LETTER

Density-dependent survival varies with species life-history strategy in a tropical forest

Y. Zhu,[1,2]* S. A. Queenborough,[1]
R. Condit,[3,4] S. P. Hubbell,[5,6]
K. P. Ma,[2] and L. S. Comita[1,6]

Abstract

Species coexistence in diverse communities likely results from multiple interacting factors. Mechanisms such as conspecific negative density dependence (CNDD) and varying life-history strategies related to resource partitioning are known to influence plant fitness, and thereby community composition and diversity. However, we have little understanding of how these mechanisms interact and how they vary across life stages. Here, we document the interaction between CNDD and life-history strategy, based on growth-mortality trade-offs, from seedling to adult tree for 47 species in a tropical forest. Species' life-history strategies remained consistent across stages: fast-growing species had higher mortality than slow-growing species at all stages. In contrast, mean CNDD was strongest at early life stages (i.e. seedling, sapling). Fast-growing species tended to suffer greater CNDD than slow-growing species at several, but not all life stages. Overall, our results demonstrate that coexistence mechanisms interact across multiple life stages to shape diverse tree communities.

Keywords

fast–slow continuum, growth-mortality trade-off, intraspecific competition, Janzen–Connell hypothesis, niche partitioning, regeneration niche, shade tolerance, species coexistence.

Ecology Letters (2018) **21**: 506–515

INTRODUCTION

How hundreds of species coexist in diverse plant communities remains a challenging issue in community ecology (Chesson 2000). In both tropical and temperate plant communities, considerable evidence supports the idea that diversity is maintained by multiple coexistence mechanisms, including conspecific negative density dependence and resource niche partitioning (MacArthur & Levins 1967; Wright 2002). Conspecific negative density dependence (CNDD), i.e. when individual fitness declines with increasing density of conspecific neighbours, can promote species coexistence if effects on conspecifics are stronger than effects on heterospecifics (Chesson 2000), due to strong intraspecific competition or host-specific natural enemies (Janzen 1970; Connell 1971). A growing number of studies supports the idea that CNDD is a widespread and key regulating mechanism in structuring tree spatial patterns, species relative abundance and diversity in forests (e.g. Harms *et al.* 2000; Zhu *et al.* 2010, 2015a,b; Hille Ris Lambers *et al.* 2012; Terborgh 2012; Bagchi *et al.*2014; Comita *et al.* 2014). More recently, studies have shown that while CNDD is prevalent in plant communities, the strength of conspecific neighbour effects (i.e. per neighbour CNDD) varies widely among species within a community (Comita *et al.* 2010; Kobe & Vriesendorp 2011; Johnson *et al.* 2012). Attempts to identify the species attributes underlying this

variation in CNDD have produced conflicting results and remains under debate (e.g. Kobe & Vriesendorp 2011; Zhu *et al.* 2015b; Comita 2017).

Resource niche partitioning can also contribute to the coexistence in plant communities (Silvertown 2004). In forests, much work has focused on species' niche differences related to light availability. Specifically, there is clear evidence for a trade-off between a species' ability to grow quickly under high light conditions vs. its ability to survive in deep shade (Wright *et al.* 2010; Kobe & Vriesendorp 2011). This growth-mortality trade-off relates more generally to species differences in life-history strategies, with species' location along the trade-off axis linked to functional traits that influence species performance (Reich 2014). For example, slow growing shade-tolerant tree species tend to have higher wood density (Wright *et al.* 2010; Rüger *et al.* 2012) and better defended, longer lived leaves (Reich *et al.* 1997; Wright *et al.* 2004; Poorter & Bongers 2006; Kitajima & Poorter 2010) compared to fast-growing, light-demanding species. Thus, traits that determine where species fall along the growth-mortality trade-off axis not only relate to species shade tolerance but also govern species' susceptibility to natural enemies (Coley 1988; Fine *et al.* 2006; Adler *et al.* 2014). In addition, in a recent global-scale analysis of plant functional traits, fast maximum growth rates were associated with low values of wood density, which tend to also be correlated with higher sensitivity to competition

[1]*School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA*
[2]*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China*
[3]*Morton Arboretum, 4100 Illinois Rte. 53, Lisle, IL 60532, USA*

[4]*Field Museum of Natural History, 1400 S. Lake Shore Dr., Chicago, IL 60605,USA*
[5]*Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA*
[6]*Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancón, Panama*
Correspondence: E-mail: zhuyan1205@gmail.com

(Kunstler *et al.* 2016). As a result, a species' location along the growth-mortality trade-off axis may influence the degree to which a species is impacted by conspecific neighbour density.

While most previous studies of species coexistence mechanisms have examined only resource niche partitioning or only CNDD, there is increasing evidence that these two mechanisms occur simultaneously and interact to influence species' performance (Comita & Hubbell 2009; Chen *et al.* 2010; Inman-Narahari *et al.* 2016; LaManna *et al.* 2016). For example, Kobe & Vriesendorp (2011) found that seedlings of shade-tolerant tree species were less sensitive to conspecific neighbour density compared to shade-intolerant species, potentially due to their lower susceptibility to soil pathogens (McCarthy-Neumann & Kobe 2008). Similarly, Lebrija-Trejos *et al.* (2016) found that first-year seedlings of species with larger seeds, which tended to be slow-growing and shade-tolerant, were less negatively impacted by conspecific neighbours than seedlings of species with smaller seeds.

These studies demonstrate that species' life-history strategy, especially with respect to shade tolerance and related growth-mortality trade-offs, influences the strength of conspecific NDD. However, past studies have focused on early life stages. Assessing the influence of coexistence mechanisms for long-lived species, such as trees, requires an understanding of dynamics across all life stages. There is evidence that the strength of both growth-mortality trade-offs and CNDD may vary with life stages of tropical trees (Comita *et al.* 2014; Kunstler *et al.* 2016). For example, Wright *et al.* (2010) found that the growth-mortality trade-off was substantially weaker for adult trees compared to saplings in a tropical forest in central Panama. In the same forest, we previously demonstrated that CNDD was strongest at the seedling stage and became progressively less negative at later life stages (Zhu *et al.* 2015b). In addition to these community-wide trends, individual species' position along the growth-mortality trade-off axis, as well as their ranking in terms of strength of CNDD, could shift with life stage (e.g. Sack & Grubb 2001; Valladares & Niinemets 2008; Kunstler *et al.* 2009; LaManna *et al.* 2016). Therefore, relationships between species' shade tolerance and strength of CNDD that have been reported for early life stages may not hold for later life stages, potentially weakening or even reversing their effects at the population and community level.

