Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest

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Abstract. Abiotic constraints and biotic interactions act simultaneously to shape communities. However, these community assembly mechanisms are often studied independently, which can limit understanding of how they interact to affect species dynamics and distributions. We develop a hierarchical Bayesian neighborhood modeling approach to quantify the simultaneous effects of topography and crowding by neighbors on the growth of 124,704 individual stems ≥1 cm DBH for 1,047 tropical tree species in a 25-ha mapped rainforest plot in Amazonian Ecuador. We build multi-level regression models to evaluate how four key functional traits (specific leaf area, maximum tree size, wood specific gravity and seed mass) mediate tree growth response to topography and neighborhood crowding. Tree growth is faster in valleys than on ridges and is reduced by neighborhood crowding. Topography and crowding interact to influence tree growth in ~10% of the species. Specific leaf area, maximum tree size and seed mass are associated with growth responses to topography, but not with responses to neighborhood crowding or with the interaction between topography and crowding. In sum, our study reveals that topography and neighborhood crowding each influence tree growth in tropical forests, but act largely independently in shaping species distributions. While traits were associated with species response to topography, their role in species response to neighborhood crowding was less clear, which suggests that trait effects on neighborhood dynamics may depend on the direction (negative/positive) and degree of symmetry of biotic interactions. Our study emphasizes the importance of simultaneously assessing the individual and interactive role of multiple mechanisms in shaping species dynamics in high diversity tropical systems.

Key words: community dynamics; functional traits; growth model; spatial interactions; species coexistence; topographic gradients; tropical forests.

Introduction

Species distributions and dynamics are generated by many ecological mechanisms acting simultaneously (HilleRisLambers et al. 2012). The vast majority of studies so far focused on the role of a single class of mechanism such as abiotic filters (Engelbrecht et al. 2007, Fortunel et al. 2014) or biotic interactions (Comita et al. 2010, Kunstler et al. 2016) in shaping plant community structure and dynamics. A smaller number of studies have examined the joint effects of several mechanisms on community structure and function (e.g., Gross et al. 2013, Gallien et al. 2015). However, many of these studies are limited in their ability to distinguish the signatures of different coexistence mechanisms because they typically analyze species co-occurrence patterns, while most coexistence theory requires an understanding of variation in species vital rates (Adler et al. 2013). Combining individual demographic data with insights from community assembly theory allows a richer understanding of how ecological

processes affect variation in species performance (Uriarte et al. 2010, Kraft et al. 2015, Kunstler et al. 2016). Despite the growth of community neighborhood dynamics analyses in recent years, only a small number of studies have simultaneously tested for the importance of multiple mechanisms (e.g. Canham et al. 2006, Uriarte et al. 2016), with even fewer studies assessing the interactions between mechanisms (Baribault and Kobe 2011, Coates et al. 2013). As much of the previous work on these questions focused on temperate and secondary tropical forest, it remains unclear whether combinations of community assembly mechanisms have interactive effects on the diversity and dynamics of old-growth tropical rainforests.

In tropical forests, elevation gradients at local scales (<1 km²) create spatial environmental heterogeneity driven by hydrology, resulting in greater soil moisture and fertility in bottomland areas (John et al. 2007, Mage and Porder 2013, Allié et al. 2015). Because of topographic gradients in soil fertility, growth and mortality of tropical tree species are generally faster in valleys than on ridges (Korning and Balslev 1994). In addition, basal area, stem density and aboveground biomass can vary strongly with elevation in tropical forests (Valencia et al. 2004, 2009, Homeier et al. 2010,

Detto et al. 2013). While there is growing evidence for the negative impacts of neighbors that arise through competition for shared resources or through shared natural enemies (Uriarte et al. 2010, Lasky et al. 2014, Fortunel et al. 2016), it is unclear how neighborhood crowding interacts with topography to shape species performance. To address this challenge, we develop a modeling approach to evaluate the individual and interactive effects of topographic gradients and neighborhood crowding on tree performance in an old-growth, hyperdiverse tropical rainforest.

Differential species responses to environmental heterogeneity (both spatial and temporal) are the foundation of many theories of species coexistence (Chesson 2000, Adler et al. 2013, Usinowicz et al. 2017). In tropical forests, there is substantial evidence that tree species can specialize to distinct microtopographic habitats such as valleys or ridges (Clark et al. 1998, Condit et al. 2000, Valencia et al. 2004, Lasky et al. 2013), and that physiological or functional traits can help to understand the mechanisms involved in specialization (Liu et al. 2014, Asner and Martin 2016). Habitat specialization can then be reinforced by interactions with neighbors in a variety of ways. For example, habitat specialists dispersing into non-preferred habitats can be excluded over time by resident habitat specialists that are superior competitors for shared resources or better defended against shared natural enemies in that habitat (Mayfield and Levine 2010, Kunstler et al. 2012). Alternatively, specialists may persist in non-preferred habitats as a sink population (Hurtt and Pacala 1995, Mouquet and Loreau 2003). In addition, specialists growing in their preferred habitat may experience stronger neighborhood effects because of higher densities of conspecifics or other species specialized on the same habitat (Paine et al. 2012, Lebrija-Trejos et al. 2014). This positive covariance between environmental preference and the strength of competition is an essential part of spatial coexistence theories (Chesson 2000, Adler et al. 2013). However, it is logistically challenging to evaluate this covariance empirically for long-lived tropical trees, and in particular to estimate species responses to the environment in the absence of competitors (Kraft et al. 2015). As a first step here, we evaluate whether habitat specialist species suffer more from crowding in their preferred habitat. By testing for variation in the strength of neighborhood crowding effects across environmental gradients, we can begin to explore the role of resource partitioning and natural enemies in shaping species coexistence across heterogeneous forest landscapes.

