RESEARCH ARTICLE

The scale dependency of trait-based tree neighborhood models

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Abstract

Questions: We asked: (a) whether the strength of conspecific and heterospecific neighborhood crowding effects on focal tree survival and growth vary with neighborhood radii; and (b) if the relative strength of the effect of neighborhood interactions on tree growth and survival varies with neighborhood scale.

Location: Luquillo Forest Dynamics Plot, Puerto Rico.

Methods: We used tree survival and growth data and included information on species-mean trait values related to several leaf traits, maximum height, seed mass and wood density. We incorporated a tree neighborhood modeling approach that uses an area around a focal tree with a specified radius, to describe the interactions between a focal tree and its neighbors. We constructed survival and growth models for each functional trait using a Bayesian approach, and varied the size of the radius from 5 m to 30 m, at 5-m intervals.

Results: The results suggested that the estimated effects of conspecific and heterospecific neighbors on tree performance do not vary based on the size of the neighborhood (5–30 m), suggesting that the effects of conspecific and heterospecific neighbors on the performance of a focal tree likely do not vary substantially beyond a neighborhood radius of 5 m in the Luquillo forest. In contrast, the estimated strength of the functional neighborhood (effect of neighbors based on their functional trait values) on tree performance was dependent on the neighborhood range. Our results also suggested that the effects of trait distances and trait hierarchies on tree survival and growth are acting simultaneously and at the same spatial scales.

Conclusion: Findings from this study highlight the importance of spatial scale in community assembly processes, and specifically, call for increased attention when selecting the radius that defines the neighborhood around a focal tree as the selected neighborhood radius influences the community patterns discovered, and affects the conclusions about the drivers that control community assembly.

KEYWORDS
hierarchical competition, Luquillo Forest Dynamics Plot, niche differentiation, plant functional traits, subtropical forest

1 | INTRODUCTION

Plant functional traits are increasingly used to help elucidate the drivers of forest community structure and dynamics (Suding *et al.*, 2005; McGill *et al.*, 2006; Spasojevic and Suding, 2012). They have also been used in neighborhood models for tree communities, were experimentation is not amenable, to address classic questions regarding the processes structuring communities (Uriarte *et al.*, 2010, 2016; Kunstler *et al.*, 2012; Liu *et al.*, 2016; Uriarte *et al.*, 2016). Neighborhood analyses of trait and demographic rates in plant ecology usually take one of two forms. The first is to model demographic rates given trait values of the plants, irrespective of the context in which the plants are found (Poorter *et al.*, 2008; Iida *et al.*, 2014a, b; Wright *et al.*, 2010a). The second is to model demography using individual plants and their trait values, together with the trait values of neighboring plants (Kunstler *et al.*, 2012; Lasky *et al.*, 2014; Fortunel *et al.*, 2016; Uriarte *et al.*, 2016; Zambrano *et al.*, 2017). Analyses that combine functional trait and demographic data provide a mechanistic understanding of observed patterns of community structure and dynamics, by directly investigating the critical linkages between phenotypes and the environment (McGill *et al.*, 2006). Specifically, trait-based approaches provide evidence of two distinct patterns resulting from competitive exclusion (Kraft *et al.*, 2015). As competition increases, greater differences in traits (i.e., niche differentiation), measured by distances among trait values, promote species coexistence (Kraft *et al.*, 2014; Fortunel *et al.*, 2016), and lead to high phenotypic disparity among co-occurring species (Webb *et al.*, 2002; Stubbs and Wilson, 2004). Conversely, competition may be driven by hierarchical differences (i.e., trait hierarchies) in species' competitive ability resulting in a phenotypic clustering of co-occurring species (Mayfield and Levine, 2010; Uriarte *et al.*, 2010; Kunstler *et al.*, 2012). Environmental filtering or tolerance of local abiotic conditions and competition for light leads to a functional clustering with species possessing traits associated with high fitness excluding species with unfavorable traits (Grime, 2006).

The first neighborhood models focused on focal plant responses to the species identity of neighboring individuals (Weiner, 1982; Pacala and Silander, 1985; Hubbell *et al.*, 2001; Canham *et al.*, 2004; Uriarte *et al.*, 2005), but over the past decade these models have transitioned toward quantifying neighborhood effects based upon the combined attributes (e.g., traits or relatedness) of all trees in a defined area around the focal tree (Uriarte *et al.*, 2004; Uriarte *et al.*, 2005; Uriarte *et al.*, 2010; Kunstler *et al.*, 2012; Paine *et al.*, 2012). While the exact details of the neighborhood models used in studies vary, tree-based studies often employ some type of crowding index. Crowding indices have been used as a proxy to determine the effects of competition on tree survival and growth and usually take into account the diameter of the neighboring trees and their distance from the focal tree. For example, a commonly used crowding index is a direct function of the squared diameter of the neighbors and an inverse function of the squared distances to the neighbor (Canham *et al.*, 2004).

For computational and practical reasons, the neighborhood is defined using a fixed radius around the focal individual tree (Canham *et al.*, 2004; but see Wills *et al.*, 2016). Using a fixed radius may appear suboptimal for examining neighborhood effects, but the inverse weighting by distance between trees, and the average canopy spreads of trees, could make the decision regarding the radius size inconsequential. Indeed, some studies have suggested that scale dependency does not exist in their neighborhood models (Fortunel *et al.*, 2016). Conversely, spatial analyses of forest plots that have analyzed individual species–area curves using concentric circular neighborhoods around focal trees have uncovered strong scale dependency (Wiegand *et al.*, 2007; Yang *et al.*, 2013), as have temporally static analyses of trait and phylogenetic dispersion (Swenson *et al.*, 2006; Swenson and Enquist, 2009; Kraft and Ackerly, 2010).

