shade-tolerant species but was not associated with local abundance. Conspecific adult trees often have a negative influence on seedling survival in temperate forests, particularly for tree species with certain traits. Here we found strong experimental and observational evidence that ectomycorrhizal-associating species consistently exhibit CNDD. Moreover, similarities in the relative strength of density dependence from experiments and observations of sapling mortality suggest a mechanistic link between negative effects of conspecific adults on seedling and sapling survival and local tree species distributions.

KEYWORDS
arbuscular mycorrhizae, conspecific negative density dependence, diversity, ectomycorrhizae, mycorrhizal fungi, saplings, seedling survival, shade tolerance, temperate forest

INTRODUCTION

Conspecific negative density dependence (CNDD), whereby population growth rates decline with increasing population density due to a negative feedback on recruitment or survival, is a critical mechanism that can support local tree diversity (Chesson, 2000). One example of CNDD is known as the Janzen-Connell hypothesis. This hypothesis suggests that specialized enemies, such as herbivores or pathogens, reduce the recruitment of offspring nearby parent trees in highly diverse tropical forests (Connell, 1971; Janzen, 1970). This process hinders the formation and preservation of monodominant stands, and the resulting spatial distribution of trees supports the coexistence of many species. It is broadly assumed that CNDD can operate as a stabilizing mechanism to support diverse communities; however, very few studies of density dependence have quantified the effects of CNDD on diversity. Theoretical work (Chesson, 2000) and observational studies (Johnson et al., 2012; LaManna et al., 2017) have linked higher species diversity to stronger CNDD, but experimental evidence of this link remains rare (Bagchi et al., 2014; Levine & HilleRisLambers, 2009). In particular, few studies show whether and how CNDD can produce greater diversity over ecological time.

Strong CNDD is pervasive in the tropics (Comita et al., 2014; Terborgh, 2012), making it an attractive potential driver of latitudinal patterns of tree diversity. However, there is also increasing support for CNDD as a mechanism that influences tree communities in temperate forests (Jiang et al., 2020, 2021; Johnson et al., 2012, 2014; McCarthy-Neumann & Kobe, 2010; Ramage et al., 2017). While this work illustrates the potential for CNDD to drive population dynamics in temperate systems, there is wide variation in the strength of CNDD among tree species (Bennett et al., 2017; Johnson et al., 2014) and along environmental gradients (LaManna et al., 2016; Smith & Reynolds, 2015).

Plant functional traits provide one potential means for predicting differences in the strength of density dependence among species (Bennett et al., 2017; Brown et al., 2019; Jia et al., 2020). In particular, functional traits that confer resistance to attack from herbivores or pathogens, the primary drivers of CNDD, may be associated with the strength of density dependence. For tree species, the type of mycorrhizal association, either arbuscular (AM) or ectomycorrhizal (ECM), has been associated with patterns in CNDD. In previous studies, ECM-associated tree species tend to exhibit weaker or even positive density dependence (Bennett et al., 2017; Chen et al., 2019; Jiang et al., 2020, 2021; Qin et al., 2021), possibly due to the greater protection from soil pathogens that the fungi confer to their tree host (Bennett et al., 2017; Corrales et al., 2016). Indeed, recent work suggests that while both AM and ECM fungal networks may partially counteract conspecific negative density-dependent mortality, ECM fungi may be more effective than AM fungi at countering the mortality agents that typically drive CNDD patterns (Liang et al., 2021). However, in other studies, the strength of CNDD was similar in AM and ECM associated tree species (Jia et al., 2020).

In addition to mycorrhizal association, shade tolerance has been associated with species-specific patterns in CNDD; shade-tolerant tree species are less susceptible to microbial attack due to conservative life history strategies, suggesting that they should exhibit weaker CNDD (McCarthy-Neumann & Kobe, 2008; Song et al., 2021).

However, shade-tolerant species are also more likely to be infected by necrotrophic fungal pathogens, which kill their hosts and feed on the decaying tissue, while shade-intolerant species are more likely to be infected by biotrophs, which feed on live tissue without killing their hosts (García-Guzmán & Heil, 2014). Indeed, low-light areas of the forest where shade-tolerant seedlings are likely to be found typically contain higher pathogen loads (Augspurger & Kelly, 1984). Therefore, despite their conservative allocation strategy, shade-tolerant species may be more affected by CNDD, if the pathogens driving density dependence are more abundant and virulent. Indeed, the few explicit tests of how shade tolerance relates to CNDD in temperate forests are conflicting: shade-tolerant species may be more (Jia et al., 2020) or less (Brown et al., 2019) likely to exhibit CNDD than shade-intolerant species within temperate forests.

Additionally, temperate species do not always follow the same patterns as tropical species: in the tropics, rare species typically exhibit stronger CNDD, which helps maintain diverse communities with many rare species (Comita et al., 2010; Mangan et al., 2010; Xu et al., 2015). In temperate forests, the pattern between CNDD and local abundance is less clear: while some studies show that rare species exhibit stronger negative density feedbacks (Johnson et al., 2012), others show the opposite pattern, with more abundant species exhibiting stronger CNDD (LaManna et al., 2016; Zhu, Woodall, et al., 2015). Quantifying the strength of CNDD across multiple co-occurring species can help to detangle sources of variability in CNDD studies and is needed to generalize the importance of CNDD in temperate, as well as tropical, forests.

In this study, we used a combination of experimental and observational approaches to ask how prevalent CNDD is in a temperate forest, with particular emphasis on whether ECM-associated species commonly exhibit CNDD. We used a seedling planting experiment to test whether the species identity (conspecific versus heterospecific) of neighboring mature trees influences seedling survival in ECM-associating tree species, and whether CNDD effects on ECM seedling mortality alter seedling community diversity. We then used the survival of naturally occurring saplings to quantify the strength of CNDD across 28 co-occurring woody species. Finally, we asked whether mycorrhizal type, shade tolerance, and local abundance predict variation in the strength of CNDD among species.

