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10 *Research Article*

11 **The scale dependency of trait-based tree neighborhood models**

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Accepted Article

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41 **Abstract**

42 **Questions:** We asked whether: 1) the strength of conspecific and heterospecific neighborhood
43 crowding effects on focal tree survival and growth vary with neighborhood radii and 2) if the relative
44 strength of the effect of neighborhood interactions on tree growth and survival varies with
45 neighborhood scale?

46

47 **Location:** Luquillo Forest Dynamics Plot, Puerto Rico.

48

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

55

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

64

65 **Conclusion:** Findings from this study highlight the importance of spatial scale in community
66 assembly processes, and specifically, a call for increased attention when selecting the radius that
67 defines the neighborhood around a focal tree as the selected neighborhood radius influences the

68 community patterns discovered, and affects the conclusions about the drivers that control community
69 assembly.

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72 **Keywords:** hierarchical competition, Luquillo Forest Dynamics Plot, niche differentiation, plant
73 functional traits, subtropical forest,

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85 **Introduction**

86 Plant functional traits are increasingly used to help elucidate the drivers of forest community structure
87 and dynamics (Suding et al. 2005; McGill et al. 2006; Spasojevic & Suding 2012). They have also
88 been used for tree communities not amenable to experimentation to address classic questions
89 regarding the processes structuring communities (e.g. Uriarte et al. 2010, 2016; Kunstler *et al.* 2012,
90 2016; Liu et al. 2016). Neighborhood analyses of trait and demographic rates in plant ecology usually
91 take one of two forms. The first is to model demographic rates given trait values of the plants,
92 irrespective of the context in which the plants are found (e.g. Poorter et al. 2008; Wright et al. 2010a;
93 Iida, Kohyama, et al. 2014; Iida, Poorter, et al. 2014). The second is to model demography using
94 individual plants and their trait values, together with the trait values of neighboring plants (e.g.
95 Kunstler et al. 2012; Lasky et al. 2014; Fortunel et al. 2016; Uriarte et al. 2016; Zambrano et al.

96 2017). Analyses that combine functional trait and demographic data provide a mechanistic
97 understanding of observed patterns of community structure and dynamics, by directly investigating
98 the critical linkages between phenotypes and the environment (McGill et al. 2006). Specifically, trait-
99 based approaches provide evidence of two distinct patterns resulting from competitive exclusion
100 (Kraft et al. 2015). As competition increases, greater differences in traits (i.e. niche differentiation),
101 measured by distances among trait values, promote species coexistence (Kraft et al. 2014; Fortunel et
102 al. 2016), and lead to high phenotypic disparity among co-occurring species (Webb et al. 2002;
103 Stubbs & Wilson 2004). Conversely, competition may be driven by hierarchical differences (i.e. trait
104 hierarchies) in species' competitive ability resulting in a phenotypic clustering of co-occurring species
105 (Mayfield & Levine 2010; Uriarte et al. 2010; Kunstler et al. 2012). Environmental filtering or
106 tolerance of local abiotic conditions and competition for light leads to a functional clustering with
107 species possessing traits associated with high fitness excluding species with unfavourable traits
108 (Grime 2006).

109 The first neighborhood models focused on focal plant responses to the species identity of
110 neighboring individuals (Weiner 1982; Pacala & Silander, 1985; Hubbell et al. 2001a; Canham et al.
111 2004a; Uriarte, Canham, et al. 2005), but over the past decade these models have transitioned towards
112 quantifying neighborhood effects based upon the combined attributes (e.g. traits or relatedness) of all
113 trees in a defined area around the focal tree (e.g. Uriarte et al. 2004, 2005b, 2010, Kunstler et al. 2012,
114 Paine et al. 2012). While the exact details of the neighborhood models used in studies vary, tree-based
115 studies often employ some type of crowding index. Crowding indices have been used as a proxy to
116 determine the effects of competition on tree survival and growth and usually take into account the
117 diameter of the neighboring trees and their distance from the focal tree. For example, a commonly
118 used crowding index is a direct function of the squared diameter of the neighbors and inverse function
119 of the squared distances to the neighbor (Canham et al. 2004b). For computational and practical
120 reasons, the neighborhood is defined using a fixed radius around the focal individual tree (Canham et
121 al. 2004a; but see Wills et al. 2016). Using a fixed radius may appear suboptimal for examining
122 neighborhood effects, but the inverse weighting by distance between trees, and the average canopy
123 spreads of trees, could make the decision regarding the radius size inconsequential. Indeed, some
124 studies have suggested that scale dependency does not exist in their neighborhood models (e.g.

125 Fortunel et al. 2016). Conversely, spatial analyses of forest plots that have analyzed individual
126 species-area curves using concentric circular neighborhoods around focal trees have uncovered strong
127 scale dependency (Wiegand et al. 2007; Yang et al. 2013), as have temporally static analyses of trait
128 and phylogenetic dispersion (e.g. Swenson *et al.* 2006; Swenson & Enquist 2009; Kraft & Ackerly
129 2010).

130 The scale dependency of ecological processes structuring natural communities has long been
131 recognized (Wiens 1989; Levin 1992; Brown 1995; Chase 2014; Garzon-Lopez et al. 2014). At small
132 spatial scales, the probability of two species co-occurring may be most influenced by trait distances
133 (MacArthur and Levins 1967). At larger spatial scales, trait hierarchies may drive the competitive
134 exclusion of species that are not so well suited to the environment (Kunstler et al. 2012). The
135 tendency for traits to be overdispersed among species at small spatial scales and clustered or
136 underdispersed at larger spatial scales have been used as evidence of scale-dependent processes (e.g.
137 Weiher & Keddy 1995, 1999; Weiher *et al.* 1998). Opposing deterministic processes have been
138 reported by static analyses of trait dispersion (e.g. Swenson & Enquist 2009), and it may be that
139 neighborhood models could be susceptible to the same problem. The measured effect of trait distances
140 and trait hierarchies on community dynamics may vary greatly with the size of the area used to define
141 the local neighborhood, but few neighborhood models address this potential scale dependency.