The scale dependency of ecological processes structuring natural communities has long been recognized (Levin, 1992; Wiens, 1989; Brown, 1995; Chase, 2014; Garzon-Lopez *et al.*, 2014). At small spatial scales, the probability of two species co-occurring may be most influenced by trait distances (MacArthur and Levins, 1967). At larger spatial scales, trait hierarchies may drive the competitive exclusion of species that are not so well suited to the environment (Kunstler *et al.*, 2012). The tendency for traits to be overdispersed among species at small spatial scales and clustered or underdispersed at larger spatial scales have been used as evidence of scale-dependent processes (Weiher and Keddy, 1995a, 2001; Weiher *et al.*, 1998). Opposing deterministic processes have been reported by static analyses of trait dispersion (Swenson and Enquist, 2009), and it may be that neighborhood models could be susceptible to the same problem. The measured effect of trait distances and trait hierarchies on community dynamics may vary greatly with the size of the area used to define the local neighborhood, but few neighborhood models address this potential scale dependency.

To examine the dependence of spatial scale on plant growth and survival in response to neighbors, we constructed neighborhood models using a Bayesian approach and demographic and functional trait tree data from the Luquillo Forest Dynamics Plot (LFDP), Puerto Rico. We hypothesized that processes driving negative density dependence of plant growth and survival in response to conspecifics and heterospecifics operate within neighborhoods smaller than 20m, as previous studies in tropical forests have shown that neighborhood effects on tree survival and growth should dissipate beyond that distance (Hubbell *et al.*, 2001b; Uriarte *et al.*, 2004, 2010; Lasky *et al.*, 2014). Hence, we predicted that strength of the effects of heterospecific neighbors' traits on the survival and growth of a focal tree, measured as trait distances, will be stronger within local neighborhoods less than 20 m radius compared with greater radii, and the strength of the effects of competitive exclusion on the survival and growth of a focal tree, measured as trait hierarchies, and analyzed using neighborhood models will be stronger in neighborhoods with larger radii (>20 m) compared with smaller radii (<20 m). Alternatively, the effects of functional neighborhood (effect of neighbors based on their functional trait values) on tree

performance might be insensitive to the choice of spatial scale used to model the neighborhood, as some studies have suggested (Fortunel *et al.*, 2016).

2 | METHODS

2.1 | Study site

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 per year. The plot has been censused approximately every five 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). Over time 150 species have been recorded in the LFDP, but in any given census the species richness is ~120 species (Hogan *et al.*, 2016). In the 20 years before the censuses used in this study, the forest experienced major hurricane disturbances in 1989 and 1998, which resulted in extraordinary temporal dynamics with tens of thousands of individuals recruiting and dying during some census intervals (Hogan *et al.*, 2016). In this study, we used relative growth rates and survival data for 22,596 individuals from a single census interval (2005–2010), which was chosen to reflect the most stable census period since the LFDP was established (at the time of this analysis), to reduce the effect of the rapid community dynamics caused by hurricane disturbances.

2.2 | Functional trait data

For this study, we used species-level functional trait data that represent the main ecological strategies for resource acquisition (Westoby *et al.*, 2002; Wright *et al.*, 2010a) and that were measured from adult trees (≥1 cm in DBH) in the Luquillo forest (Swenson *et al.*, 2012b; Swenson and Umaña, 2015; Umaña *et al.*, 2016). Leaf traits included leaf area and specific leaf area. Leaf area has been shown to strongly correlate with competitive ability for light (Bloom *et al.*, 1985), while specific leaf area is a key trait reflecting the trade-off between a leaf's lifespan and carbon capture (Westoby *et al.*, 2002; Wright *et al.*, 2004b). Other leaf traits used were nitrogen, phosphorus, and carbon content that reveal a trade-off between rapid acquisition and efficient conservation of resources (Reich *et al.*, 1997; Wright *et al.*, 2004a). Leaf N content plays a strong role in photosynthesis as the proteins of the Calvin cycle and thylakoids account for the majority of N in leaves (Evans, 1989). We also included seed mass, which is indirectly related to physiological and structural traits that influence plant survival and growth, (e.g., leaf area and photosynthetic rate (Reich *et al.*, 1992), and represents a trade-off between producing several small stress-intolerant seeds or few large stress-tolerant seeds (Coomes and Grubb, 2003; Muller-Landau, 2010). Finally,

we incorporated in our analyses wood density of stems, a critical component for many essential functions, such as mechanical support, hydraulic transport, and nutrient storage (Westoby and Wright, 2006) (also Chave *et al.*, 2009), and maximum tree height that varies across light resource gradients (Gaudet and Keddy, 1988) and with the type and frequency of disturbance events (Schamp and Aarssen, 2009). With the exception of leaf carbon content, wood density, and seed mass, trait values were log-transformed to approximate normality. All traits were then standardized across species to a mean of 0 and a standard deviation of 1 prior to the analyses.

To reduce the number and collinearity of traits we applied a principal component analysis (PCA). Traits were log-transformed for the PCA analysis. Two major axes of variation were determined in which the first axis (PC1) explained 30% of the variation and the second axis (PC2) 21% of the variation. We used the broken-stick criterion using the "PCA significance" function from the *Biodiversity* package (Kindt and Kindt, 2019) to identify the main principal components responsible for trait variation (Legendre and Legendre, 2012). The first axis was significantly associated with leaf phosphorus and nitrogen content, specific leaf area and wood density, while the second axis represented leaf area, maximum height and seed mass (see results in Appendix S1), confirming previous findings (see Díaz *et al.*, 2016). We fitted separate growth and survival models, for each functional trait and each of the two main PCA axes, as described in the next sections.

2.3 | Neighborhood survival and growth models

To examine scale-dependent effects of neighborhood crowding and plant functional traits on tree survival and growth, we constructed separate hierarchical generalized linear mixed models for each functional trait and the two main PCA axes using a Bayesian approach, as well as simpler models that only included conspecific density, heterospecific density, or initial tree DBH. We defined neighborhood radii from 5 m to 30 m from each focal tree, at 5 m intervals. We excluded from the analyses trees that were located within 30 m of the edges of the LFDP. We characterized the "neighborhood" of a focal tree in terms of the summed tree size (DBH) of conspecific and heterospecific neighbors irrespective of their trait values, and also the "functional neighborhood" in which the abundance of neighbors was calculated in terms of both their DBH size and their functional values. Due to the distinct growth pattern of the palms (Arecaceae) *Prestoea acuminata* var. *montana* and *Roystonea borinquena*, these species were not included as target trees in growth models but were incorporated as neighbors. We quantified conspecific and heterospecific competition of neighbors using a Neighborhood Crowding Index (NCI), where the negative influence of neighbors varies as a direct function of the squared diameter of the neighbor j (DBH_j) and inverse function of the squared distance to the neighbor (d_{ij}) (Uriarte *et al.*, 2010). This effect is summed over all neighbors j within the pre-defined radius around the focal individual i (separately for conspecifics and heterospecifics).

