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1 **The role of functional uniqueness and spatial aggregation in explaining rarity in**  
2 **trees**

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3 **47 Abstract:**

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6 **48 Aim:**

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8 **49** Determining the drivers of species rarity is fundamental for our understanding and con-  
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10 **50** servation of biodiversity. The rarity of a given species within its community may arise  
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12 **51** due to exclusion by other ecologically similar species. Conversely, rare species may oc-  
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14 **52** cupy habitats that are rare on the landscape or they may be ill-suited to all available habi-  
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16 **53** tats. The first mechanism would lead to common and rare species occupying similar eco-  
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18 **54** logical space **defined by functional traits**. The second mechanism would result in com-  
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20 **55** mon and rare species occupying dissimilar ecological space and spatial aggregation of  
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22 **56** rare species either because they are specialist in rare habitats, or because of rare species  
23  
24 **57** tend to be dispersal limited. Here, we quantified the contribution of locally rare species to  
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26 **58** community functional richness, and the spatial aggregation of species across tree com-  
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28 **59** munities worldwide to address these hypotheses.  
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35 **60**

36 **61 Location:**

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38 **62** Asia and the Americas.  
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44 **64 Methods:**

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46 **65** We compiled a dataset of functional traits from all the species present in 8 tree plots  
47  
48 **66** around the world to evaluate the contribution of locally rare species to tree community  
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50 **67** functional diversity using multi- and uni-variate approaches. We also quantified the spa-  
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52 **68** tial aggregation of individuals within species at several spatial scales as it relates to abun-  
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54 **69** dance.  
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7 71 Results:

8 72 Locally rare tree species in temperate and tropical forests tended to be functionally  
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10 73 unique and are consistently spatially clustered. Furthermore, there is no evidence that this  
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12 74 pattern is driven by pioneer species being locally rare.  
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17 76 Main conclusions:

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20 77 This evidence shows that locally rare tree species disproportionately contribute to commu-  
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22 78 nity functional diversity and we therefore can reject the hypothesis that locally rare spe-  
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24 79 cies [are suppressed](#) by ecologically similar, but numerically dominant, species. Rather,  
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26 80 locally rare species are likely specialists on spatially rare habitats or they may be ill-  
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29 81 suited to the locally available environments.  
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## 82 **Introduction**

83 Virtually every natural community is comprised of a few common species and many rare  
84 species (Wallace, 1878; Preston, 1948; Hubbell & Foster, 1986; Brown, 1995; Lawton &  
85 Lawton, 1999). The large number of rare species in ecological communities becomes  
86 even more pronounced in tropical regions where community ecology effectively becomes  
87 a study of rare species (Hubbell & Foster, 1986; Pitman *et al.*, 1999; Ricklefs, 2000). 88  
Thus, our understanding of how ecological communities are themselves structured de682  
89 depends on our ability to uncover the processes driving rarity. Further, identifying the driv629  
90 ers of rarity is of fundamental importance for society's efforts to conserve biodiversity 91  
91 through space and time.

92 In tree communities, the rarity of species can be explained by a few, potentially  
93 overlapping, processes. First, a species may be locally rare because its niche is being oc6  
94 cupied by ecologically similar species that are more numerically dominant in the com6  
95 munity. For example, priority effects could promote the rarity of late arriving species  
96 even though these late arrivals are ecologically similar to the early arriving individuals  
97 (Chase, 2007). Second, a species may be a habitat specialist and the habitat it specializes  
98 on is itself rare in the landscape (MacArthur, 1957; MacArthur & MacArthur, 1961;  
99 Sugihara, 1980; Kunin & Gaston, 1997). A prediction arising from the first possibility is  
100 that rare species should be functionally similar to common species. The second hypothe-  
101 sis, however, predicts that rare species should be functionally dissimilar to common spe-  
102 cies because they specialize on different and rarer habitats than common species. Further,  
103 rare species may be spatially clustered on a preferred habitat that is itself aggregated  
104 (Kunin & Gaston, 1997). Given that in undisturbed forests pioneer species, specializing

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3 105 on light gap environments, may be rare in the community (Hubbell & Foster, 1986;  
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5 106 Denslow, 1987), a possibility that emerges is that rare species will be functionally dissim-  
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8 107 ilar from common species. For example, pioneer species are characterized by having low  
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10 108 wood density, high specific leaf area, high leaf nutrients (Bazzaz, 1980) and are often  
11  
12 109 clumped distributed in gaps (Seidler & Plotkin, 2006).

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15 110 Despite the great interest in rarity in ecology (Rabinowitz, 1981; Rabinowitz *et*  
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17 111 *al.*, 1986; Gaston, 1994; McGill, 2006), quantitative tests of the hypotheses described  
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19 112 above are lacking. Specifically, comparative quantitative tests of the contribution of rare  
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21 113 versus common species to community functional diversity and whether rare species tend  
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23 114 to be spatially aggregated on spatially rare habitats are needed.

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27 115 In this study, we analyzed long-term forest plot data from the temperate zone to  
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29 116 the tropics. Four of the plots are located in Asia and four are located in the Americas. In  
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31 117 each forest plot, we quantified several plant functional traits that are associated with spe-  
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33 118 cies performance, functional trade-offs and ecological strategies. Our approach is a trait-  
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35 119 based extension of a method recently proposed by Mi *et al.* (2012) that integrates relative  
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37 120 abundance distributions with phylogenetic diversity measures (Figure 1). The specific  
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39 121 questions we addressed in this study are: (1) do locally rare tree species contribute more  
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41 122 than expected to community functional diversity by virtue of their being on the periphery  
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43 123 of community trait space?; (2) do species with pioneer traits consistently occupy periph-  
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45 124 eral positions within the trait space of tree communities?; (3) are locally rare tree species  
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47 125 more spatially clustered than common species? The answers to these key questions are  
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49 126 largely consistent across forest plots from the temperate zone to the tropics on two conti-  
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51 127 nents. Specifically, rare species tend to contribute more than expected to community  
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3 128 functional diversity, species with pioneer traits are not consistently occupying the periph-  
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5 129 eral positions, and rare species tend to be more spatially aggregated than common spe-  
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## 132 **Methods**

### 133 *Data collection*

134 This study analyzed eight forest dynamics plots from Asia and the Americas. For each  
135 forest plot, all individuals with a diameter at breast height greater than or equal to one  
136 centimeter were identified, measured and spatially mapped. The Guanacaste forest plot in  
137 Costa Rica was the only exception, where only individuals greater than or equal to three  
138 centimeters were recorded. The plots have experienced relatively little disturbance re-  
139 cently aside from the Luquillo forest plot in Puerto Rico which has experienced severe  
140 hurricane damage from Hurricane Hugo in 1989 and Hurricane Georges in 1998  
141 (Zimmerman *et al.*, 1994; Comita *et al.*, 2009) and the Wabikon Lake, Wisconsin forest  
142 plot has experienced selective logging in the past (early 1900's). The forest plots are lo-  
143 cated in temperate, subtropical and tropical regions and the plot species richness ranges  
144 from 34 with 27,8- 1 individuals in Indiana, USA to 4- 9 with 95,- 09 individuals in  
145 Xishuangbanna, China (Table 1).

146 At each forest plot, we compiled trait data for each of the species and calculated a  
147 species-level mean value for six functional traits: leaf area (LA), maximum height, spe-  
148 cific leaf area (SLA), leaf nitrogen content (%N), leaf phosphorus content (%P) and  
149 wood specific gravity. The trait database for the Xishuangbanna forest plot did not con-  
150 tain %N, %P or wood specific gravity values. Rather, these axes of function were repre-

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3 151 sented by leaf chlorophyll content and wood specific resistance (measured with a resisto-  
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6 152 graph; Rennitech Co., Germany). Leaf chlorophyll content and wood resistance values  
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8 153 have been shown to be highly correlated with %N, and %P and wood density, respective-  
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10 154 ly (Vos & Bom, 1993; Loh *et al.*, 2002; Isik & Li, 2003; Netto *et al.*, 2005; Yang *et al.*,  
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12 155 2014). Thus the leaf and wood axes of plant function were measured in each of the forest  
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14 156 plots. Trait data were collected from the plots or in some instances from the area immedi-  
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16 157 ately next to them and followed standardized methodology (Cornelissen *et al.*, 2003). For  
17  
18 158 further details on trait data collection please see Appendix A in Supporting Information.  
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22 159 The traits quantified approximate the position of species along a continuum of  
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24 160 ecological strategies on several axes (Díaz *et al.*, 2015). The SLA, %N, %P and chloro-  
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26 161 phyll content of a species are components of the ‘leaf economics spectrum’ (Wright *et*  
27  
28 162 *al.*, 2004). Leaves with low structural and high nutrient investment tend to have higher  
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30 163 photosynthetic rates and shorter leaf lifespans. The wood specific gravity and its corre-  
31  
32 164 late, wood specific resistance, represent the ‘wood economics spectrum’ (Chave *et al.*,  
33  
34 165 2009). Species with low wood specific gravity or resistances tend to exhibit rapid volu-  
35  
36 166 metric growth rates and higher mortality rates compared to those species with higher  
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38 167 wood specific gravities and resistances. The maximum height of species relates to the  
39  
40 168 adult light niche of species and light gradient partitioning. Finally, the LA reflects the leaf  
41  
42 169 area deployed for resource (i.e. light) capture and is known to vary along forest scale abi-  
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44 170 otic gradients as well as along local light gradients (Dolph & Dilcher, 1980; Cornelissen  
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46 171 *et al.*, 2003).  
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55 173 *Measuring functional diversity*  
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3 174 This work integrates functional diversity with the species rank abundance distribution in  
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5 175 forest plots. It is important to note that this means that our approach and inferences are  
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8 176 limited to the topic of local rarity and not the regional scale rarity of species. Our ap-  
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10 177 proach provides information about the relative contribution of each of the species to the  
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12 178 community functional diversity (Gaston, 2012; Mi *et al.*, 2012). We quantified functional  
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14 179 diversity using the functional richness (FRic) metric from Laliberté & Legendre (2010).  
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17 180 The FRic is the volume of a convex hull encompassing the multivariate trait space of the  
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19 181 species in a sample and therefore approximates the multivariate range of traits in the  
20  
21 182 samples. The FRic metric is a good indicator of environmental filtering acting on the  
22  
23 183 edges of trait space and it conceptually aligns with the goals of the present work, which  
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25 184 asks whether increasingly rare species tend to occupy the periphery of multivariate trait  
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27 185 space (Cornwell *et al.*, 2006). Furthermore, it does not include abundance information,  
28  
29 186 which is critical for our study that required a measure of functional diversity that is inde-  
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31 187 pendent of the abundance distribution. We utilized the function *dbFD* in R package ‘FD’  
32  
33 188 (Laliberté & Legendre, 2010) to calculate FRic. Trait values were log-transformed, if  
34  
35 189 necessary, to approximate normality prior to the *dbFD* analyses. The *dbFD* function  
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37 190 scales all trait data and performs a principal coordinate analysis (PCoA) to provide or-  
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39 191 thogonal axes prior to calculating FRic. The number of PCo axes selected to calculate  
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41 192 FRic followed Laliberté & Legendre (2010) where the number of PCo axes retained is  
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43 193 equal to the number of the species in the community minus 1.  
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53 195 *Integrating abundance distributions and functional richness*  
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3 196 To quantify the contribution of locally rare species to community functional richness for  
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5 197 each assemblage, we integrated the standardized effect size (SES) for FRic with species  
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7 198 rank abundance. In the following, we will describe the method to obtain the SES FRic  
8  
9 199 values and how we compared it with the species abundance rank values. Our method fol-  
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11 200 lows that developed by Mi *et al.* (2012) who related phylogenetic diversity to rank abun-  
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13 201 dance distributions. The first step was to calculate the observed FRic values. This method  
14  
15 202 first computes the functional richness for the first and second most abundant species in  
16  
17 203 the forest. Next, the third most abundant species is added to the sample and the functional  
18  
19 204 richness metric is again computed and recorded. This is repeated adding increasingly rare  
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21 205 species to the sample until the second most rare species is added (Figure 1).

26  
27 206 The FRic metric is correlated with species richness (Laliberté & Legendre, 2010).  
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29 207 Thus, it is not possible to compare the FRic value across samples including increasingly  
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31 208 rare species that differ in their number of species. A null model is, therefore, necessary to  
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33 209 produce the expected distribution of FRic values given the observed species richness of a  
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35 210 sample. Thus, for the second step in our analyses we generated a null distribution of val-  
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37 211 ues to estimate standardized FRic values. The null model was accomplished by random-  
38  
39 212 izing the names of species 999 times on the trait data matrix in a plot. Thus, the species  
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41 213 pool for the randomizations consisted of only the species within each plot. The FRic val-  
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43 214 ues for samples with increasingly rare species were computed as before, but this time  
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45 215 with randomized trait data. At the end we had a distribution of 999 random FRic-  
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47 216 abundance relationships [per plot](#) that could be compared to our observed relationship. For  
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49 217 each species along the species abundance rank distribution we calculated a SES FRic by  
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51 218 subtracting the mean of the null distribution of FRic values for that species from the ob-  
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3 219 served FRic and divided by the standard deviation of the null distribution. Therefore, pos-  
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6 220 itive SES FRic values indicated a higher than expected observed FRic value and negative  
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8 221 SES FRic values indicated a lower than expected observed FRic value. Since a FRic of  
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10 222 only one species cannot be computed, the most abundant species is never analyzed by  
11  
12 223 itself and the rarest species is never analyzed because the standardized effect size must be  
13  
14 224 zero when all species are sampled (i.e. there is no variance in the null distribution). At the  
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16 225 end we obtained a set of SES FRic values equal to the length of the total number of spe-  
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18 226 cies minus two for each plot.