Functional traits reflect important ecological tradeoffs (Wright et al. 2004, Chave et al. 2009) and can capture inherent variation in species performance. For instance, tropical tree species with high specific leaf area (SLA) and low wood density, maximum size and seed mass have the potential for rapid growth (Westoby et al. 2002, Poorter et al. 2008, Wright et al. 2010, Visser et al. 2016). In addition, trait differences can capture variation in species responses to environmental heterogeneity and neighborhood interactions that subsequently shape community dynamics and species coexistence. For example, functional traits influence tropical tree species response to variation in soil fertility and water availability (ter Steege et al. 2006, Engelbrecht et al. 2007, Lasky et al. 2013, Fortunel et al. 2014). In

Amazonian forests, shifts in tropical tree species distributions along local topographic gradients produce changes in community-average trait means, with communities found on ridge tops exhibiting lower specific leaf area, greater maximum size, denser wood and heavier seeds than species found in valleys (Kraft et al. 2008, Allié et al. 2015). In addition, trait differences among co-occurring species mediate the effects of neighborhood interactions on tree growth and mortality in tropical forests (Uriarte et al. 2010, Lasky et al. 2014). Specifically, tropical tree species with greater maximum size and lower wood specific gravity appear more sensitive to neighborhood effects (Fortunel et al. 2016, Kunstler et al. 2016). However, it is unclear how functional traits mediate species joint responses to abiotic and biotic gradients. Here we examine how species functional traits mediate neighborhood effects on tree growth across a topographic gradient from valleys to ridgetops.

We use census data over 11 yr and trait information for over 1,000 tree species in a 25-ha plot of lowland rainforest in Amazonian Ecuador to develop spatially explicit models of tree growth. We specifically ask the following questions:

Q1: What are the individual and interactive effects of topography and neighborhood crowding on variation in species growth?

We expect faster tree growth in valleys than on ridges, and slower tree growth with increasing neighborhood crowding. Because of strong size-asymmetry in plant competition, we expect crowding will reduce growth more in smaller trees than in taller trees. In addition, we test for two distinct patterns in relation to habitat specialization that relate to broader questions of community assembly and species coexistence. First, we test if biotic interactions may be reinforcing habitat specialization via habitat specialists experiencing stronger competition in non-preferred habitats. Second, as positive covariation between environmental preference and the strength of competition is a prerequisite for spatial coexistence mechanisms (Chesson 2000, Adler et al. 2013), we test if habitat specialists experience stronger neighborhood crowding effects in their preferred habitats.

Q2: What traits are associated with species responses to topographic gradients and neighborhood crowding?

We expect species exhibiting faster growth in valleys to have higher specific leaf area, smaller maximum size, less dense wood and lighter seeds than species growing faster on ridges. We expect species more sensitive to neighborhood crowding to have greater maximum size and less dense wood. As community-level traits vary from valleys to ridges, we expect resource acquisitive species (e.g., with high SLA or low wood density) to be even more sensitive to neighbors than resource conservative species.

METHODS

Study site

We studied the tree community at the Yasuní Forest Dynamics Plot, which is part of an international network of

long-term forest dynamics research sites (CTFS-ForestGEO, Anderson-Teixeira et al. 2015). The Yasuní plot is a 25-ha permanent forest census plot situated in lowland old-growth rainforest in Yasuní National Park and Biosphere Reserve in Ecuador. The climate is aseasonal, with a mean annual rainfall of 3,270 mm and mean annual temperatures of 25.9°C (Anderson-Teixeira et al. 2015). Soils are primarily classified as ultisols (Baldeck et al. 2013), and as such are clay-rich, acidic and relatively nutrient poor.

Tree growth data

All stems ≥1 cm in diameter at breast height (DBH) in the Yasuní plot are identified to species, tagged and mapped, giving a total of over 150,000 mapped trees from ~1,100 species, lianas excluded (Valencia et al. 2004). The forest was censused in 1997, 2004 and 2008, and the DBH of every living individual was recorded at each census. We calculated annualized absolute growth rates in diameter (cm/yr) for each living individual at each census interval (1997–2004 and 2004–2008).

Topographic gradient

The Yasuní plot ranges from 216 to 248 m above sea level, with an average slope of 12% (Valencia et al. 2004). The plot is crossed by two ridges rising 25–40 m above a main intervening valley, plus a smaller valley in the northeastern corner. We used three topographic variables to describe each 10 m by 10 m quadrat: elevation, convexity and slope (Fig. 1a–c). Total basal area in each 10 m by 10 m quadrat ranged from 3 to 281 m^2/ha during the first census and from 3 to 291 m^2/ha during the second census (Fig. 1d, e). Valleys

have lower basal area, stem density and aboveground biomass than ridges (Valencia et al. 2004, 2009).

Species topography association

Evaluating species-level associations between individual trees and plot elevation requires accounting for spatial autocorrelation present within elevation data (Allié et al. 2015). We used an unbiased Monte Carlo test of pairwise association based on the generation of 999 surrogate raster images of plot elevation that preserve the autocorrelation of the original raster image of plot elevation (following Deblauwe et al. 2012, see details in Appendix S1). We calculated the Pearson correlation coefficient ($r_{Pearson}$) between species abundance maps and the original plot elevation map (Canty and Nielsen 2008). To evaluate its significance, we used a two-tailed test to compare the observed $r_{Pearson}$ with the 999 $r_{Pearson}$ values obtained between species abundance maps and each of the 999 surrogate plot elevation maps (Deblauwe et al. 2012). We found that 378 species are strongly associated with elevation, with 232 species associated with the ridges and 146 species associated with the valleys, while the remaining 724 species were classified as generalist for the purposes of our analysis.