$$NCI_i = \sum_j \frac{DBH_j^2}{d_{ij}^2}$$

We calculated two separate indices of functional neighborhoods to quantify the effect of trait hierarchies (NCIH) and trait distances (NCIS) among heterospecific neighbors (Lasky *et al.*, 2014):

$$NCIH_i = \sum_j \left(F_{s[i]} - F_{s[j]} \right) \frac{DBH_j^2}{d_{ij}^2}$$

and

$$NCIS_i = \sum_j \left| F_{s[i]} - F_{s[j]} \right| \frac{DBH_j^2}{d_{ij}^2}$$

where $F_{s[i]}$ and $F_{s[j]}$ represent the values of the functional trait of interest for focal individual i and neighbor j belonging to their respective species $s[i]$ and $s[j]$. Increased neighborhood crowding may lead to a trait hierarchy that results in the competitive exclusion of inferior competitors, where the competitive advantage of the focal individual i over neighbor j will be represented by an increasing value of $F_{s[i]} - F_{s[j]}$. Similarly, increased crowding may lead to more intense competition for resources between functionally similar individuals, where the competitive effect of the focal individual i and neighbor j decreases with trait distance, measured by the absolute trait difference $|F_{s[i]} - F_{s[j]}|$. We log-transformed the NCI and NCIS to reduce the skewness of their distributions and the influence of their extreme values. Since the NCIH distribution was symmetric with extreme negative and positive values, we applied a log-modulus transformation, where the new value has the same sign as the original but the log of its magnitude (John and Draper, 1980).

Since trait distances may covary with heterospecific density, we used a null modeling approach to test whether the observed amount of functional dissimilarity among co-occurring species ($NCIS_i$), within a defined neighborhood radius, differed from what is expected when trait values were randomly assigned to species. For each trait, we created 999 random permutations of the trait values assigned to each species and used these permutations to compute a null distribution of the NCIS for each focal tree. We then transformed the original NCIS values by subtracting the mean and dividing by the standard deviation of that null distribution, resulting in the standardized effect size of NCIS (S.E.S NCIS).

For each studied radius, survival and growth were separately modeled as functions of a linear predictor z_i. We included separate fixed-effect terms for the crowding effects of conspecifics versus heterospecific neighbors, trait distances, and trait hierarchies, and included species as a random effect as follow:

$$z_i = \beta_{1s} + \beta_{2s}NCI_i + \beta_{3s}NCI_i + \beta_{4s}S.E.S\,NCIS_i + \beta_{5s}NCIH_i + \beta_{6s}DBH_i$$

where the β are species-specific coefficients representing the intercept (β_{1s}), the effect of conspecific neighborhood density (β_{2s}), the effect of heterospecific neighborhood density (β_{3s}), the effect of crowding based on standardized trait distances between heterospecific neighbors (β_{4s}), the effect of crowding based on trait hierarchies (β_{5s}), and the effect of initial tree size (DBH) (β_{6s}). To prevent confounding of the species-specific effects with inter-specific variation in mean diameter, we standardized tree size (DBH) by subtracting the species-specific mean ($\overline{DBH_s}$) from their individual initial DBH values and then log-transformed the values to reduce the skewness of their distributions. All predictor variables were scaled to a mean of 0 and a standard deviation of 1 to allow comparisons across effect sizes (R scripts related to the survival and growth models can be found in https://github.com/jzambranom/neighborhood-models/blob/master/tree-demography).

Tree growth was modeled as a linear function of z with Gaussian errors, while survival was modeled as a logistic function of z with binomial errors. The species-specific coefficient was drawn from a normal distribution modeled as a linear function of each functional trait and the two main PCA axes F_s:

$$\beta_{1s} \sim N \left(\mu_{\beta_1} + \gamma_1 F_s, \sigma_{\beta_1} \right).$$

Other species-specific coefficients (β_2 to β_6) were also drawn from a normal distribution, but did not include a trait effect. For the $\mu\beta$ and γ hyperparameters, we specified normal priors: N (mean = 0, precision = 0.01). We expressed the variance hyperparameters (the σ_b and σ_z) as precisions ($\tau = 1/s^2$) and gave the latter diffuse gamma priors: *Gamma* (shape = 0.001, rate = 0.001). We fitted all models using JAGS (Plummer, 2003) and parameter estimates and 95% credible intervals were obtained from the quantiles of their posterior distribution, using the median as a point estimate. All models were fit using Markov Chain Monte Carlo (MCMC) sampling techniques in *JAGS* 4.3.0 (Plummer, 2003) using the *rjags* (Plummer, 2016) and *runjags* (Denwood, 2016) packages.

We simulated six MCMC chains for 50,000 iterations with a burn-in period of 10,000 iterations to obtain a sufficient number of effectively independent samples from the posterior distribution. Convergence of the MCMC chains was assessed visually with traceplots and the Gelman–Rubin convergence diagnostic, ensuring values of the latter were <1.2 (Gelman and Rubin, 1992). Finally, we assessed the models' goodness of fit via posterior predictive checks. At each MCMC iteration, 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. The loss function was defined either as the sum of squared differences between the data vector and z for growth, or as the negative of the log-likelihood of the data vector given z for survival. If the model fits the observed data, the probability that the simulated loss is greater than the observed loss should be approximately 0.5. Goodness-of-fit tests were used to exclude models with poor fit. We visually inspected variograms of the model residuals, computed with the *gstat* package, to verify the absence of spatial autocorrelation of residuals between nearby trees (see example in Appendix S2). We tested for monotonic trends by computing the non-parametric Kendall correlation between effect size and neighborhood radius for traits displaying significant effects on individual tree survival and growth.

A 95% credible interval was estimated by computing the Kendall correlation from random draws from the posterior distribution of effect sizes at each radius.

