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

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YZ and LC conceived the study, performed data analysis, and wrote the first draft of the manuscript; SQ provided feedback and revised the manuscript; RC oversaw the collection and management of the tree data; all authors contributed to revisions.

Data accessibility statement:

Survival data from the BCI seedling census are available on Dryad (doi:10.5061/dryad.fm654), and data from the BCI census of trees ≥ 1 cm dbh are archived and available online at <http://ctfs.si.edu/webatlas/datasets/bci/>.

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.

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 neighbors, 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; Hille Ris Lambers et al. 2012; Terborgh 2012; Bagchi et al. 2014; Comita et al. 2014; Zhu et al. 2015a; Zhu et al. 2015b). More recently, studies have shown that while CNDD is prevalent in plant communities, the strength of conspecific neighbor effects (i.e., per neighbor 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 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 versus 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 (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 neighbor density.

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

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

117 In the present study, we use long-term, spatially-explicit data on individual growth and
118 survival in a lowland tropical forest in central Panama to quantify the strength of CNDD and
119 growth-mortality trade-offs at multiple life stages, from seedling to adult tree, for 47 tree species.
120 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 neighbor 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 neighbors 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 x 500 m 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 x 1 m seedling plot was established in the center of each 5 x 5 m subquadrat of the BCI 50-ha plot, for a total of 20,000 1-m² 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; Comita et al. 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; Condit et al. 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-yr census intervals for stems ≥ 1 cm dbh (1985-90, 1990-95, 1995-2000, 2000-05, 2005-10) and across two 5-yr census intervals for seedlings (2001-06, 2006-11). RGR was calculated as $(\log(\text{size}_{t+1}) - \log(\text{size}_t)) / \text{time}$, 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 favorable 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 neighbor densities

To test for negative density dependence, we first calculated the densities of conspecific and heterospecific neighbors for each focal individual. For all life stages, we calculated conspecific neighbor density and heterospecific neighbor 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 neighbor density for each focal species can be found in Table S2. For the seedling stage, we also calculated the density of neighboring seedlings by counting the number of conspecific and heterospecific seedlings alive at the start of the census interval in the same 1x1 m seedling plot as the focal seedling.

Survival analysis

We used generalized linear mixed-effects models (GLMMs; Gelman & Pardoe 2006; Bolker et al. 2009) with binomial errors to examine the influence of neighborhood densities and RGR_{90} , as well as their interactive effect, on the probability of survival. We modeled 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 modeled the probability of an individual surviving to the end of the census interval as a function of conspecific neighbor density (CON), heterospecific neighbor 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 20x20 m 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 1x1 m seedling plot in which the individual was located, nested within the 20x20m 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 the present 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 neighbor densities, RGR_{90} , and species relative abundance, as well as interactions of neighbor 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 standardized 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, Maechler & Bolker 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 neighbors 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 neighbor 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 neighborhood 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 neighbors 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 stronger CNDD; Fig S2), but was not significant due to large standard errors, particularly for conspecific seedling neighbors (Fig. 2E). There were not significant interactions between species’ RGR_{90} and heterospecific neighbor

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 neighbor density compared to slower growing species; Fig. 2F; Fig. 3A; Fig S3 & S4). The effects of size, RGR_{90} , and conspecific and heterospecific neighbors on survival remained qualitatively the same for all life stages when species relative abundance, and its interactions with conspecific and heterospecific neighbor 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 neighbors: fast growing species not only had higher mean mortality than slower growing species, but were also more sensitive to the density of conspecific neighbors 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 neighbor 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 neighbor effects

Originally proposed to explain the maintenance of high tree diversity in tropical forests (Janzen 1970; Connell 1971), negative effects of conspecific neighbor 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, for example with precipitation (Comita et al. 2014) and latitude (Johnson et al. 2012; LaManna et al. 2017). At the same time, there is

increasing 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 neighbor 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 defense (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 neighboring 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 defense (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-Neuman & Kobe 2008; McCarthy-Neuman & Ibanez 2013; but see Pringle et al. 2007). Although we did not explicitly test the mechanisms underlying CNDD in the present study, evidence from our study site, as well as other forests, suggests that negative conspecific neighbor 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 neighbor density on survival for slower vs. faster growing species is likely the result of life history trade-offs that govern allocation to growth vs. defense 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 and 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 neighbors, as well as higher susceptibility to soil 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 neighbors than species with lower seed mass. These previous studies, in conjunction with the results presented here, emphasize 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 neighbor 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 neighbor 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 the present study, that previous study did not find a significant relationship between the strength of conspecific neighbor effects and species' shade tolerance at the seedling stage. In the present 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 neighbors were only detected at the seedling and sapling stages, with conspecific seedling neighbors 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. defense 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 neighbor effects at multiple life stages. RGR_{90} was a significant driver of among-species variation in conspecific neighbor 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 neighbor 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 neighbor 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 significant driver of variation among species in heterospecific seedling neighbor effects, with faster growing species more negatively impacted by heterospecific seedling neighbor density (Fig. S3 & S4). Thus, at the seedling stage, species life history strategy appears to influence response to overall seedling neighbor density, with negative effects of neighbor 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, emphasizing 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.