Species trait data

We followed standardized protocols (Perez-Harguindeguy et al. 2013) to measure four traits describing the four major axes of plant functional strategies: leaf, wood, height and seed (Westoby et al. 2002, Chave et al. 2009, Rüger et al. 2018). We measured specific leaf area (SLA) on randomly selected, censused individuals within the Yasuní plot (Kraft
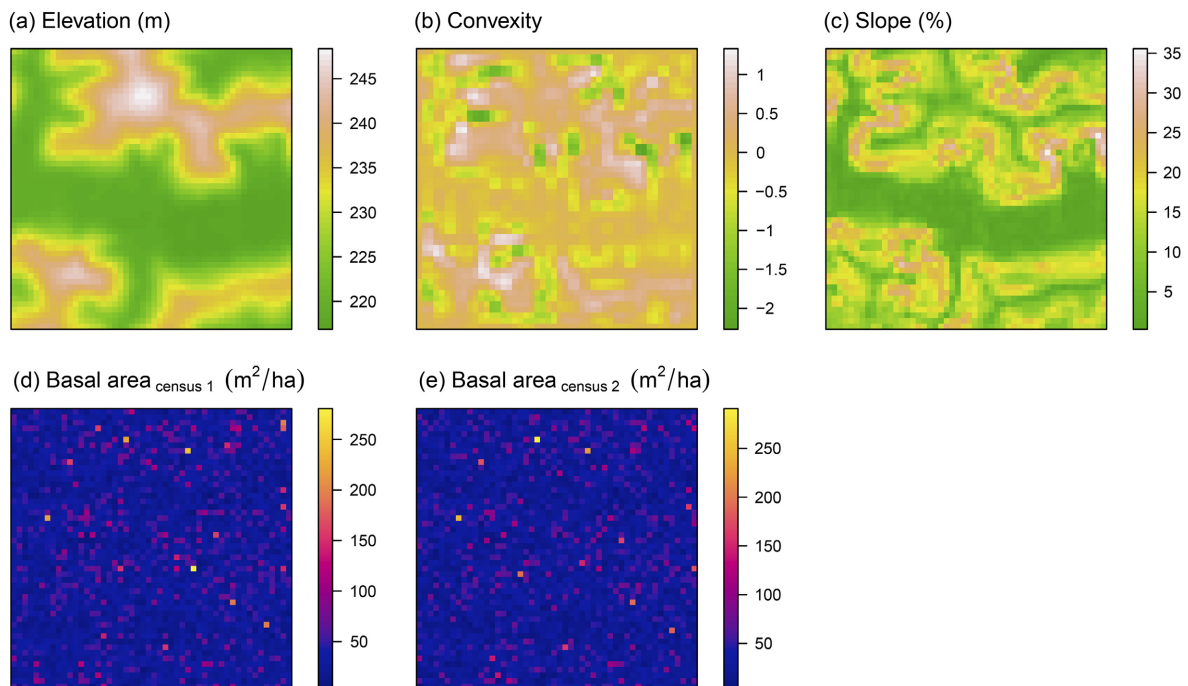

FIG. 1.   (a) Elevation, (b) convexity, (c) slope, and basal area at the (d) first and (e) second censuses in each 10 m by 10 m quadrat in the Yasuní Forest Dynamics Plot.

et al. 2008, Kraft and Ackerly 2010). Following previous analyses at the site (Kraft and Ackerly 2010), we used the measure $D95_{0.1}$ from King et al. (2006) as a proxy (Chave et al. 2005) for maximum height. This measure is derived from the 95th quantile of the diameter distribution of individuals at the site. As $D95_{0.1}$ cannot be used reliably for exceedingly rare species, for species with <20 individuals we used the maximum observed diameter, recognizing that this is likely an underestimate of maximum size for the rarest species. We refer to these measures collectively as DBH_{max} throughout for simplicity. Since increment borers are prohibited in the permanent plot, we measured wood specific gravity (WSG) of 670 species on trees located within 5 km of the plot (Hietz et al. 2013). From or underneath fruiting trees in and around the plot, we collected fresh seeds or fruits of 477 species, removed the seeds from fruit when necessary, cleaned them of any fleshy parts, then oven-dried them at 65°C for a minimum of 48 h to obtain their dry mass. For rarer species that have yet to be sampled locally, we used published WSG and seed mass data (Chave et al. 2009, Royal Botanic Gardens Kew 2015), and when these were unavailable, we substituted genus or family means (45% and 51% of the 1,100 species for WSG and seed mass data, respectively).

Statistical analyses

We built a hierarchical Bayesian model of annual diameter growth across all tree species in the Yasuní plot. The hierarchy includes an upper community-level response above a lower species-level response, similarity in individual-level responses among members of the same species, and similarity in growth measurements for observations from the same individual (Clark et al. 2005). The higher level evaluates the community-wide response to model covariates via the hyperdistribution, whereas the lower level captures species-specific response to model covariates and individuals with correlated but unexplained growth across censuses (Lasky et al. 2014, Uriarte et al. 2016). Using a hierarchical approach allows including species according to their frequency, thus preventing overfitting rare species (Condit et al. 2013).

To test the effects of topography, neighborhood crowding and their interaction on tree growth (Q1), we built a community-level regression as function of tree size, topography and neighborhood crowding over each census interval. We calculated a neighborhood crowding index $NCI_{t,s,i}$ for each focal stem i of species s based on the size (DBH) and distance (d) of its J_k individual neighbors of species K within a 10 m radius at the start of census interval t (Lasky et al. 2014, Uriarte et al. 2016) as:

$$NCI_{t,s,i} = \sum_{k=1}^{K} \sum_{\substack{j=1 \\ j \neq i}}^{J_k} \frac{DBH_{t,k,j}^2}{d_{k,j}} \quad (1)$$

Aboveground biomass scales with the square of tree size in tropical forests (Chave et al. 2005), so we assumed that neighborhood effects on tree growth increase with the square of their size. As the effects of a neighboring tree decrease with increasing distance from the focal stem in

forest systems (Ribbens et al. 1994, Canham et al. 2006, Uriarte et al. 2010), we assumed that neighborhood effects on tree growth decline with the inverse of their distance from the focal tree. We used a radius of 10 m because it is sufficient to capture the great majority of neighborhood effects (Hubbell et al. 2001, Uriarte et al. 2004, Lasky et al. 2014). To avoid edge effects, trees located within 10 m of the edge of the plot served as neighbors but not as focal trees.

