LETTER

Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly

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Abstract

The phylogenetic structure and distribution of functional traits in a community can provide insights into community assembly processes. However, these insights are sensitive to the spatial scale of analysis. Here, we use spatially explicit, neighbourhood models of tree growth and survival for 19 tree species, a highly resolved molecular phylogeny and information on eight functional traits to quantify the relative efficacy of functional similarity and shared ancestry in describing the effects of spatial interactions between tree species on demographic rates. We also assess the congruence of these results with observed phylogenetic and functional structure in the neighbourhoods of live and dead trees. We found strong support for models in which the effects of spatial neighbourhood interactions on tree growth and survival were scaled to species-specific mean functional trait values (e.g., wood specific gravity, leaf succulence and maximum height) but not to phylogenetic distance. The weak phylogenetic signal in functional trait data allowed us to independently interpret the static neighbourhood functional and phylogenetic patterns. We observed greater functional trait similarity in the neighbourhoods of live trees relative to those of dead trees suggesting that environmental filtering is the major force structuring this tree community at this scale while competitive interactions play a lesser role.

Keywords

Environmental filtering, Luquillo Forest Dynamics Plot, niche differentiation, phylogenetic conservatism, spatially explicit models, species interactions.

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INTRODUCTION

A fundamental goal in community ecology is to understand the processes that drive community assembly. Several non-exclusive mechanisms ranging from entirely deterministic to stochastic have been proposed to explain the high number of species present in some ecological communities such as tropical forests (Wright 2002). These include environmental filtering (i.e., tolerance of the abiotic environment; Weiher and Keddy 1999), interspecific competition for resources (Tilman 1982), enemy-mediated negative density dependence (Janzen 1970; Connell 1971) and limited dispersal coupled with demographic stochasticity (Hubbell 2001). The outcome of these processes may be reflected in the phylogenetic structure and distribution of functional traits in a community (Webb *et al.* 2002; Cavender-Bares *et al.* 2004, Kraft *et al.* 2007).

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Interpretation of these patterns depends on the spatial scale of analyses and the degree of functional trait conservatism (Webb *et al.* 2002, Cavender-Bares *et al.* 2006). When functional traits are phylogenetically conserved, environmental filtering at the community scale from a regional pool of species should lead to a clustered (i.e., more related than expected) phylogenetic community structure while competitive interactions between co-existing species should result in the opposite (i.e., overdispersed) pattern, albeit at a neighbourhood (<100 m) scale. However, environmental filtering can generate phylogenetic overdispersion when traits from distantly related taxa have converged in response to similar niche use. In reality, simple interpretations of phylogenetic overdispersion and clustering patterns gloss over much of the complexity inherent in community assembly processes (Vamosi *et al.* 2009). For instance, habitat filtering occurs at multiple spatial scales (Kraft *et al.* 2008) and competitive interactions are not limited to neighborhood scale interactions if multiple trophic levels are considered.

Most empirical studies that have simultaneously investigated phylogenetic and functional community structure as a means to provide insights into community assembly processes have done so by comparing static community patterns at various spatial scales (e.g., Swenson & Enquist 2009). The implicit assumption of this research is that phylogenetic or functional community structure reflects the influence of antecedent processes, such as environmental filtering or competitive interactions, on demographic rates. A number of studies have also investigated how the nature and spatial scale of phylogenetic community structure changes with life-history stage or tree size (e.g., Swenson *et al.* 2007), as well as the relationship between demographic rates and functional characteristics of species (e.g., Poorter *et al.* 2008). Despite these advances, no empirical studies have simultaneously quantified and compared the relative importance of functional similarity and shared ancestry in shaping spatial interactions among tree species, the effects that these interactions have on demographic rates and the observed phylogenetic and functional structure at the neighbourhood spatial scale at which these processes take place.

Understanding the relative importance of phylogenetic and functional traits in predicting the effect of interactions among species on tree demography will provide important insights into community assembly processes. Given that key functional traits are robust indicators of plant performance and competitive strategies (Grime 1977; Reich *et al.* 1997; Weiher *et al.* 1999; Westoby *et al.* 2002), a superior predictive performance of functional traits relative to phylogeny in shaping spatial interactions between neighbouring trees might suggest that niche differentiation in resource capture is more important in shaping community assembly at this scale than phylogenetic relatedness.

However, if phylogenetic relatedness better predicts the demographic effect of neighbourhood (<20 m) spatial interactions between tree species, phylogenetically conserved species characteristics different from commonly measured functional traits, such as defensive compounds against shared enemies, may be important for community assembly (Gilbert & Webb 2007).

Our goal in this article is to use spatially explicit, neighbourhood models of tree growth and survival for 19 tree species, together with a highly resolved DNA barcode molecular phylogeny and information on eight functional traits, to examine the relative importance of phylogeny and functional trait values in structuring neighbourhood interactions between tree species. The detection of a phylogenetic signal for biotic interactions may be more easily detected at small (<100 m^2) spatial scales (Webb *et al.* 2002). By focusing our analyses at the neighbourhood scale, we expect to simultaneously quantify the effect of individual interactions that lead to competitive exclusion and the degree to which environmental filtering operates at this scale. We employ tree growth and survival data collected in the successional communities in the Luquillo Forest Dynamics Plot (LFDP), in Puerto Rico.

Our analyses address three fundamental questions for species coexistence. First, we ask whether the strength of neighbourhood interactions between species is proportional to relative distance in mean trait values. The rationale for this hypothesis is that species with higher mean trait values (e.g., leaf N) would compete more strongly for resources (e.g., N) than species with lower values. Support for this premise would suggest that competitive interactions for limiting resources among trees may have contributed to community assembly. Second, we ask whether greater phylogenetic relatedness results in stronger negative neighbourhood interactions between tree species. Interpretation of these patterns depends on the degree of phylogenetic trait conservatism (Webb *et al.* 2002). Third, we ask whether the answers to questions 1 and 2 can be interpreted in light of observed changes in the phylogenetic and functional trait composition of tree neighbourhoods over time. To do so, we compared the composition of phylogenetic and functional traits in the neighbourhoods (including all trees) of dead and live focal trees for each focal species. We expect that if functional traits modulate the demographic effects of neighbourhood interactions (i.e., that focal tree survival and growth are lower in the neighbourhood of functionally similar species), the trait structure of tree neighbourhoods will reflect the relative strength of environmental filtering vs. species interactions at the local spatial scale. Prevalence of trait-mediated competitive interactions may result in greater trait similarity in the neighbourhoods of dead trees relative to those of live trees, while predominance of local-scale environmental filtering should result in the opposite pattern

