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1 **TRAIT SIMILARITY, SHARED ANCESTRY, AND THE STRUCTURE OF NEIGHBORHOOD**

2 **INTERACTIONS IN A SUBTROPICAL WET FOREST: IMPLICATIONS FOR COMMUNITY**

3 **ASSEMBLY**

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6   **ABSTRACT**

7   The phylogenetic structure and distribution of functional traits in a community provide insights

8   into community assembly processes. However, these insights are sensitive to the spatial scale of

9   analysis. Here we use spatially-explicit, neighborhood models of tree growth and survival for 19

10   tree species, a highly-resolved molecular phylogeny, and information on eight functional traits to

11   quantify the relative efficacy of functional similarity and shared ancestry in describing the effects

12   of spatial interactions between tree species on demographic rates. We also assess the congruence

13   of these results with observed phylogenetic and functional structure in the neighborhoods of live

14   and dead trees.

15   We found strong support for models in which the effects of spatial neighborhood

16   interactions on tree growth and survival were scaled to species-specific mean functional trait

17   values (e.g., wood specific gravity, leaf succulence, maximum height) but not to phylogenetic

18   distance. The weak phylogenetic signal in functional trait data allowed us to interpret

19   independently the static neighborhood functional and phylogenetic patterns. We observed greater

20   functional trait similarity in the neighborhoods of live trees relative to those of dead trees

21   suggesting that environmental filtering is the major force structuring this tree community at this

22   scale while competitive interactions play a lesser role.

23

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).

Interpretation of these patterns depends on the spatial scale of analyses and the degree of functional trait conservatism (Webb *et al*. 2002). 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. On the other hand, 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).

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 and Enquist 2009). The implicit assumption of this research is that phylogenetic or functional community structure reflects the

1   influence of antecedent processes, such as environmental filtering or competitive interactions, on

2   demographic rates. A number of studies have also investigated how the nature and spatial scale of

3   phylogenetic community structure changes with life history stage or tree size (e.g., Swenson *et al.* 2007),

4   as well as the relationship between demographic rates and functional characteristics of species (e.g,,

5   Poorter *et al.* 2008). Despite these advances, no empirical studies have simultaneously quantified and

6   compared the relative importance of functional similarity and shared ancestry in shaping spatial

7   interactions among tree species, the effects that these interactions have on demographic rates, and the

8   observed phylogenetic and functional structure at the neighborhood spatial scale at which these processes

9   take place.

10   Understanding the relative importance of phylogenetic and functional traits in predicting the

11   effect of interactions among species on tree demography will provide important insights into community

12   assembly processes. Given that key functional traits are robust indicators of plant performance and

13   competitive strategies (Grime 1977; Reich *et al.* 1997; Weiher *et al.* 1999; Westoby *et al.* 2002), a

14   superior predictive performance of functional traits relative to phylogeny in shaping spatial interactions

15   between neighboring trees might suggest that niche differentiation in resource capture is more important

16   in shaping community assembly at this scale than phylogenetic relatedness. On the other hand, if

17   phylogenetic relatedness better predicts the demographic effect of neighborhood (<20 m) spatial

18   interactions between tree species, phylogenetically conserved species characteristics different from

19   commonly measured functional traits, such as defensive compounds against shared enemies, may be

20   important for community assembly (Gilbert and Webb 2007).

21   Our goal in this paper is to use spatially-explicit, neighborhood models of tree growth and

22   survival for 19 tree species, together with a highly-resolved DNA barcode molecular phylogeny and

23   information on eight functional traits, to examine the relative importance of phylogeny and functional

24   trait values in structuring neighborhood interactions between tree species. The detection of a phylogenetic

25   signal for biotic interactions may be more easily detected at small (< 100 m^2) spatial scales (Webb *et al.*

26   2002). By focusing our analyses at the neighborhood scale, we expect to simultaneously quantify the

1 effect of individual interactions that lead to competitive exclusion and the degree to which

2 environmental filtering operates at this scale. We employ tree growth and survival data collected in

3 the successional communities in the Luquillo Forest Dynamics Plot (LFDP), in Puerto Rico.

4   Our analyses address three fundamental questions for species coexistence. First, we ask whether

5 the strength of neighborhood interactions between species is proportional to relative distance in mean trait

6 values. The rationale for this hypothesis is that species with higher mean trait values (e.g., leaf N) would

7 compete more strongly for resources (e.g., N) than species with lower values. Support for this premise

8 would suggest that competitive interactions for limiting resources among trees may have contributed to

9 community assembly. Second, we ask whether greater phylogenetic relatedness results in stronger

10 negative neighborhood interactions between tree species. Interpretation of these patterns depends on the

11 degree of phylogenetic trait conservatism (Webb *et al*. 2002). Third, we ask whether the answers to

12 questions 1 and 2 can be interpreted in light of observed changes in the phylogenetic and functional trait

13 composition of tree neighborhoods over time. To do so, we compared the composition of phylogenetic

14 and functional traits in the neighborhoods (including all trees) of dead and live focal trees for each focal

15 species. We expect that if functional traits modulate the demographic effects of neighborhood interactions

16 (i.e., that focal tree survival and growth are lower in the neighborhood of functionally similar species) the

17 trait structure of tree neighborhoods will reflect the relative strength of environmental filtering versus

18 species interactions at the local spatial scale. Prevalence of trait-mediated competitive interactions may

19 result in greater trait similarity in the neighborhoods of dead trees relative to those of live trees while

20 predominance of local-scale environmental filtering should result in the opposite pattern (Table 1)**.** This

21 belief stems from the assumption that there are environmental factors (e.g., soil moisture) that influence

22 demographic rates at this scale independently from spatial interactions between neighbors. The same

23 predictions hold when neighborhood interactions are affected by phylogenetic relatedness.

24   Because they reflect community assembly in action, successional tropical forests provide an ideal

25 natural laboratory for testing the power of an integrated functional trait and phylogenetic approach to

1	community assembly. High leaf nitrogen content and low wood density, functional traits associated with

2	fast growth, are characteristic of early successional species (Bazzaz and Pickett 1980). In contrast, later in

3	succession, biotic filters associated with Janzen-Connell effects may play a more important role in species

4	dynamics and therefore species with functional traits related to defense (e.g., leaf toughness) should be

5	favored; these effects may also extend to closely related species (Uriarte *et al.* 2004b).

6	**METHODS**

7	**Study site and field surveys**

8	The Luquillo Forest Dynamics Plot (LFDP) is a 16-ha permanent forest plot (SW corner *18° 20' N, 65°*

9	*49' W*) located in the Luquillo Mountains of Puerto Rico. The forest is classified as subtropical wet in the

10	Holdridge life zone system (Ewel and Whitmore 1973). Rainfall averages 3,500 mm per year. Elevation

11	ranges from 333 to 428 m a.s.l. The LFDP was established in 1990. Censuses are carried out every five

12	years. All free- standing woody stems ≥1 cm diameter at 130 cm from the ground (dbh) in the LFDP are

13	tagged, identified to species, mapped, and measured (Thompson *et al.* 2002).

14	*Species selection* -- The LFDP contains on average 89 species of trees with stems ≥ 10 cm dbh

15	distributed over 72 genera and 38 families. Our research and modeling focus on 19 species that display a

16	wide variation of life history characteristics (Table 2) (Zimmerman *et al.* 1994, Uriarte *et al.* 2004a), had

17	more than 400 individuals ≥ 1cm dbh of which at least 70 died between the 1990 and 1995 censuses.

18	These criteria ensured that we could obtain robust parameter estimates. Together these species account for

19	approximately 85% of stems ≥10 cm dbh in the plot.

20	*Hurricane damage*--Hugo, a category 4 hurricane, struck the LFDP in 1989 causing significant

21	damage (Zimmerman *et al.* 1994). The first census started in 1990, the year after Hurricane Hugo. This

22	census included an initial categorical estimate of damage for all stems ≥10 cm dbh to prevent loss of data

23	due to decomposition of trees killed or damaged by Hurricane Hugo. Damage observations were

24	classified into three categories: (1) no or light damage (≤ 25% of crown volume removed by the storm),

1   (2) medium damage (25 – 75% of crown volume lost), or (3) heavy or complete (> 75% of the crown lost,

2   stem snapped, root break, or tip-up).

