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**Relating leaf traits to seedling performance in a tropical forest: building a hierarchical functional framework**

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32 **Abstract**

33 Trait-based approaches have been extensively used in community ecology to provide a  
34 mechanistic understanding of the drivers of community assembly. However, a foundational  
35 assumption of the trait framework – traits relate to performance – has been mainly examined  
36 through univariate relationships that simplify the complex phenotypic integration of organisms.  
37 We evaluate a conceptual framework in which traits are organized hierarchically combining trait  
38 information at the individual- and species-level from biomass allocation and organ-level traits.  
39 We focus on photosynthetic traits and predict that the positive effects of increasing plant leaf  
40 mass on growth depend on species-level leaf traits. We modeled growth data on more than 1,500  
41 seedlings from 97 seedling species from a tropical forest in China. We found that seedling  
42 growth increases with allocation to leaves (high leaf area ratio and leaf mass fraction) and this  
43 effect is accentuated for species with high specific leaf area and leaf area. Also, we found that  
44 light has a significant effect on growth, and this effect is additive with leaf allocation traits. Our  
45 work offers an approach to gain further understanding of the effects of traits on the whole plant  
46 level growth via a hierarchical framework including organ-level and biomass allocation traits at  
47 species- and individual-levels.

48

49 **Keywords:** Biomass allocation traits, canopy openness, China, leaf area, leaf thickness,  
50 seedlings, specific leaf area, relative growth rates.

51

52 **Introduction**

53 Tropical forests harbor the majority of Earth's tree diversity, yet ecologists still have a limited  
54 understanding of forest dynamics and factors determining community structure in these regions.  
55 A promising approach for predicting changes in community structure and dynamics is the use of  
56 functional traits –morphological and physiological features that have an impact on organisms'  
57 performance (growth, survival, reproduction) (Arnold 1983, McGill et al. 2006, Violle et al.  
58 2007). However, previous analytical approaches examining the trait-performance relationship  
59 have been largely focused on examining univariate relationships in which tree performance is  
60 predicted from individual traits (Poorter et al. 2008, Wright et al. 2010, Paine et al. 2015), but

61 traits typically work in combination with other traits to achieve particular functions (Olson and  
62 Miller 1958). Thus, the univariate approach is an inaccurate representation of organismal  
63 function (Berg 1960, Arnold 1983, Armbruster et al. 2014, Laughlin and Messier 2015). It is  
64 therefore important to develop models that integrate the effect of different traits to drive  
65 performance (Laughlin and Messier 2015, Yang et al. 2018).

66         Among all plant traits, leaf traits are the best studied (Reich et al. 1999, Bonser 2006,  
67 Poorter 2009); however, surprisingly, their ability to predict plant demographic rates has been,  
68 generally modest (Sterck et al. 2006, Poorter et al. 2008, Adler et al. 2014, Paine et al. 2015).  
69 Leaf traits are mostly responsible for carrying out photosynthesis that results in carbon gain for  
70 the plant and, therefore, should contribute to increasing plant size (i.e. plant growth). While this  
71 prediction has been corroborated by previous studies showing that leaf traits such as specific leaf  
72 area relate positively to maximum photosynthetic rates (Reich et al. 1999, Wright et al. 2004)  
73 and tree growth (Sterck et al. 2006), the effects of these organ-level leaf traits on carbon gain and  
74 plant demography have been rarely integrated at the whole organism level (Sterck et al. 2011).  
75 The total carbon gain of a given tree does not only depend on the photosynthetic capacity of  
76 individual leaves, but also on the total biomass/area allocated to photosynthetic tissues (foliage)  
77 (Poorter and Remkes 1990, Garnier 1991, Niklas and Enquist 2001, Niinemets et al. 2002). For  
78 instance, species with high specific leaf area (SLA, leaf area divided by dry mass) that allocate  
79 high biomass to photosynthetic tissues should obtain higher total carbon than a species with the  
80 same SLA, but that allocate less biomass to photosynthetic tissues. The combined effect of traits  
81 (biomass allocation and organ-level leaf traits) could lead to important variations in total carbon  
82 gain and tree demography that should be considered when studying trait-performance  
83 relationships (Yang et al. 2018).

84         The integrated effects of different traits on tree performance have been often represented  
85 through a hierarchical framework in which traits at low levels of organization have effects on  
86 traits at higher levels of organization that in turn have effects on performance (Arnold 1983,  
87 Marks and Lechowicz 2006, Marks 2007). This framework could be applied to build a  
88 hierarchical arrangement of trait interactions in which the effect of traits at lower organizational  
89 levels (i.e. organ-level traits, such as SLA) is scaled up at the whole organism level via another  
90 set of traits (i.e. biomass allocation traits) and, ultimately, to performance. In other words, theory  
91 on carbon economy states that relative growth rate depends on the biomass allocated to tissues

92 for capturing carbon (Evans 1972, Poorter 1989a, Garnier 1991). As biomass allocation traits  
93 tend to be quite plastic in response to environmental variation and show a high variation within  
94 species (Umaña et al. 2018), the growth-allocation trait relationships should be defined at the  
95 individual level. These growth-allocation trait relationships may, in turn, vary by species  
96 depending on whether species have conservative or acquisitive traits for resource acquisition  
97 (Lambers and Poorter 1992, Poorter and van der Werf 1998). This species-level variation along  
98 the acquisitive-conservative spectrum for carbon processing is defined by organ-level leaf  
99 economics traits (Reich et al. 1999, Wright et al. 2004) that tend to be more variable across  
100 species than within species (Messier et al. 2010, 2017b, Umaña et al. 2018). This multilevel  
101 organization depicting the trait effects on performance not only represents a more realistic  
102 approach to understand the trait relationships in which a distinction in different organization  
103 levels (species and individuals) and trait types is explicitly considered, but also could explain the  
104 existence of the diverse range of phenotypes found in tropical regions and that seem to represent  
105 alternative ecological strategies (i.e., combinations of different traits such as biomass allocation  
106 and organ-level traits, that lead to equivalent performance) (Laughlin et al. 2018, Umaña et al.  
107 2020a, Worthy et al. 2020).

108 An additional factor that needs to be considered when modeling growth as a function of  
109 traits is the role of the environmental conditions (Grime 1979, Violle et al. 2007). Micro-  
110 environmental variation in abiotic factors has shown to have significant effects on plant  
111 demography (Blonder et al. 2018). In particular, for aboveground strategies, light availability is  
112 one of the most important resources determining plant strategies and functional diversity (Poorter  
113 and van der Werf 1998, Poorter and Rozendaal 2008, Umaña et al. 2020a). Further, for tropical  
114 forests, light in the understory is highly limiting and key for determining the successful  
115 recruitment and establishment of seedlings (Chazdon and Fetcher 1984, Denslow 1987, Umaña  
116 et al. 2020b). Therefore, predictions of plant demography should consider light heterogeneity in  
117 the understory when modeling plant growth rates as a function of functional traits.