2.4 | Criteria for scale dependency

We looked at whether the 95% credible interval did not include zeros for all neighborhood radii (scale-independent significant effect), some neighborhood radii (scale-dependent significant effect) or none of the neighborhood radii (insignificant effect) for model terms representing the effect of conspecifics density (NCIcons), heterospecific density (NCIhetero), trait distances (NCIS) and trait hierarchies (NCIH). We recognize that some effects may be significant at all scales, but with varying magnitude, following one of the three trends we hypothesized: the effect could be larger at the smallest (<20 m) or the largest (>20 m) neighborhood radius or show no support. Given that we only have estimates at six radii and that those estimates are not independent (each neighborhood includes all the smaller ones), we do not have sufficient power to test for all types of trends for every coefficient.

3 | RESULTS

Overall, models that included functional traits were better predictors of tree survival and growth (see results in Appendix S3), than models that included only conspecific and heterospecific density or initial size (DBH). Goodness of fit of the models did not vary much across neighborhood radii for either survival (Table S2) or growth (Table S3). Initial focal tree size (DBH) had a strong positive effect on focal tree survival and negative effect on focal tree growth, with small-sized individuals showing low survivorship (Fig. S3), but growing faster than larger individuals. Below we discuss the results of functional traits with significant effect (95% CI not crossing zero),

and the Supplementary Information (Appendix S4) includes results for all other traits studied.

3.1 | Does neighborhood radius influence the strength of conspecific and heterospecific density dependence effects on tree performance?

Conspecific density had a significant negative scale-dependent effect on focal tree survival (Figure 1a) and growth (Figure 1b), with a small effect occurring at 5 m. Heterospecific neighborhood density tended to have a positive effect on focal tree survival, but this was not significant (Figure 1a). In contrast, heterospecific density had a positive scale-independent effect on focal tree growth (Figure 1b).

3.2 | Does neighborhood radius influence the strength of the effects of the functional neighborhood on focal tree performance?

The strength of the effects of the functional neighborhood on survival of focal trees varied with neighborhood radius (Figure 2). We found evidence for a positive scale-dependent significant effect of trait hierarchies on focal tree survival. Specifically, species with higher maximum height, greatest seed mass and with bigger leaves survive better than species that are shorter in height and have small seed mass and small leaf area (Figure 2). The strength of these effects depended on the neighborhood radius, with effects being stronger at 10 m (radius around focal tree) for leaf area, 25 m for maximum height and at 30 m for seed mass when compared to other radii (Figure 2). Similarly, species with low leaf nitrogen and phosphorus content had better survival (especially at 15 m) than species with high leaf nitrogen and phosphorus content (Figure 2). Finally, high values on PC1 (i.e., plant economics) and PC2 (i.e., variation in plant size) resulted in high focal tree survival, particularly at 15 m
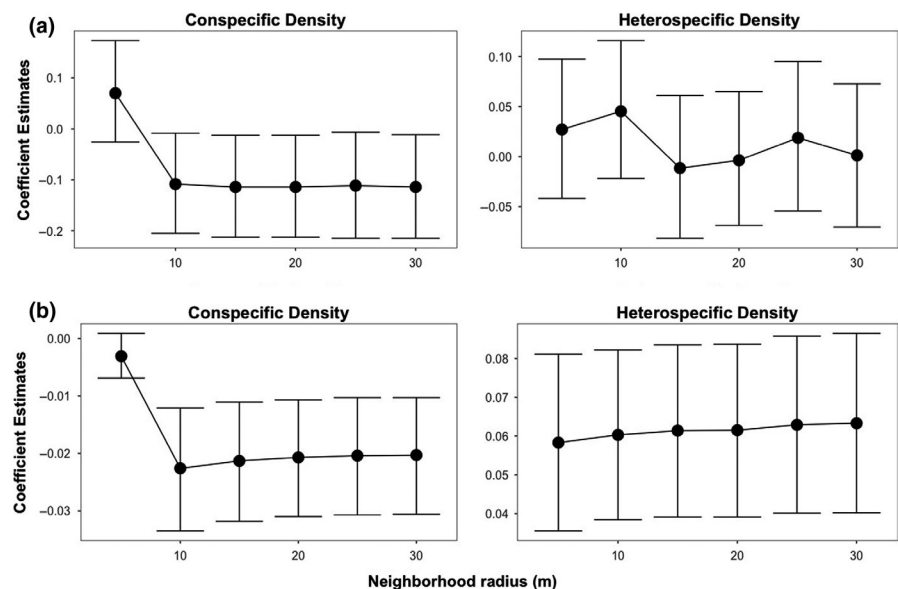