The tree growth model is assumed to have a non-linear, multiplicative form (Canham et al. 2006, Uriarte et al. 2010, Fortunel et al. 2016). To evaluate relative changes in tree growth with model covariates (Lasky et al. 2014, Kunstler et al. 2016, Uriarte et al. 2016) and to stabilize variance and reduce the strength of outliers (Emerson 2008), we log-transformed annual diameter growth. We modeled the expected log-transformed annual diameter growth $g_{t,s,I}$ of an individual stem i of species s between censuses t and $t + 1$ as:

$$\begin{aligned} E\left[\log(g_{t,s,i})\right] = {} & \beta_{1s} + \beta_{2s} \log(DBH_{t,s,i}) + \beta_{3s} TH_{s,i} \\ & + \beta_{4s} \log(NCI_{t,s,i}) + \beta_{5s} TH_{s,i} \log(NCI_{t,s,i}) \\ & + \beta_{6s} \log(DBH_{t,s,i}) \log(NCI_{t,s,i}) + \delta_t + \gamma_i \end{aligned}$$
$$(2)$$

where, for a given stem i of species s, $DBH_{t,s,i}$ is the diameter at 1.3 m height at the start of the census interval t, $TH_{s,i}$ is the topographic variable of the quadrat, and $NCI_{t,s,i}$ is the neighborhood crowding index at the start of the census interval t. Fixed effects for year and random effects for individual tree are denoted as δ_t and γ_i, respectively. For each model covariate $c \in (1,2,\ldots,6)$, the β_{cs} parameters are modeled as if arising from a normal distribution with mean $\beta_{c,0}$.

To evaluate the diversity of ways that traits can mediate tree growth and responses to topography, neighborhood crowding and their interaction (Q2), we built five species-level regressions as functions of species mean trait values. We modeled species-specific average growth rate (β_{1s}), sensitivity to topography (β_{3s}), neighborhood crowding (β_{4s}) and the interactions between neighborhood crowding with topography (β_{5s}) and tree size (β_{6s}) as:

$$\beta_{cs} = \beta_{c,0} + \beta_{c,1} F_s \quad (3)$$

where $\beta_{c,0}$ represents the mean value across all species for the model covariate c, and $\beta_{c,1}$ represents departure from the mean effect with one standard deviation change in the value of trait F_s of species s.

The first term of the regression β_{1s} is a species-specific intercept that represents species average growth rate. The next five β-parameters determine the species-specific effects of each model covariate. Ontogenetic changes in tree growth are modeled by the β_{2s} parameter. Positive values of β_{2s} indicate that tree growth increases with tree size in species s. Topographic effects on tree growth are evaluated by the β_{3s} parameter. Negative values of β_{3s} indicate that tree growth is faster at lower values of the topographic covariate. Species responses to neighborhood crowding are modeled by the β_{4s} parameter. Negative values of β_{4s} indicate that greater crowding effects lead to lower tree growth. The topography-crowding interaction is modeled by the β_{5s}

parameter. Because neighborhood crowding tends to vary with topography within the Yasuní plot (r_{Pearson} = 0.22, 0.18 and 0.02 with elevation, convexity and slope), negative values of β_{5s} indicate that tree growth is further reduced by greater neighborhood crowding effects found at higher values of the topographic covariate. The interactive effects of tree size and neighborhood crowding are modeled by the β_{6s} parameter. Positive values of β_{6s} indicate that smaller trees are more sensitive to neighborhood crowding than larger trees, thus capturing the strong size-asymmetry in plant competition.

We standardized all model covariates to enable direct comparisons of the relative importance of each effect in our system (Schielzeth 2010). We standardized the topographic covariate ($\text{TH}_{s,i}$) by subtracting mean and dividing by one standard deviation computed across the dataset. $\text{DBH}_{t,s,i}$ and $\text{NCI}_{t,s,i}$ were log-transformed prior to standardization. Because species can vary in tree size range as well as experience different ranges of neighborhood crowding, we standardized $\text{DBH}_{t,s,i}$ and $\text{NCI}_{t,s,i}$ by subtracting species-specific means and dividing by species-specific standard deviations to prevent confounding of interspecific differences in mean growth (ideally captured by β_{1s} parameter) with interspecific variation in mean DBH or NCI (Uriarte et al. 2016). We considered species with fewer than three individuals (representing 93 and 94 species at the first and second census intervals, respectively) as a single species, and used their combined mean and standard deviations to standardize their $\text{DBH}_{t,s,i}$ and $\text{NCI}_{t,s,i}$. All traits but WSG were log-transformed prior to scaling to prevent the tail of their skewed distribution from dominating the model fit, and then all traits were scaled with mean = 0 and standard deviation = 1. Standardizing trait values to have mean = 0 implies that parameter β_{cs} equals $\beta_{c,0}$ at mean community trait values.

We fit models separately (1) for each of the three topographic variables and (2) for each of the four traits (12 models total) to manage model complexity and correlations among topographic variables and traits, respectively. All parameters were fit simultaneously, including second-level regressions. We specified vague priors for all parameters and estimated their posterior distributions via Markov chain Monte Carlo routines (model code available in Appendix S2) implemented in JAGS (http://mcmc-jags.sour ceforge.net/). We fit models on the Hoffman2 High-Performance Computing cluster at the University of California, Los Angeles. We evaluated the goodness of fit for each model using standard major axis regression between observed growth and modeled growth simulated from the posterior samples. Chains generally converged within 40,000 iterations (Appendix S3). We retrieved the summary statistics (mean, median and 95% credible interval) from the β-parameters posterior distributions. β-parameters were considered (1) significant when 95% credible intervals did not overlap with zero, and (2) biologically important when greater than 0.20 (Cohen 1988).