3   *Trait and phylogeny data*-- Trait data for all woody species present in the LFDP were derived

4   from vegetation samples collected using standardized protocols (Cornelissen *et al*. 2003). Samples were

5   collected to calculate species mean leaf traits (25 samples) and wood specific gravity (10 samples). We

6   selected eight functional traits that are believed to represent fundamental functional trade-offs in life-

7   history differentiation among tree species (Wright *et al*. 2007). These include leaf area (cm^2), specific leaf

8   area (cm^2/g), leaf nitrogen content (%N), leaf phosphorus content (%P), leaf succulence (g H_2O/cm^2 leaf

9   area), wood specific gravity (g/cm^3), maximum tree height (m), and seed mass (g). Details on phylogeny

10 construction and results are provided in Kress *et al*. (In press).

11

12 **Spatially-explicit models of tree growth and survival**

13 We used data from the 1990 and 1995 censuses of the LFDP to develop neighborhood models of tree

14 growth and survival for 19 of the common tree species (Table 2). The difference in dbh between the first

15 and second census together with the time difference between censuses were used to calculate average

16 annual growth rate for each tree. Annual mortality estimates were obtained from mortality records from

17 the second census and time between censuses for each individual tree. Although the palm *Prestoea*

18 *acuminata* is the most abundant species at the site, we did not analyze it as a focal species in our growth

19 model because diameter measurements do not reflect growth for this species. We considered all species in

20 the plot as potential neighbors.

21   Our modelling approach relies on traditional distance-dependent analyses of competition, in which

22 tree growth is analysed as a function of the sizes and distances to neighbouring trees (see references in

23 Uriarte et al. 2004b). We assume that each individual has a species-specific maximum potential growth

24 rate, which is adjusted to account for the size of the focal tree, the structure and composition of its

25 neighborhood, and previous hurricane damage to both the focal tree and its neighbors (Uriarte *et al*.

26 2004a). A similar approach was used to estimate survival. Our models take the form:

1    $g = g_m \, \varphi \; \delta \, v$ [Eqn. 1]

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

3   hurricane effect, δ is the size effect and v is the neighborhood effect. A similar approach was taken for

4   survival analyses.

5   *Hurricane Effects.*-- Hurricane damage affects potential maximum growth rate and probability of

6   survival of the focal tree species (φ, in Eqns. 1a & b). Damage also alters the crowding effects of

7   neighbors (see *Neighborhood Effects*).

8   *Size Effects on Growth.*-- Potential radial growth is assumed to vary with the dbh of the focal tree.

9   We use a lognormal function for the shape of this effect, because it is flexible, and supported by both

10   theoretical and empirical evidence (Uriarte *et al*. 2004a):

11   $$g = g_m * exp^{\left[-\frac{1}{2} \left[\frac{ln(DBH / X_0)}{X_b} \right]^2 \right]}$$ [Eqn. 2]

12   where g_m is the maximum potential radial growth (cm/yr) in the absence of neighbors (i.e. at the peak of

13   the lognormal shape), X_0 is the dbh at which g_m occurs, and X_b determines the breadth of the function.

14   *Neighborhood Effects*-- The net effect of a neighboring tree on the growth of a focal tree of a

15   given species is assumed to vary as a function of the size of the neighbor, and inversely with distance to

16   the neighbor. The effect of an individual neighbor is multiplied by a species-specific scalar λ_s [0 –1]

17   which allows for differences among species in their competitive effect on a focal tree. The neighborhood

18   crowding index for individual *focal* of species k is:

19   $$NCI_{focal,k} = DBH^{\gamma}_{focal,k} \sum_{i=1}^{S} \sum_{j=1}^{n_i} \lambda_{ik} \frac{DBH_j^{a_k}}{Distance_j^{\beta_k}}$$ [Eqn. 3]

20   where $DBH^{\gamma}_{focal,k}$ is the DBH of that focal individual, weighted by an exponent γ that characterizes the

21   size sensitivity of individuals the focal species k to neighborhood effects. The double sum is over S

22   species and the n_i neighbors of each species i in the focal individual's neighborhood of estimated

23   maximum radius R. The parameter λ_{ik} is a pairwise competition coefficient, and it estimates the per-

1   capita effect of species *i* on species *k*. Parameters α_k and β_k allow non-linear scaling of the effects of

2   neighbor size and distance on focal species *k*. The parameter η is drawn from a vector with three possible

3   values that correspond to the three levels of hurricane damage to a neighboring tree. Neighborhood effects

4   *(v)* are translated into actual effect on growth or survival by using a negative exponential function of NCI.

5     $$v = exp^{-CNCI_i^{D}}$$ [Eqn. 4]

6   where C and D are species-specific estimated parameters, and NCI$_i$ is the neighborhood competition

7   index for focal tree *i.* To avoid edge effects, we excluded from the analyses all focal trees that were within

8   20 m of the edge of the plot.

9   Our motivation for this study was to explore the degree to which species functional traits and

10   phylogenetic relatedness can explain the effects of spatial interactions between species on tree

11   demography. To this end, we compared 13 models that make different assumptions about the nature of

12   these interactions (i.e., values of λ in Eqn. 3). The simplest "control" model assumed that only tree size

13   influenced focal tree growth and survival. The second model assumed that all neighbors had equivalent

14   effects on the focal tree regardless of phylogenetic relatedness or functional similarity. The third model

15   differentiated between conspecific and heterospecific neighbors. In a fourth set of models, we assigned a

16   fixed λ to each competitor scaled to the maximum phylogenetic distance calculated using the DNA

17   barcode phylogeny. Values of λ for conspecifics for this model were assumed to be 1 (no distance) and

18   effects of neighbors were scaled from 0-1 according to phylogenetic distance to the focal species. Finally,

19   we evaluated a set of 9 trait-based models (Models #5-12) by assigning λ values based on the difference

20   in mean trait values among species. For each of the 8 traits considered, competition coefficients were

21   scaled to the maximum observed values in the community with 1 being the effect of a neighbor from the

22   species with the highest mean value for that trait (e.g., highest wood specific gravity). Leaf area and seed

23   weight were log-transformed prior to scaling. As many of the traits are correlated, a PCA was conducted

24   to reduce the dimensionality of the data. The first three axes of the PCA were used in a hierarchical

25   clustering algorithm that produced a trait distance matrix (Appendix II). Using this matrix, we considered

1   an additional trait-based model (Model #13) that scaled λ values based on composite trait distance. Note

2   that this formulation of competitive effects based on trait data assumes that the strongest competitive

3   effect accrues to the species with the highest trait value. For instance, if species A has the maximum trait

4   value of 1, sp. B of 0.5, and species C of 0.1, our formulation scales the relative trait dissimilarity

5   between species B and species C to 0.4 and but that between species A and C to 0.9. As such, it provides

6   an index of niche differentiation (i.e., trait dissimilarity) among species.

7   Model parameters were estimated using maximum likelihood. Initial parameter values are

8   summarized in Appendix III. We calculated asymptotic 95% support limits for each of the parameters.

9   The 13 models were compared using Akaike's Information Criterion (AIC) and Akaike weights with the

10   best candidate model having the lowest AIC and highest weightm (Burnham and Anderson 2002). We

11   assessed the goodness of fit of our growth models using traditional regression statistics (R^2) and the slope

12   of the regression of observed radial growth on predicted radial growth was used to measure bias. For

13   mortality analyses, we used compared the percentage of trees in a given predicted survival bin (0-10%,

14   10.01-20%, etc) (Hosmer and Lemeshow 1989).

15

16   **Comparison of neighborhood models of tree demography with phylogenetic and functional trait**

17   **structure**

18   To assess the congruence of our models with static phylogenetic and trait structure patterns, we calculated

19   abundance weighted neighborhood (20 m) phylogenetic relatedness indices (NRI) and functional trait

20   similarity (TSI) for live and dead trees in census 2 for all focal species. Live trees recruited between the

21   1990 and 1995 censuses were excluded from all calculations because they did not enter into the

22   neighborhood models. We considered all the species in the LFDP as the community pool. The trait

23   distance matrix was used as input to calculate TSI using the same procedure as for NRI.

24   Interpretation of our results regarding the importance of niche differentiation versus

25   environmental filtering in structuring the phylogenetic structure of neighborhoods depends on the degree

26   of phylogenetic trait conservatism. We employed trait data and the LFDP phylogeny to test whether

1 functional traits were phylogenetically using Blomberg's K statistic (Blomberg *et al*. 2003). Where

2 necessary, trait values were normalized using log transformations. All analyses were conducted using R

3 statistical software (R Development Team 2008).

4 <center>**RESULTS**</center>

5 <center>*Likelihood and Goodness of Fit of Growth and Survival Models*</center>

6 We estimated maximum likelihood parameter values for 13 growth and survival models for 19 selected

7 focal species with the goal of quantifying the importance of phylogenetic distance and trait similarity in

8 structuring neighborhood interactions (Table 3, Appendix IV). The percent of variance in individual

9 growth rates explained by the most parsimonious models ranged from 2% for *Trichilia pallida* to 23% for

10 *Schefflera morototoni* while the fit of the survival model ranged from 29% for *Myrcia deflexa* to 99% for

11 several species (Table 3)..