In this study, we use long-term, spatially explicit data on individual growth and survival in a lowland tropical forest in central Panama to quantify the strength of CNDD and growth-mortality trade-offs at multiple life stages, from seedling to adult tree, for 47 tree species. We ask (1) does a species' life-history strategy (i.e. its location along the growth-mortality trade-off axis) influence the strength of conspecific neighbour effects the species experiences? and (2) Does the relationship between life-history strategy and strength of CNDD change with life stage?

Our results reveal that growth-mortality trade-offs occur at multiple life stages, from the seedling through adult stage, and influence the strength of CNDD, with faster growing species more negatively affected by conspecific neighbours than slower growing species, especially at the seedling stage. Our results suggest that CNDD contributes to species coexistence partly by increasing niche differences and that mechanisms of species coexistence interact across multiple life stages to shape diverse tree communities.

METHODS

Site and data collection

The study was conducted in the 50-ha tropical forest dynamics plot on Barro Colorado Island (BCI), Panama (9°9′ N, 79°51′ W). On BCI, average annual rainfall on BCI is ~ 2600 mm, with a distinct 4-month dry season from January to April (Windsor 1990). Within the $1000 \times 500 \ m^2$ plot, all woody trees and shrubs ≥ 1 cm diameter at 1.3 m above ground (dbh) were tagged, mapped, measured and identified to species in 1982–1983 (Hubbell & Foster 1983; Hubbell *et al.* 2005). The plot was subsequently recensused in 1985 and every 5 years thereafter (see Condit 1998 for detailed methods). In 2001, a $1 \times 1 \ m^2$ seedling plot was established in the centre of each $5 \times 5 \ m^2$ subquadrat of the BCI 50-ha plot, for a total of 20,000 1-m^2 plots (Comita *et al.* 2007). All free-standing, woody seedlings and small saplings ≥ 20 cm tall and < 1 cm dbh (hereafter referred to simply as seedlings) were tagged, mapped, measured and identified to species within each seedling plot in 2001 and every 1 to 2 years thereafter (Comita *et al.* 2007, 2010).

Focal species and life stages

To examine growth-mortality trade-offs and CNDD across life stages, we first divided stems into four life stages based on size cutoffs: seedlings (≥ 20 cm tall − < 1 cm dbh), saplings (1–4.9 cm dbh), juveniles (5–9.9 cm dbh) and adults (≥ 10 cm dbh). These cutoffs are consistent with previous studies at our study site (Peters 2003; Condit *et al.* 2006; Zhu *et al.* 2015b). For our analyses, we included only tree species that had ≥ 30 individuals in each of the above life stages in the 2005 and 2010 censuses of stems ≥ 1 cm dbh and the 2006 and 2011 censuses of seedlings (to ensure adequate sample sizes for all focal species in each stage), and with > 10 individuals surviving across those census intervals (to avoid biased estimates of RGR_{90}). This left a total of 47 focal tree species (out of the 236 tree species present in the BCI 50-ha plot during the study period) from 40 genera and 26 families (Table S1; Condit *et al.* 1996, 2017).

Growth rate calculations

For the 47 focal tree species, we quantified their position along the growth-mortality trade-off axis using relative growth rates (RGR) under optimal conditions. We first calculated RGR for each individual in five 5-year census intervals for stems ≥ 1 cm dbh (1985–90, 1990–95, 1995–2000, 2000–05, 2005–10) and across two 5-year census intervals for seedlings (2001–06, 2006–11). RGR was calculated as $(\log(size_{t+1}) - \log(size_t))/time$, where size in census *t* corresponds to dbh for saplings, juveniles and adults and height for seedlings. For each species, we then used the 90 percentile relative growth rate (RGR_{90}) as a proxy for growth under favourable conditions (Wright *et al.* 2010). Because

growth rates change with tree size (Hunt 1982; Kobe *et al.* 1995; Rüger *et al.* 2012), we calculated RGR_{90} separately for each life stage of each species. To assess whether species' rankings along the growth-mortality trade-off axis were consistent across life stages, we tested for correlations between species' RGR_{90} values for all combinations of life stages (e.g. seedling RGR_{90} vs. sapling RGR_{90}) using reduced major axis regression.

Calculation of neighbour densities

To test for negative density dependence, we first calculated the densities of conspecific and heterospecific neighbours for each focal individual. For all life stages, we calculated conspecific neighbour density and heterospecific neighbour density as the sum of the basal area of all conspecific and heterospecific trees ≥ 1 cm dbh, respectively, within a radius of 15 m at the start of the census interval (as in Zhu *et al.* 2015b). The maximum and median conspecific neighbour density for each focal species can be found in Table S2. For the seedling stage, we also calculated the density of neighbouring seedlings by counting the number of conspecific and heterospecific seedlings alive at the start of the census interval in the same 1×1 m² seedling plot as the focal seedling.

Survival analysis

We used generalised linear mixed-effects models (GLMMs; Gelman & Pardoe 2006; Bolker *et al.* 2009) with binomial errors to examine the influence of neighbourhood densities and RGR_{90}, as well as their interactive effect, on the probability of survival. We modelled survival over the most recent 5 year census interval for which data were available (2005–2010 for saplings, juveniles and adults; 2006–2011 for seedlings). For each life stage separately, we modelled the probability of an individual surviving to the end of the census interval as a function of conspecific neighbour density (CON), heterospecific neighbour density (HET), RGR_{90} of the species to which the individual belonged (Table S3), and interactions between CON and RGR_{90}, and between HET and RGR_{90}. For the seedling stage, we first ran the model with CON and HET calculated using densities of trees ≥ 1 cm dbh and then ran a separate model in which CON and HET were calculated using seedling densities.

Because initial size can significantly affect survival (e.g. Comita *et al.* 2009; Wang *et al.* 2012; Piao *et al.* 2013), we also included log-transformed size (dbh for stems ≥ 1 cm dbh, height for seedlings) at the start of the census interval as a fixed effect in the model. We also included species as a random effect in the model because species' baseline survival rates can vary widely. In addition, we allowed the effects of initial size, CON and HET to vary among species (i.e. as random slopes). Because individuals located close to each other are likely to have similar probabilities of survival (i.e. spatial autocorrelation), we divided the plot into 20×20 m² quadrats and assigned each individual ≥ 1 cm dbh to the quadrat number where it was located. Quadrat was then included as a random effect in the model. For seedlings, the quadrat random effect included the 1×1 m² seedling plot in which the individual was located, nested within the 20×20 m² quadrat. See Table S4 for model structure.

