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The scale dependency of trait-based tree neighborhood models

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42

43 **Abstract**

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

48

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

50

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

58

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

68

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

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

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89 **Introduction**

90 Plant functional traits are increasingly used to help elucidate the drivers of forest
91 community structure and dynamics (Suding et al. 2005; McGill et al. 2006; Spasojevic &
92 Suding 2012). They have also been used for tree communities not amenable to
93 experimentation to address classic questions regarding the processes structuring
94 communities (e.g. Uriarte et al. 2010, 2016; Kunstler *et al.* 2012, 2016; Liu et al. 2016).
95 Neighborhood analyses of trait and demographic rates in plant ecology usually take one
96 of two forms. The first is to model demographic rates given trait values of the plants,
97 irrespective of the context in which the plants are found (e.g. Poorter et al. 2008; Wright
98 et al. 2010a; Iida, Kohyama, et al. 2014; Iida, Poorter, et al. 2014). The second is to
99 model demography using individual plants and their trait values, together with the trait
100 values of neighboring plants (e.g. Kunstler et al. 2012; Lasky et al. 2014; Fortunel et al.
101 2016; Uriarte et al. 2016; Zambrano et al. 2017). Analyses that combine functional trait
102 and demographic data provide a mechanistic understanding of observed patterns of
103 community structure and dynamics, by directly investigating the critical linkages between
104 phenotypes and the environment (McGill et al. 2006). Specifically, trait-based
105 approaches provide evidence of two distinct patterns resulting from competitive
106 exclusion (Kraft et al. 2015). As competition increases, greater differences in traits (i.e.
107 niche differentiation), measured by distances among trait values, promote species
108 coexistence (Kraft et al. 2014; Fortunel et al. 2016), and lead to high phenotypic disparity
109 among co-occurring species (Webb et al. 2002; Stubbs & Wilson 2004). Conversely,
110 competition may be driven by hierarchical differences (i.e. trait hierarchies) in species'
111 competitive ability resulting in a phenotypic clustering of co-occurring species (Mayfield
112 & Levine 2010; Uriarte et al. 2010; Kunstler et al. 2012). Environmental filtering or
113 tolerance of local abiotic conditions and competition for light leads to a functional
114 clustering with species possessing traits associated with high fitness excluding species
115 with unfavourable traits (Grime 2006).

116 The first neighborhood models focused on focal plant responses to the species
117 identity of neighboring individuals (Weiner 1982; Pacala & Silander, 1985; Hubbell et al.
118 2001a; Canham et al. 2004a; Uriarte, Canham, et al. 2005), but over the past decade these

119 models have transitioned towards quantifying neighborhood effects based upon the
120 combined attributes (e.g. traits or relatedness) of all trees in a defined area around the
121 focal tree (e.g. Uriarte et al. 2004, 2005b, 2010, Kunstler et al. 2012, Paine et al. 2012).
122 While the exact details of the neighborhood models used in studies vary, tree-based
123 studies often employ some type of crowding index. Crowding indices have been used as a
124 proxy to determine the effects of competition on tree survival and growth and usually
125 take into account the diameter of the neighboring trees and their distance from the focal
126 tree. For example, a commonly used crowding index is a direct function of the squared
127 diameter of the neighbors and inverse function of the squared distances to the neighbor
128 (Canham et al. 2004b). For computational and practical reasons, the neighborhood is
129 defined using a fixed radius around the focal individual tree (Canham et al. 2004a; but
130 see Wills et al. 2016). Using a fixed radius may appear suboptimal for examining
131 neighborhood effects, but the inverse weighting by distance between trees, and the
132 average canopy spreads of trees, could make the decision regarding the radius size
133 inconsequential. Indeed, some studies have suggested that scale dependency does not
134 exist in their neighborhood models (e.g. Fortunel et al. 2016). Conversely, spatial
135 analyses of forest plots that have analyzed individual species-area curves using
136 concentric circular neighborhoods around focal trees have uncovered strong scale
137 dependency (Wiegand et al. 2007; Yang et al. 2013), as have temporally static analyses
138 of trait and phylogenetic dispersion (e.g. Swenson *et al.* 2006; Swenson & Enquist 2009;
139 Kraft & Ackerly 2010).

140 The scale dependency of ecological processes structuring natural communities has
141 long been recognized (Wiens 1989; Levin 1992; Brown 1995; Chase 2014; Garzon-
142 Lopez et al. 2014). At small spatial scales, the probability of two species co-occurring
143 may be most influenced by trait distances (MacArthur and Levins 1967). At larger spatial
144 scales, trait hierarchies may drive the competitive exclusion of species that are not so
145 well suited to the environment (Kunstler et al. 2012). The tendency for traits to be
146 overdispersed among species at small spatial scales and clustered or underdispersed at
147 larger spatial scales have been used as evidence of scale-dependent processes (e.g.
148 Weiher & Keddy 1995, 1999; Weiher *et al.* 1998). Opposing deterministic processes
149 have been reported by static analyses of trait dispersion (e.g. Swenson & Enquist 2009),

150 and it may be that neighborhood models could be susceptible to the same problem. The
151 measured effect of trait distances and trait hierarchies on community dynamics may vary
152 greatly with the size of the area used to define the local neighborhood, but few
153 neighborhood models address this potential scale dependency.

154 To examine the dependence of spatial scale on plant growth and survival in response
155 to neighbors, we constructed neighborhood models using a Bayesian approach and
156 demographic and functional trait tree data from the Luquillo Forest Dynamics Plot
157 (LFDP), Puerto Rico. We hypothesized that processes driving negative density
158 dependence of plant growth and survival in response to conspecifics and heterospecifics
159 operate within neighborhoods smaller than 20m, as previous studies in tropical forests
160 have shown that neighborhood effects on tree survival and growth should dissipate
161 beyond that distance (Hubbell et al. 2001b; Uriarte et al. 2004; Uriarte et al. 2010; Lasky
162 et al. 2014). Hence, we predicted that strength of the effects of heterospecific neighbors'
163 traits on the survival and growth of a focal tree, measured as trait distances, will be
164 stronger within local neighborhoods less than 20m radius compared to greater radii, and
165 the strength of the effects of competitive exclusion on the survival and growth of a focal
166 tree, measured as trait hierarchies, and analyzed using neighborhood models will be
167 stronger in neighborhoods with larger radii (>20 m) compared to smaller radii (< 20 m).
168 Alternatively, the effects of functional neighborhood (effect of neighbors based on their
169 functional trait values) on tree performance might be insensitive to the choice of spatial
170 scale used to model the neighborhood, as some studies have suggested (e.g. Fortunel et
171 al. 2016).

172

173 **Methods**

174 **Study site**

175 The Luquillo Forest Dynamics Plot (LFDP) (18°20' N, 65°49' W, 333-428 m. asl) is a
176 16-ha forest plot located in the Luquillo Experimental Forest in northeast Puerto Rico
177 (Thompson et al. 2002). This is a subtropical wet forest with an average precipitation of
178 3500 mm per year. The plot has been censused approximately every 5 years since 1990
179 and every free-standing individual with a woody stem ≥ 1 cm in diameter at breast height

180 (DBH measured at 1.3 m from the ground) is tagged, mapped, measured and identified to
181 species (Thompson et al. 2002). Over time 150 species have been recorded in the LFDP,
182 but in any given census the species richness is ~120 species (Hogan et al. 2016). In the 20
183 years before the censuses used in this study, the forest experienced major hurricane
184 disturbances in 1989 and 1998, which resulted in extraordinary temporal dynamics with
185 tens of thousands of individuals recruiting and dying during some census intervals
186 (Hogan et al. 2016). In this study, we used relative growth rates and survival data for
187 22596 individuals from a single census interval (2005-2010), which was chosen to reflect
188 the most stable census period since the LFDP was established (at the time of this
189 analysis), to reduce the effect of the rapid community dynamics caused by hurricane
190 disturbances.

