

LETTER

Negative density dependence is stronger in resource-rich environments and diversifies communities when stronger for common but not rare species

Joseph A. LaManna,^{1,*} Maranda L. Walton,¹ Benjamin L. Turner² and Jonathan A. Myers¹

¹Department of Biology & Tyson Research Center, Washington University in St. Louis, St. Louis, Missouri 63130, USA

²Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama

*Correspondence: E-mail: jlamanna@wustl.edu

Abstract

Conspecific negative density dependence is thought to maintain diversity by limiting abundances of common species. Yet the extent to which this mechanism can explain patterns of species diversity across environmental gradients is largely unknown. We examined density-dependent recruitment of seedlings and saplings and changes in local species diversity across a soil-resource gradient for 38 woody-plant species in a temperate forest. At both life stages, the strength of negative density dependence increased with resource availability, becoming relatively stronger for rare species during seedling recruitment, but stronger for common species during sapling recruitment. Moreover, negative density dependence appeared to reduce diversity when stronger for rare than common species, but increase diversity when stronger for common species. Our results suggest that negative density dependence is stronger in resource-rich environments and can either decrease or maintain diversity depending on its relative strength among common and rare species.

Keywords

Density dependence, diversity maintenance, diversity–environment relationship, Janzen–Connell hypothesis, natural enemies, resource availability, seedling and sapling recruitment, species coexistence, species relative abundance, temperate forest.

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INTRODUCTION

Conspecific negative density dependence (CNDD) is a widespread population process thought to maintain high species diversity by imposing intrinsic limits on population densities of individual species (Harms *et al.* 2000; HilleRisLambers *et al.* 2002; Comita *et al.* 2014; Bever *et al.* 2015). A classic model invoking CNDD is the Janzen–Connell hypothesis, which predicts that density- or distance-dependent specialised enemies reduce recruitment near conspecific adults, making space available for other species and enhancing local diversity (Janzen 1970; Connell 1971; Hubbell 1979; Carson *et al.* 2008). Many studies have found support for density- or distance-dependent growth, survival, or recruitment near conspecific adults (reviewed in Carson *et al.* 2008; Comita *et al.* 2014). Yet the ways by which CNDD maintains diversity remain unclear, likely because few studies have explicitly examined the relationship between CNDD and diversity (Harms *et al.* 2000; Johnson *et al.* 2012; Bagchi *et al.* 2014).

CNDD can influence diversity through two non-mutually exclusive mechanisms operating at different levels (Kobe & Vriesendorp 2011; Lin *et al.* 2012). First, if common species encounter higher local conspecific densities than rare species, CNDD will more strongly limit populations of common species and maintain diversity by allowing abundances of rare species to increase via a ‘community-compensatory trend’ (*sensu* Connell *et al.* 1984). Second, the strength of CNDD on a per-neighbour basis may differ among common and rare species due to life-history or other trait differences (Comita *et al.* 2010; Mangan *et al.* 2010; Kobe & Vriesendorp 2011). If so, the influence of CNDD on local diversity will depend on how both the strength of per-neighbour CNDD and local

conspecific densities vary among species. For example, rare species can often be more spatially aggregated than common species (Hubbell 1979; Condit *et al.* 2000), yielding similar or higher local conspecific densities for rare species. In this case, stronger per-neighbour CNDD for common than for rare species should still limit common species and maintain local diversity, but stronger per-neighbour CNDD for rare than for common species might limit populations of rare species and decrease local diversity. Yet studies examining the relative strength of per-neighbour CNDD among common and rare species have found mixed results (Comita *et al.* 2010; Mangan *et al.* 2010; Johnson *et al.* 2012; Bagchi *et al.* 2014; Zhu *et al.* 2015a). This complexity highlights the need to examine factors that might change the relative strength of CNDD across species and how these changes contribute to community assembly (Paine *et al.* 2012), species coexistence (Yenni *et al.* 2012) and gradients of species diversity (HilleRisLambers *et al.* 2002; Johnson *et al.* 2012).

Changes in the relative strength of per-neighbour CNDD (hereafter CNDD) among species might depend on underlying environmental conditions. Recent studies suggest that the strength of CNDD in woody-plant species increases with precipitation and productivity at continental to global scales (Johnson *et al.* 2012; Comita *et al.* 2014). This pattern might reflect stronger intraspecific competition, increased virulence and/or abundance of host-specific pathogens, or increased pressure from species-specific herbivores in resource-rich environments (Mangan *et al.* 2010; Bever *et al.* 2012; Terborgh 2012). These same processes might alter the relative importance of CNDD as a mechanism underlying patterns of species composition and diversity across local resource gradients. However, the extent to which CNDD increases with local

resource availability and contributes to variation in species diversity across local resource gradients remains untested. Moreover, relative increases in the strength of CNDD across local resource gradients may differ among common and rare species, with important implications for diversity. For example, greater increases in the strength of CNDD for rare than for common species across local resource gradients may lead to local extinction of rare species and decrease diversity in resource-rich relative to resource-poor environments. Alternatively, greater increases in the strength of CNDD for common than for rare species across local resource gradients may increase diversity in resource-rich environments by reducing the strength of interspecific competition (Huston 2014). To the extent that the strength of CNDD changes in different ways for common and rare species across local resource gradients, this mechanism could help explain why patterns of local species diversity often show variable responses to changes in productivity and resource availability within and among landscapes (Chase & Leibold 2002; Chalcraft *et al.* 2008; Adler *et al.* 2011).

The relative strength of CNDD can also differ among life stages, potentially altering the relative strength of CNDD among common and rare species and influencing species diversity. CNDD can be stronger at earlier than at later life stages (Comita *et al.* 2014; Zhu *et al.* 2015b), and processes that structure communities at earlier life stages are generally thought to have a disproportionately strong influence on the maintenance of local diversity (Harms *et al.* 2000; HilleRisLambers *et al.* 2002; Comita *et al.* 2010; Green *et al.* 2014; Zhu *et al.* 2015b). However, CNDD at later life stages may contribute more to local patterns of species diversity if CNDD becomes relatively weaker for rare or common species at later life stages (Wright 2002). Thus, changes across life stages in the relative strength of CNDD among common and rare species might impact patterns of diversity, but empirical tests of this idea are lacking.

We examined the strength of CNDD at two life stages (seedling and sapling recruitment) across a soil-resource gradient for 38 woody-plant species in a large (20 ha) stem-mapped temperate forest. We also examined changes in local species diversity across the soil-resource gradient at four life stages (seed, seedling, sapling and adult). To assess whether stronger CNDD could be responsible for observed changes in species diversity across the soil-resource gradient, we predicted seedling and sapling diversity in resource-poor and resource-rich environments using only our estimates of CNDD at both ends of the soil-resource gradient. At both life stages, the strength of CNDD increased with local resource availability. Our results suggest that CNDD is stronger in resource-rich environments and can either decrease or maintain diversity depending on its relative strength among common and rare species.