FIGURE 1 Scale-dependent significant effects of conspecific and heterospecific neighborhood on individual (a) tree survival and (b) tree growth at the Luquillo forest. Points indicate posterior medians for each studied parameter and bars represents the 95% Bayesian credible interval
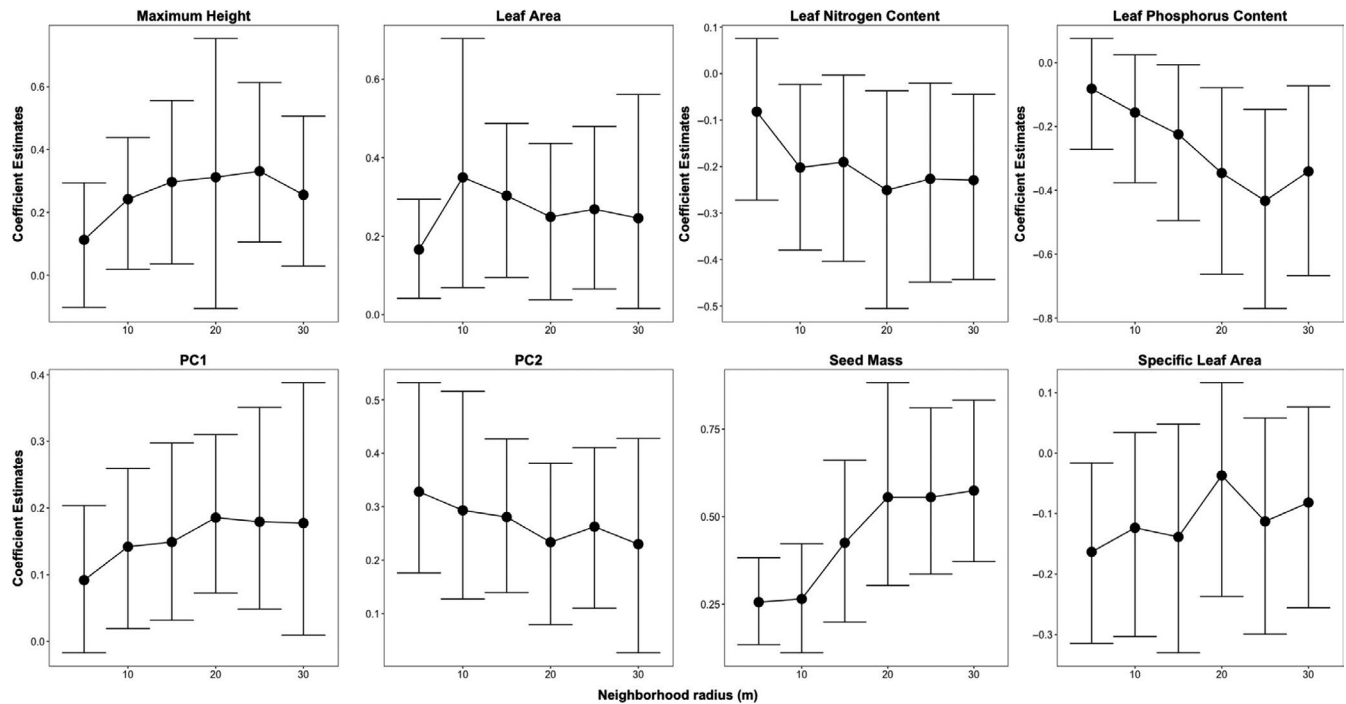
FIGURE 2 Scale-dependent significant effects of trait hierarchies on individual tree survival at the Luquillo forest. Increased neighborhood crowding led to significant trait hierarchies where individuals with high maximum tree height and leaf area values experienced better survival, with stronger effects at 25 m and 10 m respectively, when compared to other radii. Individuals with low nitrogen and phosphorus content values showed high survivorship, with stronger effects at 15 m when compared to other radii. High PC1 (plant economics) and PC2 (variation in plant size) values resulted in increased survival, particularly at 20 m and 5 m respectively. Finally, individuals with great seed mass and low specific leaf area values showed high survivorship, with stronger effects at 30 m and 20 m respectively when compared to other radii. Points indicate posterior medians for each studied parameter and bars represents the 95% Bayesian credible interval

neighborhood radius (Figure 2). Moreover, results from the Kendall correlation test showed evidence of a significant negative correlation for leaf phosphorus content, while seed mass displayed a significant positive trend (Table 1), supporting the idea of a strong scale dependency occurring for these traits.

We found evidence of a scale-dependent significant effect of trait hierarchies on focal tree growth (Figure 3). Individuals from tall species grew faster in diameter than individuals from shorter species in areas with high neighborhood density, with the strongest effect at 20 m and 30 m radii (Figure 3). Similarly, focal trees of species with greater seed mass grew faster in diameter, when compared to focal trees of species with small seeds (Figure 3), particularly at 30 m. Furthermore, higher neighborhood density led to significant trait hierarchies. Species with low nitrogen and phosphorus content experienced lower growth rates particularly in neighborhoods of 10 m radius, than species with higher values of N and P, in neighborhoods of 30 m (Figure 3). In addition, we found evidence of a significant positive trend, but only for maximum height as revealed by the Kendall correlation test (Table 1).

Significant scale-dependent effects of trait distances were found only for focal tree survival (Figure 4). When neighbors had small trait differences for leaf traits, wood density, and maximum height focal trees experienced greater survival, with stronger effects observed at 10 m for leaf nitrogen content (Figure 4), 20 m and 25 m for leaf

phosphorus content, 20 m for specific leaf area (Figure 4) and 5 m for wood density (Figure 4), when compared to other radii. However, a large difference in leaf area between focal trees and their neighbors resulted in high survivorship of the focal tree, with strong effects occurring at 20 m (Figure 4). Similarly, large differences in PC1 resulted in better survival particularly at 25 m (Figure 4). Finally, we found strong evidence of a significant positive correlation for leaf area and PC1 (Table 1).

Survival neighborhood models including 10 m and 20 m radii and leaf area revealed the combined effects of trait hierarchies and trait dissimilarity interactions (Figure 4). This was also the case for models that incorporated leaf nitrogen content and when the neighborhood radius was defined by 15 m and 30 m radii. Similarly, we found the simultaneous effects of both trait hierarchies and trait dissimilarities on tree survival when models included the first major axis of variation (PC1) and the neighborhood radius was defined by 15 m and 25 m radii (Figure 2). We found no evidence of simultaneous effects of both trait hierarchies and trait dissimilarities on tree growth.

4 | DISCUSSION

Neighborhood models have facilitated the investigation of drivers of community structure and dynamics, but often such studies

TABLE 1 Median values (with 95% credible intervals) of the Kendall correlation, a non-parametric measure of a monotonic trend, between the estimated effect of trait hierarchies (NCIH) or trait distance interactions (NCIS) and the neighborhood radius (5–30 m)

	Survival		Growth	
	NCIH	**NCIS**	**NCIH**	**NCIS**
Leaf carbon content	0.07 (−0.6, 0.73)	**0.47 (0.2, 0.73)**	−0.2 (−0.73, 0.47)	0.07 (−0.6, 0.73)
Maximum height	0.33 (−0.33, 0.73)	−0.07 (−0.47, 0.47)	**0.6 (0.2, 1)**	0.2 (−0.6, 0.73)
Leaf area	0.07 (−0.47, 0.73)	**0.6 (0.2, 0.73)**	−0.2 (−0.87, 0.47)	0.07 (−0.47, 0.73)
Leaf nitrogen content	−0.2 (−0.8, 0.6)	**0.6 (0, 1)**	−0.47 (−0.87, 0.2)	0.2 (−0.47, 0.73)
Leaf phosphorus content	**−0.6 (−0.87, −0.07)**	−0.2 (−0.6, 0.2)	−0.47 (−1, 0.33)	0.07 (−0.6, 0.73)
PC1	0.33 (−0.33, 0.87)	**0.6 (0.2, 1)**	0.2 (−0.33, 0.87)	0.2 (−0.47, 0.73)
PC2	−0.33 (−0.87, 0.47)	0.2 (−0.33, 0.73)	0.2 (−0.73, 0.47)	−0.07 (−0.6, 0.6)
Seed mass	**0.6 (0.2, 1)**	0.07 (−0.47, 0.6)	0.475 (−0.07, 1)	0.2 (−0.47, 0.73)
Specific leaf area	0.2 (−0.47, 0.73)	−0.33 (−0.73, 0.2)	−0.47 (−0.87, 0.07)	0.33 (−0.33, 0.87)
Wood density	0.2 (−0.47, 0.73)	0.47 (−0.07, 0.87)	0.47 (−0.07, 0.87)	0.07 (−0.6, 0.73)

We included functional traits showing scale-dependent significant effects on individual tree survival and growth.

