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Abundance-dependent effects of neighbourhood dissimilarity and growth rank reversal in a neotropical forest

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Why tropical forests harbour an exceptional number of species with striking differences in abundances remains an open question. We propose a theoretical framework to address this question in which rare species may have different extirpation risks depending on species ranks in tree growth and sensitivities to neighbourhood interactions. To evaluate the framework, we studied tree growth and its responses to neighbourhood dissimilarity (ND) in traits and phylogeny for 146 species in a neotropical forest. We found that tree growth was positively related to ND, and common species were more strongly affected by ND than rare species, which may help delay dominance of common species. Rare species grew more slowly at the community-wide average ND than common species. But rare species grew faster when common species tended to dominate locally, which may help reduce extirpation risk of rare species. Our study highlights that tree growth rank among species depends on their responses to neighbourhood interactions, which can be important in fostering diversity maintenance in tropical forests.

1. Introduction

Most tropical forests support hundreds of co-occurring tree species, most of which are rare, but a few are common [1]. Why common species do not dominate these forests remains an open question. Theories propose that both species difference in niches (i.e. niche theory) and similarity in competitive ability (i.e. neutral theory) can help species to coexist [2–6]. Conspecific negative density dependence (CNDD) is one of the most important niche-based processes that promote high diversity when species limit themselves more than they limit heterospecifics [2,3,7]. Both conspecific and heterospecific interactions can vary across species, which may further modify species abundances and community structures. For instance, previous studies have suggested that the strength of CNDD varies with species abundance, but the results are not always consistent, with reports of positive [8–10], negative [11–15], equivocal or mixed relationships [16–18]. The role of neighbourhood interactions in structuring species-rich communities remains uncertain.

At least two limitations of previous analyses might contribute to this uncertainty. The first limitation concerns lumping all heterospecifics into a single homogeneous group [8,10,13]. Heterospecifics can vary greatly in their effects on focal tree performance with phylogenetic distance and/or trait distance from focal species, leading to large dissimilarity among neighbourhoods even when densities are constant [19–25]. Heterospecifics usually account for a larger proportion of neighbours than do conspecifics in tropical forests, so it is important to more fully characterize neighbourhoods. Trait- and phylogeny-based approaches provide the information to differentiate among heterospecifics and
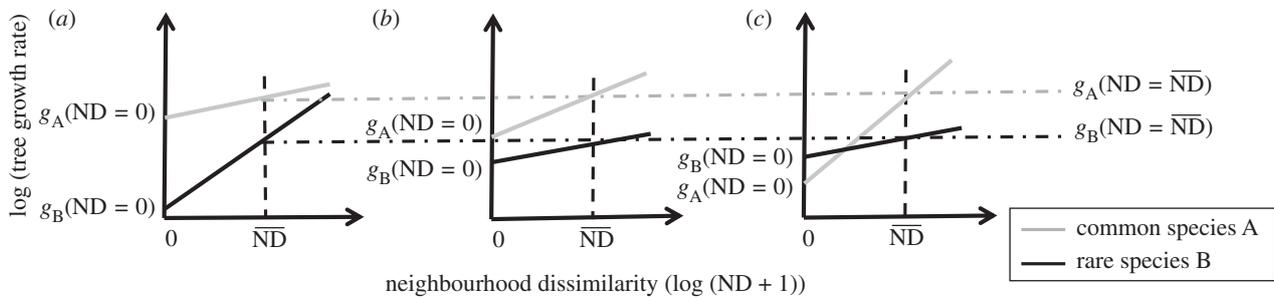
Figure 1. Conceptual diagrams illustrating three potential scenarios of diversity maintenance, arising from species variation in tree growth rates and responses to neighbourhood interactions (e.g. ND). Communities are composed of one common (A, grey) and one rare (B, black) species. The x-axis represents ND based on trait or phylogenetic information. Individuals of common species A have faster tree growth rates than do rare species B at community-wide average ND ($\overline{\text{ND}}$). Tree growth is positively related to ND for both species. Three scenarios may lead to different extirpation risks for rare species B. (a) Highest risk: common species A is subjected to weaker ND effect than rare species B, and their growth lines do not cross between zero ND and community-wide average ND. (b) Medium risk: ND effect is slightly stronger for common species A than rare species B, and their growth lines do not cross within the possible range of ND values. (c) Lowest risk: common species A is subjected to much stronger ND effect than rare species B, and their growth lines cross between zero ND and community-wide average ND.

better describe neighbourhood interactions. Interspecific interactions are usually influenced by functional trait similarity [20,24]. Some functional traits tend to be conserved phylogenetically [19,26], and closely related species also tend to share natural enemies [27] and have similar niches [23]. Therefore, trait- and phylogeny-based approaches allow us to better characterize how individuals respond to neighbourhood with dissimilar characteristics.

