LETTER

Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest

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Abstract

Multiple niche-based processes including conspecific negative density dependence (CNDD) determine plant regeneration and community structure. We ask how interspecific and intraspecific density-dependent interactions relate to plant life histories and associated functional traits. Using hierarchical models, we analysed how such interactions affected first-year survival of seedling recruits of 175 species in a tropical forest, and how species abundances and functional traits are related to interspecific variation in density-dependent effects. Conspecific seedling neighbour effects prevailed over the effects of larger conspecific and all heterospecific neighbours. Tolerance of seedling CNDD enhanced recruit survival and subsequent abundance, all of which were greater among larger seeded, slow-growing and well-defended species. Niche differentiation along the growth–survival trade-off and tolerance of seedling CNDD strongly correlated with regeneration success, with manifest consequences for community structure. The ability of larger seeded species to better tolerate CNDD suggests a novel mechanism for CNDD to contribute to seed-size variation and promote species coexistence through a tolerance–fecundity trade-off.

Keywords

Conspecific, density dependence, functional traits, growth–survival trade-off, heterospecific, niche differentiation, seed mass, seedling survival, seed-size–seed-number trade-off, tolerance–fecundity trade-off.

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INTRODUCTION

Plant community structure and diversity integrate the effects of differential species performance relative to multiple interactions with the abiotic and biotic environment. This complexity has challenged ecologists to assess the ecological role of the functional adaptations and trade-offs involved in differential species performance and of the multiple interactions responsible for the observed abundance and coexistence of species (Adler *et al.* 2013). In species-rich tropical forests, studies suggest that species differentiation along resource and stress gradients as well as density-dependent interactions, especially with conspecifics, are two main causes of community structure and species coexistence. Most empirical studies have considered these two causes separately, so little is known about how they jointly affect species performance and community structure.

Functional traits have helped ecologists to understand differences in species performance and mechanisms of species coexistence. There is ample evidence that functional traits are associated with interspecific variation in growth, survival and reproduction and that trait differentiation often involves trade-offs that characterise species ecological strategies (or niches), which result in context-dependent variation in species performance (Reich 2014). In tropical forests for instance, the functional traits that enhance growth rates when light and other limiting resources are readily available trade-off against traits that enhance survival rates when resources are limiting (Kitajima & Poorter 2010; Wright *et al.* 2010; Sendall *et al.* 2015). Species (resource-niche) differentiation along this growth–survival trade-off explains species distributions and abundances along gradients of availability of resources such as light, water and nutrients (Reich 2014). A second widespread trade-off involves investment in numerous small seeds vs. fewer larger seeds. This seed-number–seed-size trade-off is hypothesised to confer greater fecundity and colonisation ability vs. greater competitive ability and stress tolerance (Moles & Westoby 2004; Muller-Landau 2010). The mechanisms that link growth–survival and seed-number–seed-size trade-offs to differential species success, community structure and species coexistence are uncertain (Moles & Westoby 2004; Muller-Landau 2010).

Most studies of trait-based differences in species performance focus on species average performance over gradients of abiotic stress or resource availability and do not consider density dependence (Kunstler *et al.* 2016). Studies of trait-based performance differences in relation to density-dependent

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interactions associated with conspecifics (henceforth, conspecific negative density dependence or CNDD) are extremely rare (Adler et al. 2013; Comita et al. 2014). This void is significant because CNDD is pervasive (Wright 2002; Comita et al. 2014), central to species coexistence and community structure, and linked to species (niche) differentiation. CNDD promotes coexistence because, at high conspecific densities, intraspecific interactions increase relative to interspecific interactions and conspecifics come to limit themselves more than other species (Chesson 2000; Adler et al. 2007). CNDD further influences community structure via its effects on species abundances (Comita et al. 2010; Chisholm & Muller-Landau 2011). CNDD is mediated by direct intraspecific competition for resources and/or by indirect effects of host-specific enemies, as predicted by the Janzen–Connell hypothesis and supported experimentally (Mangan et al. 2010; Terborgh 2012; Bagchi et al. 2014; Comita et al. 2014). CNDD is related to species differentiation because interspecific differentiation implies that conspecific individuals are most similar in resource requirements and natural enemies (Chesson 2000). Variation in the strength of CNDD among species with different ecological roles and strategies suggests further links between CNDD and species differentiation (Bagchi et al. 2014; Comita et al. 2014). Analysing the links between CNDD and the traits underpinning trade-offs and niche differentiation would advance a broader understanding of the functional dimensions of species ecological strategies and of (niche-based) mechanisms regulating species performance and plant communities.

In a previous study on how phylogenetic similarity influenced density-dependent (DD) interactions, we noted striking interspecific differences in mean seedling survival and susceptibility to DD interactions, especially with conspecifics (Lebrija-Trejos et al. 2014). Here, we use hierarchical Bayesian models to analyse, first, how such striking differences relate to variation in species functional traits and strategies (characterised by syndromes of covariation in traits), and second, how species abundances and community structure are affected. To the best of our knowledge, this is the first study to jointly analyse these relationships for tropical forests. We include traits consistently linked to two prominent performance trade-offs underpinning species ecological strategies, the growth–survival trade-off and the seed-number–seedling-survival trade-off. This allows us to infer functional links between species (niche) differentiation and CNDD. Results are based on functional traits of 175 species and 15 years of first-year survival of 34 851 newly recruited seedlings that co-occurred with 375 290 individuals of 439 species of seedlings and larger neighbours.

