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Effects of biotic interactions on tropical tree performance depend on abiotic conditions

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Abstract. Predicting biotic responses to environmental change requires understanding the joint effects of abiotic conditions and biotic interactions on community dynamics. One major challenge is to separate the potentially confounding effects of abiotic environmental variation and local biotic interactions on individual performance. The stress gradient hypothesis (SGH) addresses this issue directly by predicting that the effects of biotic interactions on performance become more positive as the abiotic environment becomes more stressful. It is unclear, however, how the predictions of the SGH apply to plants of differing functional strategies in diverse communities. We asked (1) how the effect of crowding on performance (growth and survival) of trees varies across a precipitation gradient, and (2) how functional strategies (as measured by two key traits: wood density and leaf mass per area, LMA) mediate average demographic rates and responses to crowding across the gradient. We built trait-based neighborhood models of growth and survival across a regional precipitation gradient where increasing precipitation is associated with reduced abiotic stress. In total, our dataset comprised ~170,000 individual trees belonging to 252 species. The effect of crowding on tree performance varied across the gradient; crowding negatively affected growth across plots and positively affected survival in the wettest plot. Functional traits mediated average demographic rates across the gradient, but we did not find clear evidence that the strength of these responses depends on species' traits. Our study lends support to the SGH and demonstrates how a trait-based perspective can advance these concepts by linking the diversity of species interactions with functional variation across abiotic gradients.

Key words: *functional traits; hierarchical models; leaf mass per area; neighborhood interactions; stress gradient hypothesis; tropical forest; wood density.*

Introduction

Predicting ecological responses to environmental change requires understanding the interactive effects of abiotic conditions and biotic interactions on individual performance and community dynamics (Araújo and Luoto 2007, Clark et al. 2011, Wisz et al. 2012, Fichtner et al. 2017). Few studies, however, have measured fitness components across environmental gradients while also quantifying the effects of local biotic interactions (Clark et al. 2011, Ehrlén and Morris 2015). As a consequence, we have a limited understanding of demographic responses to environmental heterogeneity across broad scales (but see Clark et al. 2011, Gómez-Aparicio et al. 2011, Canham and Murphy 2016, Ford et al. 2016, Putnam and Reich 2017 for some exceptions).

The stress gradient hypothesis (SGH) explicitly addresses the links between abiotic conditions and local biotic interactions (Bertness and Callaway 1994, Maestre et al. 2009, Soliveres et al. 2015). Under the SGH, plant–plant interactions are expected to have a negative effect on performance in conditions of low physiological stress and a positive effect in conditions of high physiological stress. The underlying rationale is that individuals compete for shared resources when abiotic conditions are most favorable, but buffer one another from adverse environmental conditions when abiotic conditions are harsh (Bertness and Callaway 1994, Maestre et al. 2009). For example, shading and hydraulic redistribution of soil water can benefit neighboring plants in arid regions (Dawson 1993, Caldwell et al. 1998, Prieto et al. 2012). The SGH has received considerable support based largely on studies of pairwise species interactions across environmental gradients (Callaway 2007, He et al. 2013), but few empirical studies have studied multiple interacting species (Maestre et al. 2009, Soliveres et al. 2015). As a result, we lack a general understanding of how species interactions change along stress gradients, especially in highly diverse systems like tropical forests.

Characterizing species based on traits that reflect their functional strategies provides a tractable way to study the role of biotic interactions in diverse communities across abiotic gradients because species with differing functional strategies may respond differently to stress (Maestre et al. 2009, Adler et al. 2013, Soliveres et al. 2015, Kunstler et al. 2016). In light-limited wet tropical forests, for example, contrasting functional strategies are characterized by a trade-off between shade tolerance and maximum growth rate. Species with traits associated with shade tolerance and resistance to natural enemies tend to have relatively high average survival (Kobe 1999, Rüger et al. 2012). High wood density (WD; g/cm^3),

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for instance, is associated with shade-tolerant regeneration (Valladares and Niinemets 2008, Ameztegui et al. 2017) and resistance to natural enemies (Alvarez-Clare and Kitajima 2007). Some work also suggests that leaf mass per area (LMA; $g/m^2 = 1/SLA$) is positively associated with shade tolerance (Valladares and Niinemets 2008, Ameztegui et al. 2017) and resistance to herbivory (Wright et al. 2004, Poorter and Bongers 2006). These survival advantages associated with "resource-conservative" functional strategies are opposed by the higher potential growth rates afforded by alternative "resource-acquisitive" strategies (Visser et al. 2016). Specifically, low values of WD and LMA are associated with efficient hydraulic structures and high photosynthetic rates, respectively, which enable trees to rapidly capitalize on pulses of light availability (e.g., small-scale disturbances such as tree-fall gaps) (Pacala and Rees 1998, Wright et al. 2004, Poorter and Bongers 2006, Brenes-Arguedas et al. 2011, Rüger et al. 2012). Overall, in wet tropical forests, we expect shade-tolerant species to have higher survival and lower growth rates, and for these rates to be less sensitive to crowding than species with light-demanding strategies (Fig. 1).