The second limitation is that most empirical CNDD analyses focus only on species variation in the strength of CNDD while usually overlooking species difference in demographic performance (e.g. species average tree growth and survival rates) [10,11,13,18] (but see [8]). Interspecific differences in demographic performance can overwhelm CNDD effects and prevent coexistence even when CNDD is strong [2,3]. Thus, interspecific differences in the strength of CNDD are insufficient to determine the dynamics of common and rare species. We must also assess species variation in demographic performance besides neighbourhood interactions.

We propose an analytical framework to evaluate how species variation in one component of tree demographic performance (tree growth) together with its response to neighbourhood dissimilarity (ND) can have different implications for diversity maintenance (figure 1). To our knowledge, our framework is the first one to integrate both aspects of species variation in explaining the roles of density dependence in fostering diversity maintenance. We hypothesize that species responses to ND may vary across species (i.e. rare and common) and species rank in tree growth may reverse depending on ND magnitude (figure 1). Depending on how ND influences tree growth, rare species may experience different extirpation risks (three hypothesized scenarios presented in figure 1 and *Theoretical framework*). We tested our framework using data from a neotropical forest in Panama. We found that individuals of common species grew faster than rare species in a community-wide average neighbourhood. However, this growth rank reversed when common species tended to dominate locally due to stronger limitation by similar neighbours, which may help reduce the extirpation risk of rare species.

2. Material and methods

(a) Theoretical framework
We assume a hypothetical community composed of two tree species, one common (A) and one rare (B). Focal tree growth

increases with ND, defined as dissimilarity in trait and/or phylogeny between a focal tree and its neighbours. Higher ecological dissimilarity is expected to diminish negative neighbourhood effects, leading to faster tree growth [20,24]. Thus, growth rates are positive, saturating functions of ND for both species, $g_A(\text{ND})$ and $g_B(\text{ND})$ (note the log scale and slopes less than 1 in figure 1). We assume that common species A is better suited to the community-wide average abiotic and biotic environment, including ND, than rare species B [3,5,28–30]. Thus, when ND = $\overline{\text{ND}}$ (community-wide average ND, while all others equal), individuals of common species A grow faster than do rare species B such that $g_A(\text{ND} = \overline{\text{ND}}) > g_B(\text{ND} = \overline{\text{ND}})$ (figure 1). Species can vary in responses to neighbourhood interactions (i.e. difference in the slopes of growth–ND relationships) and tree growth at local/neighbourhood mono-dominance (i.e. tree growth at ND = 0). We then examine three potential scenarios in which species variation in tree growth rates and responses to ND may have different implications to species dynamics. Rare species B may have the highest extirpation risk when it is subjected to stronger ND effects than common species A (the first scenario, figure 1a). With weaker ND effects, rare species B may have the lowest or medium extirpation risk when growth rank reverses (the last scenario, figure 1c) or not (the second scenario, figure 1b), respectively.

(i) In the first scenario, common species A is subjected to weaker ND effect (i.e. flatter slope in figure 1a), and thus weaker *self-limitation* than rare species B (assuming that the weaker ND effect is primarily contributed by conspecifics). Therefore, neighbourhood interactions may have the weakest effects among the three scenarios in delaying the dominance of common species A. The strong ND effect for rare species B may enable rare species B to recover its population quickly, but the strong *self-limitation* can also restrain its population size [31], which may increase the risk of stochastic extirpation in the long term [32].

(ii) In the second scenario, ND effect is slightly stronger for common species A than rare species B, and there is no intersection or growth rank reversal within the possible range of ND values (figure 1b). A stronger effect of ND may occur for common species when rare species host fewer specialized natural enemies [33] or have lower disease transmission rates through the dilution effect [34]. In this case, neighbourhood interactions can operate to delay the dominance of common species A but with limited strength. Rare species B only obtains a small relative growth advantage when common species A tends to dominate locally (i.e. ND of common species A approximates to zero), and thus has a medium risk of extirpation.