21  
22 227 The last step was to compare the SES FRic values along the species rank abun-  
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24 228 dance axis. On the left-hand side of the x-axis is the sample containing only the two most  
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26 229 abundant species and increasingly rare species are added as one moves along the x-axis.  
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28 230 A change in the y-axis value, the SES FRic, is expected if the added species to the sample  
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30 231 (i.e. the next rarest species) increases or decreases the functional diversity more than ex-  
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32 232 pected based on a randomly added species. If there is a decreasing trend in SESs along  
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34 233 the x-axis this indicates that as one adds less and less abundant species to the sample, less  
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36 234 than expected functional diversity accumulates. In other words, the less abundant species  
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38 235 are generally functionally similar to the more abundant species already in the sample.  
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40 23- Conversely, if there is an increasing trend in the SESs along the x-axis, less abundant  
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42 237 species are more functionally diverse than expected and functionally divergent from the  
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44 238 more abundant species already in the sample.  
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53 240 *Quantifying trends in functional diversity along the abundance distribution*  
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3 2K1 Trends in the SES FRic values along the rank abundance distribution are used to indicate  
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5 2K2 the relative contribution of increasingly rare species to community FRic. Thus, a critical  
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7 2K3 step for interpreting FRic-rank abundance relationships is to determine: first, whether  
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9 2KK there are breaking points along the curve that indicate a change in the trend of the curve;  
10  
11 2K5 and second, whether the trends in the curve are significantly increasing or decreasing,  
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13 2K- which would be indicative of rarer species adding more than expected or less than ex-  
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15 2K7 pected functional diversity to the community. Thus, we first used piece-wise regression to  
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17 2K8 identify subseries (i.e. significant breakpoints) in each of the analyses and significance  
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19 2K9 was assessed with a structural change test using the vhowws F- statistic method as de-  
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21 250 scribed in Mi *et al.* (2012). We used Akaike information criteria (AIV) to compare a sim-  
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23 251 ple linear model with the piecewise linear model. For all the plots piece-wise linear mod-  
24  
25 252 els were consistently better than simple linear model (lower AIV values for piece-wise  
26  
27 253 linear models than for simple linear models, Appendix B Table B1 in Supporting Infor-  
28  
29 25K mation). Second, we used a Mann-Kendall test to quantify whether each sub- eries exhib-  
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31 255 ited a non-randomly increasing or decreasing trend in the standardized effect size values.  
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33 25- Since the Mann-Kendall test may be sensitive to autocorrelation in the data a permutation  
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35 257 approach using block bootstrapping is recommended (Wilks, 1997). erved autocorrela-  
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37 259 tion where block size was set at the maximum size at which continuous lag correlations  
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39 2-0 were significant. Thus, blocks were randomly sampled with replacement to construct null  
40  
41 2-1 sub- eries of standardized effect sizes. A Mann-Kendall was then calculated for the null  
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43 2-2 sub- eries and this was repeated 999 times to generate a null distribution to which the ob-  
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45 2-3 served Mann-Kendall for that sub- eries could be compared and a p-value could be esti-  
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3 264 mated. We utilized the function *MannKendal* in R package ‘Kendall’ and function  
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5 265 *tsboots* in R package ‘boot’ to perform these analyses.  
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### 10 267 *Evaluating individual trait ranges*

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12 268 In order to determine: (a) whether rare species increase FRic because they are potentially  
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14 269 pioneer species with low wood density, high leaf nutrient content (i.e. %P and %N) or  
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16 270 high specific leaf area (Bazzaz, 1980) and (b) whether increases in FRic with rarity  
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18 271 across all forests are generally associated with the increase in the range for a particular  
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20 272 trait across all forests, we plotted the range of individual trait values as increasingly rare  
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22 273 species are added. This allowed us to visualize how the range of an individual trait  
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24 274 changes as increasingly rare species are added and it is the uni-variate analog to our mul-  
25  
26 275 tivariate FRic analyses. As in our multivariate analyses, our uni-variate analyses also es-  
27  
28 276 timated breakpoints and performed the structural test using the Chow's F- statistic method  
29  
30 277 to evaluate whether the increases in the ranges of leaf traits and decreases in wood specif-  
31  
32 278 ic gravity were consistently associated with rare species. We used piece-wise regression  
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34 279 to identify subseries in relationships between maximum trait range and rank abundance as  
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36 280 well as minimum trait range and rank abundance.  
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### 45 282 *Quantifying spatial aggregation of individuals within species*

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47 283 We quantified the spatial aggregation of individuals within species at several scales by  
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49 284 computing the omega ( $\Omega$ ) metric developed by Condit *et al.* (2000). Omega evaluates the  
50  
51 285 population density of each focal tree of each species within concentric circles with radii  
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53 286 of 5, 10, 20, 30, 40 and 50 m. Thus, for a given species,  $\Omega$  indicates the density of con-  
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3 287 specifics in the neighborhood. This value is divided by the total population density of a  
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5 288 particular species for the entire plot. Omega values equal to one indicate a perfectly ran-  
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7  
8 289 dom distribution. At short distances,  $\Omega$  values higher than one indicates aggregation and  
9  
10 290  $\Omega$  values lower than one indicates more even spacing. To ensure that our aggregation  
11  
12 291 analyses were not inherently biased by differences in species abundance, we used a com-  
13  
14 292 plete spatial randomness simulation to test whether species had  $\Omega$  values that were signif-  
15  
16 293 icantly higher or lower than expected from a randomly dispersed species. In particular,  
17  
18 294 we calculated 999 random  $\Omega$  values by shuffling species names across the XY locations  
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20 295 of all individuals in the forest plot each time calculating an  $\Omega$  value for each species. This  
21  
22 296 randomization considers the simplest null scenario assuming complete spatial random-  
23  
24 297 ness and independence. The mean of the null distribution of  $\Omega$  values was subtracted  
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26 298 from the observed  $\Omega$  values and divided by the standard deviation of the null omega val-  
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28 299 ues to result in a standardized effect size (SES) of  $\Omega$ . A SES of  $\Omega$  higher than zero indi-  
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30 300 cates a species is more spatially aggregated than expected whereas a SES  $\Omega$  value less  
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32 301 than zero indicates a species is more evenly dispersed in space than expected. In order to  
33  
34 302 examine whether rare species tended to be more spatially clustered than common species,  
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36 303 we performed Spearman correlations between SES  $\Omega$  values and log-transformed species  
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38 304 abundance. If rare species are more spatially clustered than common species, then a nega-  
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40 305 tive Spearman correlation is expected.  
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## 307 **Results**

53 308 The results from six of the eight forest plots (Indiana, Changbaishan, Fushan, Guana-  
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55 309 caste, Gutianshan and Xishuangbanna) were consistent with downward trends on the left  
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3 310 side and upward trends on the right side of the SES FRic curves (Figure 2, Appendix B  
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5 311 Table B1, Table B2 in Supporting Information). The breakpoints for these six plots were  
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7  
8 312 located in the right hand of the curve (rare species) indicating that there are significant  
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10 313 changes of these downward trends to upward trends (Figure 2, Appendix B Table B1). In  
11  
12 314 other words, the rarest species in these forest plots were adding more to the overall com-  
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14 315 munity FRic than expected.

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17 316 We further considered the results using an ad-hoc criterion for describing rare  
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19 317 species (<1 individuals for a species per hectare) (Hubbell & Foster, 1986) to evaluate if  
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21 318 the breakpoints were associated with what may commonly be considered "rare" species.  
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23 319 The results show that, in general, the breakpoints were very close to values that match the  
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25 320 criteria for "rare" species used by Hubbell & Foster (1986) (Figure 2). Combined, the re-  
26  
27 321 sults for the trends and the breakpoints indicate that the progressively rare species add  
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29 322 more than expected to the functional diversity of the tree community (Figure 2, Appendix  
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31 323 B Table B1, Table B2). For the other two plots (Wabikon Lake and Luquillo), the trends  
32  
33 324 were more complex and rare species did not consistently contribute more than expected  
34  
35 325 to the functional diversity of the community (Figure 2, Table B1, Table B2). For these  
36  
37 326 two plots, the breakpoints were located on both the left and the right hand of the curve  
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39 327 (Table B1), and the trends were downwards (Figure 2, Table B2).

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41 328 When the ranges of individual traits were evaluated, we found no consistent  
42  
43 329 trends across the different plots indicating that traits related with pioneer species (i.e. low  
44  
45 330 wood density, high leaf nutrient content, high specific leaf area) are not consistently as-  
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47 331 sociated with the rarest species (Appendix B Table B3 Figures B1-B8). Specifically, for  
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49 332 Indiana, Changbaishan, Fushan, Guanacaste, Gutianshan and Xishuangbanna plots, the  
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3 333 breakpoints on the right hand of the curve (rare species) were not consistently found for  
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5 334 leaf trait maximum values and wood density minimum values (Table B3, Figures B1-B8).  
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8 335 The results for the plots with historical disturbance, Wabikon Lake and Luquillo showed  
9  
10 336 significant changes in the trends in the left-hand of the curves (common species), but  
11  
12 337 again the traits were not always consistent with the expectation for pioneer species (Table  
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14 338 B3). Overall, we found no consistent support for our results being due to pioneer species  
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16 339 being rare.  
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20 340 We further tested for evidence regarding whether rare species are spatially aggre-  
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22 341 gated. This was done by evaluating the correlation between species abundance and SES  
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24 342  $\Omega$  values. The results show strong evidence that rare species tend to be more spatially ag-  
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26 343 gregated than common species in all forests and spatial scales (Figure 3, Appendix B Ta-  
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28 344 ble B4). Common species tended to have negative SES  $\Omega$  values while rare species tend-  
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30 345 ed to have positive SES  $\Omega$  values. Some rare species were highly clustered distributed at  
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32 346 the smallest annulus size (5m) (Figure 3) as shown in the Wisconsin, Luquillo, Guana-  
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34 347 caste and Gutianshan plots (Figure 3b, e, f, g).  
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#### 41 349 **Discussion**

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43 350 A central goal of this study was to quantify whether rare species are functionally distinct  
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45 351 from more common species, thereby adding more than expected functional diversity to  
46  
47 352 tree communities worldwide (Lawton, 1999; Gaston, 2012). Our results show that in six  
48  
49 353 of the eight plots, rare species tend to be functionally unique indicating rare species are  
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51 354 not rare because functionally similar species have pre-empted or excluded them. These  
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53 355 results suggest that species abundance distribution is not only the result of historically  
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3 356 contingent factors where the sequence and timing of functionally similar species arriving  
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5 357 is the main determinant of their abundance (Chase, 2003, 2007; Fukami, 2015). Instead  
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8 358 the combination of traits that characterize rare species may allow them to exploit differ-  
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11 359 ent resources and therefore play an alternative role within the community as suggested by  
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13 360 similar results for other taxa (Mouillot *et al.*, 2011, 2013; Leitaõ *et al.*, 2016). However,  
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15 361 in two of our study plots, the Wabikon Lake, Wisconsin and Luquillo, Puerto Rico, the  
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17 362 results showed different trends and the breakpoints were associated to common species.  
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20 363 These two forests have both experienced past human disturbance via selective logging.  
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22 364 The Luquillo plot has experienced two major hurricanes in the past 30 years (Thompson  
23  
24 365 *et al.*, 2002) and the dynamics at Luquillo plot have shown a higher functional turnover  
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27 366 during the last 10 years compared with a non-disturbed tropical forest in Panama  
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29 367 (Swenson *et al.*, 2012). It is possible that this disturbance has affected the dynamics of  
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31 368 these forests having an important effect on the functional composition of the plant com-  
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34 369 munities. As forested ecosystems become increasingly disturbed in the future, it may well  
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36 370 be that functional diversity will be reduced through the loss of rare functionally divergent  
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39 371 species, and functional homogenization through space and along the abundance distribu-  
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41 372 tion may become more common.  
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#### 374 *Rarity and specialization*

375 A potential explanation for unifying the results for the eight plots is that weedy pioneer  
376 tree species with unique peripheral trait values (Bazzaz, 1980) are driving all of the ob-  
377 served results across forests. Specifically, in the six undisturbed forests, pioneer species,  
378 usually described as rare members of pristine communities and specialized on rare gap