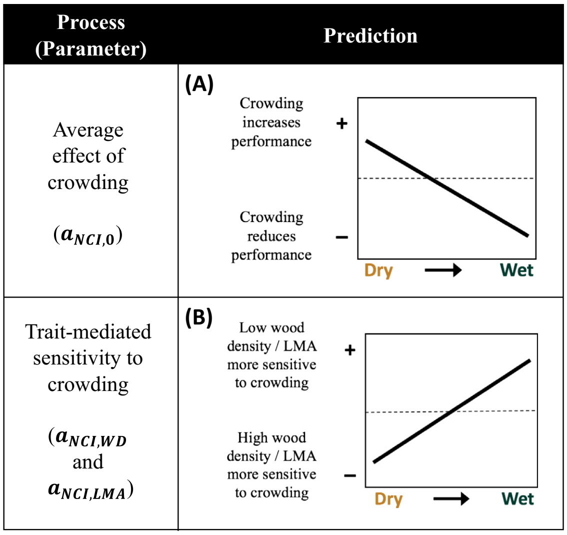

FIG. 1. Predictions for the average effect of crowding (top row) and trait-mediated effect of crowding (bottom row) on tree performance (growth and survival) along a precipitation gradient. Model parameters in the left column correspond to the models described in the methods section. (A) In high stress conditions (e.g., dry forest), crowding may have a relatively weak negative (or positive) effect on performance, assuming that abiotic conditions are the strongest determinants of performance, or if neighboring plants ameliorate harsh conditions. In contrast, in low stress conditions (e.g., wet forest), crowding is associated with competition for light that should reduce performance compared to open sites. High crowding (especially by conspecifics) can also be associated with higher natural enemy pressure. (B) In high stress conditions (e.g., dry forest), species with conservative traits (i.e., high wood density [WD] and leaf mass per area) may be more sensitive to crowding than species with acquisitive traits (i.e., crowding has a relatively strong negative impact on performance of conservative species) if acquisitive species are better able to rapidly exploit belowground resources than their neighbors. Additionally, if deciduous (i.e., drought-avoiding) species have acquisitive traits, they may avoid competition for water when it is strongest. In contrast, in low stress conditions (e.g., wet forest), acquisitive species may be more sensitive to crowding than conservative species because they are shade intolerant.

In seasonally dry tropical forests, in contrast, belowground resources (i.e., water and nutrient availability) are typically more limiting than light (Brenes-Arguedas et al. 2011, Lohbeck et al. 2013). Numerous functional traits are related to drought strategies of dry forest tropical trees, but, in general, two main strategies with respect to water limitation can be identified: drought tolerance and drought avoidance (Goldstein and Santiago 2016). Species with high WD, for instance, tend to be more resistant to drought-induced embolism and thus better able to tolerate the physiological stress of drought (Hacke et al. 2001, Mitchell et al. 2008). Other species avoid drought by shedding their leaves during the dry season and thus minimize transpirational water loss (Borchert 1980, 1994, Poorter and Markesteijn 2008, Brenes-Arguedas et al. 2013). The negative impacts of crowding may differ between drought-tolerant evergreen species and drought-avoiding deciduous species for at least two reasons. First, drought-tolerant evergreen species (but not drought-avoiding deciduous species) may compete for water in the dry season, when it is most limiting. Second, during the wet season, drought-avoiding deciduous species may exploit belowground resources more efficiently than drought-tolerating evergreen species if they have more efficient hydraulic architectures (Reich et al. 1991, Eamus 1999). Consequently, we might expect drought-avoiding deciduous species to be less sensitive to crowding compared to drought-tolerating evergreen species (Fig. 1). The results of competitive dynamics may be more complicated in these forests, however, if individuals compete for multiple limiting resources (e.g., water and light in different seasons). In general, we expect species with contrasting functional strategies to respond differently to crowding along a gradient of water availability. Integrating information on species functional strategies will help advance the SGH and clarify how functional strategies mediate the effects of biotic interactions across abiotic gradients.

We used hierarchical Bayesian models to investigate the interactive effects of abiotic conditions, functional traits, and tree crowding on growth and survival of tropical trees in three permanent forest plots across a regional rainfall gradient in Panama. One plot is classified as seasonally dry tropical forest, and the other two as wet tropical forest. Annual precipitation in the plots ranges from ca. 1,900 to 3,000 mm of rain/yr, and prior work has shown that this gradient (especially variation in dry season length) has pronounced effects on species distributions and community composition (e.g., Condit et al. 2000, 2013, Engelbrecht et al. 2007). Additionally, canopy openness (i.e., light availability) is higher (Condit et al. 2004, Brenes-Arguedas et al. 2011, Gaviria and Engelbrecht 2015), while soil nutrient availability (Condit et al. 2013) and natural enemy pressure are lower in the dry forest plot compared to the wet forest plots (Spear et al. 2015 but also see Gaviria and Engelbrecht 2015). We focus on trees 1–10 cm in diameter because small trees are particularly sensitive to size-asymmetric resource competition (DeMalach et al. 2016). The dataset comprises ~170,000 individual trees belonging to 252 species that have been identified, mapped, and measured during at least two census intervals (Condit et al. 2004, Hubbell et al. 2005). We addressed the following specific questions:

1. *How does the effect of crowding on tree growth and survival change along the precipitation gradient*? Based on

the SGH, we predict that the effect of crowding on both growth and survival will be negative in the wet sites where it reflects strong competition for light, nutrients, and potentially exposure to natural enemies (Fig. 1). In the dry forest plot, we expected crowding to have a relatively weak negative effect on growth and survival compared to the wet forest if seasonal drought has a stronger effect on performance than local biotic interactions. We would expect a positive effect of crowding on plant performance if neighboring plants reduce abiotic stress.