We have previously reported that species relative abundance in the community is related to the strength of CNDD at our study site (Comita *et al.* 2010). Thus, in this study, we examined whether the relationship between CNDD and RGR_{90} remained qualitatively the same when including species relative abundance, and its interaction with CNDD, in the model. We ran models including neighbour densities, RGR_{90} and species relative abundance, as well as interactions of neighbour densities with both RGR_{90} and species relative abundance (see Table S4; Fig. S1). Relative abundance was calculated as the total basal area of trees ≥ 1 cm dbh of the species in the 2005 census of the BCI 50-ha plot (i.e. size-weighted abundance; Comita *et al.* 2010).

For all models, values of all continuous independent variables were standardised prior to entering the model by subtracting the mean of the variable and dividing by one standard deviation. All analyses were performed in R 3.3.0 statistical software package (R Development Core Team 2016) with GLMMs run using the 'lme4 1.1-12' package (Bates *et al.* 2016).

RESULTS

Species showed a consistent growth strategy across all life stages, with significant correlations between species' RGR_{90} values for all pairs of life stages (all $P < 0.001$; Fig. 1, Table S3). Closer life stages showed stronger correlations: RGR_{90} values were highly correlated for sapling and juvenile stages ($r^2 = 0.73$; Fig. 1d), and for juvenile and adult stages ($r^2 = 0.80$; Fig. 1f). RGR_{90} values remained significantly, although more weakly, correlated even for seedlings and adult trees ($r^2 = 0.23$; Fig. 1c).

For all life stages, RGR_{90} had a significant negative effect on the probability of survival (Fig. 2b). Specifically, faster growing species consistently had lower survival than slow growing species throughout their entire lifetime. In contrast, significant community-level effects of conspecific neighbours on survival were detected only for early life stages, with both seedlings and saplings showing a lower probability of survival at higher conspecific densities (Fig. 2c). Conversely, heterospecific tree neighbour density tended to be positively related to survival (Fig. 2d). The effect of the focal individual's size on the probability of survival shifted with life stage: larger seedlings and saplings had significantly higher survival than smaller seedlings and saplings, but larger adult trees had significantly lower survival than smaller adult trees (Fig. 2a).

We detected a significant interaction between species' RGR_{90} and conspecific neighbourhood density for survival at the sapling and adult life stages (Fig. 2e). At these two stages, faster growing species tended to experience stronger (i.e. more negative) effects of conspecific neighbours compared to slower growing species (Fig. 3b,c; Fig. S2). In contrast, at the seedling and juvenile stages there was not a significant interaction between RGR_{90} and conspecific density. At the seedling stage, the coefficient for the interaction between RGR_{90} and CON was negative (i.e. faster growing species tending to have
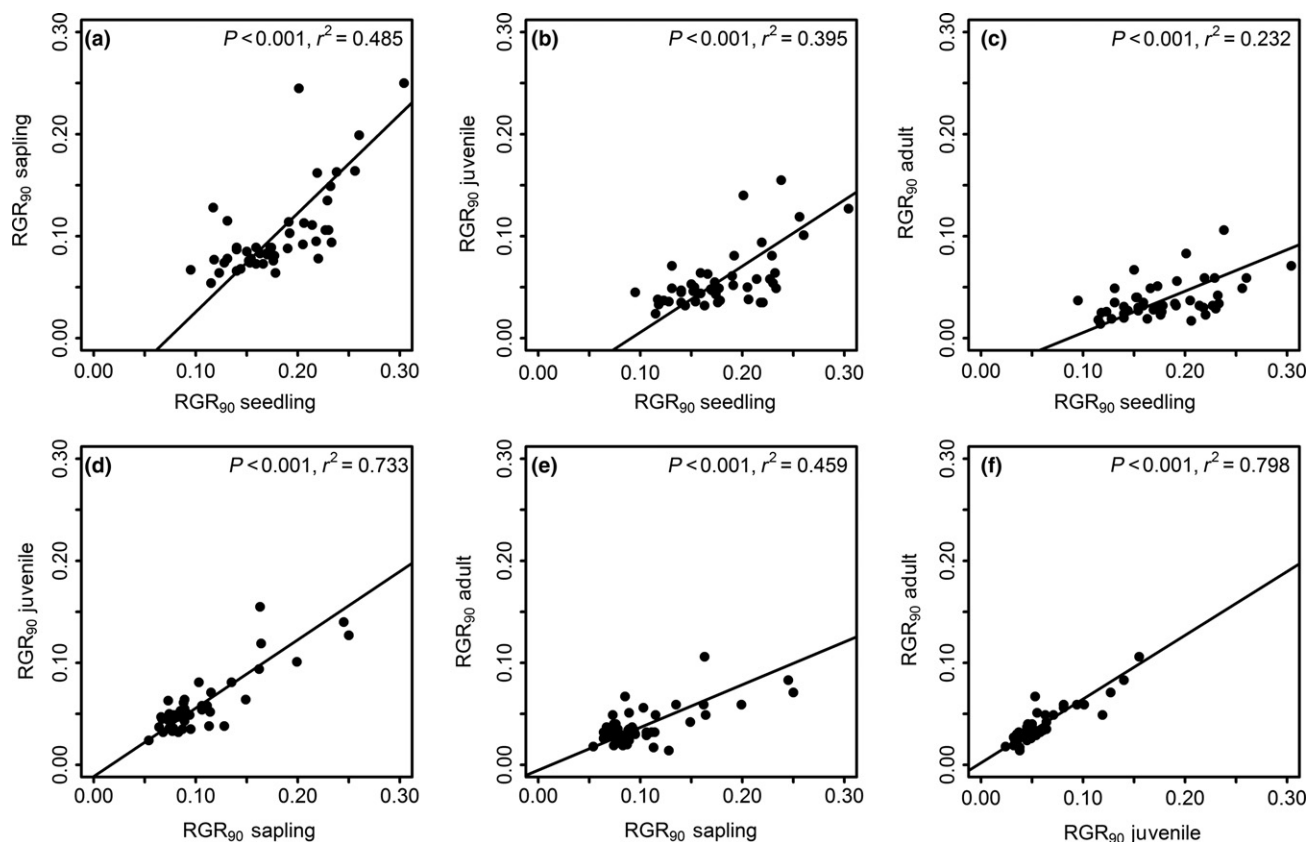
Figure 1 Relationships between species' 90th percentile growth rate (RGR_{90}) at the seedling, sapling, juvenile and adult tree stages for 47 tree species in the Barro Colorado Island 50-ha Forest Dynamics Plot (Panama).

stronger CNDD; Fig. S2), but was not significant due to large standard errors, particularly for conspecific seedling neighbours (Fig. 2e). There were not significant interactions between species' RGR_{90} and heterospecific neighbour effects at most stages, with the exception of a significant negative interaction in the model examining the effect of heterospecific seedling density on seedling survival (i.e. faster growing species being more negatively impacted by the heterospecific seedling neighbour density compared to slower growing species; Figs. 2f and 3a; Figs. S3 and S4). The effects of size, RGR_{90} and conspecific and heterospecific neighbours on survival remained qualitatively the same for all life stages when species relative abundance, and its interactions with conspecific and heterospecific neighbour densities, were included in the model (Fig. S1).