191

192 Functional trait data

193 For this study, we used species-level functional trait data that represent the main
194 ecological strategies for resource acquisition (Westoby et al. 2002; Wright et al. 2010a)
195 and that were measured from adult trees (≥ 1 cm in DBH) in the Luquillo forest
196 (Swenson et al. 2012, Umaña et al. 2016, Swenson and Umaña 2015). Leaf traits
197 included leaf area and specific leaf area. Leaf area has been shown to strongly correlate
198 with competitive ability for light (Bloom et al. 1985), while specific leaf area is a key
199 trait reflecting the trade-off between a leaf's lifespan and carbon capture (Westoby et al.
200 2002; Wright, Westoby, et al. 2004). Other leaf traits used were nitrogen, phosphorus,
201 and carbon content that reveal a trade-off between rapid acquisition and efficient
202 conservation of resources (Reich et al. 1997; Wright, Reich, et al. 2004). Leaf N content
203 plays a strong role in photosynthesis as the proteins of the Calvin cycle and thylakoids
204 account for the majority of N in leaves (Evans 1989). We also included seed mass, which
205 is indirectly related to physiological and structural traits that influence plant survival and
206 growth, (e.g. leaf area and photosynthetic rate (Reich et al. 1992), and represents a trade-
207 off between producing several small stress-intolerant seeds or few large stress-tolerant
208 seeds (Coomes & Grubb 2003; Muller-Landau 2010). Finally, we incorporated in our
209 analyses wood density of stems, a critical component for many essential functions, such

210 as mechanical support, hydraulic transport, and nutrient storage (Westoby & Wright
211 2006) (Also Chave et al. 2009), and maximum tree height that varies across light resource
212 gradients (Gaudet & Keddy 1988) and with the type and frequency of disturbance events
213 (Schamp & Aarssen 2009). With the exception of leaf carbon content, wood density, and
214 seed mass, trait values were log-transformed to approximate normality. All traits were
215 then standardized across species to a mean of 0 and a standard deviation of 1 prior to the
216 analyses.

217 To reduce the number and collinearity of traits we applied a Principal Component
218 Analysis (PCA). Traits were log-transformed for the PCA analysis. Two major axes of
219 variation were determined in which the first axis (PC1) explained 30% of the variation
220 and the second axis (PC2) 21% of the variation. We used the broken-stick criterion using
221 the “PCA significance” function from the *Biodiversity* package (Kindt 2019) to identify
222 the main principal components responsible for trait variation (Legendre & Legendre
223 2012). The first axis was significantly associated with leaf phosphorus and nitrogen
224 content, specific leaf area and wood density, while the second axis represented leaf area,
225 maximum height and seed mass (see results in Appendix S1), confirming previous
226 findings (see Díaz et al. 2016). We fitted separate growth and survival models, for each
227 functional trait and each of the two main PCA axes, as described in the next sections.

228

229 Neighborhood survival and growth models

230 To examine scale-dependent effects of neighborhood crowding and plant functional traits
231 on tree survival and growth, we constructed separate hierarchical generalized linear
232 mixed models for each functional trait and the two main PCA axes using a Bayesian
233 approach, as well as simpler models that only included conspecific density, heterospecific
234 density, or initial tree DBH. We defined neighborhood radii from 5m to 30m from each
235 focal tree, at 5m intervals. We excluded from the analyses trees that were located within
236 30m of the edges of the LFDP. We characterized the “neighborhood” of a focal tree in
237 terms of the summed tree size (DBH) of conspecific and heterospecific neighbors
238 irrespective of their trait values, and also the “functional neighborhood” in which the
239 abundance of neighbors was calculated in terms of both their DBH size and their

240 functional values. Due to the distinct growth pattern of the palms (Arecaceae) *Prestoea*
241 *acuminata var montana* and *Roystonea borinquena*, these species were not included as
242 target trees in growth models but were incorporated as neighbors. We quantified
243 conspecific and heterospecific competition of neighbors using a Neighborhood Crowding
244 Index (NCI), where the negative influence of neighbors varies as a direct function of the
245 squared diameter of the neighbor j (DBH_j) and inverse function of the squared distance to
246 the neighbor (d_{ij}) (Uriarte et al. 2010). This effect is summed over all neighbors j within
247 the pre-defined radius around the focal individual i (separately for conspecifics and
248 heterospecifics).

249

$$250 \quad NCI_i = \sum_j \frac{DBH_j^2}{d_{ij}^2}$$

251

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

255

$$256 \quad NCIH_i = \sum_j (F_{s[i]} - F_{s[j]}) \frac{DBH_j^2}{d_{ij}^2}$$

257 and

$$258 \quad NCIS_i = \sum_j |F_{s[i]} - F_{s[j]}| \frac{DBH_j^2}{d_{ij}^2}$$

259

260 where $F_{s[i]}$ and $F_{s[j]}$ represent the values of the functional trait of interest for focal
261 individual i and neighbor j belonging to their respective species $s[i]$ and $s[j]$. Increased
262 neighborhood crowding may lead to a trait hierarchy that results in the competitive
263 exclusion of inferior competitors, where the competitive advantage of the focal individual
264 i over neighbor j will be represented by an increasing value of $F_{s[i]} - F_{s[j]}$. Similarly,
265 increased crowding may lead to more intense competition for resources between
266 functionally similar individuals, where the competitive effect of the focal individual i and
267 neighbor j decreases with trait distance, measured by the absolute trait difference $|F_{s[i]} -$
268 $F_{s[j]}|$. We log-transformed the NCI and NCIS to reduce the skewness of their

269 distributions and the influence of their extreme values. Since the NCIH distribution was
270 symmetric with extreme negative and positive values, we applied a log-modulus
271 transformation, where the new value has the same sign as the original but the log of its
272 magnitude (John & Draper 1980).

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

282

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

287

$$288 \quad z_i = \beta_{1s} + \beta_{2s}CI_i + \beta_{3s}NCI_i + \beta_{4s}S.E.S\ NCIS_i + \beta_{5s}NCIH_i + \beta_{6s}DBH_i$$

289

290 where the β are species-specific coefficients representing the intercept (β_{1s}), the effect of
291 conspecific neighborhood density (β_{2s}), the effect of heterospecific neighborhood density
292 (β_{3s}), the effect of crowding based on standardized trait distances between heterospecific
293 neighbors (β_{4s}), the effect of crowding based on trait hierarchies (β_{5s}), and the effect of
294 initial tree size (DBH) (β_{6s}). To prevent confounding of the species-specific effects with
295 inter-specific variation in mean diameter, we standardized tree size (DBH) by subtracting
296 their species-specific mean (\overline{DBH}_s) from their individual initial DBH values and then log-
297 transformed the values to reduce the skewness of their distributions. All predictor
298 variables were scaled to a mean of 0 and a standard deviation of 1 to allow comparisons

299 across effect sizes (Rscripts related to the survival and growth models can be found in
300 <https://github.com/jzambranom/neighborhood-models/blob/master/tree-demography>).

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

305

$$306 \quad \beta_{1s} \sim N(\mu_{\beta_1} + \gamma_1 F_s, \sigma_{\beta_1})$$

307

308 Other species-specific coefficients (β_2 to β_6) were also drawn from a normal distribution,
309 but did not include a trait effect. For the \square_\square and \square hyper-parameters we specified normal
310 priors: $N(\text{mean} = 0, \text{precision} = 0.01)$. We expressed the variance hyper-parameters (the
311 \square_b and \square_z) as precisions ($\square = 1/\square^2$) and gave the latter diffuse gamma priors: *Gamma*
312 (shape = 0.001, rate = 0.001). We fitted all models using JAGS (Plummer 2003) and
313 parameter estimates and 95% credible intervals were obtained from the quantiles of their
314 posterior distribution, using the median as a point estimate. All models were fit using
315 Markov Chain Monte Carlo (MCMC) sampling techniques in *JAGS* 4.3.0 (Plummer
316 2003) using the *rjags* (Plummer 2016) and *runjags* (Denwood 2016) packages.