MATERIALS AND METHODS

Site and data collection

Barro Colorado Island, Panama (9.15° N, 79.85° W), supports tropical moist forest in the Holdridge Life Zone System. Annual rainfall averages 2600 mm, with just 10% falling during a 4-month dry season. Temperature averages ≈ 26 °C in every month. Community structure and dynamics of free-standing woody plants ≥ 1 cm diameter at breast height (DBH) were obtained from a 50-ha, old-growth Forest Dynamics Plot (FDP) established in 1982 and censused every 5 years since 1985 (Hubbell et al. 1999; Condit et al. 2012) (see Condit 1998 for methods). First-year survival of all newly emerged seedlings, hereafter called recruits, was obtained from 800 $1 - m^2$ seedling plots located around 250 seed-trap stations in the FDP. All woody seedlings and vines are censused each dry season in these plots (see Wright et al. 2005a for methods).

Neighbourhood characteristics

For each recruit, we determined the density of conspecific and heterospecific neighbours in two size classes: seedlings and larger plants. The density of seedling and larger neighbours were calculated as the number of individuals < 1 cm DBH within the same $1 - m^2$ plot as the focal recruit and as the number of trees ≥ 1 cm DBH within 1.15 crown radii of the $1 - m^2$ seedling plot, respectively. The crown radius of every individual ≥ 1 cm DBH was estimated from its DBH and allometric relationships between DBH and crown diameter of BCI trees (Muller-Landau et al. 2006). The distance for inclusion of larger neighbours is thus adjusted to the size of each individual neighbour (see Appendix S1A in Supporting Information and Lebrija-Trejos et al. (2014) for an overview of census data, details on crown radii selection and a description of the advantages of the variable-radius neighbour-selection approach).

Species characteristics

We selected eight key functional traits to assess whether functional traits were related to interspecific differences in mean first-year survival and strength of DD interactions. The traits included leaf mass per area (LMA), leaf nitrogen content (LN), leaf phosphorus content (LP), leaf lamina toughness (LTGH), lamina tissue density (LD), wood density (WD), maximum adult stature (H_{max}) and seed mass (SM). These traits relate to resource acquisition and competitive ability (LMA, LN, LP, WD, H_{max}, SM), physical defence (LMA, LTGH, LD, WD) and tolerance to stress by drought, shade, defoliation and mechanical damage (LMA, LTGH, LD, WD, SM). Moreover, they constitute the functional basis of the growth–survival trade-off (especially the first six traits listed; Kitajima & Poorter 2010; Wright et al. 2010; Reich 2014) and the seed-number–seedling-survival trade-off (SM; Moles & Westoby 2004; Muller-Landau 2010). We expressed leaf phosphorus and nitrogen content on both area and mass bases and refer to them as LP_{area}, LP_{mass}, LN_{area} and LN_{mass}. We used species scores on the first three Principal Component (PC) axes of a Principal Component Analysis (PCA) of traits as additional species characteristics. Appendix S1B provides details on trait data collection and the PCA.

To analyse how species performance differences affect community structure and, more specifically, whether abundant species have higher first-year survival and suffer less from DD interactions (Comita et al. 2010; Chisholm & Muller-Landau 2011), we also characterised species by their abundances (total number of individuals). Species abundances were estimated

for four ontogenetic stages: recruits, established seedlings, saplings and adults. Except for recruits, size classes were used as surrogates of ontogenetic stages. Established seedlings were defined as those that had survived two or more years after germinating and had stems < 1 cm DBH. Saplings and adults were smaller or larger than species-specific reproductive DBH-size thresholds respectively (thresholds were obtained from Wright *et al.* (2005b) and Visser *et al.* (2016)). We excluded species with reproductive size thresholds < 1 cm DBH from these performance-abundance analyses since reproductive adults were smaller than the size threshold for inclusion in the 50-ha FDP. This excluded species with $H_{max} < 4$ m. For comparison with other studies, species abundances were also characterised as the sum of the basal area of all individuals ≥ 1 cm DBH.

Analysis

We used generalised linear two-level hierarchical Bayesian models with a logit-link function to analyse 15 years of first-year survival data (alive/dead) and evaluate how interspecific variation in mean first-year survival and the strength of DD neighbour effects related to species characteristics (abundances, individual traits and positions along PC axes). Separate models were fitted for each species characteristic and each combination of PC axes. The first level of the hierarchical models specified individual survival as a species-specific linear function of average first-year survival (β_0) and the effects of the density of conspecific seedlings (CONS, β_1), large conspecifics (CONL, β_2), heterospecific seedlings (HETS, β_3) and large heterospecifics (HETL, β_4). In the second level of the hierarchical models, the species-specific β parameters of the first level of the model were a linear function of a single or multiple species characteristics n (i.e. abundances, traits or positions along PC axes). The gamma parameters ($\gamma_{0-4,n}$) of this second-level linear function represent relationships between species characteristics n and mean first-year survival (β_0) or neighbour effects on first-year survival (β_{1-4}). All models included random effects for seedling plot, seed-trap station (which group three or four nearby seedling plots), and year to capture spatial and temporal variation in survival. Appendix S1C provides detailed model specification and fitting procedure.

Models that included multiple species characteristics (namely multiple PC axes) were compared with the Widely Applicable Information Criterion (WAIC), a Bayesian extension of the Akaike Information Criterion recommended for hierarchical models (Gelman *et al.* 2013). We also used WAIC to compare each separate hierarchical model with a model excluding species characteristics (hereafter called the single-level model) and assess whether the addition of species characteristics improved the model fit by significantly increasing the interspecific variation in mean and DD survival explained. We report estimates of mean survival and DD effects based on the single-level model.