12 <center>*Neighborhood effects on growth and survival*</center>

13 *Growth*.-- For the growth analyses, 12 of the 18 species examined (*i.e.*, excluding *Prestoea acuminata*)

14 provided support for a model for which differences among species in mean trait values structured

15 neighborhood interactions (Table 3, Appendix IV). Of these 12 species, six supported a model that scaled

16 neighborhood interactions according to differences in wood specific gravity, two in species leaf

17 succulence, and two in maximum tree height. The final two species in this group of 12 exhibited support

18 for more than one growth model: *Tabebuia heterophylla* had similar Akaike weights for the wood specific

19 gravity and leaf succulence models, and *Drypetes glauca* supported the maximum tree height and

20 equivalent competitor model. The six species in the growth analyses that did not support a trait-based

21 model were distributed among the size only model (2 species), the equivalent competitors model (2

22 species), and the model that differentiated between conspecifics and heterospecific neighbors (2 species)

23 (Table 3). None of the 18 species included in the growth analyses displayed any support for the

24 phylogenetic distance neighborhood model as evidenced by extremely low Akaike weights for this set of

25 models (Appendix IV).

1 *Survival.*--In general, the relative strength of evidence in support of any one particular model at

2 the community level was weaker for survival than growth (Appendix IV). Three species, *Cecropia*

3 *schreberiana*, *Casearia sylvestris*, and *Inga laurina*, supported the phylogenetic distance model although

4 only *C. schreberiana* exhibited strong support of this model. For five of the focal species, *Alchornea*

5 *latifolia, Casearia arborea, Ocotea leucoxylon, Schefflera morototoni* and *Trichilia pallida,* a simplified

6 model that distinguished between conspecific and heterospecific neighbors was the most parsimonious

7 (Table 3). Only size influenced the probability of survival for *Cordia borinquensis* and *Myrcia deflexa*.

8 For the remaining nine species, models that distinguished between neighbors on the basis of mean

9 functional trait values provided a significantly better fit to the data. Nevertheless, there were no clear

10 patterns in the success of any one trait in predicting neighborhood effects on survival. Interestingly, none

11 of the 19 species supported the equivalent competitor model for survival, in contrast to the results for the

12 growth models.

13   *Comparison of Model Results and Neighborhood Structure*

14   To assess the congruence of the results of the neighborhood analyses with phylogenetic and

15 functional neighborhood structure, we compared phylogenetic distance (NRI) and trait similarity (TSI) of

16 all trees (live and dead) in a 20 m radius surrounding live or dead trees for the 19 focal species. Overall,

17 the NRI and TSI of neighbors surrounding live trees was greater than around dead trees, indicating greater

18 phylogenetic and trait dispersion in neighborhoods of dead focal trees (Mean NRI Dead = -0.43 ±0.04

19 S.E, mean NRI Alive = -0.26± 0.04 S.E.; ANOVA, F=9.65, d.f.= 1, 38, p=0.003, mean TSI dead= -0.10

20 ±0.08 S.E, mean TSI Alive= 0.32 ±0.10 S.E, ANOVA, F= 13.14, d.f. = 1, 38, p<0.0001, Fig. 2, Table 4).

21 All species that supported trait-mediated, neighborhood survival models had greater trait similarity in the

22 neighborhoods of live trees relative to those of dead trees (Table 4). In contrast, for two out of the three

23 species that supported the phylogenetic distance survival model, *Casearia sylvestris* and *Cecropia*

24 *schreberiana,* phylogenetic relatedness was greater in the neighborhood of live relative to dead trees

1 (Tables 3 & 4). For the third species, *Inga laurina*, the NRI for neighborhoods of live trees was greater

2 than for dead trees.

3   We also detected an effect of successional status on the phylogenetic structure of neighborhoods.

4 Specifically, neighborhoods (dead and live trees combined) of late-successional species were more

5 phylogenetically clustered than those of pioneer species (ANOVA, $F = 4.19$, d.f. = 2, 37, $p=0.02$, Fig. 2a).

6 Functional trait similarity varied in a similar manner across successional groups; neighborhoods of late

7 successional species had greater functional similarity than those of pioneer and secondary forest species

8 (ANOVA, $F= 7.15$, d.f. = 2,37, $p=0.002$, Fig. 2b).

9   Results from our analyses must be interpreted in light of the degree of phylogenetic trait

10 conservatism found for this community. Contrary to previous analyses (Swenson *et al*. 2007), we relied

11 on a more resolved phylogeny with trait data collected at the site, rather than taken from the literature. We

12 found a significant phylogenetic signal for only three of the nine traits tested: leaf % phosphorus, leaf

13 area, and seed mass (Appendix VI). For those three traits, values were more phylogenetically conserved

14 than would be predicted by a random association between phylogeny and traits.

15   **DISCUSSION**

16   *Effects of Phylogenetic Distance and Trait Similarity on Neighborhood Interactions*

17 Only three of the 19 species included in these analyses support a model that assumes that phylogenetic

18 proximity augments the strength of neighborhood interactions between species. In contrast, over 60% of

19 the 19 species supported models in which the effects of spatial neighborhood interactions on tree growth

20 and survival were scaled to species-specific mean functional trait values. Consequently, for the majority

21 of abundant tree species in the LFDP, shared ancestry, at least beyond the conspecific/heterospecific

22 dichotomy, does not mediate the effects of neighborhood interactions on tree growth and survival. Rather,

23 differences in trait values that reflect plant performance and functional competitive strategies moderate

24 negative competitive interactions among species at this stage (Grime 1977, Reich *et al*. 1997, Westoby *et*

25 *al*. 2002). These results suggest that stronger negative density dependent effects among conspecifics

26 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 neighborhood interactions (Canham *et al.* 2006), or legacies of historical negative competitive interactions between seedlings.

The lack of a strong phylogenetic signal in neighborhood 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 BCI, Panama). In a study in the BCI plot, Uriarte *et al*. (2004b) found that con-familiar neighbors 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 trait may be more informative as at finer resolutions. Previous analyses at this site using Phylomatic found phylogenetic signal in trait data (Swenson *et al*. 2007), in contrast to the present 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 tree diversity, resolution, and topology on these metrics (Vamosi *et al.* 2009, Cavender-Bares *et al.* 2009).

There were no clear patterns in the groupings of species that supported different models. Membership in a family, genus, or functional group was not a good predictor of the response of species to the structure of the neighborhood interactions. For instance, species that supported the wood specific

1   gravity growth models ranged from pioneer (*Schefflera morototoni*) to late successional (*Manilkara*

2   *bidentata*). Similarly, there were no clear patterns along taxonomic lines. The congeners *Casearia*

3   *arborea* and *Casearia sylvestris* supported different growth and survival models. Despite this variation,

4   there are several conclusions we can draw from the analyses. First, the strong showing of wood specific

5   gravity in the growth models corroborates results from other studies that found a strong link between

6   growth and wood specific gravity, presumably because diameter growth is directly related to the

7   construction costs of wood (Poorter *et al.* 2008). Similarly, leaf succulence plays an important role in the

8   maintenance of green foliage during drought, a critical requirement for sustained growth in forests subject

9   to dry spells (Cornelissen *et al.* 1997). Maximum tree height, which found some support in both survival

10 and growth models, is a good predictor of crown exposure and hence, competition for light (Kohyama

11 1993). Second, effects of traits that were phylogenetically conserved (leaf % P, leaf area, and seed mass)

12 had very weak support in the neighborhood models of growth and survival. This finding suggests that

13 evolutionary lability (i.e., the absence of trait conservatism) may facilitate species coexistence

14 (Silvertown *et al.* 2006, but see Ackerly *et al.* 2006). Third, growth of focal species was more sensitive to

15 finer gradations in the identity of neighbors than survival. This may simply reflect the fact that the

16 majority of mortality occurred in small size classes whereas growth was estimated across the whole range

17 of sizes therefore incorporated a greater range of responses to crowding. Alternatively, relatively low

18 numbers of dead trees or lack of variation in the composition of tree neighborhoods for some species may

19 have hindered our ability to detect distinct responses to the identity of neighbors.