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

154 smaller radii (< 20 m). Alternatively, the effects of functional neighborhood (effect of neighbors
155 based on their functional trait values) on tree performance might be insensitive to the choice of spatial
156 scale used to model the neighborhood, as some studies have suggested (e.g. Fortunel et al. 2016).

157

158 Methods

159 Study site

160 The Luquillo Forest Dynamics Plot (LFDP) (18°20' N, 65°49' W, 333-428 m. asl) is a 16-ha forest
161 plot located in the Luquillo Experimental Forest in northeast Puerto Rico (Thompson et al. 2002).
162 This is a subtropical wet forest with an average precipitation of 3500 mm per year. The plot has been
163 censused approximately every 5 years since 1990 and every free-standing individual with a woody
164 stem >=1cm in diameter at breast height (DBH measured at 1.3 m from the ground) is tagged,
165 mapped, measured and identified to species (Thompson et al. 2002). Over time 150 species have been
166 recorded in the LFDP, but in any given census the species richness is ~120 species (Hogan et al.
167 2016). In the 20 years before the censuses used in this study, the forest experienced major hurricane
168 disturbances in 1989 and 1998, which resulted in extraordinary temporal dynamics with tens of
169 thousands of individuals recruiting and dying during some census intervals (Hogan et al. 2016). In
170 this study, we used relative growth rates and survival data for 22596 individuals from a single census
171 interval (2005-2010), which was chosen to reflect the most stable census period since the LFDP was
172 established (at the time of this analysis), to reduce the effect of the rapid community dynamics caused
173 by hurricane disturbances.

174

175 Functional trait data

176 For this study, we used species-level functional trait data that represent the main ecological strategies
177 for resource acquisition (Westoby et al. 2002; Wright et al. 2010a) and that were measured from adult
178 trees (>=1cm in DBH) in the Luquillo forest (Swenson et al. 2012, Umaña et al. 2016, Swenson and
179 Umaña 2015). Leaf traits included leaf area and specific leaf area. Leaf area has been shown to
180 strongly correlate with competitive ability for light (Bloom et al. 1985), while specific leaf area is a

181 key trait reflecting the trade-off between a leaf's lifespan and carbon capture (Westoby et al. 2002;
182 Wright, Westoby, et al. 2004). Other leaf traits used were nitrogen, phosphorus, and carbon content
183 that reveal a trade-off between rapid acquisition and efficient conservation of resources (Reich et al.
184 1997; Wright, Reich, et al. 2004). Leaf N content plays a strong role in photosynthesis as the proteins
185 of the Calvin cycle and thylakoids account for the majority of N in leaves (Evans 1989). We also
186 included seed mass, which is indirectly related to physiological and structural traits that influence
187 plant survival and growth, (e.g. leaf area and photosynthetic rate (Reich et al. 1992), and represents a
188 trade-off between producing several small stress-intolerant seeds or few large stress-tolerant seeds
189 (Coomes & Grubb 2003; Muller-Landau 2010). Finally, we incorporated in our analyses wood
190 density of stems, a critical component for many essential functions, such as mechanical support,
191 hydraulic transport, and nutrient storage (Westoby & Wright 2006) (Also Chave et al. 2009), and
192 maximum tree height that varies across light resource gradients (Gaudet & Keddy 1988) and with the
193 type and frequency of disturbance events (Schamp & Aarssen 2009). With the exception of leaf
194 carbon content, wood density, and seed mass, trait values were log-transformed to approximate
195 normality. All traits were then standardized across species to a mean of 0 and a standard deviation of
196 1 prior to the analyses.

197 To reduce the number and collinearity of traits we applied a Principal Component Analysis
198 (PCA). Traits were log-transformed for the PCA analysis. Two major axes of variation were
199 determined in which the first axis (PC1) explained 30% of the variation and the second axis (PC2)
200 21% of the variation. We used the broken-stick criterion using the "PCA significance" function from
201 the *Biodiversity* package (Kindt 2019) to identify the main principal components responsible for trait
202 variation (Legendre & Legendre 2012). The first axis was significantly associated with leaf
203 phosphorus and nitrogen content, specific leaf area and wood density, while the second axis
204 represented leaf area, maximum height and seed mass (see results in Appendix S1), confirming
205 previous findings (see Díaz et al. 2016). We fitted separate growth and survival models, for each
206 functional trait and each of the two main PCA axes, as described in the next sections.