MATERIALS AND METHODS

Study site and data collection

Our study was conducted at the Tyson Research Center Forest Dynamics Plot located on the northeastern edge of the

Ozark Plateau, 40 km southwest of St. Louis, MO, USA (38° 31' N, 90° 33' W). This late-successional oak-hickory-dominated forest has been relatively undisturbed for ~ 80 years, and tree cores collected in the early 1980s from large individuals of dominant species indicated tree ages of 120–160 years (Zimmerman & Wagner 1979; Hampe 1984). In 2013, we identified, tagged, measured and mapped all free-standing stems of woody species greater than 1 cm diameter at breast height (dbh) in a 20-ha (480 × 420 m) section of a 25-ha plot following CTFS-ForestGEO protocols (Condit 1998).

In 2013, we measured 13 soil variables and four topographic variables across the 20 × 20 m quadrat and the 10 × 10 m subquadrat grid across the 25 ha plot (Fig. 1; Spasojevic *et al.* 2014). We used principle component analysis to determine the major axis of environmental variation at the 20 × 20 m scale for adults and saplings and at the 10 × 10 m scale for seeds and seedlings. The first principle component (PC1) at both scales described 52.8% and 59.8% of total environmental variation respectively (Fig. S1). As expected, loadings for PC1 were highly correlated between the two scales ($r = 0.99$), indicating that PC1 described the same environmental axis at both scales. Per cent soil moisture by mass was also collected from 254 sampling locations across the plot in 2013 and was positively correlated with PC1 ($r = 0.66$). Thus, PC1 described a change from drier acidic soil with high concentrations of iron and aluminium to moist pH-neutral soil with high concentrations of nitrogen, manganese, phosphorus and base cations. Drier acidic soil was associated with southwest-facing slopes and ridges, and moist pH-neutral soil was associated with northeast-facing slopes and valleys (Fig. 1). This topographic gradient is widespread across the Ozark region and linked to changes in slope, aspect and geological transitions from more acidic chert to cherty-limestone to more pH-neutral limestone (Hampe 1984; Nelson 2010).

Seed densities ($\text{m}^{-2} \text{year}^{-1}$) were calculated from collections at 200 0.5 m² traps stratified across the soil-resource gradient (Fig. 1). Seeds were collected from 140 traps during 2012 and from all 200 traps between 2013 and 2015. We collected and identified potentially viable seeds from March to December each year (six to seven seed collections/year). Seedling densities ($\text{m}^{-2} \text{year}^{-1}$) were measured during 2014–2015 from 600 1 m² plots. Three seedling plots were paired with each seed trap. We defined seedling as any individual shorter than 50 cm, which includes younger individuals that have retained cotyledons as well as older individuals. Seed traps and paired seedling plots were arranged on the landscape to minimise the correlation between geographic distance and environmental dissimilarity among plots ($r = 0.12$; Fig. 1).

CNDD and resource availability

We examined CNDD at the 10 × 10 m scale for seedling recruitment and at the 20 × 20 m scale for sapling recruitment because CNDD effects are known to decay strongly beyond distances of 10–20 m from a given adult tree in both tropical and temperate forests (Hubbell *et al.* 2001; Johnson *et al.* 2014). Saplings were generally defined as trees smaller than 10 cm dbh, but 5 cm dbh or 2 cm dbh were used for small-stature understory species (e.g. *Cornus florida* or *Lindera*

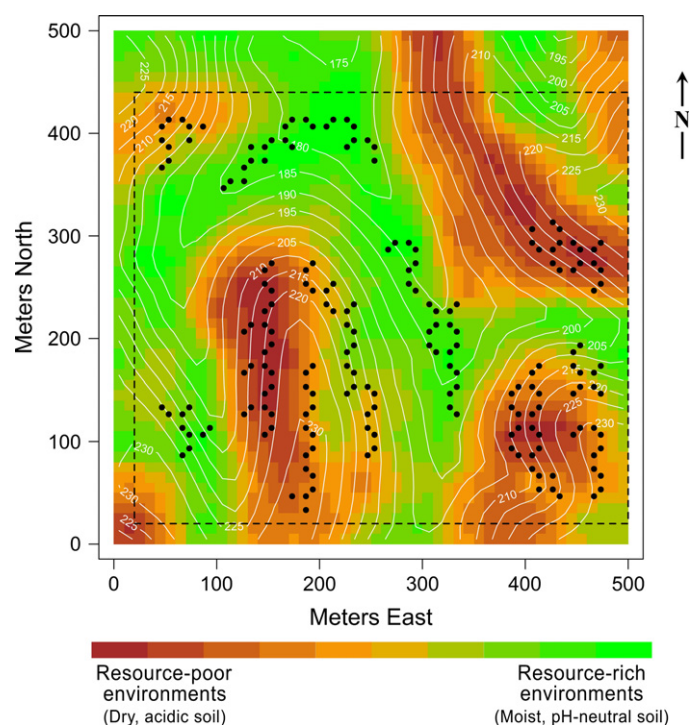


Figure 1 Map of the Tyson Research Center Forest Dynamics Plot (Missouri, USA) showing spatial variation in soil-resource availability across resource-poor environments (brown) and resource-rich environments (green). Topography (white contour lines; elevation in metres), locations of paired seed traps and seedling plots (black points) and the 20 ha section in which adults and saplings were censused (black dashed line) are also shown.

benzoin) that never or rarely reach 10 cm dbh or 5 cm dbh respectively. Adults were defined as individuals larger than the sapling size class for each species. We tested for increases in the strength of CNDD along the soil-resource gradient using hierarchical mixed models for each life stage (i.e. seedling and sapling recruitment; see Table S1 for complete model list). Following Harms *et al.* (2000), we estimated CNDD at the seedling stage as the slope of the line between log-transformed seed density and log-transformed seedling density, with slopes progressively lower than one representing stronger CNDD (Fig. S2). To examine whether CNDD became stronger with increasing resource availability, we also tested for a significant negative interaction between log-transformed seed density and the soil-resource gradient (PC1). We also tested for additive effects of log-transformed heterospecific seed and log-transformed heterospecific seedling density as well as heterospecific adult basal area in our models to control for potential heterospecific density effects on seedling density (heterospecific negative density dependence, hereafter HNDD). To control for potentially stronger HNDD with increasing resource availability, we also tested for interactions between the soil-resource gradient (PC1) and all heterospecific variables. Models were compared using sample-size corrected AIC (AIC_c; Burnham & Anderson 2002). Data from all woody-plant species shared between seed traps and seedling plots were pooled in our analysis. We incorporated random effects that allowed

the effect of conspecific seed density to vary among species and incorporated random interactions that allowed the interaction between conspecific seed density and the resource gradient to vary among species. These random effects therefore estimated the strength of CNDD for seedling recruitment (random slopes) and changes in the strength of CNDD across the soil-resource gradient (random interactions) for each species. Seedling plots were excluded from analyses when paired seed traps lacked conspecific seed, as including these can bias estimates of density dependence (Harms *et al.* 2000). We evaluated spatial auto-correlation in our model with variograms that test for patterns in residual semi-variance with increasing distance.