118 Here, we study trait-growth relationships in a plant-level integrated framework, using a  
119 combination of organ-level and biomass allocation traits. Our model also accounts for potential  
120 effects of light heterogeneity in the understory on plant performance. To do this, we use growth  
121 data on over 1,500 seedlings from tree seedling species distributed across > 200 1m<sup>2</sup> plots in a  
122 tropical forest in China. All seedlings in these plots were monitored for growth for one year and

123 collected for trait measurements at the end of the study. We paired these measurements with  
124 information on canopy openness (a proxy for light availability in the understory) that was  
125 assessed for all plots.

126 We hypothesize that biomass allocation to leaves will result in increased growth rates, but  
127 this effect will be magnified when species have acquisitive traits –high specific leaf area, high  
128 leaf area, or low leaf thickness (Poorter and Nagel 2000). Biomass allocation traits, unlike organ-  
129 level traits, exhibit higher variability across individuals of the same species than across species  
130 that is attributed to the ability of species to adjust their ecological strategies to maximize  
131 resource acquisition (Poorter et al., 2012; Umaña, Zhang, Cao, Lin, & Swenson, 2018). Organ-  
132 level traits, on the other hand, exhibit higher variation across, than within species (Umaña et al.,  
133 2018). The heterogeneity in the degrees of trait variation between trait types is likely the result  
134 of different ecological and evolutionary constraints operating on these two types of traits  
135 (Armbruster 1991, Armbruster and Schwaegerle 1996). We propose a multi-level approach to  
136 account for this differential variation in traits by implementing a hierarchical framework. We  
137 modify a recent approach that modeled adult tree growth as a function of individual-level tree  
138 crown and leaf area index (LAI) data (LAI is a measure of the total area of leaves per unit of  
139 ground area) and species-level leaf mass per area (LMA) (Yang et al., 2020). Here, we  
140 implement community-level analyses for seedlings that include individual-level biomass  
141 allocation and species-level organ-level traits. We also compare the performance of our  
142 hierarchical models with models that evaluate the interaction between species-level organ-level  
143 traits and biomass allocation (Poorter 1989b, Garnier 1991). These (interaction) models, do not  
144 consider the differential degree of variation between both types of traits and assume that biomass  
145 allocation traits are species-specific fixed values.

146

## 147 **Material and methods**

### 148 *Study Site*

149 The study was conducted in a seasonal tropical rainforest in Xishuangbanna, Yunnan province in  
150 China (101 340 E, 21 360 N), where we established 218 1m<sup>2</sup> seedling plots. The site is  
151 characterized by a monsoonal climate, with distinct seasons, the dry season (November to April),  
152 and the wet season (May to October). The annual average temperature is 21°C and the annual  
153 mean rainfall is 1493 mm which mainly occurs in the wet season (a total of 1256 mm, 84% of

154 the annual average rainfall) (Cao et al. 2008). Seedling plots were spaced every 10 m covering an  
155 approximate area of 2-ha. In each plot, we identified and tagged all free-standing woody  
156 seedlings with a maximum height lower than 50 cm and we monitored all individuals for growth  
157 and survival during 1 year between April 2013 and April 2014 (Umaña, Zhang, Cao, Lin, &  
158 Swenson, 2015).

159

### 160 *Relative growth rates and trait measurements*

161 We calculated the relative growth rate of each individual by computing the change in log-  
162 transformed height over one year. For functional traits, we collected trait data from all  
163 individuals that were monitored in the seedling plots. All seedlings were harvested at the end of  
164 the study period by excavating the soil surrounding the seedlings with a shovel. Next, we put  
165 them in plastic bags with water and transported them to the lab. Once in the lab, the seedlings  
166 were carefully cleaned, dissected, and measured for traits (additional details can be found in  
167 (Umaña et al. 2015)). The traits included biomass allocation traits (leaf area ratio, and leaf mass  
168 fraction,) and organ-level leaf functional traits (specific leaf area, leaf area, and leaf thickness).  
169 Leaf area ratio (LAR,  $\text{cm}^2 \text{g}^{-1}$ ) represents the amount of leaf area per unit of plant mass (Poorter  
170 et al. 2012). Leaf mass fraction (LMF,  $\text{g g}^{-1}$ ) represents the biomass organ fraction. Specific leaf  
171 area (SLA,  $\text{cm g}^{-1}$ ) is a leaf economics trait that describes carbon acquisition and processing  
172 strategies in which species with high SLA are more acquisitive than species with low SLA  
173 (Wright et al. 2004, Díaz et al. 2016). Leaf area (LA  $\text{cm}^2$ ) reflects the photosynthetic area  
174 displayed to capture light (Poorter and Rozendaal 2008) and leaf thickness is a mechanical trait  
175 (Th, mm) (Onoda et al. 2011). For all organ-level traits, we calculated the species average trait  
176 values and this value was used in posterior analyses. We also checked for trait correlations for  
177 biomass allocation and organ-level traits (Appendix S1: Tables S1 and S2).

178

### 179 *Light availability in the understory*

180 To measure light conditions in the understory we took hemispherical photographs at the center of  
181 each seedling plot. The photos were taken at 1 m above the ground using a Nikon FC-E8 lens  
182 attached to a Nikon Coolpix 4500 camera (Japan, Nikon). All photographs were taken with  
183 uniform light conditions before sunrise between March and April 2014 and posteriorly analyzed  
184 using Gap Light Analyzer software (Frazer et al. 2000) (<http://www.caryinstitute.org/science->

185 program/our-scientists/dr-charles-d-canham/gap-light-analyzer-gla). The analysis consisted of  
186 classifying all pixels in the photograph into two categories: sky and vegetation. After the  
187 classification, the program calculated the percentage of light in each photograph.

188

## 189 *Analyses*

190 To evaluate the relationship between traits and performance we constructed a hierarchical  
191 Bayesian model. At the first level, we modeled the expected individual-level relative growth rate  
192 of tree  $i$  of species  $j$  in a plot  $p$  as a power function of individual-level biomass allocation traits  
193 (BAT) (i.e., LAR or LMF) and canopy openness (Light) (equation 1). We also included seedling  
194 maximum height (MH) (measured per seedling) in the first level since size can affect seedling  
195 demography (Comita and Hubbell 2009). At the second level, we specified species-specific  
196 intercepts ( $\beta_0$ ) and slopes ( $\beta_1$ ) as linear functions of species-level organ-level leaf traits (OLT,  
197 which are SLA, LA, or leaf thickness) (equation 2). Our multispecies approach allows us to  
198 account for between-species variation in growth that is explained by organ-level leaf traits, as  
199 well as other unexplained factors shared by individuals of the same species (via the random  
200 effects). In total, we fitted 6 models that considered all possible combinations of individual-level  
201 biomass allocation and species-level leaf traits.

$$202 \quad \log(RGR_{i,j,p}) = \beta_{0,j} + \beta_{1,j} \times BAT_{i,j} + \beta_2 \times \text{Light}_p + \beta_3 \times MH_{i,j,p} + \varphi_p + \varepsilon_{i,j} \quad (1)$$

$$203 \quad \beta_{n,j} = \gamma_0 + \gamma_1 \times OLT_j + v_{n,j} \quad (n = 0, 1 \text{ in Eq. 1}) \quad (2)$$

204 The intercept,  $\beta_{0,j}$ , represents the log-transformed seedling relative growth rate of species  
205  $j$  for the community average values of BAT, Light, and MH. The slope of BAT ( $\beta_{1,j}$ ) represents  
206 the effects of biomass allocation traits on seedling growth (RGR). The slope  $\gamma_1$  between OLT  
207 and species-specific slope of BAT ( $\beta_{1,j}$ ) represents the relationship between species-specific  
208 OLT and the slope of the RGR–BAT relationship. The slope  $\gamma_1$  between OLT and species-  
209 specific intercept ( $\beta_{0,j}$ ) represents the species-specific OLT effect on RGR at community  
210 average BAT, Light, and MH.  $\varphi_p$  represents plot random effects,  $v_{n,j}$  represents species random  
211 effects and  $\varepsilon_{i,j}$  represents individual residuals; random effects and residuals are normally  
212 distributed.