To account for differences in the natural variation of neighbour densities (CONS, HETS, CONL and HETL), we scaled (divided) the neighbour densities by their interquartile range (IQR), a basic but robust measure of variability. The slopes

of the IQR-scaled first-level model predictors (β_{1-4}) indicate the increase in DD- effects with an increase in neighbour density by a magnitude equal to the IQR of their distribution. The IQR equals the difference between the upper quartile (the 75th percentile value) and the lower quartile (the 25th percentile value). Thus, slopes β_{1-4} represent the change in effects from neighbourhoods with a typical 'low' (25th percentile) density to neighbourhoods with a typical 'high' (75th percentile) density of neighbours. We additionally ran a single-level model using raw densities to obtain estimates of per-capita effects. In all models, the intercept (β_0) indicates mean survival (in log-odds unless otherwise stated) when local-scale neighbour densities (i.e. within 1 m^2 and 1.15 crown radii) are set to zero. All species characteristics were standardised to Z scores. We used STAN 2.6.0 (Stan Development Team; http://mc-stan.org) called from R version 3.0.0 (R Core Team; http://www.r-project.org) for model fitting. Parameter estimates and their Bayesian credible intervals (CrI) were obtained from the quantiles of their posterior distributions. Results are statistically supported (significant) when 95% CrI do not overlap zero.

RESULTS

Neighbourhood characteristics

Table S1 provide summary statistics for neighbourhood density. The median size of neighbours ranged among years from 9.5 to 13.5 cm tall for seedling neighbours and from 10.3 to 10.5 cm DBH for larger neighbours. The median age of seedling neighbours was 1 or 2 years (for years with more than 80% of seedling of known age). The ages of larger neighbours are unknown.

Species characteristics

Table S2 provides the interspecific mean and range of values for the eight traits. The first three PC axes explained 75% of the variation in traits (Fig. S1), and none of the remaining PC axes included most of the variation of any individual trait (Table S3). The first three PC axes also corresponded closely to worldwide strategy spectra, including the leaf economics spectrum (PC1), the plant height and seed size spectrum (PC2), and the wood economics spectrum (PC3) (Fig. S1). Close correspondence means that traits associated with these spectra had Pearson's correlations > 0.71 with the corresponding PC axis (Table S3). PC axes were rotated as needed to ensure that increasing scores corresponded to shifts from cheaply constructed 'acquisitive' leaves to more costly 'conservative' leaves (PC1), from short to tall species and small to large seeds (PC2), and from light to dense wood (PC3).

First-year survival and density dependence

The density of all four types of neighbours affected recruit survival significantly (Table 1). Neighbour effects were negative except for the positive effect of heterospecific seedling neighbours. The per-capita effect of large neighbours was

Table 1 Neighbour effects on the log-odds of first-year seedling survival estimated by a single-level (logit) regression model and scaled by the interquartile range (IQR) and per-capita (in parentheses)

	Mean first-year survival [β₀]	Seedling neighbours		Large neighbours	
		Conspecific [β₁]	Heterospecific [β₂]	Conspecific [β₃]	Heterospecific [β₄]
Effect estimate*	−0.24 (−0.24)	−0.45 (−0.04)	0.16 (0.01)	−0.16 (−0.16)	−0.12 (−0.04)
Credible interval	[−0.49, −0.01] ([−0.49, 0.02])	[−0.74, −0.15] ([−0.06, −0.01])	[0.10, 0.21] ([0.01, 0.01])	[−0.29, −0.01] ([−0.30, −0.01])	[−0.18, −0.05] ([−0.07, −0.02])

*The exponential of the intercept ($β_0$) indicates mean (first-year) survival odds, $P/(1 − P)$, with neighbour densities set to zero; thus $e^{−0.24} = P/(1 − P) = 0.79$. By rearranging, mean (first-year) survival probability without neighbours, $P_{zero} = 0.79/(1 + 0.79) = 0.44$. The exponential of the slopes indicates the proportional change in survival odds with a one IQR increase in neighbour density (i.e. from 25th to 75th percentile density). Thus, for conspecific seedling neighbours (CONs) for instance, $e^{−0.45} = 0.64$ indicates that a one IQR increase in CONs reduces survival odds by 36% (i.e. $1 − 0.64 * 100$); this translates to a reduction in survival probability from 0.44 without neighbours (P_{zero}) to 0.33 with a one IQR increase in CONs (i.e. $P = 0.79*0.64/(1 + 0.79*0.64) = 0.33$. For per-capita effects, densities increase by one individual.

greater than the per-capita effect of seedling neighbours for both conspecifics and heterospecifics. In contrast, the IQR-scaled effect of seedling neighbours was greater than the IQR-scaled effect of large neighbours for both conspecifics and heterospecifics. The scaled effect-size for conspecific seedlings was three to four times larger than the effect sizes of any other neighbour type. A one IQR increase in conspecific seedling density reduced mean first-year survival probability by 25% relative to the probability with neighbour densities set to zero (P_{zero}). The same one IQR increase in large conspecific and heterospecific neighbour densities reduced survival probability by 9 and 6% respectively. In contrast, a one IQR increase in heterospecific seedling density was associated with a 9% increase in survival probability (Table 1) (Table S1 provides all IQR values).

Interspecific variation was large for mean survival (log-odds, $β_0$) and conspecific seedling effects ($β_1$) and much lower for large conspecific, large heterospecific and heterospecific seedling effects (Fig. S2). Mean survival and conspecific seeding effects were positively related (Fig. 1; Pearson's correlation $r = 0.76$; 95% CI = $0.69 < r < 0.81$), suggesting a significant role for tolerance of conspecific seedling neighbours in interspecific differences in first-year survival and recruitment success.