We used a similar approach to examine CNDD at the sapling stage. Because adults are hypothesised to have strong negative density-dependent effects on saplings (Janzen 1970; Connell 1971), we used conspecific adult density to estimate CNDD at the sapling stage across the entire 20 ha plot (Johnson *et al.* 2012). While adult density in the 10 × 10 m sub-quadrats that contained seed traps was positively correlated with conspecific seed density ($r = 0.21$, $P < 0.001$), we note that this analysis encompasses all processes acting on sapling recruitment between the adult and sapling stages (e.g. seed production, pre-dispersal seed predation, seedling survival). CNDD was measured as the slope between log-transformed sapling density and log-transformed conspecific adult density (Fig. S2), and we also included log-transformed heterospecific sapling density and heterospecific adult basal area in our model to test for effects of HNDD on sapling recruitment. Interactions with the soil-resource gradient, random effects and interactions for species, and assessment of spatial auto-correlation were also examined as detailed for seedling recruitment above (Table S1). We also tested for a positive association between the strength of CNDD at seedling and at sapling recruitment.

CNDD in common and rare species

We assessed if CNDD was stronger for rare or common species, and if changes in resource availability altered the relative strength of CNDD among species. To assess if CNDD was stronger in rare or common species, we examined regressions between estimates of CNDD and adult size-weighted abundance (basal area summed across the 20 ha plot) across species. These across-species tests were performed for both life stages (seedling and sapling recruitment) at average resource availability (mean of PC1). To assess if CNDD became relatively stronger with resource availability for common or rare species, we examined regressions between the estimates of the change in CNDD with resource availability and adult size-weighted abundance. Size-weighted abundance was used to measure commonness/rarity instead of numerical abundance due to differences in size-age distributions across species and because it better represents the influence that a given tree will have on its surrounding environment (Comita *et al.* 2010). Nonetheless, numerical abundance and basal area were correlated across species ($r = 0.69$, $P < 0.001$). These regressions were weighted by the error around CNDD estimates for each species at each life stage.

CNDD and species diversity

We evaluated if changes in the strength of CNDD during seedling and sapling recruitment were associated with changes in woody-plant species diversity along the soil-resource gradient. We first assessed changes in three measures of species diversity (Shannon's diversity index, or S ; species richness; and rarefied species richness) across the soil-resource gradient at each of four life stages (seeds, seedlings, saplings and adults). We also measured the change in diversity across the resource gradient from the seed to the seedling stage ($S_{\text{seedling}} - S_{\text{seed}}$) as well as from the seedling to the sapling stage ($S_{\text{sapling}} - S_{\text{seedling}}$). To measure the change in diversity from seedlings to saplings, we only included saplings in the 10×10 m subquadrats that contained seedling plots. For all diversity analyses along the resource gradient, spatial auto-correlation was explicitly controlled using generalised least squares models.

Predicted effects of CNDD on species diversity

To assess whether CNDD could be responsible for observed changes in species diversity across the soil-resource gradient, we predicted seedling and sapling diversity in resource-poor and resource-rich environments using only our estimates of CNDD at both ends of the gradient. For seedling recruitment, we simply multiplied observed seed abundance of each species in each seed trap by the estimate of CNDD for that species in either resource-poor (minimum observed value of PC1) or resource-rich (maximum observed value of PC1) environments. This approach generated two predicted seedling communities under contrasting conditions: (1) if the entire forest plot was resource-poor; and (2) if the entire forest plot was resource-rich. We then compared community-wide species diversity (Shannon's diversity index) of both communities and determined if CNDD increased or decreased diversity in resource-rich relative to resource-poor environments. We did the same for sapling recruitment, but used observed seedling abundances and estimates of the strength of CNDD during sapling recruitment for each species in either resource-poor or resource-rich environments. Estimates of CNDD controlled for heterospecific effects on seedling and sapling recruitment, and so differences in diversity among these predicted communities should only reflect the influence of CNDD on diversity and not generalised effects of heterospecifics (see supplemental methods for more detailed methods).

RESULTS

In total, 19 776 seeds and 5715 seedlings from 29 species were used to estimate changes in CNDD during seedling recruitment and seed and seedling diversity across the soil-resource gradient. The top-ranked model for seedling recruitment ($R^2 = 0.64$) included effects of conspecific seed density, heterospecific seedling density, the soil-resource gradient, plus interactions of conspecific seed density and heterospecific seedling density with the resource gradient (Table S1, S2). In addition, 15 369 saplings and 14 863 adults from 35 species were used to estimate changes in CNDD during sapling recruitment

and sapling and adult diversity across the soil-resource gradient. The top-ranked model for sapling recruitment ($R^2 = 0.71$) included effects of conspecific adult density, heterospecific sapling density, heterospecific adult basal area, the soil-resource gradient, plus interactions of conspecific adult density and heterospecific sapling density with the resource gradient (Table S1, S2). We found no strong evidence of spatial auto-correlation in the residuals for either model (Fig. S3), and variograms showed little to no spatial auto-correlation (Fig. S4).

CNDD and resource availability

CNDD during both seedling and sapling recruitment was stronger in resource-rich than in resource-poor environments across species (Fig. 2, 3a, c). CNDD during seedling recruitment was strong for nearly all species (Fig. 2a), whereas CNDD during sapling recruitment was more variable across species (Fig. 2b). Nonetheless, the strength of CNDD during sapling recruitment increased with the strength of CNDD during seedling recruitment among species ($r = 0.48$; $P = 0.012$). The strength of CNDD increased significantly along the soil-resource gradient at both stages after controlling for additive effects of resource availability and potential effects of heterospecific densities (Fig. 2, right panels). HNDD during seedling and sapling recruitment also became stronger along the soil-resource gradient at both life stages (Fig. 3b, d). However, HNDD was non-existent in resource-poor environments and relatively weak compared to CNDD in resource-rich environments (Fig. 3). Moreover, the strength of CNDD increased twice as much along the resource gradient as HNDD (Fig. 3b, d). Thus, the strength of CNDD increased with resource availability and was generally stronger than heterospecific effects. We therefore focus our remaining results on trends in CNDD.

