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Tree crown overlap improves predictions of the functional neighbourhood effects on tree survival and growth

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Abstract

1. Investigations of forest community structure and dynamics have been facilitated by the use of neighbourhood models that examine the interactions between a focal tree and its neighbours using a fixed radius. However, different studies have chosen different radii without clear reasons, hampering the understanding of mechanisms structuring tree communities.
2. Using functional trait and tree demography data from the Luquillo subtropical forest in Puerto Rico, we compared fixed-neighbourhood models with a canopy overlap model, in which tree crown overlap is used as an indicator of neighbourhood crowding. Analyses that combine functional trait and demographic data provide a mechanistic understanding of observed patterns of community structure and dynamics as they provide insights into the linkages between phenotypes and the environment.
3. Overall, canopy overlap models had better support when compared to neighbourhood models using a fixed radius, suggesting that the fixed radius approach does not capture the full extent of competitive interactions among trees. Moreover, the effects of functional neighbourhood on tree survival and growth differ depending on the type of approach used and lead to different conclusions with respect to the drivers of tree community dynamics.
4. *Synthesis.* In summary, our findings highlight the utility of neighbourhood models based on tree crown overlap, and suggest that applying this same approach to different plots and forests will facilitate comparisons across systems and improve our understanding of the mechanisms that drive the structure and dynamics of tree communities.

KEYWORDS

functional traits, Luquillo Forest, neighbourhood models, niche differentiation, trait hierarchy, tree competition

1 | INTRODUCTION

Functional ecology has facilitated many recent mechanistic insights into the structure and dynamics of forest communities (Kunstler et al., 2016, 2012). Competitive exclusion and niche differentiation based on functional traits are important mechanisms that produce a subset of species within sites, driving community assembly (Kunstler et al., 2012). Evidence for both mechanisms comes from quantifying how trait values of neighbouring individuals influence individual performance that ultimately determines community structure and dynamics (Lasky, Uriarte, Boukili, & Chazdon, 2014; Uriarte et al., 2010; Uriarte, Lasky, Boukili, & Chazdon, 2016). Analyses that combine functional trait and demographic data, such as neighbourhood modelling (Uriarte et al., 2010) provide an understanding of observed patterns of community structure and dynamics.

Neighbourhood models have transitioned from modelling species responses to local interactions to describing trait-demography relationships that ultimately determine community structure (e.g. Uriarte et al., 2010; Kunstler et al., 2012). Specifically, neighbourhood models have allowed us to determine the importance of stabilising and equalising mechanisms such as hierarchical competition or niche differentiation on structuring plant communities (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; Kunstler et al., 2012). Neighbourhood models generally integrate a Crowding Index (NCI), where the influence of neighbours on demographic rates (e.g. growth, survival) within a fixed radius around a focal tree varies directly with the squared diameter of the neighbour (DBH_j^2) and inversely with the squared distance from the focal tree to the neighbour (d_{ij}^2) (Canham, LePage, & Coates, 2004; Uriarte, Condit, Canham, & Hubbell, 2004). The NCI is summed over all neighbours within the fixed radius containing the focal individual i .

$$NCI_i = \sum_j \frac{DBH_j^2}{d_{ij}^2} \quad (1)$$

The specific fixed radius used in previous studies to define the local neighbourhood has varied among forests. For example, a 10 m radius was used in studies conducted in a Costa Rican lowland forest (Lasky et al., 2014), temperate forests in the north-central British Columbia (Thorpe, Astrup, Trowbridge, & Coates, 2010), and the Mediterranean forests of Spain (Gómez-Aparicio, García-Valdés, Ruíz-Benito, & Zavala, 2011). In the French Alps (Kunstler et al., 2012) and the Ecuadorian forest of Yasuní (Fortunel, Valencia, Wright, Garwood, & Kraft, 2016), the competitive interactions effects on tree growth were determined using a 15 m radius. A fixed 25 m radius was used to explore the effects of local neighbourhood on tree survival and growth in temperate forest in the Southeastern U.S.A. (Zhao, Borders, Wilson, & Rathbun, 2006). Finally, in order to explore the effects of neighbourhood complementarity on tree growth, a 30 m radius cut-off was used on Barro Colorado Island (Chen et al., 2016). An investigation into the effective radius for neighbourhood competition was previously conducted for the Luquillo forest to determine the effects of functional similarity on

tree growth and survival (Uriarte et al., 2010) using a 20 m radius. Given this methodological variation (i.e. a range of different fixed radii with no apparent well-grounded biological reason for their selection), it is difficult to know whether the variation in inferences across the studies is the result of methodological choices or biological differences, and suggests that a more biologically relevant measure of neighbourhoods should be used instead of a fixed radius.

As neighbourhood models are increasingly recognised as useful, and have become more popular in functional and community ecology, a pressing question is how to deal with the scale dependency of these models? One option is to use different fixed radii, repeat the analyses each time, and report the functional sensitivity to the different scales. However, this option is computationally intensive and inefficient for large-scale data, and might complicate comparisons among different forests. Another option would be to avoid fixed radii to define the neighbourhood and instead define neighbourhoods based upon neighbours that have crowns that overlap with the focal individual. Using this approach, the extent of the crown overlap becomes a proxy for neighbourhood crowding. The crown position index (Dawkins & Field, 1978) and modified by Clark and Clark (1992) as the crown illumination index has been frequently used to assess the competition for light and the effect on tree growth and survival (Keeling & Phillips, 2007). The crown overlap index developed here provides an alternative method based upon the allometries of the tree species rather than on the subjective and difficult field assessment.

Neighbourhood competition for light ultimately depends on crown structure (Horn, 1971), with species diversity contingent on the distinct species responses to light. Size-asymmetric competition occurs when larger plants have a disproportionately larger effect in competition, affecting the growth of their smaller neighbours (Chazdon & Fetcher, 1984; Schwinning & Weiner, 1998; Weiner, 1990). Larger plants are expected to be less affected by the interaction with smaller individuals as a larger proportion of their “zone of influence (ZOI)” is unaffected by neighbour interactions (Weiner, 1990). Thus, competition for canopy space is a key mechanism structuring forest ecosystems (Oliver & Larson, 1996). Including crown overlap, therefore, provides a mechanistic, computationally direct approach for characterising tree neighbourhoods. A type of variable-neighbourhood approach using crown overlap has been previously used by Lebrija-Trejos, Wright, Hernández, and Reich (2014). Specifically, they quantified the effects of the local neighbourhood on seedling performance using spatial overlap of adult crowns, in order to refine an analysis investigating Janzen–Connell effects (Connell, 1971; Janzen, 1970). However, this approach did not explicitly quantify the impact of the local neighbourhood of tree growth and survival.