DISCUSSION

Results from our analysis of spatially explicit, long-term demographic data of 47 species demonstrate that both species life-history strategy and conspecific negative density dependence influence tree survival. Specifically, we found that slow growing species tended to have higher survival across all life stages compared to faster growing species, consistent with growth-mortality trade-offs predicted to underlie species' differential strategies for coping with abiotic stress (Kitajima 1994; Hubbell *et al.* 1999; Kobe 1999; Westoby *et al.* 2002;

Rüger *et al.* 2012). At the same time, our results also reveal that a species' position along this growth-mortality trade-off axis can influence the degree to which it is negatively impacted by conspecific neighbours: fast-growing species not only had higher mean mortality than slower growing species, but were also more sensitive to the density of conspecific neighbours at some life stages. At the community level, conspecific negative density dependence was strongest at earlier life stages. Nonetheless, we found that species' life-history strategy explained variation among species in the strength of conspecific neighbour effects at both early (sapling) and later (adult tree) stages. Thus, our study demonstrates that key species coexistence mechanisms do not act independently, but rather interact across multiple life stages to shape diverse tree communities.

Species' growth rates explain variation in conspecific neighbour effects

Originally proposed to explain the maintenance of high tree diversity in tropical forests (Janzen 1970; Connell 1971), negative effects of conspecific neighbour density on survival have been well documented in plant communities worldwide (Comita *et al.* 2014). Studies have found that the strength of CNDD varies among communities, e.g. with precipitation (Comita *et al.* 2014) and latitude (Johnson *et al.* 2012; LaManna *et al.* 2017). At the same time, there is increasing
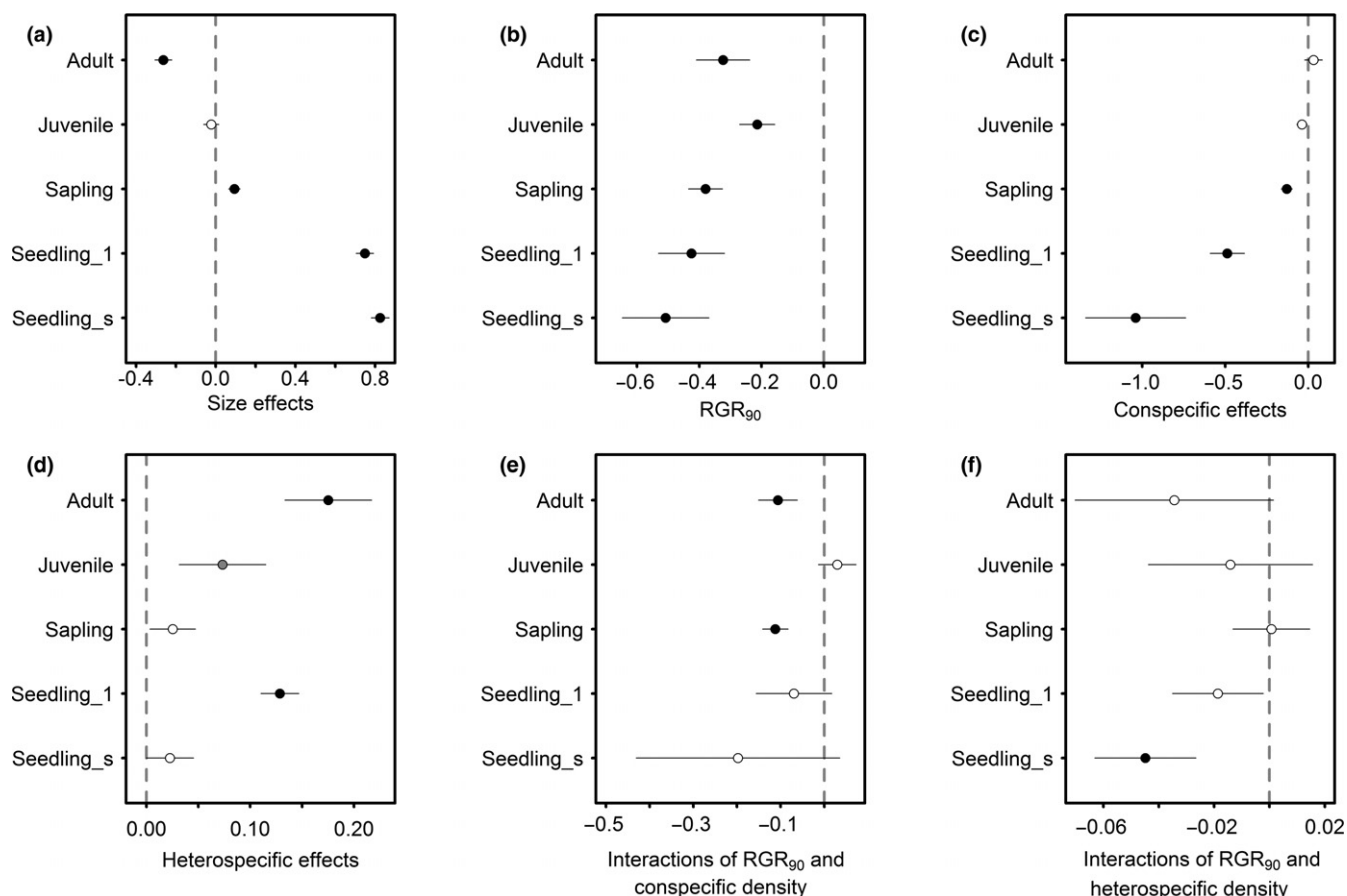
Figure 2 Parameter estimates ($\pm$ 1 SE) of effects of (a) tree size, (b) species' 90th percentile growth rate (RGR_{90}), (c) conspecific neighbour density, (d) heterospecific neighbour density, and interactions between RGR_{90} and (e) conspecific and (f) heterospecific neighbour density on individual survival at the seedling, sapling, juvenile and adult stages in the BCI forest. Survival was modelled separately for each life stage using GLMMs (see Methods). Solid circles indicate significant effects ($P < 0.05$). Seedling_s denotes the model of seedling survival when neighbour densities were calculated as number of conspecific or heterospecific seedlings in the same 1 m^2 seedling plot. For all other models, neighbour densities were based on total basal area of conspecific or heterospecific stems $\geq$ 1 cm dbh within 15 m of the focal individual.