Table 1 Expected relationships between outcomes of neighbourhood demographic models and phylogenetic (NRI) and functional trait similarity (TSI) in the neighbourhoods of live and dead trees

	Predominant process structuring community at neighbourhood scale	
Demographic model supported	Environmental filtering	Competitive exclusion
Traits mediate spatial interactions		
Neighbourhood predictions	TSI live > TSI dead	TSI dead > TSI live
Relatedness mediates spatial interactions		
Neighbourhood predictions	NRI live > NRI dead	NRI dead > NRI live

These predictions hinge on the degree of phylogenetic trait conservatism. See Introduction for more details on the rationale behind these predictions. TSI, Trait Similarity Index; NRI, Net Relatedness Index.

(Table 1). This belief stems from the assumption that there are environmental factors (e.g., soil moisture) that influence demographic rates at this scale independently from spatial interactions between neighbours. The same predictions hold when neighbourhood interactions are affected by phylogenetic relatedness.

Because they reflect community assembly in action, successional tropical forests provide an ideal natural laboratory for testing the power of an integrated functional trait and phylogenetic approach to community assembly. High leaf nitrogen content and low wood density, functional traits associated with fast growth, are characteristic of early successional species (Bazzaz & Pickett 1980). In contrast, later in succession, biotic filters associated with Janzen-Connell effects may play a more important role in species dynamics and therefore species with functional traits related to defense (e.g., leaf toughness) should be favoured; these effects may also extend to closely related species (Uriarte *et al.* 2004b).

METHODS

Study site and field surveys

The LFDP is a 16-ha permanent forest plot (SW corner 18°20′ N, 65°49′ W) located in the Luquillo Mountains of Puerto Rico. The forest is classified as subtropical wet in the Holdridge life zone system (Ewel & Whitmore 1973). Rainfall averages 3500 mm per year. Elevation ranges from 333 to 428 m a.s.l. The LFDP was established in 1990. Censuses are carried out every 5 years. All free-standing woody stems ≥ 1 cm diameter at 130 cm from the ground DBH (Diameter at Breast Height) in the LFDP are tagged, identified to species, mapped and measured (Thompson *et al.* 2002).

Species selection
The LFDP contains on average 89 species of trees with stems ≥ 10 cm DBH distributed over 72 genera and 38 families. Our research and modelling focus on 19 species that display a

wide variation of life-history characteristics (Table 2) (Zimmerman *et al.* 1994; Uriarte *et al.* 2004a), had more than 400 individuals ≥ 1 cm DBH of which at least 70 died between the 1990 and 1995 censuses. These criteria ensured that we could obtain robust parameter estimates. Together these species account for *c.* 85% of stems ≥ 10 cm DBH in the plot.

Hurricane damage
Hugo, a category 4 hurricane, struck the LFDP in 1989 causing significant damage (Zimmerman *et al.* 1994). The first census started in 1990, the year after Hurricane Hugo. This census included an initial categorical estimate of damage for all stems ≥ 10 cm DBH to prevent loss of data due to decomposition of trees killed or damaged by Hurricane Hugo. Damage observations were classified into three categories: (1) no or light damage (≤ 25% of crown volume removed by the storm), (2) medium damage (25–75% of crown volume lost) or (3) heavy or complete damage (> 75% of the crown lost, stem snapped, root break or tip-up).

Trait and phylogeny data
Trait data for all woody species present in the LFDP were derived from vegetation samples collected using standardized protocols (Cornelissen *et al.* 2003). Samples were collected to calculate species mean leaf traits (25 samples) and wood specific gravity (10 samples). We selected eight functional traits that are believed to represent fundamental functional trade-offs in life-history differentiation among tree species (Wright *et al.* 2007). These include leaf area (cm^2), specific leaf area ($cm^2\ g^{-1}$), leaf nitrogen content (%N), leaf phosphorus content (%P), leaf succulence (g $H_2O\ cm^{-2}$ leaf area), wood specific gravity (g cm^{-3}), maximum tree height (m) and seed mass (g). Details on phylogeny construction and results are provided in Kress *et al.* (in press) (Fig. 1).

Spatially explicit models of tree growth and survival

We used data from the 1990 and 1995 censuses of the LFDP to develop neighbourhood models of tree growth and

Table 2 Species included in the neighbourhood analyses, including their successional status (P = pioneer, S = secondary forest species; L = late successional species), life form (L = large tree, M = medium tree, S = small tree), % trees > 1 cm DBH that died between the census starting in 1990 and 1995, % total adult (≥ 10 cm DBH) abundance, total number of stems > 1 cm DBH and maximum DBH in the 16-ha Luquillo Forest Dynamics Plot

Species	Family	Successional status	Life form	Per cent tree mortality	Per cent total adult abundance	# stems > 1 cm DBH	Max DBH (cm)
Alchornea latifolia (*ALCLAT*)	Euphorbiaceae	S	L	33.26	1.19	1271	66
Buchenavia tetraphylla (*BUCTET*)	Combretaceae	L	L	20.64	1.17	406	151
Casearia arborea (*CASARB*)	Salicaceae	S	S	22.65	4.93	6168	48
Casearia sylvestris (*CASSYL*)	Salicaceae	S	S	15.45	1.15	3085	27
Cecropia schreberiana (*CECSCH*)	Cecropiaceae	P	M	48.51	3.13	11 220	48
Cordia borinquensis (*CORBOR*)	Boraginaceae	L	S	10.51	0.05	1266	25
Dacryodes excelsa (*DACEXC*)	Burseraceae	L	L	3.67	6.84	1731	82
Drypetes glauca (*DRYGLA*)	Euphorbiaceae	L	S	14.80	0.99	617	38
Guarea guidonia (*GUAGUI*)	Meliaceae	L	L	28.44	1.98	1132	96
Inga laurina (*INGLAU*)	Fabaceae	S	S	15.55	2.75	1607	87
Manilkara bidentata (*MANBID*)	Sapotaceae	L	L	4.13	4.53	1803	78
Myrcia deflexa (*MYRDEF*)	Myrtaceae	S	S	13.47	0.03	520	31
Ocotea leucoxylon (*OCOLEU*)	Lauraceae	S	M	11.28	0.95	984	52
Ormosia krugii (*ORMKRU*)	Leguminosae	S	M	32.67	0.56	497	69
Prestoea acuminata (*PREMON*)	Arecaceae	S	M	5.50	49.43	8521	42
Schefflera morototoni (*SCHMOR*)	Araliaceae	P	M	38.83	0.99	4726	75
Sloanea berteriana (*SLOBER*)	Elaeocarpaceae	L	L	5.82	3.20	3622	93
Tabebuia heterophylla (*TABHET*)	Bignoniaceae	S	M	13.29	1.92	826	69
Trichilia pallida (*TRIPAL*)	Melicaceae	L	M	7.41	0.27	857	43