317 We simulated six Markov Chain Monte Carlo chains (MCMC) for 50,000
318 iterations with 10,000 adaptation iterations and a burn-in period of 10,000 iterations to
319 obtain a sufficient number of effectively independent samples from the posterior
320 distribution. Convergence of the MCMC chains was assessed visually with traceplots and
321 the Gelman-Rubin convergence diagnostic, ensuring values of the latter were less than
322 1.2 (Gelman & Rubin 1992). Finally, we assessed the models' goodness of fit via
323 posterior predictive checks. At each MCMC iteration, we simulated a new data vector for
324 growth rates or survival status from the model and calculated a loss function on both the
325 simulated and observed data. The loss function was defined either as the sum of squared
326 differences between the data vector and z for growth, or as the negative of the log-
327 likelihood of the data vector given z for survival. If the model fits the observed data, the
328 probability that the simulated loss is greater than the observed loss should be
329 approximately 0.5. Goodness-of-fit tests were used to exclude models with poor fit. We

330 visually inspected variograms of the model residuals, computed with the *gstat* package, to
331 verify the absence of spatial autocorrelation of residuals between nearby trees (see
332 example in Appendix S2). We tested for monotonic trends by computing the non-
333 parametric Kendall correlation between effect size and neighborhood radius for traits
334 displaying significant effects on individual tree survival and growth. A 95% credible
335 interval was estimated by computing the Kendall correlation from random draws from the
336 posterior distribution of effect sizes at each radius.

337

338 Criteria for scale dependency

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

350

351 **Results**

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

359 results of functional traits with significant effect (95% CI non-crossing zero), and the
360 Supplementary Information (Appendix S4) includes results for all other traits studied.
361

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

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

369

370 Does neighborhood radius influence the strength of the effects of the
371 functional neighborhood on the focal tree performance?

372 The strength of the effects of the functional neighborhood on survival of focal trees
373 varied with neighborhood radii (Fig. 2). We found evidence for a positive scale-
374 dependent significant effect of trait hierarchies on focal tree survival. Specifically,
375 species with higher maximum height, greatest seed mass and with bigger leaves survive
376 better than species that are shorter in height and have small seed mass and small leaf area
377 (Fig. 2). The strength of these effects depended on the neighborhood radius, with effects
378 being stronger at 10m (radius around focal tree) for leaf area, 25m for maximum height
379 and at 30m for seed mass when compared to other radii (Fig. 2). Similarly, species with
380 low leaf nitrogen and phosphorus content had better survival (especially at 15m) than
381 species with high leaf nitrogen and phosphorus content (Fig. 2). Finally, high values on
382 PC1 (i.e. plant economics) and PC2 (i.e. variation in plant size) resulted in high focal tree
383 survival, particularly at 15m neighborhood radius (Fig. 2). Moreover, results from the
384 Kendall correlation test showed evidence of a significant negative correlation for leaf
385 phosphorus content, while seed mass displayed a significant positive trend (Table 1),
386 supporting the idea of a strong scale dependency occurring for these traits.

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

398
399 Significant scale-dependent effects of trait distances were found only for focal tree
400 survival (Fig 4). When neighbors had small trait differences for leaf traits, wood density,
401 and maximum height focal trees experienced greater survival, with stronger effects
402 observed at 10m for leaf nitrogen content (Fig. 4), 20m and 25m for leaf phosphorus
403 content, 20m for specific leaf area (Fig. 4) and 5m for wood density (Fig. 4), when
404 compared to other radii. However, a large difference in leaf area between focal trees and
405 their neighbors resulted in high survivorship of the focal tree, with strong effects
406 occurring at 20m (Fig. 4). Similarly, large differences in PC1 resulted in better survival
407 particularly at 25m (Fig. 4). Finally, we found strong evidence of a significant positive
408 correlation for leaf area and PC1 (Table 1).

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

417

418 **Discussion**

419 Neighborhood models have facilitated the investigation of drivers of community structure
420 and dynamics, but often such studies have arbitrarily defined the local neighborhood
421 radius, thus hampering our understanding of the spatial scales across which different
422 mechanisms operate in different ecosystems. In our study, we investigated the variation
423 in estimates of the effects of the local neighborhood on tree survival and growth based on
424 neighborhood radius, density and identity of neighbors, and functional traits. Contrary to
425 expectation, the strength of conspecific and heterospecific density dependence on tree
426 survival and growth was invariant with neighborhood (radii from 5-30 m). As expected,
427 the strength of the effects of the functional neighborhood on focal tree survival and
428 growth varied with neighborhood radius and the effects on tree survival and growth went
429 beyond the 20m radius. Moreover, both ecological mechanisms, i.e. environmental
430 filtering estimated from the effects of trait distances and niche differentiation estimated
431 from the effects of trait hierarchies, had significant effects at the same neighborhood
432 radii. Our results strongly suggest that the choice of the neighborhood radius when
433 analyzing neighborhood effects is critical, as different radii may lead to very different
434 conclusions on the drivers of tree community dynamics as discussed in more detail
435 below.

436

437 **Effects of neighborhood crowding and functional neighborhood on tree**
438 **performance: a matter of scale**

439 Our results show that heterospecific density dependent effects on tree growth had overall
440 consistent effects across the variety of neighborhood radii tested. Thus, it is likely that the
441 link between heterospecific neighborhood density and tree growth might not be sensitive
442 to the variation in neighborhood radius in the Luquillo forest. Furthermore, we were not
443 able to capture the effects of conspecific density on tree survival and growth at 5m, as
444 previously reported (Zhu et al. 2017), and the strength of the effect did not change for
445 larger neighborhood radii. This could be because the 5m radius neighborhood was so
446 narrow that the probability of encountering a conspecific neighbor was very small,
447 especially for neighbor trees > 10 cm DBH. Moreover, the probability of encountering

448 neighbors of the same species in small neighborhoods might vary with ontogeny, with
449 earlier stages experiencing stronger neighborhood effects at short radii. Nonetheless, it is
450 important to note that the average negative effects of conspecifics on individual survival
451 and growth were much larger than the average negative effects of heterospecifics across
452 the range of neighborhood scales investigated here. Negative conspecific density
453 dependence has been described as a driving force controlling plant survival and growth,
454 that ultimately shape tropical and temperate forest communities (Harms et al. 2000;
455 HilleRisLambers et al. 2002; Wills et al. 2006; Comita et al. 2010; Johnson et al. 2012);
456 thus our findings are consistent with previous evidence highlighting the role of density-
457 dependent patterns in structuring forest systems. Therefore, species identity, tree size, and
458 its ontogeny, which vary with the type of forest being studied, may be critical when
459 defining the local neighborhood and require further study.

460 Furthermore, interspecific variation in key functional traits (e.g. leaf N content,
461 SLA, WD) on tree survival and growth varied with neighborhood radius thus, exhibiting
462 spatial dependency. For example, greater neighborhood density led to significant trait
463 hierarchies with stronger effects at a radius larger than 20m. Interestingly, trait
464 differences were evidenced at radius larger than 20m (i.e. 25m and 30m), contrary to our
465 expectation that neighborhood models using small radii (<20m) will be those best able to
466 capture the importance of trait distances. The variation in neighborhood effects observed
467 in this study could be related to the past land use history and natural hurricane
468 disturbance in LFDP. Historical land-use intensity has influenced the species and
469 functional composition of the plot (Thompson et al. 2002) and the relative density of
470 species with different functional traits. This resulted in greater hurricane damage and in
471 the northern portion of the LFDP compared to the southern portion (Uriarte et al. 2004,
472 Hogan et al. 2016) as species in the northern part were more likely to suffer hurricane
473 damage (Zimmerman et al. 1994). Our findings that trait differences are significant at
474 large neighborhoods suggest that the disturbance gradient across the LFDP and the
475 resultant distribution of species across the plot with different functional traits might be
476 reflected in the differences in scale at which the functional trait effects are captured.
477 Thus, disturbance can potentially mediate the relationship between the local
478 neighborhood and tree survival and growth, and is likely to be a source of spatial

479 heterogeneity occurring at large scales (regional scale) that future studies need to
480 consider.