Bold values represent a $p < 0.05$ showing a strong correlation between coefficients.
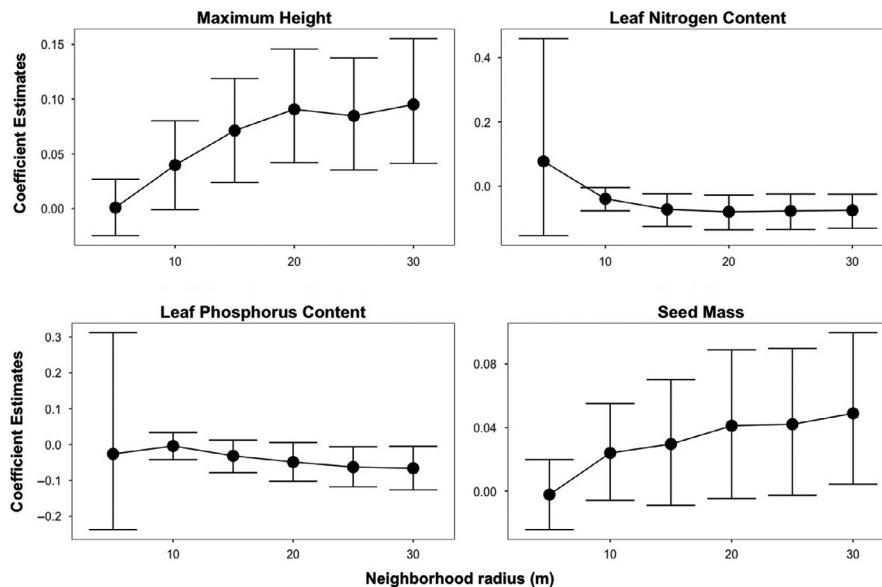

FIGURE 3 Scale-dependent significant effects of trait hierarchies on individual tree growth at the Luquillo forest. Increased crowding led to significant trait hierarchies where individuals with high maximum tree height had greater growth rates, with stronger effects at 20 m and 30 m when compared to other radii. Individuals with low nitrogen and phosphorus content experienced lower growth rates than individuals with higher values, particularly at 10 m and 30 m respectively. Finally, focal trees with greater seed mass grew faster in diameter, when compared to focal trees with small seeds, particularly at 30 m. Points indicate posterior medians for each studied parameter and bars represents the 95% Bayesian credible interval

have arbitrarily defined the local neighborhood radius, thus hampering our understanding of the spatial scales across which different mechanisms operate in different ecosystems. In our study, we investigated the variation in estimates of the effects of the local neighborhood on tree survival and growth based on neighborhood radius, density and identity of neighbors, and functional traits. Contrary to expectation, the strength of conspecific and heterospecific density on tree survival and growth was invariant with neighborhood (radii of 5–30 m). As expected, the strength of the effects of the functional neighborhood on focal tree survival and growth varied with neighborhood radius and the effects on tree survival and growth went beyond the 20 m radius. Moreover, both ecological mechanisms, i.e., environmental filtering estimated from the effects of trait distances and niche differentiation estimated from the effects of trait hierarchies, had significant effects at the same neighborhood radii. Our results strongly suggest that the choice of the neighborhood radius when analyzing neighborhood effects is critical, as different radii may lead to very different conclusions on the drivers of tree community dynamics as discussed in more detail below.
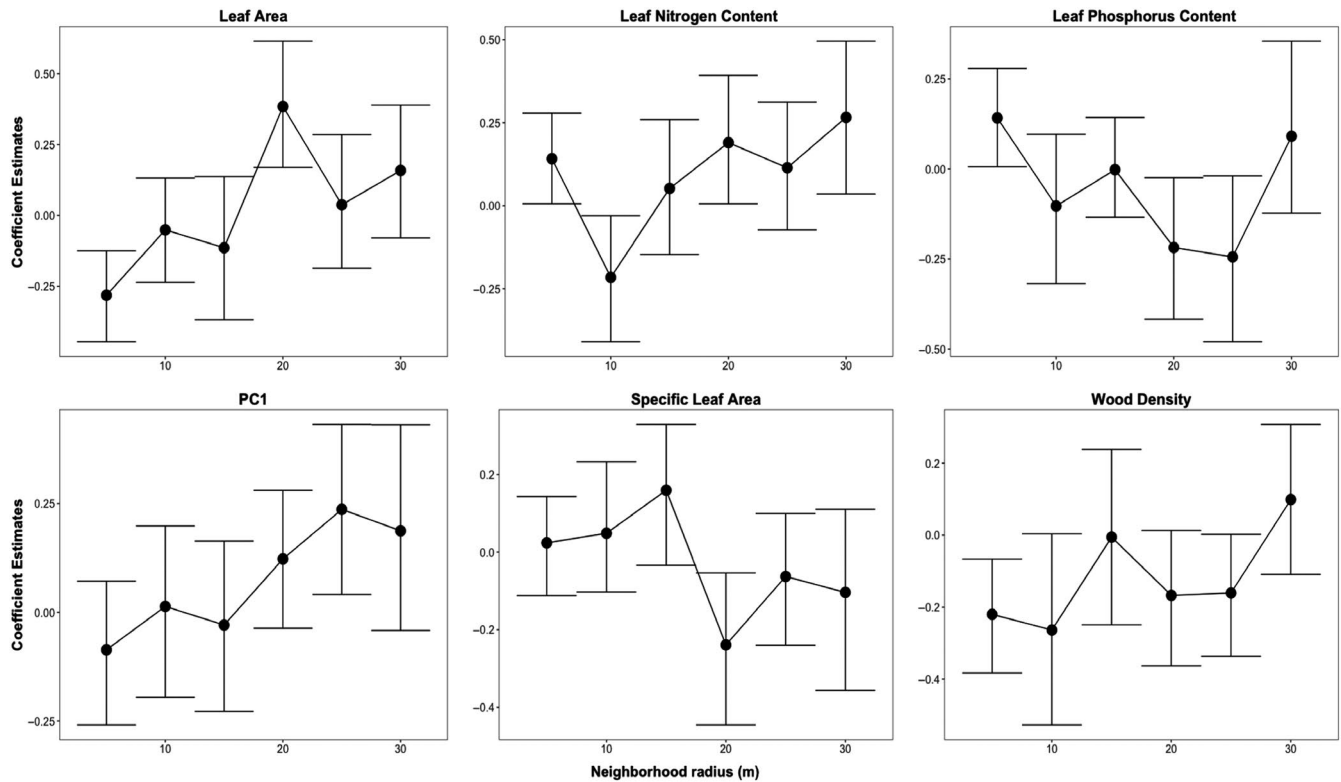
FIGURE 4 Scale-dependent significant effects of trait distances interactions (niche differentiation) on individual tree survival at the Luquillo forest. Large differences in leaf area and PC1 (plant economics) between focal trees and their neighbors resulted in high survivorship of the focal tree, with strong effects occurring at 20 m and 25 m respectively. Low trait differences with neighbors in leaf nitrogen and phosphorus content, specific leaf area and wood density were associated with high survivorship of focal trees, with overall stronger effects at 5 m, 10 m, 20 m and 25 m when compared to other radii. Points indicate posterior medians for each studied parameter and bars represents the 95% Bayesian credible interval