(iii) In the last scenario, common species A is subjected to much stronger ND effect than rare species B, and their growth lines cross between $ND = 0$ and $ND = \overline{ND}$ (figure 1c). The strong *self-limitation* for common species A indicates the important roles of neighbourhood interactions in delaying the dominance of common species A. The intersection of both lines reverses the growth rank at $ND = 0$ (i.e. $g_A(ND = 0) < g_B(N = 0)$) from $ND = \overline{ND}$ (figure 1c). This rank reversal grants rare species B a growth advantage relative to common species A when common species A tends to dominate locally (note that ND of common species A will approximate to zero when common species A tends to dominate locally, while ND of rare species B will be larger than $\overline{ND}$ when common species A tends to dominate locally, and growth increases with ND; therefore, we can derive $g_A(ND = 0) < g_B(ND = 0) < g_B(ND|ND > \overline{ND})$), which can reduce the risk of local extinction for rare species B.

(b) Empirical approach

To evaluate the three hypothetical scenarios (figure 1), we fitted spatially explicit individual-based hierarchical Bayesian models using tree diameter growth, traits and phylogeny data collected for 146 species in a 50 ha tropical forest plot. First, we assessed how tree growth rate responds to variation of ND in functional traits and/or phylogeny between a focal tree and its neighbours. Then we tested how species of different abundances vary in their responses to ND (discriminating between scenario (a) and scenarios (b) and (c) in figure 1), and in tree growth ranks at community-wide average ND and zero ND (discriminating between scenarios (b) and (c) in figure 1), respectively. We present an overview of the methods in the main text below, while we provide the complementary details in the electronic supplementary material.

(i) Study site

This study uses tree census data from a 50 ha plot of neotropical forest located on Barro Colorado Island (BCI), Panama (9°10′ N, 79°51′ W) [35–37]. Within the plot, all free-standing woody stems greater than or equal to 1 cm diameter at breast height (DBH) were mapped, measured and identified to species using standardized methods [36]. We used census data for 2000 and 2005.

(ii) Diameter growth rate

For every tree alive in 2000, we identified its neighbours within a radius of 30 m. To avoid edge effects, trees less than or equal to 30 m from the plot edge were excluded as focal plants. The 30 m cut-off was chosen because previous research at this forest found that neighbourhood conspecific effects were insignificant beyond this distance [38]. Preliminary analyses using other radius cut-offs (25 and 35 m) showed qualitatively similar results (electronic supplementary material, figures S1–S4). For each focal tree, we calculated its annual absolute diameter growth from 2000 to 2005. We obtained a dataset containing 125 514 growth records for 261 species after procedures of data quality controls (see the electronic supplementary material).

(iii) Species abundance

We calculated species abundance as the sum of basal area of all living stems from each species present in the 50 ha plot based on the DBH measurement taken in 2000. We used species-specific basal area instead of number of individuals to measure species abundance because this metric may better capture resource space occupied and natural enemies held by a species, given the high tree size variation in natural forests [8,15].

(iv) Shade tolerance

We found that shade-tolerant species had slower tree growth rates and were less sensitive to neighbourhood interactions than shade-intolerant species in our previous work [24]. Thus, we included shade tolerance as a covariate when assessing abundance-dependent effects of neighbourhood interactions and growth ranks. We defined species with higher shade tolerance as those with lower diameter growth and mortality rates of saplings or poles following Comita *et al.* [8] (see the electronic supplementary material). After excluding the 80 species missing shade tolerance information, we retained 102 471 growth records for 181 species. The correlation between the shade tolerance index and log-transformed species abundance is not significant ($r = 0.063$, $p = 0.398$).

(v) Neighbourhood dissimilarity

For each growth record, we calculated its trait dissimilarity from a focal tree to its neighbours in 2000 using three traits (electronic supplementary material, table S1): maximum height (mean height of up to six largest individuals in the 50 ha plot), wood density (WD) and leaf mass per area (LMA). Maximum height determines tree species' abilities to intercept light in forests [39]. Both WD and LMA are associated with a trade-off between rapid resource acquisition and high tolerance to environmental stress [39,40]. Maximum height, WD and LMA are all conserved in phylogeny [19]. Trait measurement methods can be found in [40]. We calculated neighbourhood trait dissimilarity as the weighted average trait distance between a focal tree and all its neighbours [24,41]. We weighted the pairwise trait distance by neighbour tree basal area and inversely by spatial distance (see the electronic supplementary material) because larger and spatially closer neighbours are expected to have a greater influence on focal trees [20]. As niche differences are co-determined by multiple traits [42], we also calculated the multi-trait-based ND through measuring the Euclidean trait distance in standardized three-dimensional trait space [41].