2. *How do functional strategies influence average demographic rates and the sensitivity of demographic rates to crowding across the gradient*? Across the precipitation gradient, we expect species with resource conservative functional strategies (i.e., high values of WD and LMA) to have lower average growth and higher average survival compared to species with resource-acquisitive strategies (i.e., low WD and LMA). Additionally, in wet forests, we expect crowding to have a weaker negative effect on demographic performance for shade-tolerant species compared to shade-intolerant species (Fig. 1) if crowding reflects competition for light—the limiting resource in these locations. In dry forests, in contrast, we expect the negative effects of crowding to be less pronounced for species with acquisitive functional strategies than for species with conservative strategies (despite having potentially lower average survival) because they are capable of rapid uptake and exploitation of belowground resources during the wet season. This effect could be exacerbated if species with acquisitive strategies tend to avoid drought by being deciduous and thus avoiding competition for water when it is most limiting.

Materials and Methods

Tree census and demographic data

We analyzed data from three permanent forest plots located across a regional rainfall gradient in Panama (Condit 1998, Hubbell et al. 1999, 2005, Condit et al. 2004). In each plot, all stems ≥1 cm diameter at 1.3 m above the ground (DBH) have been identified, mapped, and measured during at least two censuses. Here, we briefly summarize key information on these plots (for more complete descriptions, see Condit 1998, Hubbell et al. 1999, Pyke et al. 2001, Condit et al. 2004, Hubbell et al. 2005, Feeley et al. 2011). The 4-ha Cocoli plot is located in dry forest on Panama's Pacific coast (8.988 N, 79.598 W) and receives ca. 1,900 mm of rain/yr. For this plot, we used data from censuses conducted in 1994, 1997, and 1998. The 50-ha plot on Barro Colorado Island (BCI; 9.158 N, 79.858 W) receives a mean annual rainfall of ca. 2,500 mm/yr. The BCI plot has been censused approximately every five years since 1981. To maximize the overlap among census periods, we only used data from the 1995 and 2000 BCI censuses (Condit et al. 2012). The 6-ha Sherman plot is located on Panama's wet Caribbean coast (9.368 N, 79.958 W) and receives ca. 3,000 mm rain/yr. For the Sherman plot, we used data from three censuses in 1996, 1997–1998, and 1999, and we excluded 1-ha of early successional forest (Condit et al. 2004). The mean dry season length (i.e., days per year when potential evapotranspiration exceeds rainfall) for these plots is Cocoli = 129 d, BCI = 118 d, and Sherman = 106 d (Condit et al. 2000).

For each stem that survived a census interval, we calculated the annual diameter growth rate as $(DBH_2 - DBH_1/t) \times 365$, where t is the number of days between measurements. When modeling tree growth, we excluded palms (because they do not produce secondary growth), stems that were measured at different heights in consecutive censuses, and outliers that grew or shrunk more than five standard deviations around the mean growth values in each plot because these are likely to represent measurement or data entry errors. We based our exclusion of outliers (<0.1% of total records) on prior work in this study system (see, for example, Condit et al. 2004, Rüger et al. 2011*a*, *b*) and the fact that our models would not converge with such extreme values. Aside from these outliers, we included instances of negative growth in our analyses.

Functional traits

We focused our analyses on two traits that have been linked to functional strategies in our system (Wright et al. 2010, Rüger et al. 2012) and along abiotic gradients more generally (Poorter 2009, Markesteijn et al. 2011*a*): WD (g/cm^3) and leaf dry mass per area (LMA; g/cm^2). Wood density reflects a trade-off between hydraulic safety and efficiency and is also associated with shade tolerance (Valladares and Niinemets 2008) and resistance to natural enemies (Chave et al. 2009). Wood density was measured using cores of 1–11 individuals collected nearby BCI (Wright et al. 2010). LMA is a key trait of the leaf economics spectrum; low and high values are generally associated with acquisitive and conservative carbon strategies, respectively (Westoby et al. 2002, Wright et al. 2004), and this relationship holds for our study system (Messier et al. 2010). For LMA, we used data from Wright et al. (2010) for trees at BCI. For trees in the Cocoli and Sherman plots, whenever possible we used LMA data from corresponding dry and wet sites studied by Messier et al. (2010). For species in the Cocoli or Sherman plots that were absent from the Messier et al. (2010) dataset but included in the Wright et al. (2010) dataset, we used the LMA data from BCI. In all cases, LMA was measured on shade leaves from 1 to 54 individual leaves per species. Species lacking trait data were generally rare; the trait dataset covered >85% and >95% of the observed species and individuals, respectively, for both traits. In addition, we classified 82% of the recorded species (representing 94% of the individuals) as evergreen or deciduous based on expert knowledge (O. Calderon and S.J. Wright, *unpublished data*), and we used *t*-tests to compare trait values between these groups.

Statistical analyses

We used hierarchical Bayesian models to quantify the effects of neighborhood crowding on growth and survival of individual stems. Models of growth included a level to account for two sources of measurement error following Rüger et al. (2011*a*, *b*) and Chen et al. (2016). Specifically, we assumed that the observed annual growth rates for individual trees (mm/yr) incorporate size-dependent measurement errors (e.g., placement of measurement tools) and size-independent errors (e.g., data recording). We fit these errors using a normal mixture distribution,

$$\text{Obs.}g_{is} \sim (1-f) \times \mathrm{N}\left(\text{True.}g_{is}, \frac{\mathrm{SD}_1}{\mathrm{int}_i}\right) + f \times \mathrm{N}\left(\text{True.}g_{is}, \frac{\mathrm{SD}_2}{\mathrm{int}_i}\right) \quad (1)$$

where Obs.g_{is} and True.g_{is} are the observed and true growth rates for tree i of species s, respectively; SD_1 and SD_2 are the size-dependent and size-independent errors that affect 97.3% ($1-f$) and 2.7% (f) of the observations, respectively (based on Rüger et al. 2011*a*, *b*); and int_i is the census interval for tree i, which scales both types of measurement error (Rüger et al. 2011*a*, *b*, Chen et al. 2016).