207

208 Neighborhood survival and growth models

209 To examine scale-dependent effects of neighborhood crowding and plant functional traits on tree
210 survival and growth, we constructed separate hierarchical generalized linear mixed models for each
211 functional trait and the two main PCA axes using a Bayesian approach, as well as simpler models that
212 only included conspecific density, heterospecific density, or initial tree DBH. We defined
213 neighborhood radii from 5m to 30m from each focal tree, at 5m intervals. We excluded from the
214 analyses trees that were located within 30m of the edges of the LFDP. We characterized the
215 “neighborhood” of a focal tree in terms of the summed tree size (DBH) of conspecific and
216 heterospecific neighbors irrespective of their trait values, and also the “functional neighborhood” in
217 which the abundance of neighbors was calculated in terms of both their DBH size and their functional
218 values. Due to the distinct growth pattern of the palms (Arecaceae) *Prestoea acuminata var montana*
219 and *Roystonea borinquena*, these species were not included as target trees in growth models but were
220 incorporated as neighbors. We quantified conspecific and heterospecific competition of neighbors
221 using a Neighborhood Crowding Index (NCI), where the negative influence of neighbors varies as a
222 direct function of the squared diameter of the neighbor j (DBH_j^2) and inverse function of the squared
223 distance to the neighbor (d_{ij}^2) (Uriarte et al. 2010). This effect is summed over all neighbors j within
224 the pre-defined radius around the focal individual i (separately for conspecifics and heterospecifics).
225

$$226 NCI_i = \sum_j \frac{DBH_j^2}{d_{ij}^2}$$

227
228 We calculated two separate indices of functional neighborhoods to quantify the effect of trait
229 hierarchies ($NCIH$) and trait distances ($NCIS$) among heterospecific neighbors (Lasky et al. 2014):
230

$$231 NCIH_i = \sum_j (F_{s[i]} - F_{s[j]}) \frac{DBH_j^2}{d_{ij}^2}$$

232 and

$$233 NCIS_i = \sum_j |F_{s[i]} - F_{s[j]}| \frac{DBH_j^2}{d_{ij}^2}$$

234
235 where $F_{s[i]}$ and $F_{s[j]}$ represent the values of the functional trait of interest for focal individual i and
236 neighbor j belonging to their respective species $s[i]$ and $s[j]$. Increased neighborhood crowding may

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

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

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

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

where the β are species-specific coefficients representing the intercept (β_{1s}), the effect of conspecific neighborhood density (β_{2s}), the effect of heterospecific neighborhood density (β_{3s}), the effect of crowding based on standardized trait distances between heterospecific neighbors (β_{4s}), the effect of crowding based on trait hierarchies (β_{5s}), and the effect of initial tree size (DBH) (β_{6s}). To prevent

266 confounding of the species-specific effects with inter-specific variation in mean diameter, we
267 standardized tree size (DBH) by subtracting their species-specific mean (\overline{DBH}_s) from their individual
268 initial DBH values and then log-transformed the values to reduce the skewness of their distributions.
269 All predictor variables were scaled to a mean of 0 and a standard deviation of 1 to allow comparisons
270 across effect sizes (Rscripts related to the survival and growth models can be found in
271 <https://github.com/jzambranom/neighborhood-models/blob/master/tree-demography>).

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

276

277
$$\beta_{1s} \sim N(\mu_{\beta_1} + \gamma_1 F_s, \sigma_{\beta_1})$$

278

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

287 We simulated six Markov Chain Monte Carlo chains (MCMC) for 50,000 iterations with
288 10,000 adaptation iterations and a burn-in period of 10,000 iterations to obtain a sufficient number of
289 effectively independent samples from the posterior distribution. Convergence of the MCMC chains
290 was assessed visually with traceplots and the Gelman-Rubin convergence diagnostic, ensuring values
291 of the latter were less than 1.2 (Gelman & Rubin 1992). Finally, we assessed the models' goodness of
292 fit via posterior predictive checks. At each MCMC iteration, we simulated a new data vector for
293 growth rates or survival status from the model and calculated a loss function on both the simulated
294 and observed data. The loss function was defined either as the sum of squared differences between the

295 data vector and z for growth, or as the negative of the log-likelihood of the data vector given z for
296 survival. If the model fits the observed data, the probability that the simulated loss is greater than the
297 observed loss should be approximately 0.5. Goodness-of-fit tests were used to exclude models with
298 poor fit. We visually inspected variograms of the model residuals, computed with the *gstat* package,
299 to verify the absence of spatial autocorrelation of residuals between nearby trees (see example in
300 Appendix S2). We tested for monotonic trends by computing the non-parametric Kendall correlation
301 between effect size and neighborhood radius for traits displaying significant effects on individual tree
302 survival and growth. A 95% credible interval was estimated by computing the Kendall correlation
303 from random draws from the posterior distribution of effect sizes at each radius.

304

305 Criteria for scale dependency

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

316

317 Results

318 Overall, models that included functional traits were better predictors of tree survival and growth (see
319 results in Appendix S3), than models that included only conspecific and heterospecific density or
320 initial size (DBH). Goodness of fit of the models did not vary much across neighborhood radii for
321 either survival (Table S2) or growth (Table S3). Initial focal tree size (DBH) had a strong positive

322 effect on focal tree survival and negative effect on focal tree growth, with small sized individuals
323 showing low survivorship (Fig. S3), but growing faster than larger individuals. Below we discuss the
324 results of functional traits with significant effect (95% CI non-crossing zero), and the Supplementary
325 Information (Appendix S4) includes results for all other traits studied.

326

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

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

333

334 Does neighborhood radius influence the strength of the effects of the functional
335 neighborhood on the focal tree performance?