recognition that the strength of CNDD often varies widely among species within communities (e.g. Comita *et al.* 2010; Kobe & Vriesendorp 2011; Lin *et al.* 2012; Lebrija-Trejos *et al.* 2014; Zhu *et al.* 2015a). Our results here demonstrate that such variation among species in the strength of conspecific neighbour effects is not random, but rather is driven at least in part by species' life-history strategy.

The relationship we found between species RGR_{90} and CNDD is most likely the result of differences in allocation related to shade tolerance (Valladares & Niinemets 2008). In closed-canopy forests, shade-tolerant species grow slowly, but are able to persist in the shaded understory due to their ability not only to tolerate low light levels but also to withstand or prevent attack by herbivores and pathogens by allocating resources to storage and defence (Coley & Barone 1996; Kobe 1997; Myers & Kitajima 2007; Kitajima & Poorter 2010; Queenborough *et al.* 2013). In contrast, light-demanding species are highly sensitive to shading by neighbouring plants, but are able to grow quickly in response to high light availability as a result of preferential allocation to growth rather than storage or defence (Herms & Mattson 1992; Kitajima 1994; Reich *et al.* 1998; Fine *et al.* 2006). Consistent with this allocation trade-off, several experiments have demonstrated

that fast-growing, shade-intolerant tree species are more susceptible to pathogens (Augspurger & Kelly 1984; McCarthy-Neumann & Kobe 2008; McCarthy-Neumann & Ibáñez 2013; but see Pringle *et al.* 2007). Although we did not explicitly test the mechanisms underlying CNDD in this study, evidence from our study site, as well as other forests, suggests that negative conspecific neighbour effects are often due to host-specific, density-responsive natural enemies (Terborgh 2012), particularly soil pathogens (Augspurger 1984; Freckleton & Lewis 2006; Mangan *et al.* 2010; Bagchi *et al.* 2014). Thus, our finding of weaker effects of conspecific neighbour density on survival for slower vs. faster growing species is likely the result of life-history trade-offs that govern allocation to growth vs. defence against (or recovery from) pathogen and herbivore attack.

Our results are consistent with previous studies that have found a link between CNDD and shade tolerance, or traits related to shade tolerance. In a study of seedling mortality in a wet tropical forest in Costa Rica, Kobe & Vriesendorp (2011) found a correlation between species responses to shade and responses to conspecific seedling density, with species that were more sensitive to shade also showing higher sensitivity to conspecific neighbours, as well as higher susceptibility to soil
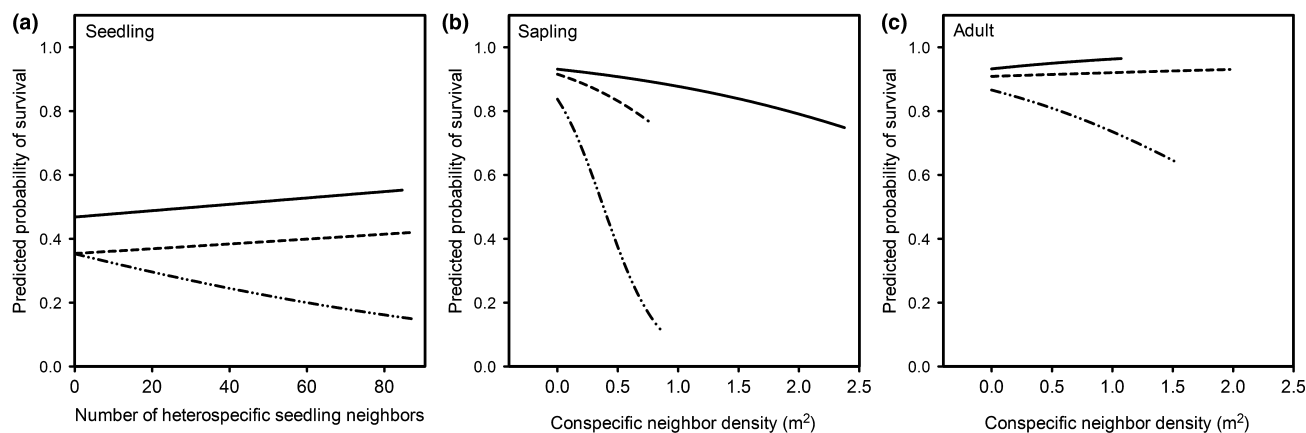
Figure 3 Predicted effects of neighbour density on the probability of individual survival in the Barro Colorado Island forest for tree species grouped as slow (solid line), intermediate (dashed line) or fast (dotted-dashed lines) growing (based on quantiles of RGR_{90}). Results are shown for life stages where a significant ($P < 0.05$) interaction between conspecific and heterospecific density and RGR_{90} were detected: (a) seedling stage, (b) sapling stage and (c) adult stage. Lines show predictions based on model results (for the basic model; see Methods), with all independent variables assigned to their mean values except conspecific density.

pathogens (McCarthy-Neumann & Kobe 2008), compared to more shade-tolerant species. Similarly, in a study of first-year seedling survival in the BCI forest, Lebrija-Trejos *et al.* (2016) found that species with greater seed mass, which tend to be slow-growing and shade-tolerant, were less negatively impacted by conspecific neighbours than species with lower seed mass. These previous studies, in conjunction with the results presented here, emphasise that tree life-history strategies related to growth-mortality trade-offs encompass tolerance of not only abiotic stress (e.g. shade), but also negative biotic interactions (e.g. density-dependent pathogen attack), consistent with the stress tolerance hypothesis (Kitajima 1994).