481

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

484 Habitat filtering, leading to trait hierarchies, mainly acts at a regional scale, and selects a
485 set of species with similar functional attributes that enable them to withstand the
486 environmental conditions encountered by the forest community (Diaz et al. 1998; Grime
487 2006). Trait hierarchies due to habitat preferences, can lead to similar species co-
488 occurring and performing better when located near to analogous neighbors (Kunstler et
489 al. 2012). In contrast, niche differentiation, acting at small to intermediate spatial scales,
490 prevents the co-occurrence of ecologically similar species (Weiher & Keddy 1995a;
491 Grime 2006). There is growing evidence, including our study, that the observed spatial
492 patterns of plant communities may be a combination of both processes occurring at
493 similar scales. For example, results from an investigation into the variation in trait
494 diversity along a stress-resource gradient suggested that both environmental filtering and
495 local competition operated simultaneously to structure plant communities in the alpine
496 tundra of the Colorado Rocky Mountains (Spasojevic & Suding 2012). A strong
497 interaction between regional scale climate and local scale neighborhood shaping tree
498 communities has been described for the Northeastern US and Puerto Rico (Zambrano et
499 al. 2017). Similarly, both environmental filtering and local competition explain
500 differences in trait axes due to habitat disturbance in grassland communities (Mason et al.
501 2011). In sum, results from the Luquillo forest are consistent with these previous studies
502 and demonstrate that habitat filtering and niche differentiation effects, occurring at the
503 same scale, are strong enough to structure forest systems.

504 Focal trees of species with greater maximum height experienced better survival
505 and grew faster than small-statured focal trees. This finding emphasize that light
506 competition is likely to play a major role in the dynamics. Light is a directional resource
507 resulting in an asymmetrical competition and explaining the hierarchy observed in this
508 study. Asymmetric competition for light has been described as a major driver of

509 community assembly of forests (Goldberg & Miller 1990; Freckleton & Watkinson 2001;
510 Westoby et al. 2002; Canham et al. 2004b) by exerting a constraint in species co-
511 occurrence and reducing the opportunities for niche differentiation. Interestingly, focal
512 trees growing with more functionally similar individuals in terms of wood density,
513 maximum height, and specific leaf area experienced greater survival than individuals
514 growing in more diverse neighborhoods. Wood density has been positively associated to
515 tree survival as it is a critical component for many essential functions, such as mechanical
516 support, hydraulic transport, and nutrient storage (Westoby & Wright 2006; Chave et al.
517 2009), while SLA is related to carbon investment as due has a direct impact of plant
518 survival (Wright et al. 2010b). It is possible that habitat heterogeneity, as a result of past
519 anthropogenic disturbance and recurrent natural events (e.g. hurricanes), and recent
520 natural disturbance might be promoting the co-occurrence of both functionally dissimilar
521 and similar competitors at varying scales as previously suggest in this forest (e.g.
522 Swenson, Erickson, et al. 2012). Previous studies have described tree communities at the
523 LFDP as a mix of early and late-successional species after Hurricane Georges potentially
524 the result of an increase in light in the understory allowing more pioneer species to grow
525 (Zimmerman et al. 2010; Hogan et al. 2016; Hogan et al. 2018; Uriarte et al. 2018).
526 Habitat heterogeneity along with species habitat preferences have been described as
527 important factors determining the spatial distribution of tree species in forest systems
528 (Harms et al. 2001; John et al. 2007; Chen et al. 2010; Shen et al. 2013).

529

530 How do we improve local neighborhood models?

531 As neighborhood models become more popular in our efforts to understand functional
532 and community ecology, a pressing question is how we deal with the scale dependency of
533 these models? As explored in this study, one could select a range of pre-determined radii,
534 repeat the analyses for each radius and report the functional sensitivity to scales. While
535 this is possible for small- scale data, this option is computationally intensive and
536 inefficient for large-scale forest plots with many trees. This might also complicate
537 comparisons among forests as the most useful scale may be different for forests with
538 different scales of environmental heterogeneity, vegetation structure, and species

539 composition, rendering generalizations of the processes structuring tree communities very
540 difficult. Furthermore, the radius of importance may be tree species- and size-specific
541 depending, not only on the canopy and root system of the focal tree, but the canopy and
542 root systems of the neighbors. Ideally, we would want to define a metric that describes
543 the local neighborhood without having to pre-select the radius. Tree survival and growth
544 are greatly affected by the light environment experienced by individual trees, which
545 ultimately depends on the crown structure (Horn 1971). An alternative to preselecting a
546 radius is to include only those neighboring individuals that have overlapping or
547 interwoven crowns with the focal individual and to include the magnitude of that overlap
548 in the crowding index. In a previous study conducted at the LFDP (see Zambrano et al.
549 2019), we found that models including crown overlap had better support than models that
550 incorporated a fixed-radius. Furthermore, we reached different conclusions, depending on
551 the type of approach, with respect to the drivers affecting plant performance and
552 subsequent forest dynamics. Therefore, the use of models that integrate information of
553 crown overlap provides a mechanistic, computationally rationale and direct approach for
554 characterizing and analyzing tree neighborhood-

555

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

569 pattern methods and neighborhood models would greatly improve our understanding of
570 spatial patterns structuring tree communities.

571

572 **Conclusion**

573 Scaling has long been recognized as a major challenge and opportunity in ecology (Levin
574 1992). Identifying spatial structures is a key step toward an improved understanding of
575 the ecological processes that explain species diversity and distribution patterns (Legendre
576 and Fortin 1989). The findings from our study clearly call for more attention to the choice
577 of the radius size encompassing a neighborhood, as the interpretation of the relative
578 importance of the functional neighborhood on tree survival and growth is prone to
579 differences in neighborhood radius. Our results indicate that interspecific effects are
580 relative stable at spatial scales > 5 m, but are likely stronger and more variable at scales $<$
581 5 m. Therefore, our findings suggest that inferences drawn in previous work utilizing a
582 single spatial definition of a neighborhood may be biased. By not accounting for the
583 variation in the effects of functional traits on tree survival and growth as these are
584 dependent on the size of the neighborhoods. The neighborhood radius affects the
585 processes driving community assembly and may be different in each forest. Furthermore,
586 the effects of functional neighborhood in each studied forest will vary with habitat
587 heterogeneity such as the abiotic environment (e.g. topography and soil moisture), the
588 land use history and natural disturbances. Thus, conclusions drawn from neighborhood
589 models will be context dependent. A potential alternative to the scale dependency
590 exhibited by current neighborhood models are approaches that do not depend on a pre-
591 defined single radius. These may provide a more mechanistic understanding of the drivers
592 controlling community assembly and allowing comparisons across different forests to
593 describe more general patterns.

594

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606 **Author's contributions**

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

610

611 **Data accessibility statement**

612 Long-term tree data is available on the Luquillo LTER data website ([http://luq.lter-
613 net.edu/data/datacatalog](http://luq.lter-
613 net.edu/data/datacatalog)), while functional trait data is available in Dryad
614 (<https://datadryad.org/resource/doi:10.5061/dryad.j2r53/1>).