Using species level functional trait and tree demography data from the Luquillo forest dynamics plot (LFDP) in Puerto Rico and a Bayesian modelling approach, we introduce an approach where crown overlap is used as an indicator of neighbourhood crowding, without having to use an arbitrary and fixed-neighbourhood radius. We then compare the performance of these crown overlap models

with models using a fixed-neighbourhood from the focal tree approach. If crown overlap is a good metric for capturing species effects and responses to competition, we should expect traits that relate to competition for light (e.g. leaf N, maximum height) to exhibit a stronger pattern (i.e. significance) than those related to competition for water. By allowing comparisons among different forests, the crown overlap approach introduced here will facilitate generalisations of the mechanisms driving the structure and dynamics of tree communities.

2 | MATERIALS AND METHODS

2.1 | Study area

The Luquillo Forest Dynamics Plot (LFDP) (18°20'N, 65°49'W, 333–428 m a.s.l.) is a 16-ha forest plot located in the Luquillo Experimental Forest in northeast Puerto Rico (Thompson et al., 2002). This is a subtropical wet forest with an average precipitation of 3,500 mm/year. The plot has been censused approximately every 5 years since 1990 and every free-standing individual with a woody stem ≥ 1 cm in diameter at breast height (DBH measured at 1.3 m from the ground) is tagged, mapped, measured, and identified to species (Thompson et al., 2002). In this study, we used growth and survival data from a single recent census interval (2005–2010) as the Luquillo forest has experienced major disturbance from Hurricane Hugo in 1989 and Hurricane Georges in 1998, with elevated recruitment and growth rates resulting in significant temporal dynamics (Swenson et al., 2012). We discarded the few cases where the stem was broken off in 2010 below the point of measurement in the 2005 census or when trait data were not available for the species. We also discarded focal individuals found <20 m from the edge of the plot to avoid edge effects from incomplete neighbourhoods. These actions resulted in a dataset containing 38,495 individuals of 128 species.

2.2 | Functional trait data and allometric relationships

We selected eight key functional traits, measured for all species included in this study, to assess whether traits were related to interspecific differences in individual growth and survival and the strength of neighbourhood crowding. We included leaf nitrogen content (LNC, %), leaf phosphorus content (LPC, %) and leaf carbon content (LCC, %), leaf area (LA, cm²), specific leaf area (SLA, cm²/g), maximum height for the species ($H_{\max}$, meters), seed mass (SM, grams), and wood density (WD, g/cm³). These traits have been reported previously (Swenson & Umana, 2015; Swenson et al., 2012; Umaña et al., 2016) and are known to be closely related to resource acquisition and competitive ability (Wright et al., 2010). With the exception of LCC, WD, and SM, trait values were log transformed before standardisation to approximate normality. All functional trait values were standardized to a mean of 0 and a standard deviation of 1 before conducting a Principal Component Analysis (PCA) to reduce the number and collinearity of traits. We determined two major axes

of variation. The first axis was primarily associated with LPC and LNC, WD and SLA explained 30% of the variation, while the second axis was mainly represented by LA, $H_{\max}$ and SM and explained 21% of the variation.

We generated general allometric equations relating DBH to tree height and to crown radius from field measurements in order to estimate the crown area and height of every individual tree in the forest plot. Measurements were made by NGS on 198 individuals ranging in diameter from 1 cm to >100 cm in DBH from 14 species that dominate the forest (Supporting Information Table S1). The DBH of each tree was measured using a diameter tape and a Nikon Forestry 550 hypsometer was utilised to measure the tree height. The radius of the crown was measured in two cardinal directions by standing under the outer edge of the crown and using the hypsometer to measure the distance to the trunk. When the individual was shorter than 2 m, the height and crown measurements were made by hand with a meter tape. We utilised the average crown radius for generating allometric relationships. While the major and minor axes of the crown were known and, therefore, could be modelled, assigning the direction of these axes to each individual tree in the forest would introduce more noise into the analyses. Similarly, general allometric equations for DBH-height and DBH-crown radius were used because we only had data for 14 species out of the 128 species and assigning species-specific estimates to only ~10% of the species could introduce unintended biases. Ideally, equations for each species will be derived in the future. The height or crown radius were plotted against DBH on log-log axes and fitted with a power function (radius) or a second order polynomial function (height) where AIC was utilized to select the best model. The resulting equations were: $\log_{10}(\text{tree crown radius}) = 0.6598 \cdot \log_{10}(\text{DBH}) - 0.3918$ ($r^2 = 0.8139$); $\log_{10}(\text{height}) = -0.1318 \cdot (\log_{10}(\text{DBH}))^2 + 0.8888 \cdot \log_{10}(\text{DBH}) + 0.2708$ ($r^2 = 0.91$). Lastly, the palm species *Prestoea acuminata* and *Roystonea borinquensis* are a dominant feature of this forest, but have distinct canopy growth forms as compared to dicots. Thus, their data were used along with a power function to estimate a palm-specific canopy: $\log_{10}(\text{tree crown radius}) = \log_{10}(0.1762) + 0.8233 \cdot \log_{10}(\text{DBH})$ ($r^2 = 0.61$).

2.3 | Neighbourhood models based on a variable crown-radius approach

Our crown overlap model was based on an approach that measured the proportion of crown overlap as an estimate of neighbourhood crowding and used a modified neighbour crowding index (NClmod). We quantified conspecific and heterospecific competition of neighbours by modifying NCI and replacing distance and size of neighbours by the proportion of crown overlap (CO) as follows:

$$\text{NClmod}_i = \sum_j \text{CO} \quad (2)$$

Crown overlap requires us to know the radius of tree crowns and height for every studied individual. This can be accomplished using general allometric equations relating diameter to height and

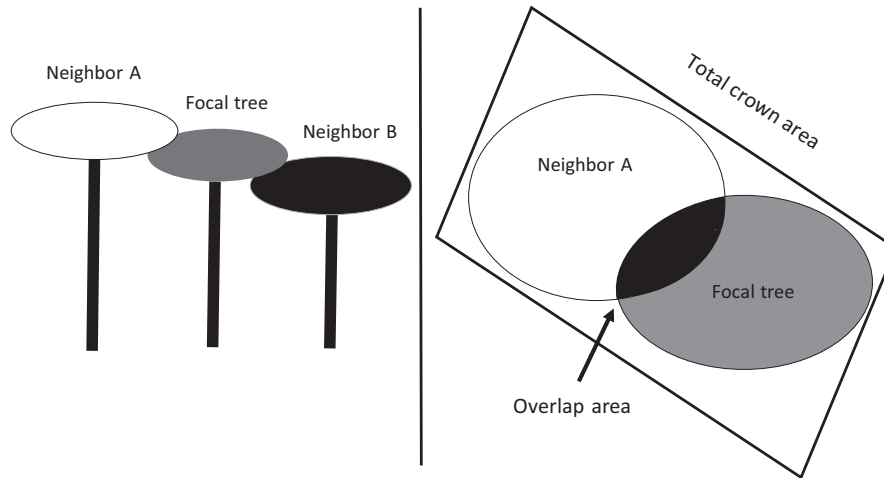


FIGURE 1 Estimation of the proportion of total crown area occupied by overlapping crown areas of a focal tree and a taller neighbour (neighbour A). Overlap with shorter neighbours (e.g. neighbour B) was not included in the estimation