survival for 19 of the common tree species (Table 2). The difference in DBH between the first and second censuses together with the time difference between censuses were used to calculate average annual growth rate for each tree. Annual mortality estimates were obtained from mortality records from the second census and time between censuses for each individual tree. Although the palm *Prestoea acuminata* is the most abundant species at the site, we did not analyse it as a focal species in our growth model because diameter measurements do not reflect growth for this species. We considered all species in the plot as potential neighbours.

Our modelling approach relies on traditional distance-dependent analyses of competition, in which tree growth is analysed as a function of the sizes and distances to neighbouring trees (see references in Uriarte *et al.* 2004b). We assume that each individual has a species-specific maximum potential growth rate, which is adjusted to account for the size of the focal tree, the structure and composition of its neighbourhood, and previous hurricane damage to both the focal tree and its neighbours (Uriarte *et al.* 2004a). A similar approach was used to estimate survival. Our models take the form:

$$g = g_m \varphi \delta \nu, \tag{1}$$

where g is predicted growth, g_m is an estimated species-specific maximum potential growth, φ is the hurricane

effect, δ is the size effect and ν is the neighbourhood effect. A similar approach was taken for survival analyses.

Hurricane effects
Hurricane damage affects potential maximum growth rate and probability of survival of the focal tree species (φ, in eqn 1). Damage also alters the crowding effects of neighbours (see Neighbourhood effects).

Size effects on growth
Potential radial growth is assumed to vary with the DBH of the focal tree. We use a lognormal function for the shape of this effect, because it is flexible, and supported by both theoretical and empirical evidence (Uriarte *et al.* 2004a):

$$g = g_m \times \exp\left[-\frac{1}{2}\right]\left[\frac{\ln(DBH/X_0)}{X_b}\right]^2, \tag{2}$$

where g_m is the maximum potential radial growth (cm year^{-1}) in the absence of neighbours (i.e., at the peak of the lognormal shape), X_0 is the DBH at which g_m occurs and X_b determines the breadth of the function.

Neighbourhood effects
The net effect of a neighbouring tree on the growth of a focal tree of a given species is assumed to vary as a function of the size of the neighbour, and inversely with distance to

the neighbour. The effect of an individual neighbour is multiplied by a species-specific scalar λ_s [0 − 1] which allows for differences among species in their competitive effect on a focal tree. The neighbourhood crowding index for individual *focal* of species *k* is:

$$\mathrm{NCI}_{\mathrm{focal},k} = \mathrm{DBH}_{\mathrm{focal},k}^{\gamma} \sum_{i=1}^{S} \sum_{j=1}^{n_i} \lambda_{ik} \frac{\mathrm{DBH}_j^{a_k}}{\mathrm{Distance}_j^{\beta_k}}, \qquad (3)$$

where $\mathrm{DBH}_{\mathrm{focal},k}^{\gamma}$ is the DBH of that focal individual, weighted by an exponent γ that characterizes the size sensitivity of individuals the focal species *k* to neighbourhood effects. The double sum is over *S* species and the n_i neighbours of each species *i* in the focal individual's neighbourhood of estimated maximum radius *R*. The parameter λ_{ik} is a pairwise competition coefficient, and it estimates the per-capita effect of species *i* on species *k*. Parameters α_k and β_k allow for nonlinear scaling of the effects of neighbour size and distance on focal species *k*. The parameter η is drawn from a vector with three possible values that correspond to the three levels of hurricane damage to a neighbouring tree. Neighbourhood effects (*v*) are translated into actual effect on growth or survival by using a negative exponential function of NCI.

$$v = \exp^{-C\mathrm{NCI}_i^D}, \qquad (4)$$

where *C* and *D* are species-specific estimated parameters and NCI_i is the neighbourhood competition index for focal tree *i*. To avoid edge effects, all focal trees that were within 20 m of the edge of the plot were excluded from the analyses.

Our motivation for this study was to explore the degree to which species functional traits and phylogenetic relatedness can explain the effects of spatial interactions between species on tree demography. To this end, we compared 13 models that make different assumptions about the nature of these interactions (i.e., values of λ in eqn 3). The simplest 'control' model assumed that only tree size influenced focal tree growth and survival. The second model assumed that all neighbours had equivalent effects on the focal tree regardless of phylogenetic relatedness or functional similarity. The third model differentiated between conspecific and heterospecific neighbours. In a fourth set of models, we assigned a fixed λ to each competitor scaled to the maximum phylogenetic distance calculated using the DNA barcode phylogeny. Values of λ for conspecifics for this model were assumed to be 1 (no distance) and effects of neighbours were scaled from 0 to 1 according to phylogenetic distance to the focal species. Finally, we evaluated a set of nine trait-based models (Models #5–12) by assigning λ values based on the difference in mean trait values among species. For each of the eight traits considered, competition coefficients were scaled to the maximum observed values in

the community with one being the effect of a neighbour from the species with the highest mean value for that trait (e.g., highest wood specific gravity). Leaf area and seed weight were log-transformed prior to scaling. As many of the traits are correlated, a Principal Component Analysis was conducted to reduce the dimensionality of the data. The first three axes of the PCA were used in a hierarchical clustering algorithm that produced a trait distance matrix (Appendix S2). Using this matrix, we considered an additional trait-based model (Model #13) that scaled λ values based on composite trait distance. Note that this formulation of competitive effects based on trait data assumes that the strongest competitive effect accrues to the species with the highest trait value. For instance, if species A has the maximum trait value of 1, species B of 0.5 and species C of 0.1, our formulation scales the relative trait dissimilarity between species B and species C to 0.4 and but that between species A and C to 0.9. As such, it provides an index of niche differentiation (i.e., trait dissimilarity) among species.