Estimated P_{zero} was high, 0.44 (95% CrI = 0.38–0.50). Overall, estimated survival probability (P) was greater when growing with heterospecific than conspecific neighbours (i.e. the vast majority of species performed better among
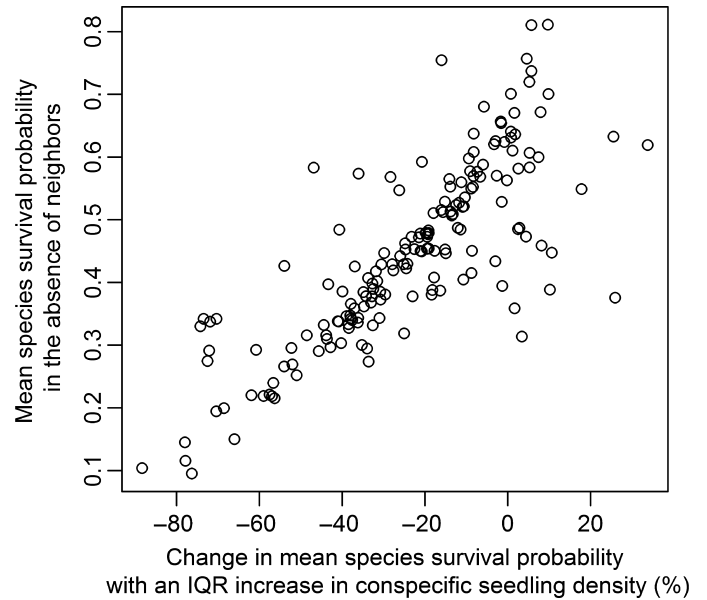

Figure 1 Positive relation between tolerance of conspecific seedlings and mean first-year survival. Relationship between species mean first-year survival probability in the absence of neighbours (P_{zero}) and the effect of conspecific seedling density on first-year survival. Coefficients were obtained from species-level model estimates. P_{zero} is the intercept of the relationship between first-year survival and neighbour density, transformed from log-odds to probability. The effect of conspecific seedling density is calculated as the percent difference between P_{zero} and the survival probability P estimated for an interquartile range increase in conspecific seedling density.

heterospecific neighbours; Appendix S2A). *P* with a one IQR increase in all heterospecific neighbours was 0.45 (95% CrI = 0.42 < *P* < 0.48), with positive and negative effects of seedling and larger heterospecifics largely offsetting one another. In contrast, *P* with a one IQR increase in all conspecific neighbours was significantly lower, *P* = 0.30 (95% CrI 0.22 < *P* < 0.40), with negative effects of seedling and larger conspecifics reinforcing one another.

Abundance, first-year survival and density dependence

The strength of seedling CNDD has a strong signature in the abundance of larger, older trees. Separate models were fitted for species abundances at each of four ontogenetic stages: recruits, established seedlings, saplings and adults. The abundances of established seedlings, saplings and adults, but not recruits, were significantly, positively related to mean first-year survival and the strength of CNDD of seedling neighbours (Table 2). Species abundance expressed as basal area was also positively related to conspecific seedling density effects, but was unrelated to mean first-year survival (Table S4).

Traits, first-year survival and density dependence

We fitted models for three PC axes (including all seven unordered combinations of the three axes) and 10 individual-trait metrics (including two variants for leaf N and P concentrations) to evaluate relationships between traits and first-year survival and density dependence (Tables 3 and S5). The hierarchical model was an improvement over the single-level

Table 2 Parameter estimates (γ) from the second (species) level hierarchical model relating species abundance at four ontogenetic stages to species mean first-year survival (log-odds) and the effects of neighbourhood composition on seedling survival. The parameters β_{0-4} and $\gamma_{0-4,n}$ are defined in the text (see Methods: Analysis)

| | Mean first-year seedling survival [$\beta_0 = -0.24$] $\gamma_{0,n}$ | Seedling neighbours | | Large neighbours | |
| | | Conspecific [$\beta_1 = -0.45$] $\gamma_{1,n}$ | Heterospecific [$\beta_2 = 0.16$] $\gamma_{2,n}$ | Conspecific [$\beta_3 = -0.16$] $\gamma_{3,n}$ | Heterospecific [$\beta_4 = -0.12$] $\gamma_{4,n}$ |
Abundance of					
Recruits	0.10 (0.11)	0.21 (0.19)	−0.06 (0.03)	0.02 (0.07)	0.01 (0.03)
Established seedlings	**0.38 (0.09)**	**0.38 (0.14)**	−0.05 (0.02)	−0.03 (0.07)	0.04 (0.03)
Saplings	**0.41 (0.11)**	**0.25 (0.13)**	−0.03 (0.03)	−0.03 (0.09)	0.05 (0.03)
Adults	**0.40 (0.10)**	**0.24 (0.13)**	−0.04 (0.03)	−0.02 (0.07)	0.04 (0.03)

The IQR-scaled beta coefficients, β_{0-4}, of the model including only density-dependent effects (single-level model in Table 1) are shown below the column headings. Gamma coefficients indicate how species abundances increase (positive slopes) or decrease (negative slopes) when the beta coefficients increase. Bold values indicate statistically significant gamma coefficients (slopes). The standard deviation of the posterior density of the gamma coefficients, $\gamma_{0-4,n}$, is given in parenthesis after each gamma parameter estimate.