MATERIALS AND METHODS

Site description

This study took place on the Prospect Hill tract of the Harvard Forest (HF) located in Petersham, Massachusetts. This forest is in the northern-hardwood–hemlock–white-pine transition zone (42.530° N, 72.190° W, 300 m elevation above sea level). The mean annual temperature and precipitation are 7.1°C and 1066 mm, respectively. For the observational part of our study, we utilized the 35-ha HF ForestGEO plot where every woody stem >1 cm diameter at breast height (DBH) has been identified to species, tagged, geolocated, and its diameter measured (Orwig, Aylward, et al., 2022). The experimental portion of our study took place in plots that are adjacent to the ForestGEO plot (Appendix S1: Figure S1).

Experimental methods

We selected three ECM species, *Pinus resinosa*, *Quercus rubra*, and *Pinus strobus*, which represent a range in other plant traits, including shade tolerance (Niinemets & Valladares, 2006). All three species are common at our study site, although the population of *P. resinosa* were planted there in the early 1900s and now consist of both planted and naturally regenerated individuals. In the forest adjacent to the mapped ForestGEO plot, we located 30 experimental plots (Appendix S1: Figure S1). Each circular plot had a diameter of 20 m and was centered on a focal *P. resinosa*, *Q. rubra*, or *P. strobus* with a DBH greater than 28 cm such that there were 10 plots centered on each of the three species. We chose locations where none of the other study species occurred; for example, in a plot centered on a *Q. rubra* tree, there were no *P. resinosa* or *P. strobus*. We used these plots to plant seedlings of each of the three species beneath both conspecific and heterospecific "adult" trees (defined as trees with a DBH greater than 28 cm).

In addition to these three species, we also planted *Picea abies* seedlings. *P. abies* are present at this site but not native to the area. Like *P. resinosa*, *P. abies* was commonly planted in the early 1900s and now naturally regenerate at this site. We included this species in the seedling planting primarily to increase the diversity of our planted seedling communities. *P. abies* was chosen as it was available from the same nursery as the three experimental species, was a similar size and age to the other three species, associates with the same type of mycorrhizal fungi, and is a common species at this study site (Table 1). We purchased bare-root seedlings in May 2019 that were grown outdoors at the New Hampshire State Nursery in Boscawen, NH. *P. abies* and *Q. rubra* seedlings were 2 years old at planting while *P. strobus* and *P. resinosa* were 3 years old.

Experimental planting

Within each plot, we constructed two subplots, 1 × 1 m, into which the seedlings were planted. Subplots were

TABLE 1 Characteristics of species included in the analysis of CNDD for saplings from two censuses.

Species	Total abundance	Mycorrhizal association	Median DBH	Species code
Viburnum dentatum	53	AM	1.1	Vibude
Viburnum lantanoides	96	AM	1.2	Vibual
Viburnum cassinoides	1846	AM	1.3	Vibuca
Lindera benzoin	83	AM	1.4	Lindbe
Ilex verticillata	1266	AM	1.5	Ilexve
Amelanchier laevis	354	AM	1.4	Amella
Crataegus spp.	259	AM	1.5	Cratsp
Acer pennsylvanicum	425	AM	1.8	Acerpe
Nemopanthus mucronatus	377	AM	1.8	Nemomu
Castanea dentata	1020	ECM	2.2	Castde
Hamamelis virginiana	3578	AM	2.45	Hamavi
Fagus grandifolia	4362	ECM	3.0	Fagugr
Sorbus americana	74	AM	3.25	Sorbam
Tsuga canadensis	24,222	ECM	5.4	Tsugca
Betula alleghaniensis	5015	ECM	5.6	Betula
Betula lenta	1545	ECM	8.6	Betule
Betula populifolia	123	ECM	9.5	Betupo
Fraxinus americana	197	AM	10.1	Fraxam
Nyssa sylvatica	193	AM	10.6	Nysssy
Acer rubrum	12,967	AM	11.9	Acerru
Prunus serotina	266	AM	13.3	Prunse
Betula papyrifera	590	ECM	15.35	Betupa
Picea abies	911	ECM	16.5	Piceab
Picea rubens	106	ECM	18.15	Piceru
Pinus strobus	2149	ECM	22.1	Pinust
Quercus rubra	4407	ECM	28.6	Querru
Quercus velutina	227	ECM	30.4	Querve
Pinus resinosa	789	ECM	32.8	Pinure

Note: Species used in the planting experiment are in boldface type. AM, species that typically associate with arbuscular mycorrhizae; ECM, species that typically associate with ectomycorrhizae (mycorrhizal associations determined according to the FungalRoot database [Soudzilovskaia et al., 2020]). The operational cutoff between saplings and adults was the median DBH for species with DBH < 12.7 cm, and 12.7 cm for the remaining species (see *Methods*). Abbreviations: CNDD, conspecific negative density dependence; DBH, diameter at breast height.

located approximately 1 m apart and within 2 m of the base of the trunk of the focal tree, and subplot type ("even" or "uneven") was randomly assigned. In each subplot, we planted 20 seedlings. To test whether CNDD promotes diversity, and whether the effects of CNDD on diversity were dependent on the initial diversity of the community, in one subplot (even), we planted five individuals of each species. In the other (uneven), we planted 11 individuals of the same species as the focal tree (conspecifics), and three of each of the heterospecific species. Thus, the two subplots had the same total number of seedlings, but the conspecific seedling was either at the same density as each of the heterospecifics, or at a much higher density, as would be more likely under natural regeneration conditions. We used a standard, randomized planting design such that the spatial arrangement of conspecific seedlings relative to heterospecific seedlings was consistent across all subplots of the same type (Appendix S1: Figure S2). All 1200 seedlings were planted between 31 May and 7 June 2019.

Before planting, each subplot was cleared of aboveground stems greater than 20 cm in height with hand clippers, so that competition with herbaceous plants and ferns was minimized across all plots. Resprouts from clipped vegetation, primarily ferns, were rare and were re-clipped when they emerged. Next, leaf litter was removed and set aside. A wooden 1-m^2 frame with grid lines at 20-cm intervals, creating a 5×5 grid, was then placed on the ground to serve as the planting guide (Appendix S1: Figure S2). Using an auger (7.6 cm diameter), we dug holes in 20 locations in each subplot. Removed soil was placed on a tarp and homogenized. The individually tagged seedlings were then planted and covered by the homogenized soil. Throughout the planting process, the roots of the seedlings were kept moist with water in spray bottles. After the 20 seedlings were planted, the subplot was flagged, watered, and covered by leaf litter.