Model parameters were estimated using maximum likelihood. Initial parameter values are summarized in Appendix S3. We calculated asymptotic 95% support limits for each of the parameters. The 13 models were compared using Akaike's Information Criterion (AIC) and Akaike weights with the best candidate model having the lowest AIC and highest weight (Burnham & Anderson 2002). We assessed the goodness-of-fit of our growth models using traditional regression statistics (R^2) and the slope of the regression of observed radial growth on predicted radial growth was used to measure bias. For mortality analyses, we compared the percentage of trees in a given predicted survival bin (0–10, 10.01–20%, etc.) (Hosmer & Lemeshow 1989).

Comparison of neighbourhood models of tree demography with phylogenetic and functional trait structure

To assess the congruence of our models with static phylogenetic and trait structure patterns, we calculated abundance weighted neighbourhood (20 m) phylogenetic relatedness indices [Net Relatedness Index (NRI)] and functional trait similarity [Trait Similarity Index (TSI)] for live and dead trees in census 2 for all focal species. Live trees recruited between the 1990 and 1995 censuses were excluded from all calculations because they did not enter into the neighbourhood models. We considered all the species in the LFDP as the community pool. The trait distance matrix was used as input to calculate TSI using the same procedure as for NRI.

Interpretation of our results regarding the importance of niche differentiation vs. environmental filtering in structuring the phylogenetic structure of neighbourhoods depends on the degree of phylogenetic trait conservatism.

We employed trait data and the LFDP phylogeny to test whether functional traits were phylogenetically using Blomberg's *K* statistic (Blomberg *et al.* 2003). Where necessary, trait values were normalized using log transformations. All analyses were conducted using R statistical software (R Development Team 2008).

RESULTS

Likelihood and goodness-of-fit of growth and survival models

We estimated maximum likelihood parameter values for 13 growth and survival models for 19 selected focal species with the goal of quantifying the importance of phylogenetic distance and trait similarity in structuring neighbourhood interactions (Table 3; Appendix S4). The per cent of variance in individual growth rates explained by the most parsimonious models ranged from 2% for *Trichilia pallida* to 23% for *Schefflera morototoni*, while the fit of the survival model ranged from 29% for *Myrcia deflexa* to 99% for several species (Table 3).

Neighbourhood effects on growth and survival

Growth
For the growth analyses, 12 of the 18 species examined (i.e., excluding *P. acuminata*) provided support for a model for which differences among species in mean trait values

structured neighbourhood interactions (Table 3; Appendix S4). Of these 12 species, six supported a model that scaled neighbourhood interactions according to differences in wood specific gravity, two in species leaf succulence and two in maximum tree height. The final two species in this group of 12 exhibited support for more than one growth model: *Tabebuia heterophylla* had similar Akaike weights for the wood specific gravity and leaf succulence models, and *Drypetes glauca* supported the maximum tree height and equivalent competitor model. The six species in the growth analyses that did not support a trait-based model were distributed among the size only model (two species), the equivalent competitors model (two species) and the model that differentiated between conspecifics and heterospecific neighbours (two species) (Table 3). None of the 18 species included in the growth analyses displayed any support for the phylogenetic distance neighbourhood model as evidenced by extremely low Akaike weights for this set of models (Appendix S4).

Survival
In general, the relative strength of evidence in support of any one particular model at the community level was weaker for survival than growth (Appendix S4). Three species, *Cecropia schreberiana*, *Casearia sylvestris* and *Inga laurina*, supported the phylogenetic distance model although only *C. schreberiana* exhibited strong support of this model. For five of the focal species, *Alchornea latifolia*, *Casearia arborea*, *Ocotea leucoxylon*, *S. morototoni* and *T. pallida*, a simplified

Table 3 Most parsimonious model and goodness-of-fit statistics for the 19 focal species. See Methods for a detailed description of goodness-of-fit metric for survival data

Focal species	Best growth model	R^2	Best survival model	R^2
Alchornea latifolia	Leaf succulence	0.09	Conspecific vs. heterospecific	0.99
Buchenavia tetraphylla	Size only	0.14	Leaf P	0.99
Casearia arborea	Wood specific gravity	0.12	Conspecific vs. heterospecific	0.99
Casearia sylvestris	Conspecific vs. heterospecific	0.03	Phylogenetic distance	0.92
Cecropia schreberiana	Equal neighbours	0.19	Phylogenetic distance	0.99
Cordia borinquensis	Max height	0.05	Size only	0.64
Dacryodes excelsa	Wood specific gravity	0.17	Leaf succulence	0.64
Drypetes glauca	Equal neighbours/max height	0.02	Leaf N/specific wood gravity	0.77
Guarea guidonia	Wood specific gravity	0.18	Composite trait distance	0.99
Inga laurina	Wood specific gravity	0.19	Phylogenetic distance	0.82
Manilkara bidentata	Wood specific gravity	0.18	Max height	0.73
Myrcia deflexa	Equal neighbours	0.07	Size only	0.29
Ocotea leucoxylon	Size only	0.18	Conspecific vs. heterospecific	0.93
Ormosia krugii	Max height	0.04	Leaf area	0.99
Prestoea acuminata	NA	NA	Max height	0.34
Schefflera morototoni	Wood specific gravity	0.23	Conspecific vs. heterospecific	0.99
Sloanea berteriana	Leaf succulence	0.06	Leaf succulence	0.63
Tabebuia heterophylla	Leaf succulence/specific wood gravity	0.08	Specific Leaf Area	0.88
Trichilia pallida	Conspecific vs. heterospecific	0.02	Conspecific vs. heterospecific	0.76

model that distinguished between conspecific and heterospecific neighbours was the most parsimonious (Table 3). Only size influenced the probability of survival for *Cordia borinquensis* and *M. deflexa*. For the remaining nine species, models that distinguished between neighbours on the basis of mean functional trait values provided a significantly better fit to the data. Nevertheless, there were no clear patterns in the success of any one trait in predicting neighbourhood effects on survival. Interestingly, none of the 19 species supported the equivalent competitor model for survival, in contrast to the results for the growth models.