213 We compared the performance of our hierarchical models with models that included an  
214 interaction effect between species-level BAT and OLT (hereafter referred as to species-level

215 interaction models) using Leave-One-Out Information Criterion (LOOIC) (function  
216 "loo\_compare" from package "loo" in R (Vehtari et al. 2017a)). LOO uses log-likelihoods from  
217 posterior simulations of the parameter values to estimate point-wise out-of-sample prediction  
218 accuracy and determine the relative predictive performance of the model to the data. The lower  
219 LOOIC the higher the predictive accuracy (Vehtari et al. 2017b).

220 We also considered another set of models that included an interacting term between  
221 biomass allocation trait (BAT) and light in the first level, instead of considering these terms as  
222 separate factors. However, these models performed worse (higher LOOIC values) than the first  
223 set of models and were no longer considered for discussion (Appendix S1: Table S3).

224 Before the analyses, we log-transformed SLA, LA, and Th in order to reduce skewness  
225 and centered all the traits, MH, and Light (mean = 0 and standard deviation = 1) for easy  
226 interpretation and comparison. All analyses were performed using Stan via the R package "rstan"  
227 (R Development Core Team 2017, Stan Team 2020). Each model was fitted using uninformative  
228 priors (all details can be found in Data S1), 4 chains with 3,000 iterations, and a warmup of  
229 1,500 iterations. To assess parameter convergence, we used the Gelman and Rubin's convergence  
230 diagnostics (cut-off= 1.01). The code used to run the model and diagnostics are included as  
231 supplementary information (Data S1 and Appendix S2).

232

## 233 **Results**

### 234 *Overview*

235 In total, we analyzed growth rates of 1,574 seedlings from 97 species. The mean seedling relative  
236 growth rate was around 0.19 cm·cm<sup>-1</sup>·year<sup>-1</sup> but there was a high variation across species  
237 (Appendix S1: Figure S1). Our dataset consists of many species that were rare with less than 15  
238 individuals per species and few common species (Appendix S1: Table S4 includes the  
239 abundances for the species used in the analyses). Also, the percentage of canopy openness in our  
240 study site ranged between 0.66 to 10.10 (coefficient of variation = 0.49, Appendix S1: Figure  
241 S2), and this variable had a significant effect on seedling growth across all models (Table 1).

242

### 243 *Comparing hierarchical and species-level interaction models*

244 We compared two sets of models, the hierarchical models –which used a combination of  
245 individual-level and species-level trait information– and the interaction models –that used



246 species-level trait information. Consistently, the hierarchical models outperformed the  
247 interaction models (Table 2). Below, we only describe the results of the hierarchical models.

248

#### 249 *Effects of biomass allocation on seedling growth*

250 We found that increases in leaf mass per area (LMF) and leaf area ratio (LAR) result in higher  
251 seedling growth ( $\mu\beta_1$ ) (Figure 1, Appendix S1: Table S5).

252

#### 253 *Effects of species-level leaf traits on seedling growth at mean biomass allocation trait*

254 For models using leaf area (LA), we found non-significant effects on growth when LAR and  
255 LMF were at their mean community values (Figure 2, Appendix S1: Table S5). For models using  
256 specific leaf area (SLA), instead, we found that species with low SLA grew slower than species  
257 with high SLA when LAR and LMF were at their mean community values (intercept) (Figure 2,  
258 Appendix S1: Table S5). For models using leaf thickness, we found non-significant effects on  
259 growth when LAR and LMF were at their mean community values (95% credible intervals  
260 overlapped zero).

261

#### 262 *Effects of species-level leaf traits on biomass allocation trait-growth effect*

263 We found that the positive effect of LAR on seedling growth was significant and positively  
264 related to species-level LA, with large-leaved species exhibiting the highest growth rates (Figure  
265 3, Appendix S1: Table S5). Similarly, we found that the positive effect of LMF on seedling  
266 growth was positively related to species LA and SLA with species having acquisitive traits (i.e.,  
267 high LA and SLA) exhibiting the highest growth, but was only significant for SLA (Figure 3,  
268 Appendix S1: Table S5). Species-level leaf thickness was not related to biomass allocation trait  
269 effect on seedling growth for any of the biomass allocation traits used (LAR, and LMF) (Figure  
270 3, Appendix S1: Table S5).

271

## 272 **Discussion**

273 In this study, we implement an approach that moves beyond the univariate trait classical  
274 analytical methods to contribute to an integrated understanding of the effect of leaf traits on  
275 performance using a hierarchical framework for plant communities. We show that seedling  
276 growth results from the integrated effect of individual-level and species-level leaf traits in which

277 increased biomass allocation to leaves and high values of SLA and LA result in high plant  
278 growth. Our findings represent a multi-level perspective on trait integration and highlight the  
279 importance of combining biomass allocation and organ-level trait information at the individual  
280 and species-level to gain further insights about the whole plant level strategies in species-rich  
281 tropical forests.

282

### 283 *Increased allocation to leaves leads to high seedling growth*

284 As predicted, we found that allocation to leaves results in high relative growth rates for tropical  
285 seedlings suggesting that the more the plants invest in photosynthetic tissues, the more the  
286 carbon gain that contributes to seedling growth. These results agree with previous findings that  
287 indicate that fast-growing plants are those that allocate more biomass to leaf tissues (Garnier  
288 1991, Lambers and Poorter 1992). In particular, our results show that the strength of the LAR  
289 effect in growth was larger than the models with LMF and suggest that LAR is a predominant  
290 factor explaining variation in RGR. These results are concordant with the conclusions presented  
291 by Poorter (1989a) who suggested that the amount of area allocated to leaves for a given dry  
292 mass is more relevant for determining plant growth than the allocation to dry weight into leaves  
293 (LMF).