Within each 10-m radius plot, we also identified and measured the diameter of each tree >2.5 cm DBH as well as the distance of each stem to the seedling subplots. To account for possible differences in light environment that could influence seedling survival, we took a hemispherical photo using a fisheye lens from the center of each plot to capture the light environment. Photographs were taken between 7:30 and 9:30 AM to avoid overexposure. Images were analyzed with WINSCANOPY (Regent Instruments Inc., Quebec, Canada) to calculate the gap fraction (a metric of canopy openness) of each of the 30 plots.

Seedlings were tracked individually throughout the summer. After all seedlings had been in the ground for 2 weeks, seedlings were censused for survival and their initial heights were measured to account for any differences in survival that were due to variation in initial seedling size. Seedlings were censused again after an additional 10 weeks for their final survival status. Seedlings were presumed dead if their needles had all turned brown (conifers) and if they had no remaining leaves (*Q. rubra*). We continued to monitor all seedlings, regardless of status, for the full 12 weeks of the experiment.

Statistical analysis of experimental seedling mortality

We removed 17 individual seedlings from the analysis (1 *P. strobus*, 13 *Q. rubra*, and 3 *P. resinosa*) that died within the first 2 weeks, presumably due to transplant shock rather than as a result of our experimental treatments. For each seedling species, we calculated the overall odds ratio of survival under conspecific and heterospecific focal adults, such that an odds ratio <1 indicates a lower chance of survival beneath a conspecific adult. We then fit a binomial mixed model using the R package *lme4* (Bates et al., 2015) to predict seedling survival as a function of the adult species identity of the plot (based on whether the focal tree in the plot was a conspecific or heterospecific), initial seedling height, subplot type (even or uneven), and canopy gap fraction, with the plot as a random effect. For the *P. abies* seedlings, we fit the same model without the adult identity variable as all seedlings were growing in heterospecific plots.

To account for possible effects of both the focal tree in each plot (our experimental treatment), and also the effects of neighboring trees, we used the full 314-m^2 plot to calculate a neighborhood competition index (NCI) following Canham et al. (2004) and modified as in other similar analyses (Bai et al., 2012; Magee et al., 2020; Zhang et al., 2017). For each plot, we calculated NCI values to compare the effects of conspecific and heterospecific adults within 10 m as follows:

$$\mathrm{NCI}_{\mathrm{conspecific}} = \sum \frac{\mathrm{DBHconspecific}}{\mathrm{distance}} \tag{1}$$

$$\mathrm{NCI}_{\mathrm{heterospecific}} = \sum \frac{\mathrm{DBHheterospecific}}{\mathrm{distance}}. \tag{2}$$

We then used the results of the first set of models (using the identity of the focal adult tree as our treatment) to inform which parameters to include in the second set (including the NCI as our treatment), including any parameter from the first model set with $p < 0.1$. We ran a second set of binomial mixed models that did not include adult identity, but did include $\mathrm{NCI}_{\mathrm{conspecific}}$, $\mathrm{NCI}_{\mathrm{heterospecific}}$, and any of the parameters identified from model set 1 with plot ID as a random variable.

Finally, we tested whether the observed seedling mortality affected the diversity of the seedling community. To do this, we calculated the overall survival of each seedling subplot. We then simulated random mortality at that level for each subplot, by randomly assigning a survival code to each seedling until the overall observed mortality of the plot was met. We ran this simulation 1000 times for each subplot. As all our experimental plots were planted with the same species richness (4), we used the Shannon's Equitability Index (J) (Begon et al., 1996)

$$J = \frac{-\sum_{i=1}^{S} p_i \times \log(p_i)}{\log(\mathrm{SR})} \tag{3}$$

where p_i is the proportion of each species and SR is the species richness. We used this metric to assess whether the diversity we observed at the end of our experiment differed from what the diversity would be if mortality had occurred randomly with respect to species identity of the seedlings.

Observational sapling survival

To determine whether naturally regenerating saplings exhibited a similar pattern to those we experimentally planted, as well as to quantify density dependence in a wider variety of naturally occurring saplings, we used the subset of the HF ForestGeo plot that has been re-censused as of 2021. The first census occurred from June 2010 through January 2014. The re-census occurred from May 2018 to September 2019. Individual trees were revisited and their survival status was recorded.

Using the initial census, we calculated the same metrics of neighborhood competition as for our experimental plots (Equations (1) and (2)) for each individual stem in the forest. We used a maximum distance of 20 m. We only assessed patterns for species with more than 10 individual saplings and more than 20 individual adults. To account for differences in average size of each species as well as maximize the number of species included in our analysis, we defined individuals as saplings if their DBH was less than the median DBH of that species, up to a maximum cutoff of 12.7 cm DBH, and individuals greater than the median as "adults" (Table 1). To confirm that our results were not sensitive to the choice of methods, we re-ran the CNDD estimation using 15 m maximum distance to neighbors and 25 m maximum distance to neighbors. We also re-ran the CNDD estimation using an alternative method to distinguish between saplings and adults: using a DBH cutoff of either 3, 8, or 12.7 cm for species with a median DBH < 5 cm, >5 but <12.7 cm, and >12.7 cm, respectively, as a common concern with CNDD analyses is that the distinction can be arbitrary (Detto et al., 2019). Results of from these alternative analyses can be found in Appendix S1: Figure S3.

To calculate the overall effect of neighborhood on sapling mortality, we fit a generalized linear mixed-effects model (GLMM) with binomial errors and a complementary log–log link to assess the relative importance of factors determining individual sapling mortality using the R package *lme4* (Bates et al., 2015). To account for differences in the length of time between the two censuses for individual trees, we used a log(time) offset of the number of years between the two censuses (range: 5.25–9.5 years) for each individual stem as in Johnson et al. (2017). The DBH of the sapling at the first census was included as a covariate (Johnson et al., 2017). Both NCI_{con} and NCI_{het} were also included in the model to account for the overall effects of competition as well as the specific effects of conspecific neighbors. All three variables were scaled by subtracting the overall mean and dividing by two SDs (Gelman, 2008). Species was included as a random effect, and both NCI_{con} and NCI_{het} were estimated with random slopes for each species. The model coefficients for each species of NCI_{con} and NCI_{het} were used to estimate $\text{CNDD}_{\text{coeff}}$, such that $\text{CNDD}_{\text{coeff}}$ was the difference between the model coefficient for NCI_{con} and NCI_{het}.