336 The strength of the effects of the functional neighborhood on survival of focal trees varied with
337 neighborhood radii (Fig. 2). We found evidence for a positive scale-dependent significant effect of
338 trait hierarchies on focal tree survival. Specifically, species with higher maximum height, greatest
339 seed mass and with bigger leaves survive better than species that are shorter in height and have small
340 seed mass and small leaf area (Fig. 2). The strength of these effects depended on the neighborhood
341 radius, with effects being stronger at 10m (radius around focal tree) for leaf area, 25m for maximum
342 height and at 30m for seed mass when compared to other radii (Fig. 2). Similarly, species with low
343 leaf nitrogen and phosphorus content had better survival (especially at 15m) than species with high
344 leaf nitrogen and phosphorus content (Fig. 2). Finally, high values on PC1 (i.e. plant economics) and
345 PC2 (i.e. variation in plant size) resulted in high focal tree survival, particularly at 15m neighborhood
346 radius (Fig. 2). Moreover, results from the Kendall correlation test showed evidence of a significant
347 negative correlation for leaf phosphorus content, while seed mass displayed a significant positive
348 trend (Table 1), supporting the idea of a strong scale dependency occurring for these traits.

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

358

359 Significant scale-dependent effects of trait distances were found only for focal tree survival (Fig 4).
360 When neighbors had small trait differences for leaf traits, wood density, and maximum height focal
361 trees experienced greater survival, with stronger effects observed at 10m for leaf nitrogen content
362 (Fig. 4), 20m and 25m for leaf phosphorus content, 20m for specific leaf area (Fig. 4) and 5m for
363 wood density (Fig. 4), when compared to other radii. However, a large difference in leaf area between
364 focal trees and their neighbors resulted in high survivorship of the focal tree, with strong effects
365 occurring at 20m (Fig. 4). Similarly, large differences in PC1 resulted in better survival particularly at
366 25m (Fig. 4). Finally, we found strong evidence of a significant positive correlation for leaf area and
367 PC1 (Table 1).

368

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

376

Discussion

377 Neighborhood models have facilitated the investigation of drivers of community structure and
378 dynamics, but often such studies have arbitrarily defined the local neighborhood radius, thus
379 hampering our understanding of the spatial scales across which different mechanisms operate in
380 different ecosystems. In our study, we investigated the variation in estimates of the effects of the local
381 neighborhood on tree survival and growth based on neighborhood radius, density and identity of
382 neighbors, and functional traits. Contrary to expectation, the strength of conspecific and
383 heterospecific density dependence on tree survival and growth was invariant with neighborhood (radii
384 from 5-30 m). As expected, the strength of the effects of the functional neighborhood on focal tree
385 survival and growth varied with neighborhood radius and the effects on tree survival and growth went
386 beyond the 20m radius. Moreover, both ecological mechanisms, i.e. environmental filtering estimated
387 from the effects of trait distances and niche differentiation estimated from the effects of trait
388 hierarchies, had significant effects at the same neighborhood radii. Our results strongly suggest that
389 the choice of the neighborhood radius when analyzing neighborhood effects is critical, as different
390 radii may lead to very different conclusions on the drivers of tree community dynamics as discussed
391 in more detail below.

392

393 Effects of neighborhood crowding and functional neighborhood on tree performance: a
394 matter of scale

395 Our results show that heterospecific density dependent effects on tree growth had overall consistent
396 effects across the variety of neighborhood radii tested. Thus, it is likely that the link between
397 heterospecific neighborhood density and tree growth might not be sensitive to the variation in
398 neighborhood radius in the Luquillo forest. Furthermore, we were not able to capture the effects of
399 conspecific density on tree survival and growth at 5m, as previously reported (Zhu et al. 2017), and
400 the strength of the effect did not change for larger neighborhood radii. This could be because the 5m
401 radius neighborhood was so narrow that the probability of encountering a conspecific neighbor was
402 very small, especially for neighbor trees > 10 cm DBH. Moreover, the probability of encountering
403 neighbors of the same species in small neighborhoods might vary with ontogeny, with earlier stages
404 experiencing stronger neighborhood effects at short radii. Nonetheless, it is important to note that the

405 average negative effects of conspecifics on individual survival and growth were much larger than the
406 average negative effects of heterospecifics across the range of neighborhood scales investigated here.
407 Negative conspecific density dependence has been described as a driving force controlling plant
408 survival and growth, that ultimately shape tropical and temperate forest communities (Harms et al.
409 2000; HilleRisLambers et al. 2002; Wills et al. 2006; Comita et al. 2010; Johnson et al. 2012); thus
410 our findings are consistent with previous evidence highlighting the role of density-dependent patterns
411 in structuring forest systems. Therefore, species identity, tree size, and its ontogeny, which vary with
412 the type of forest being studied, may be critical when defining the local neighborhood and require
413 further study.

414 Furthermore, interspecific variation in key functional traits (e.g. leaf N content, SLA, WD) on
415 tree survival and growth varied with neighborhood radius thus, exhibiting spatial dependency. For
416 example, greater neighborhood density led to significant trait hierarchies with stronger effects at a
417 radius larger than 20m. Interestingly, trait differences were evidenced at radius larger than 20m (i.e.
418 25m and 30m), contrary to our expectation that neighborhood models using small radii (<20m) will be
419 those best able to capture the importance of trait distances. The variation in neighborhood effects
420 observed in this study could be related to the past land use history and natural hurricane disturbance in
421 LFDP. Historical land-use intensity has influenced the species and functional composition of the plot
422 (Thompson et al. 2002) and the relative density of species with different functional traits. This
423 resulted in greater hurricane damage and in the northern portion of the LFDP compared to the
424 southern portion (Uriarte et al. 2004, Hogan et al. 2016) as species in the northern part were more
425 likely to suffer hurricane damage (Zimmerman et al. 1994). Our findings that trait differences are
426 significant at large neighborhoods suggest that the disturbance gradient across the LFDP and the
427 resultant distribution of species across the plot with different functional traits might be reflected in the
428 differences in scale at which the functional trait effects are captured. Thus, disturbance can potentially
429 mediate the relationship between the local neighborhood and tree survival and growth, and is likely to
430 be a source of spatial heterogeneity occurring at large scales (regional scale) that future studies need
431 to consider.