We also calculated phylogenetic dissimilarity of each focal tree to its neighbours. Phylogenetic distance was assessed as the cophenetic distance in the phylogenetic tree, and has units of millions of years. We calculated neighbourhood phylogenetic dissimilarity as the weighted average phylogenetic distance between a focal tree and all its neighbours. The weight function was defined the same as that in calculating neighbourhood trait dissimilarity. We used a node age-calibrated phylogenetic tree based on molecular markers sampled from this forest [43] and extracted the 181 species present in our analyses.

(vi) Abundance-dependent effects of neighbourhood dissimilarity and growth ranks

We constructed hierarchical Bayesian models to assess how species with different abundances vary in their responses to ND, and their growth ranks at community-wide average ND and zero ND, respectively. We first excluded the 35 extremely rare species with less than 10 focal individuals because their small sample sizes preclude reliable estimates of species-level ND effects. Thus, the subsequent analyses contained 146 species.

We modelled the expected true absolute growth rate of focal tree i of species j ($\overline{TAGR_{i,j}}$), after correcting measurement errors (see the electronic supplementary material), as a power function of initial DBH ($DBH_{i,j}$), neighbourhood crowding ($NC_{i,j}$) and ND ($ND_{i,j}$). The model is similar to the model used in our previous research [24]:

$$\log(\overline{TAGR_{i,j}}) = \beta_{0,j} + \beta_{1,j} \times \log(DBH_{i,j}) + \beta_{2,j} \times \log(NC_{i,j})$$
$$+ \beta_{3,j} \times \log(ND_{i,j} + 1) + \varphi, \qquad (2.1)$$

where φ represents a normally distributed random effect for 10×10 m quadrats, which was used to control spatial variation in tree growth possibly associated with environmental variation. Each independent variable was centred at its community-wide average and divided by its standard deviation (s.d.) for easier

interpretation and faster parameter convergence [44]. The community-wide average values of initial size, NC and ND were calculated over all focal individuals of all species in the community. The intercept ($\beta_{0,j}$) represents the log-transformed tree growth rate of species j at community-wide average DBH, NC and ND. We used $\log(ND_{i,j} + 1)$ instead of $\log(ND_{i,j})$ because we need to compare growth ranks at zero ND, and both methods produced similar results in our previous study [24]. We calculated NC for each focal tree as the sum of its neighbours' basal areas with inverse weighting by spatial distance.

At the second level, we modelled the species-specific intercept ($\beta_{0,j}$), and slopes associated with NC ($\beta_{2,j}$) and ND ($\beta_{3,j}$) as linear functions of the log-transformed species abundance and shade tolerance index (see the electronic supplementary material). The slope between species abundance and species-specific intercept ($\beta_{0,j}$) represents the $g_j(ND = \overline{ND})$ of figure 1 or the relationship between species-specific abundance and average tree growth rate at the community-wide average ND, after controlling species variation in shade tolerance. The slope between species abundance and species-specific slope of ND ($\beta_{3,j}$) represents the relationship between species-specific abundance and the slope of the growth–ND relationship in figure 1. We modelled NC effects as a function of log-transformed species abundance and shade tolerance because we expect common, shade-tolerant species to be more tolerant to crowding [24]. We modelled the initial size effect ($\beta_{1,j}$) as the sum of a community-wide average effect and a normally distributed species-level random effect because we lack explicit hypotheses about how size effect might vary with shade tolerance and abundance. We standardized log-transformed species abundance and shade tolerance index (zero mean and unit standard deviation) to facilitate parameter convergence [44].

We also conducted an analysis which decomposed the overall ND (including both conspecific and heterospecific neighbours) into a conspecific neighbourhood crowding and a heterospecific neighbourhood dissimilarity (HND). HND considers only the trait distances between a focal tree and its heterospecific neighbours, and used the same weight function as overall ND [24]. This analysis facilitates the comparison with previous studies focusing on CNDD and also allows us to test whether the ND effects might be primarily driven by negative effects of conspecifics [24]. We performed the decomposition analysis for NDs based on phylogeny and multiple traits only because the results associated with these two variables were more consistent with the predictions of our theoretical framework than the results from single trait-based NDs.

Finally, to examine whether growth rank reversed when common species tends to dominate locally, we predicted species-specific log-transformed growth rate at zero ND (Pred.log.AGR$_j$, while all other covariates are at their average). To assess the relationship between species abundance and growth rank at zero ND, we did a weighted linear regression with the posterior mean value of Pred.log.AGR$_j$ as response variable and the log-transformed species abundance and shade tolerance index as independent variables. The linear relationship was fitted by inversely weighting the range of 95% credible interval of Pred.log.AGR$_j$.