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3 379 environments, might be the species responsible of the observed pattern of functionally  
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5 380 distinct rare species (Hubbell & Foster, 1986). Under this scenario, rarity would primarily  
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8 381 be driven by the availability of habitats and functional specialization. However, upon ex-  
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10 382 amination of increases in individual trait ranges as progressively rare species are added in  
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12 383 each forest plot, we find no clear and consistent evidence that pioneer species with  
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14 384 unique trait values are the determinant of our results. For example, some leaf traits  
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16 385 showed increases associated with rare species, as it is the case for *Trevesia palmata* (Ara-  
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18 386 liaceae), a tree characterized by big leaves and no side branches, which is a very rare spe-  
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20 387 cies in the Xishuangbanna tree community. However, the increases in leaf traits for other  
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22 388 non-disturbed forest plots were not always evident or were also associated with signifi-  
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24 389 cant decreases in leaf trait values. For example, *Lonicera monantha* (Caprifoliaceae) is  
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26 390 one of the rarest species in the Changbaishan plot, but it is not a pioneer species, instead  
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28 391 is an understory tree and shade tolerant. Therefore, these results provide little support for  
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30 392 the pioneer habitat specialization hypothesis linked to rarity.  
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36 393 Rare species might not be necessarily pioneers, but they may be specialized in  
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38 394 other ways. We attempted to explore this possibility by analyzing the strength of the as-  
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40 395 sociation between rare species and elevationally rare habitats compared to common spe-  
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42 396 cies, suggesting potential specialization to particular elevations (Appendix C). Elevation,  
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44 397 often linked to other topographical variables, has been found to play an important role in  
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46 398 determining species distribution in tropical forest and potentially a key factor determining  
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48 399 habitat associations (Baldeck *et al.*, 2013). We evaluated the preferred elevation of spe-  
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50 400 cies, ordered from most rare to most common, against the relative abundance of the ele-  
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52 401 vation bins ordered from most rare to most common. We failed to find evidence support-  
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3 402 ing the habitat specialization for rare species aside from a very weak positive correlation  
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5 403 in a few plots and this was consistent across bin sizes (Appendix C). However, we cau-  
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7 404 tion that the analytical approach used had several flaws that hinder our ability to com-  
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9 405 pletely reject the rare species-specialists relationship. Specifically, other habitat variables  
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11 406 that were not measured that are not or loosely correlated with elevation in the plots may  
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13 407 be axes upon which rare species specialize. Furthermore, it is also important to recall that  
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15 408 our analyses concern local rarity both in species and elevation and we cannot speak to  
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17 409 whether the rare species-specialists relationship is supported at larger spatial scales.  
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411 *Rarity and spatial aggregation*

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27 412 We further tested whether locally rare species are spatially aggregated. Our results show  
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29 413 that locally rare species are more spatially aggregated than common species in all forests  
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31 414 and spatial scales suggesting that populations of locally rare species are small because:  
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33 415 (1) they are specialized on rare habitats; (2) locally rare species are sink populations and  
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35 416 their spatial dispersion is limited due to rare dispersal events and a lack of reproduction  
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37 417 and population spread, which combined drive the clustered individual spatial patterns.  
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39 418 Although previous studies have found similar patterns, where locally rare species tend to  
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41 419 be more clumped than common species (Hubbell, 1979; Condit, 2000; Li *et al.*, 2009),  
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43 420 one additional hypothesis that would help to clarify the role of rare species should be to  
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45 421 evaluate their performance. In this respect, Hubbell (1979), showed that for a tropical  
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47 422 forest analyzed in this study (Guanacaste, Costa Rica), rare species tend to exhibit poor  
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49 423 reproductive performance compared with common species, suggesting that specialization  
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51 424 might not be the main factor driving rarity. Supporting these results, recent work by  
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3 425 Mangan *et al.* (2010) experimentally demonstrated that rare species are more susceptible  
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6 426 to pathogens. However, previous work by Wills *et al.* (2006) that included two of our  
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8 427 study forests showed that rare species have preferential recruitment, but quantifying de-  
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10 428 mographic rates for rare species can be challenging (Condit *et al.*, 2006). Wills *et al.*  
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12 429 (2006) argued that their results were evidence of frequency-dependent selection favoring  
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14 430 rare species thereby maintaining tree diversity. Thus, more studies are needed in order to  
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17 431 fully support or reject the specialization hypothesis.

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20 432 In some ways, it may be useful to consider our results in the context of the core-  
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22 433 satellite hypothesis (Hanski, 1982). Hanski (1982) presented a classification of species  
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24 434 according to their abundance and spatial distribution (regionally). In this context, locally  
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26 435 small populations in a region may be considered satellite and perhaps sink populations,  
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29 436 whereas locally large populations in a region may be considered core and perhaps source  
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32 437 populations. One prediction arising from this would be that the locally rare populations  
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34 438 like those we presently analyze are satellite and perhaps sink populations ill-suited to the  
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36 439 local environment. Due to data limitations we were unable to address whether locally rare  
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39 440 species were ill-suited to local conditions and we have in many cases little information  
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41 441 regarding whether the species in our forest plots are locally *and* regionally rare. Thus, at  
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43 442 present we cannot fully address the predictions arising from the core-satellite literature. It  
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46 443 is interesting to note, however, that recent work by Ricklefs & Renner (2012) has indicat-  
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48 444 ed that there is phylogenetic signal in local abundance in forest plots worldwide. This  
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50 445 may indicate that there is inherent rarity in lineages that is evident locally and regionally,  
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53 446 but it is still unclear from this evidence whether this rarity is due to specialization on rare  
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56 447 habitats or some other process.

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3 448 Together, our results fail to support the notion that rarity is driven by the ecologi6  
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5 442 cal similarity between rare species and competitively superior or earlier arriving common  
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8 450 species. Also, we present tentative evidence that did not support the link between special6  
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10 451 ization and rarity based upon our analyses of elevational data and shade tolerance strate6  
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12 452 gies. We do note, however, that soil nutrient and light data would be preferred for such an  
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14 453 analysis and future work on this topic is merited. Our results have additional implications  
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16 454 beyond those for community structure and assembly. First, because locally rare species  
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18 455 disproportionately contribute to community functional diversity, it is expected that they 456  
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20 may also disproportionately contribute to ecosystem function (Tilman *et al.*, 1997;  
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22 457 Mouillot *et al.*, 2011). Recent work has indicated this may be the case in several tropical  
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24 458 systems (Mouillot *et al.*, 2013). The present work show that rare species tend to be func64  
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26 52 tionally unique, but they may not be disproportionately influencing present day function64(9  
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28 ing. However, functionally unique rare species are still likely to be critical for the stabil64(1  
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30 ity of ecosystems undergoing change. Thus, the loss of rare species in ecosystems not on64(2  
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32 ly reduces the species and functional dimensions of biological diversity (Hector &  
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34 463 Bagchi, 2007), but it also likely has the potential to negativs are still likely to be critical  
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36 for the stabil6 !(1 ity of ecosystems undergoing change. Thus, the loss of rare species in  
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38 ecosystems not on6 !(2 ly reduces the species and functional dimensions of biolely impact the  
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40 ability of eco64(4 systems to respond to change or forcing. Second, a great deal of emphasis is  
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42 now being 465 placed on building large plant trait and spatial datasets for the purpose of  
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44 mapping the 466 distribution and diversity of plant function worldwide to facilitate vegetation  
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46 modeling 467 and biodiversity science (Kattge *et al.*, 2011; Lamanna *et al.*, 2014; van  
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48 Bodegom *et al.*, 468 2014). Such databases will inevitably be biased towards the inclusion of  
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50 locally common 469 species and the exclusion of locally rare species. This problem will be  
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52 exacerbated in 470 tropical systems where it is likely that such efforts will be prone to  
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54 underestimate tropi6  
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3 471 cal functional diversity compared to temperate functional diversity. Thus, future analyses  
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5 472 should attempt to avoid such biases and, just as importantly, a great deal more infor-  
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7 473 mation regarding the functional diversity of entire tropical assemblages will be needed.  
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13 475 **Acknowledgments**

14  
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39 488 versity of Puerto Rico, working with the International Institute of Tropical Forestry  
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49 492 **Appendix A: Supplementary methods on trait data collection.**50  
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52 493 **Appendix B: Supplementary results.**  
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3 494 **Appendix C: Supplementary methods and results on elevational data.**  
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8 496 **Biosketch**  
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10 497 María Natalia Umaña is a PhD student at the University of Maryland, USA, and is broad-  
11  
12 498 ly interested in disentangling the mechanisms that maintain tree diversity in natural  
13  
14 499 communities. The co-authors are plant ecologists and evolutionary biologists interested in  
15  
16 500 understanding the diversity, dynamics and functioning of tropical and temperate forest.  
17  
18 501 MNU and NGS designed the study; all authors conducted the study; MNU, NGS, XM, I-  
19  
20 502 FS, DJ and YI performed all data analyses; MNU and NGS wrote the manuscript; MC,  
21  
22 503 BE, ZH, RH, DJ, YI, LL, XL, KM, I-FS, JT, MU, XW, AW, JY and JKZ commented on  
23  
24 504 and edited the manuscript.  
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29 505 Census and trait data are available on (to be filled upon acceptance).  
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695 **Table 1.** Location and description of the forest dynamics plots.

Forest Plot	Latitude	Longitude	Forest Type	Plot Size (ha)	Census Year	Species Richness
Lilly Dickey Woods, Indiana, U.S.A.	39.2361	-86.2204	Temperate forest	25	2004	34
Wabikon Lake, Wisconsin, U.S.A	45.5508	-88.7964	Temperate forest	25.6	2008	38
Changbaishan, China	42.3833	128.083	Korean pine mixed forest	25	2004	51
Fushan, Taiwan	24.7614	121.555	Subtropical evergreen forest	25	2002	110
Luquillo, Puerto Rico	18.3262	-65.816	Lowland moist forest	16	2012	125
Guanacaste, Costa Rica	10.8833	-85.44	Tropical dry forest	14.44	2006	136
Gutianshan, China	29.25	118.117	Subtropical evergreen forest	24	2012	159
Xishuangbanna, China	21.6117	101.574	Tropical forest	20	2007	469

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3 697 **Figure captions**  
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5 698 **Figure 1.** A conceptual figure depicting how the species rank abundance distribution was  
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8 699 integrated with functional diversity. In this highly simplified example there are five indi-  
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10 700 vidual species represented by different colors and shapes, sorted from most to least abun-  
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12 701 dant based on the number of individuals in the forest plot. Notice that in this example the  
13  
14 702 rarest species in the community is functionally unique and that is why its shape is differ-  
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16 703 ent from the other species. The multivariate trait volume (in this simplified example, rep-  
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18 704 resented by the gray area) for the first three most abundant species is computed to repre-  
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20 705 sent the functional diversity. This measure is also referred to as functional richness. The  
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22 706 volume is measured again including the fourth most abundant species. Here, the fourth  
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24 707 species does not expand the volume. This process is repeated until we add the rarest spe-  
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26 708 cies, which in this case adds substantially to the functional richness.  
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34 710 **Figure 2.** The standardized effect sizes of functional diversity. a) Indiana, USA, b) Wis-  
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36 711 consin, USA, c) Changbaishan, China, d) Fushan, Taiwan, e) Luquillo, Puerto Rico, f)  
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38 712 Guanacaste, Costa Rica, g) Gutianshan, China, h) Xishuangbanna, China. Positive values  
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40 713 on the y-axis indicate that the species included in that calculation contribute more than  
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42 714 expected to the functional diversity and negative values indicate that they contribute less  
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44 715 than expected to the functional diversity. Positive trends indicate that increasingly rare  
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46 716 species are disproportionately increasing the functional diversity of the system. Vertical  
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48 717 dotted grey lines in the panels indicate significant breakpoints in the piecewise regression  
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50 718 (Appendix B Table B1). Dashed portions of the trend lines indicate species that have less  
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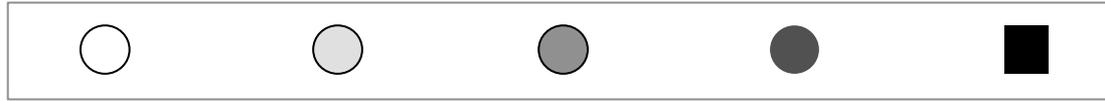
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3 719 than one individual per hectare, which is a commonly used categorization for 'rarity' in  
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6 720 tree communities.