We assessed the potential for spatial environmental heterogeneity to influence species coexistence in Yasuní by looking for evidence of covariance between the effects of the topography and neighborhood crowding. Specifically, we examined whether neighbors reduce the growth of habitat specialists most strongly in their preferred habitats (Q1). To evaluate this possibility, we built contingency tables between species association with elevation (i.e. ridge-specialist, valley-specialist or generalist) and the elevation location where their growth suffered more from crowding (i.e. ridge, valley or everywhere) and used a Pearson χ^2 test to evaluate the independence. For each species, we used the β_{5s} parameter to evaluate where neighborhood crowding significantly reduced tree growth. When the 95% credible interval of the β_{5s} parameter overlapped zero, it indicates insufficient evidence in the data to support a meaningful variation of the effect of crowding on tree growth across elevations and the corresponding species falls into the 'everywhere' category.

All analyses were conducted in the R 3.4.2 statistical platform (R Development Core Team 2018) using packages spatstat (Baddeley et al. 2015), dynatopmodel (Metcalfe et al. 2015), raster (Hijmans and van Etten 2012), rjags (Plummer et al. 2016), smatr (Warton et al. 2012) and gmodels (Warnes et al. 2015).

RESULTS

In total, we analyzed 201,351 growth-census observations representing 124,704 individuals and 1,047 species, including 232 ridge-associated species, 145 valley-associated species and 669 habitat generalist species. Across the 12 combinations of the three topographic variables and the four traits, our neighborhood models explained on average 87.3% of the variance in tree growth (Appendix S4). The standardized regression coefficients showed consistent responses of tree growth to each of the model covariates between topography models (Fig. 2, see details in Appendix S3). Because results were qualitatively similar between topography models, we focus hereafter on results from the elevation model. Full results for the convexity and slope models are available in the supporting information.

Effects of tree size, topography and neighborhood crowding on species growth

Consistent with our predictions, tree growth increased with increasing tree size, and smaller trees were more sensitive to neighborhood crowding than larger trees (positive ranges of values for the $\beta_{2,0}$ and $\beta_{6,0}$ parameters; Fig. 2; Appendix S3).

As predicted, tree growth overall decreased with increasing elevation (negative range of values for the $\beta_{3,0}$ parameter; Fig. 2; Appendix S3). On average across the four trait models, 4.7% of the 1,047 species- together representing 21.4% of plot stems- showed significant response of tree growth to elevation (β_{3s} parameter in Appendix S5), although the effects of topography were relatively weak (median values of the β_{3s} parameter in Appendix S3).

As expected, tree growth decreased with increasing crowding by neighbors (negative range of values for the $\beta_{4,0}$ parameter; Fig. 2; Appendix S3). Across all 12 models, neighborhood crowding significantly and strongly influenced tree growth in 26.0% of the 1,047 species (β_{4s} parameter in Appendices S3 and S5), together representing 45.7% of the plot stems. Among those species, 95.7% showed
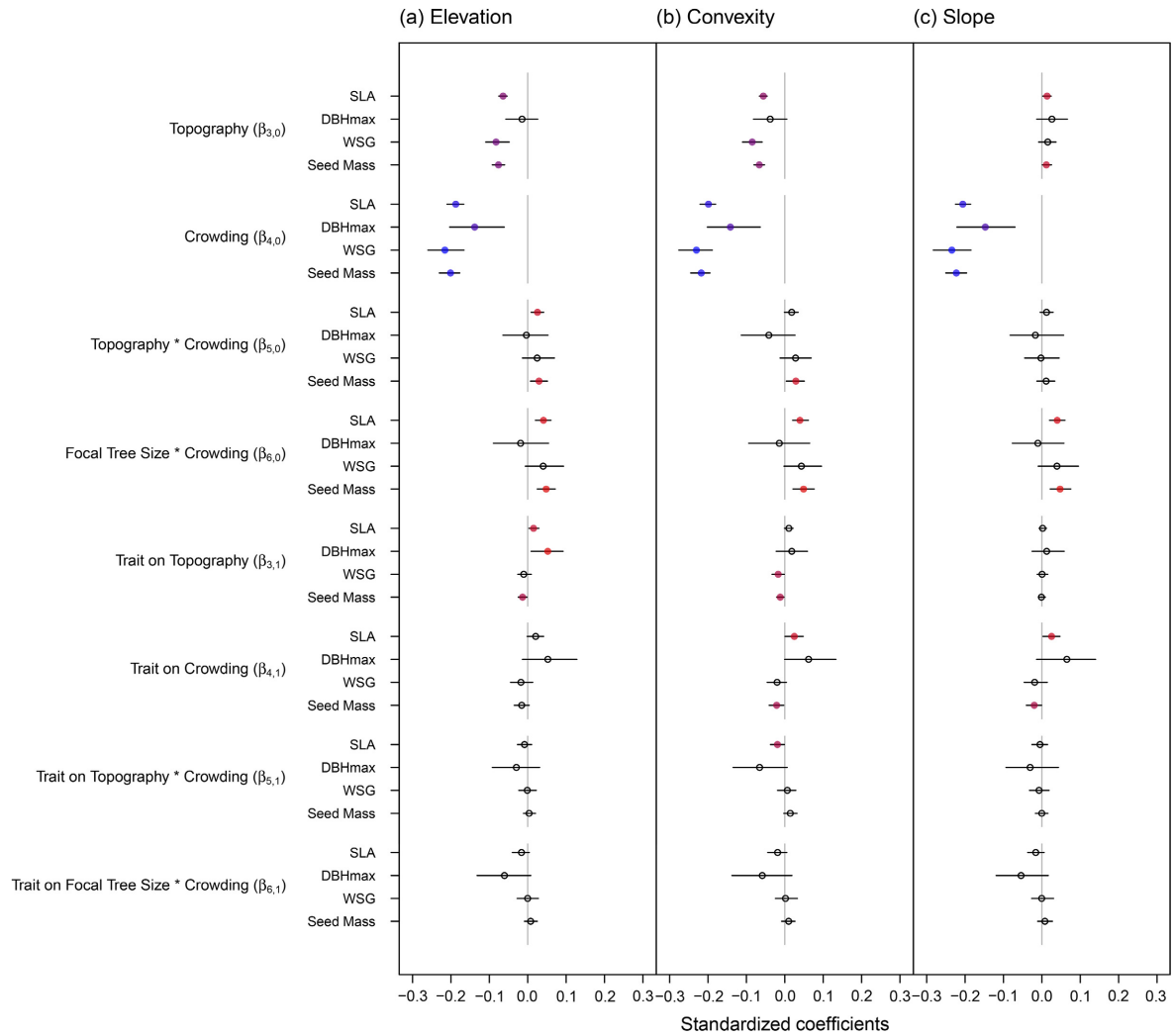
FIG. 2. Standardized regression coefficients modeling the effects of topography ($\beta_{3,0}$), neighborhood crowding ($\beta_{4,0}$), the topography-crowding interaction ($\beta_{5,0}$) and the tree size-crowding interaction (β_{6s}) on tree growth, and the trait effects on the effects of topography ($\beta_{3,1}$), crowding ($\beta_{4,1}$), the topography-crowding interaction ($\beta_{5,1}$), and the tree size-crowding interaction (β_{61}). Coefficients for (a) elevation, (b) convexity and (c) slope models are shown for each of the four trait models: specific leaf area (SLA), maximum tree size (DBH$_{max}$), wood specific gravity (WSG) and seed mass. Circles show posterior medians of β-coefficients, and lines indicate 95% credible intervals (empty circles indicate non-significant effects). Positive β values (in red) indicate faster growth with increasing values of the covariate, while negative β values (in blue) indicate slower growth with increasing values of the covariate.