615

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906 **Supporting Information**

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

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

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

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

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917 **TABLES**

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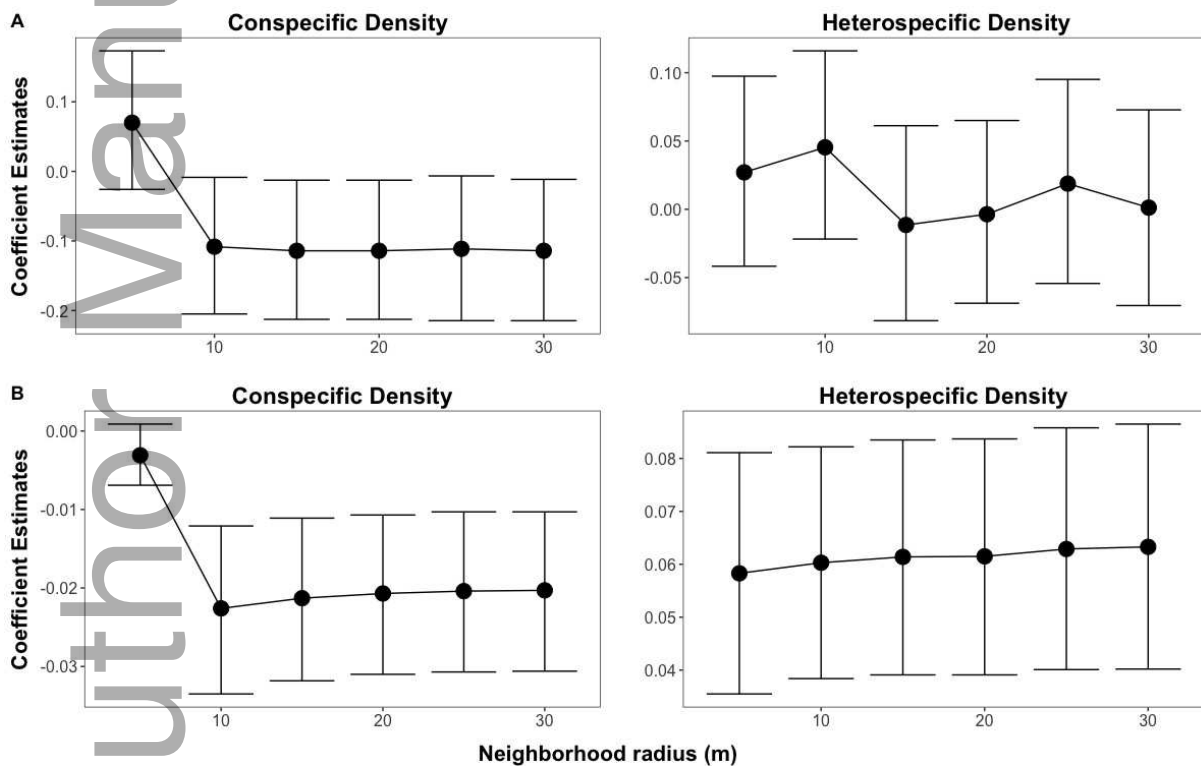
	Survival		Growth	
	<i>NCIH</i>	<i>NCIS</i>	<i>NCIH</i>	<i>NCIS</i>
Leaf Carbon Content	0.07 (-0.6, 0.73)	0.47 (0.2, 0.73)	-0.2 (-0.73, 0.47)	0.07 (-0.6, 0.73)
Maximum Height	0.33 (-0.33, 0.73)	-0.07 (-0.47, 0.47)	0.6 (0.2, 1)	0.2 (-0.6, 0.73)
Leaf Area	0.07 (-0.47, 0.73)	0.6 (0.2, 0.73)	-0.2 (-0.87,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

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

924

925 **FIGURES**



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927 **Figure 1.** Scale-dependent significant effects of conspecific and heterospecific
 928 neighborhood on individual A) tree survival and B) tree growth at the Luquillo forest.

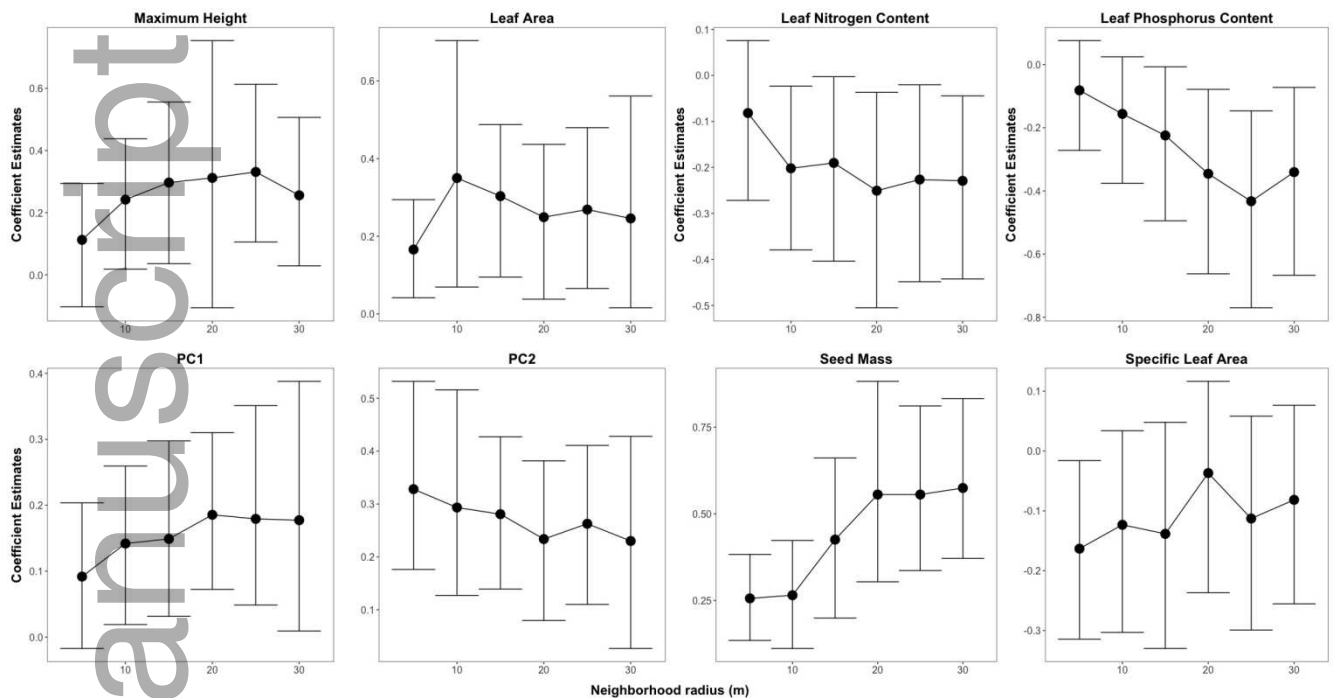
929 Points indicate posterior medians for each studied parameter and the shaded area
 930 represents the 95% Bayesian credible interval.

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936 **Figure 2.** Scale-dependent significant effects of trait hierarchies on individual tree

937 survival at the Luquillo forest. Increased neighborhood crowding lead to significant trait

938 hierarchies where individuals with high maximum tree height and leaf area values

939 experienced better survival, with stronger effects at 25m and 10m respectively, when

940 compared to other radii. Individuals with low nitrogen and phosphorus content values

941 showed high survivorship, with stronger effects at 15m when compared to other radii.