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8 721

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10 722 **Figure 3.** The degree of spatial aggregation of individuals within a species. SES  $\Omega$  values  
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12 723 were plotted against their forest-wide abundance. The radius circle ( $\Omega$ ) surrounding each  
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15 724 individual used for this figure was 5m. Positive SES  $\Omega$  values indicate a higher degree of  
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17 725 spatial aggregation. All correlations were statistically significant ( $P < 0.01$ ). Species with  
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20 726 no conspecific individuals within the 5m radius were omitted from these analyses but the  
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22 727 correlations were still significant. Overall the trends show that rare species tend to be  
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25 728 more clustered than common species.  
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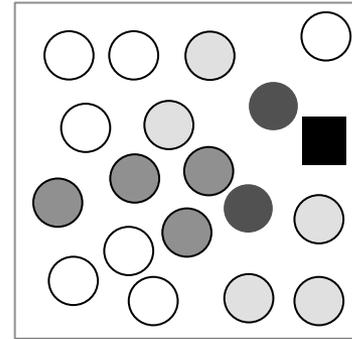
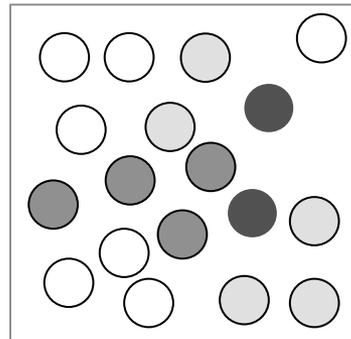
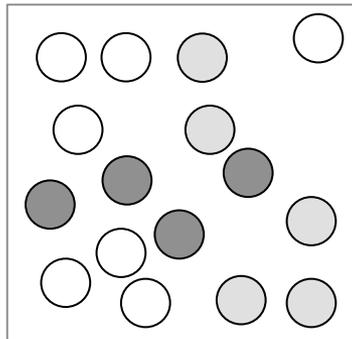
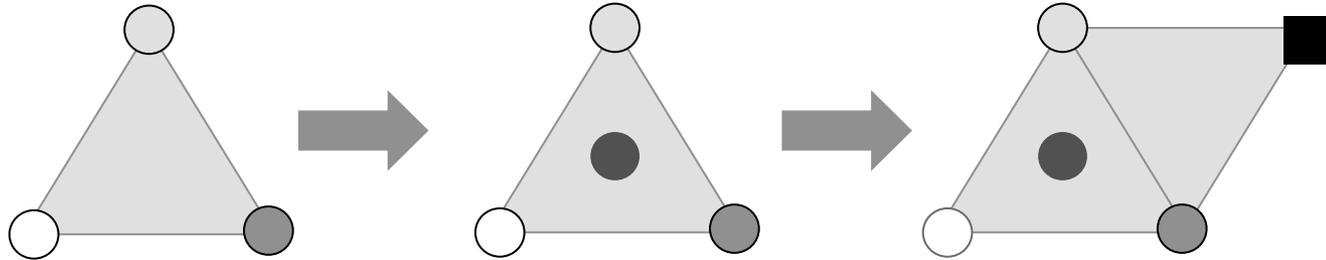
Species



Abundance Rank

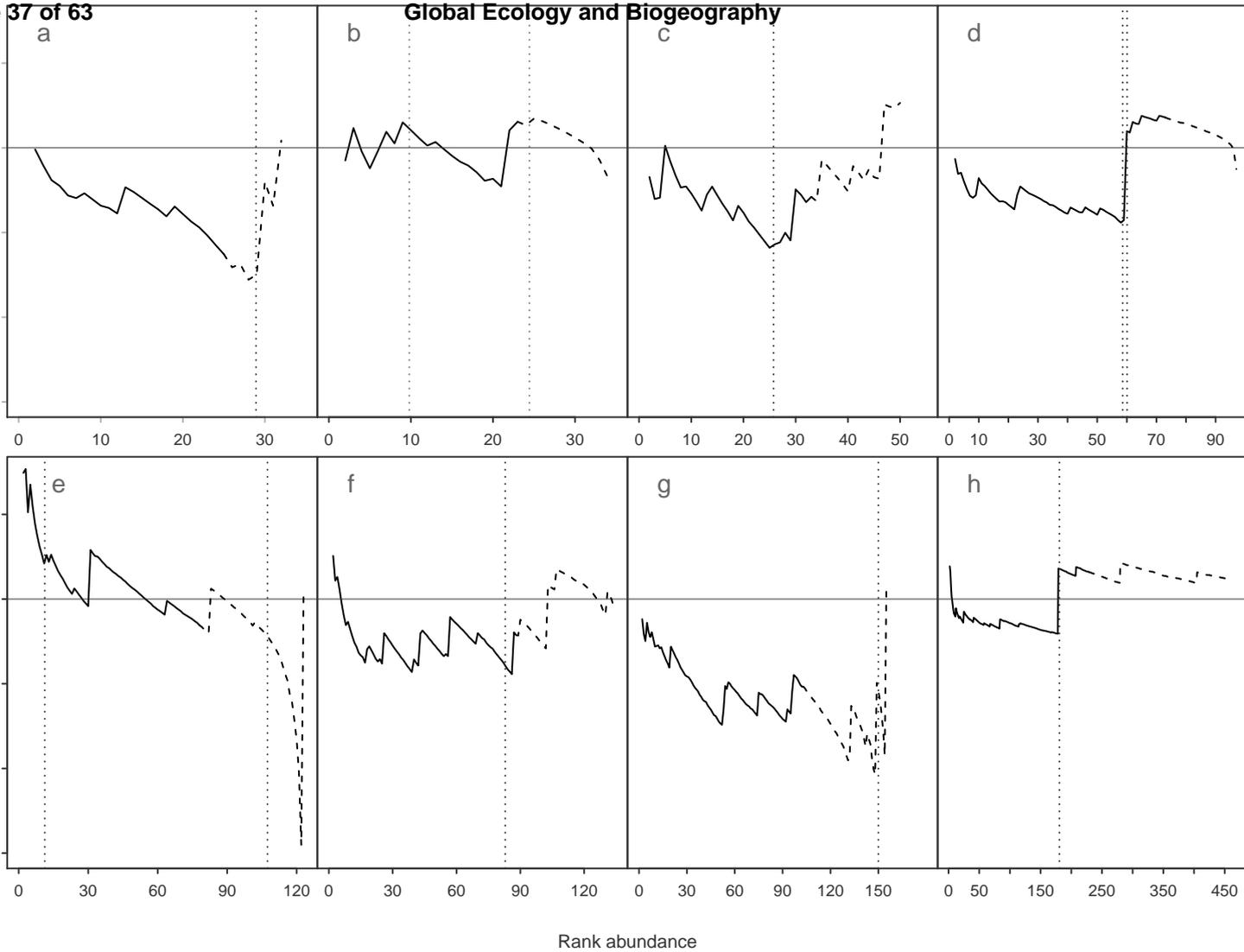


Functional diversity

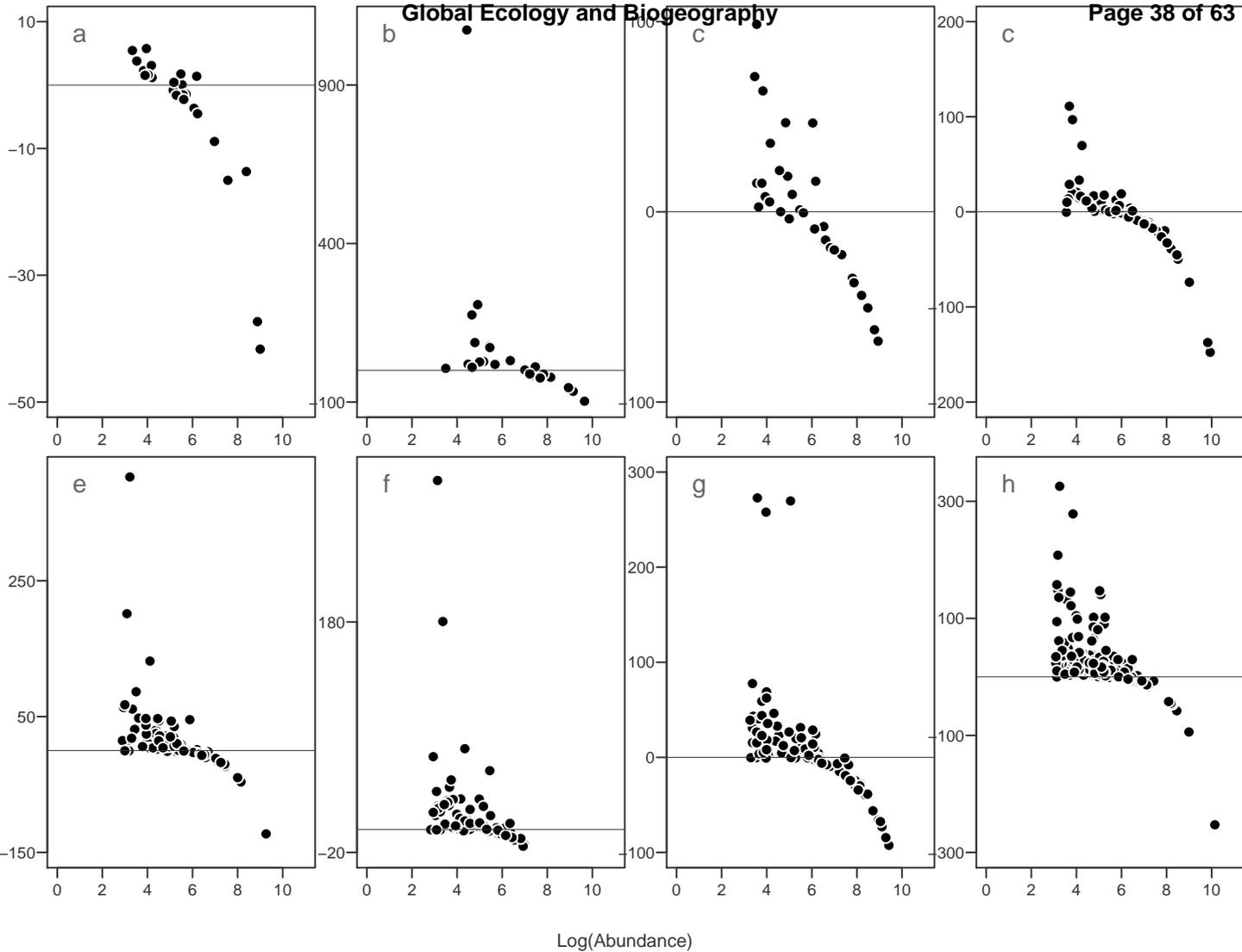


Global Ecology and Biogeography

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Rank abundance



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Log(Abundance)

## Supporting Information

### The role of functional uniqueness and spatial aggregation in explaining rarity in trees

María Natalia Umaña, Xiangcheng Mi, Min Cao, Brian J. Enquist, Zhanqing Hao, Robert Howe, Yoshiko Iida, Daniel Johnson, Luxiang Lin, Xiaojuan Liu, Keping Ma, I-Fang Sun, Jill Thompson, Maria Uriarte, Xugao Wang, Amy Wolf, Jie Yang, Jess K. Zimmerman, and Nathan G. Swenson.

#### Appendix A: Supplementary methods on trait data collection.

##### Contents:

1. Text: Methods
2. Table A1. Trait ranges for all the plots.

##### Text: Supplementary methods on trait data collection.

Traits were collected from 5-10 individuals per species from the area within and around the forest dynamics plots when possible or all available individuals when not possible. In some instances, the trait data were not collected in, or in the area immediately around, the forest plot. Specifically, maximum height was compiled from literature. For the species in Lilly Dickey Woods, Indiana, traits were collected during 2010 from forests in Michigan and Wisconsin. Trait data for Wabikon Lake, Wisconsin were collected in 2010 in the plot; trait data for Changbaishan, China were collected in 2011 in the plot; trait data for Fushan, Taiwan were collected in 2011 in the plot; trait data for Luquillo, Puerto Rico were collected between 2007 and 2008 in the plot; trait data for Guanacaste, Costa Rica, were collected between 2006 and 2007 in the plot; trait data for Gutianshan, China were collected between 2009 and 2010 in the plot; and trait data for Xishuangbanna, China species were collected between 2010 and 2011 in the plot. **Table A1 (Appendix A1)** shows all the ranges from the different traits across all the plots.

**Table A1.** Trait ranges for all the plots.

Plot	Maximum Height	WSG/WSR	%P /Chlorophyll content	%N	SLA	LA
Indiana, USA	3	0.3	0.1	1.3	30.0	0.5
	60	0.8	0.9	3.9	585.2	405.5
Wisconsin, USA	8	0.3	0.1	1.0	77.6	1.1
	150	0.7	0.4	2.9	585.2	530.3
Changbaishan, China	1.5	0.3	1.2	1.3	57.1	6.0
	32	0.7	2.9	3.6	585.0	796.1
Fushan, Taiwan	2.3	0.2	0.0	0.9	86.8	4.4
	28.6	0.8	0.3	4.1	400.2	1658.8
Luquillo, Puerto Rico	1.524	0.3	0.0	1.0	18.8	10.0
	30.48	1.0	0.3	5.1	1304.2	60383.3
Guanacaste, Costa Rica	3	0.2	0.0	1.3	33.5	1.4
	45	1.0	0.2	5.8	406.0	212.4
Gutianshan, China	0.8	0.3	0.0	0.9	59.6	0.5
	45	0.8	0.2	3.7	460.9	229.5
Xishuangbanna, China	2	11.22	24.98	NA	14.48	1.86
	60	1109.39	67.12	NA	394.34	2395.26

**Note:** The plot in Xishuangbanna, China did not contain wood specific gravity, %N and %P values, instead these axes of function were represented by leaf chlorophyll content and wood specific resistance (WSR). WSG represents wood specific gravity, SLA represents specific leaf area, LA represents leaf Area.

## Supporting Information

### The role of functional uniqueness and spatial aggregation in explaining rarity in trees

María Natalia Umaña, Xiangcheng Mi, Min Cao, Brian J. Enquist, Zhanqing Hao, Robert Howe, Yoshiko Iida, Daniel Johnson, Luxiang Lin, Xiaojuan Liu, Keping Ma, I-Fang Sun, Jill Thompson, Maria Uriarte, Xugao Wang, Amy Wolf, Jie Yang, Jess K. Zimmerman, and Nathan G. Swenson.

#### Appendix B: Supplementary results.

##### Contents:

1. Table B1. Breakpoints for functional richness metrics.
2. Table B2. Man-Kendall.
3. Table B3. Breakpoints associated for leaf ranges.
4. Table B4. Spatial aggregation.
5. Figures B1-B8. Variation in individual trait ranges for each plot.

## TABLES

**Table B1.** Breakpoints and significance values associated to the structural change test for relationships between SES FRic values and rank species abundance.