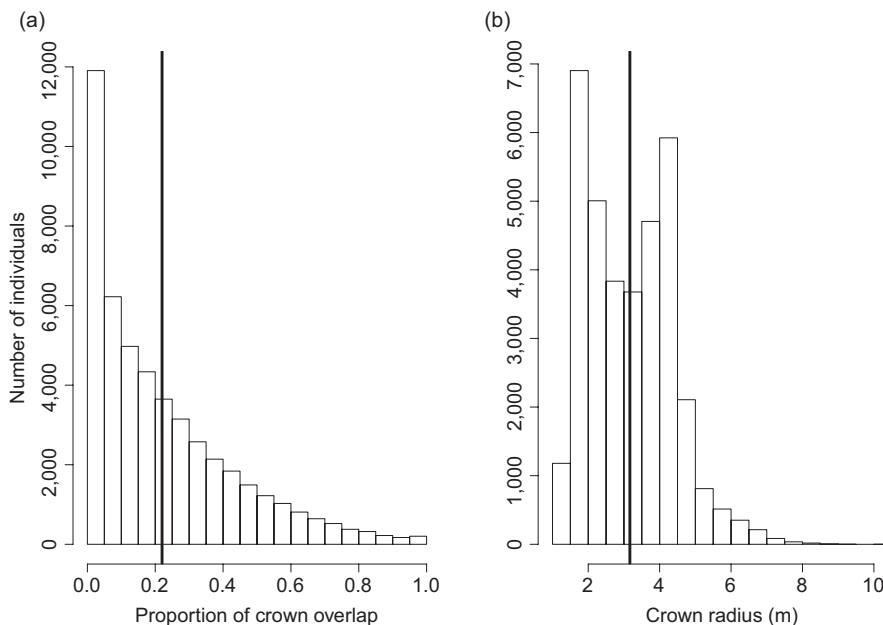


FIGURE 2 Histogram showing proportion of crown overlap (a) and crown radius (m) (b) for trees (≥ 1 cm dbh) located at the Luquillo Experimental Forest Plot located in the northeast of Puerto Rico and included in the neighbourhood analyses. Black line depicts the mean

crown dimensions. Allometric equations were built from both monocots and dicots. Tree crowns were assumed to be elliptical, then considering only trees that were taller than each focal tree, we determined the intersection area among the crowns for each focal tree and its neighbours (Figure 1), using the `joinPolys` function from the `PBSmapping` package (Schnute, Boers, & Haigh, 2006). We then determined the proportion of total crown area (combined areas of the focal tree and its neighbour) occupied by the intersection of crowns from focal trees and its neighbours to estimate the proportion of crown overlap (Figure 2a). This was then used as a measure of neighbourhood crowding. We characterised a functional neighbourhood in which the effects of neighbours were calculated in terms of their functional values at the species level and calculated modified indices of functional neighbourhoods, previously used in other studies (see Kunstler et al., 2012; Lasky et al., 2014; Uriarte et al., 2016), to quantify the effect of trait hierarchies (NCIhmod) and

absolute trait differences (NCISmod) for each individual focal tree as follows:

$$\text{NCIhmod}_i = \sum_j (F_{s,i} - F_{s,j}) \text{DBH}_j^2 \quad (3)$$

and

$$\text{NCISmod}_i = \sum_j |F_{s,i} - F_{s,j}| \text{DBH}_j^2 \quad (4)$$

where $F_{s,i}$ and $F_{s,j}$ are the values of the functional trait of the focal individual i and neighbour j for species s . We used a species trait distance matrix to determine the variation in species traits (multivariate trait). We then conducted a null model approach to account for the fact that heterospecific abundance and neighbourhood dissimilarity might be correlated, potentially leading to uncertainties associated with NCIhmod being highly inflated. Thus, we tested whether observed amount of

functional dissimilarity among co-occurring species in the neighbourhood area (NCImod) differed from what was expected as heterospecific density increases. For this purpose, we calculated the standardized effect sizes (SES) using the mean and standard deviation of the null distribution of 999 expected neighbourhood dissimilarity indices for each focal tree.

We then used a hierarchical approach to model both survival and growth as a linear predictor z_i :

$$\begin{aligned} z_i = & \beta_{1s} + \beta_{2s} \text{NCImod}_i + \beta_{3s} \text{NCImod}_i + \beta_{4s} \text{SES NCImod}_i \\ & ; + \beta_{5s} \text{NCImod}_i + \beta_{6s} \log(\text{DBH}_i) \\ & ; + \beta_{7s} \text{NCImod}_i * \log(\text{DBH}_i) + \beta_{8s} \text{NCImod}_i * \log(\text{DBH}_i) \end{aligned} \quad (5)$$

where β represented species-specific coefficients describing the intercept (β_{1s}), the effect of conspecific neighbourhood density independent of species functional traits (β_{2s}), the effect of heterospecific neighbourhood density independent of species functional traits (β_{3s}), the effect of crowding based on standardised effect size values for functional dissimilarity between the focal tree and its neighbours (β_{4s}), the effect of crowding based on trait hierarchies between the focal tree and its neighbours (β_{5s}), the effect of initial tree size (DBH) (β_{6s}). To account for the possibility that small trees might respond more strongly to competition than large trees, we included an interaction between initial size and conspecific (β_{7s}) and heterospecific neighbourhood (β_{8s}). We standardised the size by subtracting their species-specific means from their initial DBH size values and dividing by species-specific standard deviations to prevent confounding of the species-specific effects with interspecific variation in mean diameter. Each of the species-specific coefficients followed a normal distribution and hyper-parameters were specified using diffuse normal priors: N (mean = 0, precision = 0.001). We expressed the variance of hyper-parameters (the s_b and s_γ) as precisions ($t = 1/s^2$) and gave the latter diffuse gamma priors: Gamma (shape = 0.001, rate = 0.001). All predictor variables were scaled to zero to allow comparisons across effect sizes. Models included both the uncertainty in the data (observation error) and the variability of the process (process error).