Changes in CNDD across the resource gradient did not appear to be caused by changes in relative densities across the resource gradient. Seed densities increased with resources for seven of 29 species and decreased for one species (mean r among species = 0.18). Seedling densities increased with resources for five of 29 species and decreased for three species (mean $r = -0.02$). At the 20 ha scale, adult densities increased with resources for five of 35 species and decreased for four species (mean $r = 0.03$). Sapling densities increased with resources for three of 35 species and decreased for eight species (mean $r = -0.06$). Only three of 29 species had higher seed but not higher seedling densities in resource-rich environments, and only three of 35 species had higher adult but not higher sapling densities. This pattern indicates that increases in CNDD were generally not linked to higher initial densities in resource-rich environments.

CNDD in common and rare species

The relative strength of CNDD among common and rare species differed across life stages and changed along the soil-resource gradient at the seedling stage. CNDD during seedling recruitment was equally strong for common and rare species (Fig. 4a), but became relatively stronger for rare species as resources increased (Fig. 4b). In contrast, CNDD during

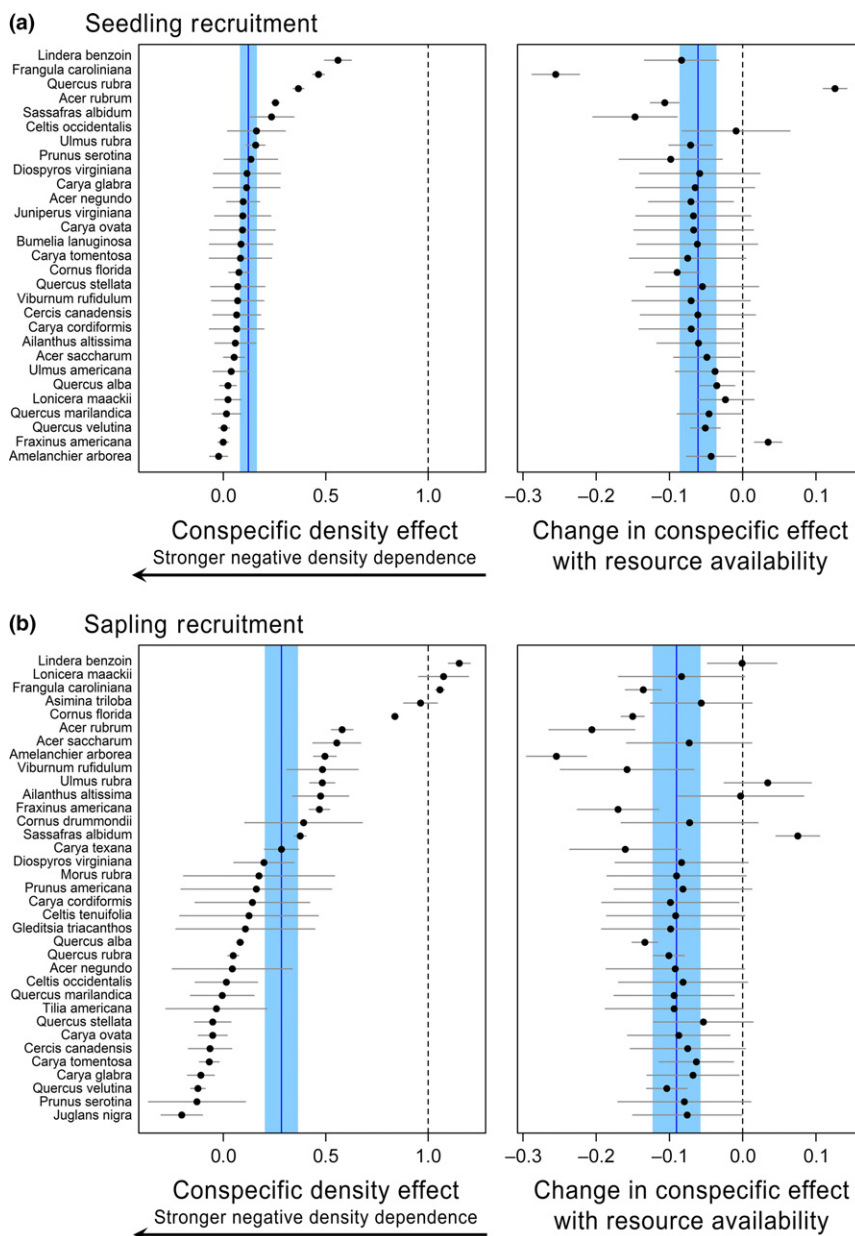


Figure 2 The strength of conspecific negative density dependence (CNDD) on (a) seedling recruitment for 29 woody-plant species and (b) sapling recruitment for 35 woody-plant species. A slope of one between seedling or sapling density and conspecific seed or adult density, respectively, is expected given no CNDD (dashed line in left panels). Estimates of CNDD progressively lower than one represent stronger negative density-dependent recruitment. The change in the strength of CNDD with a 1 SD change in PC1 along the soil-resource gradient is also shown for all species at both life stages (right panels), with a null expectation of no change with increasing resource availability (dashed line in right panels). Negative values in right panels indicate stronger CNDD with increasing resource availability. Species are ordered from top to bottom by increasing CNDD. The estimated mean effects across all species (± 1 SE) are shown in blue.

sapling recruitment was much stronger for common than for rare species across the entire soil-resource gradient (Fig. 4c). The strength of CNDD also increased equally for all species with resource availability at the sapling stage (Fig. 4d), meaning that common species were most suppressed near conspecifics in resource-rich environments. Thus, common species increasingly had a recruitment advantage over rare species as resources increased at the seedling stage, but recruitment of common species was increasingly suppressed as resources increased at the sapling stage.

CNDD and species diversity

Different effects of resource availability on the relative strength of CNDD for common and rare species (Fig. 4) corresponded to different effects of resource availability on species diversity across life stages (Fig. 5). At both seedling and sapling life stages, CNDD was generally stronger in resource-rich environments (Fig. 2). However, stronger CNDD corresponded to decreased seedling diversity but increased sapling diversity in resource-rich environments. As resources increased,

