

Positive effects of neighborhood complementarity on tree growth in a Neotropical forest

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Abstract. Numerous grassland experiments have found evidence for a complementarity effect, an increase in productivity with higher plant species richness due to niche partitioning. However, empirical tests of complementarity in natural forests are rare. We conducted a spatially explicit analysis of 518 433 growth records for 274 species from a 50-ha tropical forest plot to test neighborhood complementarity, the idea that a tree grows faster when it is surrounded by more dissimilar neighbors. We found evidence for complementarity: focal tree growth rates increased by 39.8% and 34.2% with a doubling of neighborhood multi-trait dissimilarity and phylogenetic dissimilarity, respectively. Dissimilarity from neighbors in maximum height had the most important effect on tree growth among the six traits examined, and indeed, its effect trended much larger than that of the multi-trait dissimilarity index. Neighborhood complementarity effects were strongest for light-demanding species, and decreased in importance with increasing shade tolerance of the focal individuals. Simulations demonstrated that the observed neighborhood complementarities were sufficient to produce positive stand-level biodiversity–productivity relationships. We conclude that neighborhood complementarity is important for productivity in this tropical forest, and that scaling down to individual-level processes can advance our understanding of the mechanisms underlying stand-level biodiversity–productivity relationships.

Key words: *biodiversity and ecosystem functioning; complementarity; individual-based method; neighborhood dissimilarity; phylogeny; plant functional trait; productivity; shade tolerance.*

INTRODUCTION

The accelerating loss of biodiversity has focused attention on the relationship between biodiversity and ecosystem functioning (Hooper et al. 2005, Loreau 2010, Cardinale et al. 2012). More than 400 experiments have been conducted to study the relationship between primary producer diversity and productivity, a fundamental ecosystem function (Cardinale et al. 2011). Most of these experiments found positive biodiversity–productivity relationships. The complementarity effect, which arises from niche differentiation or facilitation (Loreau and Hector 2001), was proposed as a key mechanism for the positive biodiversity–productivity relationships. Experimental tests in grasslands and microcosms have provided considerable evidence for complementarity (Cardinale et al. 2011); however, empirical tests of complementarity in forests are rare (Ruiz-Benito et al. 2014, Jucker et al. 2015), and tests in tropical forests are entirely lacking.

Studies of biodiversity–productivity relationships in natural forests have used quadrat-based methods to analyze the relationships of spatial variation in diversity to productivity (Chisholm et al. 2013, Ruiz-Benito et al. 2014). Although quadrat-based methods provide a direct characterization of the shape of the biodiversity–productivity relationship, the use of quadrats as the unit of analysis inevitably obscures factors operating at spatial scales smaller than the chosen quadrat size (e.g., spatial distribution of tree sizes and species identities within quadrats). In sessile forest trees, the potential for niche complementarity is expected to be restricted to interactions among near neighbors (Weiner 1990).

Individual-based methods can overcome this limitation of quadrat-based methods. Individual-based methods use a regression-based framework that explicitly incorporates neighborhood spatial structure (e.g., Uriarte et al. 2004, 2010, Lasky et al. 2014). Importantly, individual- or species-level effects identified by individual-based methods can be scaled up to the stand level through simulations that quantify and distinguish the potential consequences for productivity of complementarity and selection mechanisms (i.e., niche

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differentiation among neighboring species vs. sampling species with specific traits). Individual-based methods have been used to link interactions among individuals with stand-level diversity effects in plantations (Sapjanskas et al. 2013), but this approach has not yet been applied in natural forests.

The complementarity effect can be evaluated at the neighborhood scale using individual-based methods. The independent variable of interest is a measure of the niche similarity of neighbors to the focal individual. Trait and phylogenetic similarities are frequently used as surrogates for niche similarity and the relative strength of interspecific interactions (Uriarte et al. 2010, Paine et al. 2012, Lasky et al. 2014, Lebrija-Trejos et al. 2014). Key functional traits are associated with resource acquisition and natural enemy defense (Augspurger and Kelly 1984, Coley and Barone 1996, Westbrook et al. 2011), and many important plant functional traits are phylogenetically conserved (Swenson et al. 2007, Lebrija-Trejos et al. 2014). Evolutionarily related plant species also share natural enemies (Gilbert et al. 2012) and have similar germination and early survival niches (Burns and Strauss 2011). Thus, focal trees living with more dissimilar neighbors are expected to suffer less from resource competition or natural enemy attack and thereby achieve higher productivity.

We defined this phenomenon as neighborhood complementarity to distinguish it from stand-level complementarity, which measures the average difference between species' yields observed in monoculture and in mixture (Loreau and Hector 2001). Stand-level complementarity represents the net balance of all biological processes that influence biomass and, for this reason, could be a weak indicator of the existence of niche differentiation (Cardinale et al. 2011). In contrast, neighborhood complementarity measures niche partitioning more directly by explicitly assessing how functional or evolutionary dissimilarity among neighboring individuals affects their performance.