In the middle level, we modeled the expected value of log true growth of individual tree i belonging to species s as,

$$\log(\text{True.}g_{is}) = b_{0_s} + b_{\mathrm{NCI}_s} \times \log(\mathrm{NCI}_{is}) + b_{\mathrm{DBH}_s} \times \log(\mathrm{DBH}_{is}) + \varphi_{is} + \varepsilon_{is} \quad (2)$$

where the intercept term, b_{0_s}, represents the species-specific average growth rate (i.e., predicted growth for a stem of average size under average crowding conditions), b_{NCI_s} describes the species-specific response to the neighborhood crowding index (NCI, see below; Canham et al. 2004), b_{DBH_s} is the species-specific effect of the logarithm of the initial stem diameter (DBH), φ is normally distributed individual random effect, and ε is a normally distributed error term. Survival models were identical except that they (1) did not include the level accounting for measurement errors, (2) used logistic regression, and (3) included the length of the census interval to scale expected survival (*see* Data S1).

We calculated a NCI for each focal tree i based on the size and distance of all K neighbors located within a 15 m radius at the beginning of a census interval:

$$\mathrm{NCI}_{ij} = \sum\nolimits_{j=1, j\neq i}^{k} (\mathrm{DBH}_j)^2 / d_{ij}^2 \quad (3)$$

where d_j and DBH_j represent the distance from focal tree i and stem diameter of neighbor tree j, respectively. We chose the neighborhood radius based on previous studies, suggesting that this distance captures the major neighborhood effects (Uriarte et al. 2004). Scaling exponents were based on previous work (Canham et al. 2004, Uriarte et al. 2004, Lasky et al. 2015), but note that models using either 1 or 2 as exponents for DBH and d gave similar results (Appendix S1: Fig. S1).

The final level of the model quantified species-specific effects of traits on b_{0_s} and b_{1_s}:

$$b_{0_s} = a_{0,0} + a_{0,\mathrm{WD}} \times \text{wood density}_s + a_{0,\mathrm{LMA}} \times \mathrm{LMA}_s + \varepsilon_{0s} \quad (4)$$

$$b_{\mathrm{NCI}_s} = a_{\mathrm{NCI},0} + a_{\mathrm{NCI,WD}} \times \text{wood density}_s + a_{\mathrm{NCI,LMA}} \times \mathrm{LMA}_s + \varepsilon_{1s} \quad (5)$$

where $a_{0,0}$ and $a_{\mathrm{NCI},0}$ are community-level intercept terms, $a_{0,\mathrm{WD}}$ and $a_{1,\mathrm{WD}}$ determine the effect of WD of species s, $a_{0,\mathrm{LMA}}$ and $a_{\mathrm{NCI,LMA}}$ determine the effect of LMA of species s, and ε_{0s} and ε_{1s} are normally distributed species random effects. To help account for intraspecific trait variation, we used site-specific species trait values whenever possible (see *Functional traits*). Traits were not used to estimate the species-specific effect of initial size (b_{DBH_s}). We analyzed trees 1–10 cm DBH because crowding is likely to have especially strong effects on understory trees. While arbitrary, this cutoff should capture major differences experienced by understory and canopy trees (Pacala et al. 1994, Wright et al. 2010).

To facilitate direct comparison of parameter estimates and model convergence, we standardized all predictor variables within plots by subtracting their mean and dividing by their standard deviation (Gelman and Hill 2006). We gave all parameters proper, diffuse (“uninformative”) priors, and we estimated posterior distributions via Markov chain Monte Carlo (MCMC) simulation. To address question 1, we examined the posterior distributions of hyperparameter $a_{\mathrm{NCI},0}$, which reflects the average effect of crowding on performance in each plot. Negative values of $a_{\mathrm{NCI},0}$ indicate a negative effect of crowding (NCI) on performance and vice versa. To address question 2, we examined the posterior distributions of hyperparameters $a_{0,\mathrm{WD}}$ and $a_{0,\mathrm{LMA}}$, which reflect how traits mediate average demographic rates, as well as hyperparameters $a_{\mathrm{NCI,WD}}$, $a_{\mathrm{NCI,LMA}}$, which indicate how traits mediate sensitivity to crowding. Positive values of $a_{\mathrm{NCI,WD}}$ and $a_{\mathrm{NCI,LMA}}$ indicate that species with higher trait values (which correspond to more conservative functional strategies in this study) experience a smaller reduction in performance in response to crowding (i.e., they are less sensitive to crowding).

We fit growth models with JAGS 4.3.0 using the “rjags” package (Plummer 2015) and survival models with Stan using the “rstan” package (Stan Development Team 2016) in R version 3.5.1 (R Development Core Team 2018). We considered models to have converged when the Gelman and Rubin statistic (Rhat) was < 1.1 (Gelman and Rubin 1992), and we refer to parameter estimates as statistically significant when 95% credible intervals did not overlap zero. We evaluated model fit using the R^2 between the observed data and predicted values for the growth models, and the proportion of correctly identified outcomes for the survival models. We also evaluated model performance by fitting models with a training dataset (85% of the full dataset based on a random split) and then calculating the predictive ability of these models to predict the 15% withheld data. Note that our main results are based on parameters estimated with the full dataset. We provide full results in Appendix S1 and Data S1.