942 High PC1 and PC2 values resulted in increased survival, particularly at 20m and 5m

943 respectively. Finally, individuals with great seed mass and low specific leaf area values

944 showed high survivorship, with stronger effects at 30m and 20m respectively when

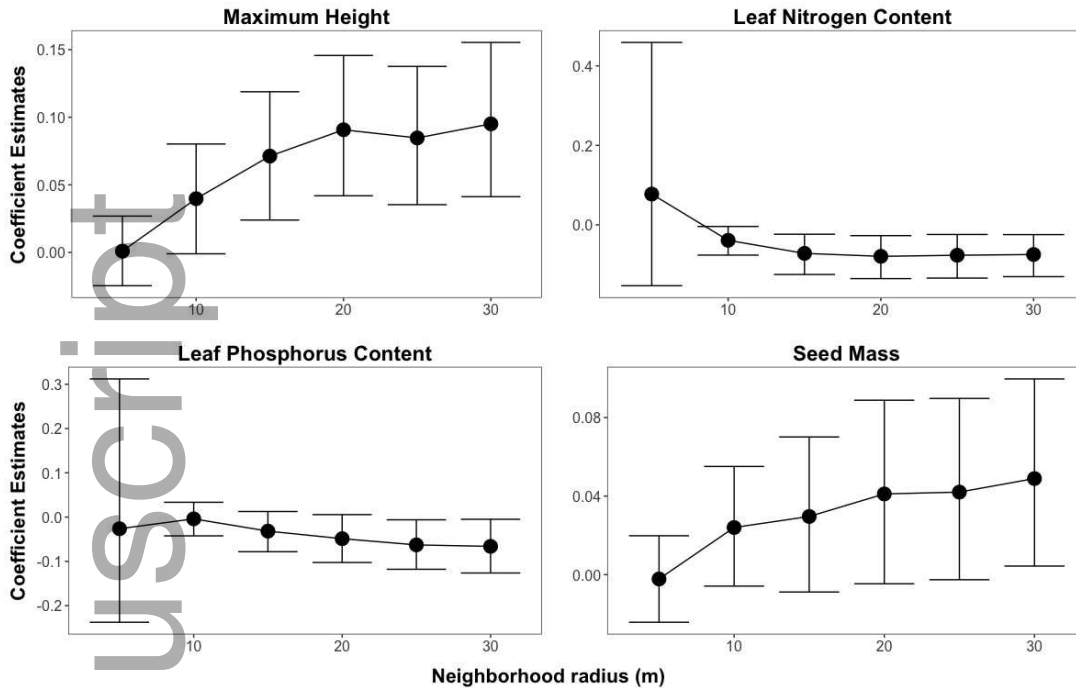
945 compared to other radii. Points indicate posterior medians for each studied parameter and

946 the shaded area represents the 95% Bayesian credible interval.

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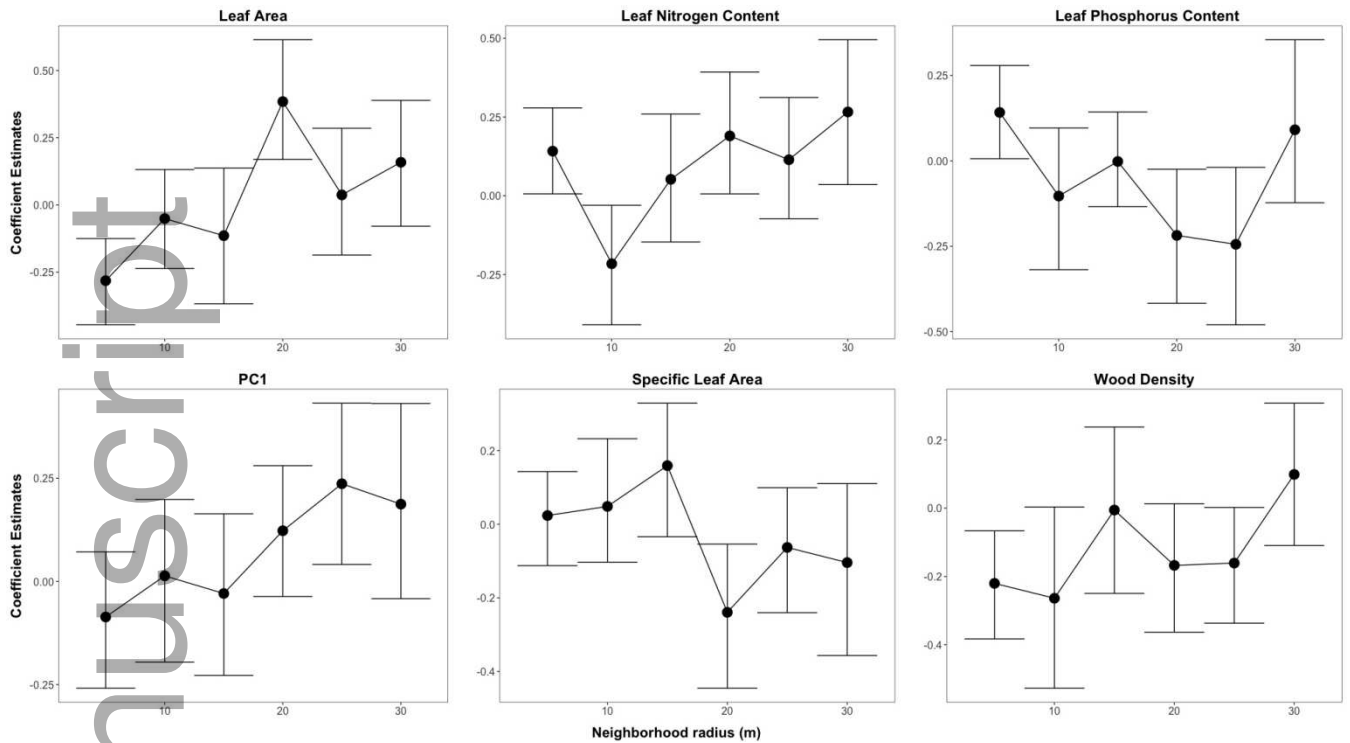
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951 **Figure 3.** Scale-dependent significant effects of trait hierarchies on individual tree
 952 growth at the Luquillo forest. Increased crowding lead to significant trait hierarchies with
 953 individuals with high maximum tree height had greater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