The strength of neighborhood complementarity may vary with life history strategies. For example, species varying in shade tolerance often have different sensitivities to natural enemies, with light-demanding species being more vulnerable to insects and pathogens (Augspurger and Kelly 1984, Coley and Barone 1996, McCarthy-Neumann and Kobe 2008). We expected that these differences in natural enemy susceptibility would make light-demanding species more susceptible than shade-tolerant species to neighborhood species composition changes (Comita et al. 2010, Kobe and Vriesendorp 2011). Thus, we hypothesized that light-demanding species would benefit more from neighborhood complementarity than shade-tolerant species.

In this study, we quantified neighborhood complementarity in woody productivity to establish a more mechanistic basis for biodiversity–productivity relationships in natural forests. Specifically, we predicted that

(1) an individual tree's growth benefits from greater dissimilarity to its neighbors due to niche partitioning, i.e., there is a positive neighborhood complementarity effect on individual growth, (2) the strength of this effect is stronger for light-demanding species than for shade-tolerant species, and (3) neighborhood complementarity is sufficient to produce a positive stand-level biodiversity–productivity relationship. To test these hypotheses, we analyzed 518 433 growth records for 274 species from a 50-ha tropical forest plot. We used these data to construct individual-based models to assess how neighborhood dissimilarity, measured as functional trait and phylogenetic differences between focal trees and neighbors, affects focal tree growth and stand-level wood production.

MATERIALS AND METHODS

Study site

This study was conducted using 1990, 1995, 2000, 2005, and 2010 census data from a 50-ha plot of lowland moist tropical forest located on Barro Colorado Island (BCI), Panama (9°10' N, 79°51' W) (Condit 1998, Hubbell et al. 1999, 2005). In each census, all free-standing woody stems ≥ 1 cm diameter at breast height (DBH) were tagged, mapped, identified to species and measured in diameter using standardized methods (Condit 1998).

Growth rates

For every plant alive in the 1990, 1995, 2000, and 2005 censuses, we identified its neighbors within a radius of 30 m. The 30-m cut-off was chosen because previous research at this forest found that neighborhood conspecific effects were insignificant beyond 30 m (Hubbell et al. 2001). We also used other neighborhood cut-offs (20 and 25 m) in preliminary analyses, with qualitatively similar results (Appendix S2: Figs. S2 and S3). To avoid edge effects, plants < 30 m from the plot edge were excluded as focal plants. For each census interval, we calculated the annual absolute diameter growth of every focal individual. We discarded the cases where a tree (1) was measured at a different height in two consecutive censuses; (2) had its main stem broken and the resprouted stem measured instead; (3) grew at a rate > 75 mm in diameter per year (presumed measurement errors); (4) was a hemiepiphytic or palm species; or (5) had multiple stems. This produced a data set containing 518 452 growth records for 191 630 individuals of 278 species.

Neighborhood dissimilarities

For each growth record, we calculated the weighted average phylogenetic dissimilarity of each focal individual to its neighbors at the start of the relevant

census interval. Larger and spatially closer neighbors were expected to have a greater influence (Uriarte et al. 2010), so we calculated the average neighborhood phylogenetic dissimilarity by weighting pairwise phylogenetic distance by neighbor tree basal area and inversely by spatial distance. We used a DNA barcode phylogeny of 270 species (Kress et al. 2009), which lacked eight of the species present in this analysis. We attached four of the eight missing species to the phylogeny as polytomies at the genus level. The four remaining species absent from the phylogeny were rare and represented <0.01% of the overall growth records. Phylogenetic distance was assessed as the cophenetic distance in the phylogenetic tree, and has units of millions of years. If a neighbor's phylogenetic information was absent (about 0.01% of neighbors), we set its phylogenetic distance to the focal tree as the average phylogenetic distance of the other individuals to the focal tree in that neighborhood community. We excluded the 19 focal individuals whose phylogenetic information was absent from the phylogenetic dissimilarity analysis, leaving 518 433 growth records covering 274 species.

We also calculated the weighted average functional dissimilarity from a focal individual to its neighbors at the start of each census interval. To facilitate comparisons of neighborhood phylogenetic and trait dissimilarity effects on growth, we dropped the four species whose phylogeny data were missing, and used the trimmed data in the subsequent trait dissimilarity analyses. Eight functional traits were initially included in the analysis: maximum tree height, leaf mass per area, leaf nitrogen content, leaf area, wood density, leaf tissue density, leaf dry matter content, and leaf lamina toughness (Appendix S1: Table S1). These traits are thought to be closely related to resource acquisition and/or natural enemy defenses (Augsburger and Kelly 1984, Coley and Barone 1996, Westbrook et al. 2011). We removed collinearity among these traits by sequentially deleting the trait variable with the largest variance inflation factor until all remaining variables had variance inflation factors <2 (Dormann et al. 2013). Leaf mass per area and leaf dry matter content were removed in this process, leaving six traits in the subsequent analyses (Table A2 presents the pairwise correlations among these six traits). We substituted the mean value of the next higher taxonomic level for missing species because the six remaining traits are all phylogenetically conserved in this forest (Lebrija-Trejos et al. 2014). Leaf area was highly right skewed so we used its log-transformed values. To calculate trait distance, we first standardized each trait (to mean zero and unit standard deviation), and then calculated the pairwise Euclidean distances between focal trees and their neighbors in standardized multivariate trait space (Paine et al. 2012). Finally, we obtained the average neighborhood trait dissimilarity by weighting the pairwise trait distance by neighbor tree basal area