294 Further, we found a positive and significant effect of light availability on seedling growth  
295 that agrees with previous findings on other tropical forests and highlights the importance of this  
296 resource for seedling performance (Augsburger 1984, Popma and Bongers 1988). Yet, the effect  
297 of light interacting with allocation traits did not improve the model fit, which suggests that  
298 variation in growth is better predicted by a consistent effect of leaf allocation traits that does not  
299 depend on the light conditions. Although previous studies have reported similar results in which  
300 light effects are independent of trait effects, other studies have reported an interactive effect of  
301 both factors (reviewed by Poorter & Nagel 2000). Combined, our results indicate that in our  
302 study site, light is one of the main resources limiting seedling growth, and those organisms that  
303 allocate more biomass to leaf tissues have a demographic advantage.

304

### 305 *Species-level leaf traits relate to seedling growth*

306 We observed that species-level leaf area and leaf thickness were not directly related to seedlings  
307 RGR (at mean community LAR and LMF), whereas species with high SLA (more acquisitive

308 carbon processing strategies) grew faster than seedlings with low SLA. While the SLA result  
309 agrees with our predictions, the LA and thickness results do not, as we predicted that species  
310 displaying larger areas for light acquisition and lower leaf thickness should attain high seedling  
311 growth. One potential explanation for this is that LA and thickness are structural traits involved  
312 in several functions that may lead to conflicting responses to enhance growth. For example,  
313 having large leaves is beneficial for capturing light but may bring costs for mechanical support  
314 that impair performance (Niklas 1992, 1999), self-shading (Sterck and Bongers 2001), or costs in  
315 transpiration (McDonald et al. 2003). For leaf thickness, although leaves with thick mesophyll  
316 layers may display low photosynthetic capacity, these leaves might be more resistant to drought  
317 and herbivore damage that ultimately is advantageous for growth (Onoda et al. 2011). We  
318 suggest that different trade-offs involved in the variation of these traits may obscure their direct  
319 effect on RGR. However, as discussed below, the effects of LA were better captured via the  
320 integrated effect on biomass allocation traits. On the other hand, results for SLA were consistent  
321 with our predictions. SLA is more strongly linked to physiological functions as maximum  
322 photosynthetic rate and carbon processing strategies than LA and Lth (Wright et al. 2004) and, as  
323 such, it is expected that SLA will show stronger effects on carbon gain that is ultimately  
324 translated into seedling growth than of compared to LA or leaf thickness.

325

### 326 *Species-level leaf traits mediate the effect of leaf allocation on growth*

327 Consistent with our predictions we found that the positive effects of LAR and LMF on growth  
328 were magnified for species with more acquisitive traits, high LA, and SLA (Figure 3). Our  
329 results agree with previous studies showing that higher values of SLA and LA may lead to higher  
330 plant growth (Sterck et al. 2006, Poorter et al. 2008). Yet, our analyses go one step further by  
331 indicating that the positive effects of acquisitive species-level leaf traits on plant demography  
332 depend and can be modified by individual-level leaf allocation traits. Our approach allows to  
333 model the integrated effect of different traits via a hierarchical arrangement to predict variation  
334 in plant growth across distinct organizational levels (within and across species). This approach  
335 has important implications in terms of defining functional trade-offs for species, given that if we  
336 only focus on examining one trait –SLA– for classifying species as acquisitive and conservative  
337 for resource uptake we will be ignoring important information regarding how these strategies are  
338 modified by foliage allocation. The combined effect of SLA and leaf allocation traits could result

339 in alternative phenotypes with equivalent carbon gains and therefore equivalent performance  
340 (Hirose and Werger 1995, Marks 2007, Worthy et al. 2020).

341 Although trait integration has long been studied in ecological and evolutionary studies  
342 (Olson and Miller 1958, Berg 1960, Cheverud and Cheverud 1982, Schlichting 1989), there are  
343 still a limited number of studies that examine the integrated effects of traits on performance for  
344 communities with high species diversity species (but see, Yang et al., 2020, Freschet et al., 2015;  
345 Messier et al., 2017). Some key results from previous studies show that trait effects on plant  
346 performance can be contingent to the effects of other traits (Wildová et al. 2007, Blonder et al.  
347 2018, Pistón et al. 2019, Worthy et al. 2020) and suggest that variations in plant performance are  
348 highly sensitive to the interactive effect of functional traits. Our results suggest that we can gain  
349 additional insights about the role of traits predicting variation in growth not only by accounting  
350 for trait interactions but by considering the different patterns of trait variation (individual- and  
351 species-level) across trait types (Armbruster 1991) using hierarchical approaches (Marks 2007)  
352 (Table 2). The individual-level traits would represent the adjustability to local conditions  
353 showing high intraspecific variation (biomass allocation) (Umaña et al. 2020b), while the  
354 species-level traits are likely subject to different types of constraints that makes them less  
355 variable within species than across species (i.e. SLA) (Umaña et al., 2018). We suggest,  
356 therefore, that traits should be modeled by recognizing differences in constraints across trait  
357 types such that biomass allocation traits display high within species variation, have a more direct  
358 effect on performance, and interact with organ-level traits.

359 Among all species-level leaf traits studied here, leaf thickness showed the weakest effects  
360 on growth. We expected that higher leaf thickness would result in lower seedling growth given  
361 that high leaf thickness implies higher construction cost (high carbon investments) (Chabot et al.  
362 1979, Poorter et al. 2006). However, none of the relationships examined in this study were  
363 significant or close to being significant for any of the models tested. We infer from this that leaf  
364 thickness might not strongly and directly affect carbon processing strategies and this would  
365 explain the weak relationships we found. Instead, leaf thickness, as a mechanical trait, might  
366 relate to structural resistance but less directly to photosynthetic functions that can translate into  
367 carbon gain (Onoda et al. 2011).

368

369 *Conclusion*

370 The integration of functional traits to understand variations in plant demography is central for  
371 building a robust predictive functional framework. Here, we propose a hierarchical framework  
372 that combines two trait types measured at two organization levels – individual-level biomass  
373 allocation and species-level leaf traits– to predict seedling growth. Our results indicate that the  
374 effects of species-level leaf traits on demography depend on the individual variation in biomass  
375 allocation traits. This study represents an effort for describing the complex relationships between  
376 traits that underly organisms' function. We suggest that recognizing and explicitly accounting for  
377 the differences in trait variation across organization levels and trait types reveals functional  
378 interactions that improve our understanding of the link between plant functionality and variation  
379 in performance for species-rich communities.

380

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391 MC, LL, and NGS conducted the study and contributed to the project design; MNU performed  
392 all data analyses, PM contributed to code writing and interpretation of the model results; CZ,  
393 MC, and LL coordinated the light analyses; MNU wrote the first draft of the manuscript; all  
394 authors contributed to editing the manuscript.

395

### 396 **Supporting Information**

397 Additional supporting information may be found online at: [link to be added in production]

398

### 399 **Open Research**

400 Trait and demographic data for seedlings (Umaña et al. 2019) is available from the Dryad Digital  
401 Repository: <https://doi.org/10.5061/dryad.6d1qm1j>. Canopy openness data (Umaña et al. 2020c)  
402 is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bk3j9kd93>.

403

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603 TABLES

604 **Table 1.** Posterior mean of light and seedling height effects on seedling growth, 95% credible  
605 interval, and Gelman-Rubin diagnostic value (Rhat). Light effect on seedling growth rates for all  
606 six models. LAR – leaf area ratio, LMF – leaf mass fraction, LA – leaf area, SLA – specific leaf  
607 area, Thickness – leaf thickness.