reduction in growth with increasing crowding, while the remaining 4.3% exhibited increased growth with increasing crowding (Appendix S5).

Tree growth showed no consistent response to the topography-crowding interaction at the plot level (the 95% credible intervals of the $\beta_{5,0}$ parameter included zero in 9 out of 12 models; Fig. 2; Appendix S3). This overall lack of support for the role of the topography-crowding interaction at the community level, however, masks some discrepancies at the species level. On average across the four trait models in the elevation model, the topography-crowding interaction significantly affected tree growth in 8.7% of the 1,047 species (β_{5s} parameter in Appendix S5), together representing 17.0% of the plot stems. Among those species, 33.5% exhibited reduced growth with increasing neighborhood crowding at higher elevation, whereas the remaining respective 66.5% showed the opposite pattern (Appendix S5).

Among the species showing significant tree growth response to topography, crowding and their interaction, we generally could detect these effects in lesser abundant species only when very strong (i.e., more negative or positive values of the β_{3s}, β_{4s} and β_{5s} parameters; Appendix S6).

Species traits associated with variation in tree growth with tree size, topography and neighborhood crowding

Species traits influenced tree growth response to topography ($\beta_{3,1}$ parameter; Fig. 2; Appendix S3). In particular, species with heavier seeds had faster tree growth at lower elevation (negative values of $\beta_{3,1}$ parameter moved β_{3s} parameter further away from zero). Species with higher SLA and greater maximum size had a weaker growth response to elevation (positive values of $\beta_{3,1}$ parameter moved β_{3s} parameter closer to zero). Contrary to our

expectation, species traits did not consistently influence tree growth response to neighborhood crowding ($\beta_{4,1}$ parameter; Fig. 2; Appendix S3). We found some limited evidence that neighborhood crowding further reduced tree growth in species with heavier seeds (negative values of $\beta_{4,1}$ parameter moved β_{4s} parameter further away from zero). In addition, species with higher SLA tend to have a weaker growth response to neighborhood crowding (positive values of $\beta_{4,1}$ parameter moved β_{4s} parameter closer to zero). In line with these results, we found that species traits did not mediate tree growth response to the tree size-crowding interaction ($\beta_{6,1}$ parameter; Fig. 2; Appendix S3). Finally, associated with the overall insignificant effects of the topography-crowding interaction on tree growth, we found that trait values overall did not influence tree growth response to the topography-crowding interaction ($\beta_{5,1}$ parameter; Fig. 2; Appendix S3). The species that show a significant response to model covariates span the entire range of values found for SLA, WSG and seed mass in the Yasuní plot (Appendix S7).

Tree growth response of habitat specialists to the interaction between topography and neighborhood crowding

We found a strong correlation between species association with elevation (calculated from species occurrence in the plot) and the topographic position where their growth suffered more from crowding (evaluated by the $\beta_{5,0}$ parameter) (Table 1). In particular, on average across the four trait models, 17 ridge-associated species and 11 valley-associated species (together representing 5.4% of the plot stems) suffered from stronger crowding effects where they did not

commonly occur. In addition, on average across the four trait models, 10 ridge-associated species and 15 valley-associated species (together representing 5.2% of the plot stems) suffered significantly from stronger crowding effects where they are most commonly found.

Discussion

Understanding how multiple ecological mechanisms interact to shape community dynamics is essential to improve our predictions of species responses to global change (Alexander et al. 2015, Franklin et al. 2016). Here we use spatially explicit demographic censuses to examine how abiotic conditions and neighborhood crowding interact to drive variation in tree performance in a hyperdiverse, old-growth tropical forest.

Topographic effects

In tropical forests, the interaction of rainfall with local topography can lead to soil water and fertility gradients, with lower soil moisture and fertility on the ridges than in the valleys (John et al. 2007, Mage and Porder 2013, Allié et al. 2015). As predicted, topographic gradients strongly influenced tree growth in the Yasuní plot, resulting in individual trees growing faster at lower elevation. If individual trees with faster growth rates also tend to exhibit higher mortality rates, as found at the species-level (Wright et al. 2010, Salguero-Gómez et al. 2016), tree turnover could be faster in the valleys than on the ridges in the Yasuní plot, which can create more treefall gaps and lead to higher frequency of smaller trees at lower elevation.

TABLE 1. Contingency tables between species habitat association (i.e., ridge-specialist, valley-specialist or generalist) and the topographic variable where their growth suffered more from crowding for each topography model (elevation, convexity and slope) and each trait model (specific leaf area [SLA], maximum tree size [DBH_{max}], wood specific gravity [WSG] and seed mass). Number of ridge-associated, valley-associated, and generalist species are indicated for each topographic variable where tree growth suffers more from crowding. Pearson χ^2 tests and significance (P) are indicated.