and inversely by spatial distance. To better understand the relationship between neighborhood trait dissimilarity and individual growth, we also used each standardized trait separately to calculate single-trait based dissimilarity indices.

To test whether neighborhood complementarity might be driven purely by the negative effects of conspecifics, we calculated neighborhood dissimilarity indices both with and without conspecifics. We refer to the indices without conspecifics as heterospecific dissimilarity indices.

Shade tolerance

We characterized the shade-tolerance of each species based on the mean growth and mortality rates for smaller individuals, following Comita et al. (2010). We first log-transformed the mean mortality and growth rates of saplings and poles reported in Condit et al. (2006). Then we conducted a principal components analysis on the transformed growth and mortality rates for the 191 species present in our analysis. The first axis explained 72.56% of overall variation. We use this axis to define a shade-tolerance index, oriented so that more positive values were associated with slower growth, lower mortality, and greater shade-tolerance (Appendix S3: Fig. S1).

Neighborhood dissimilarity effects on tree growth

We constructed a three-level hierarchical Bayesian model to assess neighborhood dissimilarity effects on tree growth. At the first level, we assumed the observed annual growth rate (Obs.AGR) was subjected to two types of measurement errors (Rüger et al. 2011): the size dependent error caused by slightly different placement of measurement tools, and the size independent error due to recording errors. These errors were fitted as a normal mixture distribution (Eq. 1a),

$$\text{Obs.AGR}_{ij} \sim (1-f) \times N \left(\text{True.AGR}_{ij}, \frac{\text{SD}_1}{\text{int}_i} \right) + f \times N \left(\text{True.AGR}_{ij}, \frac{\text{SD}_2}{\text{int}_i} \right) \quad (1a)$$

where Obs.AGR_{ij} and True.AGR_{ij} are the observed and true growth rate of focal tree *i* of species *j*, respectively; and SD₁ and SD₂ represent the size-dependent and size-independent error components affecting 97.3% (1 - *f*) and 2.7% (*f*) of the observations, respectively (Rüger et al. 2011). Each type of measurement error was scaled by the census interval (int_{*i*}). This error distribution was fitted by Rüger et al. (2011) using 1562 remeasured DBHs from this forest, and was entered as a fixed prior in our model.

At the second level, we modeled the true growth rate as a power function of initial DBH, neighborhood

crowding (NC), and neighborhood dissimilarity (ND), with normally distributed random effects (RE) for individual, census interval, and 10 × 10 m quadrat (Eq. 1b)

$$\log(\text{True.AGR}_{i,j}) \sim N(\beta_{0,j} + \beta_{1,j} \times \log(\text{DBH}_{i,j}) + \beta_{2,j} \times \log(\text{NC}_{i,j}) + \beta_{3,j} \times \log(\text{ND}_{i,j}) + \text{RE}, \sigma_p) \quad (1b)$$

where $\log(\text{True.AGR}_{i,j})$, $\log(\text{DBH}_{i,j})$, $\log(\text{NC}_{i,j})$, and $\log(\text{ND}_{i,j})$ represent the log-transformed true growth rate (mm/yr), initial DBH (mm), neighborhood crowding, and weighted average neighborhood phylogenetic or trait dissimilarity of focal tree i of species j , respectively, and σ_p represents the process error. We used the power function in this study because (1) previous research from this forest found that the growth–DBH relationship of most species followed power functions (Rüger et al. 2012); (2) application of log transformations led residuals to be more normally distributed; and (3) the probability two plant species share a pest species decreases approximately exponentially with their phylogenetic distance (Gilbert et al. 2012). We standardized each independent variable to mean zero and unit standard deviation to speed up convergence and to facilitate comparison of the relative importance of the different explanatory variables. We calculated NC for each focal tree based on the size and spatial distance of its neighbors within 30 m

$$\text{NC}_i = \sum_{m=1, m \neq i}^M \frac{\text{BA}_m}{\text{Dist}_{i,m}} \quad (1c)$$

where $\text{Dist}_{i,m}$ is the spatial distance between focal tree i and its neighbor tree m , BA_m is the basal area of neighbor tree m (mm²), and there are M total neighbors.