Table 3 Parameter estimates (γ) from the second level of the hierarchical model relating species mean first-year survival (β_0) and neighbour effects on first-year survival (β_{1-4}) to individual functional traits and to functional strategies captured by Principal Component Axes (PCs). The parameters β_{0-4} and $\gamma_{0-4,n}$ are defined in the text (see Methods: Analysis)

| | Mean first-year survival [$\beta_0 = -0.24$] | Seedling neighbours | | Large neighbours | | ΔWAIC [44296] |
		Conspecific [$\beta_1 = -0.45$]	Heterospecific [$\beta_2 = 0.16$]	Conspecific [$\beta_3 = -0.16$]	Heterospecific [$\beta_4 = -0.12$]	
	A) Functional strategies (PC axes)					
	$\gamma_{0,n}$	$\gamma_{1,n}$	$\gamma_{2,n}$	$\gamma_{3,n}$	$\gamma_{4,n}$	
PC2	**0.20 (0.10)**	**0.35 (0.16)**	−0.04 (0.03)	**−0.23 (0.09)**	0.00 (0.03)	−14
+ PC3	**0.30 (0.10)**	0.07 (0.16)	−0.00 (0.03)	−0.03 (0.07)	0.02 (0.03)	−21
+ PC1	**0.37 (0.09)**	−0.06 (0.17)	−0.03 (0.03)	0.08 (0.08)	0.05 (0.03)	−26
	B) Single functional traits					
SM	**0.58 (0.08)**	**0.26 (0.13)**	−0.04 (0.03)	−0.10 (0.07)	0.01 (0.03)	−12
LMA	**0.31 (0.10)**	−0.09 (0.15)	−0.05 (0.03)	0.09 (0.08)	**0.07 (0.03)**	−12
LTGH	**0.24 (0.10)**	0.07 (0.15)	−0.1 (0.03)	−0.04 (0.07)	0.05 (0.03)	−12
H_{max}	−0.08 (0.11)	0.25 (0.15)	−0.04 (0.03)	**−0.15 (0.08)**	0.00 (0.03)	−11
WD	**0.39 (0.11)**	−0.01 (0.18)	−0.04 (0.03)	0.02 (0.07)	0.05 (0.03)	−8
LP_{mass}	**−0.32 (0.11)**	0.13 (0.17)	0.03 (0.03)	−0.08 (0.08)	−0.02 (0.04)	−8
LD	**0.36 (0.10)**	0.05 (0.15)	−0.03 (0.03)	−0.01 (0.07)	0.05 (0.03)	−7
LN_{area}	**0.22 (0.10)**	0.08 (0.15)	−0.04 (0.03)	0.01 (0.08)	0.05 (0.03)	−5
LP_{area}	−0.08 (0.11)	0.02 (0.16)	−0.03 (0.03)	−0.01 (0.07)	0.06 (0.03)	1
LN_{mass}	−0.10 (0.10)	0.12 (0.15)	0.02 (0.03)	−0.5 (0.06)	−0.02 (0.03)	1

Parameters β_{0-4} and the WAIC of the single-level model (in Table 1) appear in brackets below the column headings. ΔWAIC indicates the difference in WAIC between the hierarchical and the single-level model. In section A, the effects of each PC in the best multiple-PC model are shown yet the ΔWAICs represent changes in WAIC that occur when each axis is added to the model. Bold numbers indicate significant relationships. Traits and PCs in bold indicate models with ΔWAIC<−2. The standard deviation of the posterior density of the parameters $\gamma_{0-4,n}$ is given in parentheses after each parameter estimate.

model for eight individual traits (Table 3B), for each PC axis and their pairwise combinations (Table S5), and especially for the model combining all three PC axes (Table 3A).

Relationships between traits and mean first-year survival (β_0), described by the gamma parameters ($\gamma_{0,n}$) in the hierarchical models, were significant in 14 of the 17 hierarchical models. Mean first-year survival related significantly to all three PC axes, increased significantly with six individual traits (LMA, SM, LTGH, WD, LD and LN_{area}) and decreased significantly with LP_{mass} (Table 3, Fig. 2a).
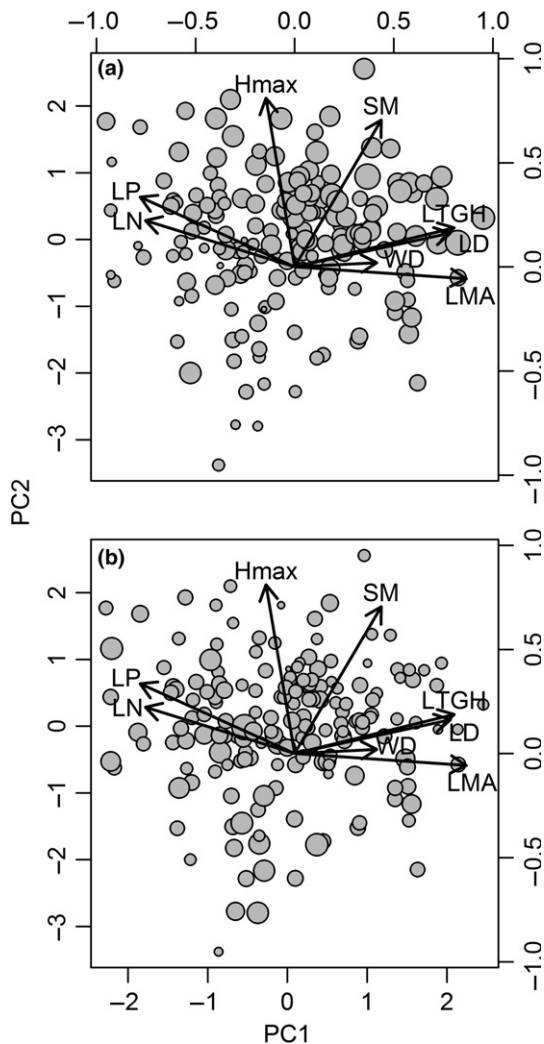
Figure 2 Variation in species (a) mean first-year seedling survival and (b) conspecific seedling negative density dependence (CNDD) associated to species positioning along the first two principal components (PCs) of a Principal Components Analysis on species functional traits. The functional trait-space is defined by eight key functional traits related to resource acquisition and competitive ability: leaf mass per area (LMA), leaf nitrogen content mass-based (LN), leaf phosphorus content mass-based (LP), wood density (WD), maximum adult stature (H_{max}) and seed mass (SM); physical defence: LMA, leaf lamina toughness (LTGH), leaf tissue density (LD) and WD; and stress tolerance: LMA, LTGH, LD, WD and SM. Circles represent species and are scaled proportional to the species mean first-year seedling survival (in a) and strength of CNDD (in b). Arrows represent the direction and strength of change of trait values. The left and bottom axes represent PCs scores. The top and right axes represent Pearson correlations between traits and the PCs.