The growth and survival models were fitted separately for each functional trait, as well as for each of the two main PCA axes and the multivariate trait. Relative diameter growth rate followed a normal distribution, while survival followed a binomial distribution. It is important to highlight that for this analysis, we only included neighbours that were taller (calculated from allometric equations using initial DBH in 2005) than the focal trees and, thus might be exerting stronger competitive effects.

2.4 | Models based on a fixed-neighbourhood approach

We also constructed neighbourhood models at different fixed radii, using the same approach and the same individuals as used for the crown overlap models (Equations 3–5). We calculated a Crowding Index (NCI) (Equation 1), where the negative influence of neighbours varied directly with the squared diameter of the neighbour j (DBH_j) and inversely with the squared distance to the neighbour (d_{ij})

(Canham et al., 2004). Neighbours were identified within the areas of different radii (10, 15, 20, 25 and 30 m) from the focal tree. Both survival and growth were model as a linear predictor as follows:

$$\begin{aligned} z_i = & \beta_{1s} + \beta_{2s} \text{NCI}_i + \beta_{3s} \text{NCI}_i + \beta_{4s} \text{SES NCI}_i \\ & ; + \beta_{5s} \text{NCI}_i + \beta_{6s} \log(\text{DBH}_i) + \beta_{7s} \text{NCI}_i * \log(\text{DBH}_i) \\ & ; + \beta_{8s} \text{NCI}_i * \log(\text{DBH}_i) \end{aligned} \quad (6)$$

where β represented species-specific coefficients describing the intercept (β_{1s}), the effect of conspecific neighbourhood density independent of species functional traits (β_{2s}), the effect of heterospecific neighbourhood density independent of species functional traits (β_{3s}), the effect of crowding based on standardised effect size values for functional dissimilarity between the focal tree and its neighbours (β_{4s}), the effect of crowding based on trait hierarchies between the focal tree and its neighbours (β_{5s}), the effect of initial tree size (DBH) (β_{6s}), the interaction between conspecific density and initial size (β_{7s}) and the interaction between heterospecific density and initial size (β_{8s}).

In addition, we evaluate whether neighbourhood effects, using variable-fixed neighbourhood and canopy overlap models, were different to community-level data when only dominant species were included. We selected 12 species that account for 75% of adult stems in the plot and represent a broad range of life-history strategies (Uriarte, Turner, Thompson, & Zimmerman, 2015), these included *Alchornea latifolia* (Euphorbiaceae), *Buchenavia tetraphylla* (Combretaceae), *Casearia arborea* (Salicaceae), *Cecropia schreberiana* (Cecropiaceae), *Dacryodes excelsa* (Burseraceae), *Guarea guidonia* (Meliaceae), *Inga laurina* (Fabaceae), *Manilkaria bidentata* (Sapotaceae), *Prestoea acuminata* (Arecaceae), *Schefflera morototoni* (Araliaceae), *Sloanea berteriana* (Elaeocarpaceae) and *Tabebuia heterophylla* (Bignoniaceae).

2.5 | Model evaluation

We fitted all models using JAGS (Plummer, 2013) and simulated six Markov Chain Monte Carlo chains (MCMC) for 50,000 iterations to obtain a sufficient number of effectively independent samples from the posterior distribution. We then performed a Gelman–Rubin convergence diagnostic (Gelman & Rubin, 1992). Parameter estimates and 95% credible intervals were obtained from the quantiles of their posterior distribution. Results were statistically supported when credible intervals did not overlap zero. We compared the variable-fixed-neighbourhood and canopy overlap models using the Deviance Information Criterion (DIC) to determine the most parsimonious models ($\Delta\text{DIC} < 5$). We also use this approach to compare “full” models with more simple models that included initial size, heterospecific/conspecific density (Supporting Information Tables S2 and S3), or crown overlap. We used the DIC to determine the most parsimonious models between full models with simpler models (Supporting Information Tables S2 and S3) for each model type (various-neighbourhood or canopy overlap models). In addition, we assessed the models' goodness-of-fit via posterior predictive checks by determining the probability that a posterior simulation is further away from the expected value than the observed data (Bayesian p-values) (Gelman, 1996). At every step in

the MCMC chain, we simulated a new data vector for growth rates or survival status from the model and calculated a loss function on both the simulated and observed data. For growth, p-values equals to 1 if the sum of square deviations is greater for the simulated growth than the observed growth. For survival, p-values equals to 1 if the log-likelihood of the observed values are greater than the simulated one. The closer the p-values to 0.5, the better the values calculated from the simulated data distributed around the observed values.

3 | RESULTS

3.1 | Comparison between variable- and fixed-neighbourhood models

Overall, the most parsimonious models comprised were those models that included a variable-neighbourhood approach, or that incorporated crown overlap as a measure of neighbourhood crowding, for both survival (Table 1) and growth (Table 2), as revealed by the DIC and Bayesian p-values. Survival models that included WD had better support for crown overlap models, while the best growth models included $H_{\max}$. Among the fixed-neighbourhood models, the most parsimonious models included 10 m models for survival and 30 m for growth. Survival models using 10 m neighbourhoods that included SLA had better support and, similarly, the best growth model with 30 m neighbourhoods included SLA. Mean proportion of crown overlap was 0.22 at the Luquillo plot (Figure 2a). Crown radii ranged between 1.34 and 10.04 m and had a mean of 3.17 m at the Luquillo plot (Figure 2b); thus, a 30 m radius was able to capture all neighbourhood interactions, in contrast to a 10 m radius. In general, survival and growth models that included functional traits performed better when compared to more simple models (Tables 1 and 2) or when compared to models that only included crown overlap as revealed by the AIC values for both survival (AIC = 12,064) and growth (AIC = -40,874).

Community-level models had greater support than models that included the most common species at the Luquillo forest for both survival (Supporting Information Table S4) and growth (Supporting Information Table S5), as revealed by the DIC and Bayesian p-values. The best survival and growth crown overlap models included $H_{\max}$. Among the fixed-neighbourhood models, the most parsimonious models included 10 m models for survival and 20 m for growth. Survival models using 10 m neighbourhoods that included LA had better support and, similarly, the best growth model with 20 m neighbourhoods included WD. In general, survival and growth models that included functional traits performed better when compared to more simple models (Supporting Information Tables S4 and S5) or when compared to models that only included crown overlap as revealed by the AIC values for both survival (AIC = 7,106) and growth (AIC = -21,551).