Variation among species in the strength of conspecific neighbour effects has also been linked to tree species relative abundance. In a previous analysis of seedling data from BCI, Comita *et al.* (2010) found that seedlings of more abundant species suffered less from conspecific neighbour effects compared to rare species in the community, likely due to strong effects of soil pathogens on rare species (Mangan *et al.* 2010; Marden *et al.* 2017). As in this study, that previous study did not find a significant relationship between the strength of conspecific neighbour effects and species' shade tolerance at the seedling stage. In this study, however, we found a significant relationship between CNDD and RGR_{90} at the sapling and adult life stages, even when accounting for species relative abundance (Fig. S1). Thus, by examining multiple life stages, our current analysis was able to detect a relationship between life-history strategy and CNDD.

Interactive effects of CNDD and RGR_{90} across life stages

Previous community-level studies examining CNDD or growth-mortality trade-offs in trees have typically focused only on a single life stage. However, understanding the contribution of these processes to shaping community composition and maintaining diversity requires an understanding of how they impact dynamics across the life cycle. Consistent with our previous study (Zhu *et al.* 2015b), we found that CNDD was strongest at earlier life stages. Specifically, significant negative effects of conspecific neighbours were only detected at the seedling and sapling stages, with conspecific seedling neighbours having a particular strong impact on seedling survival. Stronger CNDD at earlier life stages may be due to higher vulnerability to natural enemies or lower ability to recover from attack due to limited light availability in the forest understory (Walters & Reich 1996; Wright 2002; Valladares & Niinemets 2008; Niinemets 2010). While CNDD can result from intense intraspecific competition for resources, direct intraspecific competition between tree seedlings has been shown to be weak in tropical forests (Paine *et al.* 2008) and therefore unlikely to drive CNDD at the seedling stage. Decreasing CNDD with life stages could also arise if spatial variation in local abiotic factors (e.g. soil moisture) becomes a more important driver of survival at later stages. If such environmental filtering occurs at later stages, species with strong habitat preferences would survive well in their optimal habitat where conspecific densities tend to be high (Getzin *et al.* 2008; Zhu *et al.* 2010), thereby offsetting negative effects of density-responsive natural enemies.

In contrast to CNDD, we found evidence that growth-mortality trade-offs influence forest dynamics across all life stages. Species with fast optimal growth rates consistently had a significantly higher probability of mortality within each life stage. Across life stages, species' positions along the growth-mortality trade-off axis were largely consistent from one stage to the next, indicating that ontogenetic shifts in life-history strategy are rare, at least for these relatively common tree species. As discussed above, growth-mortality trade-offs are typically driven by allocation to growth vs. defence and storage. For individuals in the shaded understory, which would include the majority of seedlings and saplings (since canopy gaps are rare), this trade-off is likely driven predominantly by light availability. However, growth of adult tree species is likely not as strongly light limited since they are closer to or

in the canopy (but see Wright *et al.* 2010). Instead, growth-mortality trade-offs at later life stages may be driven more by soil resources, i.e. the ability to grow fast when water or nutrients are abundant vs. the ability to survive drought or withstand low nutrient availability. At the same time, slower growing species typically have higher wood density than faster growing species (Muller-Landau 2004; Chave *et al.* 2009), which makes them less susceptible to stem breakage during storms (Zimmerman *et al.* 1994) and more resistant to drought (Pratt *et al.* 2007; Greenwood *et al.* 2017). Nonetheless, our results suggest that species' life-history strategies remain consistent across life stages even though the factors driving trade-offs, as well as the functional traits underlying species' demographic rates (Visser *et al.* 2016), change with tree size.

In addition to having a lower mean probability of survival, species with faster growth rates were also more sensitive to conspecific neighbour effects at multiple life stages. RGR_{90} was a significant driver of among-species variation in conspecific neighbour effects at the sapling and adult stages, indicating that species life-history strategy shapes patterns of CNDD at both early and later life stages. The significant interaction between RGR_{90} and CNDD at the adult tree stage is somewhat surprising given that CNDD was generally weak at that stage. Although less studied than at the seedling stage, pathogens may also drive density-dependent mortality of large trees and susceptibility may be linked to life-history strategy. For example because fast-growing species typically have lower wood density, they may be more susceptible to heart-rot fungi that attack large trees and increase mortality risk (Heilmann-Clausen & Christensen 2004). At the same time, competition for below-ground resources may become stronger at later life stages when light is less limiting, with faster growing species potentially having roots better able to acquire limited nutrients (but possibly also more susceptible to soil pathogens, see Laliberté *et al.* 2015). In contrast, at the juvenile stage, survival was significantly related to species RGR_{90}, but we found no effects of conspecific neighbour density and no interaction between RGR_{90} and CNDD. Individuals in this size class would have higher maintenance costs compared to seedlings and saplings, but would still likely be shaded by larger adult trees. Thus, light availability, coupled with species' ability to tolerate low light, may be the predominant drivers of survival at this life stage.

While CNDD itself was strongest at the seedling stage, the relationship between RGR_{90} and conspecific neighbour effects was not significant at that stage. Instead, variation in CNDD at the seedling stage was significantly related to species relative abundance in the community (Fig. S1; Comita *et al.* 2010). RGR_{90} was, however, a signification driver of variation among species in heterospecific seedling neighbour effects, with faster growing species more negatively impacted by heterospecific seedling neighbour density (Figs. S3 and S4). Thus, at the seedling stage, species life-history strategy appears to influence response to overall seedling neighbour density, with negative effects of neighbour density likely resulting from general competition or generalist natural enemies. Although our study did include some common fast-growing pioneer species (e.g. *Miconia argentea*, *Croton*

billbergianus), it is important to note that many of the fastest growing species in the BCI forest were not included in our analysis because they did not have sufficient numbers of seedlings in the understory (since their seedlings typically die quickly if in the shade or grow rapidly into the next life stage if in a light gap). Experimental studies manipulating conspecific seedling densities of both faster and slower growing species would help determine whether CNDD is influenced by species location on the growth-survival trade-off axis at the seedling stage.

CONCLUSIONS

Overall, our results demonstrate how species life-history strategies interact with conspecific density dependence to influence forest dynamics across multiple life stages. Our findings support the idea that conspecific density dependence contributes to species coexistence, and that this occurs at least in part through heightening abiotic niche differences (McCarthy-Neumann & Kobe 2008). Effects of CNDD on mortality were strongest at the seedling stage, emphasising the importance of non-random mortality at early life stages in structuring diverse tree communities (Grubb 1977; Green *et al.* 2014). At the same time, significant effects of life-history strategy and its interaction with CNDD at both early (sapling) and later (adult) stages underscore the critical need to examine multiple life stages when assessing mechanisms of species coexistence in long-lived organisms. Our results further suggest that similar physiological trade-offs may govern susceptibility to density-dependent mechanisms and responses to resource availability. Identifying the predominant drivers underlying these trade-offs for each life stage (e.g. light limitation and pathogen impacts at early life stages vs. stem breakage and drought at later stages), as well as the functional traits governing species responses to these drivers, would greatly improve understanding of community dynamics and species coexistence in diverse forests.

