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abstract protons faster from the cytoplasmic than from the periplasmic side. The rate of proton abstraction must be reversed for NO intermediates, perhaps because a high  $pK_a$  value prohibits protonation from a donor loaded from the cytoplasm (33, 34). How these intricate processes are spatially and temporally coordinated on an atomic scale remains open. The structure will, however, facilitate focused site-directed mutagenesis and functional experiments that will contribute to a better understanding of the fundamental HCO reaction and of redox-driven proton translocation processes in general.

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Figs. S1 to S3

Table S1

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# Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community

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The factors determining species commonness and rarity are poorly understood, particularly in highly diverse communities. Theory predicts that interactions with neighbors of the same (conspecific) and other (heterospecific) species can influence a species' relative abundance, but empirical tests are lacking. By using a hierarchical model of survival for more than 30,000 seedlings of 180 tropical tree species on Barro Colorado Island, Panama, we tested whether species' sensitivity to neighboring individuals relates to their relative abundance in the community. We found wide variation among species in the effect of conspecific, but not heterospecific, neighbors on survival, and we found a significant relationship between the strength of conspecific neighbor effects and species abundance. Specifically, rare species suffered more from the presence of conspecific neighbors than common species did, suggesting that conspecific density dependence shapes species abundances in diverse communities.

**A**n understanding of the causes of commonness and rarity in ecological communities is essential for determining how communities are structured and for designing

effective strategies for biodiversity conservation (1–3). However, such understanding has eluded scientists (3–5), particularly in highly diverse communities such as tropical forests (6), where hundreds of species coexist with abundances that vary by several orders of magnitude. In these communities, individuals that are surrounded by neighbors of the same species (that is, conspecifics) often exhibit lower growth and survival (7–11). This phenomenon is attributed to shared natural enemies or strong intraspecific competition for resources (12, 13). Many studies have emphasized the importance of such negative density dependence (NDD) for species coexistence

(14–17), yet little attention has been paid to variation among species in the strength of NDD experienced and the possible consequences of that variation for determining species abundances (11).

The strength of NDD that is experienced by a species, defined here as the degree to which an individual's probability of survival is reduced by the addition of a conspecific neighbor, could, in theory, be positively or negatively related, or unrelated, to species abundance in natural communities. First, rare species may be rare because they suffer more when local densities are high (11), resulting in a positive relationship between the effect of conspecific neighbors and species abundance in the community (that is, more-common species are less negatively affected by conspecifics). Alternatively, rare species may occur at densities that are too low to sustain viable populations of specialist enemies (18) and thus may be less affected by density dependence than more-common species are (19). Another possibility is that the strength of NDD varies among species but shows no relationship to species abundance in the community. Species abundance is influenced by a number of factors, including habitat affinity (2), regeneration requirements (20), and resource use (21), which could override the effect of NDD on abundance. Landscape-scale processes, such as predator satiation and long-distance seed dispersal (22, 23), may further decouple the relationship between species abundance and NDD, which typically acts over smaller spatial scales [ $<30$  m (11)].

To evaluate these competing hypotheses, we used a hierarchical Bayesian approach (24)

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to analyze recently collected data from 20,000 1-m<sup>2</sup> seedling plots in the lowland tropical forest of Barro Colorado Island (BCI), Panama. We specifically evaluated how survival was influenced by the density and identity of neighboring seedlings and trees. A key challenge in quantifying interspecific variation within diverse plant communities is that many species occur at extremely low densities, making it infeasible to collect sufficient data for meaningful statistical analyses at the species level for most species (25). Previous studies of density dependence have dealt with this by limiting analyses to the most abundant species in the community [for example (15, 16)] or lumping species into broad functional groups [for example, (8)] or abundance classes [for example, (11)]. In contrast, our hierarchical (that is, mixed model) approach allows us to quantify the distribution of density-dependent effects and their relationship to abundance across the entire community, including rarer species, while properly accounting

for differences in sample size, and thus confidence (25), among the 180 tree species encountered. We used a two-level hierarchical model in which individual survival is a species-specific function of the density of conspecific and heterospecific neighbors, and species-level parameters are functions of species abundance in the community (26). We also included shade tolerance as a species-level covariate in the model, because shade tolerance may influence both species abundance and the strength of NDD in tropical tree communities (27, 28). In this way, we not only quantified the strength and variation of NDD for the community but also tested whether variation in the effect of neighbors among species is related to differences in relative abundance or life-history strategy (specifically, shade tolerance).