There were fewer significant relationships between traits and neighbour density dependence. The gamma parameters ($\gamma_{1-4,n}$) represent the relationships between traits and neighbour density effects on first-year survival (β_{1-4}). Just two of 12 gamma parameters were significant for the model combining all three PC axes, and both parameters were associated with the plant-height/seed-size strategy spectrum (PC2) (Table 3A). Just three of 40 gamma parameters were significant for individual traits (Table 3B). PC2 and the two individual traits strongly associated with PC2, SM and H_{max}, showed consistent relationships in models involving individual traits and PC2 (Tables 3 and S5). Large values of SM moderated the strong negative relationship ($\beta_1 = -0.45$) between survival and conspecific seedling density (Figs 2b and 3). Large values of H_{max} strengthened the weaker effect of larger conspecifics ($\beta_1 = -0.16$) (Table 3B). Additionally, large values of LMA moderated the weak negative relationship ($\beta_4 = -0.12$) between survival and large heterospecific neighbour density (Table 3B).

DISCUSSION

Tolerance of negative density dependence associated with conspecific seedlings and traits associated with the growth–survival trade-off strongly correlated with first-year survival of 34 851 seedling recruits, with manifest consequences for species abundances and community structure. Scaled coefficients indicated that density-dependent interactions associated with conspecific seedlings (CNDD) were stronger than density-dependent interactions associated with larger conspecifics and all heterospecifics. Tolerance of conspecific seedling neighbours and recruit survival were greater among larger seeded, slow-growing and physically well-defended species (i.e. low LP_{mass} and high LMA, LTGH and tissue density). We propose that the ability of larger seeded species to tolerate
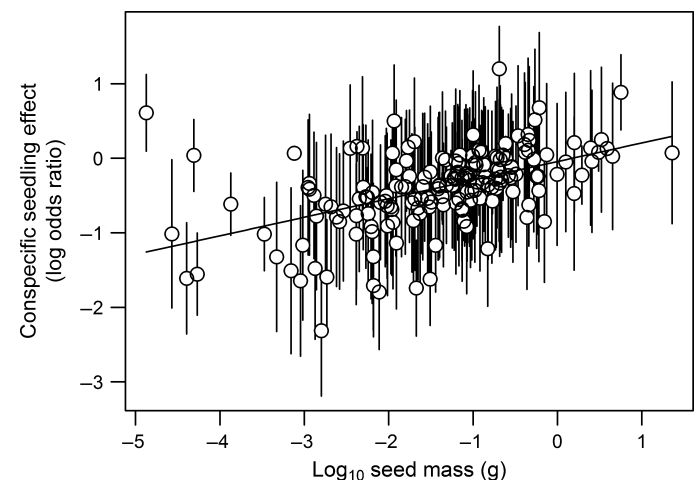

Figure 3 Relationship between seed mass (SM) and the effect of conspecific seedling density (β_1) on first-year seedling survival (log-odds ratio). Open circles represent (j) individual species estimates of β_1 (i.e. $\beta_{1,j}$) and bars represent the standard deviation of the estimates. The solid line represents the second (species) level model estimate of the regression slope of SM ($\gamma_{1,n=SM}$) on β_1 (i.e. $\beta_{1,j} = \gamma_{1,0} + \gamma_{1,n=SM} * SM_j$).

CNDD provides a novel functional mechanism that helps explain the variation in seed size observed within plant communities via a tolerance–fecundity trade-off.

Neighbour effects on first-year survival

Overall, neighbour effects largely confirm findings of our study focusing on impacts of phylogenetic relatedness (Lebrija-Trejos *et al.* 2014). Forest-wide (mean) first-year survival varied markedly among species (Figs 1 and S2A) and was most strongly affected by conspecific seedling neighbours (Table 1). The strength of CNDD associated with larger neighbours was greater in this study than in Lebrija-Trejos *et al.* (2014) possibly because we optimised the radius used to calculate large neighbour densities in this study (Appendix S1A). Larger neighbours had a stronger per-capita effect on focal seedlings that is consistent with size-asymmetric resource competition. Yet, resource competition is unlikely to be the main cause of CNDD. When differences in density are incorporated, the effect of the density of conspecific seedling neighbours was four times greater than the effect of the density of much larger conspecifics (Table 1; *Results: neighbourhood characteristics*). The comparatively strong effect of conspecific seedlings together with the low impact of first-year seedlings on resource availability (Wright 2002) is consistent with the hypothesis that natural enemies that specialise to forest strata as well as host species largely mediate CNDD in this forest (Basset 2001; Gilbert *et al.* 2007; Mangan *et al.* 2010).