3.2 | Effects of the functional neighbourhood on individual survival and growth

The effects of the local neighbourhood on tree survival varied among neighbourhood approaches. For the crown overlap model,

WD best described focal tree survival, with individuals with denser wood achieving greater survival than individuals with lighter wood (Figure 3). We also found strong evidence of a trait hierarchy, only captured by the crown overlap model, with focal trees with lighter wood experiencing lower survival than focal trees with denser wood. Moreover, we found support for a positive interaction between initial size (DBH) and heterospecific density (Figure 3), with the effects of heterospecific neighbourhood on tree survival increasing as the size of the individual increases. In contrast, the fixed-neighbourhood model (10 m) did not capture any trait effects on tree survival, but revealed a positive interaction between initial size (DBH) and conspecific density (Figure 3), with the effects of conspecific neighbourhood on tree survival increasing as the size of individual increases. Initial size had a strong effect on survival for both neighbourhood approaches with big trees experiencing high survivorship.

Similar to survival, the effects of the local neighbourhood on tree growth varied depending on the type of approach used. Models that included $H_{\max}$ best described focal tree growth for crown overlap model. Taller individuals grew faster than small statured individuals (Figure 4). We also found strong evidence of a trait hierarchy, only captured by the crown overlap model, with taller focal trees growing faster than small statured focal trees (Figure 4). In contrast, the fixed-neighbourhood model (30 m) did not capture any trait or functional neighbourhood effects on tree growth (Figure 4). Initial size (DBH) had a strong effect on growth for both neighbourhood approaches with large diameter trees growing faster than small diameter trees (Figure 4).

When only species were considered, crown overlap models revealed more consistent effects of the local neighbourhood on tree survival (Supporting Information Figure S1) and growth (Supporting Information Figure S2), while the results from the fixed-neighbourhood models differed from the results obtained at the community level. For tree survival, we found evidence of a trait hierarchy captured by the fixed-neighbourhood model (Supporting Information Figure S1) and contrasting results at the community-level that did not show strong effects of the functional neighbourhood. Crown overlap models also revealed a trait hierarchy (Supporting Information Figure S1) that was also captured by survival models at the community level. For growth, the fixed-neighbourhood model (20 m) did not capture any trait or functional neighbourhood effects, while the crown overlap model revealed a strong trait effect (Supporting Information Figure S2) thereby aligning with the results obtained at the community level.

4 | DISCUSSION

Is there an optimal radius that best describes the local neighbourhood and the competitive effect of neighbour trees on focal tree survival and growth? This question is growing in importance as neighbourhood models become more useful and more widely used in studies of community ecology. Our results revealed that neighbourhood models using crown overlap as a measure of neighbourhood

TABLE 1 Most parsimonious models and goodness-of-fit statistics including the deviance information criterion (DIC) and Bayesian *p*-values for survival models including the crown overlap model and fixed-neighbourhood (10, 15, 20, 25, and 30 m) approaches. The most parsimonious models (Δ DIC >5) are highlighted in dark grey, whereas the best fixed-neighbourhood models are in light grey

Model description	Crown overlap model		10 m		15 m		20 m		25 m		30 m	
	DIC	<i>p</i> -value	DIC	<i>p</i> -value	DIC	<i>p</i> -value	DIC	<i>p</i> -value	DIC	<i>p</i> -value	DIC	<i>p</i> -value
Leaf carbon content	12,208	0.4960	12,229	0.4518	12,292	0.4515	12,285	0.4546	12,278	0.4566	12,290	0.4555
Maximum height	12,047	0.4969	12,063	0.4523	12,147	0.4548	12,134	0.4585	12,133	0.4580	12,059	0.4548
Leaf area	12,049	0.4972	12,012	0.4529	12,099	0.4568	12,043	0.4502	12,046	0.4540	12,058	0.4569
Leaf nitrogen content	12,176	0.4925	12,027	0.4531	12,106	0.4561	12,078	0.4560	12,097	0.4514	12,109	0.4524
leaf phosphorus content	12,020	0.4935	12,076	0.4550	12,116	0.4580	12,044	0.4590	12,102	0.4559	12,122	0.4587
PC1	12,043	0.4949	12,071	0.4527	12,034	0.4492	12,020	0.4534	12,049	0.4499	12,041	0.4560
PC2	12,014	0.4931	12,048	0.4513	12,015	0.4540	12,029	0.4546	12,052	0.4561	12,070	0.4558
Seed mass	12,101	0.4974	12,116	0.4541	12,102	0.4551	12,125	0.4555	12,119	0.4539	12,114	0.4491
Specific leaf area	12,112	0.4918	12,006	0.4546	12,027	0.4576	12,033	0.4553	12,028	0.4534	12,043	0.4569
Wood density	12,001	0.4985	12,081	0.4538	12,034	0.4575	0.4563	12,062	12,128	0.4582	12,060	0.4553
Multivariate	12,118	0.4593	12,124	0.4699	12,119	0.4628	12,128	0.4709	12,125	0.4689	12,117	0.4690
Conspecific only	12,118	0.4870	12,120	0.4841	12,116	0.4947	12,116	0.4925	12,117	0.4911	12,112	0.4914
Conspecific and size only	12,244	0.4833	12,247	0.4622	12,236	0.4876	12,258	0.4839	12,249	0.4862	12,237	0.4835
Heterospecific only	12,063	0.4906	12,077	0.4838	12,068	0.4896	12,065	0.4912	12,073	0.4909	12,058	0.4918
Heterospecific and size only	12,257	0.4815	12,255	0.4668	12,268	0.4849	12,252	0.4835	12,247	0.4817	12,258	0.4832
Size only	12,228	0.4953	12,235	0.4953	12,224	0.4953	12,230	0.4953	12,226	0.4953	12,235	0.4953

TABLE 2 Most parsimonious models and goodness-of-fit statistics including the deviance information criterion (DIC) and Bayesian *p*-values for growth models including the crown overlap model and fixed-neighbourhood (10, 15, 20, 25, and 30 m) approach. The most parsimonious models (Δ DIC >5) are highlighted in dark grey, whereas the best fixed-neighbourhood models are in light grey