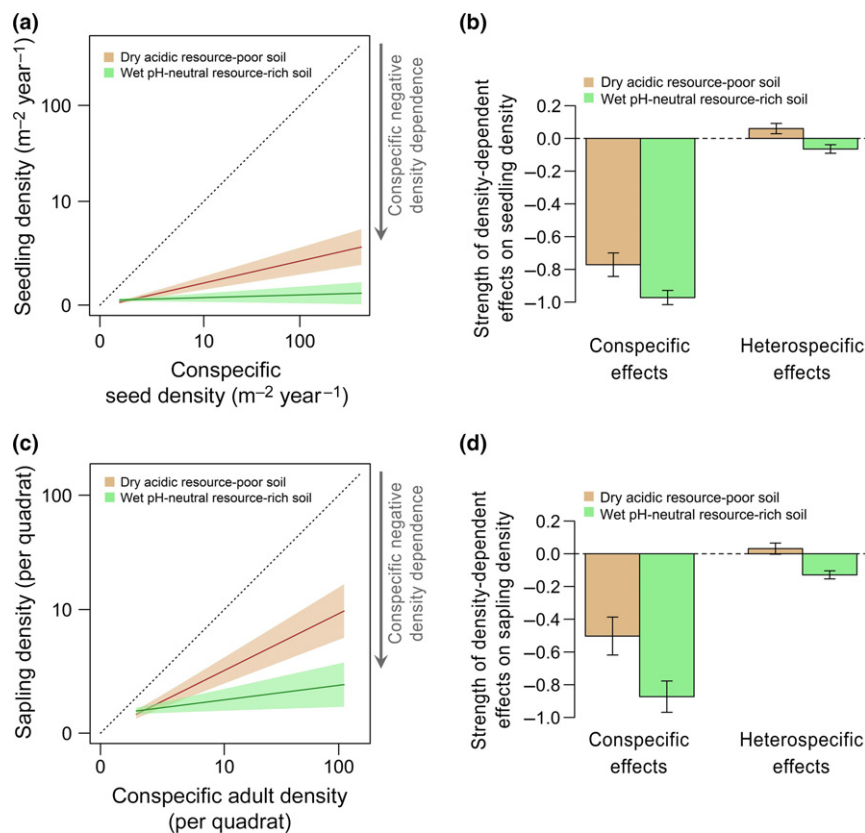


Figure 3 Average density-dependent effects in resource-poor (minimum observed value of PC1; brown) and resource-rich (maximum observed value of PC1; green) environments. (a) Conspecific negative density dependence (CNDD) during seedling recruitment is measured as slopes lower than the expected 1:1 relationship (dotted line) between conspecific seed and seedling densities. (b) Effects on seedling density (± 1 SE) of conspecific seeds [slopes in (a) subtracted from one, or grey arrow in (a)] and heterospecific seedlings (slopes measured between heterospecific seedlings and seedling density). (c) CNDD during sapling recruitment is measured as slopes lower than the expected 1:1 relationship (dotted line) between conspecific adult and sapling densities (individuals/ 20×20 m quadrat). (d) Effects on sapling density (± 1 SE) of conspecific adults (slopes in (c) subtracted from one) and heterospecific saplings (slopes measured between heterospecific saplings and sapling density). Conspecific effects control for heterospecific effects and vice versa (see Methods and Materials).

stronger seedling CNDD for rare species was associated with declines in seedling diversity relative to seed diversity (Figs. 5, 6a). This trend was also evident at a larger spatial scale when calculating changes in seedling and seed diversity across 12 clustered regions that were stratified across the soil-resource gradient (Fig. 1, S5). In contrast, stronger sapling CNDD for common than for rare species as resources increased was associated with increased sapling diversity relative to seedling diversity (Figs. 5, 6b). Similar patterns were observed for species richness and rarefied species richness (Fig. S6). These patterns indicate that CNDD reduces diversity when it becomes relatively stronger for rare than for common species (as observed for seedling recruitment in resource-rich environments) but maintains diversity when it becomes stronger for common species (as observed for sapling recruitment in resource-rich environments) in this temperate forest.

Predicted effects of CNDD on species diversity

Consistent with observed changes in diversity across the soil-resource gradient (Figs. 5 and 6), communities assembled using only observed differences in CNDD across the soil-

resource gradient revealed that strong CNDD can both decrease and maintain diversity depending on its relative strength among species (Fig. S7). Predicted seedling diversity was lower in resource-rich environments (Shannon's diversity index \pm SE = 1.49 ± 0.05), where CNDD became relatively stronger for rare than for common species, than in resource-poor environments (1.77 ± 0.05). In contrast, predicted sapling diversity was higher in resource-rich environments (2.67 ± 0.05), where CNDD became stronger for all species but was relatively stronger for common than for rare species, than in resource-poor environments (2.48 ± 0.06).

DISCUSSION

Our results support the hypothesis that the strength of per-neighbour CNDD increases across local resource gradients with implications for species diversity. A previous study of temperate forests at the continental scale (Johnson *et al.* 2012) and meta-analysis of temperate and tropical forests at the global scale (Comita *et al.* 2014) found that CNDD becomes stronger in more productive and wetter regions respectively. To our knowledge, our study is the first to demonstrate that

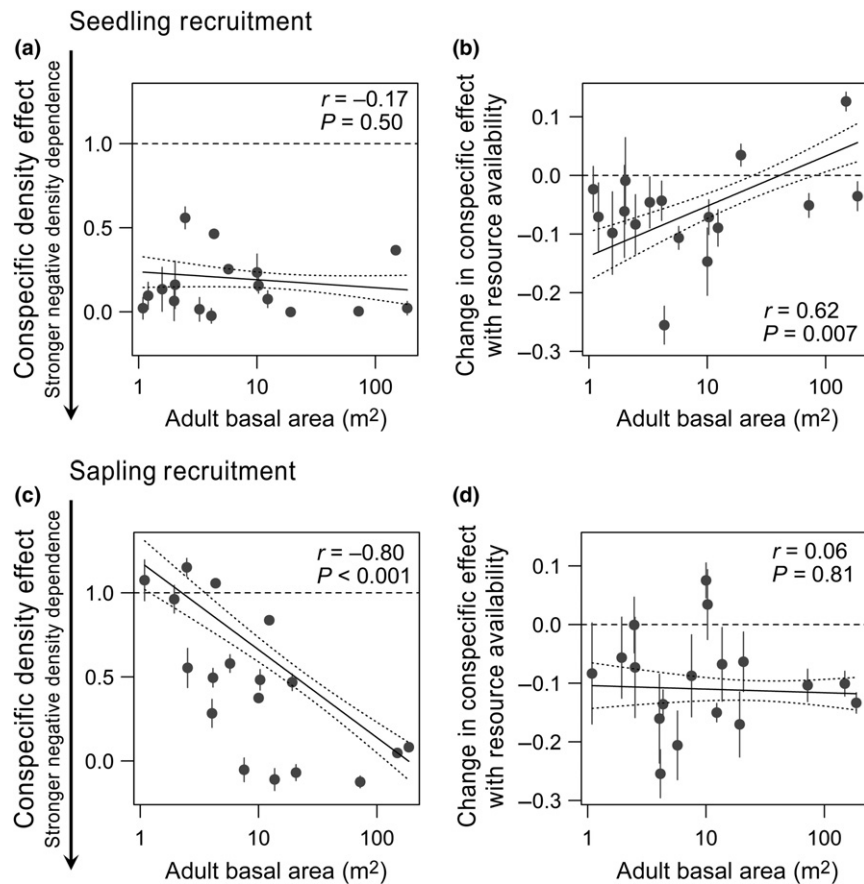


Figure 4 The relative strength of conspecific negative density dependence (CNDD) and changes in the strength of CNDD with resource availability among common and rare species. (a) Strength of CNDD during seedling recruitment as a function of size-weighted abundance, measured as adult basal area (m²). (b) The change in seedling CNDD with a 1 SD change in the soil-resource gradient (PC1) as a function of adult basal area. (c) Strength of CNDD during sapling recruitment as a function of adult basal area. (d) The change in sapling CNDD with a 1 SD change in the soil-resource gradient (PC1) as a function of adult basal area. Note that adult size-weighted abundance is plotted on a log scale.