Comparison of model results and neighbourhood structure

To assess the congruence of the results of the neighbourhood analyses with phylogenetic and functional neighbourhood structure, we compared phylogenetic distance (NRI) and trait similarity (TSI) of all trees (live and dead) in a 20-m radius surrounding live or dead trees for the 19 focal species. Overall, the NRI and TSI of neighbours surrounding live trees were greater than around dead trees, indicating greater phylogenetic and trait dispersion in neighbourhoods of dead focal trees (mean NRI dead = -0.43 ± 0.04 SE, mean NRI live = -0.26 ± 0.04 SE, ANOVA, $F = 9.65$, d.f. = 1, 38, $P = 0.003$; mean TSI dead = -0.10 ± 0.08 SE, mean TSI

live = 0.32 ± 0.10 SE, ANOVA, $F = 13.14$, d.f. = 1, 38, $P < 0.0001$; Fig. 2; Table 4). All species that supported trait-mediated, neighbourhood survival models had greater trait similarity in the neighbourhoods of live trees relative to those of dead trees (Table 4). In contrast, for two out of the three species that supported the phylogenetic distance survival model, *C. sylvestris* and *C. schreberiana*, phylogenetic relatedness was greater in the neighbourhood of live relative to dead trees (Tables 3 and 4). For the third species, *I. laurina*, the NRI for neighbourhoods of live trees was greater than for dead trees.

We also detected an effect of successional status on the phylogenetic structure of neighbourhoods. Specifically, neighbourhoods (dead and live trees combined) of late-successional species were more phylogenetically clustered than those of pioneer species (ANOVA, $F = 4.19$, d.f. = 2, 37, $P = 0.02$; Fig. 2a). Functional trait similarity varied in a similar manner across successional groups; neighbourhoods of late-successional species had greater functional similarity than those of pioneer and secondary forest species (ANOVA, $F = 7.15$, d.f. = 2, 37, $P = 0.002$; Fig. 2b).

Results from our analyses must be interpreted in light of the degree of phylogenetic trait conservatism found for this community. Contrary to previous analyses (Swenson *et al.* 2007), we relied on a more resolved phylogeny with trait data
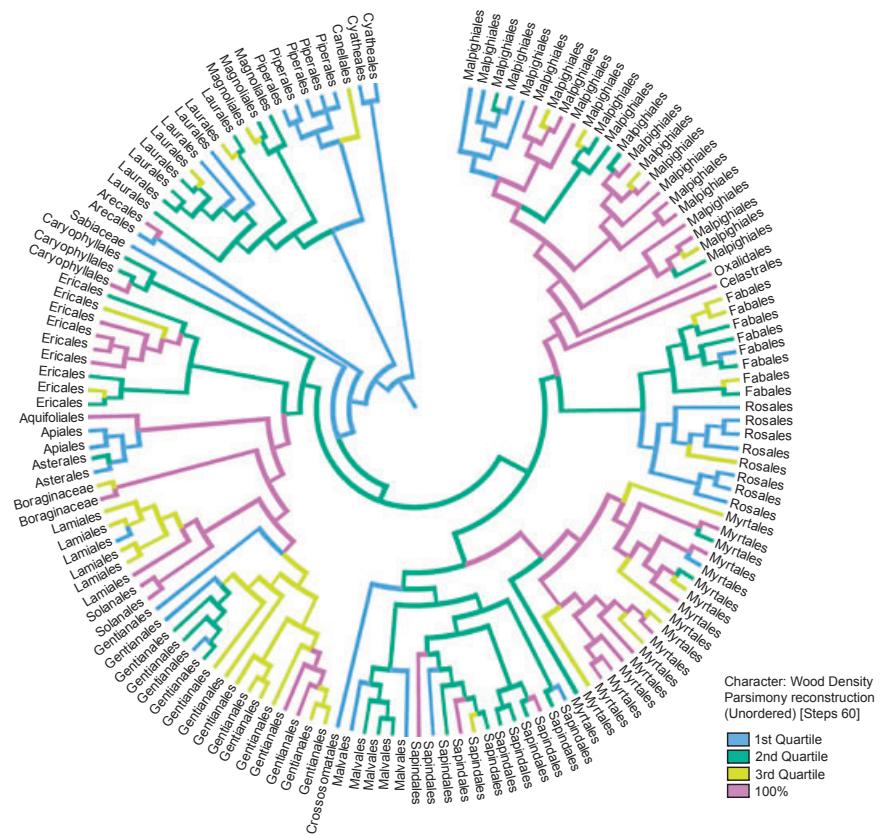
Figure 1 DNA barcode phylogeny of the woody species in Luquillo Forest Dynamics Plot. Each terminal branch represents a single species designated by its taxonomic order. Values for wood specific gravity for each species were mapped onto the tree using MESQUITE Version 2.73 (Maddison & Maddison 2010). See Methods for details on tree construction. Mapped wood specific gravity data were categorized into the following four quantiles: <0.25, 25–50, 50–75 and >75%. Details on phylogeny construction are provided in Appendix S1.
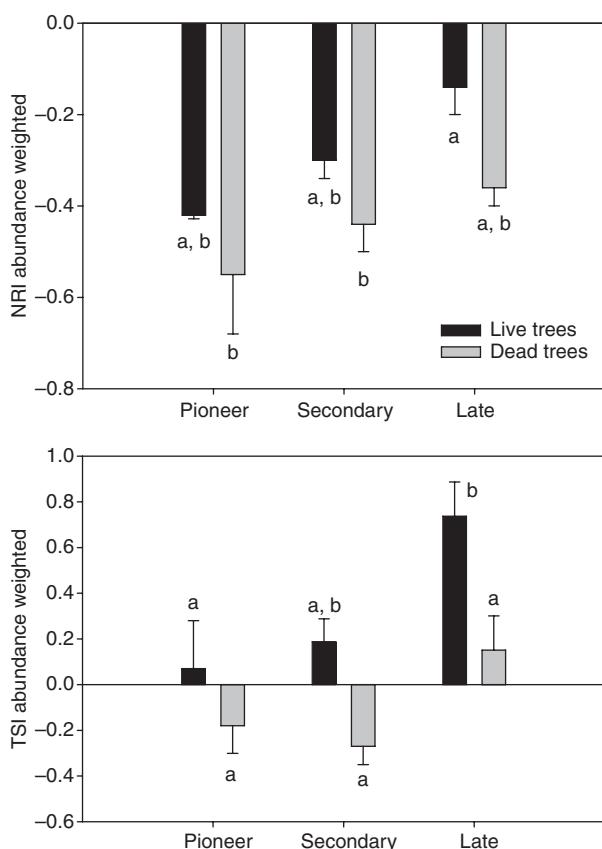
Figure 2 Net Relatedness Index (NRI) and Trait Similarity Index (NTI) for trees included within a 20-m radius of live and dead trees for pioneer, secondary forest and late-successional trees. Different letters indicate that means are significantly different at α = 0.05.