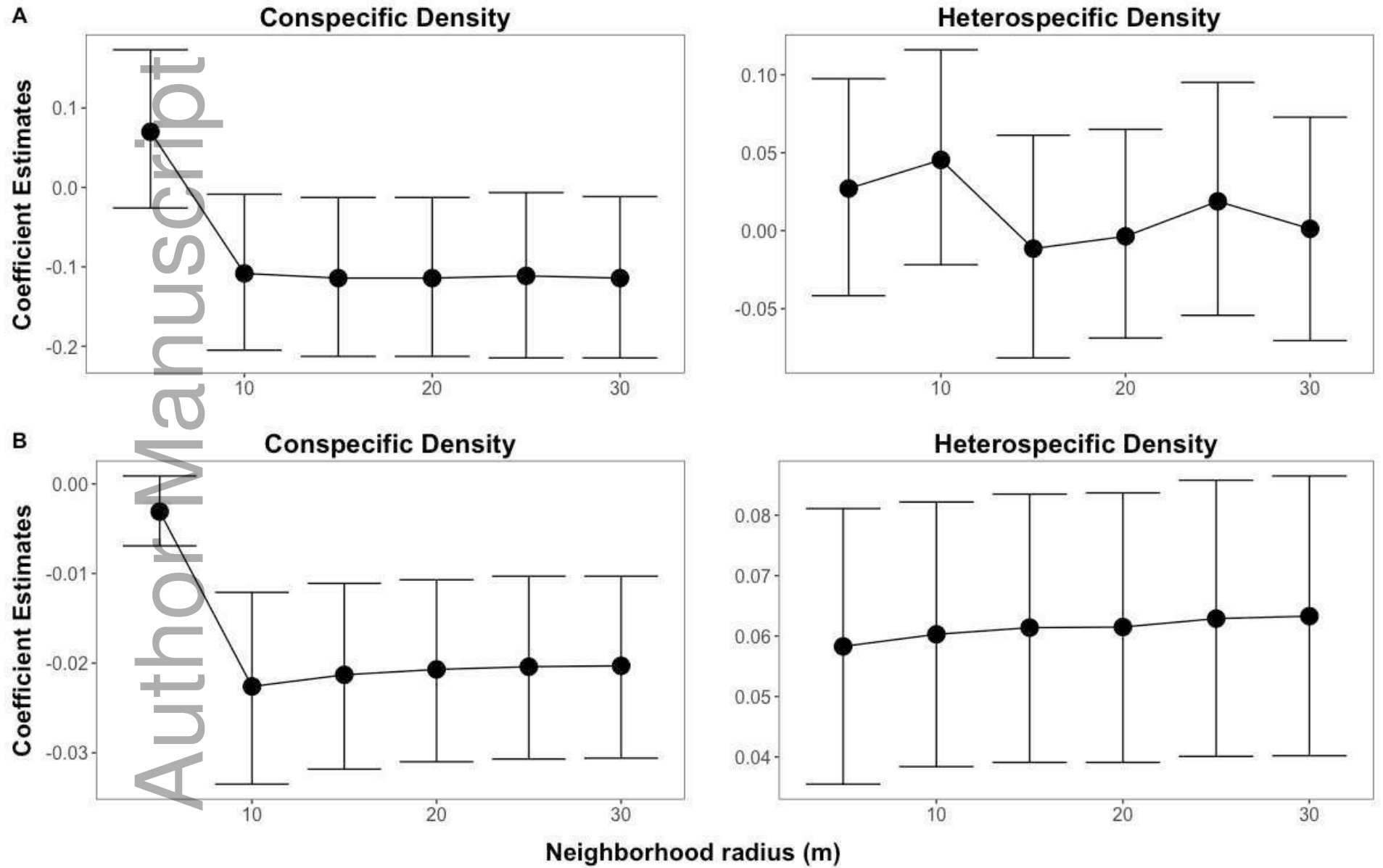
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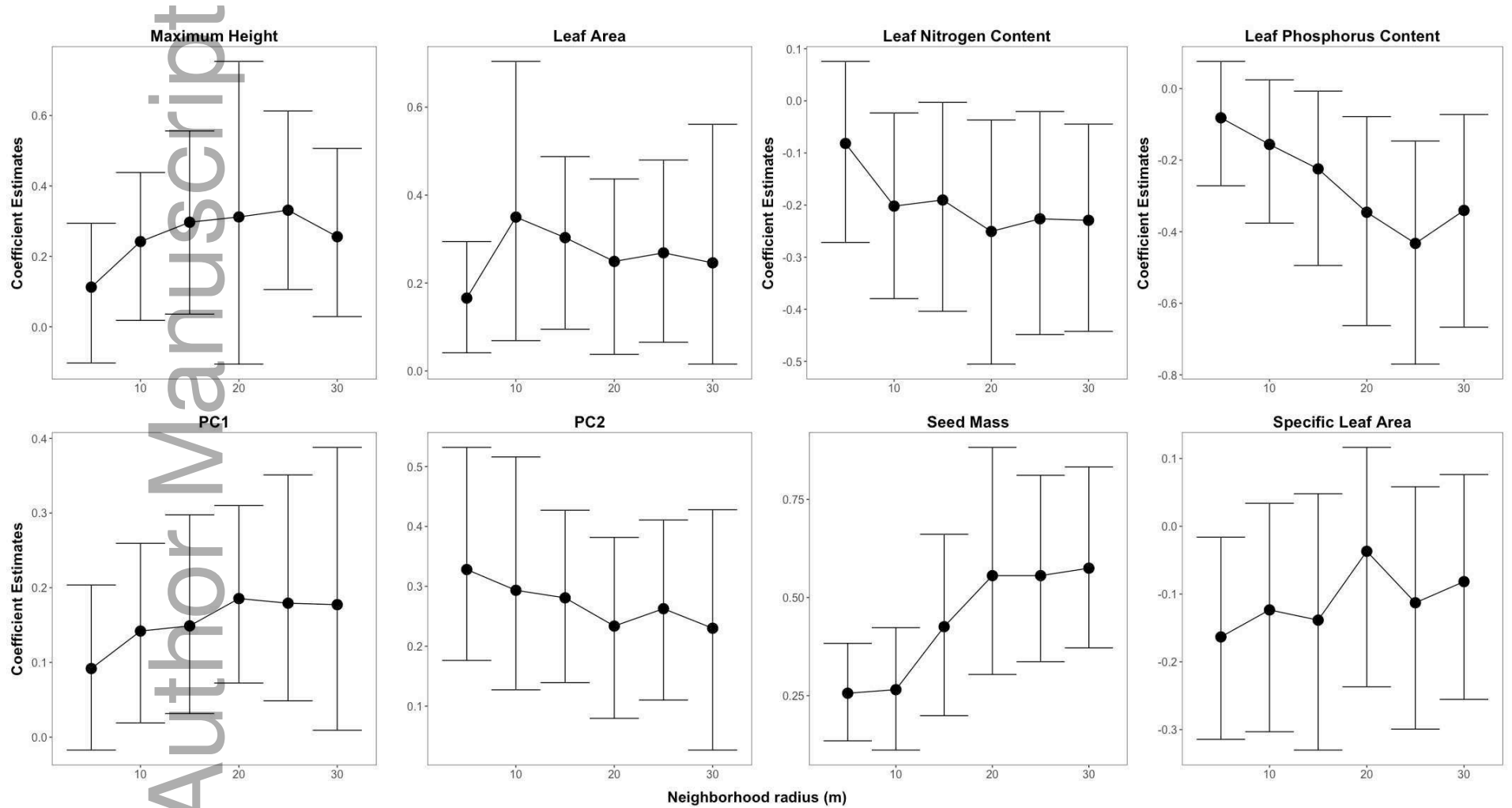