At the third level, we modeled the species-level parameters ($\beta_{0,3,j}$) from Eq. 1b as the sum of the community-wide average effect ($\beta_{0,3}$) and the normally distributed random effect for species j (ϵ_j):

$$\beta_{k,j} = \beta_k + \epsilon_j, \quad k=0,1,2,3. \quad (1d)$$

Neighborhood complementarity strength and shade tolerance relationships

We constructed another three-level hierarchical Bayesian model using data for the 191 species that had shade tolerance information so that we could assess the relationship between focal species’ shade tolerance and neighborhood complementarity strength. The first- and second-level models were the same as Eq. 1a and 1b. At the third level, we modeled the species-level parameters ($\beta_{0,3,j}$ Eq. 1b) as a linear function of the shade tolerance index (ST_{*j*}) of focal species j with normally distributed error $\sigma_{0,3}$

$$\beta_{k,j} \sim N(\alpha_k + \gamma_k \times \text{ST}_j, \alpha_k), \quad k=0,1,2,3. \quad (2)$$

where α_k and γ_k were the intercept and the slope, respectively.

These analyses were repeated for neighborhood phylogenetic dissimilarity, trait dissimilarity, heterospecific phylogenetic dissimilarity, and heterospecific trait dissimilarity indices.

We used diffuse prior distributions for all parameters (see Supplement for JAGS code), and estimated the parameters using Markov chain Monte Carlo (MCMC) sampling techniques in JAGS 3.4.0 using the *rjags* package (Plummer 2014). We ran three parallel chains with different initial values, and used Gelman and Rubin’s convergence diagnostics (with a threshold value <1.1) in the *coda* package (Plummer et al. 2006) to detect parameter convergence.

To compare how shade-tolerant species and light-demanding species respond to overall and heterospecific neighborhood dissimilarity indices, we did a linear analysis using the response difference and the shade tolerance index as response and explanatory variables, respectively. The response difference was calculated as the mean difference between the sampled posteriors of the overall and heterospecific neighborhood dissimilarity coefficients ($\beta_{3,j}$ in Eqs. 1b and 2) for each species j . The linear relationships were fitted by inversely weighting the standard deviation of the response difference.

Stand-level biodiversity–productivity relationships

We performed simulations to evaluate the consequences of the identified neighborhood complementarity for stand-level biodiversity–productivity relationships. We first fitted species-level parameters simultaneously by using the three-level Bayesian models (Eqs. 1a, 1b and 1d) in which Eq. 1b was modified by replacing $\log(\text{ND}_{i,j})$ with $\log(\text{ND}_{i,j} + 1)$

$$\log(\text{True.AGR}_{i,j}) \sim N(\beta_{0,j} + \beta_{1,j} \times \log(\text{DBH}_{i,j}) + \beta_{2,j} \times \log(\text{NC}_{i,j}) + \beta_{3,j} \times \log(\text{ND}_{i,j} + 1) + \text{RE}, \sigma_p). \quad (3)$$

In this way, we can predict individual growth rates in monoculture by setting $\text{ND}_{i,j} = 0$. The distributions of $\log(\text{ND}_{i,j} + 1)$ and $\log(\text{ND}_{i,j})$ were similar. Furthermore, species-level parameters fitted using $\log(\text{ND}_{i,j} + 1)$ were also similar to those obtained from the main models using $\log(\text{ND}_{i,j})$ (Appendix S4: Fig. S1).

We then sampled one 160 × 160 m area from the 2005 census. (We limited our simulations to this 2.56-ha area instead of the entire 50-ha plot to reduce runtime.) We simulated a series of monoculture and polyculture communities over this area by manipulating species identities of live individuals while preserving their original locations and sizes. For each monoculture, we set all the trees as the same species. In this way, we obtained 274 different monocultures. The polyculture simulations differed in species richness (2,