To further account for the possibility that our $\text{CNDD}_{\text{coeff}}$ estimate could be produced by underlying spatial or other factors not accounted for in this simple statistical model, we additionally performed null model testing (LaManna et al., 2021). Using the same model structure as above, we recalculated values of NCI_{con} and NCI_{het} for each sapling after randomizing the observed proportion of the total NCI that was conspecific: effectively keeping the total neighborhood density the same as the observed, but randomizing the density of conspecific neighbors. We also kept the observed values of DBH, and the mortality outcome. We re-ran this null model 1000 times, and estimated $\text{CNDD}_{\text{null}}$ as the difference between the mean NCI_{con} and NCI_{het} coefficients using the same model structure as described above. We then calculated the final estimate of CNDD for each species (CNDD_{est}) as follows:

$$\text{CNDD}_{\text{est}} = -\left(\text{CNDD}_{\text{coeff}} - \text{CNDD}_{\text{null}}\right) \tag{4}$$

where $\text{CNDD}_{\text{coeff}}$ is the estimate based on the difference between the model coefficients for NCI_{con} and NCI_{het} using the observed data, and $\text{CNDD}_{\text{null}}$ is the estimate based on the difference between the model coefficients for NCI_{con} and NCI_{het} using the randomized NCI_{con}. The negative sign is to make the estimate more interpretable: as all the models were run as hazard functions, with survival coded as 0 and mortality coded as 1, taking the inverse of the estimate mreans that a negative CNDD_{est} indicates a species exhibited stronger CNDD, while a positive CNDD_{est} indicates that greater conspecific adult density was associated with a higher likelihood of survival. For each species, we took the mean across the 1000 iterations of the null model randomization, and we considered our estimate of CNDD significant if the 95% confidence interval of CNDD_{est} did not cross zero. We also confirmed that the mean null model coefficients were significantly different from the coefficients based on the observed values for each species using a paired *t*-test. Full visualization of the null model distribution for each species relative to CNDD_{obs} can be found in Appendix S1: Figure S4.

Finally, we compared this species-level estimate of CNDD at this site to species-level plant traits. We assigned each species a dominant mycorrhizal association based on values from FungalRoot (Soudzilovskaia et al., 2020) and a shade-tolerance value based on Niinemets and Valladares (2006). We then used a linear model to estimate the effects of mycorrhizal association, shade tolerance, and local abundance (log transformed) on CNDD$_{est}$. Because the species in this study varied dramatically in their typical and mature size, and because AM species were generally smaller (Table 1), we also included the median DBH of the species as a predictor in the model. To ensure that our results were robust to model structure, we also iteratively checked all possible two-way interactions of the four species-level predictors (mycorrhizal association, shade tolerance, local abundance, and median DBH); none were significant, so we report the results of the additive model. All analyses were performed in R version 4.0.5.

RESULTS

Experimental seedling survival

All seedling species had higher survival rates when planted beneath heterospecific trees than when planted under conspecific trees (Figure 1, Table 2). *Q. rubra*, which had the lowest overall mortality, also exhibited the least difference in survival (88.5% under conspecifics, 96.7% under heterospecifics, odds ratio: 0.91). *P. resinosa* had the highest overall mortality, with only 3.8% seedling survival beneath conspecifics and 15.4% beneath heterospecifics (odds ratio 0.25). *P. strobus* showed the greatest absolute difference in survival between conspecifics (73.9%) and heterospecifics (94.4%) and the strongest effect of the identity of the neighboring adult tree (Table 2).

Results were qualitatively similar when comparing the density of adult trees in the surrounding community, as measured by NCI, to seedling survival. All four species exhibited declining survival with increasing conspecific adult density (NCI$_{con}$), but all but *Q. rubra* also exhibited declining survival in response to increasing heterospecific density (NCI$_{het}$) as well (Table 3). When comparing the NCI$_{con}$ coefficient estimates and SE with those of NCI$_{het}$, only *P. strobus* exhibited CNDD; in other words, the coefficient estimate for the negative effect of conspecific neighbors did not overlap with the weaker negative effect of heterospecific neighbors (Table 3).

None of the seedling species exhibited survival differences between the even and unevenly planted plots (Table 2). In the evenly planted seedling subplots, which began the experiment with perfectly even communities ($J = 1$), observed mortality caused a decline in seedling diversity; however, this decline in diversity was indistinguishable from simulated random mortality (Figure 2a). The seedling diversity in the unevenly planted subplots either stayed the same or, in the case of the unevenly planted subplots beneath *P. resinosa* adults, substantially increased (Figure 3b). In those plots, the seedling community had changed from an equitability index (J) of 0.85 (uneven) to 0.98 at the end of the experiment: almost perfectly even, and far higher than the diversity predicted if the mortality had been random. These locations