Model	Parameter	Mean	2.50%	97.50%	Rhat
LAR & LA	Height	-0.35	-0.43	-0.26	1.00
	Light	0.20	0.12	0.29	1.00
LAR & SLA	Height	-0.36	-0.45	-0.28	1.00
	Light	0.21	0.12	0.29	1.00
LAR & Thickness	Height	-0.36	-0.44	-0.27	1.00
	Light	0.21	0.12	0.29	1.00
LMF & LA	Height	-0.40	-0.49	-0.31	1.00
	Light	0.19	0.11	0.27	1.00

LMF & SLA	Height	-0.40	-0.48	-0.32	1.00
	Light	0.20	0.11	0.28	1.00
LMF & Thickness	Height	-0.41	-0.49	-0.32	1.00
	Light	0.19	0.11	0.27	1.00

608

609

610 **Table 2.** Pairwise comparisons between hierarchical models and species-level interaction  
611 models. Trait codes are the same as in Table 1. *loaic* ( $-2 * eldp$ ) is the leave-one-out cross-  
612 validation information criterion, *elpd\_diff* is the difference in *elpd* for a pair hierarchical and  
613 interaction models, *se\_diff* is the standard error of component-wide differences of *elpd* between a  
614 pair of models. If *elpd\_diff* is small than 4, the difference between models is not  
615 significant. If the *elpd\_diff* is larger than 4, then we compare the difference in standard error  
616 (*se\_diff*). In all cases, *elpd\_diff* for the interaction model was  $> 2$  times higher compared to  
617 *se\_diff*.

Traits	Model type	loaic	elpd_diff	se_diff
LAR-LA	Hierarchical	6397.2	0	0
	Interaction	6419.1	-11.1	4.9
LAR-SLA	Hierarchical	6395.0	0	0
	Interaction	6419.7	-13.2	4.7
LAR-Thickness	Hierarchical	6395.8	0	0
	Interaction	6420.2	-12.6	4.7
LMF-LA	Hierarchical	6396.0	0	0
	Interaction	6420.4	-11.7	4.9
LMF-SLA	Hierarchical	6392.9	0	0
	Interaction	6421.6	-14.2	4.7
LMF-Thickness	Hierarchical	6397.9	0	0
	Interaction	6420.3	-12.6	4.7

618

619 FIGURE LEGENDS

620

621 **Figure 1.** Histograms of species-level posterior means of biomass allocation trait effects ( $\beta_1$ ) on  
622 seedling relative growth rate (RGR,  $\text{cm}\cdot\text{cm}^{-1}\cdot\text{year}^{-1}$ ) for seedling communities in a tropical forest  
623 in China. The title in each plot corresponds to the biomass allocation trait used in the first level  
624 of the model and to the species-level organ-level trait used in the second level. Trait codes are  
625 the same as in Table 1.

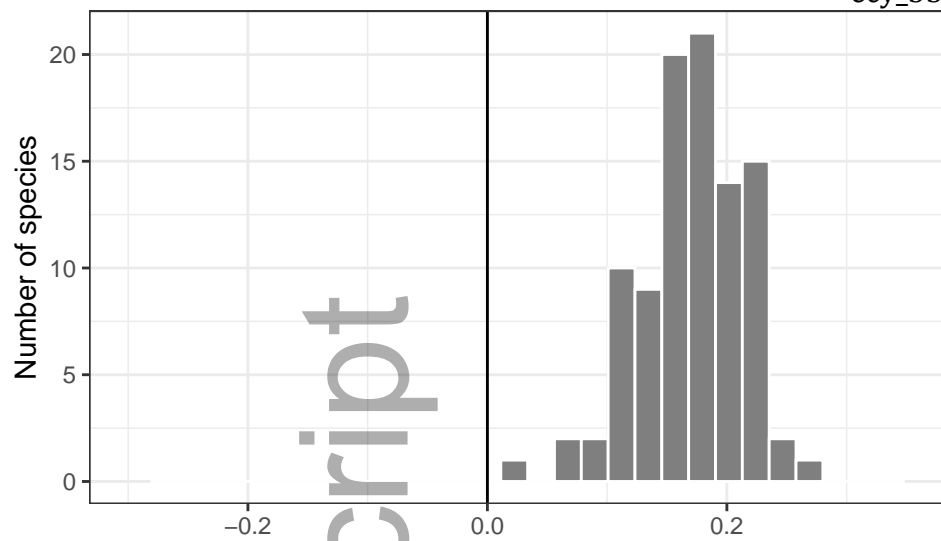
626

627 **Figure 2.** Species-level leaf trait effects on seedling relative growth rate (RGR,  $\text{cm}\cdot\text{cm}^{-1}\cdot\text{year}^{-1}$ )  
628 at community-mean biomass allocation trait (intercept,  $\beta_0$ ). BAT refers to biomass allocation  
629 trait –LAR, or LMF. Black circles and gray lines indicate the means and the 95% credible  
630 intervals of the species-specific coefficients respectively. Black lines represent fitted significant  
631 relationships (95% credible intervals did not cross zero, see Appendix S1: Table S5). Trait codes  
632 are the same as in Table 1.

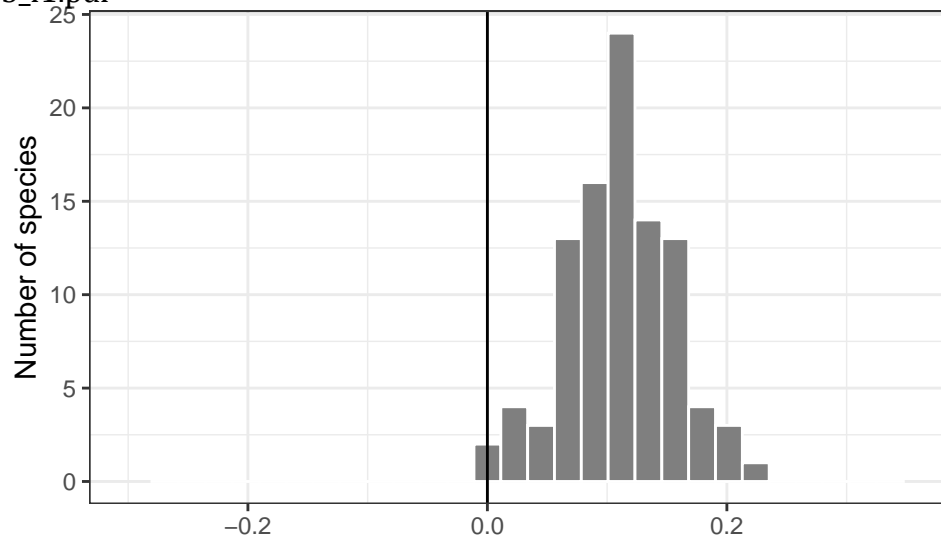
633

634 **Figure 3.** Species-level leaf trait effects on the relationship between biomass allocation trait  
635 (LAR or LMF) and relative growth rate (RGR,  $\text{cm}\cdot\text{cm}^{-1}\cdot\text{year}^{-1}$ ). Black circles and gray lines  
636 indicate the means and the 95% credible intervals of the species-specific coefficients  
637 respectively. The solid black line represents fitted significant relationships (95% credible  
638 intervals crossed zero, see Appendix S1: Table S5). Dashed line represents fitted significant  
639 relationships (90% credible intervals did not cross zero). Trait codes are the same as in Table 1.