432

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

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

453 Focal trees of species with greater maximum height experienced better survival and grew
454 faster than small-statured focal trees. This finding emphasize that light competition is likely to play a
455 major role in the dynamics. Light is a directional resource resulting in an asymmetrical competition
456 and explaining the hierarchy observed in this study. Asymmetric competition for light has been
457 described as a major driver of community assembly of forests (Goldberg & Miller 1990; Freckleton &
458 Watkinson 2001; Westoby et al. 2002; Canham et al. 2004b) by exerting a constraint in species co-
459 occurrence and reducing the opportunities for niche differentiation. Interestingly, focal trees growing
460 with more functionally similar individuals in terms of wood density, maximum height, and specific
461 leaf area experienced greater survival than individuals growing in more diverse neighborhoods. Wood

462 density has been positively associated to tree survival as it is a critical component for many essential
463 functions, such as mechanical support, hydraulic transport, and nutrient storage (Westoby & Wright
464 2006; Chave et al. 2009), while SLA is related to carbon investment as due has a direct impact of
465 plant survival (Wright et al. 2010b). It is possible that habitat heterogeneity, as a result of past
466 anthropogenic disturbance and recurrent natural events (e.g. hurricanes), and recent natural
467 disturbance might be promoting the co-occurrence of both functionally dissimilar and similar
468 competitors at varying scales as previously suggest in this forest (e.g. Swenson, Erickson, et al. 2012).
469 Previous studies have described tree communities at the LFDP as a mix of early and late-successional
470 species after Hurricane Georges potentially the result of an increase in light in the understory allowing
471 more pioneer species to grow (Zimmerman et al. 2010; Hogan et al. 2016; Hogan et al. 2018; Uriarte
472 et al. 2018). Habitat heterogeneity along with species habitat preferences have been described as
473 important factors determining the spatial distribution of tree species in forest systems (Harms et al.
474 2001; John et al. 2007; Chen et al. 2010; Shen et al. 2013).

475

476 How do we improve local neighborhood models?

477 As neighborhood models become more popular in our efforts to understand functional and community
478 ecology, a pressing question is how we deal with the scale dependency of these models? As explored
479 in this study, one could select a range of pre-determined radii, repeat the analyses for each radius and
480 report the functional sensitivity to scales. While this is possible for small- scale data, this option is
481 computationally intensive and inefficient for large-scale forest plots with many trees. This might also
482 complicate comparisons among forests as the most useful scale may be different for forests with
483 different scales of environmental heterogeneity, vegetation structure, and species composition,
484 rendering generalizations of the processes structuring tree communities very difficult. Furthermore,
485 the radius of importance may be tree species- and size-specific depending, not only on the canopy and
486 root system of the focal tree, but the canopy and root systems of the neighbors. Ideally, we would
487 want to define a metric that describes the local neighborhood without having to pre-select the radius.
488 Tree survival and growth are greatly affected by the light environment experienced by individual
489 trees, which ultimately depends on the crown structure (Horn 1971). An alternative to preselecting a
490 radius is to include only those neighboring individuals that have overlapping or interwoven crowns

491 with the focal individual and to include the magnitude of that overlap in the crowding index. In a
492 previous study conducted at the LFDP (see Zambrano et al. 2019), we found that models including
493 crown overlap had better support than models that incorporated a fixed-radius. Furthermore, we
494 reached different conclusions, depending on the type of approach, with respect to the drivers affecting
495 plant performance and subsequent forest dynamics. Therefore, the use of models that integrate
496 information of crown overlap provides a mechanistic, computationally rationale and direct approach
497 for characterizing and analyzing tree neighborhood.

498

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

512

513 Conclusion

514 Scaling has long been recognized as a major challenge and opportunity in ecology (Levin 1992).
515 Identifying spatial structures is a key step toward an improved understanding of the ecological
516 processes that explain species diversity and distribution patterns (Legendre and Fortin 1989). The
517 findings from our study clearly call for more attention to the choice of the radius size encompassing a
518 neighborhood, as the interpretation of the relative importance of the functional neighborhood on tree
519 survival and growth is prone to differences in neighborhood radius. Our results indicate that

520 interspecific effects are relatively stable at spatial scales > 5 m, but are likely stronger and more variable
521 at scales < 5m. Therefore, our findings suggest that inferences drawn in previous work utilizing a
522 single spatial definition of a neighborhood may be biased. By not accounting for the variation in the
523 effects of functional traits on tree survival and growth as these are dependent on the size of the
524 neighborhoods. The neighborhood radius affects the processes driving community assembly and may
525 be different in each forest. Furthermore, the effects of functional neighborhood in each studied forest
526 will vary with habitat heterogeneity such as the abiotic environment (e.g. topography and soil
527 moisture), the land use history and natural disturbances. Thus, conclusions drawn from neighborhood
528 models will be context dependent. A potential alternative to the scale dependency exhibited by current
529 neighborhood models are approaches that do not depend on a pre-defined single radius. These may
530 provide a more mechanistic understanding of the drivers controlling community assembly and allowing
531 comparisons across different forests to describe more general patterns.

532

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543 **Author's contributions**

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

546

547 **Data accessibility statement**

548 Long-term tree data is available on the Luquillo LTER data website (<http://luq.lter-net.edu/data/databatalog>), while functional trait data is available in Dryad
549 (<https://datadryad.org/resource/doi:10.5061/dryad.j2r53/1>).
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809 **Supporting Information**

810 **Appendix S1.** Results of the Principal Component Analysis of plant functional traits.