AUTHORSHIP

DATA ACCESSIBILITY STATEMENT

REFERENCES

Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J., Ray-Mjkherjee, J., Mbeau-Ache, C. et al. (2014). Functional traits explain variation in plant life history strategies. *Proc. Natl Acad. Sci. USA*, 111, 740–745.

Augspurger, C.K. (1984). Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, 65, 1705–1712.

Augspurger, C.K. & Kelly, C.K. (1984). Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia*, 61, 211–217.

Bagchi, R., Gallery, R.E., Gripenberg, S., Gurr, S.J., Narayan, L., Addis, C.E. et al. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, 506, 85–88.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H. et al. (2016). lme4: linear mixed-effects models using 'Eigen' and S4. R Package Version 3.3.0. Available at: https://cran.rproject.org/web/packages/lme4/index.html.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. et al. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.*, 24, 127–135.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009). Towards a worldwide wood economics spectrum. *Ecol. Lett.*, 12, 351–366.

Chen, L., Mi, X.C., Comita, L.S., Zhang, L.W., Ren, H.B. & Ma, K.P. (2010). Community-level consequences of density dependence and habitat association in a subtropical broadleaved forest. *Ecol. Lett.*, 13, 695–704.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Coley, P.D. (1988). Effects of plant growth rate and leaf life-time on the amount and type of anti-herbivore defence. *Oecologia*, 74, 531–536.

Coley, P.D. & Barone, J. (1996). Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Evol. Syst.*, 27, 305–335.

Comita, L.S. (2017). How latitude affects biotic interactions. *Science*, 356, 1328–1329.

Comita, L.S. & Hubbell, S.P. (2009). Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology*, 90, 328–334.

Comita, L.S., Aguilar, S., Perez, R., Lao, S. & Hubbell, S.P. (2007). Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest. *J. Veg. Sci.*, 18, 163–174.

Comita, L.S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C.D. & Zimmerman, J.K. (2009). Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *J. Ecol.*, 97, 1346–1359.

Comita, L.S., Muller-Landau, H.C., Aguilar, S. & Hubbell, S.P. (2010). Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, 329, 330–332.

Comita, L.S., Queenborough, S.A., Murphy, S.J., Eck, J.L., Xu, K., Krishnadas, M. et al. (2014). Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *J. Ecol.*, 102, 845–856.

Condit, R. (1998). *Tropical Forest Census Plots*. Springer-Verlag, Berlin, Germany.

Condit, R., Hubbell, S.P. & Foster, R.B. (1996). Changes in tree species abundance in a Neotropical forest: impact of climate change. *J. Trop. Ecol.*, 12, 231–256.

Condit, R., Ashton, P.S., Bunyavejchewin, S., Dattaraja, H.S., Davies, S.J., Esufali, S. et al. (2006). The importance of demographic niches to tree diversity. *Science*, 313, 98–101.

Condit, R., Aguilar, S., Pérez, R., Lao, S., Hubbell, S.P. & Foster, R.B. (2017). BCI 50-ha Plot Taxonomy as of 2017. https://doi.org/10.25570/stri/10088/32990.

Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations* (eds den Boer, P.J. & Gradwell, G.R.). Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp. 298–312.

Fine, P.V., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H. et al. (2006). The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology*, 87, S150–S162.

Freckleton, R.P. & Lewis, O.T. (2006). Pathogens, density dependence and the coexistence of tropical trees. *P. Roy. Soc. B-Biol. Sci*, 273, 2909–2916.

Gelman, A. & Pardoe, L. (2006). Bayesian measures of explained variance and pooling in multilevel (hierarchical) models. *Technometrics*, 48, 241–251.

Getzin, S., Wiegand, T., Wiegand, K. & He, F. (2008). Heterogeneity influences spatial patterns and demographics in forest stands. *J. Ecol.*, 96, 807–820.

Green, P.T., Harms, K.E. & Connell, J.H. (2014). Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. *P. Roy. Soc. B-Biol. Sci*, 111, 18649–18654.

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C.D. et al. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecol. Lett.*, 20, 539–553.

Grubb, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review*, 52, 107–145.

Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404, 493–495.

Heilmann-Clausen, J. & Christensen, M. (2004). Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. *For. Ecol. Manage.*, 201, 105–117.

Herms, D.A. & Mattson, W.J. (1992). The dilemma of plants: to grow or defend. *Q. Rev. Biol.*, 67, 283–335.

Hille Ris Lambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.*, 43, 227–248.

Hubbell, S.P. & Foster, R.B. (1983). Diversity of canopy trees in a Neotropical forest and implications for conservation. In: *Tropical Rain Forest: Ecology and Management* (eds Sutton, S.L., Whitmore, T.C. & Chadwick, A.C.). Blackwell Scientific, Oxford, UK, pp. 25–41.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B. et al. (1999). Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, 283, 554–557.

Hubbell, S.P., Condit, R. & Foster, R.B. (2005). Barro Colorado Forest Census plot data. Available at: http://ctfs.si.edu/webatlas/datasets/bci.

Hunt, R. (1982). *Plant Growth Curves: A Functional Approach to Plant Growth Analysis*. Edward Arnold, London, UK.

Inman-Narahari, F., Ostertag, R., Hubbell, S.P., Giardina, C.P., Cordell, S. & Sack, L. (2016). Density-dependent seedling mortality varies with light availability and species abundance in wet and dry Hawaiian forests. *J. Ecol.*, 104, 773–780.

Janzen, D. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.

Johnson, D., Beaulieu, W.T., Bever, J.D. & Clay, K. (2012). Conspecific negative density dependence and forest diversity. *Science*, 336, 904–907.

Kitajima, K. (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, 98, 419–428.

Kitajima, K. & Poorter, L. (2010). Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytol.*, 186, 708–721.

Kobe, R.K. (1997). Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos*, 80, 226–233.

Kobe, R.K. (1999). Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology*, 80, 187–201.

Kobe, R.K. & Vriesendorp, C.F. (2011). Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecol. Lett.*, 14, 503–510.

Kobe, R.K., Pacala, S.W., Silander, J.A. & Canham, C.D. (1995). Juvenile tree survivorship as a component of shade-tolerance. *Ecol. Appl.*, 13, 517–532.