We found significant variation in the strength of NDD among tree species in the BCI forest (Fig. 1). At the community level, both conspecific seedling and conspecific adult neighbors had a significant negative effect on the probabil-

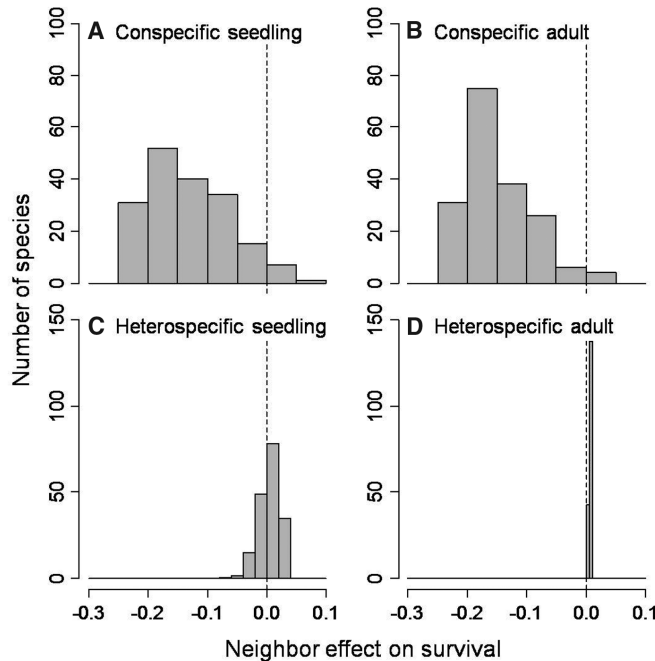
ity of seedling survival (Table 1). The strength of conspecific neighbor effects varied widely among species but was overwhelmingly negative (Fig. 1, A and B, and table S2). In contrast, effects of heterospecific seedling and adult neighbors were close to zero, with community-level means weakly positive (Fig. 1, C and D, and table S2). Compared with the variation in conspecific neighbor effects, heterospecific neighbor effects varied little among species (Fig. 1). Thus, our results suggest a limited role for heterospecific density in driving patterns of seedling survival, although heterospecific neighbors may have stronger effects at later life stages.

A significant portion of the variation among species in conspecific neighbor effects was explained by species abundance in the community. The effect of conspecific neighbors on survival was significantly and positively related to species abundance, with less-common species experiencing stronger NDD (Table 1 and Fig. 2). This relationship was found for both seedling and adult neighbors, with stronger statistical support at the seedling stage (Table 1). In principle, these relationships might be driven by shade tolerance, because light-demanding species are expected to be both rarer and more vulnerable to natural enemy attack than shade-tolerant species are (29). However, we found that species shade tolerance explained little of the variation in the strength of conspecific neighbor effects (Table 1). Conversely, effects of heterospecific neighbors were not related to species abundance in the community but were related to shade tolerance (Table 1), which is consistent with the fact that light-demanding species are more sensitive to shading by neighbors. Thus, our results indicate that species interactions with conspecific, but not heterospecific, neighbors influence species relative abundance, and this relationship is not explained by variation in species shade tolerance.

In the BCI tree community, species abundances range over more than four orders of magnitude (table S1). Our results indicate that this variation can be explained, in part, by variation in the strength of NDD experienced by species. These results suggest that local-scale density dependence constrains a species' abundance in a community and that these constraints vary among species. In our system, the most common species are those whose seedling survival is minimally affected by the local density of conspecific neighbors. In contrast, species having a strong impact on themselves typically occur at lower abundances.

Negative conspecific effects have been linked to abundance in a previous study of native and invasive species in a temperate old field (a post-agriculture successional community) (30), in which abundance was negatively related to the rate and degree to which species accumulated host-specific pathogens in the soil. Our results indicate that the extent to which species inhibit their own regeneration shapes species abundances not only during succession and invasion, but also in intact systems. In addition, given that previous studies of NDD have typically focused on the most common

**Fig. 1. (A to D)** Distribution of effects of conspecific and heterospecific neighbors on seedling survival. Histogram bars are based on posterior means of coefficients for 180 tree species in central Panama. Bars to the left of the dashed zero line indicate species whose survival is reduced by increasing density of neighbors. The same scale is used for the x axis in all panels to facilitate comparisons.