Results

Across all species and plots, WD and LMA were weakly positively correlated (Pearson’s r = 0.15, $P = 0.01$). Mean WD of trees in the dry plot was slightly higher than in either the intermediate or wet plot (0.64 g/cm^3 compared to 0.60 and 0.60 g/cm^3, respectively; Appendix S1: Table S1). Mean LMA of the wet plot was higher than the intermediate and dry plots (88 g/cm^2 compared to 68 and 64 g/cm^2, respectively; Appendix S1: Table S1). On average, deciduous species had lower WD than evergreen species in all plots, but the difference was only significant in the intermediate plot (t = −2.4, df=89.2, P = 0.02; Appendix S1: Fig. S2). Additionally, deciduous species had significantly lower LMA compared to evergreen species in the dry plot (t = −2.27, df=57.6, P = 0.03), but LMA was similar between deciduous and evergreen species in both the intermediate and wet plots (P > 0.05; Appendix S1: Fig. S2). Across species, mean annual growth was highest in the dry plot and similar in the intermediate and wet plots (Appendix S1: Fig. S3a). Average survival was also highest in the dry plot, followed by the wet and then intermediate plots (Appendix S1: Fig. S3b). Initial stem size had positive effects on growth and survival rates across plots (Appendix S1: Fig. S4).

Q1) How does the effect of crowding on growth and survival change along the gradient?

Our results were partly consistent with our predictions (Fig. 1) that local crowding would have a negative effect on performance in the wetter plots and a less negative (or positive) effect in the driest plot. Crowding had a significantly negative effect on average growth in all plots, and this effect tended to be stronger in the wetter plots (Figs. 2A, 3). On average, an increase of 1 standard deviation in the crowding index reduced annual growth by 7, 9, and 12% for the dry, intermediate, and wet plots, respectively. The mean R^2 values for the growth models (based on the relationship between observed and predicted values) were 0.10, 0.08, and 0.17 for the dry, intermediate, and wet plots, respectively (Appendix S1: Table S1). In contrast to our expectations, crowding had a significantly positive effect on average survival in the wettest plot (Figs. 2B, 3) where an increase of the crowding index by 1 standard deviation elevated the annual survival rate by 0.2%. The mean R^2 values for survival models (based on the % of stems correctly predicted as dead or alive) were 0.95, 0.79, and 0.94 for the dry, intermediate, and wet plots, respectively. The percentages of dead individuals correctly predicted across the three plots ranged from 17% to 21%.

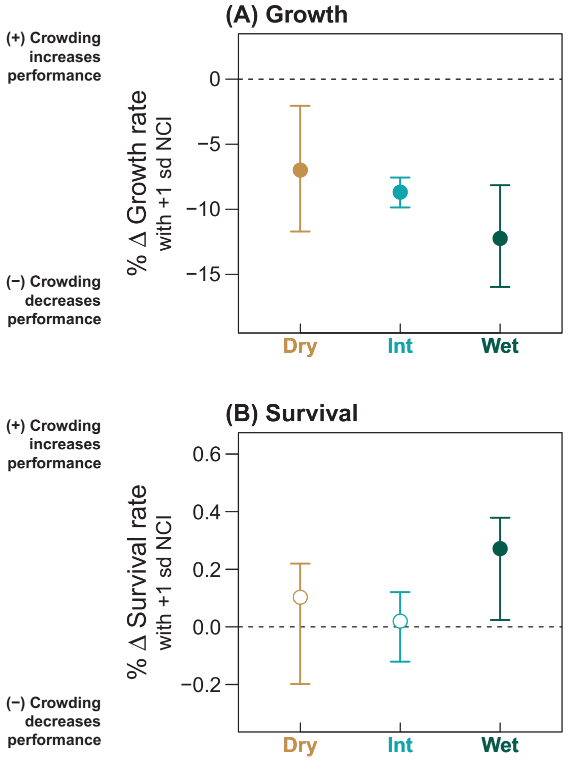

FIG. 2. Posterior means with 95% credible intervals (CIs) for the % change in average growth (A) and survival (B) with an increase of 1 standard deviation in the neighborhood crowding index (NCI) for trees 1–10 cm DBH at three forest plots in Panama. Points are solid when 95% CIs do not overlap zero.

Q2) How do functional traits influence average demographic rates and sensitivity to crowding across the gradient?

Wood density was significantly associated with average performance in ways that were consistent with our expectations. Specifically, species with higher WD had significantly lower growth in the intermediate and wet plots, and higher survival in all plots (Fig. 3A, C; Appendix S1: Fig S5). Across plots, an increase of WD by 1 standard deviation reduced growth by 10–30% and increased survival by 0.3–1%. LMA was positively associated with average growth in the wet site (Fig. 3B), where an increase of LMA by 1 standard deviation increased growth by 17%. LMA was also positively associated with average survival in the intermediate and wet sites (Fig. 3D) where a 1 standard deviation increase of the trait elevated the survival rate by 0.5–0.9%.

In addition to these trait effects on average demographic rates, we expected that, in wet forests, species with shade-tolerant functional strategies (characterized by high values of WD and LMA) would be less sensitive to crowding compared to species with shade-intolerant strategies. In dry forests, in contrast, we expected that species with conservative trait values associated with drought-tolerating strategies (high WD and LMA) would be relatively more sensitive to crowding than species with acquisitive trait values. We did not, however, find significant associations between species traits and their sensitivity to crowding (Fig. 4).