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Figure legends

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).

Figure 2. Parameter estimates (± 1 se) of effects of (A) tree size, (B) species' 90th percentile growth rate (RGR_{90}), (C) conspecific neighbor density, (D) heterospecific neighbor density, and interactions between RGR_{90} and (E) conspecific and (F) heterospecific neighbor density on

individual survival at the seedling, sapling, juvenile, and adult stages in the BCI forest. Survival was modeled 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 neighbor densities were calculated as number of conspecific or heterospecific seedlings in the same 1 m² seedling plot. For all other models, neighbor densities were based on total basal area of conspecific or heterospecific stems ≥ 1 cm dbh within 15 m of the focal individual.

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.

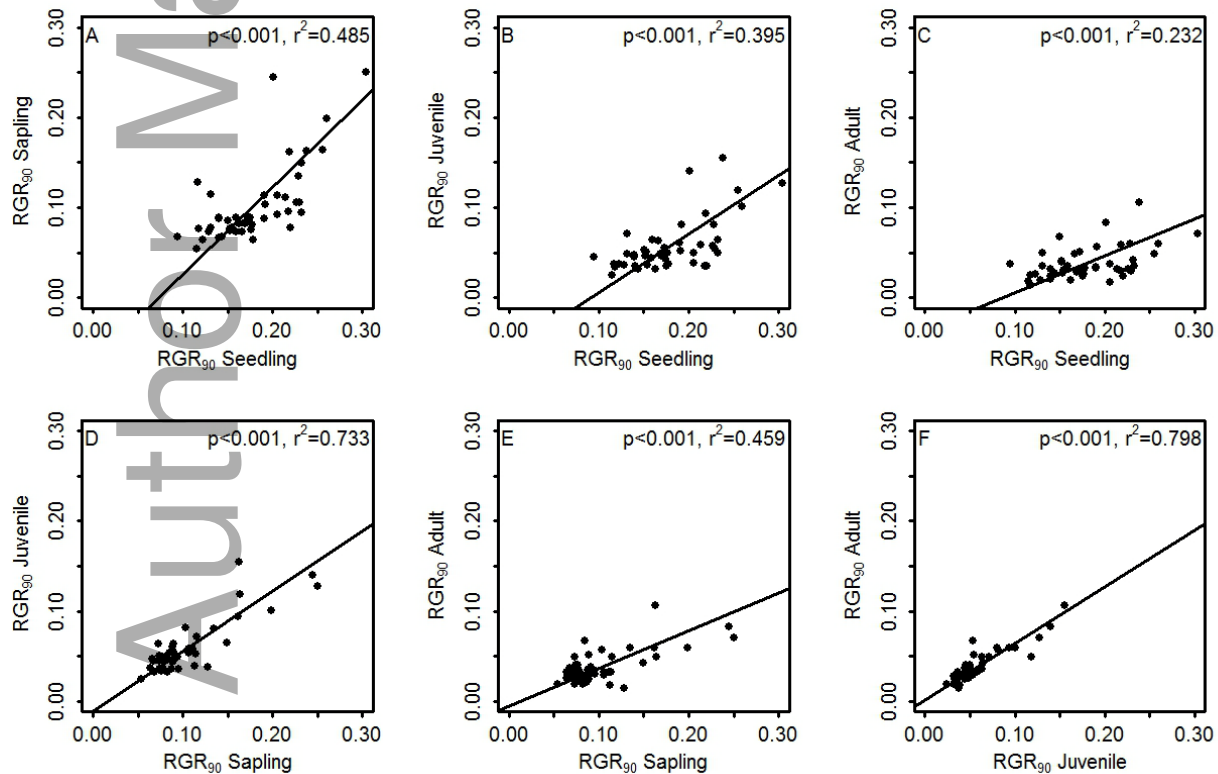


Figure 1

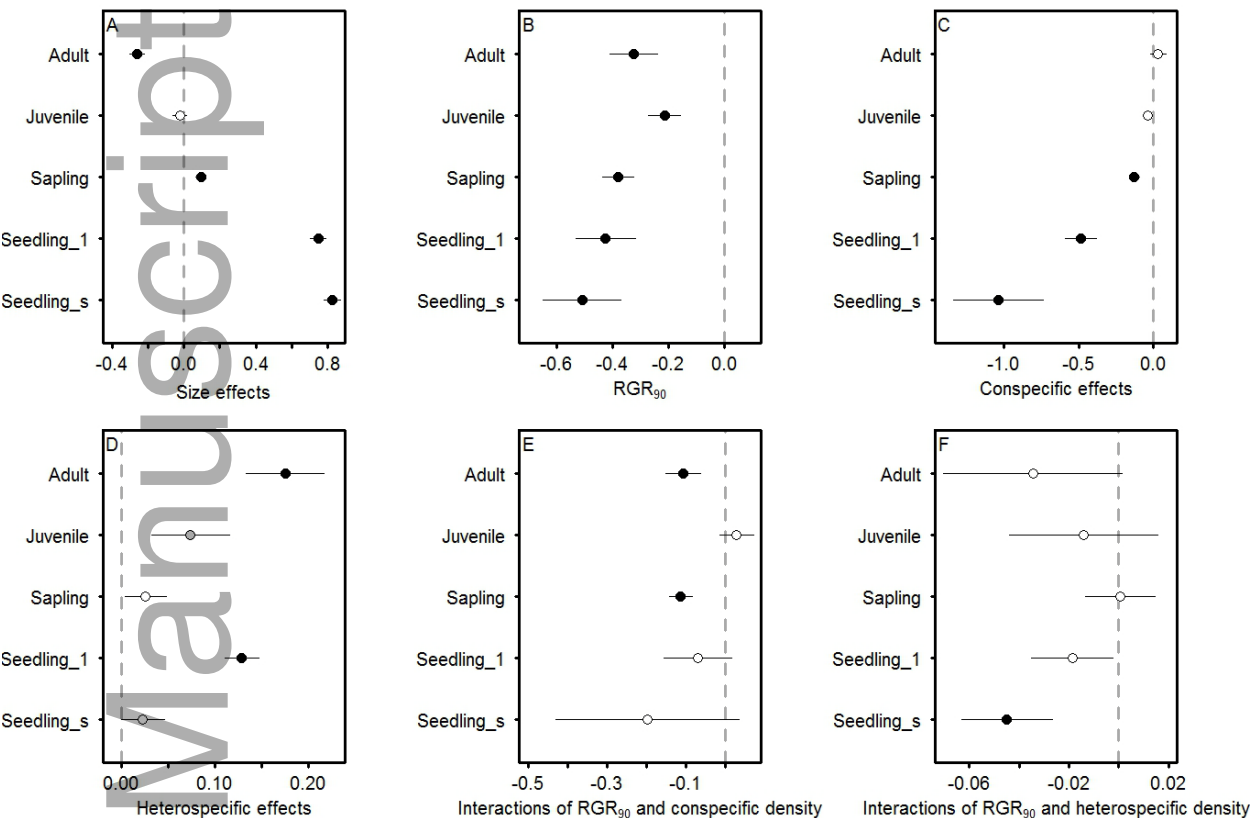


Figure 2

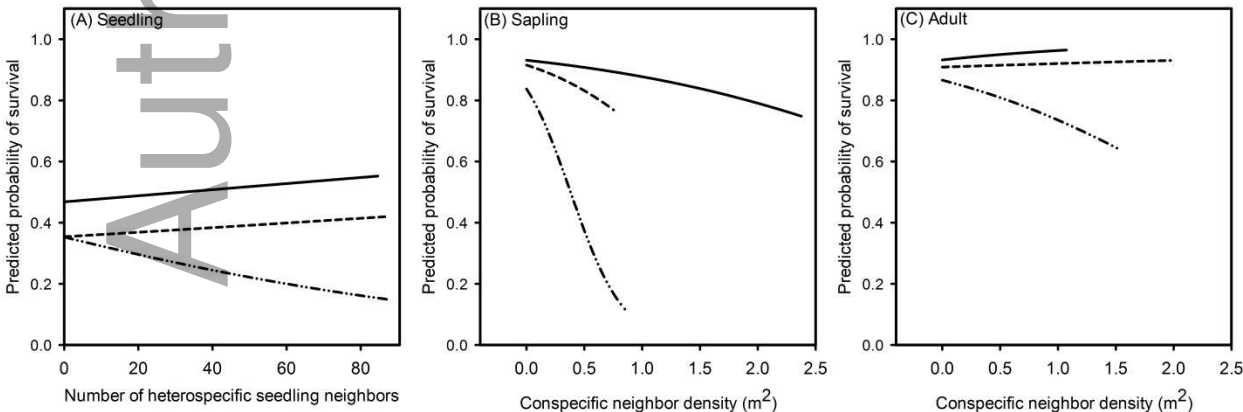
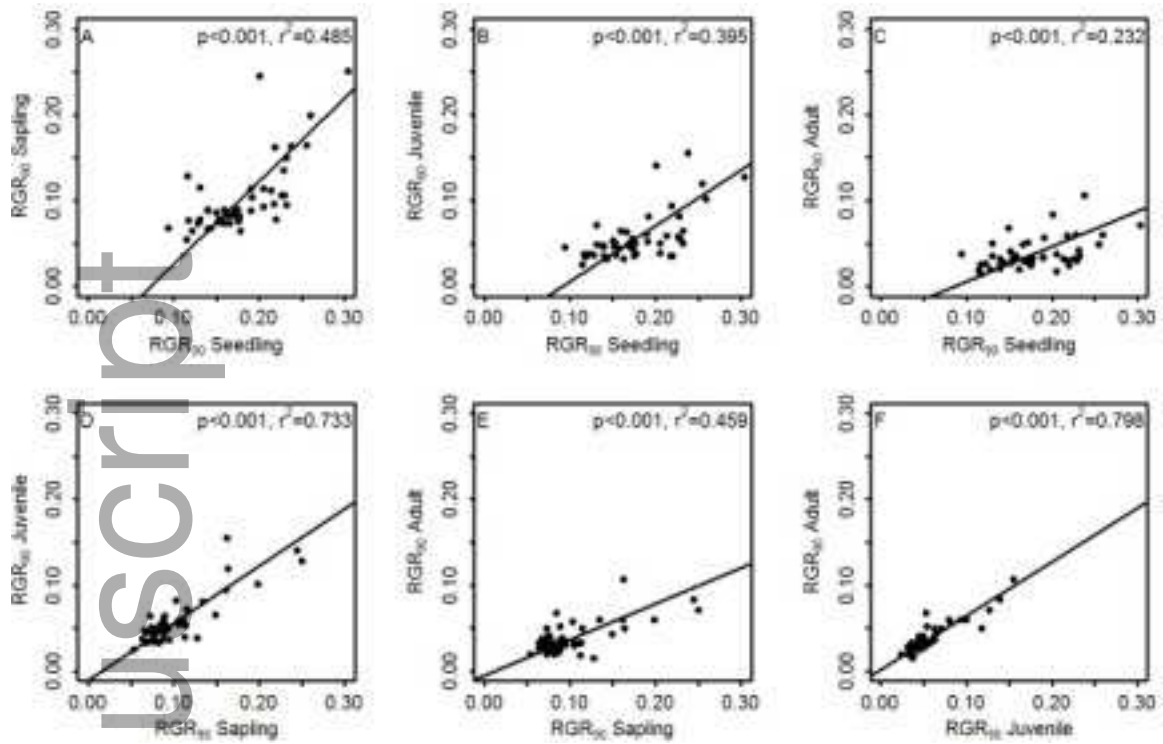
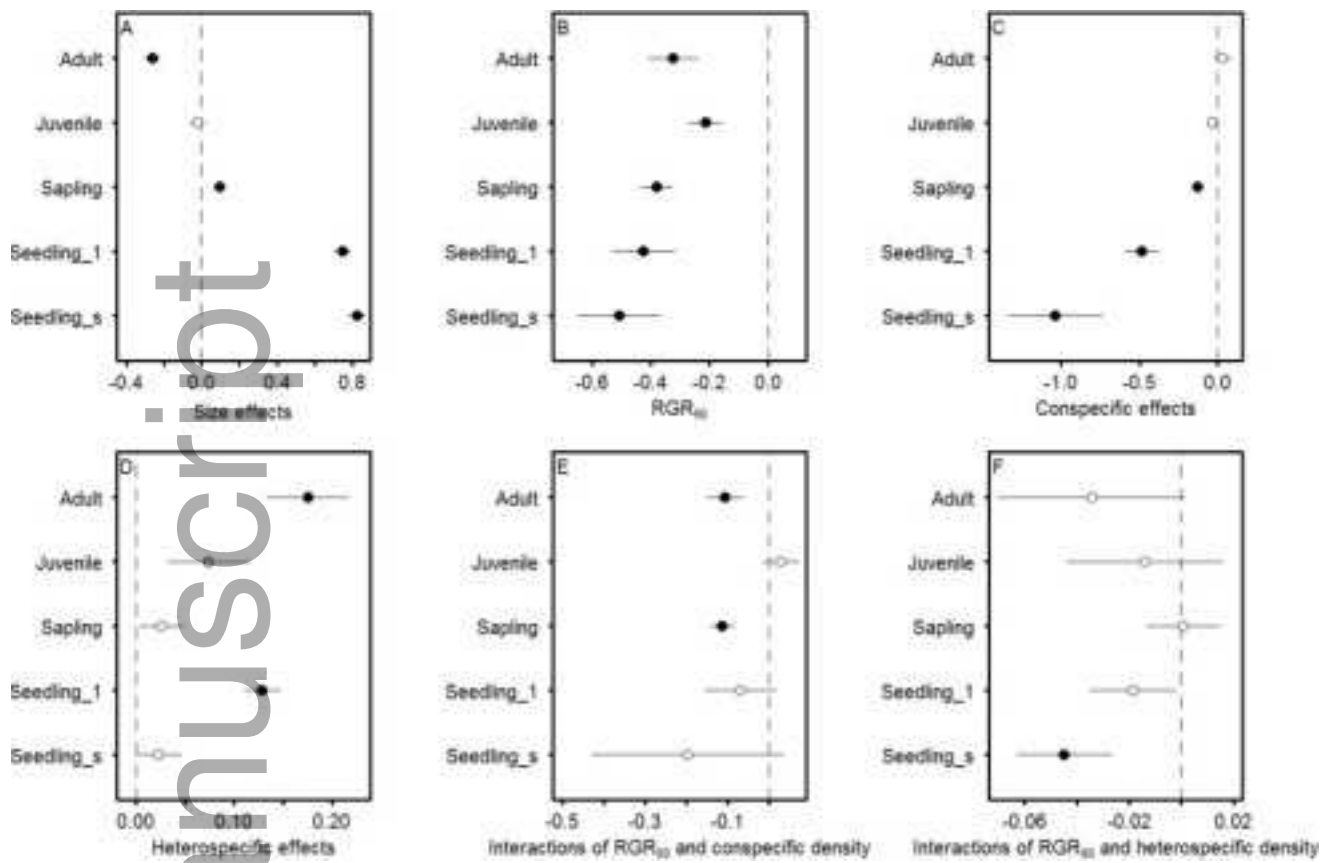