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

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

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

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820 **TABLES**

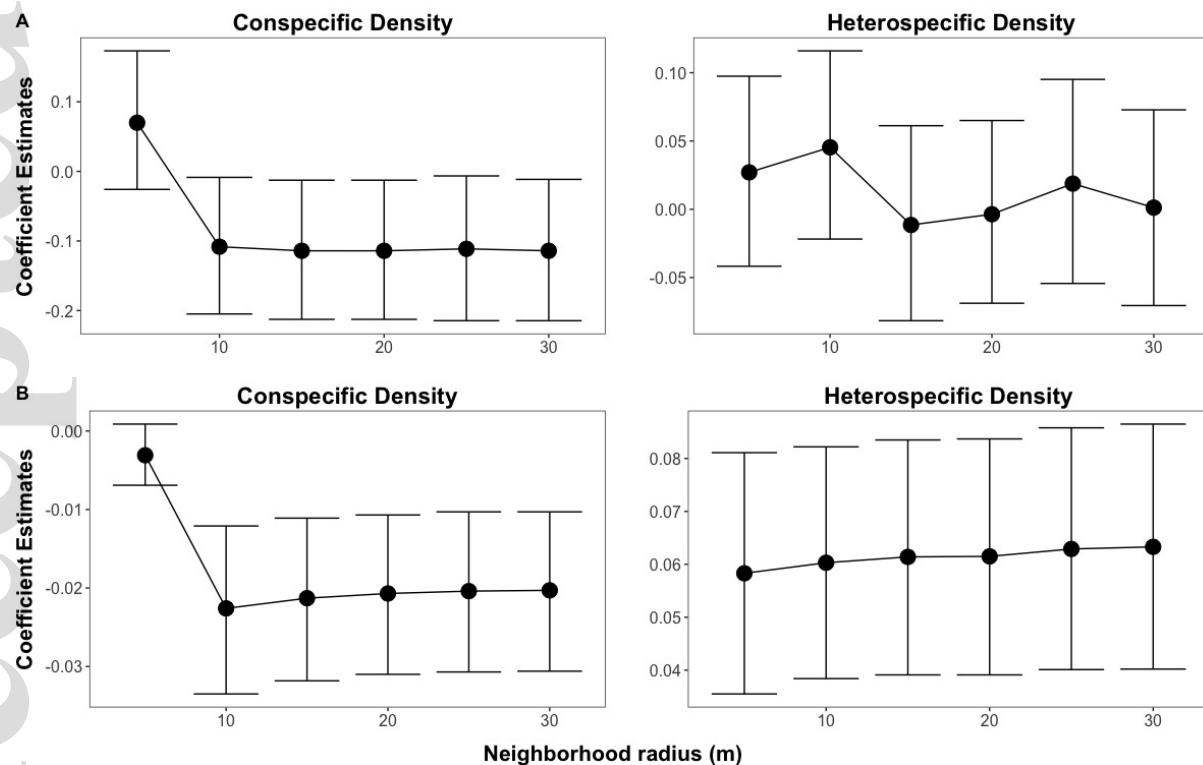
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	Survival		Growth	
	<i>NCIH</i>	<i>NCIS</i>	<i>NCIH</i>	<i>NCIS</i>
Leaf Carbon Content	0.07 (-0.6, 0.73)	0.47 (0.2, 0.73)	-0.2 (-0.73, 0.47)	0.07 (-0.6, 0.73)
Maximum Height	0.33 (-0.33, 0.73)	-0.07 (-0.47, 0.47)	0.6 (0.2, 1)	0.2 (-0.6, 0.73)
Leaf Area	0.07 (-0.47, 0.73)	0.6 (0.2, 0.73)	-0.2 (-0.87, 0.47)	0.07 (-0.47, 0.73)
Leaf Nitrogen Content	-0.2 (-0.8, 0.6)	0.6 (0, 1)	-0.47 (-0.87, 0.2)	0.2 (-0.47, 0.73)
Leaf Phosphorus Content	-0.6 (-0.87, -0.07)	-0.2 (-0.6, 0.2)	-0.47 (-1, 0.33)	0.07 (-0.6, 0.73)

PC1	0.33 (-0.33, 0.87)	0.6 (0.2, 1)	0.2 (-0.33, 0.87)	0.2 (-0.47, 0.73)
PC2	-0.33 (-0.87, 0.47)	0.2 (-0.33, 0.73)	0.2 (-0.73, 0.47)	-0.07 (-0.6, 0.6)
Seed Mass	0.6 (0.2, 1)	0.07 (-0.47, 0.6)	0.475 (-0.07, 1)	0.2 (-0.47, 0.73)
Specific Leaf Area	0.2 (-0.47, 0.73)	-0.33 (-0.73, 0.2)	-0.47 (-0.87, 0.07)	0.33 (-0.33, 0.87)
Wood density	0.2 (-0.47, 0.73)	0.47 (-0.07, 0.87)	0.47 (-0.07, 0.87)	0.07 (-0.6, 0.73)