<b>Plot</b>	<b>Estimated breakpoint</b>	<b>F</b>	<b>P-value (<math>&lt;</math>)</b>	<b>AIC(seg)</b>	<b>AIC(lm)</b>
Indiana, USA	28.92	61.91	8.21E-11	31.34695	68.24729
Wisconsin, USA	9.809	3.74	0.03598	50.64894	47.86799
Wisconsin, USA	24.44	3.38	3.38E-06		
Changbaishan, China	25.76	60.29	1.86E-13	58.69107	116.7757
Fushan, Taiwan	58.96	900.01	2.20E-16	66.14535	200.8568
Fushan, Taiwan	60.1	162.14	2.20E-16		
Luquillo, Puerto Rico	11.25	13.04	7.68E-06	195.2497	269.1527
Luquillo, Puerto Rico	107.4	69.61	2.20E-16		
Guanacaste, Costa Rica	82.43	33.66	1.72E-12	198.3929	247.3509
Gutianshan, China	154.1	255.00	2.20E-16	211.5991	284.6906
Xishuangnanna, China	180.6	996.32	2.20E-16	326.2578	453.2756

**Table B2.** Mann-Kendall trend test for each plot and block bootstrap results.

<b>Plot</b>	<b>Kendall's tau statistic (<math>\tau</math>)</b>	<b>Probability</b>	<b>Abundance rank range</b>
Indiana, USA	-0.846	<0.001	(2-28)
	0.733	0.975	(26-32)
Wisconsin, USA	-0.415	0.061	(2-10)
	0.667	0.912	(11-24)
	-0.867	0.009	(24-34)
Changbaishan, China	-0.732	<0.001	(2-26)
	0.620	0.999	(27-52)
Fushan, Taiwan	-0.599	<0.001	(2-59)
	0.145	0.858	(60-110)
	-0.867	0.028	(2-11)
Luquillo, Puerto Rico	-0.653	<0.001	(12-107)
	-1.000	<0.001	(108-125)
Guanacaste, Costa Rica	-0.927	0.015	(2-82)
	0.227	0.934	(83-136)
Gutianshan, China	-0.892	<0.001	(2-154)
	0.333	0.494	(155-159)
Xishuangbanna, China	-0.602	<0.001	(2-180)
	0.156	0.995	(180-469)

Note: Positive Mann-Kendal's statistic value indicates that the data tend to increase along the species abundance rank; a negative trend indicates the opposite. The probability column represents the probability that an observed *tau* value is greater than in null *tau* values. The rank abundance range column represents the species rank range that was used.

**Table B3.** Breakpoints and significance values associated to the structural change test for correlations between maximum trait values or minimum trait values and rank abundance.

Plot	Trait	Maximum Range				Lower range			
		Break point	Sp. Ab	F	P-value	Break point	Sp. Ab	F	P-value
Indiana, USA	LA	18.90	73	2.22	2E-04	28.99	5	1.79	7E-03
	SLA	5.31	1158	1.96	2E-03	28.31	5	1.55	3E-02
	<b>N</b>	<b>28.41</b>	<b>5</b>	<b>1.63</b>	<b>2E-02</b>	4.76	1974	2.13	5E-04
	<b>P</b>	<b>28.78</b>	<b>5</b>	<b>1.60</b>	<b>2E-02</b>	22.54	45	2.24	2E-04
	WD	25.03	28	1.63	2E-02	2.97	7912	1.14	3E-01
Wisconsin, USA	LA	4.25	3457	1.27	2E-01	4.66	3457	2.33	8E-05
	SLA	15.95	176	2.17	3E-04	4.95	3457	2.21	2E-04
	N	8.00	1751	2.25	2E-04	4.70	3457	2.07	8E-04
	P	6.01	2172	2.29	1E-04	4.69	3457	1.63	2E-02
	WD	23.99	32	1.88	3E-03	5.13	2517	2.24	2E-04
Changbaishan, China	LA	12.75	681	2.58	7E-06	7.33	1598	2.25	2E-04
	<b>SLA</b>	<b>46.06</b>	<b>2</b>	<b>1.94</b>	<b>2E-03</b>	7.62	1598	2.71	2E-06
	N	13.30	515	2.33	8E-05	7.72	1598	2.79	7E-07
	P	17.00	251	2.55	9E-06	6.41	2468	2.79	7E-07
	WD	41.23	17	1.55	3E-02	38.32	18	1.49	5E-02
Fushan, Taiwan	LA	12.98	2343	2.36	6E-05	39.34	355	3.40	4E-10
	SLA	38.56	371	3.33	1E-09	9.57	2984	3.43	3E-10
	N	63.67	64	2.73	1E-06	60.00	86	3.17	7E-09
	P	33.20	489	3.36	6E-10	77.02	17	2.24	2E-04
	<b>WD</b>	<b>14.19</b>	<b>2256</b>	<b>3.73</b>	<b>3E-12</b>	<b>79.93</b>	<b>13</b>	<b>2.22</b>	<b>2E-04</b>
luquillo, Puerto Rico	<b>LA</b>	<b>96.50</b>	<b>6</b>	<b>2.75</b>	<b>1E-06</b>	2.03	3972	3.99	6E-14
	<b>SLA</b>	<b>104.74</b>	<b>4</b>	<b>2.01</b>	<b>1E-03</b>	88.11	9	3.04	4E-08
	N	39.69	164	3.91	2E-13	59.09	69	3.44	2E-10
	P	7.96	1802	2.83	5E-07	38.42	185	3.98	7E-14
	WD	3.86	3292	2.15	4E-04	8.00	1517	4.37	1E-15
Guana- caste, Costa Rica	LA	72.83	30	4.13	6E-15	25.41	232	4.10	9E-15
	SLA	5.00	624	4.63	4E-16	21.97	311	3.20	5E-09
	N	23.48	243	4.30	4E-16	35.37	148	3.46	2E-10
	P	46.57	79	2.89	2E-07	30.81	191	2.67	3E-06
	WD	39.49	101	4.10	1E-14	3.64	921	2.71	2E-06
Gu- tianshan, China	LA	67.01	140	4.28	4E-16	28.49	1334	4.65	3E-07
	<b>SLA</b>	<b>146.00</b>	<b>2</b>	<b>2.66</b>	<b>3E-06</b>	98.39	28	3.29	2E-09
	N	71.91	93	3.97	8E-14	38.32	567	4.61	5E-07
	P	111.00	16	3.89	3E-13	118.32	13	2.73	1E-06
	WD	11.18	3508	4.06	2E-14	123.18	9	2.62	5E-06
Xishuang- banna,	<b>LA</b>	<b>260.12</b>	<b>14</b>	<b>7.89</b>	<b>2E-16</b>	264.34	13	6.45	4E-16
	<b>SLA</b>	<b>235.36</b>	<b>20</b>	<b>8.10</b>	<b>3E-16</b>	295.02	8	7.39	2E-14

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5		ll	123.32	104	7.73	2E-16	383.60	2	4.78	2E-16
6		<b>WSG</b>	380.89	2	6.25	1E-15	<b>378.39</b>	<b>2</b>	<b>4.92</b>	<b>2E-16</b>

Note: The breakpoint column indicates the abundance rank value where the trait value changed in its trend (maximum or minimum). The Sp.Ab represents the abundance of the species at the breaking point. Bold values show the candidate pioneer traits.

\* For Luquillo, Puerto Rico and Wisconsin, USA, we checked for pioneer traits associated to common species instead of rare species, according to our original hypothesis.

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**Table B4.** The degree of spatial aggregation of species in all forest dynamic plot communities.

Plot	Omega	rho	statistic S	P-value
Indiana, USA	5	-0.90	4376	<0.001
	10	-0.99	4580	<0.001
	20	-0.99	4586	<0.001
	30	-0.99	4574	<0.001
	40	-1.00	4590	<0.001
	50	-0.99	4584	<0.001
Wisconsin, USA	5	-0.78	3606	<0.001
	10	-0.75	3550	<0.001
	20	-0.84	3728	<0.001
	30	-0.87	3786	<0.001
	40	-0.89	3826	<0.001
	50	-0.91	3862	<0.001
Changbaishan, China	5	-0.86	10139	<0.001
	10	-0.90	10349	<0.001
	20	-0.96	10709	<0.001
	30	-0.98	10794	<0.001
	40	-0.99	10864	<0.001
	50	-1.00	10899	<0.001
Fushan, Taiwan	5	-0.92	140575	<0.001
	10	-0.96	143041	<0.001
	20	-0.97	143957	<0.001
	30	-0.99	145340	<0.001
	40	-0.99	145818	<0.001
	50	-0.99	145911	<0.001
Luquillo, Puerto Rico	5	-0.80	131458	<0.001
	10	-0.79	131252	<0.001
	20	-0.90	139019	<0.001
	30	-0.97	143898	<0.001
	40	-0.99	145542	<0.001
	50	-0.99	145599	<0.001
Guanacaste, Costa Rica	5	-0.64	192632	<0.001
	10	-0.82	213463	<0.001
	20	-0.84	216340	<0.001
	30	-0.92	225283	<0.001
	40	-0.95	229140	<0.001
	50	-0.96	230807	<0.001
Gutianshan, China	5	-0.87	311219	<0.001
		-0.91	318239	<0.001
	20	-0.94	323775	<0.001
	30	-0.96	326615	<0.001
	40	-0.98	329504	<0.001

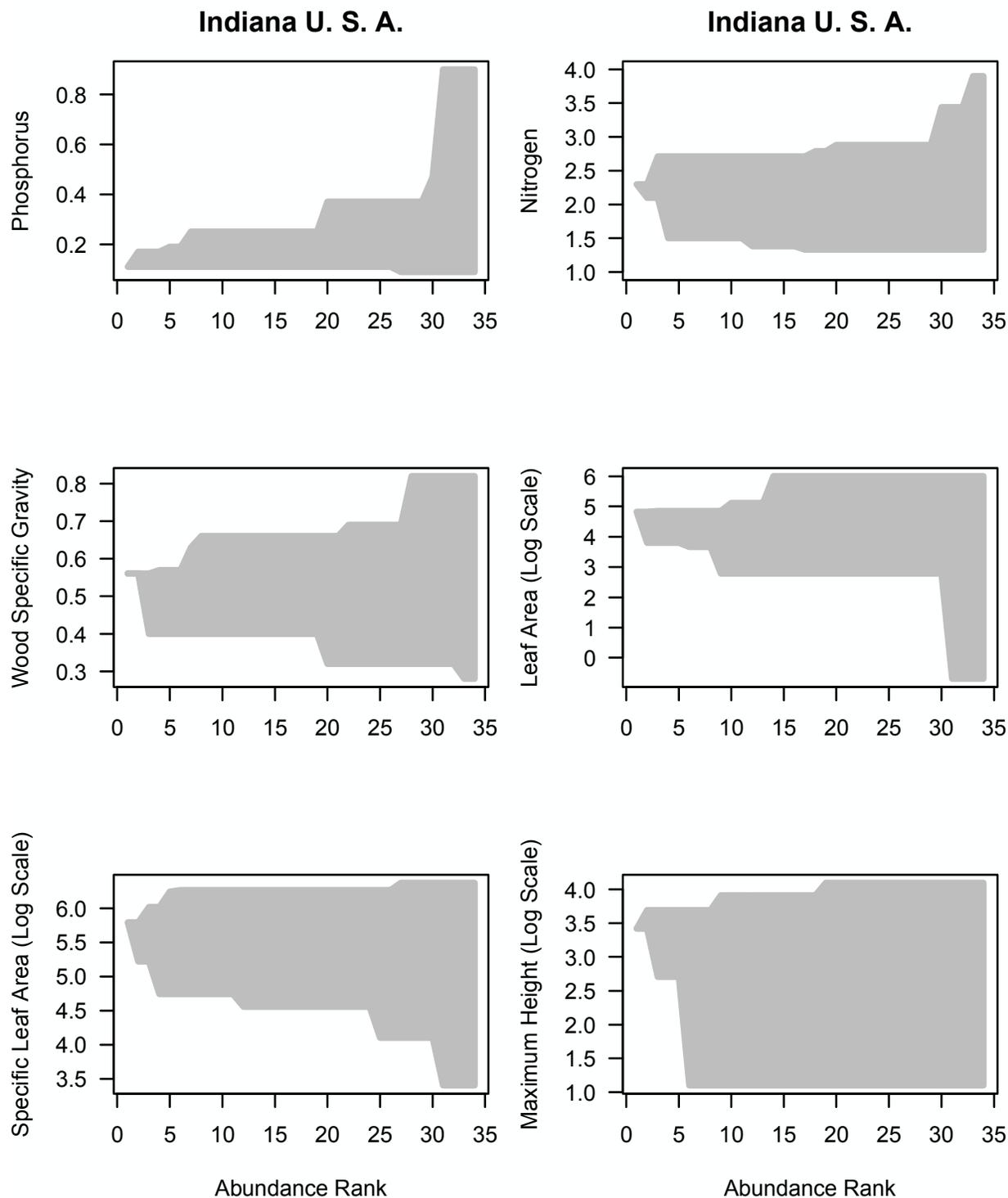
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	50	-0.98	329980	<0.001
Xishuangbanna, China	5	-0.67	4086361	<0.001
	10	-0.72	4205348	<0.001
	20	-0.86	4562793	<0.001
	30	-0.91	4688648	<0.001
	40	-0.95	4773076	<0.001
	50	-0.97	4826073	<0.001

Note: The results correspond to Spearman correlations between ( $\Omega$ ) and their forest-wide abundance. All species with abundances lower than one individual by hectare were removed from the analysis.