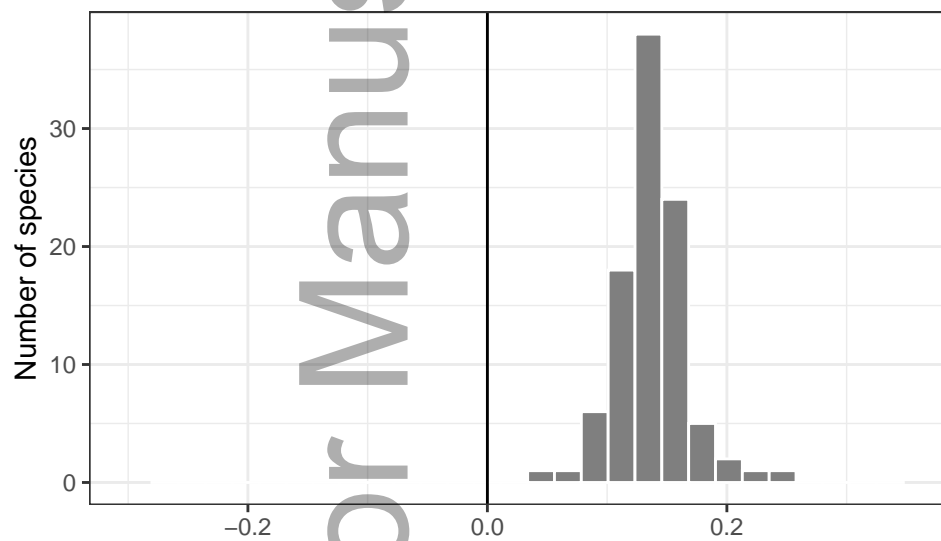
LAR & LA model



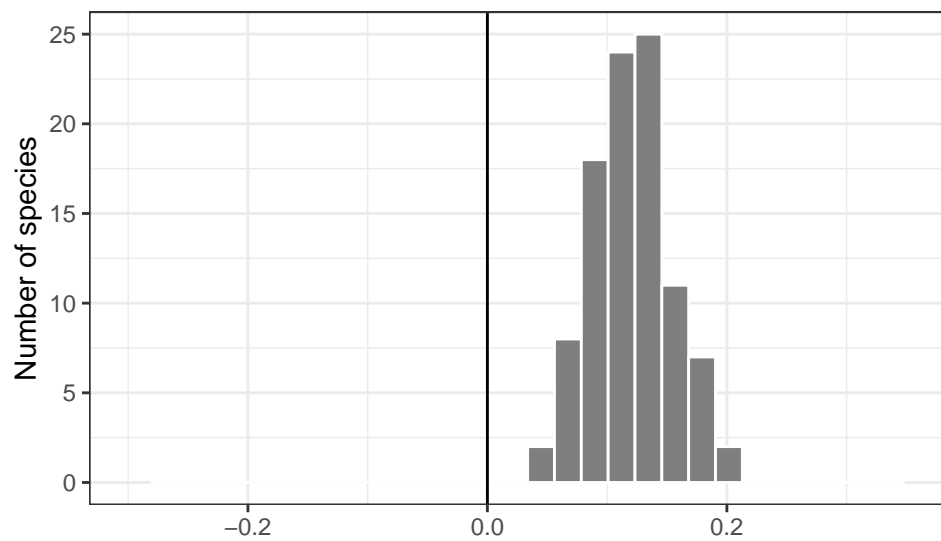
LMF & LA model



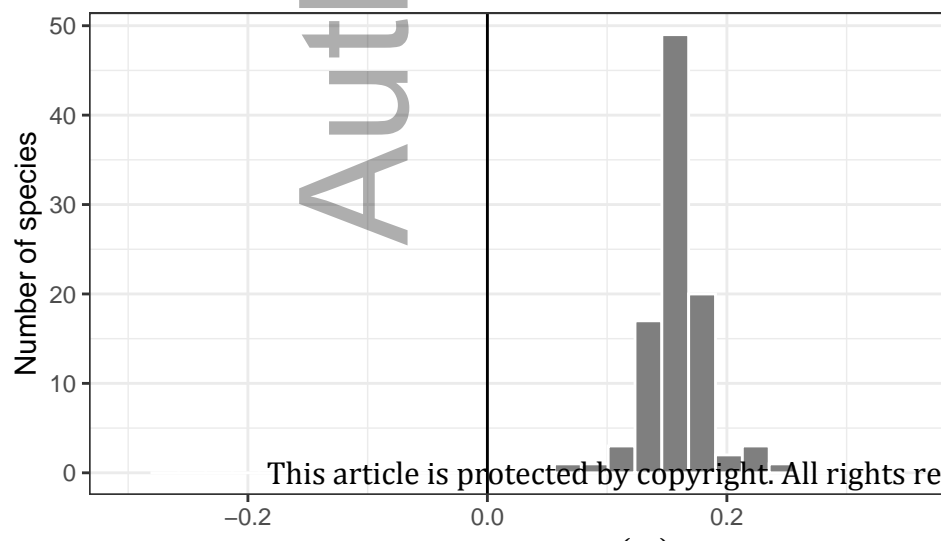
LAR & SLA model



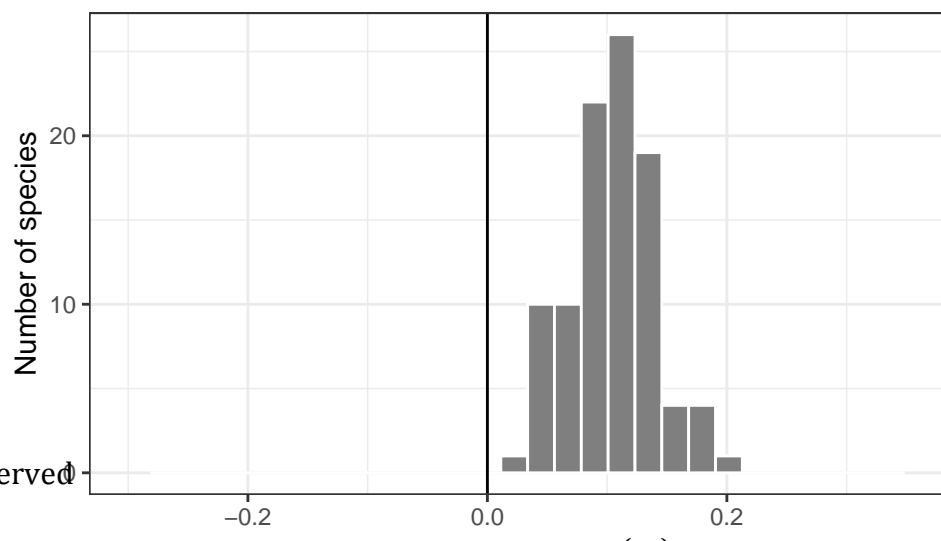
LMF & SLA model



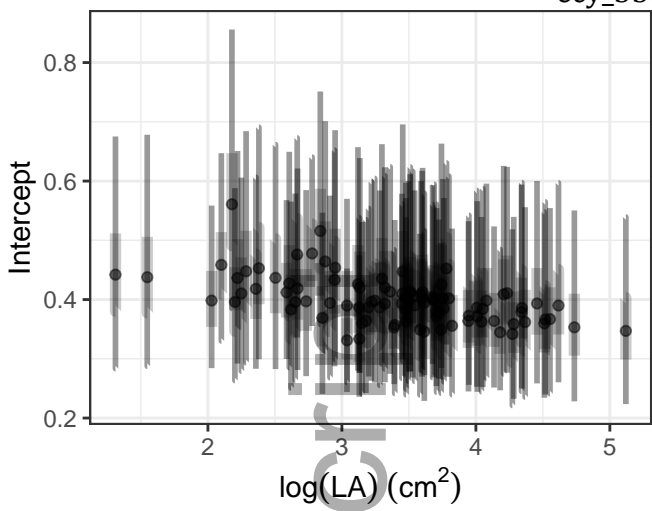
LAR & Thickness model



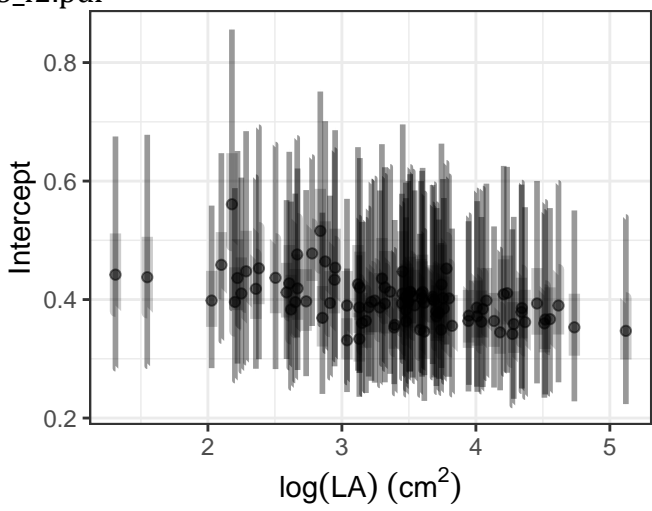
LMF & Thickness model