collected at the site, rather than taken from the literature. We found a significant phylogenetic signal for only three of the nine traits tested: leaf % phosphorus, leaf area and seed mass (Appendix S6, Fig. 1). For those three traits, values were more phylogenetically conserved than would be predicted by a random association between phylogeny and traits.

DISCUSSION

Effects of phylogenetic distance and trait similarity on neighbourhood interactions

Only three of the 19 species included in these analyses support a model that assumes that phylogenetic proximity augments the strength of neighbourhood interactions between species. In contrast, over 60% of the 19 species supported models in which the effects of spatial neighbourhood interactions on tree growth and survival were scaled to species-specific mean functional trait values. Consequently, for the majority of abundant tree species in the LFDP, shared ancestry, at least beyond the conspecific/

heterospecific dichotomy, does not mediate the effects of neighbourhood interactions on tree growth and survival. Rather, differences in trait values that reflect plant performance and functional competitive strategies moderate negative competitive interactions among species at this stage (Grime 1977; Reich *et al.* 1997; Westoby *et al.* 2002). These results suggest that stronger negative density dependent effects among conspecifics relative to interactions with heterospecifics found in previous studies may simply reflect greater similarity in resource requirements. Strong effects of shared ancestry on seedling recruitment may still be important (Webb *et al.* 2006; Gónzalez *et al.* 2010) but they do not appear to extend into the sapling and adult life-history stages for most species in this study. Moreover, the large amount of unexplained variation in growth may be the result of heterogeneity in underlying environmental gradients that influences demographic rates independently from neighbourhood interactions (Canham *et al.* 2006), or legacies of historical negative competitive interactions between seedlings.

The lack of a strong phylogenetic signal in neighbourhood interactions may reflect the relatively low number of species in this tropical forest (e.g., 140 woody species in the LFDP relative to 300 in Barro Colorado Island, Panama). In a study in the BCI plot, Uriarte *et al.* (2004b) found that con-familiar neighbours had greater effects on focal tree growth than non-confamilials, possibly the result of shared enemies. However, that sort of study is not possible in the LFDP because of the low numbers of congeners and confamilials for most species. In addition, previous studies using less well-resolved phylogenies to assess trait conservatism found that some traits included in this analysis were phylogenetically conserved (Chazdon *et al.* 2003; Chave *et al.* 2006; Swenson *et al.* 2007). Together these results suggest that phylogenetic relationships may be important in mediating species interactions at the generic or familial level but functional traits may be more informative at finer resolutions. Previous analyses at this site using Phylomatic found phylogenetic signal in trait data (Swenson *et al.* 2007), in contrast to this study which relied on a molecular phylogeny. The *K* statistic used here is quite sensitive to branch lengths. Although Phylomatic community phylogenies have crudely estimated node ages and branch lengths, it is likely that the contrasting levels of phylogenetic signal between the two studies are the result of differences in estimated branch lengths for the two trees. Refining hypotheses about the effects of shared ancestry on community assembly processes may require a better understanding of the effects of phylogenetic tree diversity, resolution and topology on these metrics (Vamosi *et al.* 2008; Cavender-Bares *et al.* 2009).

There were no clear patterns in the groupings of species that supported different models. Membership in a family,

Table 4 Mean and standard errors for Net Relatedness Index (NRI) and Trait Similarity Index (TSI) for neighbour trees included within a 20-m radius of live and dead trees for the 19 species included in the analyses

Focal species	NRI dead	NRI live	TSI dead	TSI live
Alchornea latifolia	−0.43 (0.02)	−0.32 (0.02)*	−0.28 (0.02)	−0.35 (0.02)
Buchenavia capitata‡	−0.35 (0.05)	−0.33 (0.05)	−0.22 (0.08)	0.27 (0.46)*
Casearia arborea	−0.44 (0.01)	−0.39 (0.02)	−0.56 (0.01)	−0.16 (0.00)*
Casearia sylvestris†	−0.26 (0.01)	−0.42 (0.00)*	0.11 (0.01)	−0.01 (0.01)*
Cecropia schreberiana†	−0.28 (0.00)	−0.41 (0.00)*	0.06 (0.00)	0.34 (0.01)*
Cordia borinquensis	−0.56 (0.04)	−0.39 (0.01)*	−0.36 (0.04)	0.24 (0.02)*
Dacryodes excelsa‡	−0.33 (0.06)	−0.04 (0.01)*	0.46 (0.09)	1.08 (0.01)*
Drypetes glauca‡	−0.31 (0.04)	−0.02 (0.02)*	0.26 (0.06)	0.82 (0.03)*
Guarea guidonia‡	−0.43 (0.03)	−0.16 (0.01)*	−0.12 (0.03)	0.78 (0.03)*
Inga laurina†	−0.44 (0.03)	−0.19 (0.01)*	−0.12 (0.04)	0.48 (0.02)*
Manilkara bidentata‡	−0.37 (0.05)	−0.14 (0.01)*	0.29 (0.08)	0.94 (0.01)*
Myrcia deflexa	−0.71 (0.06)	−0.41 (0.02)*	−0.43 (0.08)	−0.06 (0.03)*
Ocotea leucoxylon	−0.32 (0.02)	−0.36 (0.00)	−0.43 (0.05)	−0.04 (0.03)*
Ormosia krugii‡	−0.58 (0.04)	−0.42 (0.02)*	−0.24 (0.04)	0.05 (0.04)*
Prestoea acuminata‡	−0.25 (0.02)	−0.15 (0.02)*	−0.06 (0.03)	0.50 (0.00)*
Schefflera morototoni	−0.66 (0.01)	−0.43 (0.01)*	−0.32 (0.01)	0.24 (0.01)*
Sloanea berteriana‡	−0.18 (0.03)	0.063 (0.00)*	0.77 (0.03)	1.28 (0.01)*
Tabebuia heterophylla‡	−0.87 (0.05)	−0.33 (0.02)*	−0.54 (0.05)	0.18 (0.03)*
Trichilia pallida	−0.39 (0.05)	−0.12 (0.02)*	−0.15 (0.08)	0.51 (0.03)*