4.1 | Effects of neighborhood crowding and functional neighborhood on tree performance: a matter of scale

Our results show that heterospecific density-dependent effects on tree growth had overall consistent effects across the variety of neighborhood radii tested. Thus, it is likely that the link between heterospecific neighborhood density and tree growth might not be sensitive to the variation in neighborhood radius in the Luquillo forest. Furthermore, we were not able to capture the effects of conspecific density on tree survival and growth at 5 m, as previously reported (Zhu et al., 2017), and the strength of the effect did not change for larger neighborhood radii. This could be because the 5 m radius neighborhood was so narrow that the probability of encountering a conspecific neighbor was very small, especially for neighbor trees >10 cm DBH. Moreover, the probability of encountering neighbors of the same species in small neighborhoods might vary with ontogeny, with earlier stages experiencing stronger neighborhood effects at short radii. Nonetheless, it is important to note that the average negative effects of conspecifics on individual survival and growth were much larger than the average negative effects of heterospecifics across the range of neighborhood scales investigated here. Negative conspecific density dependence has been described

as a driving force controlling plant survival and growth, that ultimately shape tropical and temperate forest communities (Comita et al., 2010; Harms et al., 2000; HilleRisLambers et al., 2002; Wills et al., 2006; Johnson et al., 2012); thus our findings are consistent with previous evidence highlighting the role of density-dependent patterns in structuring forest systems. Therefore, species identity, tree size, and its ontogeny, which vary with the type of forest being studied, may be critical when defining the local neighborhood and require further study.

Furthermore, interspecific variation in key functional traits (e.g., leaf N content, SLA, WD) on tree survival and growth varied with neighborhood radius, thus exhibiting spatial dependency. For example, greater neighborhood density led to significant trait hierarchies with stronger effects at a radius larger than 20 m. Interestingly, trait differences were evidenced at radii larger than 20 m (i.e., 25 m and 30 m), contrary to our expectation that neighborhood models using small radii (<20 m) will be those best able to capture the importance of trait distances. The variation in neighborhood effects observed in this study could be related to the past land-use history and natural hurricane disturbance in LFDP. Historical land-use intensity has influenced the species and functional composition of the plot (Thompson et al., 2002) and the relative density of species with different functional traits. This resulted in greater hurricane damage in

the northern portion of the LFDP compared with the southern portion (Uriarte et al., 2004; Hogan et al., 2016) as species in the northern part were more likely to suffer hurricane damage (Zimmerman et al., 1994). Our findings that trait differences are significant at large neighborhoods suggest that the disturbance gradient across the LFDP and the resultant distribution of species across the plot with different functional traits might be reflected in the differences in scale at which the functional trait effects are captured. Thus, disturbance can potentially mediate the relationship between the local neighborhood and tree survival and growth, and is likely to be a source of spatial heterogeneity occurring at large scales (regional scale) that future studies need to consider.

4.2 | The effect of neighbors' functional traits on focal tree performance emerges at different spatial scales

Habitat filtering, leading to trait hierarchies, mainly acts at a regional scale, and selects a set of species with similar functional attributes that enable them to withstand the environmental conditions encountered by the forest community (Diaz et al., 1998; Grime, 2006). Trait hierarchies due to habitat preferences can lead to similar species co-occurring and performing better when located near to analogous neighbors (Kunstler et al., 2012). In contrast, niche differentiation, acting at small to intermediate spatial scales, prevents the co-occurrence of ecologically similar species (Weiher and Keddy, 1995b; Grime, 2006). There is growing evidence, including our study, that the observed spatial patterns of plant communities may be a combination of both processes occurring at similar scales. For example, results from an investigation into the variation in trait diversity along a stress-resource gradient suggested that both environmental filtering and local competition operated simultaneously to structure plant communities in the alpine tundra of the Colorado Rocky Mountains (Spasojevic and Suding, 2012). A strong interaction between regional-scale climate and local-scale neighborhood shaping tree communities has been described for the northeastern US and Puerto Rico (Zambrano et al., 2017). Similarly, both environmental filtering and local competition explain differences in trait axes due to habitat disturbance in grassland communities (Mason et al., 2011). In sum, results from the Luquillo forest are consistent with these previous studies and demonstrate that habitat filtering and niche differentiation effects, occurring at the same scale, are strong enough to structure forest systems.