Model description	Crown overlap model		10 m		15 m		20 m		25 m		30 m	
	DIC	<i>p</i> -value	DIC	<i>p</i> -value	DIC	<i>p</i> -value	DIC	<i>p</i> -value	DIC	<i>p</i> -value	DIC	<i>p</i> -value
Leaf carbon content	-40,669	0.5559	-40,697	0.5687	-40,693	0.5621	-40,674	0.5001	-40,667	0.5011	-40,651	0.5579
Maximum height	-41,691	0.4956	-41,660	0.5683	-41,675	0.5698	-41,672	0.5607	-41,684	0.5589	-41,687	0.5608
Leaf area	-40,603	0.4951	-40,592	0.5942	-40,534	0.5791	-40,552	0.5790	-40,595	0.5691	-40,565	0.5667
Leaf nitrogen content	-41,221	0.4961	-41,209	0.5840	-41,207	0.5776	-41,208	0.5737	-41,218	0.5711	-41,209	0.5692
Leaf phosphorus content	-41,044	0.4952	-41,025	0.5700	-41,021	0.5616	-41,022	0.5598	-41,016	0.5591	-41,019	0.5593
PC1	-40,991	0.4954	-40,923	0.5872	-40,931	0.5871	-40,926	0.5769	-40,924	0.5778	-40,928	0.5749
PC2	-41,023	0.4953	-41,013	0.5752	-41,017	0.5636	-41,023	0.5636	-41,027	0.5613	-41,036	0.5630
Seed mass	-41,023	0.4953	-41,036	0.5669	-41,048	0.5579	-41,035	0.5570	-41,034	0.5539	-41,028	0.5563
Specific leaf area	-41,116	0.5079	-41,011	0.5689	-41,103	0.5623	-41,105	0.5620	-41,114	0.5574	-41,096	0.5589
Wood density	-41,112	0.4964	-41,115	0.5949	-41,106	0.5857	-41,108	0.5847	-41,114	0.5819	-41,101	0.5789
Multivariate	-40,497	0.5069	-40,493	0.5023	-40,498	0.5031	-40,491	0.5010	-40,492	0.5022	-40,497	0.5014
Conspecific only	2,123	0.5001	2,129	0.5003	2,124	0.4995	2,123	0.4998	2,121	0.5002	2,118	0.5019
Conspecific and size only	-40,291	0.5064	-40,284	0.5034	-40,297	0.5024	-40,293	0.5029	-40,289	0.5014	-40,291	0.5019
Heterospecific only	3,224	0.4989	3,218	0.5003	3,229	0.5010	3,231	0.4998	3,224	0.5002	3,227	0.5008
Heterospecific and size only	-39,326	0.5065	-39,332	0.5033	-39,328	0.5028	-39,321	0.5016	-39,324	0.5014	-39,315	0.5018
Size only	-41,134	0.5058	-41,129	0.5097	-41,132	0.5094	-41,128	0.5020	-41,134	0.5014	-41,130	0.5014

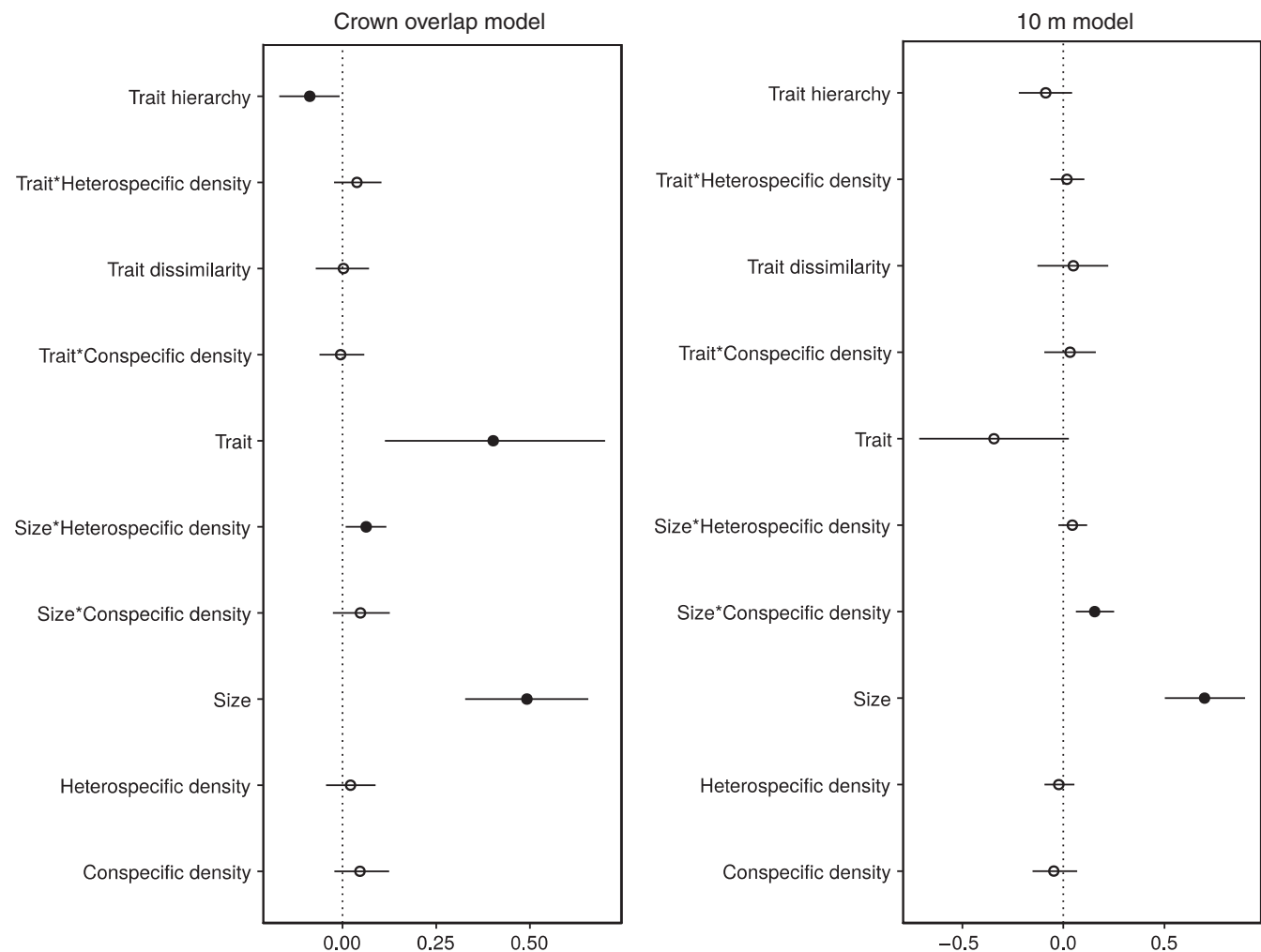


FIGURE 3 Best-fit survival models including wood density in the case of the crown overlap models and specific leaf area for the fixed-neighbourhood approach (10 m). Standardised regression coefficients included initial size effects (DBH), conspecific and heterospecific neighbourhood effects and their interaction, as well as trait effects and neighbourhood competition described by trait hierarchies and absolute trait differences among neighbours. Circles indicate posterior medians for each studied parameter and lines indicate 95% confidence intervals, with filled circles representing significant effects

crowding had a overall better support than widely used fixed-neighbourhood approaches, suggesting that the fixed radius approach might not capture the full extent of competitive interactions. Our variable-neighbourhood approach presents a viable alternative to describing the neighbourhood using a fixed radius, as it is more flexible and immediately extendable to other forest systems. In the future, defining neighbourhoods using tree crown overlap will allow comparisons among forests observed using large forest dynamics plots around the globe and facilitate movement towards the generalisation of drivers of forest structure and tree community dynamics.