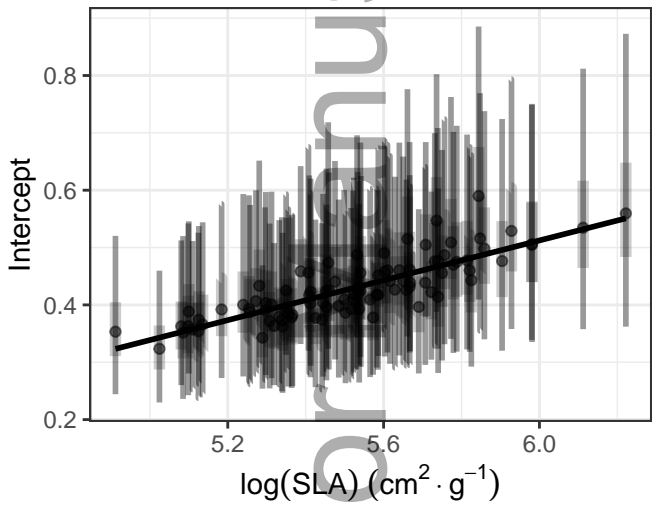
LAR & LA model



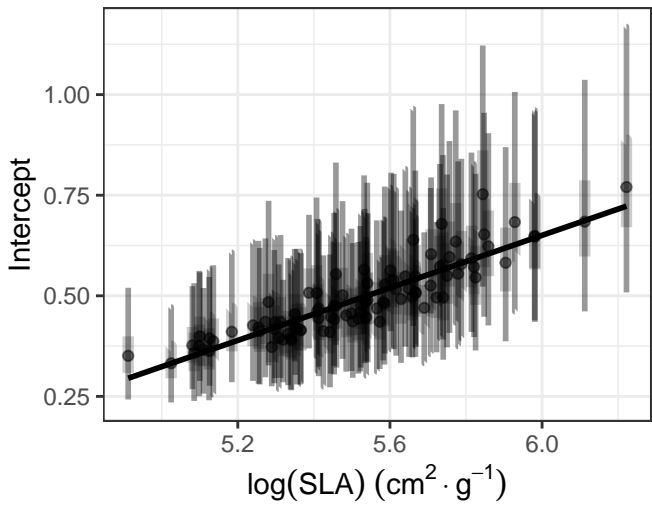
LMF & LA model



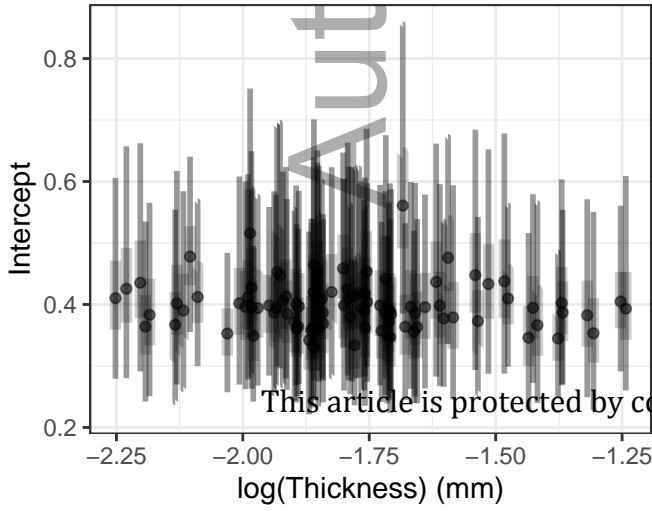
LAR & SLA model



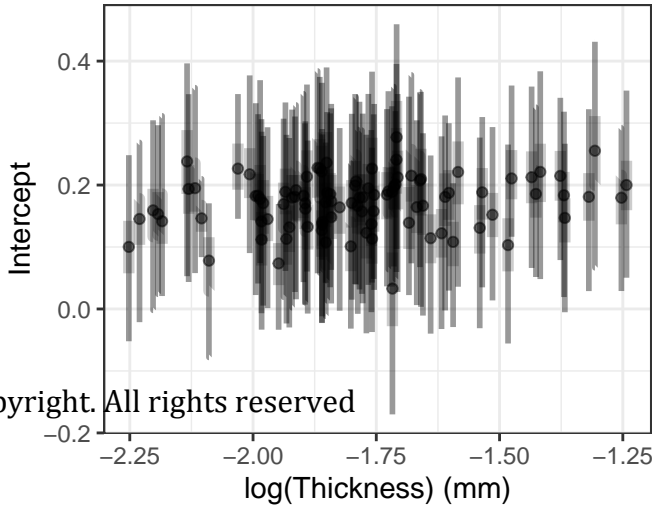
LMF & SLA model



LAR & Thickness model



LMF & Thickness model

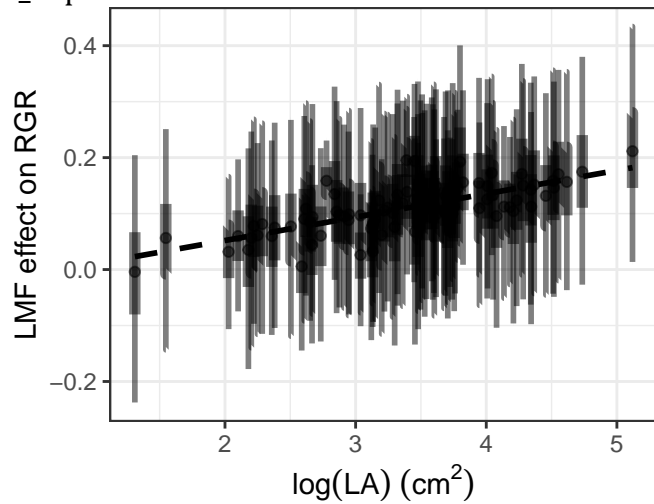
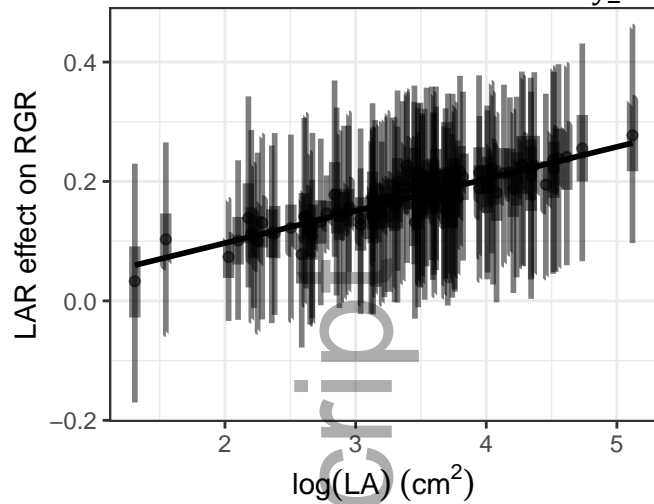




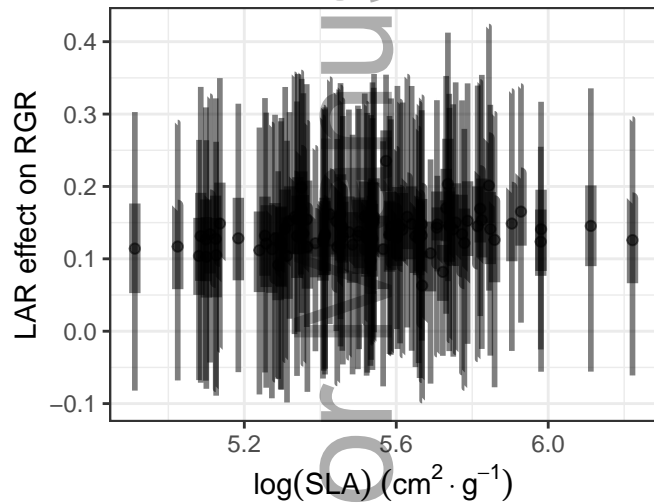