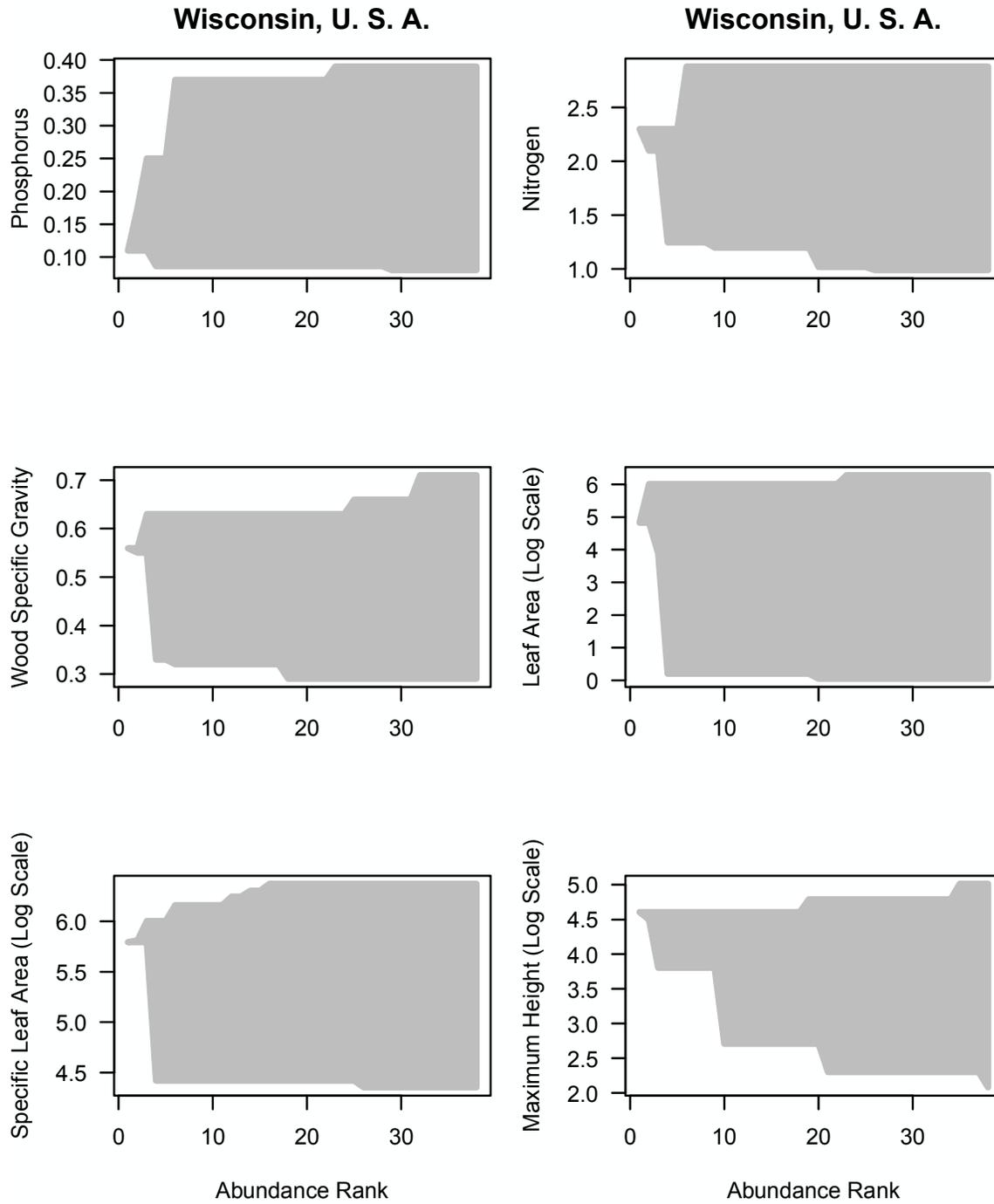
FIGURES

**Figure B1.** Change in trait ranges for the Indiana, U. S. A. forest plot as a function of rank abundance where increasingly rare species are added from left to right.



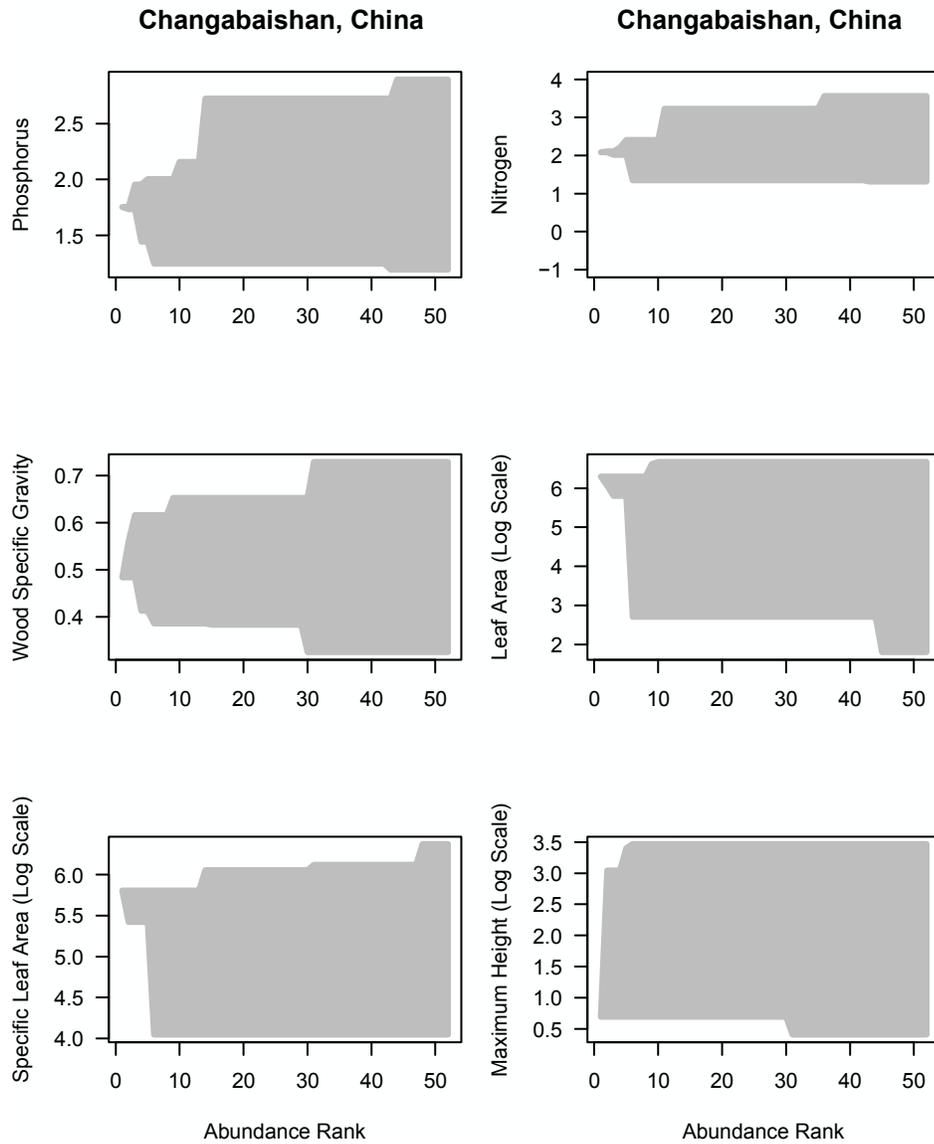
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**Figure B2.** Change in trait ranges for the Wisconsin, U. S. A. forest plot as a function of rank abundance where increasingly rare species are added from left to right.



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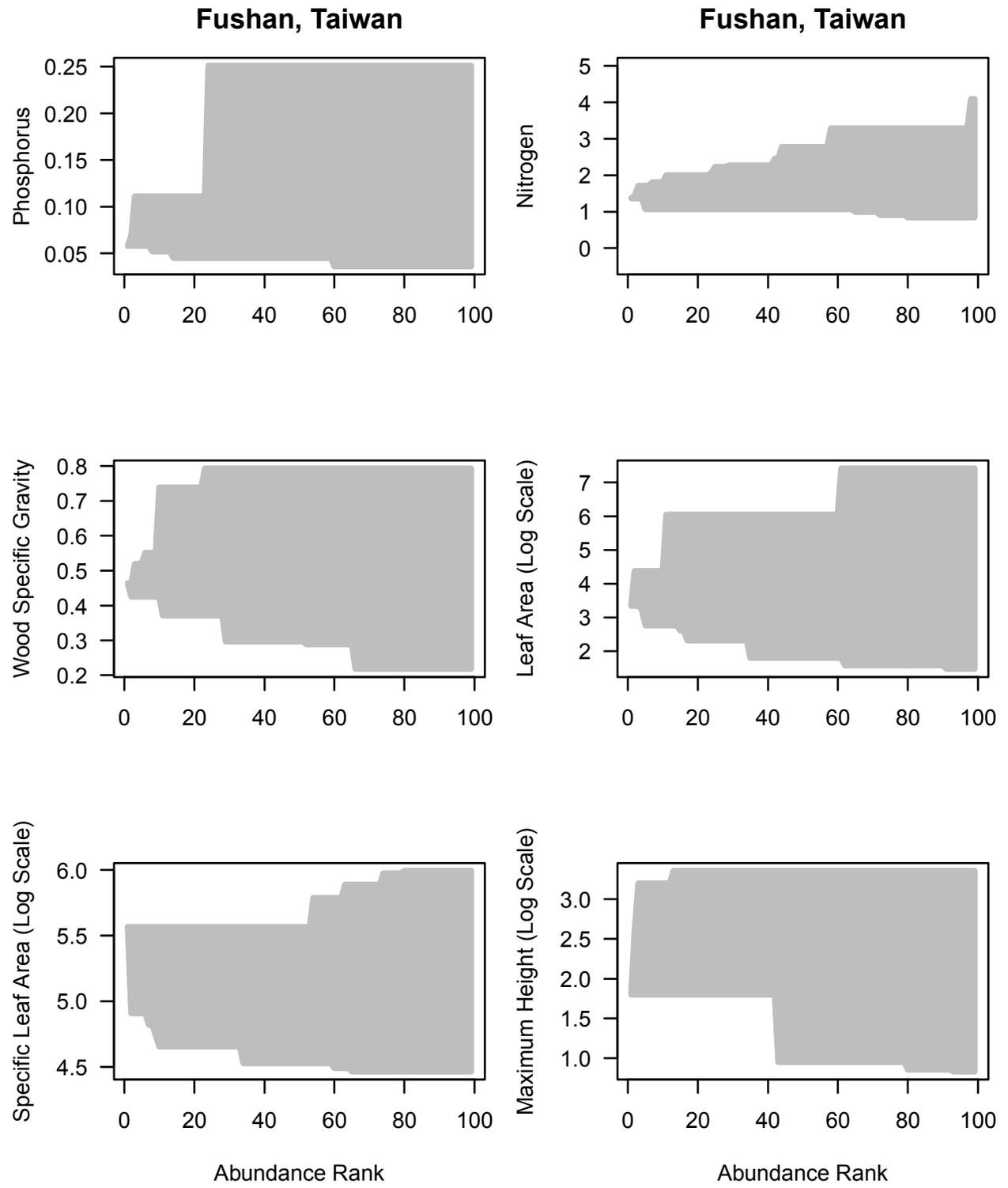
**Figure B3.** Change in trait ranges for the Changbaishan, China forest plot as a function of rank abundance where increasingly rare species are added from left to right.