4.1 | Variable- vs. fixed- neighbourhood approaches: which one best described tree survival and growth?

We found strong support for models including a crown overlap index when compared to neighbourhood models using a fixed-neighbourhood radius. Crown overlap models not only included individuals that were overlapping, but also neighbours that were taller than the

focal trees resulting in potentially strong competitive pressure. Thus, neighbourhood models that include a tree crown overlap and relative heights might prove to be more accurate, when describing the effects of local neighbourhood competition on tree demography, as fixed-neighbourhood approaches might not capture the full extent of competitive interactions. Crown size determines the amount of light capture by an individual tree, therefore, regulates species co-occurrence and community structure and composition (Poorter & Arets, 2003; Poorter, Bongers, & Bongers, 2006; Poorter, Bongers, Sterck, & Wöll, 2003). Competition for canopy space has long been recognized as a major driver of community dynamics (Purves, Lichstein, & Pacala, 2007; Terborgh, 1985) as it determines individual performance as well as the densities and size distribution of crown trees.

To date, studies have often arbitrarily defined relationships between the functional neighbourhood and tree survival and growth, with neighbourhoods defined at scales ranging from ~300 m² (10 m radius) to ~3,000 m² (30 m radius) (Chen et al., 2016; Fortunel et al., 2016; Gómez-Aparicio et al., 2011; Kunstler et al., 2012; Lasky et

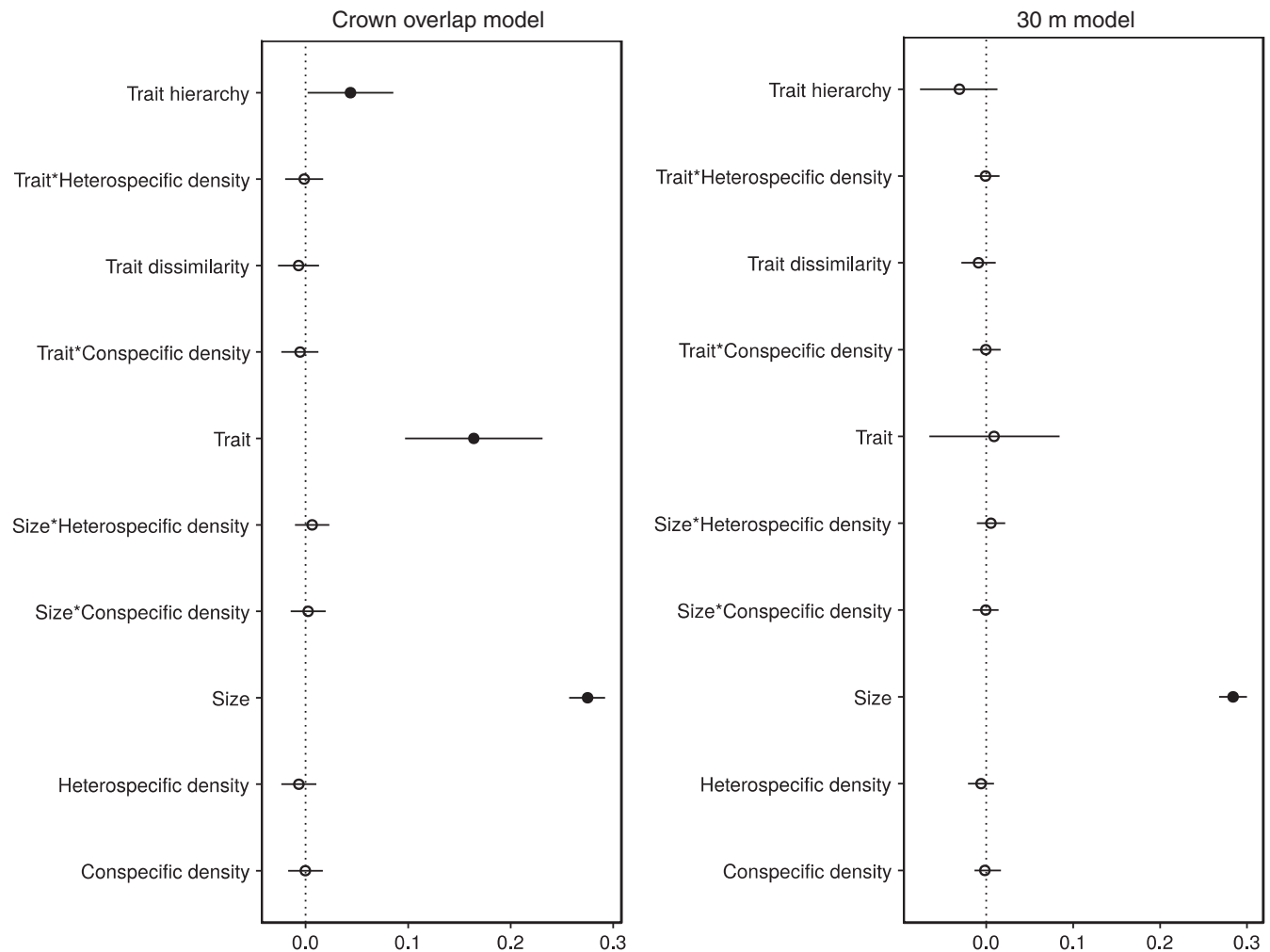


FIGURE 4 Best-fit growth models including maximum height for both the crown overlap model and for the fixed-neighbourhood approach (30 m). Standardised regression coefficients included initial size effects (DBH), conspecific and heterospecific neighbourhood effects and their interaction, as well as trait effects and neighbourhood competition described by trait hierarchies and absolute trait differences among neighbours. Circles indicate posterior medians for each studied parameter and lines indicate 95% confidence intervals, with filled circles representing significant effects

al., 2014; Thorpe et al., 2010; Uriarte et al., 2010; Zhao et al., 2006). The question remains whether there is an optimal radius able to capture processes shaping tree communities between different forests. By using a crown-based radius, our approach is flexible and offers the possibility to make comparisons among different trees, different plots, and different forests, allowing the exploration of community assembly processes at larger scales to draw generalisations of the processes structuring tree communities. With few exceptions, investigations of the drivers of plant community structure and dynamics are mostly conducted at the plot level, even though, theoretical and empirical evidence suggest that local neighbourhood competition act together with regional scale processes (Chase & Knight, 2013; Latham & Ricklefs, 1993; Ricklefs, 2004). For example, processes such as climate interact with local neighbourhood to determine tree community structure and composition (Zambrano, Marchand, & Swenson, 2017), thus trait dispersion patterns may vary significantly with the scale of investigation.