We conducted these analyses for individual-trait, multi-trait and phylogeny-based dissimilarity variables. We fitted all the Bayesian models using Markov chain Monte Carlo sampling techniques in JAGS 3.4.0 [45]. We set diffuse prior distributions for all parameters (see electronic supplementary material, for JAGS code). We ran three parallel chains and used Gelman and Rubin's convergence diagnostics to assess parameter convergence (a cut-off value of 1.1) [46].

(vii) Robustness of the empirical test

We repeated the analyses using other neighbourhood radius cut-offs or including the extremely rare species (electronic
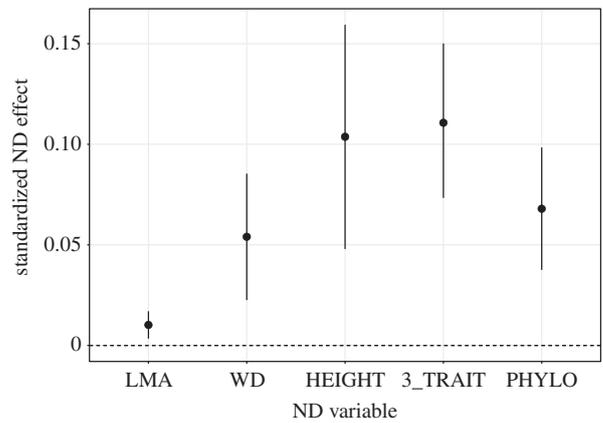

Figure 2. Standardized community-wide ND effects on tree growth from five models using ND variables based on LMA, WD, maximum height (HEIGHT), the joint three-trait (3_TRAIT) and phylogeny (PHYLO). Circles and lines show the means and 95% credible intervals of the coefficients, respectively. Filled circles represent significant results. Coefficients were considered as significant if their 95% credible intervals excluded zero.

supplementary material, figures S1–S6). We also used an alternative method, the group-level method (see the electronic supplementary material), where we separated the 181 species (146 + 35 extremely rare species) into three groups according to their ranks in species abundances, and then compared group-level responses to ND and growth ranks at community-wide average ND and zero ND (electronic supplementary material, figure S7). All these analyses produced qualitatively similar results.

3. Results

(a) Abundance-dependent effects of neighbourhood dissimilarity

We found significant community-level positive effects on tree growth for all five ND variables (based on LMA, WD, maximum height, multi-trait and phylogeny) ($\gamma_{3,0}$ in equation (S6) of electronic supplementary material; figure 2). Multi-trait and maximum-height-based NDs had the strongest effect on growth. When the overall NDs were decomposed into a conspecific and a heterospecific component, focal trees grew slower with more crowded conspecific neighbours or faster with heterospecific neighbours more dissimilar in multiple traits but not in phylogeny (electronic supplementary material, table S2). Larger ($\beta_{1,j}$ in equation (2.1)) and less crowded ($\beta_{2,j}$ in equation (2.1)) trees grew faster than smaller and more crowded trees (electronic supplementary material, figures S8–S9).