Kunstler, G., Coomes, D.A. & Canham, C.D. (2009). Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. *J. Ecol.*, 97, 685–695.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C. *et al.* (2016). Plant functional traits have globally consistent effects on competition. *Nature*, 529, 204–207.

Laliberté, E., Lambers, H., Burgess, T.I. & Wright, S.J. (2015). Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytol.*, 206, 507–521.

LaManna, J.A., Walton, M.L., Turner, B.L. & Myers, J.A. (2016). Negative density dependence is stronger in resource-rich environments and diversifies communities when stronger for common but not rare species. *Ecol. Lett.*, 19, 657–667.

LaManna, J.A., Mangan, S.A., Alonso, A., Bourg, N.A., Brockelman, W.Y., Bunyavejchewin, S. *et al.* (2017). Plant diversity increases with the strength of negative density dependence at the global scale. *Science*, 356, 1389–1392.

Lebrija-Trejos, E., Wright, S.J., Hernandez, A. & Reich, P.B. (2014). Does relatedness matter? Phylogenetic densitydependent survival of seedlings in a tropical forest. *Ecology*, 95, 940–951.

Lebrija-Trejos, E., Reich, P.B., Hernández, A. & Wright, S.J. (2016). Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest. *Ecol. Lett.*, 19, 1071–1080.

Lin, L., Comita, L.S., Zheng, Z. & Cao, M. (2012). Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *J. Ecol.*, 100, 905–914.

MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting Species. *Am. Nat.*, 101, 377–385.

Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M.L., Valencia, M.C., Sanchez, E.I. *et al.* (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, 466, 752–755.

Marden, J.H., Mangan, S.A., Peterson, M.P., Wafula, E., Fescemyer, H.W., Der, J.P. *et al.* (2017). Ecological genomics of tropical trees: how local population size and allelic diversity of resistance genes relate to immune responses, cosusceptibility to pathogens, and negative density dependence. *Mol. Ecol.*, 26, 2498–2513.

McCarthy-Neumann, S. & Ibáñez, I. (2013). Plant-soil feedback links negative distance dependence and light gradient partitioning during seedling establishment. *Ecology*, 94, 780–786.

McCarthy-Neumann, S. & Kobe, R.K. (2008). Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. *Ecology*, 89, 1883–1892.

Muller-Landau, H.C. (2004). Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, 36, 20–32.

Myers, J.A. & Kitajima, K. (2007). Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. *J. Ecol.*, 95, 383–395.

Niinemets, Ü. (2010). Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *For. Ecol. Manage.*, 260, 1623–1639.

Paine, C.E.T., Harms, K.E., Schnitzer, S.A. & Carson, W.P. (2008). Weak competition among tropical tree seedlings: implications for species coexistence. *Biotropica*, 40, 432–440.

Peters, H.A. (2003). Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecol. Lett.*, 6, 757–765.

Piao, T.F., Comita, L.S., Jin, G.Z. & Kim, J.H. (2013). Density dependence across multiple life stages in a temperate old-growth forest of northeast China. *Oecologia*, 172, 207–217.

Poorter, L. & Bongers, F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, 87, 1733–1743.

Pratt, R.B., Jacobsen, A.L., Golgotiu, K.A., Sperry, J.S., Ewers, F.W. & Davis, S.D. (2007). Life history type and water stress tolerance in nine California chaparral species (Rhamnaceae). *Ecol. Monogr.*, 77, 239–253.

Pringle, E.G., Álvarez-Loayza, P. & Terborgh, J. (2007). Seed characteristics and susceptibility to pathogen attack in tree seeds of the Peruvian Amazon. *Plant Ecol.*, 193, 211–222.

Queenborough, S.A., Metz, M.R., Valencia, R. & Wright, S.J. (2013). Demographic consequences of chromatic leaf defence in tropical tree communities: do red young leaves increase growth and survival? *Ann. Bot.*, 112, 677–684.

R Development Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Available at http://www.R-project.org.

Reich, P.B. (2014). The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *J. Ecol.*, 102, 275–301.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997). From tropics to tundra: global convergence in plant functioning. *Proc. Natl Acad. Sci. USA*, 94, 13730–13734.

Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D. & Buschena, C. (1998). Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Funct. Ecol.*, 12, 327–338.

Rüger, N., Wirth, C., Wright, S.J. & Condit, R. (2012). Functional traits explain light and size response of growth rates in tropical tree species. *Ecology*, 93, 2626–2636.

Sack, L. & Grubb, P.J. (2001). Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? *Funct. Ecol.*, 15, 145–154.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends Ecol. Evol.*, 19, 605–611.

Terborgh, J. (2012). Enemies maintain hyperdiverse tropical forests. *Am. Nat.*, 179, 303–314.

Valladares, F. & Niinemets, U. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annu. Rev. Ecol. Evol. Syst.*, 39, 237–257.

Visser, M.D., Bruijning, M., Wright, S.J., Muller-Landau, H.C., Jongejans, E., Comita, L.S. *et al.* (2016). Functional traits as predictors of vital rates across the life cycle of tropical trees. *Funct. Ecol.*, 30, 168–180.

Walters, M.B. & Reich, P.B. (1996). Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology*, 77, 841–853.

Wang, X.G., Comita, L.S., Hao, Z.Q., Davies, S.J., Ye, J., Lin, F. *et al.* (2012). Local-scale drivers of tree survival in a temperate forest. *PLoS ONE*, 7, e29469.

Westoby, M., Falster, D., Moles, A., Vesk, P. & Wright, I. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.*, 33, 125–159.

Windsor, D.M. (1990). *Climate and Moisture Variability in a Tropical Forest: long-term records from Barro Colorado Island.* Smithsonian Institution Press, Panama.

Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, 130, 1–14.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E. *et al.* (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, 91, 3664–3674.

Zhu, Y., Mi, X.C., Ren, H.B. & Ma, K.P. (2010). Density dependence is prevalent in a heterogeneous subtropical forest. *Oikos*, 119, 109–119.

Zhu, K., Woodall, C.W., Monteiro, J.V. & Clark, J.S. (2015a). Prevalence and strength of density-dependent tree recruitment. *Ecology*, 96, 2319–2327.

Zhu, Y., Comita, L.S., Hubbell, S.P. & Ma, K. (2015b). Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. *J. Ecol.*, 103, 957–966.

Zimmerman, J.K., Everham III, E.M., Waide, R.B.D., Lodge, J., Taylor, C.M. & Brokaw, N.V.L. (1994). Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *J. Ecol.*, 82, 911–922.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.