4.2 | Trait effects on tree survival and growth varied between neighbourhood approaches

Our results suggest that effects of traits on survival and growth differ depending on the type of approach. As expected, we found the effects to be more significant for traits related to competition to light. Specifically, maximum height and wood density best described survival and growth of focal trees in the crown overlap models. Taller individuals grew faster than small statured individuals; reflecting a strong asymmetric competition as light become available. Light has been described as a limited resource that significantly affects tree survival and growth with important consequences for competition (Horn, 1971). Forest ecosystems are highly heterogeneous with local light being disproportionately available depending on the spatial location of an individual (Chazdon & Fetcher, 1984). With such considerations, an approach similar to the one used in this study seems more advantageous than using a fixed radius to describe the local

neighbourhood. In addition, individuals with denser wood experienced high survivorship compared to individuals with lighter wood. Wood density has been described as a critical component for many essential functions, such as mechanical support and nutrient storage, and high wood density is associated with slow tree growth (Chave et al., 2009; Enquist, West, Charnov, & Brown, 1999; Roderick, 2000). Thus, our results suggest a potential trade-off, not captured by the fixed-neighbourhood approach, where the allocation to radial growth to acquire physical stability occurs at the expense of vertical growth, concordant with previous findings in other tropical forests (King, Davies, Tan, & Noor, 2006; Wright et al., 2010).

In addition, our crown overlap models revealed that species sensitivity to strong density dependence led to trait-mediated hierarchical interactions for both tree survival and growth. As crowding conditions increased, individuals with denser wood and with high maximum height values were better competitors than individuals with light wood and smaller in stature. In contrast, the fixed-neighbourhood approach did not capture the effects of the functional neighbourhood on tree survival and growth. Consequently, the outcome of the models varied depending on the type of approach and led to very different conclusions on the drivers of tree community dynamics at the Luquillo forest. By including overlapping neighbours that are also taller than the focal trees, crown overlap models might be able to capture stronger competitive pressures than models using a fixed radius approach. Furthermore, when considering fixed-neighbourhood models, the strength of the functional neighbourhood on tree survival and growth varied with neighbourhood size for models including the whole community or only common species; further supporting the utility of our crown overlap approach. Furthermore, results from the crown overlap models at the community level and for only common species were more consistent than the results obtained with the fixed-radius approach, suggesting that the effects of neighbourhoods are likely to be driven by different local densities and/or sizes of conspecific or heterospecific neighbouring trees. Thus, complicating the selection of an "optimal" radius able to capture intra or interspecific competitive interactions relevant to the organization of the community. Our approach allows for describing the effects of the functional neighbourhood without having to either pre-select a fixed radius or designating an arbitrary neighbourhood size.

4.3 | Caveats and future directions

It is important to highlight that this variable-neighbourhood approach assumed that the tree crowns are centred on the stem, but in general, trees develop asymmetric crowns in order to avoid competition by neighbours (Muth & Bazzaz, 2003). The canopy structure is set by the crown sizes, shapes, and positions of the individual tree crowns that in turn determines, but also is determined by, the interactions among individual trees. This requires obtaining data at the individual level that is time consuming, and thus has been difficult to obtain in very diverse systems. Low values of crown overlapping found in this study suggest that most of the focal trees at the

Luquillo forest seem to be very exposed and potentially free from the shading of other trees. It is likely that the crowns of many trees in the Luquillo plot have idiosyncratic shapes after suffering damage during Hurricanes Hugo and Georges and uneven crown regrowth. Intense hurricanes have altered crown dimensions and overlap at Luquillo (Uriarte, Canham, Thompson, & Zimmerman, 2004), with the potential that allometric models may miscalculate crown area. Consequently, future studies should consider field verification as part of the protocol proposed for the construction of crown overlap models (see Vieilledent, Courbaud, Kunstler, Dhôte, & Clark, 2010), especially in disturbance-prone forests. Individual-based simulation models such as the perfect plasticity approximation (PPA) or SORTIE have been suggested as an alternative approach to scale individuals to stand dynamics and predict canopy structure (Purves, Lichstein, Strigul, & Pacala, 2008; Strigul, Pristinski, Purves, Dushoff, & Pacala, 2008); however, similar to our allometric approach this requires collecting detailed individual data. Further progress is needed to develop approaches to increase the accuracy of the models that account for the three-dimensional structure of tree crowns and the relative positioning of the foliage in the canopy space. Alternative approaches should also consider including the light availability index of individual crowns (see Rüger, Wirth, Wright, & Condit, 2012).

Moreover, we included only trees more or equal to 1 cm DBH; thus, it is possible that we are not capturing the full extent of competitive interaction occurring at the Luquillo forest. We expect stronger effects at the seedling stages, as early life stages might experience stronger density dependent mortality than later life stages. Negative density dependence is predicted to be stronger at early life stages, but, to date, very few functional approaches have been applied in seedling communities due to time and technical constraints. With light limiting, the photosynthetic carbon gains that ultimately affect individual survival and growth rates, we expect stronger competition in the understory, where generally only 1%–3% of the radiation above the canopy reaches the forest (Chazdon & Fetcher, 1984; Clark, Clark, Rich, Weiss, & Oberbauer, 1996). Low survival and growth rates have been reported for early life stages especially for seedlings (Kobe, 1999), suggesting light availability as an important driver of community assembly contributing to species co-occurrence patterns.

We propose that a variable-neighbourhood approach will permit comparisons among different types of forests (e.g. temperate and tropical sites) to determine whether neighbourhood-performance interactions are related to latitude. Moreover, demographic responses to environmental heterogeneity may vary significantly across life stages (Visser et al., 2016). Previous studies investigating how assembly mechanisms vary across tree ontogeny in tropical forests have found significant trait-based ontogenetic trade-offs (Lasky et al., 2015). However, the spatial scale of the effect of plant traits on tree survival may shift with ontogeny, with early stages experiencing more stress and being more sensitive than adult trees (Kitajima, Cordero, & Wright, 2013; Lasky et al., 2015; Niinemets, 2010). Due to the variation in the spatial patterns among different age classes, adopting an approach as the one described here may

more effectively capture competitive interactions that may vary with ontogenetic shifts.

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AUTHORS' CONTRIBUTIONS

This study was conceived by J.Z., W.F.F., and N.G.S.; J.Z. conducted the neighbourhood analysis; N.G.S. and S.J.W. collected tree allometric data; J.Z. wrote the manuscript; W.F.F., J.T., M.U., J.K.Z., M.N.U., and N.G.S. contributed to revisions.

DATA ACCESSIBILITY

Long-term tree data are available on the Luquillo LTER data website: <https://luq.lter.network/data/luqmetadata119> (Zimmerman, 2016), while functional trait data are available in Dryad Digital Repository: <https://doi.org/10.5061/dryad.j2r53/1> (Swenson & Umana, 2015).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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