The ND effects varied across species, and were significantly positively related to species abundances for NDs based on maximum height and multi-trait ($\gamma_{3,1}$ in equation (S6) of electronic supplementary material; figures 3a and 4a–e), consistent with the hypothetical scenarios (b) and (c) (figure 1), indicating common species tend to be more strongly affected in their growth by differences in ND than rare species. The effect of phylogeny-based ND was also positively related to species abundance (figures 3a and 4e), although the effect was only marginally significant. Common species were subjected to more negative effects of conspecifics than rare species (electronic supplementary material, table S3), consistent with the hypothetical scenarios (b) and (c).
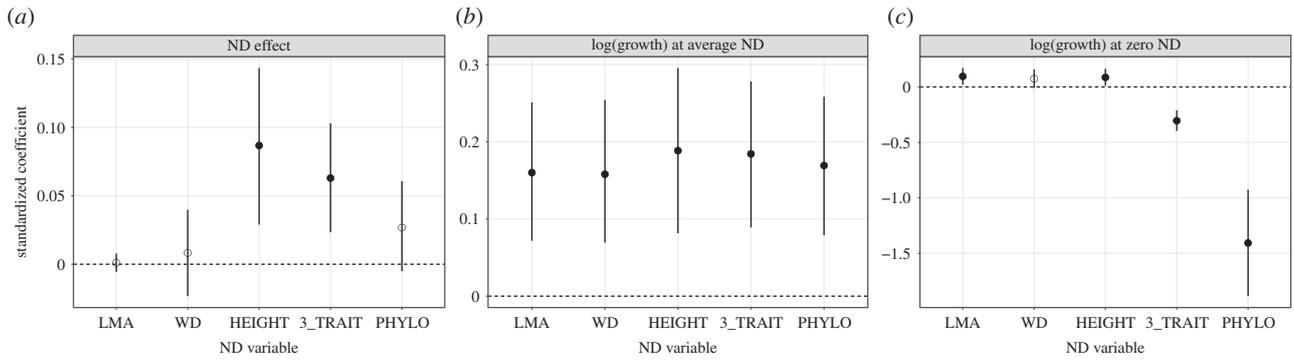
Figure 3. Standardized regression coefficients (the y-axis) representing the relationships between species-specific abundance and strength of ND effect (a), growth rate at community-wide average ND (b) and growth rate at zero ND (c), using five different ND variables shown at the horizontal axes (abbreviation defined in figure 2). Circles show the means of the coefficients. Lines represent the 95% CIs (credible or confidence intervals of coefficients). Filled circles represent significant results. Coefficients were considered as significant if their 95% CIs excluded zero.
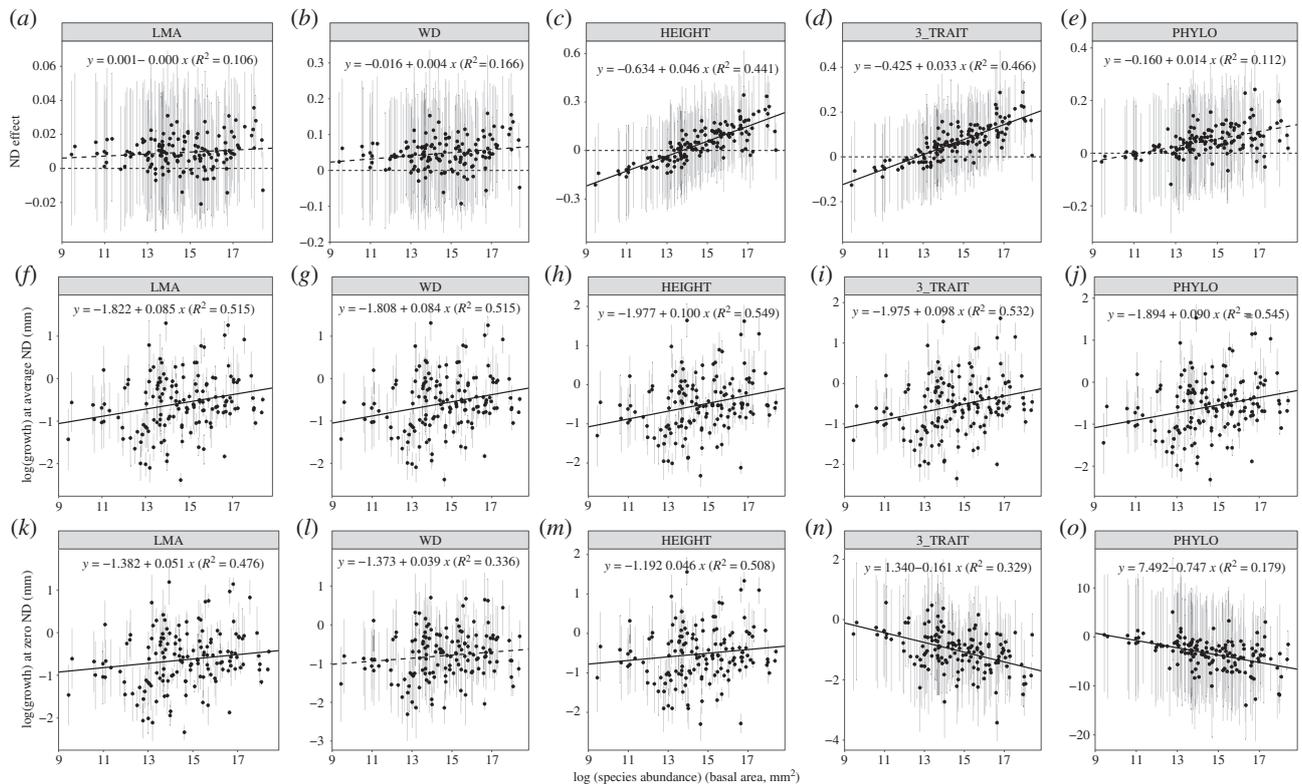

Figure 4. Relationships between species-specific abundance and ND effect (a − e), growth rate at community-wide average ND (f − j) and growth rate at zero ND (k − o), using five different ND variables (LMA, WD, HEIGHT, 3_TRAIT and PHYLO, as defined in figure 2). Circles and grey vertical lines show the means and 95% credible intervals of the species-specific coefficients, respectively. Black lines represent the fitted relationships, and solid black lines indicate significant results. Texts show the fitted equations, whose coefficients are in their original scale.