DISCUSSION

We examined how the effects of tree crowding vary along a tropical precipitation gradient, and how responses to crowding along the gradient depend on the species' functional strategy. Our main findings are that (1) the average effect of crowding on performance varied along the gradient, and (2) species traits were significantly associated with average vital rates, and these associations varied across the gradient. Our results lend some support to the SGH and reinforce the idea that the effects of local biotic interactions are contingent on abiotic conditions (Maestre et al. 2009, Soliveres et al. 2015).

Crowding effects vary across the gradient

Based on the SGH, we expected crowding to have the strongest negative effect on performance in wet sites (where

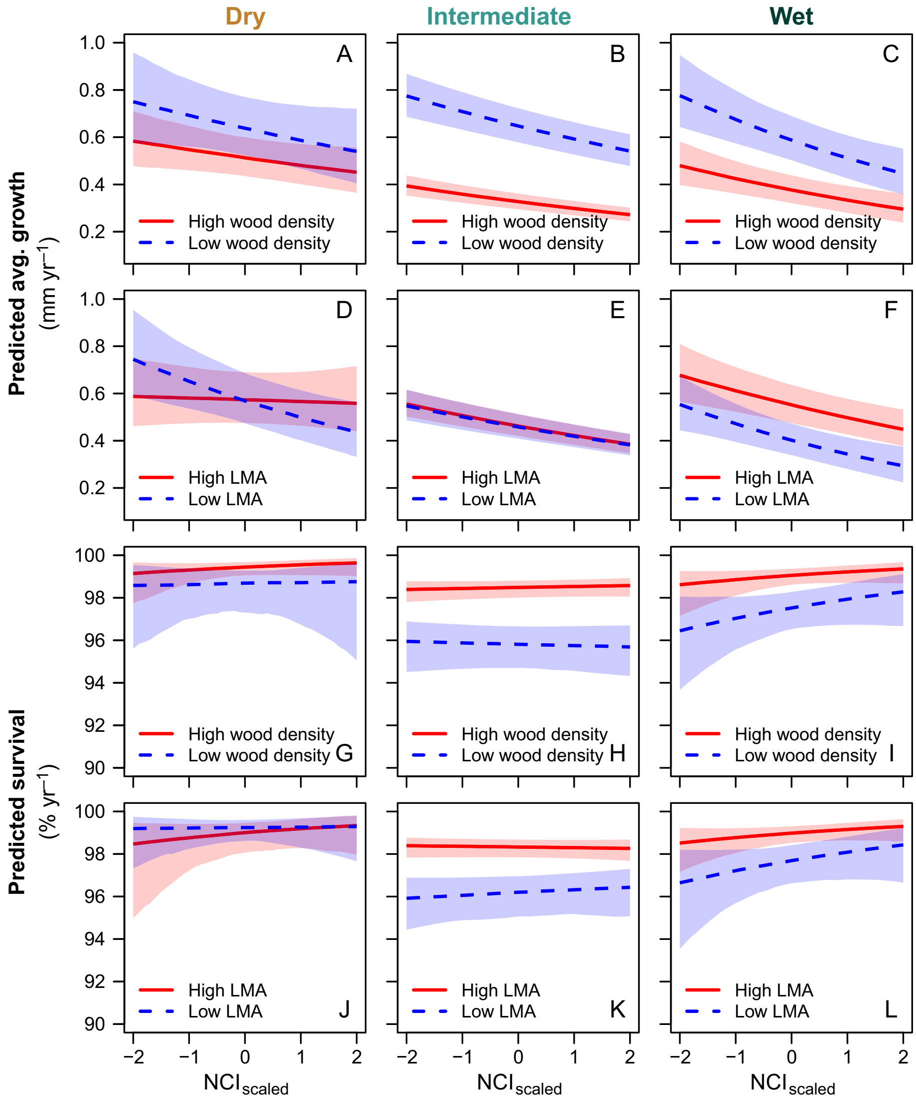

FIG. 3. Predicted annual growth (mm/yr; panels a–f) and survival (% yr^{-1}; panels g–l) for trees with high and low trait values (i.e., + or − 1 standard deviation from the mean trait value) across a range of crowding (NCI) for trees at three forest plots in Panama. Left, center, and right columns correspond to the dry, intermediate, and wet plots. Dotted (blue) and solid (red) lines represent model predictions for species with low and high trait values, respectively. Panels (A–C) and (G–I) show different responses based on variation in WD; panels (D–F) and (J–L) show different responses based on variation in leaf mass per area.

it leads to lower understory light availability) and weaker negative (or even positive) effects in the dry site if water availability is more limiting than negative biotic interactions. Our results provide some support for this hypothesis: there was a trend toward a more negative effect of crowding on growth with increasing precipitation. These results are consistent with competition for light as a key factor limiting tree performance in wet tropical forests (Uriarte et al. 2004, Brenes-Arguedas et al. 2011, Rüger et al. 2012). In our study, the weaker negative effect of crowding on growth in the dry forest suggests relatively weak influences of biotic interactions on tree growth. Stronger support for the SGH, however, would come from a significant positive effect of crowding on performance in the dry site. Because water availability (especially dry season intensity) is a major driver of forest dynamics and composition in this system (Condit et al. 2004, 2013, Engelbrecht et al. 2007), crowding could have a positive effect on performance in dry environments if it helps trees conserve or acquire water (e.g., a hydraulic lift effect; Dawson 1993). It is possible that the soil properties of our study area reduce the potential for facultative effects from, for example, hydraulic redistribution (Prieto et al. 2012). It is also possible that the range of the gradient studied here is not wide enough to observe positive interactions in the dry site. For example, in a tropical dry forest in Ecuador, Espinosa et al. (2016) found evidence of facilitation but that site has a more pronounced dry season and receives substantially less precipitation than the driest site in our study (ca. 650 mm/yr vs. ca. 1,900 mm/yr). Finally, the high incidence of deciduousness in the dry site may reduce the potential for facultative relationships because these species “opt out” of interactions when water resources are most limiting. During the rainy season, competition for light may lead to a net negative effect of crowding.