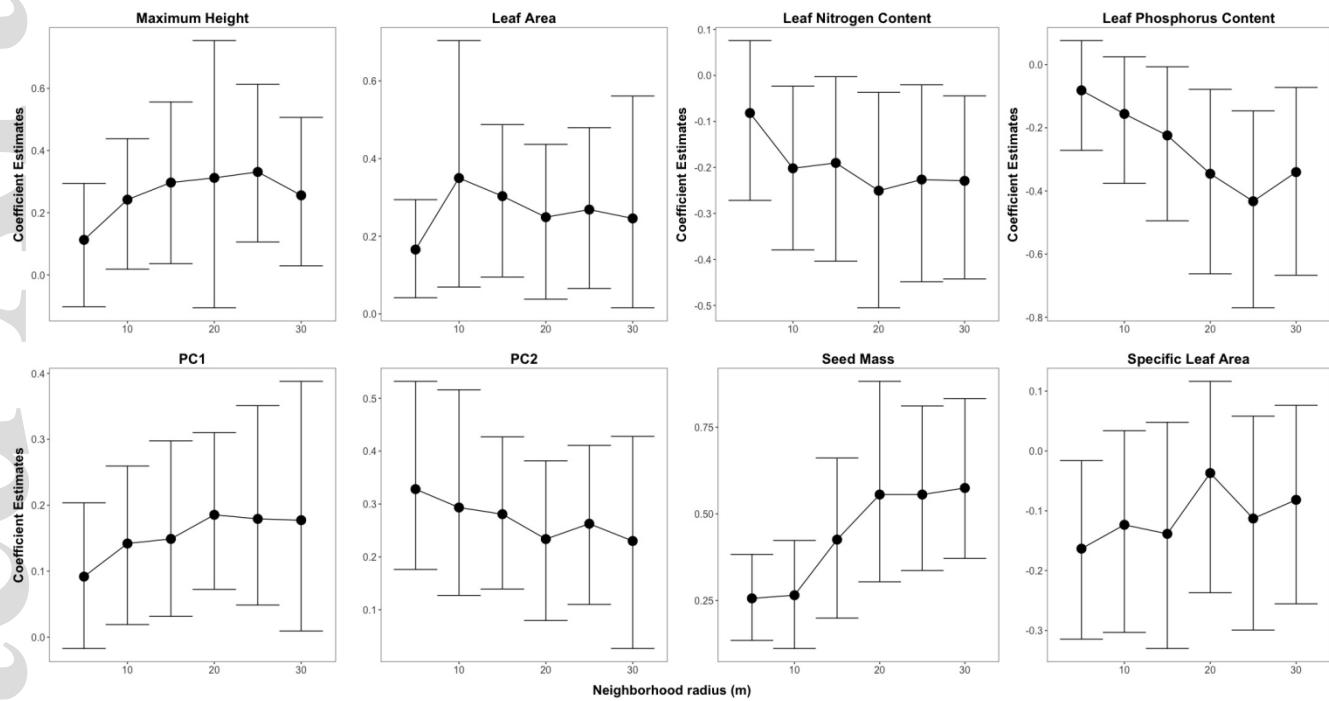
822 **Table 1.** Median values (with 95% credible intervals) of the Kendall correlation, a non-parametric
 823 measure of a monotonic trend, between the estimated effect of trait hierarchies (NCIH) or trait
 824 distance interactions (NCIS) and the neighborhood radius (5m-30m). We included functional traits
 825 showing scale-dependent significant effects on individual tree survival and growth.
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827 FIGURES