20   *Comparison of Model Results and Neighborhood Structure*

21 To assess the congruence of model results with static community patterns, we evaluated the phylogenetic

22 and functional trait structure in the neighborhoods of dead and live trees for each focal species. The

23 absence of phylogenetic signal for most of the traits supported by the neighborhood models allows us to

24 interpret trait and phylogenetic patterns largely independently. Overall, we observed greater functional

25 trait similarity in the neighborhoods of live trees relative to those of dead trees. Together with strong

1 support for trait-mediated neighborhood models, these results suggest that environmental filtering is the

2 major force structuring this community at the neighborhood scale while competitive interactions play a

3 relatively minor role. This is not surprising given that environmental filters can have strong effects on

4 demographic rates (Weiher and Keddy 1995, Cavender-Bares *et al.* 2004). In contrast to the majority of

5 species that supported trait-based models, we found greater phylogenetic relatedness in the neighborhood

6 of dead trees relative to those of live trees for two out of the three species that supported the phylogenetic

7 distance model. These outcomes are consistent with a predominance of negative competitive interaction

8 between closely related species relative to environmental filtering. High rates of tree mortality and intense

9 thinning of individuals of early- and mid- successional species as the hurricane damaged canopy closed

10 may have increased the likelihood of detecting effects of competitive interactions on demographic

11 processes for these two species. Nevertheless, we failed to find this pattern for other early succesional

12 species (e.g., *S. morototoni*) suggesting that environmental filtering is more important in driving

13 neighborhood structure for these species. One potential reason for this pattern is that mortality may be

14 less spatially clustered in these species (e.g., recruited into smaller gaps after the hurricane) allowing for

15 less taxonomic variation around dead trees.

16   Phylogenetic and functional trait structure of tree neighborhoods differed considerably between

17 successional groups. Both trait and phylogenetic similarity were greater for live late successional species

18 than for other groups. Late successional species share certain traits such as greater wood specific gravity,

19 lower leaf % N and P, larger seed weights, and low specific leaf area and may be present in areas with

20 relatively little disturbance leading to greater trait similarity in the neighborhood of these species (Bazzaz

21 and Pickett 1980). Coupled with the outcomes of the neighborhood models, these results are consistent

22 with an increasing importance of environmental filtering relative to competitive interactions during

23 succession, at least at this neighborhood scale. This was a surprising result given that pathogen-mediated

24 neighborhood interactions on seedling mortality are expected to intensify during succession (Comita *et al*.

25 2009), and may extend to closely related species (Webb *et al*. 2006, Gilbert and Webb 2007). The only

26 other study to examine shifts in phylogenetic relatedness through succession found increased

1 overdispersion in older relative to younger sites in a chronosequence (Letcher 2009). However, these

2 findings were the result of recruitment of species present in the regional pool representing different

3 lineages as succession proceeded (Norden *et al.* 2009), a factor not included in this study.

4 Despite considerable efforts to understand the processes that generate variation in functional traits

5 and phylogenetic structure across spatial scales (e.g., Silvertown *et al*. 2006, Swenson *et al*. 2007),

6 temporal comparison in communities undergoing succession remains rare (but see Letcher 2009). Yet,

7 such comparisons can provide important insights into community assembly processes. Our analyses

8 illustrate the dynamic nature of community assembly processes through succession. It also calls attention

9 to the importance of coupling an understanding of demographic processes with analyses of phylogenetic

10 and functional community structure.

11

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8

1 Table 1. Expected relationships between outcomes of neighborhood demographic models and phylogenetic (NRI) and functional trait similarity

2 (TSI) in the neighborhoods of live and dead trees. These predictions hinge on the degree of phylogenetic trait conservatism. See Introduction for

3 more details on the rationale behind these predictions.

4

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

TSI = Trait Similarity Index

NRI = Net Relatedness Index

5

6

1 Table 2. Species included in the neighborhood analyses, including their successional status (P=pioneer, S=secondary forest species; L=late

2 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

3 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

4 Plot.

Species	Family	Succ. Status	Life form	Percent tree mortality	Percent total adult abund.	# stems > 1 cm dbh	Max dbh (cm)
Alchornea latifolia (ALCLAT)	Euphorbiaceae	S	L	33.26	1.19	1,271	66
Buchenavia tetraphylla (BUCTET)	Combretaceae	L	L	20.64	1.17	406	151
Casearia arborea (CASARB)	Salicaceae	S	S	22.65	4.93	6,168	48
Casearia sylvestris (CASSYL)	Salicaceae	S	S	15.45	1.15	3,085	27
Cecropia schreberiana (CECSCH)	Cecropiaceae	P	M	48.51	3.13	11,220	48
Cordia borinquensis (CORBOR)	Boraginiaceae	L	S	10.51	0.05	1,266	25
Dacryodes excelsa (DACEXC)	Burseraceae	L	L	3.67	6.84	1,731	82
Drypetes glauca (DRYGLA)	Euphorbiaceae	L	S	14.80	0.99	617	38
Guarea guidonia (GUAGUI)	Meliaceae	L	L	28.44	1.98	1,132	96
Inga laurina (INGLAU)	Fabaceae	S	S	15.55	2.75	1,607	87
Manilkara bidentata (MANBID)	Sapotaceae	L	L	4.13	4.53	1,803	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	8,521	42
Schefflera morototoni (SCHMOR)	Araliaceae	P	M	38.83	0.99	4,726	75
Sloanea berteriana (SLOBER)	Elaeocarpaceae	L	L	5.82	3.20	3,622	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

1

2

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	Conspp. vs heterospp.	0.99
Buchenavia tetraphylla	Size only	0.14	Leaf P	0.99
Casearia arborea	Wood specific gravity	0.12	Conspp. vs heterospp.	0.99
Casearia sylvestris	Conspp. vs heterospp.	0.03	Phylogenetic distance	0.92
Cecropia schreberiana	Equal neighbors	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 neigh./Max Height	0.02	Leaf N/Spec. wood grav.	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 neighbors	0.07	Size only	0.29
Ocotea leucoxylon	Size only	0.18	Conspp. vs heterospp.	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	Conspp. vs heterospp.	0.99
Sloanea berteriana	Leaf succulence	0.06	Leaf succulence	0.63
Tabebuia heterophylla	Leaf suc./Spec. wood grav.	0.08	SLA	0.88
Trichilia pallida	Conspp. vs heterospp.	0.02	Conspp. vs heterospp.	0.76

1

1   Table 4. Mean and standard errors for Net Relatedness Index (NRI) and Trait Similarity Index (TSI) for

2   neighbor trees included within a 20 m radius of live and dead trees for the 19 species included in the

3   analyses. Trees that supported the phylogenetic distance survival model are indicated with a *P*; those that

4   supported a trait-based model with a *T*. Asterisks indicate that mean values of neighborhood NRI or TSI

5   differed between live and dead trees at α=0.05.

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[T]	-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[P]	-0.26 (0.01)	-0.42 (0.00)*	0.11 (0.01)	-0.01 (0.01)*
Cecropia schreberiana[P]	-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[T]	-0.33 (0.06)	-0.04 (0.01)*	0.46 (0.09)	1.08 (0.01)*
Drypetes glauca[T]	-0.31 (0.04)	-0.02 (0.02)*	0.26 (0.06)	0.82 (0.03)*
Guarea guidonia[T]	-0.43 (0.03)	-0.16 (0.01)*	-0.12 (0.03)	0.78 (0.03)*
Inga laurina[P]	-0.44 (0.03)	-0.19 (0.01)*	-0.12 (0.04)	0.48 (0.02)*
Manilkara bidentata[T]	-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[T]	-0.58 (0.04)	-0.42 (0.02)*	-0.24 (0.04)	0.05 (0.04)*
Prestoea acuminata[T]	-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[T]	-0.18 (0.03)	0.063 (0.00)*	0.77 (0.03)	1.28 (0.01)*
Tabebuia heterophylla[T]	-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)*

1   **FIGURES**

2   Figure 1. DNA barcode phylogeny of the woody species in Luquillo Forest Dynamics Plot. Each

3   terminal branch represents a single species designated by its taxonomic order. Values for wood specific

4   gravity for each species were mapped onto the tree using Mesquite (Version 2.0). See Methods for details

5   on tree construction. Mapped wood specific gravity data was categorized into the following four

6   quantiles:<0.25, 25-50, 50-75, > 75%. Details on phylogeny construction are provided in Appendix I.

7

8   Figure 2. Net Relatedness Index (NRI) and trait similarity index (NTI) for trees included within a 20

9   radius of live and dead trees for pioneer, secondary forest, and late successional trees. Different letters

10   indicate that means are significantly different at α=0.05.

11

Figure 1.