Tree growth suffers more from crowding	Trait	Elevation			Convexity			Slope		
		Generalist	Ridge-specialist	Valley-specialist	Generalist	Ridge-specialist	Valley-specialist	Generalist	Ridge-specialist	Valley-specialist
At higher elevation, convexity or slope	SLA	16	7	7	19	10	17	20	12	10
	DBH_{max}	17	7	7	22	11	17	25	11	11
	WSG	15	7	8	20	11	17	25	12	11
	Seed Mass	15	9	7	21	12	15	22	11	9
Everywhere	SLA	623	213	120	618	203	115	620	203	119
	DBH_{max}	618	213	122	614	203	115	615	202	119
	WSG	624	215	121	613	201	117	614	202	120
	Seed Mass	620	213	122	616	200	117	620	202	121
At lower elevation, convexity or slope	SLA	30	13	18	32	20	13	29	18	16
	DBH_{max}	34	13	16	33	19	13	29	20	15
	WSG	30	11	16	36	21	11	30	19	14
	Seed Mass	34	11	16	32	21	13	27	20	15
Pearson χ^2 and significance	SLA	$\chi^2 = 16.78$	$P = 0.0021$		$\chi^2 = 29.95$	$P < 0.0001$		$\chi^2 = 17.61$	$P = 0.0015$	
	DBH_{max}	$\chi^2 = 10.11$	$P = 0.0386$		$\chi^2 = 24.91$	$P = 0.0001$		$\chi^2 = 15.55$	$P = 0.0037$	
	WSG	$\chi^2 = 15.43$	$P = 0.0039$		$\chi^2 = 25.50$	$P < 0.0001$		$\chi^2 = 12.96$	$P = 0.0115$	
	Seed Mass	$\chi^2 = 12.34$	$P = 0.0150$		$\chi^2 = 22.60$	$P = 0.0002$		$\chi^2 = 16.01$	$P = 0.0030$	

While we identified 377 habitat-associated species (including 232 ridge-specialists and 145 valley-specialists) from species occurrence data, we only detected strong sensitivity of tree growth to elevation in 49 species (representing 21.4% of the stems in the plot). This result suggests that topographic gradients have less impact on species diameter growth rates than on species fine-scale distributions in this forest. To better understand how differential species performance can generate the observed patterns of species occurrence at the plot level, future studies would need to evaluate (1) how other components of plant performance (namely survival and reproduction) respond to topographic gradients, and (2) whether species demographic responses to environmental heterogeneity are consistent over time scales relevant to the emergence of tropical tree species distributions (i.e., decades to centuries).

Neighborhood crowding effects

While our prior work discussed how species trait differences may influence neighborhood crowding effects (Lasky et al. 2014, Fortunel et al. 2016), here we focused on the crowding effects of neighbors on focal tree growth independent of species functional identity (Uriarte et al. 2016). Competition for shared resources and attack by shared natural enemies are expected to increase with increasing neighborhood crowding (Wright 2002, Myers et al. 2013). Consistent with this expectation, neighborhood crowding strongly reduced tree growth in the Yasuní plot, which is consistent with previous work in both temperate and tropical forests (Canham et al. 2006, Uriarte et al. 2010, Lasky et al. 2014, Kunstler et al. 2016). An earlier analysis with the 315 most abundant taxa in the Yasuní plot showed that neighborhood crowding had significant effects on the growth of 89 species (Fortunel et al. 2016). Using a hierarchical Bayesian framework allowed us to include almost all species in the plot and to detect significant crowding effects on tree growth for 263 of the 1,047 species that together represent 44.6% of the stems in the Yasuní plot, yielding further evidence of the importance of neighborhood interactions on tree growth in this lowland rainforest plot.

The vast majority of species sensitive to neighbors suffered reduced growth in crowded conditions (249 out of 263 species, average $\beta_{4s} = -0.36$). However, a small minority of species sensitive to neighbors responded positively to neighbor density (14 out of 263 species, average $\beta_{4s} = 0.38$). Similar positive effects were detected on the survival of tropical seedlings in Puerto Rico (Lasky et al. 2015). Such findings could be due to positive interactions between plant species or to more favorable environmental conditions that surpassed any negative crowding effects. For example, high light availability in a recently formed gap could drive both greater community-wide growth rates as well as increased crowding. Future work will need to integrate additional environmental data, in particular light availability or canopy cover data, in order to better understand the variation in neighbor effects we report.

Although crowding effects are clear in our analysis, it is important to note a methodological issue affecting all neighborhood analyses in forest plots using tree coordinates in a projected horizontal plane such as in the CTFS-ForestGeo network (Anderson-Teixeira et al. 2015). If tree coordinates are reported in a projected horizontal plane while the underlying terrain is uneven, error can be introduced in the distances calculated from these tree coordinates. Accounting for local slope (α) may help refine the distances between neighboring trees: ground distance would be multiplied by $\sqrt{(1 + \alpha^2)}$, and ground area would be multiplied by $(1 + \alpha^2)$. With an average slope of 12% at Yasuní (Valencia et al. 2004), it would correspond to an increase of 1.44% in ground area, and an increase of same magnitude in the number of neighboring trees included in the neighborhood crowding index. Addressing this methodological issue is beyond the scope of this study, but we note that the contribution of these additional trees at the extreme margin of the neighborhood is limited in the NCI term as we assume that neighborhood crowding effects decline rapidly with distance (see Eq. 1).