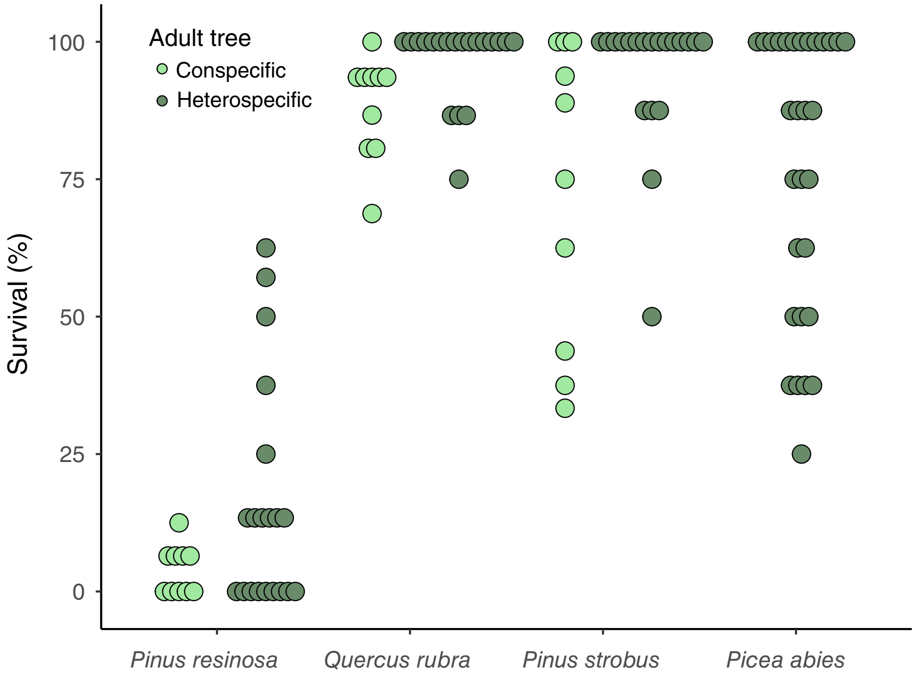

FIGURE 1 Plot-level survival of each of the four seedling species when planted beneath a conspecific (pale green) or a heterospecific (dark green) adult tree. Seedlings from both subplots in each 20 m diameter plot are included in each point, such that each point represents survival of 40 planted seedlings. $N = 30$ plots for each species.

TABLE 2 Coefficient estimates (SE in parentheses) from binomial mixed-effects model of seedling survival for each of the four seedling species.

Seedling species	Conspecific adult	Seedling height	Gap fraction	Subplot type (uneven)
Pinus resinosa	−1.96 (0.86)*	−0.10 (0.04)*	0.18 (0.12)	0.25 (0.46)
Quercus rubra	−1.38 (0.57)*	−0.01 (0.03)	0.00 (0.09)	0.07 (0.47)
Pinus strobus	−2.76 (1.09)*	−0.06 (0.03)*	−0.11 (0.17)	−0.25 (0.41)
Picea abies	Not applicable	−0.05 (0.04)	0.22 (0.13)**	−0.43 (0.38)

Note: In all models, plot was included as a random effect.
*$p < 0.05$; **$p < 0.1$.

TABLE 3 Coefficient estimates (SE in parentheses) from binomial mixed effects model of survival for each of the four experimental seedling species using the quantitative variables $\mathrm{NCI}_{\mathrm{con}}$ and $\mathrm{NCI}_{\mathrm{het}}$.

Seedling species	$\mathrm{NCI}_{\mathrm{con}}$	$\mathrm{NCI}_{\mathrm{het}}$	Seedling height	Gap fraction	Subplot type (uneven)
Pinus resinosa	−0.032 (0.013)*	−0.016 (0.015)	−0.097 (0.042)*	0.145 (0.120)	0.282 (0.463)
Quercus rubra	−0.015 (0.015)	0.005 (0.010)	−0.009 (0.031)	−0.045 (0.098)	0.029 (0.469)
Pinus strobus	−0.061 (0.021)*	−0.022 (0.016)	−0.061 (0.030)*	−0.105 (0.152)	−0.283 (0.407)
Picea abies	−0.021 (0.029)	−0.023 (0.012)**	−0.042 (0.040)	0.170 (0.118)	−0.426 (0.379)

Note: In all models, plot was included as a random effect.
Abbreviations: $\mathrm{NCI}_{\mathrm{con}}$, neighborhood competition index conspecific; $\mathrm{NCI}_{\mathrm{het}}$, neighborhood competition index heterospecific.
*$p < 0.05$. **$p < 0.1$.

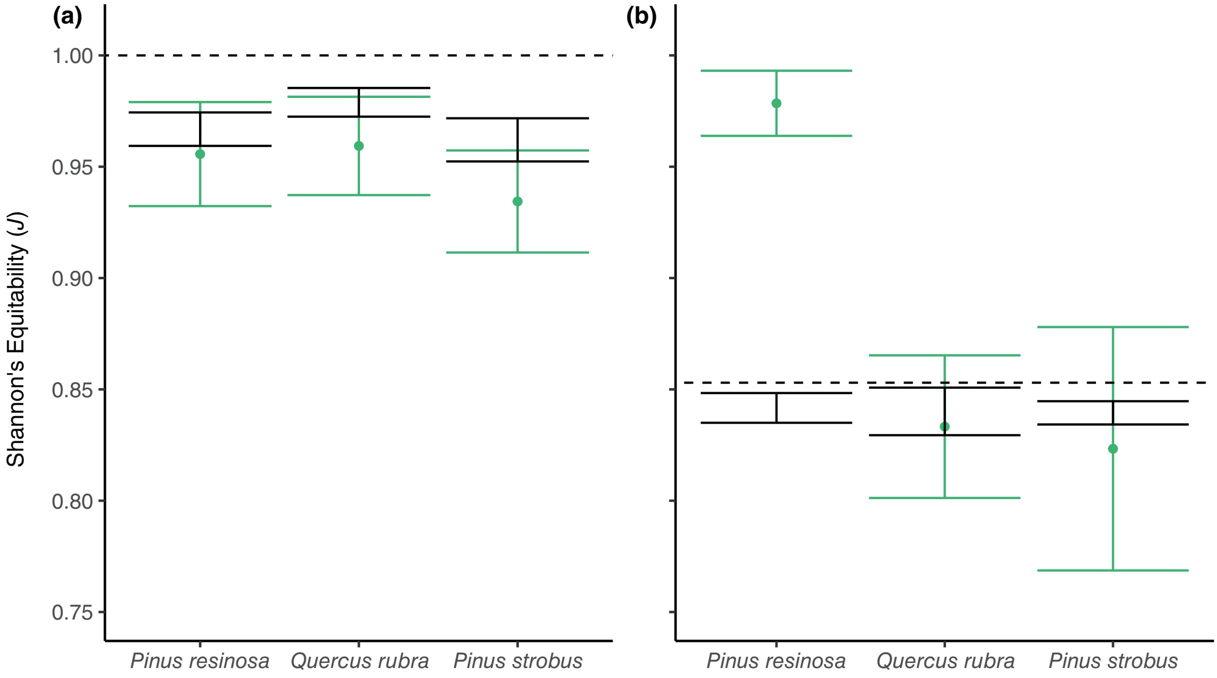

FIGURE 2 Mean Shannon's equitability index (*J*), a metric of community evenness, at the end of the experiment (green) relative to 1000 model simulations of equivalent level of mortality occurring randomly (black). Values for (a) seedling subplots that were planted with equal numbers of each seedling species and (b) subplots that were planted with the conspecific seedling dominating, averaged across the 10 replicated adult trees. Error bars represent 95% confidence intervals. Dashed lines represent Shannon's equitability index of the community as it was initially planted.

experienced the highest total mortality (59.7%), and also the highest difference between conspecific seedling mortality (96%) and heterospecific seedling mortality (12.6%).