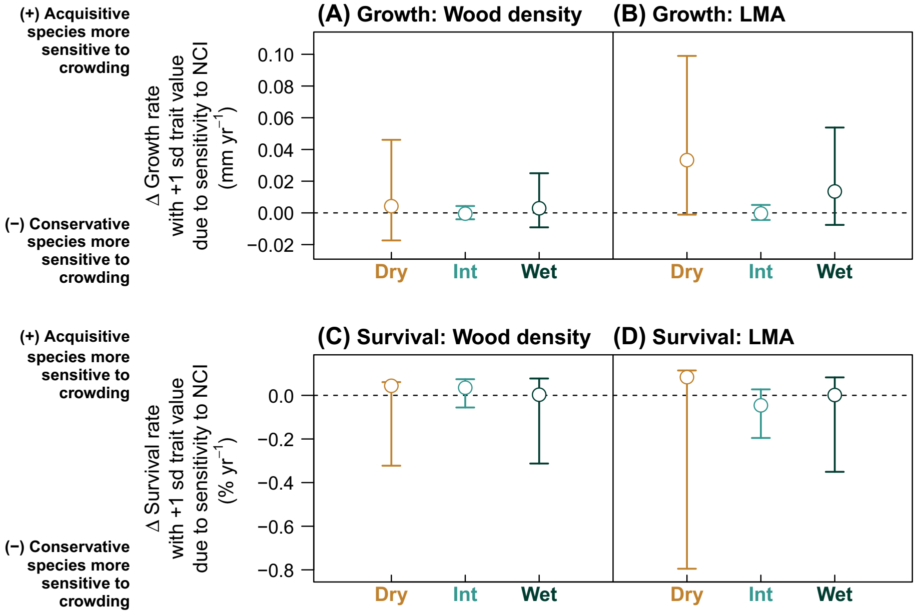

FIG. 4. Posterior means and 95% credible intervals (CIs) for the trait-mediated effect of sensitivity to neighborhood crowding index (NCI) for growth (A, B) and survival (C, D) of trees 1–10 cm DBH at three forest plots in Panama. Panels (A, C) show results for wood-specific gravity and panels (B, D) show results for leaf mass per area. Points are solid if 95% CIs do not overlap zero. *Y*-axis shows the change in the average growth (A) or survival (B) for trees with +1 standard deviation of crowding for species with 1 standard deviation higher than the mean trait value in each plot. Positive coefficients indicate that species with high trait values are relatively less sensitive to crowding (i.e., NCI has a less negative impact on their performance) and vice versa.

The two components of performance measured here (growth and survival) did not respond in the same way to crowding. In particular, the sign of the effect of crowding on growth vs. survival was opposite in the one case where they were both significant. Specifically, in the wet plot, crowding had a negative effect on growth and positive effect on survival. The positive effect of crowding on survival is nonetheless consistent with previous results from Rüger et al. (2011*a*, *b*) showing a positive association between light availability and mortality for a majority of species at BCI. Processes that elevate mortality rates in gaps relative to closed canopy forests offer a likely explanation (Coley and Barone 1996). At BCI, for example, Richards and Coley (2007) reported much higher rates of herbivory in gaps than in closed canopy conditions. The negative effect of high natural enemy pressure may outweigh an increase in survival due to increased light availability. Desiccation has also been shown to increase mortality rates in gaps, which are subject to much higher temperatures and water deficits than closed canopy forests (Denslow 1980). These potential explanations highlight the role of local environmental heterogeneity for shaping the nature of biotic interactions, which can complicate trends in the average effect of crowding across the gradient. Additionally, crowding appeared to have a stronger effect on growth than survival. A one-unit increase in the crowding term reduced growth rates by ~10% across the plot and increased survival in the wet plot by only 0.2%. Note, however, that the proportion of total variation explained by our models was modest (Appendix S1: Table S1) indicating a substantial amount of remaining individual-level variation in growth and survival rates. Additionally, it is not clear how the effects we report for trees in the 1–10 cm DBH size class translate to overall population growth rates. Some new approaches are becoming available that could help integrate findings such as those we report with models of population fitness to better understand how the longer-term consequences of crowding (Needham et al. 2018). Finally, the contrasting results between growth and survival are consistent with other studies finding that different fitness components are related to different traits (Flores et al. 2014, Visser et al. 2016). This suggests that different fitness components may be driven by different processes. Some other factors may prevent us from observing expected trade-offs. For example, fitness components expected to trade off may instead be positively correlated if the individuals vary in fitness as a result of genetic differences or environmental quality. This could lead to some individuals expressing both higher survival and growth and create the illusion of a positive correlation from the failure to control for a third missing variable involved in the trade-off (Sugiyama and Bazzaz 1998). In any case, studies that examine the responses of multiple components of fitness can help to more fully reveal community dynamics (Adler et al. 2014).