Effects of heterospecific neighbours on first-year seedling survival were comparatively weak and differed in direction for seedling and larger neighbours (Table 1, Fig. S2). Crowding and competition for light and soil resources are expected to reduce survival, as observed for larger but not for seedling heterospecific neighbours. Large heterospecifics frequently have weak effects on neighbours (reviewed by Lebrija-Trejos *et al.* 2014), which could result from early selection of competitively similar species by local habitat filtering (Swenson & Enquist 2009; Mayfield & Levine 2010). There is also evidence for limited competition or even mild facilitation among seedlings in the shaded understory of tropical forests (Svenning *et al.* 2008; Anderson 2009). The positive effects of heterospecific seedlings observed here are, however, likely to result from similar responses of seedling density and survival to light availability, with elevated seedling densities and survival in ephemeral high-light environments associated with treefalls.

Implications for community structure of neighbour effects on first-year survival

Species abundances were tightly linked to first-year survival, highlighting the importance of regeneration for later developmental stages and overall community structure. Specifically, species whose individuals survived well among high densities of conspecific seedlings had significantly higher mean first-year survival and were significantly more abundant at post-recruitment life stages (Fig. 1, Table 2). In contrast to later developmental stages, recruit abundances were unrelated to CNDD. Recruit abundances vary widely with interannual variation in seed production (Wright *et al.* 2005a) and this variation might

mask effects of CNDD. Alternatively, CNDD effects may be time- and/or size-sensitive, and become more important as seedlings grow over time. The negative relationship between seedling CNDD and species abundance (Table 2) is consistent with previous studies in tropical and temperate forests and grasslands (Klironomos 2002; Comita *et al.* 2010; Mangan *et al.* 2010; Johnson *et al.* 2012; McCarthy-Neumann & Ibáñez 2013). Theory also suggests that strong CNDD may be a widespread cause of species rarity (Chisholm & Muller-Landau 2011).

The vast majority of species (more than 95%) were more negatively affected by conspecific than by heterospecific neighbours (Fig. S3). Since CNDD promotes coexistence when conspecifics come to limit themselves more than other species, this result suggests that CNDD may contribute to species coexistence in this forest. It is also consistent with the hypothesis that CNDD can promote coexistence even when the absolute strength of self-limitation is weak for some species (Figs 1 and S2; Chisholm & Muller-Landau 2011).

Traits and neighbour effects

Just two out of 30 possible relationships between individual traits and the effects of heterospecific and large conspecific neighbours were significant (Table 3B). The negative DD effect of large conspecifics increased with species stature (with larger values of H_{max}). Both stronger size-asymmetric competition and/or greater build-up of pests associated with larger neighbours might contribute to this effect (King *et al.* 2006). The negative DD effect of large heterospecific neighbours was ameliorated in species with large LMA. This might reflect greater shade tolerance associated with greater LMA (Walters & Reich 1999) and with other high-LMA shade-tolerant adaptations such as low dark respiration rate and low leaf turnover rate (Reich 2014). The 28 insignificant relationships between traits and DD effects of heterospecific and large conspecific neighbours is unsurprising because these DD effects were relatively weak (Table 1), with minimal variation in strength among species (Fig. S2).

In contrast, DD effects of conspecific seedlings were strong (Table 1), varied widely among species (Figs 1 and S2B), and were significantly correlated with species abundances (Table 2) and mean survival (Fig. 1). Nonetheless, only seed mass (SM) was significantly related to conspecific seedling effects (Fig. 3). This strong relationship suggests a unique functional role of SM for first-year seedling survival.

Seed mass and conspecific negative density dependence

We can discount two possible causes of the observed relationship between SM and CNDD of seedling neighbours. The first possibility concerns the seed-size–seed-number trade-off. Large-seeded species might occur over a limited range of low seed densities and therefore might appear to suffer less from conspecific seedling density. To evaluate this possibility, we fitted a hierarchical model that used the maximum seedling density observed for each species as a species-level character. There was no support for a relationship between maximum seedling density and seedling CNDD (Appendix S2B), so we

discount this possible explanation. A second possibility concerns the phylogenetic conservatism of SM (Lebrija-Trejos *et al.* 2014). This raises the possibility that phylogeny underlies the apparent relationship between SM and seedling CNDD. To evaluate this possibility, we tested for phylogenetic signal among the residuals of the relationship between SM and conspecific seedling effects (Revell 2010). There was no phylogenetic signal (Appendix S2B), so we also discount a phylogenetic explanation.

Several advantages of large seeds may contribute to lower CNDD among large-seeded species. Larger seeds tend to have larger storage reserves, initial seedling size and absolute growth rates, and more rapid seedling maturation (e.g. secondary cell-wall development and lignin formation). Thus, seedlings of large-seeded species can recover better from tissue losses, are mechanically resistant and have greater access to light and soil resources (Kitajima 2007; Dalling *et al.* 2011). They may also be less dependent on fungal partners for resource supply as germinants (contrast with orchids, for example), which possibly could be associated with a generally greater resistance to microbial (including pathogenic) penetration and colonisation. Further research would be required to test any and all of these possibilities, but collectively they may improve both plant carbon balance and the ability to tolerate natural enemies, both of which are important vis-a-vis CNDD in tropical forest understories (Mangan *et al.* 2010; Bagchi *et al.* 2014).