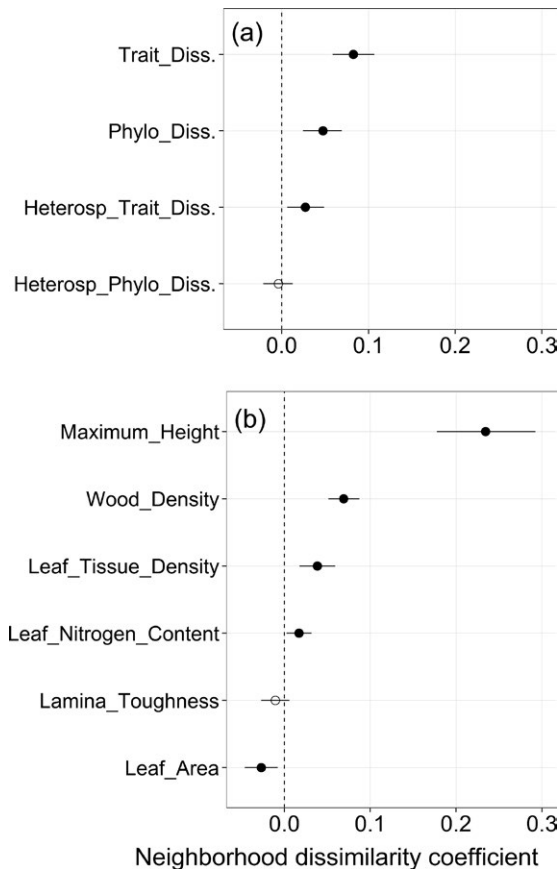


FIG. 1. Standardized slope coefficients of different neighborhood dissimilarity indices. Panel (a) shows the coefficients of neighborhood trait dissimilarity (Trait_Diss.), phylogenetic dissimilarity (Phylo_Diss.), heterospecific trait dissimilarity (Heterosp_Trait_Diss.), and heterospecific phylogenetic dissimilarity (Heterosp_Phylo_Diss.). Both Trait_Diss. and Heterosp_Trait_Diss. were calculated using the six traits together. Panel (b) shows the coefficients of single-trait-based neighborhood dissimilarity indices. Circles show the means and 95% credible intervals of the coefficients, respectively (solid circles indicate statistically significant effects if the 95% credible intervals excluded zero).

4, 8, 16, 32, 64, 128, and 256 species for which Bayesian models had been parameterized). For each polyculture, we randomly selected the desired number of species and randomly assigned these species identities to individuals with equal probability. We simulated 500 different polycultures (species compositions) for each species richness level. Overall we established 4274 virtual communities for both the phylogenetic and trait dissimilarity simulations.

After establishing the communities, we selected individuals >30 m away from the edge as focal trees, and calculated neighborhood crowding and neighborhood phylogenetic dissimilarity and trait dissimilarity for each focal tree. To estimate the relative importance of complementarity and selection mechanisms for biodiversity–productivity relationships, we calculated focal tree growth rate in three different scenarios with the simulated

community conditions and the coefficients estimated using Eq. 3 (but excluding random effects for individual, census interval, and quadrat when calculating individual growth rates) and the full data set (Appendix S4: Fig. S1). (1) Selection mechanism only: simulated focal tree growth was calculated by setting $\beta_{3,j}$ to 0 in Eq. 3. Community productivity differences thus would result only from sampling species with different intrinsic growth rates and different responses to initial size and shading, with no niche partitioning among neighbors. (2) Complementarity mechanism only: focal tree growth was calculated by setting $\beta_{0,j}$, $\beta_{1,j}$ and $\beta_{2,j}$ to their community-level average values while retaining species differences in $\beta_{3,j}$. Community productivity differences thus would be produced exclusively by niche partitioning, with no impact of species differences in growth. (3) Both complementarity and selection mechanisms: focal tree growth was calculated using Eq. 3 in its entirety. In all scenarios, we calculated community productivity as the summed basal area growth of all focal trees. Finally, we attained the 95% confidence interval of the median productivity by bootstrapping the simulated productivities at each species richness level 10 000 times. We retained exactly 1 ha of focal trees after eliminating trees within 30 m of the edge.

RESULTS

We found positive neighborhood complementarities, consistent with our predictions. Both neighborhood trait and phylogenetic dissimilarities were significantly positively related to tree growth (Fig. 1a). After back-transforming the standardized coefficients ($\frac{\text{standardized coefficient}}{\text{standard deviation}}$, standard deviations for trait and phylogenetic dissimilarities were 0.171 and 0.112, respectively), the mean effect sizes for trait and phylogenetic dissimilarities were 0.483 and 0.424, meaning that doubling trait or phylogenetic dissimilarities increased diameter growth by an average of 39.8% and 34.2%, respectively (calculated as $2^{0.483} - 1$ and $2^{0.424} - 1$). Initial DBH and neighborhood crowding had significant positive and negative effects on growth, respectively, with effect sizes that were more than double those of neighborhood dissimilarities (Appendix S2: Fig. S1)

When neighborhood dissimilarity indices were calculated without conspecifics, their effects on tree growth decreased, with a significant positive effect for heterospecific trait dissimilarity and an insignificant effect for heterospecific phylogenetic dissimilarity (Fig. 1a). The back-transformed mean effect size for heterospecific trait dissimilarity was 0.174, meaning that doubling heterospecific trait dissimilarity increased diameter growth by an average of 12.8% ($2^{0.174} - 1$).

Four of the single-trait-based trait dissimilarity indices had significant positive effects on growth: maximum height, wood density, leaf tissue density, and leaf nitrogen content (Fig. 1b). Among the six traits, maximum height had the most important effect on growth.