this interaction between CNDD and resource availability scales down to influence landscape patterns of species diversity within local ecological communities. We found that the strength of CNDD generally increased across a local soil-resource gradient for woody-plant species during two important life-stage transitions (Fig. 2). Our approach contrasts with previous studies of CNDD that examined landscape-level averages without explicitly considering changes in the strength of CNDD across local environmental gradients (Comita *et al.* 2010; Mangan *et al.* 2010; Metz *et al.* 2010; Chen *et al.* 2010; Johnson *et al.* 2012; Zhu *et al.* 2015a). Moreover, increases in the strength of CNDD with soil resources appeared to reduce diversity when CNDD was relatively stronger for rare than common species, but increase diversity when stronger for common species (Figs. 4–6, S7). Overall, these results suggest that CNDD is stronger in resource-rich environments and can either decrease or maintain diversity depending on its relative strength among common and rare species.

Two non-mutually exclusive mechanisms might cause stronger CNDD in more resource-rich environments: (1) stronger host-specific antagonistic interactions or (2) stronger intraspecific competition. Experiments in tropical and temperate forests have shown that negative host–antagonist

interactions, specifically species-specific interactions with soil pathogens and plant herbivores, are largely responsible for CNDD effects (Packer & Clay 2000; Mangan *et al.* 2010; Terborgh 2012; Liu *et al.* 2012; Bagchi *et al.* 2014). For example, survival of juvenile black cherry (*Prunus serotina*), the species in our study with the second strongest CNDD during sapling recruitment (Fig. 2b), decreases near conspecific adults as a result of soil pathogens (Packer & Clay 2000). Microbiologists have predicted that increased moisture or temperature should increase pathogen virulence (Bever *et al.* 2012), and faster plant growth in more fertile soil may trade-off with weaker pathogen or herbivore defences (Kardol *et al.* 2006; Fine *et al.* 2006). Soil properties such as pH have also been linked to changes in bacterial and fungal species diversity and composition (Fierer & Jackson 2006; Barberán *et al.* 2015), which may affect the strength of plant–soil feedbacks and CNDD. Our results largely support these ideas at a local scale, with stronger CNDD in sites associated with higher soil moisture and pH (Figs. 1 and 2). However, we cannot eliminate the possibility that changes in unmeasured microclimatic variables like temperature or stronger intraspecific competition led to our observation of stronger CNDD in resource-rich environments. Thus, increasingly negative host–antagonist interac-

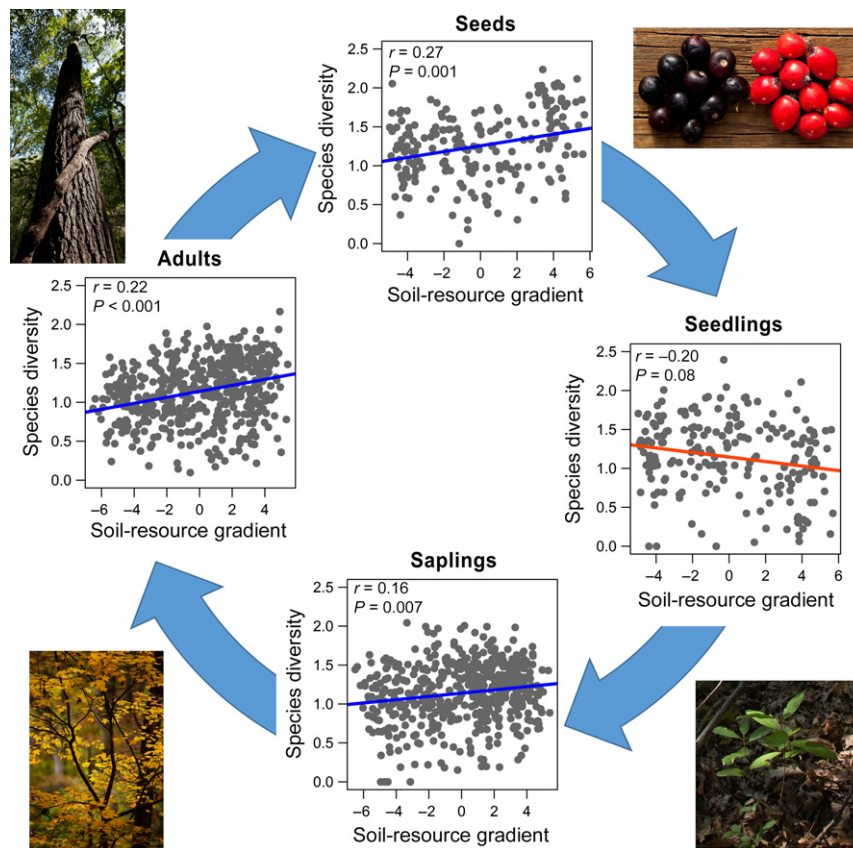


Figure 5 Changes in woody-plant species diversity (Shannon's diversity index) along the soil-resource gradient for four life stages at the Tyson Research Center Forest Dynamics Plot. Correlation coefficients, regression lines and significance tests account for spatial auto-correlation among samples. Photo credit: Jonathan A. Myers.

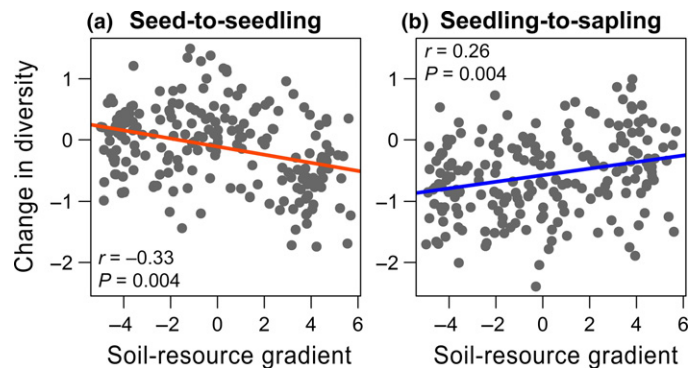


Figure 6 The change in diversity across life stages at the Tyson Research Center Forest Dynamics Plot. (a) Diversity decreased in resource-rich relative to resource-poor environments during the seed-to-seedling transition, but (b) diversity increased in resource-rich relative to resource-poor environments during the seedling-to-sapling transition. Correlation coefficients, regression lines and significance tests account for spatial auto-correlation among samples.

tions may combine with more intense intraspecific competition to strengthen CNDD in resource-rich environments, but experimental tests are needed to determine the relative importance of these two mechanisms.