Experimental seedling survival was also affected by factors other than the local neighborhood. For example, *P. strobus* and *P. resinosa* seedlings that were initially

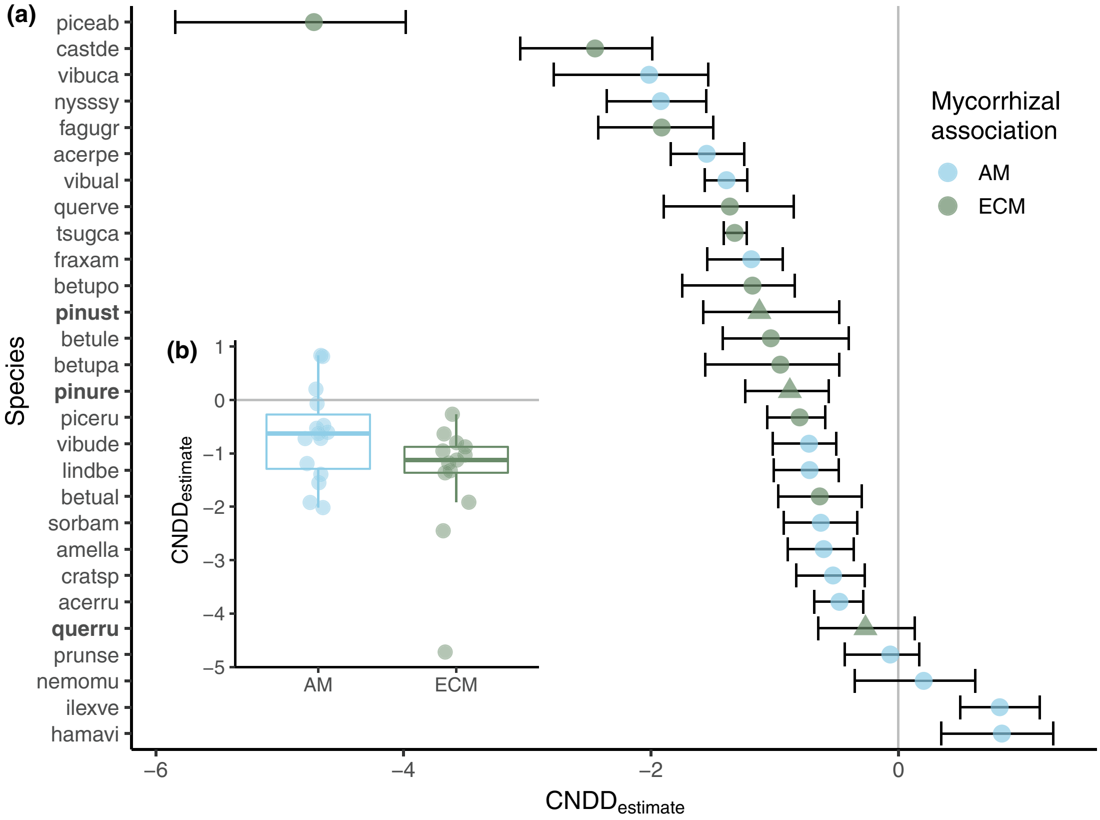

FIGURE 3 (a) Estimates of conspecific negative density dependence (CNDD) for saplings of 28 tree species at the Harvard Forest. Error bars represent the total range of estimates using 1000 iterations of the null model (see *Observational sapling survival* in the Materials and Methods section for details). Blue points represent species that typically associate with arbuscular mycorrhiza (AM), green points represent species that typically associate with ectomycorrhizae (ECM). (b) Box plot of all estimates by mycorrhizal type, showing the significant difference between AM tree species and ECM tree species. Species used in the seedling experiment are in bold. Species codes as in Table 1. Boxes represent 25th to 75th percentiles. Whiskers extend to 1.5 times the interquartile range. Thick midline represents the median.

taller had slightly lower survival. *P. abies* was the only species whose survival increased with increasing light availability as measured by the gap fraction (Table 2).

Observed sapling survival

Overall, the probability of sapling survival in our observational CNDD analysis decreased with increasing local density of conspecifics (Table 4). Sapling survival was also positively associated with sapling DBH and negatively associated with local density of heterospecifics; however, the effect of these drivers was considerably lower than the effect of conspecific neighbors (Table 4). The strength of CNDD varied substantially among species. In 23 of the 28 species used in our analysis, sapling survival decreased significantly with increasing conspecific density, whereas in two species, sapling survival increased with increasing conspecific density (Figure 3).

Tree species that typically associate with ECM fungi were much more likely to exhibit CNDD than those that typically associated with AM fungi (Figure 3b, Table 5); 12 of the 13 ECM-associated species in this analysis exhibited significant CNDD. In contrast, 4 of the 15 AM-associated species either did not exhibit

TABLE 4 Overall standardized coefficient estimates from generalized linear mixed-effects model predicting sapling mortality as a function of initial size and local tree community.

Predictor	Estimate (SE)	*p*
(Intercept)	−1.867 (0.249)	<0.001
DBH	−0.805 (0.036)	<0.001
NCI_{het}	−0.106 (0.147)	0.468
NCI_{con}	0.948 (0.271)	<0.001

Note: NCI_{con} and NCI_{het} represent local densities of conspecific trees and heterospecific trees, respectively. Species was included as a random effect with NCI_{con} and NCI_{het} both estimated with a random slope for each species. Individual random effects coefficients for each species can be found in Appendix S1: Table S1, overall random effects can be found in Appendix S1: Table S2.