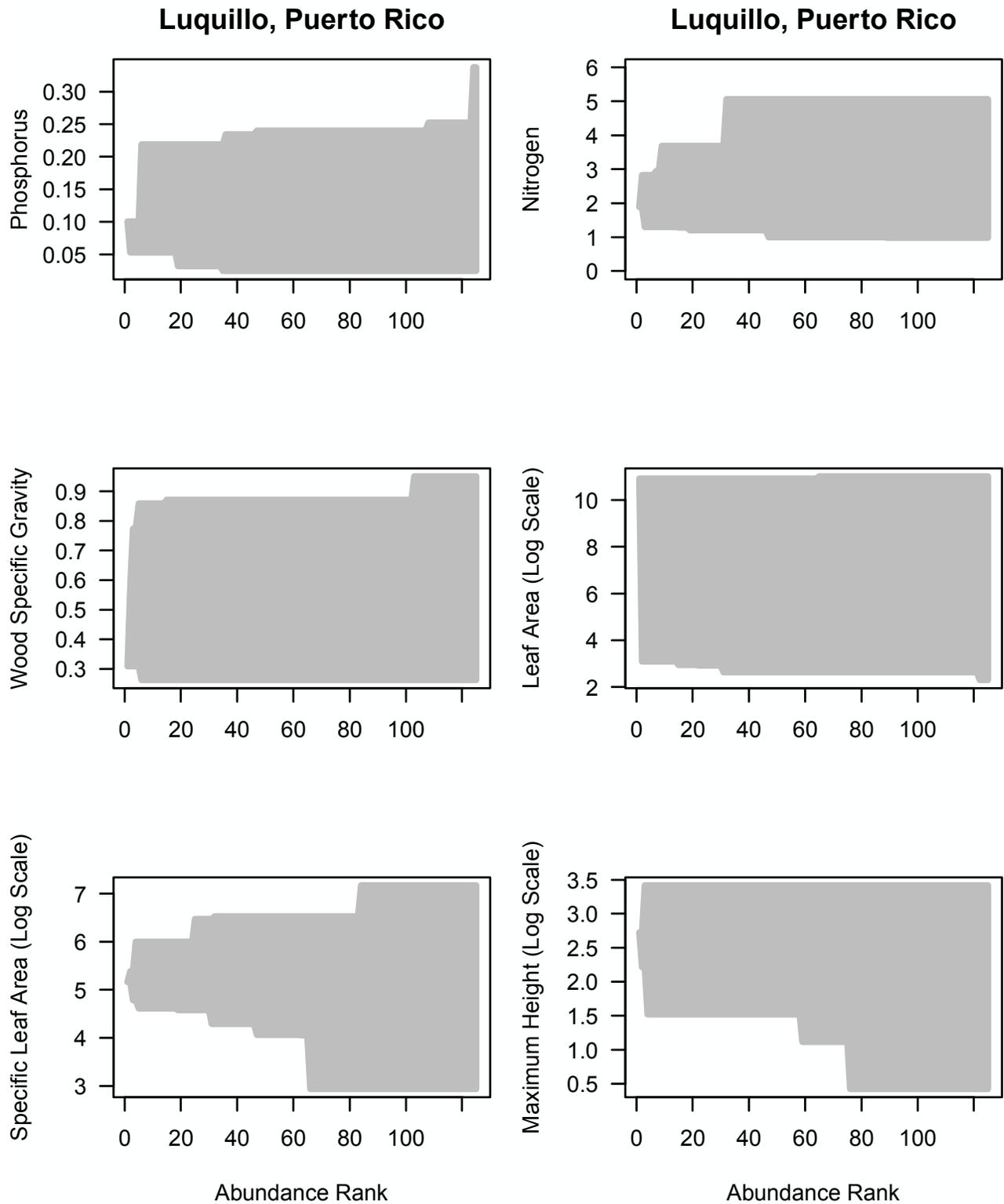
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**Figure B4.** Change in trait ranges for the Fushan, Taiwan forest plot as a function of rank abundance where increasingly rare species are added from left to right.



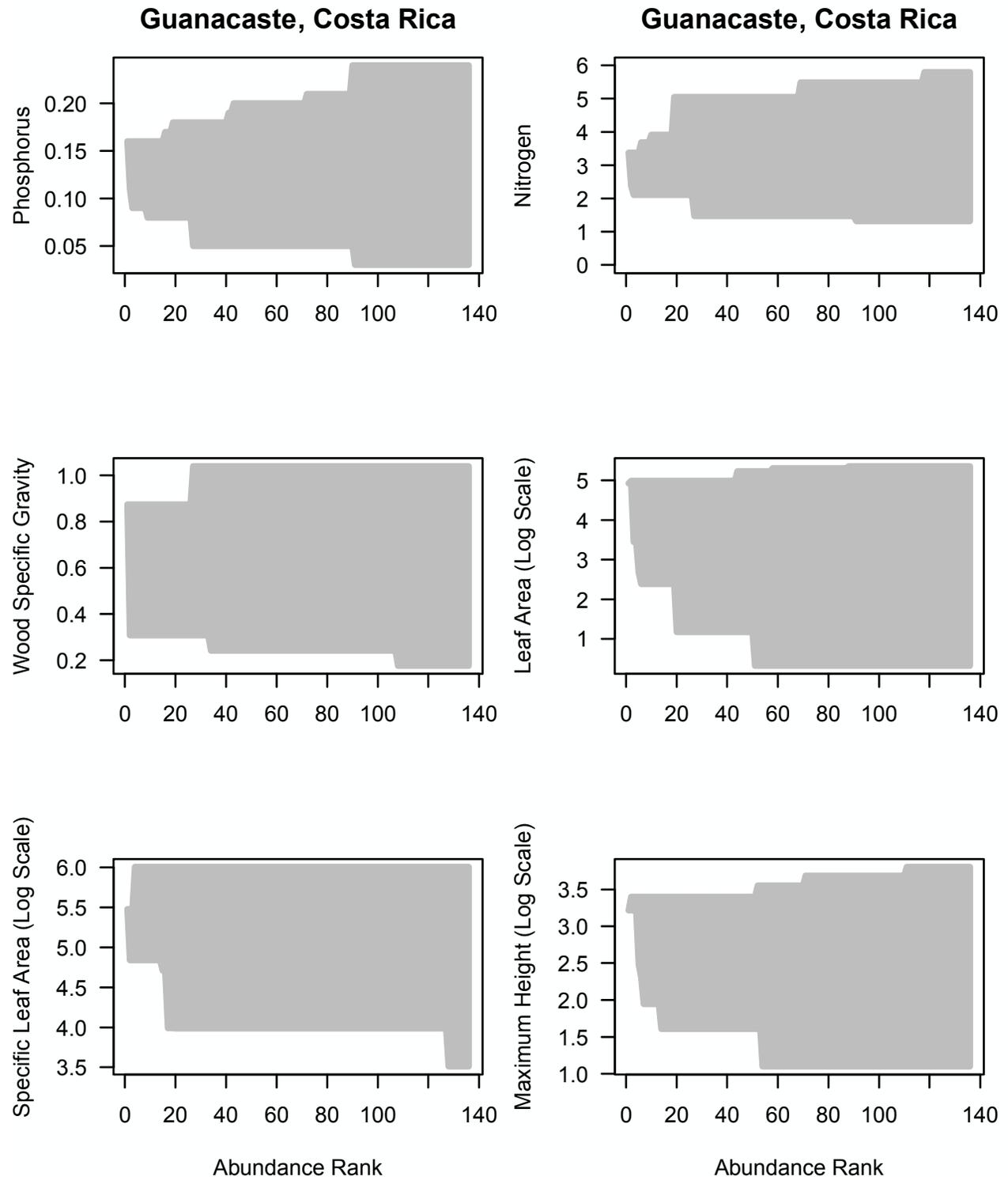
**Figure B5.** Change in trait ranges for the Luquillo, Puerto Rico forest plot as a function of rank abundance where increasingly rare species are added from left to right.



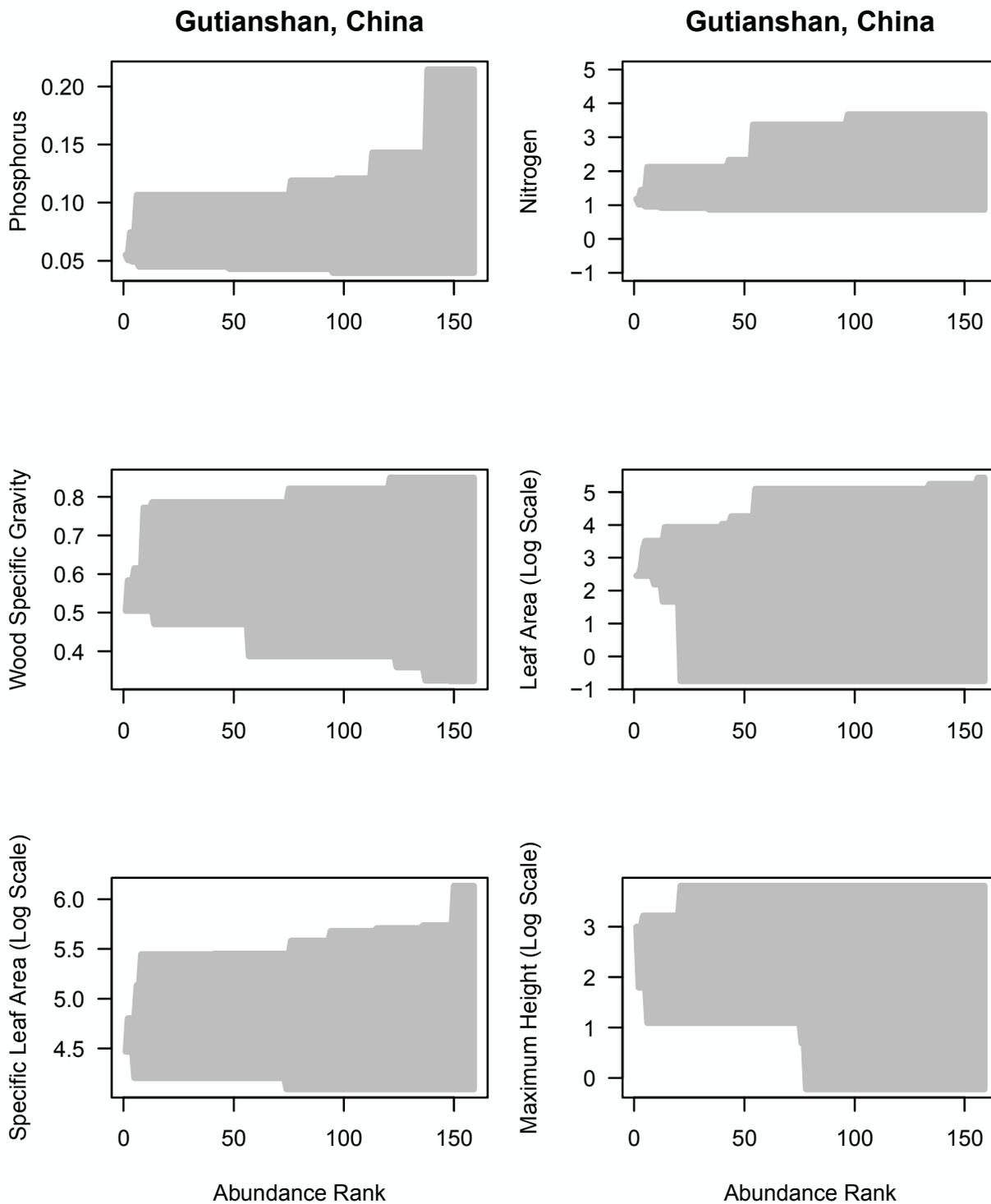
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**Figure B6.** Change in trait ranges for the Guanacaste, Costa Rica forest plot as a function of rank abundance where increasingly rare species are added from left to right.



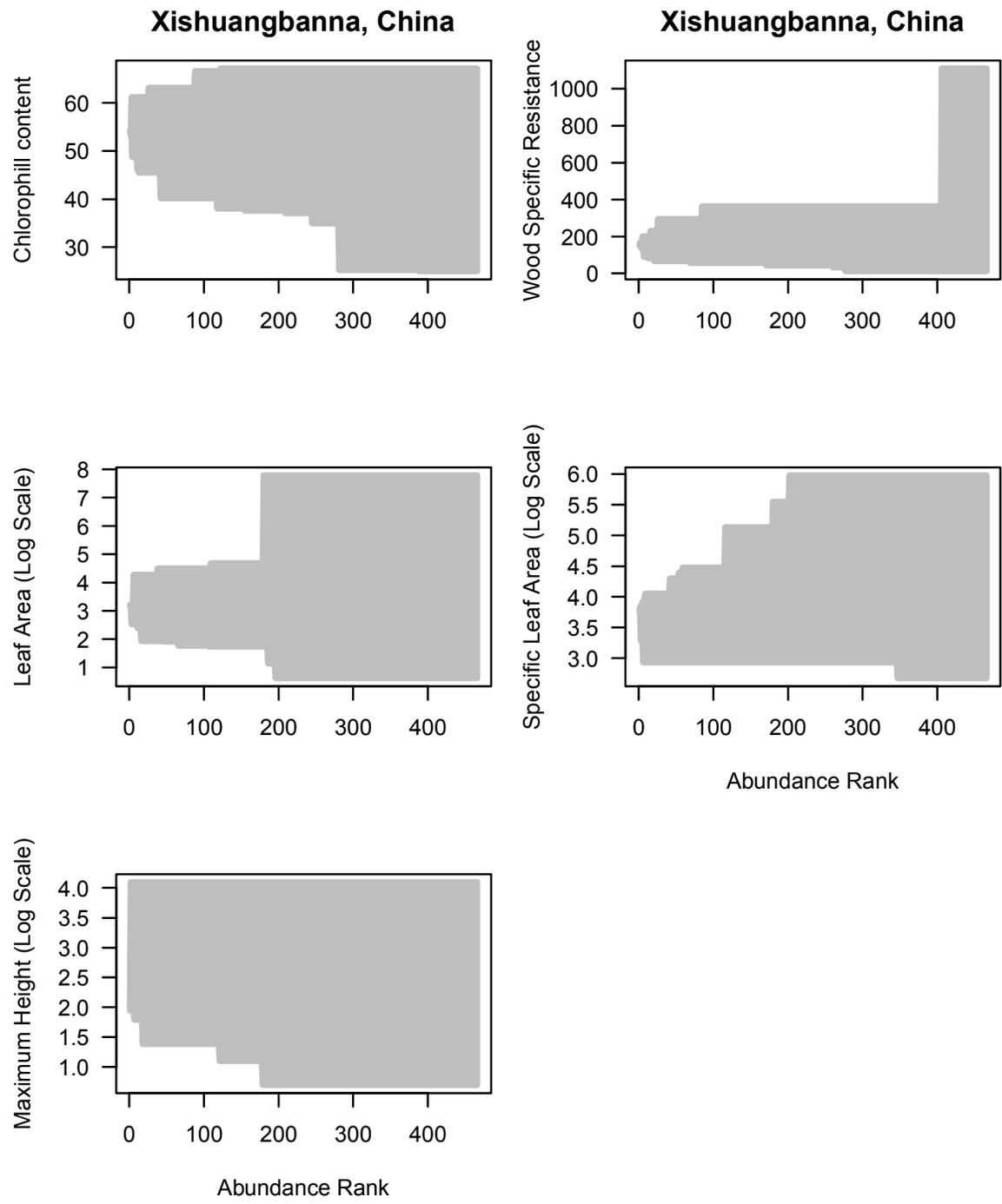
**Figure B7.** Change in trait ranges for the Gutianshan, China forest plot as a function of rank abundance where increasingly rare species are added from left to right.