We found that stronger per-neighbour CNDD in resource-rich environments can both maintain and decrease diversity

depending on its relative strength across species (Figs. 4–6). Specifically, diversity is maintained when CNDD is stronger for common than for rare species (Figs. 4c, 6b, S7), but diversity declines when CNDD becomes stronger for rare species (Figs. 4b, 6a, S7). These findings support the hypothesis that stronger CNDD for common than for rare species maintains diversity, but not via a community-compensatory trend. The traditional compensatory paradigm holds that common species have higher local conspecific densities regardless of their per-neighbour CNDD, limiting populations of common species at the community level (Connell *et al.* 1984; Wills *et al.* 2006). Yet rare species can be more spatially aggregated than common species (Hubbell 1979; Condit *et al.* 2000), yielding similar or higher local conspecific densities for rare species. In our ecosystem, neither median nor maximal local conspecific densities increased systematically with species relative abundance at the seedling (median: $r = 0.09$, $P = 0.658$; maximal: $r = -0.05$, $P = 0.809$) or sapling stage (median: $r = 0.18$, $P = 0.305$; maximal: $r = 0.05$, $P = 0.788$). Thus, innate differences in CNDD among common and rare species due to physiological, morphological, immunocompetence or other life-history trait variation may have greater influence on diversity than compensatory mechanisms (Kobe & Vriesendorp 2011). For example, stronger per-neighbour CNDD for rare species in resource-rich environments during the seedling stage was associated with decreased diversity. Since local conspecific

densities did not differ strongly among common and rare species, this pattern likely reflects increased recruitment limitation and local extinction of rare species as their per-neighbour CNDD increased along the soil-resource gradient. Thus, innate differences among species in per-neighbour CNDD can potentially have greater influence on diversity than community-compensatory mechanisms, maintaining diversity when stronger for common than for rare species but decreasing diversity when stronger for rare species.

Despite declines in species diversity linked to stronger CNDD for rare species during seedling recruitment, stronger CNDD for common species during sapling recruitment increased diversity in resource-rich environments. Moreover, this pattern of higher diversity in resource-rich environments relative to resource-poor environments was maintained into the adult life stage and likely carried over to influence the diversity of seed rain (Fig. 5). These results suggest a limited role for CNDD as a diversifying mechanism at the seed-to-seedling transition and potentially contrast with the idea that processes structuring communities at earlier life stages (e.g. seedling recruitment) have a disproportionately strong influence on species diversity and composition at later life stages (Harms *et al.* 2000; HilleRisLambers *et al.* 2002; Comita *et al.* 2010; Green *et al.* 2014; Zhu *et al.* 2015b). However, stronger CNDD for common species during sapling recruitment and associated increases in species diversity may have resulted from other early-life-stage processes (e.g. seed production, pre-dispersal seed predation, seedling survival). Our observation of stronger CNDD for rare species in resource-rich environments may also depend on the years in which we surveyed seedlings. We analysed 2 years of seedling data, but the strength of CNDD (Lin *et al.* 2012) and the relationship between CNDD and species abundance (Bachelot *et al.* 2015) can vary temporally. Overall, our results highlight the need for theoretical studies that generate predictions for when changes in the relative strength of CNDD among common and rare species and among different life stages should most strongly influence patterns of diversity.

Like CNDD, HNDD during seedling and sapling recruitment also became stronger in resource-rich environments (Fig. 3). However, heterospecifics generally had weaker influences on seedling and sapling recruitment relative to conspecifics (Fig. 3, Table S2). These results are supported by previous studies that show weaker heterospecific relative to conspecific effects on recruitment, survival and growth in temperate and tropical forests (Comita *et al.* 2010; Johnson *et al.* 2012, 2014). Stronger HNDD in resource-rich environments may reflect increased interspecific competition and/or increased mortality from generalist herbivores or seed predators (Terborgh 2012). However, recent work supports the idea that generalist enemies or interspecific competition from older age classes may contribute more to HNDD than interspecific competition within a cohort (Wright 2002; Paine *et al.* 2008; Terborgh 2012; Bever *et al.* 2015). Thus, stronger HNDD during seedling and sapling recruitment in resource-rich environments may be the result of stronger negative interactions with generalist antagonists or older heterospecifics, although experimental tests are needed to confirm these hypotheses.

Our results have broad implications for understanding how the population-level consequences of negative density dependence scale up to influence community assembly and patterns of species diversity across ecological gradients. Specifically, the relative importance of biotic interactions as a mechanism structuring species diversity and composition likely increases with the availability of local resources. We found that both CNDD and HNDD were weaker in resource-poor than in resource-rich environments, and diversity was lowest in these environments for saplings, adults and seed rain (Figs. 3 and 5). These results suggest that only species with physiological tolerances for low-resource availability can potentially occupy resource-poor environments (Grime 2001; Pianka 2011). On the other hand, biotic interactions appear to be a more important factor determining species diversity, composition and relative abundance in resource-rich environments. Theory already suggests that one type of biotic interaction, interspecific competition, should increase with resource availability, yielding a stronger influence of competition on community assembly in resource-rich environments (Grace 1991; Grime 2001). Yet we found CNDD was much stronger than HNDD in resource-rich environments (Fig. 3), suggesting that negative interactions with host-specific antagonists (pathogens, herbivores or predators), rather than increased competition for resources, may contribute most strongly to changes in the relative importance of community assembly mechanisms across resource-poor and resource-rich environments.

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AUTHORSHIP

JAL and JAM conceived the study; JAM obtained the funding; MLW, JAM and JAL collected the data and BLT

analysed the soil samples. JAL executed the statistical analyses and wrote the first draft of the manuscript, and all authors contributed to revisions.