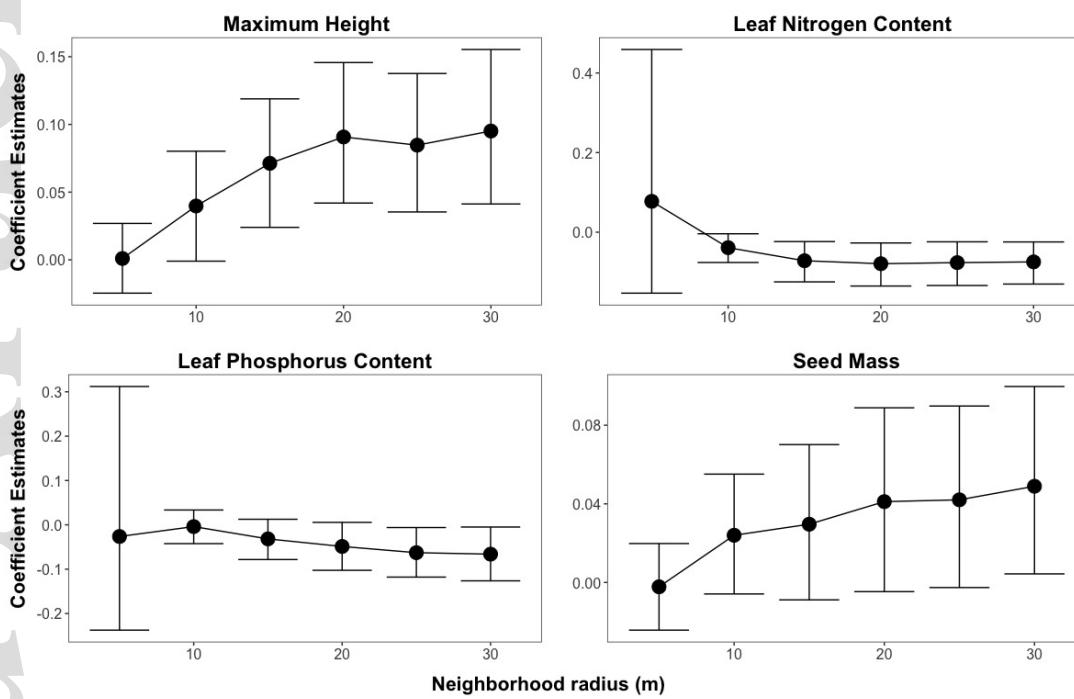
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829 **Figure 1.** Scale-dependent significant effects of conspecific and heterospecific neighborhood on
830 individual A) tree survival and B) tree growth at the Luquillo forest. Points indicate posterior medians
831 for each studied parameter and the shaded area represents the 95% Bayesian credible interval.
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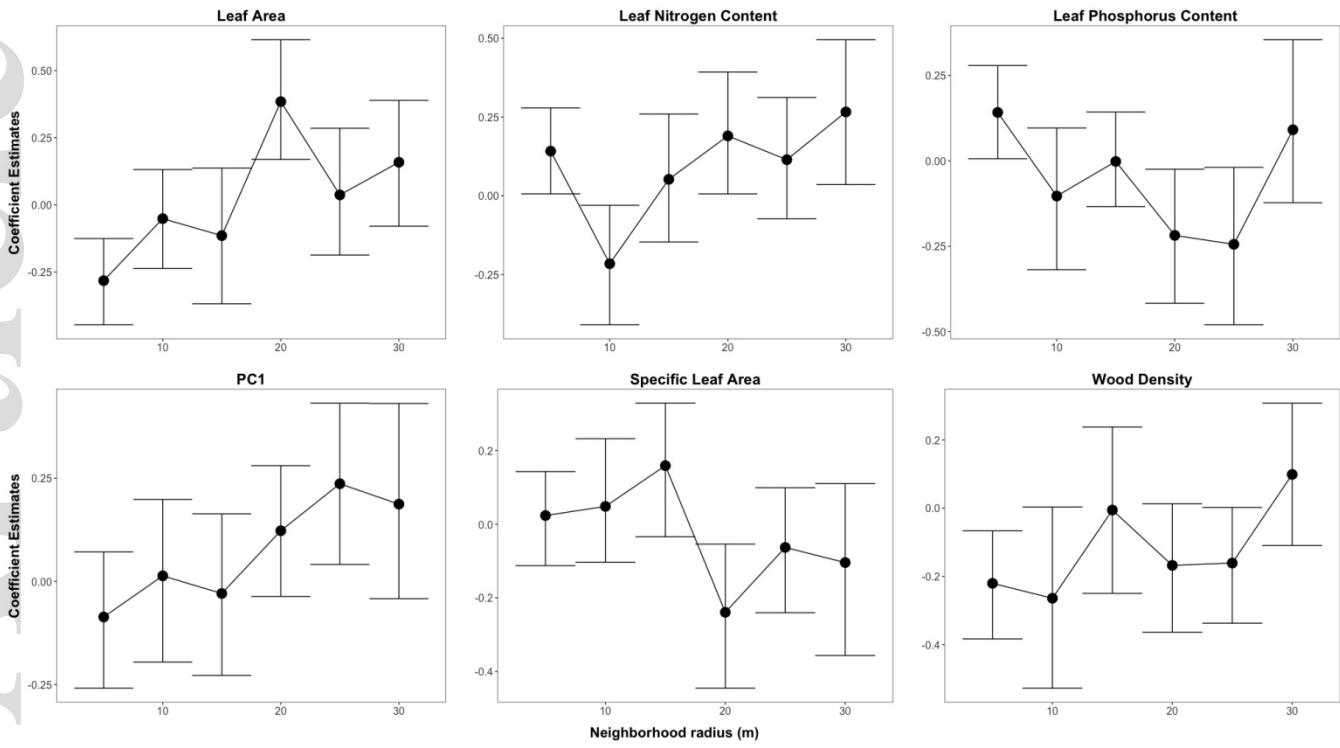


836 **Figure 2.** Scale-dependent significant effects of trait hierarchies on individual tree survival at the
837 Luquillo forest. Increased neighborhood crowding lead to significant trait hierarchies where
838 individuals with high maximum tree height and leaf area values experienced better survival, with
839 stronger effects at 25m and 10m respectively, when compared to other radii. Individuals with low
840 nitrogen and phosphorus content values showed high survivorship, with stronger effects at 15m when
841 compared to other radii. High PC1 and PC2 values resulted in increased survival, particularly at 20m
842 and 5m respectively. Finally, individuals with great seed mass and low specific leaf area values
843 showed high survivorship, with stronger effects at 30m and 20m respectively when compared to other
844 radii. Points indicate posterior medians for each studied parameter and the shaded area represents the
845 95% Bayesian credible interval.
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851 **Figure 3.** Scale-dependent significant effects of trait hierarchies on individual tree growth at the
852 Luquillo forest. Increased crowding lead to significant trait hierarchies with individuals with high
853 maximum tree height had greater growth rates, with stronger effects at 20m and 30m when compared
854 to other radii. Individuals with low nitrogen and phosphorus content experienced lower growth rates
855 than individuals with higher values, particularly at 10m and 30m respectively. Finally, focal trees with
856 greater seed mass grew faster in diameter, when compared to focal trees with small seeds, particularly
857 at 30m. Points indicate posterior medians for each studied parameter and the shaded area represents
858 the 95% Bayesian credible interval.
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861 **Figure 4.** Scale-dependent significant effects of trait distances interactions (niche differentiation) on
 862 individual tree survival at the Luquillo forest. Large differences in leaf area and PC1 between focal
 863 trees and their neighbors resulted in high survivorship of the focal tree, with strong effects occurring
 864 at 20m and 25m respectively. Low trait differences with neighbors in leaf nitrogen and phosphorus
 865 content, specific leaf area and wood density were associated with high survivorship of focal trees,
 866 with overall stronger effects at 5m, 10m, 20m and 25m when compared to other radii. Points indicate
 867 posterior medians for each studied parameter and the shaded area represents the 95% Bayesian
 868 credible interval.