Character: Wood Density
Parsimony reconstruction (
Unordered) [Steps: 60]

1st Quartile
2nd Quartile
3rd Quartile
100%
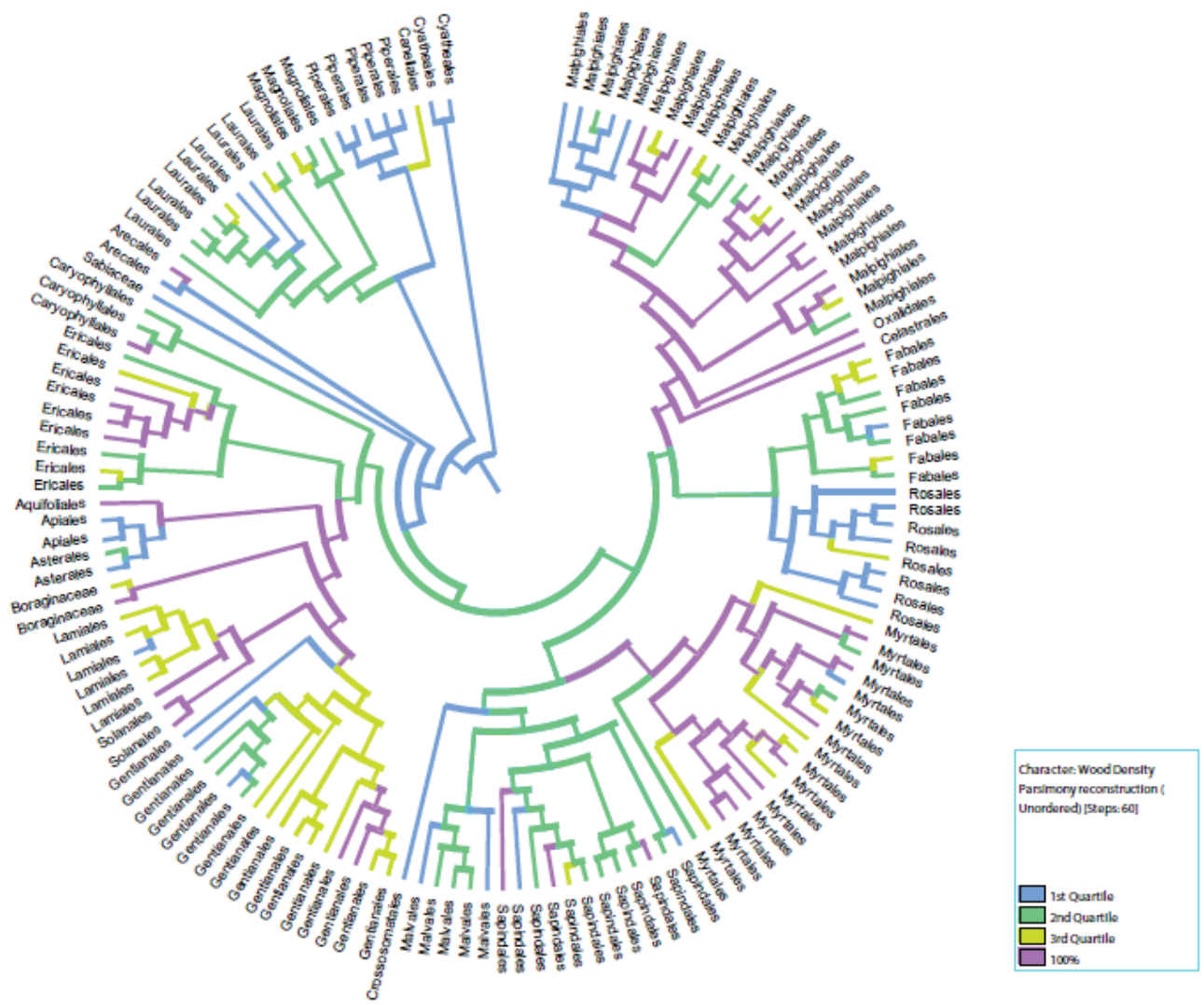
1 **Figure 2.**
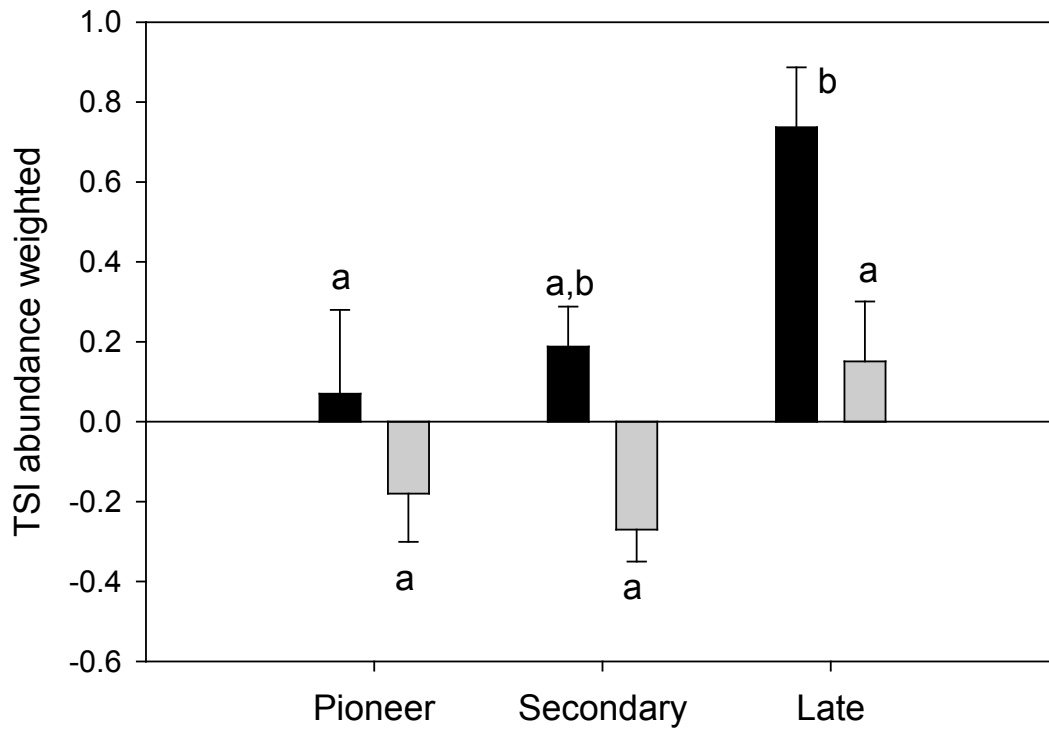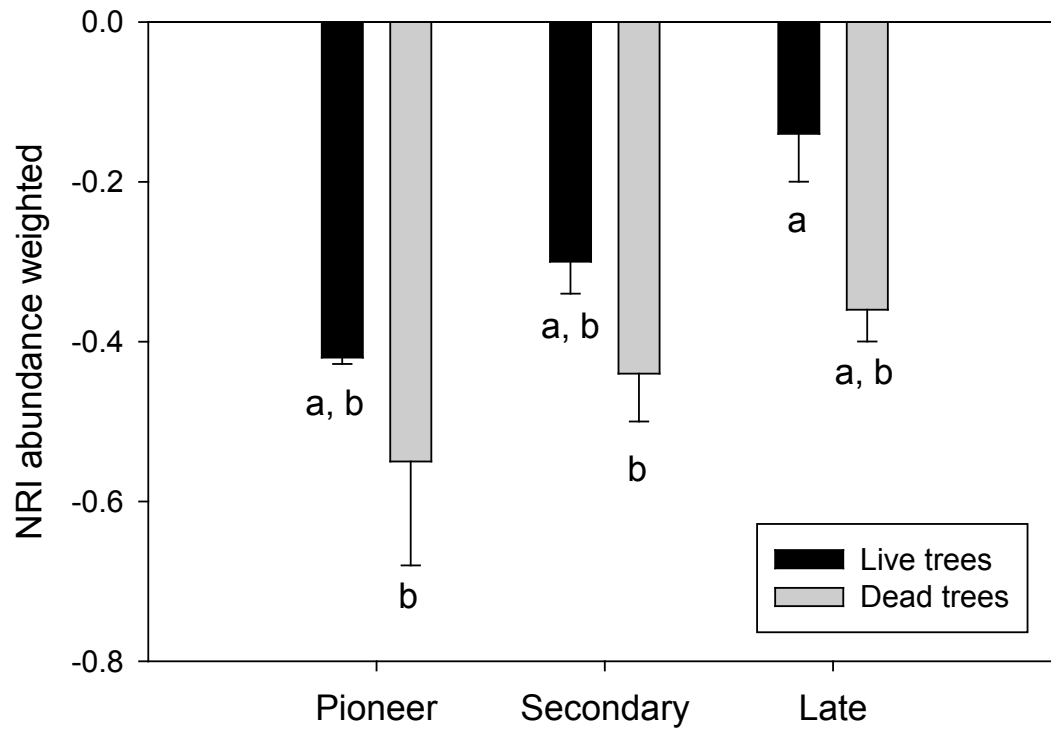
2