REFERENCES

- Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y. & Hector, A., *et al.* (2011). Productivity is a poor predictor of plant species richness. *Science*, 333, 1750–1753.
- Bachelot, B., Kobe, R.K. & Vriesendorp, C. (2015). Negative density-dependent mortality varies over time in a wet tropical forest, advantaging rare species, common species, or no species. *Oecologia*, 179, 853–861.
- Bagchi, R., Gallery, R.E., Gripenberg, S., Gurr, S.J., Narayan, L. & Addis, C.E., *et al.* (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, 506, 85–88.
- Barberán, A., McGuire, K.L., Wolf, J.A., Jones, F.A., Wright, S.J. & Turner, B.L., *et al.* (2015). Relating belowground microbial composition to the taxonomic, phylogenetic, and functional trait distributions of trees in a tropical forest. *Ecol. Lett.*, 18, 1397–1405.
- Bever, J.D., Platt, T.G. & Morton, E.R. (2012). Microbial population and community dynamics on plant roots and their feedbacks on plant communities. *Annu. Rev. Microbiol.*, 66, 265–283.
- Bever, J.D., Mangan, S. & Alexander, H. (2015). Maintenance of plant species diversity by pathogens. *Annu. Rev. Ecol. Evol. Syst.*, 46, 305–325.
- Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer Publishing, Fort Collins, CO.
- Carson, W.P., Anderson, J.T., Leigh, E. & Schnitzer, S.A. (2008). Challenges associated with testing and falsifying the Janzen–Connell hypothesis: a review and critique. In *Tropical Forest Community Ecology* (eds Carson, W.P. & Schnitzer, S.A.). Wiley-Blackwell Publishing, Oxford, UK, pp. 210–241.
- Chalcraft, D.R., Cox, S.B., Clark, C., Cleland, E.E., Suding, K.N. & Weiher, E., *et al.* (2008). Scale-dependent responses of plant biodiversity to nitrogen enrichment. *Ecology*, 89, 2165–2171.
- Chase, J.M. & Leibold, M.A. (2002). Spatial scale dictates the productivity–biodiversity relationship. *Nature*, 416, 427–430.
- Chen, L., Mi, X., Comita, L.S., Zhang, L., Ren, H. & Ma, K. (2010). Community-level consequences of density dependence and habitat association in a subtropical broad-leaved forest. *Ecol. Lett.*, 13, 695–704.
- Comita, L.S., Muller-Landau, H.C., Aguilar, S. & Hubbell, S.P. (2010). Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, 329, 330–332.
- Comita, L.S., Queenborough, S.A., Murphy, S.J., Eck, J.L., Xu, K. & Krishnadas, M., *et al.* (2014). Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *J. Ecol.*, 102, 845–856.
- Condit, R. (1998). *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer-Verlag and R. G. Landes Company, Berlin, Germany and Georgetown, TX.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S. & Gunatilleke, N., *et al.* (2000). Spatial patterns in the distribution of tropical tree species. *Science*, 288, 1414–1418.
- Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Populations* (eds den Boer, P.J. & Gradwell, G.R.). Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp. 298–312.
- Connell, J.H., Tracey, J. & Webb, L.J. (1984). Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecol. Monogr.*, 54, 141–164.
- Fierer, N. & Jackson, R.B. (2006). The diversity and biogeography of soil bacterial communities. *Proc. Natl Acad. Sci. USA*, 103, 626–631.
- Fine, P.V., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M. & Stevens, M.H.H., *et al.* (2006). The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology*, 87, S150–S162.
- Grace, J. (1991). A clarification of the debate between Grime and Tilman. *Funct. Ecol.*, 5, 583–587.
- Green, P.T., Harms, K.E. & Connell, J.H. (2014). Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. *Proc. Natl Acad. Sci. USA*, 111, 18649–18654.
- Grime, J.P. (2001). *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. John Wiley & Sons, Chichester, UK.
- Hampe, C.L. (1984). A description of species composition, population structures, and spatial patterns in a Missouri oak-hickory forest. Thesis, University of Missouri, St. Louis, MO.
- Harms, K.E., Wright, S.J., Calderón, O., Hernández, A. & Herre, E.A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404, 493–495.
- HilleRisLambers, J., Clark, J.S. & Beckage, B. (2002). Density-dependent mortality and the latitudinal gradient in species diversity. *Nature*, 417, 732–735.
- Hubbell, S.P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, 203, 1299–1309.
- Hubbell, S.P., Ahumada, J.A., Condit, R. & Foster, R.B. (2001). Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecol. Res.*, 16, 859–875.
- Huston, M.A. (2014). Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. *Ecology*, 95, 2382–2396.
- Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.
- Johnson, D.J., Beaulieu, W.T., Bever, J.D. & Clay, K. (2012). Conspecific negative density dependence and forest diversity. *Science*, 336, 904–907.
- Johnson, D.J., Bourg, N.A., Howe, R., McShea, W.J., Wolf, A. & Clay, K. (2014). Conspecific negative density-dependent mortality and the structure of temperate forests. *Ecology*, 95, 2493–532.
- Kardol, P., Martijn Bezemer, T., Der Putten, V. & Wim, H. (2006). Temporal variation in plant–soil feedback controls succession. *Ecol. Lett.*, 9, 1080–1088.
- Kobe, R.K. & Vriesendorp, C.F. (2011). Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecol. Lett.*, 14, 503–510.
- Lin, L., Comita, L.S., Zheng, Z. & Cao, M. (2012). Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *J. Ecol.*, 100, 905–914.
- Liu, X., Liang, M., Etienne, R.S., Wang, Y., Staehelin, C. & Yu, S. (2012). Experimental evidence for a phylogenetic Janzen–Connell effect in a subtropical forest. *Ecol. Lett.*, 15, 111–118.
- Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M., Valencia, M.C. & Sanchez, E.I., *et al.* (2010). Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, 466, 752–755.
- Metz, M.R., Sousa, W.P. & Valencia, R. (2010). Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology*, 91, 3675–3685.
- Nelson, P.W. (2010). *The Terrestrial Natural Communities of Missouri*, 2nd edn. Missouri Department of Conservation, Jefferson City, MO.
- Packer, A. & Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, 404, 278–281.
- Paine, C.E.T., Harms, K.E., Schnitzer, S.A. & Carson, W.P. (2008). Weak competition among tropical tree seedlings: implications for species coexistence. *Biotropica*, 40, 432–440.
- Paine, C.E.T., Norden, N., Chave, J., Forget, P., Fortunel, C. & Dexter, K.G., *et al.* (2012). Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecol. Lett.*, 15, 34–41.
- Pianka, E.R. (2011). *Evolutionary Ecology*, 7th edn. Harper Collins, New York, NY.

- Spasojevic, M.J., Yablon, E.A., Oberle, B. & Myers, J.A. (2014). Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere*, 5, 1–10.
- Terborgh, J. (2012). Enemies maintain hyperdiverse tropical forests. *Am. Nat.*, 179, 303–314.
- Wills, C., Harms, K.E., Condit, R., King, D., Thompson, J. & He, F., *et al.* (2006). Nonrandom processes maintain diversity in tropical forests. *Science*, 311, 527–531.
- Wright, J.S. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, 130, 1–14.
- Yenni, G., Adler, P.B. & Ernest, S.M. (2012). Strong self-limitation promotes the persistence of rare species. *Ecology*, 93, 456–461.
- Zhu, K., Woodall, C.W., Monteiro, J.V. & Clark, J.S. (2015a). Prevalence and strength of density-dependent tree recruitment. *Ecology*, 96, 2319–2327.
- Zhu, Y., Comita, L.S., Hubbell, S.P. & Ma, K. (2015b). Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. *J. Ecol.*, 103, 957–966.
- Zimmerman, M. & Wagner, W.L. (1979). A description of the woody vegetation of oak-hickory forest in the northern Ozark highlands. *Bull. Torrey Bot. Club*, 106, 117–122.

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