Trait effects on performance

Consistent with our predictions and previous work (e.g., Kraft et al. 2010, Wright et al. 2010, Visser et al. 2016), WD was negatively associated with average growth rates and positively associated with survival rates, and these effects were fairly consistent across the gradient. Our results further support WD, in particular, as a key trait mediating growth/survival trade-offs (Chave et al. 2009). Notably, however, WD did not have a significant effect on growth in the dry forest plot. One possible explanation could emerge from an association between deciduousness and low WD. Specifically, growth advantages of low WD (i.e., hydraulic efficiency) may not be fully realized by dry forest deciduous species because of the energetic costs associated with shedding leaves and the limited growing season (Givnish 2002). In fact, we did find an association between WD and deciduousness in the dry forest such that deciduous trees tended to have lower values of WD than evergreen trees. We found fewer (and weaker) associations between LMA and average performance across the gradient but we did find, surprisingly, LMA was positively associated with growth rates in the wettest plot. One possible explanation for this result may be that LMA integrates a variety of different processes that affect leaf tissue density, leaf area, and leaf thickness (Poorter et al. 2009, John et al. 2017), which may have contrasting effects on the expected pattern (Messier et al. 2017).

In addition to affecting average demographic rates, we expected species traits to mediate tree responses to crowding differently across the gradient. In particular, in the wet forest, we expected crowding to reduce performance of low WD species more strongly than high WD species in the wet forests because of the link between this trait and shade tolerance (e.g., Augspurger 1984, Valladares and Niinemets 2008, Ameztegui et al. 2017). Previous work at BCI (Rüger et al. 2012) as well as a recent global study (Kunstler et al. 2016) reported that high WD species have a weaker growth response to light availability compared to low WD species. While the directions of the effects estimated in our study were consistent with our expectations and previous findings, the effects were not statistically significant. The fact that we used a different census interval for the BCI data (1995–2000) compared to the intervals used by Rüger et al. (2012) (1985–1990 and 1990–1995) could offer one potential explanation for the contrasting results. In particular, the particularly dry conditions during the 1997–98 El Niño may have influenced growth rates in a way that decoupled the trait-mediated response. Further investigation into temporal variability of trait-mediated processes could provide valuable complementary insight in this respect.

In the dry site, in particular, it is also possible that tradeoffs between shade tolerance and drought tolerance could offer another potential explanation for the lack of response (Laanisto and Niinemets 2015). If traits that confer drought resistance are the same as those that confer shade tolerance, and light is still an important driver of plant performance in the rainy season, these two different tolerance strategies may interact to obscure trait-mediated effects. Additionally, the lack of significant associations between traits and sensitivity to crowding could be related to ways that trait variation is coordinated with drought strategies (i.e., drought tolerance vs. drought avoidance). For example, on the one hand, high WD of drought-tolerating evergreen species confers a survival advantage via reduced susceptibility to drought-induced embolism (Markesteijn et al. 2011*b*). High WD is, however, also associated with less efficient hydraulic transport and relatively slow uptake of belowground resources. Therefore, competition for water (and water-soluble nutrients) may be particularly elevated for drought-tolerating species in crowded conditions, especially when they compete with individuals that have relatively efficient hydraulic architectures that may preemptively monopolize belowground resources. On the other hand, by shedding their leaves during the dry season, drought-avoiding deciduous species do not compete for water when it is most scarce. The fact that drought-avoiding deciduous species tended to have lower WD and LMA values compared to co-occurring evergreen species is consistent with our hypothesis that species with resource-acquisitive strategies may be less sensitive to crowding in dry forest. However, there was a marginally significant association between sensitivity of growth to crowding and LMA in the dry plot (i.e., growth rates of species with low LMA were somewhat more reduced by crowding than species with high values of LMA). This suggests a potential competitive disadvantage for species with acquisitive strategies in the dry forest. Further work investigating how different drought strategies correspond to competitive interactions will help clarify the role of biotic interactions along water availability gradients. More generally, suites of traits providing more nuanced information about plant strategies may provide a better description of plant community dynamics than single traits (Laughlin and Messier 2015, Muscarella and Uriarte 2016).

Finally, other recent work has focused on different metrics of neighborhood crowding that consider the potential of diverse neighbors to interact in different ways (e.g., Uriarte et al. 2004, Kunstler et al. 2012, Lasky et al. 2014, 2015). For instance, closely related species may share natural enemies, functionally similar species may compete for resources more strongly, and functional strategies may correspond to competitive dominance hierarchies. In this study, we focused on a general metric of crowding (i.e., weighing the effects of all neighbors equally), but future work considering how sensitivity to crowding is related to more nuanced metrics of neighborhood diversity may provide additional insight to the ways that traits mediate biotic interactions across abiotic gradients (Fichtner et al. 2017).

Conclusion

Despite being a major challenge of ecology, few studies have disentangled the interactive effects of abiotic conditions and local biotic interactions on plant performance. By synthesizing data from multiple long-term sites across a regional gradient, we gained insight to the ways that biotic interactions vary with abiotic conditions, and how those interactions depend on functional strategies. In summary, species responses to crowding appear to be not only contingent on environmental stress, as predicted by the basic SGH, but also on the particular resources involved (e.g., water limitation vs. light limitation) and, to some extent, their functional strategies. Important nuances regarding these strategies (such as drought tolerance or drought avoidance) can be poorly captured by single traits. Thus, future work will likely need to embrace the interactions of multiple environmental variables and suites of traits.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2537/suppinfo

Data Availability

Data are available from the Smithsonian DSpace Repository at https://doi.org/10.5479/data.bci.20130603 and on the TRY Plant Trait Database (www.try-db.org) under TRY dataset IDs 112 (“Panama Leaf Traits Database”) and 113 (“Panama Plant Traits Database”).