1   **APPENDIX I.** Phylogeny construction

2   Leaf tissue samples were field collected from tagged individuals within the LFDP by NGS and

3   preserved using silica gel. Approximately 50 mg of each sample of leaf material was placed

4   within a well of a 2-mL polypropylene 96-well matrix screen-mate plate (Matrix Technologies)

5   and transferred to the Laboratories of Analytical Biology at the Smithsonian Institution for DNA

6   extraction and sequencing. The community phylogeny for the LFDP was generated using a

7   multi-locus barcode library of three markers (*rbcL*, *matK*, and *trnH-psbA*). Details of sequence

8   editing, alignment, and assembly are provided in Kress *et al.* (2009). Briefly, a data matrix was

9   constructed for 144 species with sequences from three DNA barcode regions. The matrix

10   included *rbcLa* sequences for 144 species (trees and shrubs found in the LFDP), *matK* for 100

11   species and *trnH-psbA* for 123 species. The *trnH-psbA* spacer was aligned such that only

12   members of the same family were compared with each other and when only one species per

13   family or per order was present, those sequences were not included in the sequence matrix (see

14   Kress *et al*. 2009 for details on nested super-matrix design). The sequence matrix was then

15   analyzed by parsimony implemented in PAUP (Swofford 2000); the one difference from Kress *et*

16   *al*. (2009) was the use of an ordinal constraint tree, which specified that all trees be congruent

17   with APG III (2009) in their ordinal topology. The phylogenetic reconstruction was done in two

18   steps: 1) a short search for each of 200 independent random addition phylogenetic trees with two

19   trees saved at each random addition sequence, which was followed by 2) an exhaustive heuristic

20   search using the phylogenetic trees compiled from the 200 random additions resulting in 360,000

21   equally parsimonious trees. One of the 360,000 equally parsimonious trees was then selected for

22   use in this study. The consensus tree produced from compilation of the 360,000 trees exhibited

23   very strong topological support (Kress *et al.,* In press) suggesting that the evolutionary

1   hypothesis represented by the phylogeny closely approximates true historical relationships (Fig.

2   1).

3   **References**

4   Swofford , D.L. 2000. PAUP: Phylogenetic Analysis Using Parsimony. Version 4. Sinauer

5   Associates, Sunderland, Massachusetts.

6

7

1 **APPENDIX II.** Results from the PCA analyses of 8 trait data for tree species in the LFDP.

2

Trait	Comp.1	Comp.2	Comp.3
Leaf % P	-0.01	-0.028	-0.017
Leaf % N	-0.181	-0.957	0.154
Wood spec. gravity	0.009	0.062	0.059
Leaf area	0.104	-0.187	-0.947
SLA	-0.041	-0.113	-0.028
Leaf succulence	-0.016	0.058	-0.068
Max. height	0.086	0.041	-0.221
Seed weight	0.973	-0.166	0.146
Cum. Variance Explained	0.6	0.84	0.95

3

1   **APPENDIX III.** List of parameters included in the model. We provide boundaries for parameter values in square brackets.

2

3   <u>Growth Model</u>   <u>Mortality Model</u>

4   Maximum Growth (MaxGr.)   [0-40 mm/yr]   Maximum prob. of survival (MaxSurv) [0-1]

5   Hurricane effects on: (two levels complete and intermediate damage).

6   Maximum growth (φ_g) [0-1]   Maximum prob. survival (φ_s) [0-1]

7   Effective neighborhood radius (R) [0-20]   Effective neighborhood radius (R) [0-20m]

8   Mode (X_0) and variance (X_b) for lognormal relationship between:

9   Size and growth; X_0 [0-200 cm]; X_b [0-20]   Size and prob. of survival; X_0 [0-200 cm]; X_b [0-20]

10   Coefficients of neighborhood effects

11   C [0-10]   C [0-10]

12   D [1-5]   D [1-5]

13   Competitive coefficients (λ_i)   [0-1]*   Competitive coefficients (λ_i) [0-1]*

14   Effect of neighbor size on focal growth α [0-4]   Effect of neighbor size on focal survival α [0-4]

15   Effect of neighbor distance on its effect on:

16   Focal growth β [0-4]   Focal prob. of survival β [0-4]

17   Focal sensitivity to crowding:

18   Growth γ [-2 to 2]   Survival γ [-2 to 2]

1   Adjustment in comp. effect to account for hurricane damage to neighbor (η) at two levels: complete and medium damage [0-1.]

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4   *Competitive coefficients were only estimated for the conspecific vs. heterospecific and equal competitors models

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1 **APPENDIX IV.** Akaike weights for (A) growth and (B) survival models considered in our analyses. See Methods for a detailed description of

2 the models. Most parsimonious models are highlighted in bold text. See Table 2 for species names.

3 (A)

Species	Phylogeny	Leaf % N	Leaf % P	Wood den.	SLA	Leaf Suc	Max Ht	Seed wt	Leaf Area	Comp. trait	Consp/Het	Equal
ALCLAT	0.00	0.00	0.00	0.27	0.00	**0.73**	0.00	0.00	0.00	0.00	0.00	0.00
BUCTET	0.05	0.00	0.00	0.05	0.05	0.20	0.05	0.00	0.00	0.00	0.02	0.05
CASARB	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASSYL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00
CECSCH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**
CORBOR	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00
DACEXC	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
DRYGLA	0.00	0.00	0.00	0.00	0.01	0.10	**0.45**	0.00	0.00	0.00	0.00	**0.45**
GUAGUI	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
INGLAU	0.00	0.00	0.00	**0.62**	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00
MANBID	0.00	0.00	0.00	**0.73**	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00
MICPRA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MYRDEF	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.00	**0.62**
OCOLEU	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ORMKRU	0.00	0.00	0.00	0.00	0.00	0.00	**0.91**	0.00	0.00	0.00	0.07	0.02
SCHMOR	0.00	0.00	0.00	**0.82**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SLOBER	0.00	0.00	0.00	0.08	0.00	**0.92**	0.00	0.00	0.00	0.00	0.00	0.00
TABHET	0.00	0.00	0.00	**0.50**	0.00	**0.50**	0.00	0.00	0.00	0.00	0.00	0.00
TRIPAL	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	**0.97**	0.01

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(B)

Focal sp.	Phylogeny	Leaf % N	Leaf % P	Wood den.	SLA	Leaf Suc	Max Ht	Seed wt	Leaf Area	Comp. trait	Consp/Het	Equal
ALCLAT	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00
BUCTET	0.02	0.24	**0.65**	0.00	0.00	0.00	0.00	0.02	0.05	0.00	0.00	0.01
CASARB	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00
CASSYL	**0.41**	0.03	0.06	0.03	0.09	0.00	0.03	0.06	0.15	0.02	0.01	0.09
CECSCH	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CORBOR	0.05	0.08	0.05	0.05	0.05	0.08	0.08	0.13	0.03	0.03	0.00	0.05
DACEXC	0.04	0.07	0.07	0.12	0.12	**0.33**	0.20	0.01	0.02	0.01	0.00	0.01
DRYGLA	0.04	**0.17**	0.11	**0.17**	0.11	0.11	0.11	0.06	0.04	0.04	0.01	0.04
GUAGUI	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.82**	0.18	0.00
INGLAU	**0.56**	0.08	0.03	0.03	0.08	0.00	0.05	0.05	0.02	0.05	0.01	0.08
MANBID	0.12	0.07	0.07	0.12	0.07	0.07	**0.33**	0.02	0.02	0.04	0.02	0.04
MICPRA	0.01	0.03	0.01	0.02	0.01	0.00	**0.66**	0.03	0.05	0.00	0.00	0.02
MYRDEF	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.02	0.01	0.04	0.00	0.02
OCOLEU	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.99**	0.00
ORMKRU	0.06	0.10	0.10	0.10	0.10	0.06	0.06	0.06	**0.16**	0.10	0.01	0.10
PREMON	0.00	0.00	0.00	0.00	0.00	0.00	**0.99**	0.00	0.00	0.00	0.00	0.00
SCHMOR	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00
SLOBER	0.07	0.04	0.04	0.04	0.07	**0.53**	0.07	0.03	0.02	0.02	0.02	0.04
TABHET	0.09	0.05	0.01	0.09	**0.63**	0.01	0.03	0.03	0.01	0.01	0.02	0.03
TRIPAL	0.05	0.08	0.13	0.05	0.08	0.13	0.13	0.05	0.03	0.03	**0.21**	0.05

APPENDIX V. Estimated parameters with associated support intervals for the most parsimonious growth and survival neighborhood model for
the focal species.