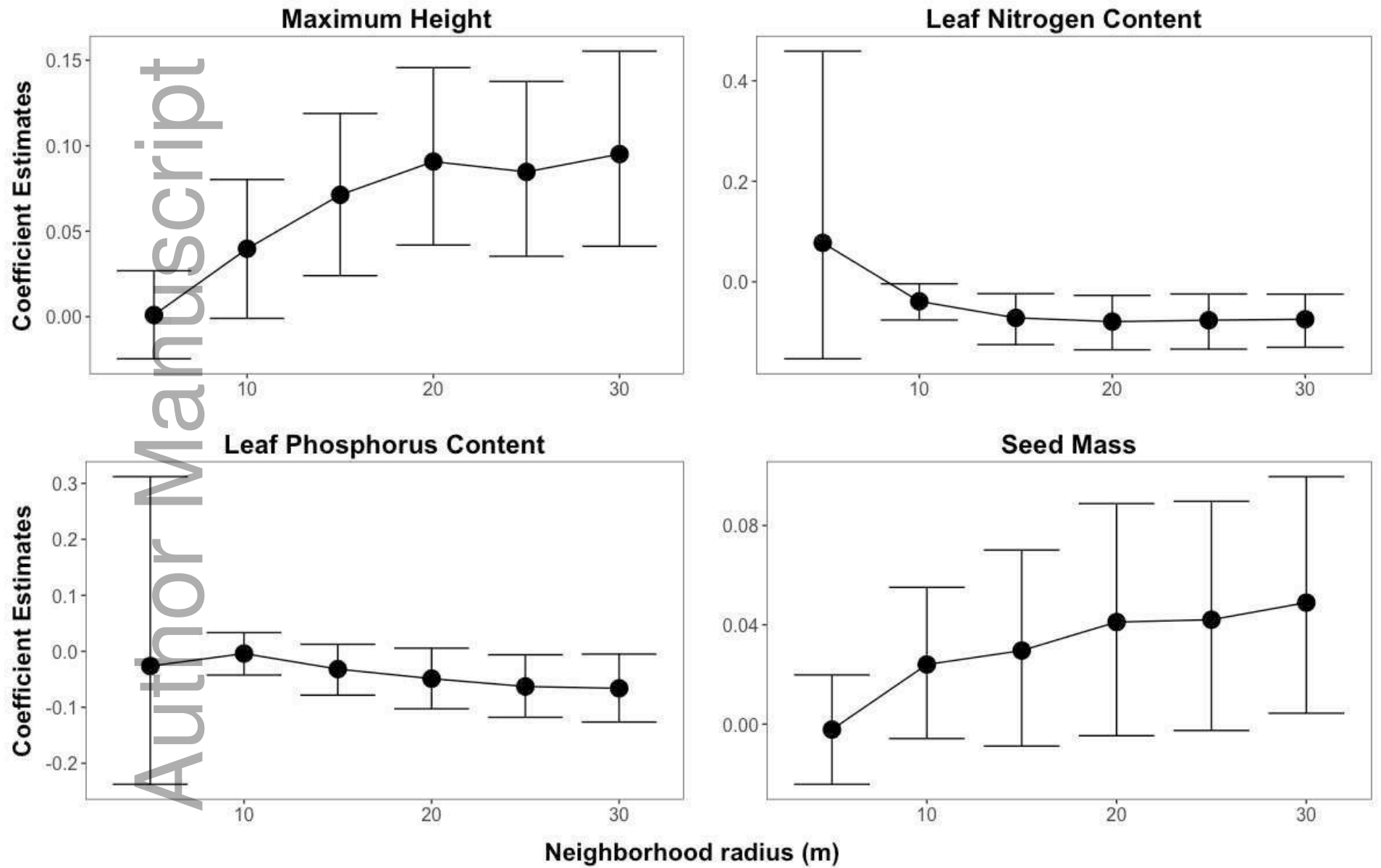
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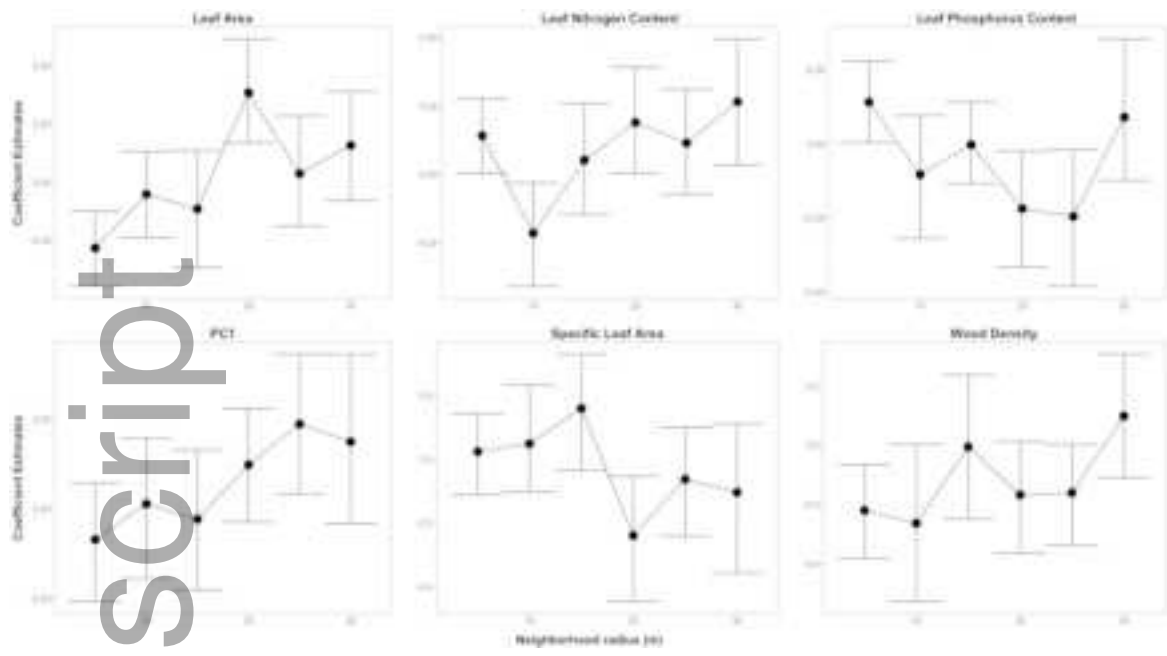
962 **Figure 4.** Scale-dependent significant effects of trait distances interactions (niche
 963 differentiation) on individual tree survival at the Luquillo forest. Large differences in leaf
 964 area and PC1 between focal trees and their neighbors resulted in high survivorship of the
 965 focal tree, with strong effects occurring at 20m and 25m respectively. Low trait
 966 differences with neighbors in leaf nitrogen and phosphorus content, specific leaf area and
 967 wood density were associated with high survivorship of focal trees, with overall stronger
 968 effects at 5m, 10m, 20m and 25m when compared to other radii. Points indicate posterior
 969 medians for each studied parameter and the shaded area represents the 95% Bayesian
 970 credible interval.

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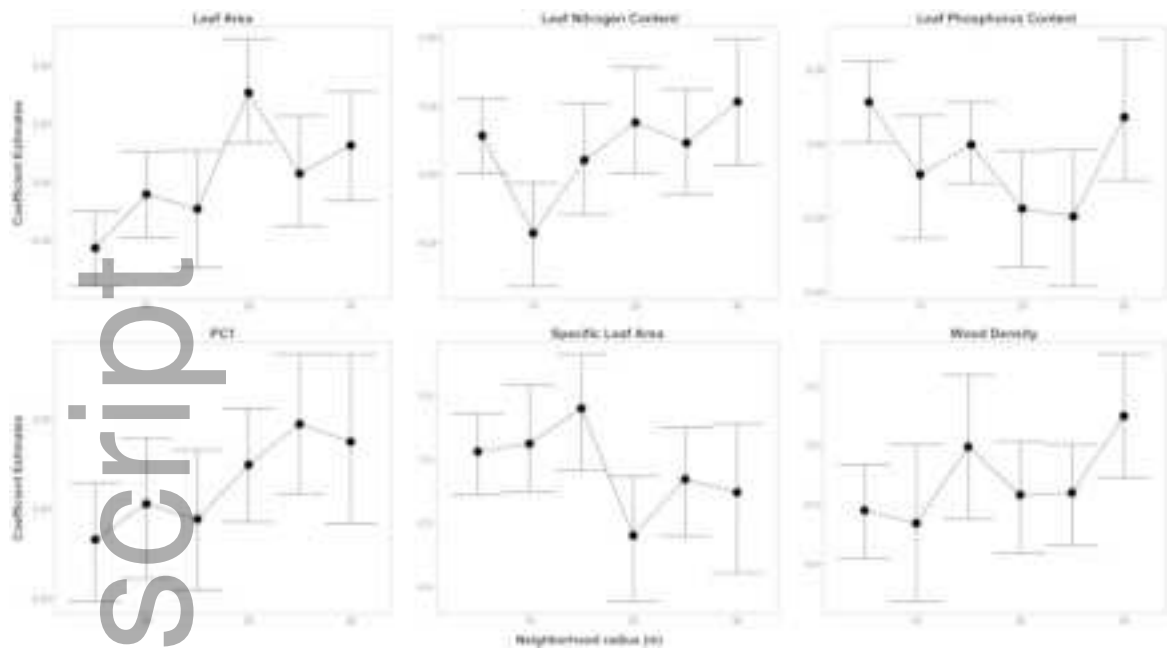








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