*Mean values of neighbourhood NRI or TSI differed between live and dead trees at α = 0.05.
†Trees that supported the phylogenetic distance survival model.
‡Trees that supported a trait-based model.

genus or functional group was not a good predictor of the response of species to the structure of the neighbourhood interactions. For instance, species that supported the wood specific gravity growth models ranged from pioneer (*S. morototoni*) to late successional (*Manilkara bidentata*). Similarly, there were no clear groupings along taxonomic lines. The congeners *C. arborea* and *C. sylvestris* supported different growth and survival models. Despite this variation, there are several conclusions we can draw from the analyses. First, the strong showing of wood specific gravity in the growth models corroborates results from other studies that found a strong link between growth and wood specific gravity, presumably because diameter growth is directly related to the construction costs of wood (Poorter *et al.* 2008). Similarly, leaf succulence plays an important role in the maintenance of green foliage during drought, a critical requirement for sustained growth in forests subject to dry spells (Cornelissen *et al.* 1997). Maximum tree height, which found some support in both survival and growth models, is a good predictor of crown exposure and hence, competition for light (Kohyama 1993). Second, effects of traits that were phylogenetically conserved (leaf % P, leaf area and seed mass) had very weak support in the neighbourhood models of growth and survival. This finding suggests that evolutionary lability (i.e., the absence of trait conservatism) may facilitate species coexistence (Silvertown *et al.* 2006; but see Ackerly *et al.* 2006). Third, growth of focal species was more

sensitive to finer gradations in the identity of neighbours than survival. This may simply reflect the fact that the majority of mortality occurred in small size classes, whereas growth was estimated across the whole range of sizes therefore incorporated a greater range of responses to crowding. Alternatively, relatively low numbers of dead trees or lack of variation in the composition of tree neighbourhoods for some species may have hindered our ability to detect distinct responses to the identity of neighbours.

Comparison of model results and neighbourhood structure

To assess the congruence of model results with static community patterns, we evaluated the phylogenetic and functional trait structure in the neighbourhoods of dead and live trees for each focal species. The absence of phylogenetic signal for most of the traits supported by the neighbourhood models allows us to interpret trait and phylogenetic patterns largely independently. Overall, we observed greater functional trait similarity in the neighbourhoods of live trees relative to those of dead trees. Together with strong support for trait-mediated neighbourhood models, these results suggest that environmental filtering is the major force structuring this community at the neighbourhood scale while competitive interactions play a relatively minor role. This is not surprising given that environmental filters can have strong effects on demographic rates (Weiher and

Keddy 1999; Cavender-Bares *et al.* 2004). In contrast to the majority of species that supported trait-based models, we found greater phylogenetic relatedness in the neighbourhood of dead trees relative to those of live trees for two out of the three species that supported the phylogenetic distance model. These outcomes are consistent with a predominance of negative competitive interaction between closely related species relative to environmental filtering. High rates of tree mortality and intense thinning of individuals of early- and mid-successional species as the hurricane damaged canopy closed may have increased the likelihood of detecting effects of competitive interactions on demographic processes for these two species. Nevertheless, we failed to find this pattern for other early successional species (e.g., *S. morototoni*) suggesting that environmental filtering is more important in driving neighbourhood structure for these species. One potential reason for this pattern is that mortality may be less spatially clustered in these species (e.g., recruited into smaller gaps after the hurricane) allowing for less taxonomic variation around dead trees.

Phylogenetic and functional trait structure of tree neighbourhoods differed considerably between successional groups. Both trait and phylogenetic similarity were greater for live late-successional species than for other groups. Late-successional species share certain traits such as greater wood specific gravity, lower leaf % N and P, larger seed weights and low specific leaf area and may be present in areas with relatively little disturbance leading to greater trait similarity in the neighbourhood of these species (Bazzaz & Picket 1980). Coupled with the outcomes of the neighbourhood models, these results are consistent with an increasing importance of environmental filtering relative to competitive interactions during succession, at least at this neighbourhood scale. This was a surprising result given that pathogen-mediated neighbourhood interactions on seedling mortality are expected to intensify during succession (Comita *et al.* 2009), and may extend to closely related species (Webb *et al.* 2006; Gilbert & Webb 2007). The only other study to examine shifts in phylogenetic relatedness through succession found increased overdispersion in older relative to younger sites in a chronosequence (Letcher 2009). However, these findings were the result of recruitment of species present in the regional pool representing different lineages as succession proceeded (Norden *et al.* 2009), a factor not included in this study.

Despite considerable efforts to understand the processes that generate variation in functional traits and phylogenetic structure across spatial scales (e.g., Silvertown *et al.* 2006; Swenson *et al.* 2007), temporal comparison in communities undergoing succession remains rare (but see Letcher 2009). Yet, such comparisons can provide important insights into community assembly processes. Our analyses illustrate the dynamic nature of community assembly processes through succession. It also calls attention to the importance of coupling an understanding of demographic processes with analyses of phylogenetic and functional community structure.

REFERENCES

Ackerly, D.D., Schwilk, D.W. & Webb, C.O. (2006). Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology*, 87, S50–S61.

Bazzaz, F.A. & Picket, S.T.A. (1980). Physiological ecology of tropical succession: a comparative review. *Annu. Rev. Ecol. Syst.*, 11, 287–310.

Blomberg, S.P., Garland, T. Jr. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer, New York, U.S.A.

Canham, C.D., Papaik, M., Uriarte, M. & McWilliams, W. (2006). Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. *Ecol. Appl.*, 16, 540–554.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A. & Bazzaz, F.A. (2004). Phylogenetic overdispersion in Floridian oak communities. *Am. Nat.*, 163, 823–843.