Abbreviations: DBH, diameter at breast height; NCI_{con}, neighborhood competition index conspecific; NCI_{het}, neighborhood competition index heterospecific.

significant CNDD or instead were more likely to survive when growing in areas with greater densities of conspecifics (e.g., had significantly positive estimates of CNDD). AM-associated saplings also had a somewhat lower overall survival (61%) than ECM-associated saplings (72%). Although there are a similar number of AM and ECM associating species at this site, ECM species tend to have higher abundance and overall about 66% of saplings are ECM-associating species. In addition, the AM-associating species at this site tend to be smaller (Table 1). However, the median DBH of the species was not associated with stronger CNDD (Table 5).

TABLE 5 Coefficient estimates from linear model predicting the strength of the species level estimate of CNDD as a function of four species level characteristics: mycorrhizal association, shade tolerance, local abundance, and median DBH of the species at this site.

Predictor	Estimate (SE)	*p*
(Intercept)	−0.250 (1.00)	0.805
Mycorrhizal type (ECM)	−1.111 (0.482)	0.033
Shade tolerance	−0.540 (0.240)	0.036
Median DBH	0.001 (0.025)	0.965
Log (abundance)	0.228 (0.130)	0.095

Note: Overall model $R^2_{\text{adjusted}} = 0.257$.
Abbreviations: CNDD, conspecific negative density dependence; DBH, diameter at breast height; ECM, ectomycorrhizal.

Shade tolerance was also a significant predictor of CNDD at the species level, such that more shade-tolerant species generally exhibited stronger, more negative CNDD than shade-intolerant species (Figure 4). In contrast, local abundance was not a significant predictor of the strength of CNDD (Figure 4).

CNDD estimated in naturally occurring saplings generally aligned with the results from the seedling experiment. *Q. rubra*, which showed the weakest response to the nearby conspecific adults (Table 2) and no response to neighborhood conspecific density (Table 3) in the seedling experiment, showed no significant evidence of CNDD at the sapling stage (Figure 3). *P. strobus*, which exhibited the strongest response to nearby conspecific adults (Table 2) and neighborhood conspecific densities (Table 3) in the experimental data, showed strong evidence of CNDD in the analysis of observed sapling survival (Figure 3). *P. resinosa*, which exhibited intermediate CNDD in the seedling experiment, was also intermediate in the observed sapling analysis.

DISCUSSION

CNDD and mycorrhizal associations

The results of both our field experiment and our analysis of sapling survival indicate that sapling mortality is

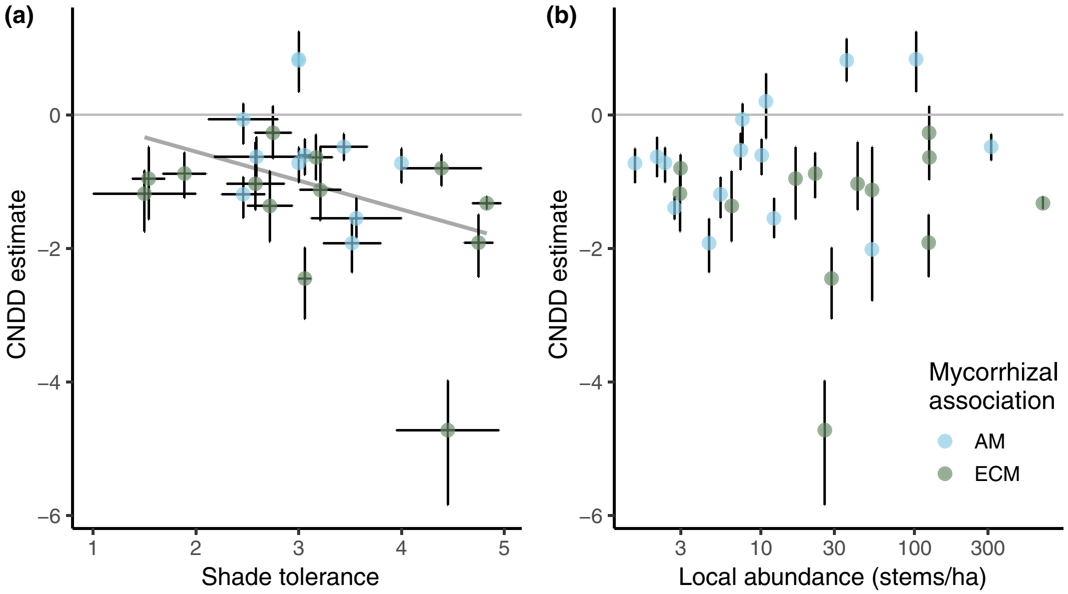

FIGURE 4 Estimates of conspecific negative density dependence (CNDD) for saplings of 28 tree species at the Harvard Forest as a function of (a) shade tolerance and (b) local abundance. Blue points represent species that typically associate with arbuscular mycorrhiza (AM), green points represent species that typically associate with ectomycorrhizae (ECM). Gray line in (a) illustrates a significant negative relationship between shade tolerance and CNDD (see Table 5). Vertical error bars represent 95% confidence intervals (see *Observational sapling survival* in the Materials and Methods section for details). Horizontal error bars in (a) are SE from Niinemets and Valladares (2006). Note that *Crataegus* sp., *Nemopanthus mucronatus*, *Viburnum lantanoides*, and *Viburnum cassinoides* are missing from (a), as there was no estimate of shade tolerance available.