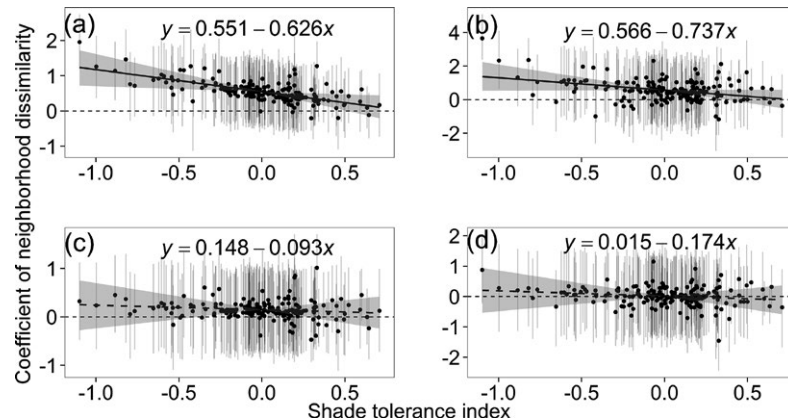


FIG. 2. Relationships between shade tolerance and species-level coefficients of (a) neighborhood trait dissimilarity, (b) phylogenetic dissimilarity, (c) heterospecific trait dissimilarity, and (d) heterospecific phylogenetic dissimilarity. Points and gray lines indicate the means and 95% credible intervals of species-level neighborhood dissimilarity coefficients. Black lines show the fitted relationships between shade tolerance and neighborhood dissimilarity coefficients, with solid lines indicating significant (a) or marginally significant (b) effects, and dashed lines representing insignificant effects. Shaded areas show the 95% credible intervals of the slope coefficients.

Its effect trended much larger than that of the multi-trait index (Fig. 1) and even approached that of initial size (Appendix S2: Fig. S1). Leaf area dissimilarity had a significant negative effect on tree growth (Fig. 1b), contrary to our prediction.

The species-level trait and phylogenetic dissimilarity effects were significantly and marginally significantly negatively related to shade tolerance, respectively (Fig. 2 and Appendix S6: Fig. S1), meaning that light-demanding species had stronger positive neighborhood complementarity effects. In contrast, the relationships between shade tolerance and species-level heterospecific phylogenetic and trait dissimilarity effects were weak and not statistically significant (Figs. 2 and Appendix S6: Fig. S1). Response differences between overall (including both conspecifics and heterospecifics) and heterospecific neighborhood distance were significantly negatively related to shade tolerance (Appendix S6: Fig. S1). Shade tolerance had significant negative effects on species-level intrinsic growth ($\beta_{0,j}$ in Eqs. 1b and 2; Appendix S6: Fig. S1), indicating faster growth for light-demanding species. Shade tolerance was significantly positively related to the neighborhood crowding effect ($\beta_{2,j}$ in Eqs. 1b and 2; Appendix S6: Figs S1 and S2), meaning that light-demanding species were more negatively affected by neighborhood crowding. Initial size effects ($\beta_{1,j}$ in Eqs. 1b and 2) increased with shade tolerance (Appendix S6: Figs S1 and S3), meaning that the growth rates of shade-tolerant species increase faster with size.

Our simulations showed that the identified neighborhood complementarities lead to strong positive stand-level biodiversity–productivity relationships. Species richness and simulated productivity showed weak positive relationships when only the selection mechanism was present (i.e., when tree species differ in intrinsic growth parameters but there is no effect

of neighborhood dissimilarity on growth, Figs. 3c,f and Appendix S7: Fig. S1), but showed strong positive relationships when only the complementarity mechanism was present (i.e., neighborhood dissimilarity affects tree growth but there are no species differences in intrinsic growth parameters; Figs. 3b,e and Appendix S7: Fig. S1). When both complementarity and selection mechanisms were present (Figs. 3a,d and Appendix S7: Fig. S1), the positive biodiversity–productivity relationships were stronger and the simulated productivities in mixtures were higher than the corresponding mixture productivities with either mechanism in isolation.

DISCUSSION

We analyzed a long-term data set from a 50-ha tropical forest plot using spatially explicit individual-based methods to evaluate neighborhood complementarity and its consequences for stand-level biodiversity–productivity relationships. We found significant positive relationships between tree growth and neighborhood multi-trait dissimilarity and phylogenetic dissimilarity, demonstrating neighborhood complementarities (Fig. 1a). Hubbell (2006) previously tested for a relationship between quadrat species richness and total quadrat basal area (a proxy for biomass) in this forest, and reported essentially no relationship, a finding he interpreted in terms of lack of niche complementarity. We argue that niche complementarity is fundamentally about productivity, which is not necessarily positively related to standing biomass in forests. Indeed, local variation in biomass within old growth forests depends mostly on local disturbance history (i.e., time since the last gap formation event). A subsequent quadrat-based analysis of the relationship between species richness and