However, species-specific effects of heterospecific dissimilarity in phylogeny or multiple traits were not significantly related to species abundance (electronic supplementary material, table S3).

(b) Abundance-dependent growth ranks
Species-specific average growth rate at community-wide average ND ($g_{A \text{ and } B}(ND = \overline{ND})$ of figure 1) increased with species abundance for all five ND variables ($\gamma_{0,1}$ in equation (S6) of electronic supplementary material; figures 3b and 4f−j), consistent with all the three hypothetical scenarios in figure 1. This indicates that individuals of common species grew faster than did rare species at community-wide average abiotic and biotic environment.

Then we assessed the abundance-dependent growth rank at zero ND, a test of growth rank reversal discriminating between scenarios (b) and (c) of figure 1. We found rank reversal at zero ND for the cases of multi-trait and phylogeny (figures 3c and 4n,o), consistent with the hypothetical scenario (c) in figure 1, indicating that common species with greater growth rates at community-wide average biotic and abiotic environment (figures 3b and 4i,j) grew slower when they tended to dominate locally (zero ND) (figures 3c and 4n,o). However, we did not find the rank reversal for the NDs based on single traits (maximum height, WD and LMA) (figures 3c and 4k−m).

Shade tolerance was important in explaining species variation in ND effects, crowding effects and average growth rates (electronic supplementary material, figure S10).

Shade-intolerant species were subjected to stronger negative crowding effects and stronger positive ND effects than shade-tolerant species. Individuals of less shade-tolerant species grew faster than did shade-tolerant species. Species of different abundances also varied in their responses to crowding, with common species more tolerant to negative crowding effect (electronic supplementary material, figure S11).

4. Discussion

A major goal of our study was to evaluate ND effect on tree growth and its variation across species. Consistent with previous studies [20,21], our results showed significant positive community-level ND effects on tree growth. The decomposition analysis with multiple trait-based ND showed negative effects of conspecific crowding and positive effect of heterospecific dissimilarity on growth, suggesting that the overall positive ND effect was contributed by both the dilution of conspecifics and more dissimilar heterospecifics. These results indicate that having neighbours exhibiting different ecological roles improves the growth of focal species, and are in agreement with the niche partitioning theory [3,30].

We also assessed the relationships between species-specific ND effect and abundance. If rare species were subjected to stronger ND effect than common species (scenario (a) in figure 1), there may be weak dominance delaying effect for common species. If common species were more sensitive to ND (scenarios (b) and (c) in figure 1), the dominance delaying effect for common species can be stronger. Consistent with the latter case, we found positive relationships between species-specific abundances and the effects of NDs based on maximum height, multi-trait and phylogeny. These results indicate that common species are subjected to stronger *self-limitations*, which may help delay their dominance in the community. The finding of abundance-dependent positive ND effect suggests that species differences in ecological roles can delay dominance in two different ways. First, interspecific differentiation in niches weakens interspecific competition relative to intraspecific competition, thus leading to positive ND effects. Second, species differentiation in responses to ND leads to stronger *self-limitations* for common species and reduces their relative advantages over rare species. The magnitude of association between species abundance and neighbourhood identity effect was stronger for the multiple trait-based overall ND than its conspecific or heterospecific components, suggesting that both conspecifics and heterospecifics play important roles in the abundance-dependent positive ND effects.

The results of stronger positive ND effects for common species appear to contradict previous research performed in the same forest, which reported rare species experienced strongest CNDD effect on seedling survival [8]. Several causes may lead to this inconsistency: first, we measured neighbourhood density effect using trait- and phylogeny-based methods rather than in summing conspecific numbers or basal area. Second, we used tree diameter growth as response variable while seedling survival was evaluated in that previous study [8]. Different demographic components could be subjected to different ecological dynamics or same ecological dynamics but varying in importance across different ontogenetic stages [13,15,21,47–49]. Future studies need to integrate individual growth, survival and reproduction over all ontogenetic stages to project population growth rates.