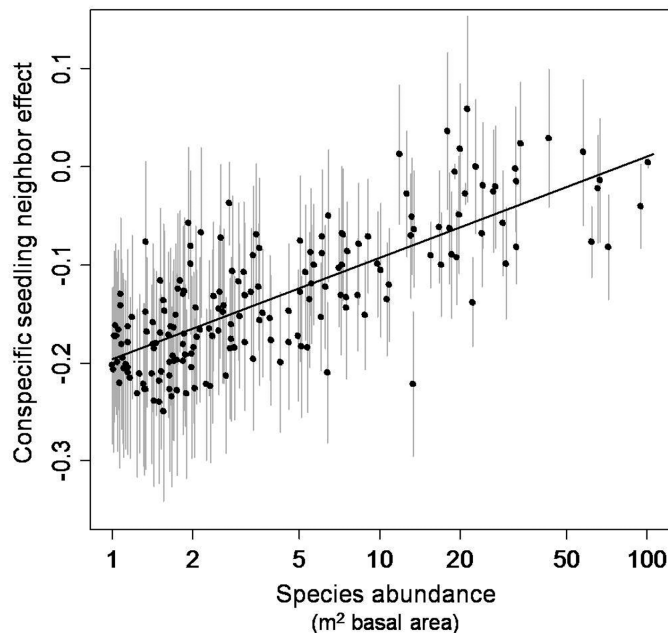


**Table 1.** Coefficient means ( $\pm 1$  SD) from the hierarchical Bayesian model of seedling survival. Survival was modeled as a function of the density of neighboring conspecific (CON) and heterospecific (HET) seedlings (S) and adult tree basal area (BA). The probability of survival ( $p$ ) for a seedling of species  $j$  in plot  $k$  was modeled as  $\text{logit}(p_{jk}) = \beta_{0j} + \beta_{1j} \times \text{CONS}_{jk} + \beta_{2j} \times \text{HETS}_{jk} + \beta_{3j} \times \text{CONBA}_{jk} + \beta_{4j} \times \text{HETBA}_{jk} + \phi_k$ , where  $\phi_k$  is a random effect for seedling plot. Values for each parameter ( $\beta_m$ ) varied among species, and were modeled as functions of size-weighted species abundance (ABUND) and shade tolerance (SHADE), where  $\beta_{mj} = \gamma_{m0} + \gamma_{m1} \times \text{ABUND}_j + \gamma_{m2} \times \text{SHADE}_j$ . Means were calculated from posterior distributions. Bold values are significantly different from zero (based on 95% credible intervals). Species information and species-specific estimates are presented in tables S1 and S2.

Survival model parameters	Intercept ( $\gamma_0$ )	Species-level predictors	
		Abundance ( $\gamma_1$ )	Shade tolerance ( $\gamma_2$ )
Intercept ( $\beta_0$ )	<b>-1.464 (0.285)</b>	0.120 (0.146)	<b>0.598 (0.141)</b>
Conspecific seedling effect ( $\beta_1$ )	<b>-0.133 (0.036)</b>	<b>0.045 (0.019)</b>	-0.029 (0.016)
Heterospecific seedling effect ( $\beta_2$ )	0.005 (0.006)	-0.004 (0.003)	<b>0.013 (0.005)</b>
Conspecific adult effect ( $\beta_3$ )	<b>-0.150 (0.037)</b>	0.032 (0.019)	0.008 (0.023)
Heterospecific adult effect ( $\beta_4$ )	<b>0.006 (0.001)</b>	-0.001 (0.001)	0.001 (0.001)



**Fig. 2.** The mean strength of conspecific NDD exhibited by individual tree species on BCI (points; vertical gray lines show  $\pm 1$  SD) is significantly related to size-weighted species abundances in the 50-ha Forest Dynamics Plot. The overall relationship fitted by the hierarchical Bayesian model is strongly positive (black line), indicating that rare species experience stronger density dependence than common species do.



species in the community, which we show exhibit the least NDD, our results indicate that past studies probably underestimated both the variation and the mean strength of density dependence in plant communities.

The mechanisms underlying the observed NDD are an important area for future investigation. In tropical forests, negative effects of conspecific neighbors are commonly thought to result primarily from density-dependent, host-specific natural enemies (12, 13), with several studies suggesting that soil pathogens play a key role at the seedling stage (23). Recent field and growing-house experiments on a subset of the species analyzed here found that soil pathogens were key drivers of density dependence, with a significant relationship between species sensitivity to negative plant-soil feedbacks and species abundance in the forest (31), which is consistent with the results presented here. Strong intraspecific competition for shared resources could, in theory, also contribute to density dependence, but probably plays a small role in explaining the patterns we found, because competition between seedlings has been shown to be weak or nonexistent in tropical forests (32). Within communities, differences among species in vulnerability to natural enemies could relate in part to the degree to which species are well adapted to the local environment; that is, species at the edge of their habitat tolerances may be more vulnerable to or less able to recover from attack. Regardless of the specific mechanisms operating, the clear negative effect of conspecific neighbor densities across the community emphasizes the importance of local-scale interactions in driving spatial patterns of survival and shaping species abundances in tropical forests.

The significant variation in NDD among species reported here and its relationship to abundance suggest that theoretical models of plant communities should incorporate this asymmetry.

Current models that include NDD almost invariably assume that it is identical in strength across all species (33). One such model, the symmetric density-dependent neutral model (34), nonetheless succeeds in providing a good fit to the species-abundance curve for the BCI tree community and other tropical forests, but recent studies show that fits to species abundance distributions are not strong tests of theoretical models, because models with different underlying mechanisms can provide equally good fits (21, 35). That we found the strength of NDD to be related to species abundance confirms that the variation in NDD is not only statistically significant but also biologically meaningful. This underscores the need to incorporate species asymmetry into future theoretical efforts (33). Understanding of the processes structuring diverse communities may be better advanced by shifting focus away from the shape of the species-abundance curve to assessing what determines the position of species on the curve (35).

Our results also have important implications for biodiversity conservation. Understanding the drivers of species abundance is critical for identifying and protecting rare species that have an inherently higher risk of extinction (2). Previous efforts to identify key traits that correlate with species rarity have had limited success (3, 5). The results here suggest that such studies should look beyond morphological and physiological traits to include species sensitivity to biotic interactions, namely, the degree to which species inhibit their own regeneration.

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