Interaction between topography and neighborhood crowding

Although neighborhood crowding was greater on ridge-tops than in the valleys in the Yasuní plot, topography and neighborhood crowding generally did not interact in shaping tree growth for the vast majority of species at Yasuní. This suggests that environmental filtering and species interactions mainly act largely independently in shaping the growth of recruited stems in this lowland rainforest, which has important implications for improving predictions of the future dynamics of tropical forests (Fisher et al. 2018). Nevertheless, the interaction between topographic variables and neighborhood crowding strongly influenced individual growth for 91 of the 1,047 species that together represent 17.0% of the stems at Yasuní, suggesting that these community assembly mechanisms can interact in shaping species dynamics in highly diverse tropical rainforests. Our findings also highlight the challenge in assessing how multiple community assembly mechanisms interact in highly diverse tropical systems, where the majority of the species are rare and thus may not be found on the entire gradients of topography and crowding (Fortunel et al. 2016). Species interactions in our study are evaluated via neighborhood crowding that encompasses the effects of both conspecific and heterospecific neighbors, but future work partitioning the relative contributions of each mechanism to variation in growth could shed more light on the ecological processes shaping the interaction between topography and crowding (Comita et al. 2010, Kunstler et al. 2016). Our study focused on stems ≥1 cm in diameter at breast height that were able to tolerate the local environmental conditions and biotic interactions and to successfully establish in the tree community. As suggested by other studies evaluating species demography across local topographic gradients in tropical forests (Kenfack et al. 2014), seedlings may be a more sensitive stage to determine whether the combined effects of environmental heterogeneity and neighborhood crowding can lead to more coexistence. Future studies would need to combine demographic data across ontogenetic stages (Lasky et al. 2015), from seedlings to adult trees, to better evaluate the role of multiple mechanisms in shaping species dynamics and coexistence in highly diverse tropical rainforests.

Role of traits in mediating species response to topography and neighborhood crowding

Species traits strongly influenced growth response to topography in the Yasuní plot. Contrary to our expectation, species with higher specific leaf area responded less strongly to topographic gradients. As this trait confers greater light capture and resource acquisition (Westoby et al. 2002), species with higher specific leaf area may be able to optimize their growth across the topographic gradient found in the plot. As expected, species growing faster in valleys have smaller maximum size (Kraft et al. 2008). This result suggests that short-stature shade-tolerant species may be benefitting from higher soil fertility and reduced shading associated with lower basal area found in the valleys compared to the ridges of the Yasuní plot (Valencia et al. 2004). Because species on ridge tops have denser wood (Kraft et al. 2008) and can thus support larger crown areas (Francis et al. 2017) than species in valleys, our result may also suggest that neighborhood crowding of dense wood neighbors reduced tree growth more because they cast more shade. Moreover, species exhibiting faster growth in valleys than on ridge-tops had heavier seeds, potentially because greater amounts of resources available to seedlings during establishment can have long-lasting effects on growth and thus long-term consequences for forest dynamics (Jansen et al. 2012).

Contrary to our expectation, we did not detect the influence of species traits on growth response to neighborhood crowding or the interaction between topography and crowding. The fact that traits did not appear to consistently mediate species response to neighborhood crowding is consistent with previous work in a subtropical forest (Lasky et al. 2015) but contradicts recent work in a secondary tropical forest (Uriarte et al. 2016) and in forests globally (Kunstler et al. 2016). The climate at Yasuní is largely aseasonal and traits associated with competition for soil water resources in local neighborhoods may not be shifting as strongly as in forests experiencing more seasonal climates (Farrior et al. 2013). In addition, the Yasuní plot is located in an old-growth tropical forest where the dynamics is relatively slow compared to other plots located in secondary tropical forests where the dynamics is comparatively high, and where the role of traits may be more prominent in shaping neighborhood interactions and forest dynamics (Lasky et al. 2014). Besides differences in climate and/or disturbance levels among study sites, possible explanations for this discrepancy between studies include the following: (1) neighborhood effects can have negative or positive effects on tree growth, and (2) neighborhood effects on tree dynamics can arise through either symmetric or asymmetric interactions between plants- typically for soil and light resources, respectively (DeMalach et al. 2016). Hence, traits may have contrasting influence in mediating species response to neighbors depending on the direction and degree of symmetry of biotic interactions. Future work would need to integrate species traits that are more mechanistically linked to specific abiotic and biotic factors to better disentangle the role of traits in shaping species response to different mechanisms of community assembly.

Response of habitat specialists to the interaction between topography and neighborhood crowding

Environmental variation can contribute to species coexistence when the effects biotic interactions on species performance vary with the environment (Adler et al. 2013, Usinowicz et al. 2017). Here, we take an important first step in examining whether neighborhood effects on tree growth vary with topography in lowland tropical forests by evaluating the relationships between species habitat association (defined from species occurrence data in the plot) and topographic location where tree growth suffered more from crowding (evaluated by the $\beta_{5,0}$ parameter in our tree growth model) in the Yasuní plot. We found that tree growth of 28 habitat specialists that represent 5.4% of the plot stems suffered more from crowding where they are not commonly found. This suggests that competition has the potential to reinforce patterns of habitat specialization by reducing growth of some species in their non-preferred environments. In addition, we found that tree growth of 25 habitat specialists (representing 5.2% of the plot stems) was reduced by neighbors in their preferred location. This positive covariance between environmental preference and the strength of competitive effects is an important element of several spatial mechanisms of species coexistence (Chesson 2000, Adler et al. 2013), though much more work is needed to fully quantify the contribution of these mechanisms to species coexistence at Yasuní. These inferences can be strengthened in future studies by better assessing species environmental preference via transplant experiments across habitats, experimental removals of competitors around focal trees or other direct measures rather than occurrence data (Kraft et al. 2015), and by better connecting growth differences to variation in long-term population dynamics, which ultimately drive coexistence processes (Adler et al. 2013).

Conclusions

Working in a highly diverse lowland rainforest, we found that environmental gradients and species interactions influenced tree growth. They acted largely independently at the plot level, though the interaction between topography and neighborhood crowding significantly shaped the growth of ~10% of the 1,047 studied species in the Yasuní plot. Traits mediated species response to topographic gradients, but had no overall effect on species responses to neighborhood crowding. This suggests that traits may have differential effects in local neighborhoods depending on the direction (negative/positive) and type (symmetric/asymmetric) of interaction. Our work highlights the value of simultaneously considering the individual and interactive effects of multiple ecological processes in driving the dynamics of high-diversity communities.

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