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**Figure B8.** Change in trait ranges for the Xishuangbanna, China forest plot as a function of rank abundance where increasingly rare species are added from left to right.



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## Supporting Information

### The role of functional uniqueness and spatial aggregation in explaining rarity in trees

María Natalia Umaña, Xiangcheng Mi, Min Cao, Brian J. Enquist, Zhanqing Hao, Robert Howe, Yoshiko Iida, Daniel Johnson, Luxiang Lin, Xiaojuan Liu, Keping Ma, I-Fang Sun, Jill Thompson, Maria Uriarte, Xugao Wang, Amy Wolf, Jie Yang, Jess K. Zimmerman, and Nathan G. Swenson.

#### Appendix C: Supplementary methods and results on elevational data.

##### Contents

1. Methods
2. Results
3. Table C1 Ranges of elevation for each plot.
4. Table C2. Correlations species rank abundance and its preferred elevation.
5. Figures C1-C4. Topography correlations for plots with significant correlations.

##### **Text: Supplementary methods on quantifying whether rare species prefer elevationally rare habitats**

We used fine-scale elevation data in order to evaluate whether the relative abundances of species in a plot were related to the relative abundances of different elevations within each plot. Ideally, additional information regarding light habitats and soil nutrients would be incorporated into our analyses, but at present this information is not available. Further, elevation tends to be a correlate of soil nutrients and water gradients in forest dynamics plots suggesting that it is a reasonable proxy of soil habitats (John *et al.*, 2007).

To accomplish our analyses we utilized the known elevation of each 20 x 20 m subplot in each forest plot. Thus, we obtained a distribution of elevations for each plot. This distribution was then binned every 1, 5 and 10 m. The number of 20 x 20 m subplots per bin represented the relative abundance of the bin. Because bin size decisions may influence the results we utilized three size intervals to quantify sensitivity to our binning decisions. Next, we calculated the elevation of each individual of each species in a plot and estimated the median value. This median value was used to estimate the preferred elevation for the species. The median values were translated into elevation bin numbers. Species and elevation bins were then sorted by their respective relative abundances and plotted against each other with the

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3 rarest species and bin nearest the origin of the  $xy$ -plot. A spearman correlation was  
4 calculated with the expectation that if rare species are rare because they specialize on  
5 rare habitats, then there should be a positive rank correlation.  
6

### 7 8 **Text: Results**

9 The results showed in general no significant correlation between the abundance and  
10 the elevation and only in few cases very weak positive correlation and this was  
11 consistent across bin sizes (Table C1, Table C2, Figures C1-C4). Thus, rare species  
12 generally do not appear to be associated with rare topographic habitats in the forests  
13 we investigated.  
14

### 15 **References**

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17 John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M.,  
18 Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M. & Foster, R.B. (2007)  
19 Soil nutrients influence spatial distributions of tropical tree species. *Proceedings*  
20 *of the National Academy of Sciences USA*, **104**, 864–869.  
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3 **Tables**

4 **Table C1.** Ranges of elevation (in meters) for each plot.

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<b>Plot</b>	<b>Min elevation (m)</b>	<b>Max elevation (m)</b>	<b>Difference</b>
Lilly Dickey Woods, Indiana, U.S.A.	230.03	302.8	72.77
Wabikon Lake, Wisconsin, U.S.A	488	514	26
Changbaishan, China	791.8	809.5	17.7
Fushan, Taiwan	400	1400	1000
Luquillo, Puerto Rico	335	371	36
Guanacaste, Costa Rica	140	779.9	639.9
Gutianshan, China	42.72	57.12	14.4
Xishuangbanna, China	724.4	842.4	118

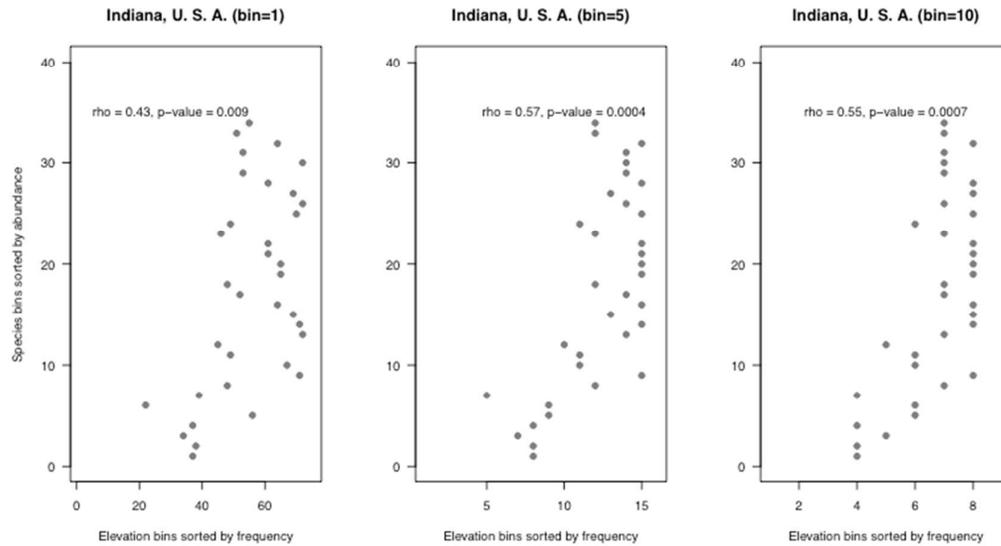
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19 **Table C2.** Correlation between species rank abundance and its preferred elevation.

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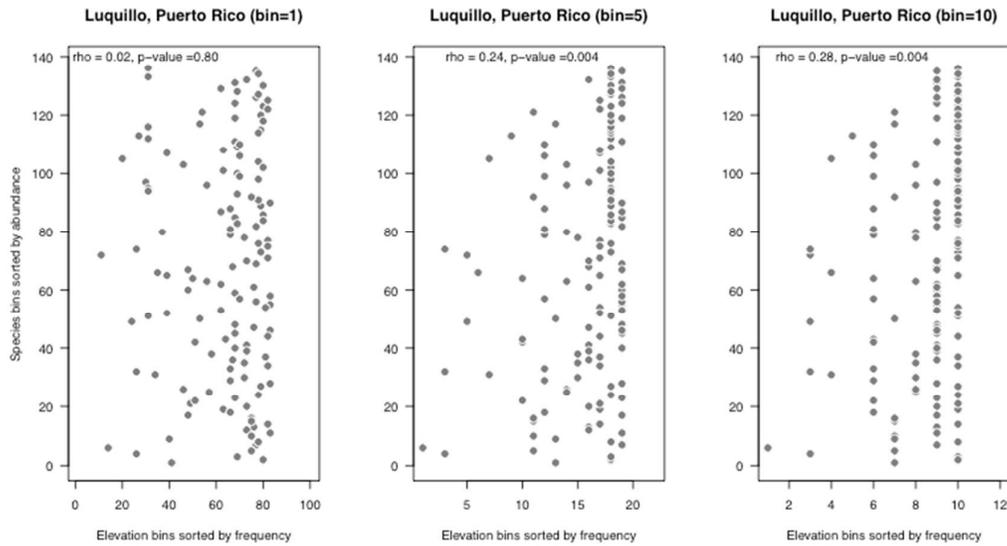
<b>Plot</b>	<b>bin=1</b>		<b>bin=5</b>		<b>bin=10</b>	
	<b>Rho</b>	<b>P-value</b>	<b>Rho</b>	<b>P-value</b>	<b>Rho</b>	<b>P-value</b>
Indiana, USA	0.43	0.01	0.57	<0.001	0.55	<0.001
Wisconsin, USA	0.29	0.07	0.26	0.10	NA	NA
Changbaishan, China	0.28	0.06	0.28	0.05	NA	NA
Fushan, Taiwan	0.15	0.80	-0.1	0.28	-0.05	0.60
Luquillo, Puerto Rico	0.02	0.80	0.24	<0.001	0.28	<0.001
Guanacaste, Costa Rica	0.11	0.15	0.13	0.11	0.39	<0.001
Gutianshan, China	0.16	0.07	0.12	0.12	0.19	<0.001
Xishuangbanna, China	0.1	0.02	0.08	0.06	0.1	0.03

**Figures**

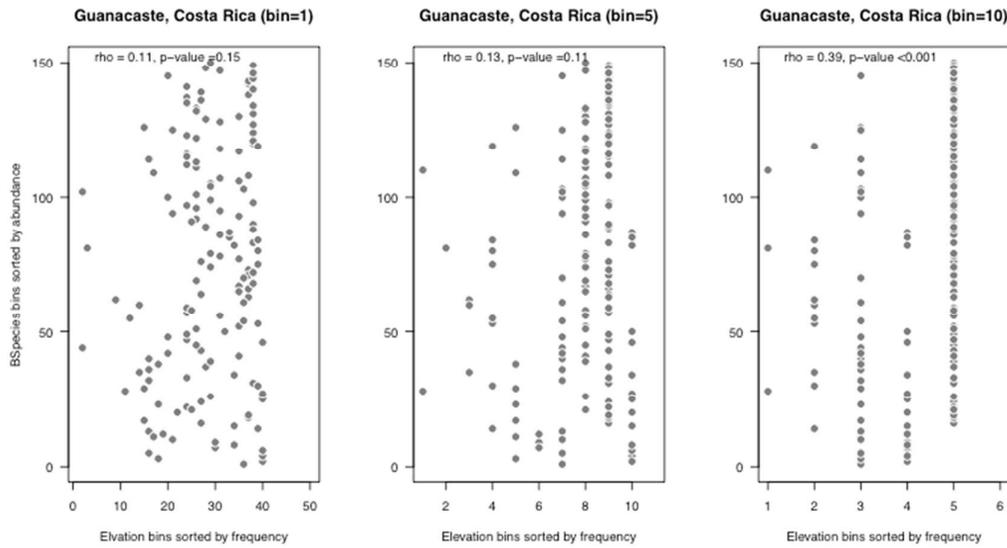
**Figure C1.** The relationship between species rank abundance (y-axis) ordered from rarest to most common and its preferred elevation ranked from the most rare elevation bin to the most common for species in the Indiana, U.S.A. forest plot. The panels represent the three elevation bin sizes used (1m, 5m, and 10m). Spearman rho correlations are provided.



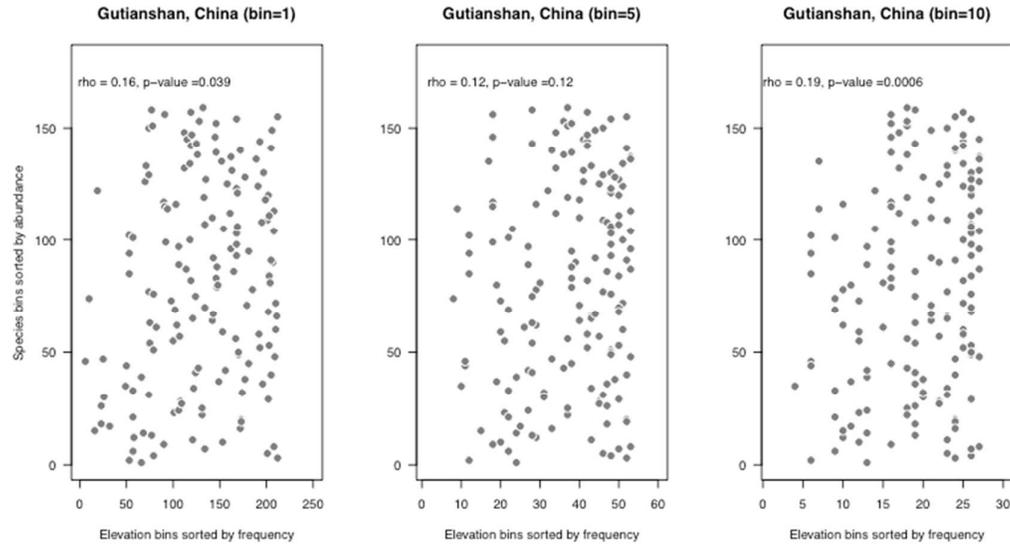
**Figure C2.** The relationship between species rank abundance (y-axis) ordered from rarest to most common and its preferred elevation ranked from the most rare elevation bin to the most common for species in the Luquillo, Puerto Rico forest plot. The panels represent the three elevation bin sizes used (1m, 5m, and 10m). Spearman rho correlations are provided.



**Figure C3.** The relationship between species rank abundance (y-axis) ordered from rarest to most common and its preferred elevation ranked from the most rare elevation bin to the most common for species in the Guanacaste, Costa Rica forest plot. The panels represent the three elevation bin sizes used (1m, 5m, and 10m). Spearman rho correlations are provided.



**Figure C4.** The relationship between species rank abundance (y-axis) ordered from rarest to most common and its preferred elevation ranked from the most rare elevation bin to the most common for species in the Gutianshan, China forest plot. The panels represent the three elevation bin sizes used (1m, 5m, and 10m). Spearman rho correlations are provided.



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