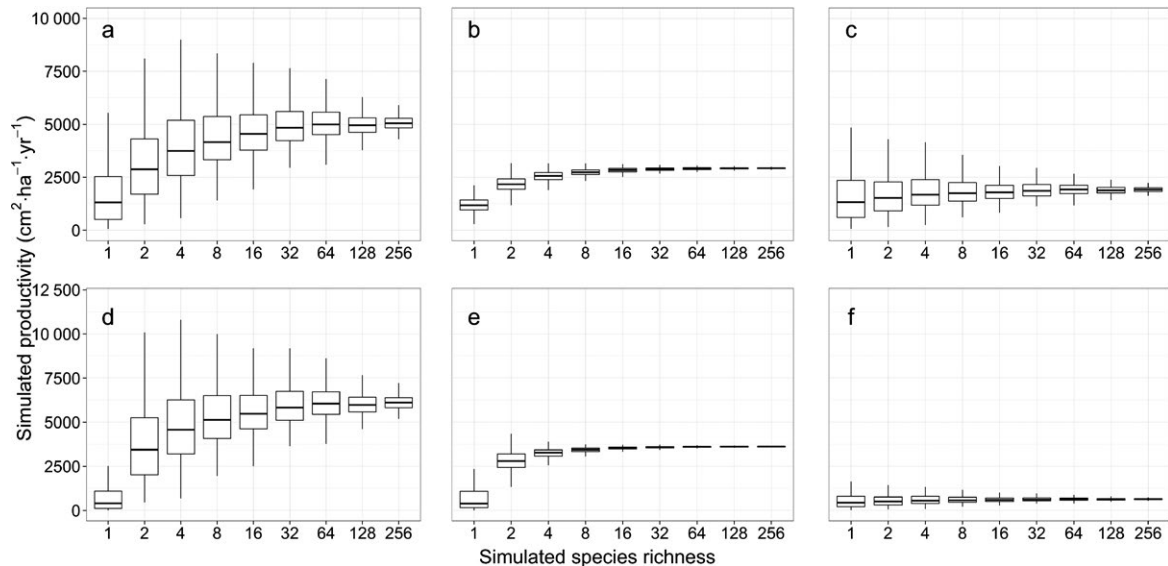


FIG. 3. The relationships between species richness and simulated productivities when growth was influenced only by (b, e) complementarity mechanism, only by (c, f) selection mechanism, or by (a, d) both mechanisms from (a–c) neighborhood trait and (d–f) phylogenetic dissimilarity models. Simulated productivities were quantified here as the total growth in basal area if all individuals survive.

productivity at this site found a significant positive relationship at the 20×20 m scale, though not at larger spatial scales (Chisholm et al. 2013). The positive relationship at small scales could be caused by the neighborhood complementarities identified in this study. While, at larger scales, the effects of environmental gradients dominate, which leads to the mixed relationships between species richness and productivity (Chisholm et al. 2013). However, environmental gradients were removed in our simulation because we excluded the random effects for quadrats when calculating simulated individual growth. Therefore, neighborhood complementarity can operate and lead to the positive diversity–productivity relationships in the simulation at large spatial scale (Fig. 3).

Four of the single-trait based trait dissimilarity indices (maximum height, wood density, leaf tissue density, and leaf nitrogen content) had significant positive effects on tree growth (Fig. 1b), suggesting multiple processes contribute to neighborhood complementarities. Maximum height and leaf nitrogen content are closely related to plant species' strategies with respect to competition for light (Wilson et al. 2000, Moles et al. 2009). Wood density and leaf tissue density are linked to herbivore and pathogen resistance (Augsburger and Kelly 1984, Coley and Barone 1996). Maximum height had the strongest effect size among the single-trait based indices; its effect size even trended larger than that of the multi-trait based index (Fig. 1). This implies that marginal overlap of the niche axis associated with maximum height may be disproportionately important relative to the niche axis associated with

the other traits (Holt 1987). However, these traits were given the same weight when calculating multi-trait distance index, which dilutes the effects of niche partitioning associated with maximum height. We found significant negative relationship between growth and leaf area dissimilarity (Fig. 1b). This result suggests that environmental filtering processes associated with leaf area might be more important than niche partitioning associated with this trait. Species with small leaf area usually are shade tolerant species (Pearson correlation between $\log(\text{leaf area})$ and shade tolerance index, $r = -0.17$, $P = 0.018$). Trees tend to have lower shade tolerance and higher leaf area under gap area, while trees under shaded area tend to have the opposite patterns. Focal trees with high leaf area under shaded areas should have more dissimilar neighbors but slower growth, while focal trees with high leaf area under gap areas should have more similar neighbors but faster growth.

The effects of neighborhood dissimilarity for growth were largest when both conspecifics and heterospecific neighbors were included (the phylogenetic and trait dissimilarity models) and smaller for heterospecifics only (the heterospecific trait and phylogenetic dissimilarity models), but were still statistically significant for heterospecific trait dissimilarity (Fig. 1a). This suggests that two different mechanisms might contribute to the observed positive neighborhood complementarity. Focal trees may benefit from the dilution effect induced by the density decrease of conspecific neighbors and from the associational effect caused by increased density of dissimilar heterospecific neighbors (Underwood et al. 2014).