We evaluated the hypothesis that seedling size advantages associated with large SM could explain differences in susceptibility to CNDD. We used species-specific mean recruit heights as a species-level character in our hierarchical model. Mean recruit height was significantly correlated with SM ($r = 0.42$, $P < 0.001$) despite variable light environments. CNDD of seedling neighbours decreased with increasing recruit height (posterior mean-effect estimate = 0.48, 95% CrI = 0.15–0.85). This result is consistent with the hypothesis that large-seeded species suffer less from CNDD during their first year in part due to an initial size advantage. Whether an advantage of larger SM is indirectly maintained beyond the first year (i.e. after seed reserves are consumed), requires further study.

Three studies have explicitly evaluated the relationship between SM and CNDD. Studies limited to abundant or wind-dispersed tropical tree species found no relationship between SM and negative effects of pathogens and pests associated with conspecifics (Augspurger & Kelly 1984; Swamy & Terborgh 2010). One pot experiment study including rare and common species found that microbial extracts from conspecific soils (excluding arbuscular mycorrhizal fungi) had no significant effect on overall survival or survival of small-seeded species, but were associated with greater survival of large-seeded species (McCarthy-Neumann & Kobe 2008). This result, which was unexplained by the original authors, is inconsistent with the pathogenicity of microbes associated with conspecific soils and is not considered further. Our analysis, unique in taxonomic spread, showed that seedling CNDD increase with decreasing seed size (Figs. 2b and 3). This result may explain the finding of Bagchi *et al.* (2014) that species most abundant as seeds, which tend to be small-seeded species (Muller-Landau *et al.* 2008), suffered stronger CNDD.

We propose that the unique role of SM in tolerance to self-limitation via CNDD represents a new functional dimension to the importance of variation in seed size and suggests a novel mechanism for CNDD to promote seed-size variation and species coexistence through a tolerance–fecundity trade-off (Muller-Landau 2010). Under this model, fecundity (small seeds) trades-off with tolerance of nearby conspecifics (large seeds) and species coexist by partitioning variation in regeneration sites caused by pests associated with changes in the density of (and presumably distance to) conspecifics. To the extent that small seeds are more easily dispersed (Muller-Landau *et al.* 2008), CNDD could also constitute a selective pressure for the evolution of small seeds, which would allow escape from high conspecific densities via enhanced dispersal (Howe & Miriti 2004).

Traits and mean first-year survival

In contrast to the limited links between functional traits and strategies with DD effects, traits were clearly related to interspecific differences in first-year survival (Table 3, Fig. 2a). These relationships closely matched performance expectations associated with functional strategies and constraints in tropical forest understory environments. Mean first-year survival increased significantly with denser tissues, tougher leaves, lower rewards for herbivores (i.e. low LP_{mass}; Santiago *et al.* 2012) and enhanced biochemical capacity to use intercepted light under shade (i.e. high LN_{area}; Niinemets 1997)(Table 3). These leaf traits together with wood density (WD) distinguish leaf and stem resource-use strategies and were associated with PC axes 1 and 3 respectively (Figs 2 and S1). The resource-use strategies range from resource-acquisitive 'fast' species to resource-conservative 'slow' species and underpin a trade-off between growth and survival rates, where species at the slow-growth end survive better in closed forest understories by allocating more resources to mechanically robust and well-defended long-lived tissues (Reich *et al.* 1999; Lusk & Reich 2000; Chave *et al.* 2009; Wright *et al.* 2010; Westbrook *et al.* 2011; Reich 2014). In line with the seedling-survival advantage of large seeds (reviewed by Kitajima 2007), mean first-year survival also increased with SM. Increased survival with higher WD and SM could also be related to increased tolerance to drought (Poorter & Markesteijn 2008; Chave *et al.* 2009), which kills many seedlings and trees in tropical forests (Poorter & Markesteijn 2008; Phillips *et al.* 2010).

The tight correspondence between first-year survival and traits and investment strategies underpinning the growth–survival trade-off indicates that niche differentiation along this trade-off is a key determinant of regeneration success. The best multiple-PC model further shows that species differentiation along the leaf economics spectrum (PC1), the plant height and seed size spectrum (PC2), and the wood economics spectrum (PC3) make independent contributions to forest-wide survival at this development stage (Table 3A).

Concluding remarks

Our analyses of first-year survival of thousands of recruits of 175 species show that regeneration success is most strongly

determined by species differences in seed mass (SM), which is related to tolerance of high local densities of conspecific seedlings, and by species positions along leaf and stem allocation strategies, which underpin the growth–survival trade-off (i.e. by resource-niche differentiation). These two aspects of species regeneration niches have manifest consequences for community structure despite the short duration of the regeneration phase, as indicated by the significant relationship between recruit survival and species abundances at subsequent life stages.

One trait, SM, plays an important role in the growth–survival trade-off and also enhances tolerance to the local density of conspecific seedlings. This specifies a functional link between CNDD and regeneration niche differentiation. Notwithstanding, SM plays a key role in tolerance to CNDD that is not shared by other traits associated with the growth–survival trade-off. This suggests a functional role of SM not necessarily related to differentiation along the growth–survival trade-off (or species resource-use strategies) and may explain why SM varies widely at all positions along the growth–survival trade-off (e.g. among both fast-growing, resource/light-demanding species and slow-growing, low-resource/shade-tolerant species). More specifically, we have shown that large variation in SM is uniquely linked to large variation in susceptibility to CNDD. This result constitutes a novel mechanism translating seed-size variation into differential species success with habitat heterogeneity and thus a new possibility for species coexistence via the tolerance–fecundity trade-off (Muller-Landau 2010).

AUTHORSHIP

ELT conceived the study together with PBR and SJW; SJW and AH designed and performed field research; ELT performed analyses and wrote the manuscript; PBR and SJW contributed substantially to revisions.

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