(A) Growth

Parameter	ALCLAT	BUCTET	CASARB	CASSYL	CECSCH	CORBOR	DACEXC	DRYGLA	GUAGUI
MaxG (mm/yr)	2.61 (2.43-2.64)	4.12 (4.03-4.16)	4.39 (4.34-4.47)	1.82 (1.80-1.86)	38.23 (37.85-38.62)	1.34 (1.3-1.36)	5.6 (5.54-5.66)	1.15 (1.09-1.17)	5.3 (5.19-5.35)
C	0.34 (0.33-0.59)	NA	1.11 (1.10-1.13)	0.90 (0.80-0.91)	2.01 (1.98-2.04)	2.04 (2.02-2.08)	3.45 (3.41-3.39)	8.37 (8.29-10)	2.26 (2.23-2.35)
D	3.96 (3.92-4.81)	NA	1.31 (1.3-1.33)	1.68 (1.67-1.73)	1.34 (1.33-1.36)	4.66 (4.46-4.5)	1.15 (1.09-1.16)	2.66 (2.61-2.69)	1.21 (1.2-1.27)
Radius (m)	3.2 (3-3.4)	NA	19.8 (19-20)	10.2 (10-12.8)	19.8 (19-20)	2.6 (2.2-3)	12.8 (12.6-13.6)	2.2 (2-2.4)	18.6 (18.4-18.8)
alpha	2.1 (2.04-2.12)	NA	1.52 (1.5-1.53)	1.70 (1.68-1.72)	1.33 (1.25-1.34)	3.17 (3.13-3.39)	1.95 (1.93-1.97)	1.1 (1.04-1.11)	1.38 (1.36-1.44)
beta	0.25 (0.03-0.26)	NA	0.26 (0.25-0.36)	0.04 (0-0.05)	0.45 (0.41-0.46)	0.06 (0.01-0.07)	0.22 (0.21-0.23)	0.2 (0-0.21)	0.01 (0-0.02)
x0	14.47 (14.33-18.38)	58.84 (58.3-62.4)	5.87 (5.81-6.1)	147 (0.001-148)	197.04 (195-200)	195.2 (93-200)	27.72 (27.44-27.9)	49.29 (48.8-60.1)	172.1 (170.4-200)
Xb	1.98 (1.8-2)	2.86 (2.8-2.89)	1.5 (1.46-1.52)	19.83 (19.63-20)	2.5 (2.47-2.53)	5.04 (4.58-5.09)	2.35 (2.27-2.37)	3.49 (3.32-3.53)	13.39 (11.78-13.52)
Complete dam Focal	0.43 (0.43-0.66)	0.52 (0.51-0.53)	0.57 (0.52-0.58)	0.13 (0.13-0.17)	0.08 (0.06-0.08)	0.17 (0.16-0.18)	0.57 (0.47-0.58)	0.21 (0-1)	0.47 (0.46-0.48)
Complete dam competitor	0.43 (0-1)	NA	0.82 (0.81-0.82)	0.44 (0-1)	0.65 (0.64-0.66)	0.63 (0-1)	0.09 (0.08-0.1)	0.84 (0-1)	0.41 (0.4-0.42)
Medium dam Focal	0.78 (0.77-0.81)	0.384 (0.38-0.39)	0.84 (0.83-0.85)	0.86 (0.73-0.87)	0.14 (0.13-0.15)	0.68 (0-1)	0.79 (0.78-0.81)	0.51 (0-1)	0.84 (0.83-0.88)
Medium dam competitor	0.49 (0-1)	NA	0.84 (0.83-0.94)	0.02 (0-1)	0.34 (0.33-0.35)	0.003 (0-1)	0.49 (0.48-0.5)	0.69 (0-1)	0.34 (0.33-0.35)
Gamma	1.82 (1.81-1.98)	NA	-0.28 (-0.31,-0.27)	-1.18 (-1.47,-1.17)	-0.09 (-0.1,-0.08)	1.82 (1.8-1.83)	-0.445 (-0.45,-0.44)	1.04 (1.03-1.05)	-0.52 (-0.53,-0.46)

Growth (continued)

Parameter	INGLAU	MANBID	MYRDEF	OCOLEU	ORMKRU	SCHMOR	SLOBER	TABHET	TRIPAL
MaxG (mm/yr)	9.61 (9.52-9.71)	4.33 (4.19-4.37)	1.15 (1.08-1.17)	3.44 (3.40-3.47)	2.03 (2.01-2.07)	7.79 (7.7-8.01)	2.04 (2.01-2.09)	1.39 (1.38-1.48)	1.02 (0.97-1.03)
C	2.64 (2.61-2.66)	3.22 (3.18-3.25)	8.37 (8.29-10)	NA	0.71 (0.7-0.97)	1.97 (1.95-1.99)	1.29 (1.27-1.45)	2.78 (2.7-2.81)	1.26 (1.24-1.76)
D	1.07 (1.04-1.08)	1.33 (1.29-1.034)	2.66 (2.61-2.69)	NA	4.91 (3.78-4.95)	1.21 (1.19-1.25)	2.63 (2.55-2.66)	4.12 (4.08-4.17)	3.97 (3.93-5)
Radius (m)	19.8 (19-20)	15.8 (15.2-16)	2.6 (2.2-3)	NA	0.4 (0.2-0.5)	19.8 (19-20)	10.2 (10-11.4)	13.4 (13.2-14)	19.4 (16.6-19.8)
alpha	1.45 (1.43-1.60)	1.56 (1.54-1.60)	1.1 (1.04-1.11)	NA	0.42 (0.41-0.48)	1.51 (1.49-1.52)	1.58 (1.56-1.64)	1.43 (1.12-1.45)	3.16 (1.39-3.19)
beta	0.44 (0.43-0.51)	0.50 (0.47-0.51)	0.2 (0-0.21)	NA	0.04 (0-0.05)	0.70 (0.69-0.71)	0.10 (0.11-0.12)	0.05 (0.04-0.32)	0.09 (0-0.1)
x0	193.8 (192-196)	129.2 (127-169)	49.29 (48.8-60.1)	18.77 (18.6-18.9)	18.45 (13.5-18.6)	9.23 (9.13-9.41)	164 (148-166)	183.5 (135-185)	36.62 (36.3-51.3)
Xb	4.72 (4.67-4.77)	6.82 (6.61-6.88)	3.49 (3.32-3.53)	1.78 (1.76-1.80)	2.56 (2.53-3.19)	1.28 (1.26-1.29)	4.25 (4.2-4.37)	6.45 (6.38-6.5)	4.79 (4.36-4.84)
Complete dam Focal	0.63 (0.38-0.64)	0.37 (0.31-0.38)	0.21 (0-1)	0.34 (0.33-0.35)	0.88 (0.87-1)	0.78 (0.77-1)	0.5 (0.49-0.52)	0.89 (0.88-1)	0.04 (0-1)
Complete dam competitor	0.97 (0-1)	0.76 (0.75-0.78)	0.84 (0-1)	NA	0.43 (0.42-0.44)	0.14 (0-1)	0.81 (0-1)	0.15 (0.14-0.16)	0.44 (0-1)
Medium dam Focal	0.86 (0.83-0.87)	0.89 (0.82-0.90)	0.51 (0-1)	0.81 (0.8-0.82)	0.66 (0.49-0.67)	0.95 (0.94-1)	0.73 (0.72-0.87)	0.96 (0.95-1)	0.55 (0.24-0.55)
Medium dam competitor	0.07 (0-1)	0.415 (0.41-0.42)	0.69 (0-1)	NA	0.99 (0.98-1)	0.96 (0-1)	0.86 (0-1)	0.23 (0.22-0.4)	0.94 (0-1)
Gamma	-0.255 (-0.26,-0.25)	-0.45 (-0.46,-0.42)	-1.99 (-2,-1.51)	NA	0.83 (0.82-0.93)	-0.16 (-0.19,-0.14)	1.82 (1.81-1.98)	-1.77 (-2,-1.75)	0.35 (0.34-0.59)