higher beneath conspecific adults in this system. In particular, the agreement between these two separate analyses for the three tree species common to the two studies provides strong evidence of CNDD in this temperate forest, particularly in ECM trees. Indeed, the apparent ubiquity of CNDD among ECM species in this forest came as a surprise, as previous work has found weaker or positive patterns of density dependence among ECM-associating trees (Bennett et al., 2017; Brown et al., 2019; Jiang et al., 2020, 2021). Notably, however, several of these studies found these patterns primarily in plant growth rates rather than in survival (Bennett et al., 2017; Brown et al., 2019). Given that there can be intraspecific trade-offs between survival and growth rates (Seiwa, 2007), it is possible that CNDD estimates based on growth and survival may differ within a species (Brown et al., 2019). In addition, the details of the species included in this study may differ from those in other locations. At this site, while there is a similar number of species that associate with AM and ECM fungi, ECM-associating trees are much more abundant. Thus, the availability of mutualists for AM-associating species is likely lower and/or patchier, and recent evidence shows that AM colonization is greater on plants that grow in stands where other AM-associating plants are more abundant (Grünfeld et al., 2020). This could have the result that regeneration near to conspecifics comes with greater access to appropriate mutualists, which could dampen the negative effects typically associated with proximity to conspecific adults for AM-associating species (Liang et al., 2021). In contrast, mutualist availability is likely ubiquitous for ECM-associating species, as ECM species are well distributed at this site. Finally, estimates of species level CNDD in one context may not generalize, as there is increasing evidence that the strength of CNDD can change due to variation in the presence of large mammals (Murphy & Comita, 2021), climate (Liu & He, 2021), and along environmental gradients (Brown et al., 2021; LaManna et al., 2016; Magee et al., 2020; Record et al., 2016).

CNDD and shade tolerance

We also found evidence that shade tolerance predicted the strength of CNDD: shade-tolerant species tended to show somewhat greater CNDD, although the effect was strongly driven by a single species (*P. abies*). This is consistent with some (García-Guzmán & Heil, 2014; Jia et al., 2020), but not other (Brown et al., 2019), studies on shade tolerance and CNDD. This discrepancy may be because there are conflicting pressures on trees that result in no clear net effect. Shade-tolerant species typically have more conservative life history strategies, which might make them less sensitive to CNDD (McCarthy-Neumann & Kobe, 2008; Song et al., 2021). However, shade-intolerant species are less likely to be limited by conspecific-associating fungal pathogens, and more likely to be limited by herbivorous insects or pathogens with weaker effects on mortality, perhaps making them less likely to exhibit CNDD (García-Guzmán & Heil, 2014; Jia et al., 2020). Taken together with results from this study, it seems that shade tolerance may not have a consistent effect on strength of CNDD in temperate forests.

CNDD and other species characteristics

Local abundance is a strong driver of CNDD in tropical trees, where rare species typically exhibit the strongest CNDD (Comita et al., 2010). In temperate forests, however, the results have been mixed, with some analyses indicating that rare species exhibit stronger CNDD (Johnson et al., 2012; Seiwa et al., 2019) and others finding that more abundant species exhibit stronger CNDD (Zhu, Woodall, et al., 2015). Indeed the effect of local abundance may also interact with other characteristics. For example, rare AM species typically exhibit stronger CNDD than common AM species, but the same may not hold true for ECM species (Jiang et al., 2020, 2021). In this study, we found that local abundance had no apparent effect on the strength of CNDD, overall or interacting with mycorrhizal type. This may be important for understanding the effects of CNDD on diversity in this forest: theoretical work suggests that if variation among species in CNDD is correlated with abundance, with stronger CNDD for rare species, then diversity may not be maintained. However, if CNDD is unrelated to abundance, as in our study here, or even stronger for common species, then CNDD may help promote the maintenance of diversity (Stump & Comita, 2018).

Additional plant characteristics may also influence species susceptibility to CNDD. For example, species with larger seeds may be more tolerant to conspecific neighbors as their seeds act as carbohydrate stores, insuring them against biomass losses to herbivores and pathogens (Lebrija-Trejos et al., 2016; Seiwa et al., 2019). This may help explain why the large-seeded *Q. rubra* exhibited either weak or no CNDD in both the experiment and the observational study; however, the effect of cotyledon reserves is likely larger at younger ages. Notably, naturally occurring *Q. rubra* seedlings at this site do exhibit CNDD, but the effect decreases as the size of the seedling increases (Jevon et al., 2020), which is consistent with what we found here (that the evidence of CNDD was stronger in the experiment, which assessed much smaller individuals) The apparent weakening of CNDD in this species as individuals increase in size in also consistent with previous work suggesting that CNDD is often strongest at the seed to seedling transition or at younger age classes (Zhu, Comita, et al., 2015). We note that, as we assessed large seedlings (2 and 3 years old) in the experiment, and saplings (up to 12.7 cm DBH) in the observational analysis, the overall results of this study are likely conservative with respect to how many species exhibit CNDD and the apparent strength of the effect relative to the true strength of CNDD that is experienced by trees in this forest.

CNDD and diversity

The change in diversity in one out of six of our experimental treatments also illustrates how CNDD mortality can affect community diversity (Figure 3). Importantly, it illustrates that alone, differences in mortality in seedlings growing near conspecific and heterospecific adults is not enough to generate greater diversity. The overall mortality must also be relatively high, and the initial diversity low, to result in meaningful changes to seedling community diversity. This is consistent with conceptual models suggesting that overall differences in mortality rates among life stages, alone or in combination with nonrandom mortality, can be an important determinant of community diversity (Green et al., 2014). The significant increase in diversity in even one treatment during this short-term experiment provides clear evidence that CNDD can act as a mechanism to support local diversity, particularly in systems or situations with high mortality.

Conclusions

Based on these patterns, we suggest that there is strong evidence for CNDD in temperate tree species. Our results also suggest that tree species associated with ECM fungi exhibit CNDD, which runs counter to previous studies (Bennett et al., 2017; Brown et al., 2019; Jiang et al., 2020, 2021). This suggests caution when generalizing about how plant traits predict CNDD. Instead, integrating information about multiple plant characteristics, as well as the environmental context, will help to better predict species-level patterns in CNDD. We found experimentally that CNDD is capable of increasing seedling community diversity. However, theoretical work suggests that, in some cases, interspecific variation in the strength of CNDD decreases its ability to promote coexistence (Stump & Comita, 2018), and results from this study and others show large variation in the strength of CNDD among co-occurring species. Therefore, although evidence of CNDD in temperate forests is accumulating, the consequences for diversity remain poorly understood.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All experimental data and code for both observational and experimental analyses (Jevon, 2022) are available in Mendeley Data at https://doi.org/10.17632/ws3cdn28n8.4. Observational tree census data (Orwig, Foster, et al., 2022) are available from the Environmental Data Initiative at https://doi.org/10.6073/pasta/4e17b7bf83b2ca4f48b7c90d0b164af2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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