Initial DBH explained more of the variation in growth than did any of the neighborhood dissimilarities indices, with the exception of the maximum height based dissimilarity index (Figs. 1 and B1). This suggests future studies should be careful with size structure variation among quadrats when conducting quadrat-based analysis on biodiversity-productivity relationships. Failure to account for differences in size structure may mask or distort diversity effects.

We further found negative relationships between shade tolerance and neighborhood dissimilarity effects (the trait and phylogenetic dissimilarity models) on tree growth (Fig. 2). Kobe and Vriesendorp (2011) tested for a relationship between species shade tolerance and negative conspecific density effects on seedling survival in Costa Rica, and found shade-tolerant species were more resistant to negative density effects, which is consistent with our findings. In contrast, Comita et al. (2010) found no relationship between shade tolerance and negative density effects on seedling survival on BCI. The negative relationships between shade tolerance and neighborhood dissimilarity effects disappeared for the heterospecific only models (the heterospecific phylogenetic and trait dissimilarity models) (Fig. 2), which lead to significantly negative relationships between shade tolerance and response differences between overall and heterospecific neighborhood dissimilarities (Fig. E1). This phenomenon can lead to asymmetric complementarity. In mixtures with both shade-tolerant and light-demanding species, overyielding primarily comes from the alleviation of negative density effects for light-demanding species, while the yields of shade-tolerant species are similar in mixtures and monocultures.

Our results suggest that complementarity in this forest may be particularly strongly related to alternative strategies for competing for light. We found maximum height had the strongest effect on tree growth among the six single-trait-based dissimilarity indices (Fig. 1b). Further, neighborhood complementarity strengths were negatively related to shade tolerance (Fig. 2). Species differences in crown architecture (e.g., height, crown width, and shape) and, in shade tolerance, can lessen light competition and contribute to stand-level productivity (Jucker et al. 2015).

Our simulations demonstrated that the identified neighborhood complementarities are sufficient to produce positive biodiversity-productivity relationships at the stand level, and that they contribute more than sampling effects to such relationships in this forest (Fig. 3). When the complementarity mechanism was present, simulated productivity increased strongly at low levels of species richness, and then became saturated at high levels (Fig. 3), consistent with the results obtained from other ecosystems (Cardinale et al. 2012). Although individual-based methods do not directly deal with stand-level species richness and productivities as Loreau and Hector's partitioning approach did in experiments (Loreau and

Hector 2001), individual-based methods can control various confounding factors (e.g., tree size and spatial distribution) when applied to observational data from natural forests. The identified individual-level mechanisms (e.g., neighborhood complementarity) can be scaled up to stand-level patterns and relationships through simulations. It is also easy to partition the influences of different mechanisms (e.g., complementarity vs. selection), and assess their relative importance in simulations. However, two caveats must be considered. First, limitations of the fitted growth model limit the accuracy of simulated production. Second, the simulations assumed zero mortality and recruitment, and thus quantified the implications of complementarity effects only for growth. However, previous studies in this forest found both survival (Hubbell et al. 2001, Comita et al. 2010, Lebrija-Trejos et al. 2014) and recruitment (Harms et al. 2000, Wright et al. 2005) were negatively related to local conspecific density. Inclusion of these effects would likely reinforce the niche complementarities quantified here and further strengthen positive stand-level biodiversity-productivity relationships.

Fundamentally, if competition is more intense among conspecifics than among heterospecifics, and if competition among heterospecifics is more intense among species that are more closely related and more similar in their traits, then neighborhood complementarity effects such as those documented here will result. We expect that these differences in the intensity of competition will prove general in other forests, and indeed, in most communities of any kind (Briones et al. 1996, Turnbull et al. 2007, Lasky et al. 2014, Kraft et al. 2015), providing a mechanism for positive biodiversity-productivity relationships in these communities.

CONCLUSIONS

Although the biodiversity-productivity relationship is a stand-level pattern, stand-level analyses may not be the best tools to elucidate the underlying mechanisms. Whichever specific process leads to the complementarity effect in plant communities, it must operate primarily among neighboring trees. Our analyses show how scaling down to individual-level processes can advance our mechanistic understanding of stand-level biodiversity-productivity relationships. Using individual-based methods, we found significant positive effects of neighborhood phylogenetic dissimilarity, multi-trait based dissimilarity and four single-trait based dissimilarities on tree growth (Fig. 1). This suggests that neighborhood complementarity is important for productivity in this tropical forest. Given that complementarity in maximum height had the most important effect on tree growth, and that neighborhood complementarity strengths were negatively related to shade tolerance, our results further suggest that complementarity in light competition strategies is central to biodiversity-productivity relationships in this forest.

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