1   (B) Survival

Parameter	ALCLAT	BUCTET	CASARB	CASSYL	CECSCH	CORBOR	DACEXC	DRYGLA	GUAGUI	INGLAU
MaxSurv	0.99	0.99	0.97	0.98	0.99	0.98	0.99	0.99	0.99	0.98
	(0.98-1)	(0.98-1)	(0.96-0.98)	(0.97-0.99)	(0.98-1)	(0.97-0.99)	(0.98-1)	(0.98-1)	(0.98-1)	(0.97-0.99)
C	4.56	5.52	0.91	0.31	6.44	NA	0.17	5.95	2.22	0.5
	(4.52-4.79)	(5.35-5.57)	(0.89-0.93)	(0.3-0.33)	(6.4-6.57)		(0.16-0.22)	(3.57-6)	(2.2-2.26)	(0.49-0.55)
D	1.1	2.03	1.92	1.12	3.13	NA	1.52	4.83	3.26	2.06
	(1.06-1.11)	(2.01-2.13)	(1.89-1.94)	(1.01-1.13)	(3.06-3.16)		(1-1.53)	(4.78-5)	(3.23-3.3)	(1.93-2.08)
Radius (m)	6.6	16	19	19.8	17.6	NA	19.8	19.2	19.2	19.8
	(6.4-6.8)	(15.8-16.2)	(18.8-19.2)	(19.6-20)	(17.4-17.8)		(19.6-20)	(19-19.4)	(19-19.4)	(19.6-20)
alpha	1.51	3.71	3.46	0.7	1.58	NA	0.48	1.16	1.46	1.57
	(1.48-1.53)	(3.67-3.81)	(3.43-3.59)	(0.69-0.73)	(1.57-1.6)		(0.46-0.49)	(0.84-1.17)	(1.44-1.54)	(1.49-1.58)
beta	0.26	0.38	0.15	0.16	0.39	NA	0.05	3.68	0.01	0.56
	(0.15-0.27)	(0.37-0.39)	(0-0.16)	(0-0.17)	(0.38-0.4)		(0-0.06)	(3.65-4)	(0-0.02)	(0.53-0.57)
x0	34.6	101.48	7.32	4.86	8.82	4.72	10.36	17.38	64.15	3.91
	(34.3-34.9)	(85.2-102.5)	(7.24-7.38)	(4.81-5.1)	(8.73-8.99)	(4.67-4.77)	(9.3-10.4)	(16.7-17.6)	(55.2-64.8)	(2.31-3.95)
Xb	6.43	9.2	3.28	4.92	1.79	3.57	14.42	4.75	19.79	17.1
	(6.24-6.49)	(9.11-9.65)	(3.25-3.31)	(4.48-4.9)	(1.74-1.81)	(3.53-3.64)	(14.3-14.3)	(4.7-4.89)	(19.6-20)	(11.8-17.3)
Complete dam Focal	0.89	0.93	0.82	0.91	0.59	0.94	0.87	0.73	0.93	0.71
	(0.85-0.89)	(0.92-0.94)	(0.81-0.83)	(0.88-0.92)	(0.57-0.6)	(0.93-0.95)	(0.85-0.88)	(0.72-0.79)	(0.92-0.96)	(0.7-0.72)
Complete dam	0.24	0.91	0.35	0.085	0.8	NA	0.21	0.19	0.89	0.27
	(0.23-0.25)	(0.9-0.92)	(0.33-0.36)	(0.08-0.09)	(0-1)		(0-1)	(0-1)	(0.88-0.9)	(0-1)
Medium dam Focal	0.97	0.99	0.98	0.99	0.99	0.98	0.99	0.99	0.99	0.99
	(0.96-0.98)	(0.98-1)	(0.97-0.99)	(0.98-1)	(0.98-1)	(0.97-0.99)	(0.98-1)	(0.98-1)	(0.98-1)	(0.98-1)
Medium dam competitor	0.83	0.36	0.83	0.31	0.74	NA	0.57	0.48	0.87	0.42
	(0.82-0.84)	(0.35-0.37)	(0.82-0.84)	(0.3-0.32)	(0-1)		(0-1)	(0-1)	(0.86-0.88)	(0-1)
Gamma	-1.93	-1.95	-1.88	-1.35	-1.99	NA	-1.89	-0.17	-1.29	-1.97
	(-2,-1.91)	(-2,-1.93)	(-1.9,-1.8)	(-1.37,-1.23)	(-2,-1.97)		(-2,-1.87)	(-2, 2)	(-1.3,-1.27)	(-2,-1.95)

2

3

Parameter	MANBID	MYRDEF	PREMON	OCOLEU	ORMKRU	SCHMOR	SLOBER	TABHET	TRIPAL
MaxSurv	0.99 (0.98-1)	0.96 (0.95-0.97)	0.99 (0.98-1)	0.99 (0.98-1)	0.99 (0.98-1)	0.99 (0.98-1)	0.98 (0.97-0.99)	0.98 (0.97-0.99)	0.99 (0.98-1)
C	0.36 (0.23-0.36)	NA	0.42 (0.37-0.42)	4.11 (1.27-4.15)	0.65 (0.64-0.77)	1.6 (1.57-1.61)	1.16 (1.15-1.26)	0.39 (0.38-0.43)	9.12 (8.4-9.2)
D	3.78 (3.75-4.23)	NA	2.31 (2.29-2.38)	4.81 (4.76-5)	4.67 (4.62-5)	1.01 (1-1.02)	4.99 (4.95-5)	4.27 (4.22-4.57)	4.6 (4.5-5)
Radius (m)	18.6 (17.2-18.8)	NA	10.4 (10.2-10.6)	11.2 (10.8-11.4)	5.8 (4.4-6)	19.8 (19.6-20)	2 (1.8-2.2)	11.6 (11.4-11.8)	6.4 (6.2-6.5)
alpha	2.81 (2.36-2.84)	NA	0.21 (0-0.22)	0.42 (0-0.43)	0.05 (0-0.06)	0.97 (0.96-1.06)	0.17 (0-0.18)	1.44 (1.42-1.45)	1.66 (1.64-1.68)
beta	0.27 (0-0.28)	NA	0.37 (0.18-0.37)	3.98 (3.94-4)	3.86 (3.82-4)	0.16 (0-0.17)	0.55 (0.54-0.7)	0.11 (0-0.12)	0.02 (0-0.03)
x0	40.47 (37.2-40.9)	1.83 (1.79-1.85)	19.1 (12.9-19.3)	43.6 (43.2-44.9)	15.61 (15.5-16.1)	6.37 (6.31-6.69)	8.47 (8.39-9.66)	23.97 (19.4-24.2)	162.9 (161.3-200)
Xb	16.07 (15.9-17.4)	3.64 (3.53-3.68)	11.2 (11.01-16.4)	8.41 (8.33-8.49)	3.19 (3.15-3.31)	4.77 (4.72-4.86)	9.86 (9.27-9.96)	15.49 (15.3-16.5)	19.18 (17.8-19.4)
Complete dam Focal	0.92 (0.91-0.93)	0.36 (0-1)	0.54 (0.53-0.54)	0.88 (0.87-0.91)	0.86 (0.85-0.87)	0.64 (0.63-0.72)	0.93 (0.9-0.94)	0.72 (0.71-0.73)	0.63 (0-0.65)
Complete dam competitor	0.36 (0-1)	NA	0.5 (0.49-0.51)	0.44 (0.43-0.45)	0.27 (0.26-0.28)	0.81 (0.8-0.82)	0.91 (0-1)	0.89 (0.88-0.9)	0.55 (0-1)
Medium dam Focal	0.99 (0.98-1)	0.23 (0-1)	0.72 (0.71-0.73)	0.97 (0.963-0.99)	0.97 (0.96-0.98)	0.99 (0.98-1)	0.98 (0.97-1)	0.99 (0.98-1)	0.99 (0.98-1)
Medium dam competitor	0.41 (0-1)	NA	0.47 (0.46-0.48)	0.93 (0.92-0.94)	0.66 (0.65-0.67)	0.17 (0.16-0.18)	0.26 (0-1)	0.72 (0.71-0.73)	0.79 (0-1)
Gamma	-1.72 (-2,-1.7)	NA	-0.94 (-0.98,-0.93)	-0.62 (-2,-0.62)	-1.25 (-1.26,-1.24)	-1.99 (-2,-1.97)	-1.36 (-2,-1.34)	-1.23 (-1.24,-0.83)	-1.06 (-1.07,-1.03)

1

1 **APPENDIX VI.** K values for phylogenetic conservatism for the nine traits included in the analyses. p-values were calculated as the proportion of

2 null K values that were greater than the observed value of K. All trait values were log-transformed except wood specific gravity and leaf % C.

Trait	Transform	K	p-value
Leaf % P	log	0.08	0.01
Leaf % N	log	0.05	0.39
Leaf % C	NA	0.06	0.43
Wood specific gravity	NA	0.07	0.28
Leaf area	log	0.10	0.01
SLA	log	0.06	0.19
Leaf succulence	log	0.06	0.21
Max. height	log	0.06	0.19
Seed mass	log	0.13	<0.0001

3

4