Cavender-Bares, J., Keen, A. & Miles, B. (2006). Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology*, 87, S109–S122.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kimbel, S.W. (2009). The merging of community ecology and phylogenetic biology. *Ecol. Lett.*, 12, 693–715.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Ter Steege, H. & Webb, C.O. (2006). Regional and phylogenetic variation in wood density across 2456 neotropical tree species. *Ecol. Appl.*, 16, 2356–2367.

Chazdon, R.L., Careaga, S., Webb, C.O. & Vargas, O. (2003). Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecol. Monogr.*, 73, 331–348.

Comita, L.S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C.D. & Zimmerman, J.K. (2009). Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *J. Ecol.*, 97, 1346–1359.

Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations* (eds den Boer, P.J. & Gradwell, G.R.). Centre for Agricultural Publishing & Documentation, Wageningen, The Netherlands, pp. 298–312.

Cornelissen, J.H.C., Werger, M.J.A. & CastroDiez, P. (1997). Foliar nutrients in relation to growth, allocation and leaf traits in seedlings of a wide range of woody plant species and types. *Oecologia*, 111, 460–469.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E. *et al.* (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.*, 51, 335–380.

Ewel, J.J. & Whitmore, J.L. (1973). *The Ecological Life Zones of Puerto Rico & the United States Virgin Islands. Forest Service Research Papers ITF-18*. International Institute of Tropical Forestry, Rio Piedras, Puerto Rico, USA.

Gilbert, G.S. & Webb, C.O. (2007). Phylogenetic signal in plant pathogen-host range. *Proc. Natl. Acad. Sci. USA*, 104, 4979–4983.

Gónzalez, M.A., Roger, A., Courtois, E.A., Jabot, F., Norden, N., Paine, C.E.T. *et al.* (2010). Shifts in species and phylogenetic diversity between sapling and tree communities indicate negative density dependence in a lowland rain forest. *J. Ecol.*, 98, 137–146.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.*, 111, 1169–1194.

Hosmer, D. & Lemeshow, S. (1989). *Applied Logistic Regression*. John Wiley & Sons, New York.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ, USA.

Janzen, D. (1970). Herbivores & the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.

Kohyama, T. (1993). Size-structured tree populations in gap-dynamic forest. The forest architecture hypothesis for the stable coexistence of species. *J. Ecol.*, 81, 131–143.

Kraft, N.J.B., Cornwell, W.K., Webb, C.O. & Ackerly, D.D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am. Nat.*, 170, 271–283.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008). Functional traits and niche based tree community assembly in an Amazonian forest. *Science*, 322, 580–582.

Kress, W.J., Erickson, D.L., Swenson, N.G., Thompson, J., Uriarte, M. & Zimmerman, J.K. (in press). Improvements in the application of DNA barcodes in building a community phylogeny for tropical trees in a Puerto Rican Forest Dynamics Plot. *PLoSOne*.

Letcher, S.G. (2009). Phylogenetic structure of angiosperm communities during tropical forest succession. *Proc. R. Soc. B-Biol. Sci.*, 277, 97–104.

Maddison, W.P. & Maddison, D.R. (2010). Mesquite: a modular system for evolutionary analysis. (Version 2.73). Available at: http://mesquiteproject.org.

Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.-H. & Vilchez-Alvarado, B. (2009). Resilience of tropical rain forests: tree community re-assembly in secondary forests. *Ecol. Lett.*, 12, 385–394.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G. *et al.* (2008). Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, 89, 1908–1920.

R Development Team. (2008). *A Language and Environment for Statistical Computing*. Vienna, Austria.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997). From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. USA*, 94, 13730–13734.

Silvertown, J., Dodd, M., Gowing, D., Lawson, C. & McConway, K. (2006). Phylogeny and the hierarchical organization of plant diversity. *Ecology*, 87, S39–S49.

Swenson, N.G. & Enquist, B.J. (2009). Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, 90, 2161–2170.

Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007). The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology*, 88, 1770–1780.

Thompson, J., Brokaw, N., Zimmerman, J.K., Waide, R.B., Everham, E.M. III, Lodge, D.J. *et al.* (2002). Land use history, environment, and tree composition in a tropical forest. *Ecol. Appl.*, 12, 1344–1363.

Tilman, D. (1982). *Resource Competition and Community Structure. Monographs in Population Biology*. Princeton University Press, Princeton, NJ, USA.

Uriarte, M., Canham, C.D., Thompson, J. & Zimmerman, J.K. (2004a). A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecol. Monogr.*, 74, 591–614.

Uriarte, M., Condit, R., Canham, C.D. & Hubbell, S.P. (2004b). A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbors matter? *J. Ecol.*, 92, 348–360.

Vamosi, S.M., Heard, S.B., Vamosi, J.C. & Webb, C.O. (2008). Emerging patterns in the comparative analysis of community structure. *Mol. Ecol.*, 18, 572–592.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.

Webb, C.O., Gilbert, G.S. & Donoghue, M.J. (2006). Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology*, 87, S123–S131.

Weiher, E. & Keddy, P.A. (1999). Assembly rules as trait-based constraints on community composition. In: *Ecological Assembly Rules* (eds Weiher, E. & Keddy, P.). Cambridge University Press, Cambridge, UK, pp. 251–271.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999). Challenging Theophrastus: a common core list of plant traits for functional ecology. *J. Veg. Sci.*, 10, 609–620.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.*, 33, 125–159.

Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, 130, 1–14.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M. *et al.* (2007). Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann. Bot.*, 99, 1003–1015.

Zimmerman, J.K., Everham, E.M., Waide, R.B., Lodge, D.J., Taylor, C.M. & Brokaw, N.V.L. (1994). Responses of tree

species to hurricane winds in subtropical wet forest in Puerto-Rico: implications for tropical tree life-histories. *J. Ecol.*, 82, 911–922.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Phylogeny construction.
Appendix S2 Results from the PCA analyses of eight trait data for tree species in the LFDP.
Appendix S3 List of parameters included in the model. We provide boundaries for parameter values in square brackets.
Appendix S4 Akaike weights for (a) growth and (b) survival models considered in our analyses.
Appendix S5 Estimated parameters with associated support intervals for the most parsimonious growth and survival neighbourhood model for the focal species.

Appendix S6 *K* values for phylogenetic conservatism for the nine traits included in the analyses.

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