Effect of LAR & LA

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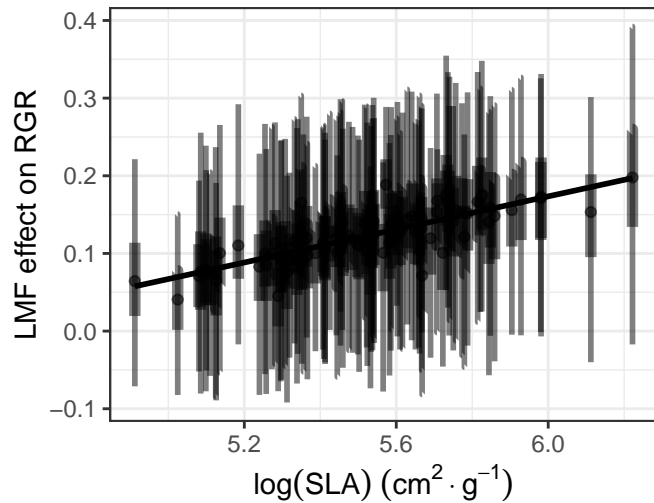
Effect of LMF & LA



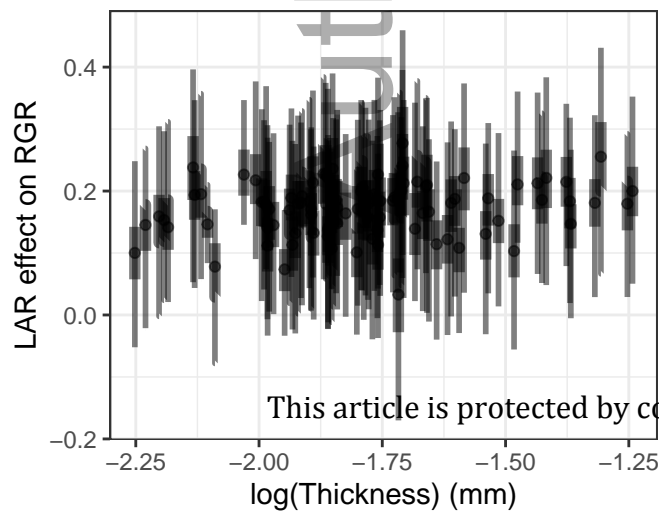
Effect of LAR & SLA



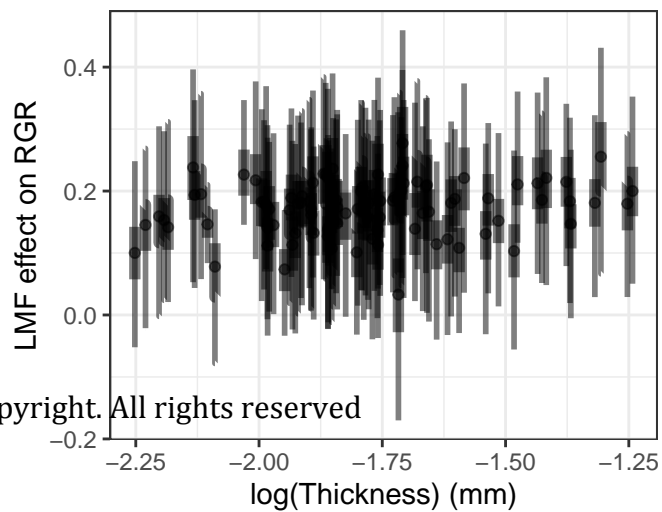
Effect of LMF & SLA



Effect of LAR & Thickness



Effect of LMF & Thickness



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