Focal trees of species with greater maximum height experienced better survival and grew faster than small-statured focal trees. This finding emphasizes that light competition is likely to play a major role in the dynamics. Light is a directional resource resulting in an asymmetrical competition and explaining the hierarchy observed in this study. Asymmetric competition for light has been described as a major driver of community assembly of forests (Goldberg and Miller, 1990; Freckleton and Watkinson, 2001; Westoby et al., 2002; Canham et al., 2004) by exerting a constraint in species co-occurrence and reducing the opportunities for niche differentiation. Interestingly, focal trees growing with more functionally similar individuals in terms of wood density, maximum height, and specific leaf area experienced greater survival than individuals growing in more diverse neighborhoods. Wood density has been positively associated to tree survival as it is a critical component for many essential functions, such as mechanical support, hydraulic transport, and nutrient storage (Westoby and Wright, 2006; Chave et al., 2009), while SLA is related to carbon investment having a direct impact on plant survival (Wright et al., 2010b). It is possible that habitat heterogeneity, as a result of past anthropogenic disturbance and recurrent natural events (e.g., hurricanes), and recent natural disturbance might be promoting the co-occurrence of both functionally dissimilar and similar competitors at varying scales as previously suggested in this forest (Swenson et al. 2012a). Previous studies have described tree communities at the LFDP as a mix of early and late-successional species potentially as the result of an increase in light in the understorey after Hurricane George, allowing more pioneer species to grow (Zimmerman et al., 2010; Hogan et al., 2016, 2018; Uriarte et al., 2018). Habitat heterogeneity along with species habitat preferences have been described as important factors determining the spatial distribution of tree species in forest systems (Chen et al., 2010; Harms et al., 2001; John et al., 2007; Shen et al., 2013).

4.3 | How do we improve local neighborhood models?

As neighborhood models become more popular in our efforts to understand functional and community ecology, a pressing question is: how do we deal with the scale dependency of these models? As explored in this study, one could select a range of pre-determined radii, repeat the analyses for each radius and report the functional sensitivity to scales. While this is possible for small-scale data, this option is computationally intensive and inefficient for large-scale forest plots with many trees. This might also complicate comparisons among forests as the most useful scale may be different for forests with different scales of environmental heterogeneity, vegetation structure, and species composition, rendering generalizations of the processes structuring tree communities very difficult. Furthermore, the radius of importance may be tree species- and size-specific depending not only on the canopy and root system of the focal tree, but also on the canopy and root systems of the neighbors. Ideally, we would want to define a metric that describes the local neighborhood without having to pre-select the radius. Tree survival and growth are greatly affected by the light environment experienced by individual trees, which ultimately depends on the crown structure (Horn, 1971). An alternative to pre-selecting a radius is to include only those neighboring individuals that have overlapping or interwoven crowns with the focal individual and to include the magnitude of that overlap in the crowding index. In a previous study conducted at the LFDP (see Zambrano et al., 2019), we found that models including crown overlap had better support than models that incorporated

a fixed radius. Furthermore, we reached different conclusions depending on the type of approach, with respect to the drivers affecting plant performance and subsequent forest dynamics. Therefore, the use of models that integrate information of crown overlap provides a mechanistic, computationally rational and direct approach for characterizing and analyzing tree neighborhood.

Other potential alternatives are spatial point pattern methods that have been broadly used in ecology to determine spatial patterns and test hypothesis related to processes structuring plant communities. A large number of methods for the analysis of spatial point pattern have been developed, such as the pair-correlation function (Illian *et al.*, 2008; Stoyan and Stoyan, 1994), the distribution function of nearest-neighborhood distance (Diggle *et al.*, 2003), Ripley's *K*-function (Ripley, 1976) or an equal-area annulus method (Wills *et al.*, 2016). For example, spatial point analysis has been used to describe the combined effects of habitat heterogeneity and non-habitat clustering processes (e.g., dispersal limitation) and, therefore, permits the quantification of the spatial correlation structure of a pattern over a range of distance scales of tree species in tropical and temperate forests (Shen *et al.*, 2013; Wang *et al.*, 2011). However, most ecological studies using spatial point patterns are static and rarely incorporate trait or demographic information. Thus, analyses that include both the advantages of point pattern methods and neighborhood models would greatly improve our understanding of spatial patterns structuring tree communities.

5 | CONCLUSION

Scaling has long been recognized as a major challenge and opportunity in ecology (Levin, 1992). Identifying spatial structures is a key step toward an improved understanding of the ecological processes that explain species diversity and distribution patterns (Legendre and Fortin 1989). The findings from our study clearly call for more attention to the choice of the radius size encompassing a neighborhood, as the interpretation of the relative importance of the functional neighborhood on tree survival and growth is prone to differences in neighborhood radius. Our results indicate that interspecific effects are relative stable at spatial scales >5 m, but are likely stronger and more variable at scales <5 m. Therefore, our findings suggest that inferences drawn in previous work utilizing a single spatial definition of a neighborhood may be biased by not accounting for the variation in the effects of functional traits on tree survival and growth as these are dependent on the size of the neighborhoods. The neighborhood radius affects the processes driving community assembly and may be different in each forest. Furthermore, the effects of functional neighborhood in each studied forest will vary with habitat heterogeneity such as the abiotic environment (e.g., topography and soil moisture), the land-use history and natural disturbances. Thus, conclusions drawn from neighborhood models will be context-dependent. A potential alternative to the scale dependency exhibited by current neighborhood models are approaches that do not depend on a pre-defined single radius. These may provide a more mechanist understanding of the drivers controlling community assembly and allow comparisons across different forests to describe more general patterns.

AUTHOR CONTRIBUTIONS
This study was conceived by JZ. JZ and PM conducted the neighborhood analysis. JZ wrote the first draft and all authors contributed significantly to the final version of the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Results of the principal component analysis of plant functional traits

Appendix S2. Example of a variogram to verify absence of spatial autocorrelation of residuals between nearby trees

Appendix S3. Goodness of fit for tree survival and growth neighborhood models

Appendix S4. Plots depicting effects of each individual trait and initial size on tree survival and growth