For WD and LMA, we did not find significant positive relationships between species-specific ND effect and abundance. This could be an outcome of relatively weak positive community-level ND effects for the models based on these two traits, suggesting weak niche differentiation associated with these two individual traits. Each species is characterized by multiple traits, which might exhibit important trade-offs. Therefore, not every individual trait can always be strongly related to interactions and demographic performance [39,40]. This could be the case of analyses that considered WD and LMA as individual traits. LMA has been found to be weakly related to demographic performance in this forest [47]. Therefore, when all traits were combined and when phylogeny was used, the effects are stronger. Indeed, multiple trait-based metrics are recommended for better understanding of species interactions in a holistic perspective [42].

Besides species variation in ND effects, we also assessed species difference in tree growth, an aspect that has often been overlooked in earlier work on density dependence [10,11,13] but which is critical to understand the roles of density dependence in fostering diversity maintenance. Our study made an important contribution in this aspect by assessing species variation in average tree growth at both community-wide average ND and zero ND. Common species may have been better suited to the average biotic and abiotic environment of the community [3,5,28–30], and the relative growth advantage at community-wide average ND may be one indication of such higher suitability. As expected by our hypothesis, we found that individuals of common species grew faster than did rare species at community-wide average ND. Together with the findings of stronger positive ND effects for common species, our results imply that common species performing well at favourable average abiotic and biotic environment are also subjected to stronger *self-limitation* than rare species.

Then we assessed whether the abundance-dependent growth rank at zero ND can reverse from the rank at community-wide average ($ND = \overline{ND}$), which would allow discriminating between the hypothetical scenarios (b) and (c) in figure 1. Consistent with the prediction of line intersection in scenario (c), our results show that individuals of rare species grew faster than did common species at zero NDs in the cases of multi-trait and phylogeny-based models (i.e. growth rank reversed from $\overline{ND}$ to zero ND). Given the positive growth–ND relationships, the growth rank reversal suggests that rare species could obtain relative growth advantage to common species across a wide range of ND values (e.g. when NDs of rare species are larger than $\overline{ND}$) while common species tended to dominate locally (i.e. their NDs approximate to zero). Together with the strong *self-limitation* from stronger ND effects for common species, the growth rank reversal may help reduce the extirpation risk of rare species and foster diversity maintenance in this forest.

One critical extension of our study to previous work is that we evaluated the often overlooked species variation in tree growth in addition to variation in density dependence as a way to explore the roles of density dependence in fostering diversity maintenance. However, our analyses come with the following caveats. (i) Like many studies that evaluated species-rich ecosystems, our analyses used the mean trait values for species. However, there is important difference among conspecifics that might explain more variation in

growth among neighbouring individuals [50]. (ii) We limited our analyses in evaluating tree growth, but we note that assessing different responses (e.g. individual growth, survival and recruitment) at different ontogenetic stages (e.g. seedlings, saplings and adult trees) might produce different results, given the high complexity of species-rich ecosystems [15,21,47,48]. When considering multiple demographic components of different ontogenetic stages, mechanisms other than density dependence may also be important in maintaining species diversity, such as growth–survival trade-off [40] and ontogenetic trade-off [21]. Therefore, it will be of high priority for future research to integrate processes of different demographic components from different ontogenetic stages and examine the ultimate consequences for population growth rates and species diversity.

Our analytic framework is complementary to a previous study addressing the contribution of CNDD to diversity maintenance: Fricke & Wright [51] developed a metric of effective density-dependence mortality, and assessed its association with species abundance. This new metric considers both species-specific strength of density dependence (considered in our study) and the frequency of conspecific interactions (not considered in our study), while removing the impact of species-specific demographic rate (e.g. species average tree growth rate considered in our study). Integrating all these three aspects is complicated but may help finally resolve the inconsistency about the roles of density dependence in diversity maintenance.

5. Conclusion

For sessile organisms, the local biotic neighbourhood is crucial in determining their success and ultimately permanence in a community. In this study, we evaluated an analytic framework of three alternative scenarios regarding with species association in responses to neighbourhood interactions and tree growth rates. We found that common and rare species varied in their growth responses to neighbourhood interactions, which enables them to reverse their growth ranks at different neighbourhood environment. Our finding implicates that common or rare species are not always superior or inferior in a community, and suggests that species ranks in tree growth with changing neighbourhood interactions can be important in fostering diversity maintenance in tropical forests. Future studies could benefit from considering species variation in both demographic performances and responses to neighbourhood interactions, and from integrating multiple demographic rates and ontogenetic stages.

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