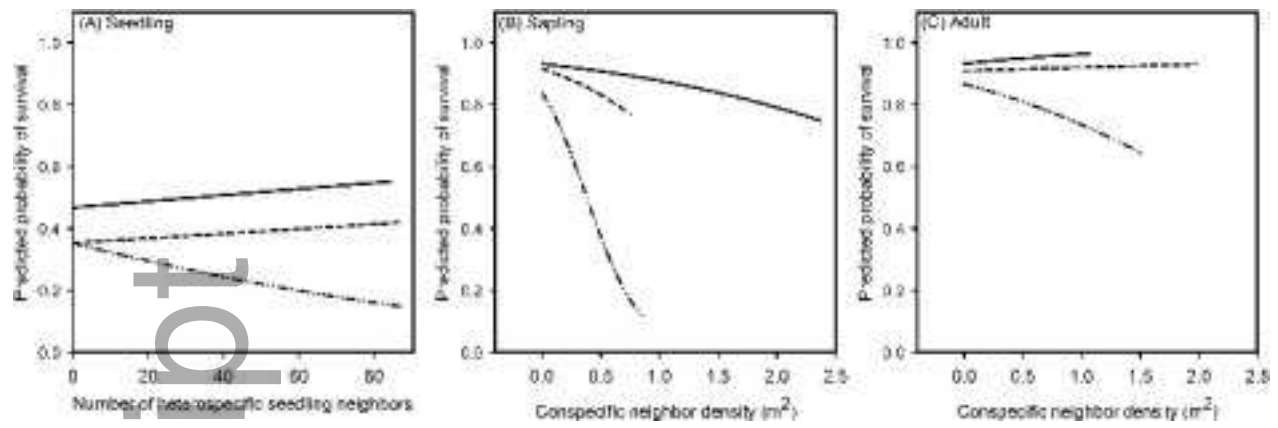
Figure 3



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