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Shifts in taxonomic and functional composition of trees along rainfall and phosphorus gradients in central Panama

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Abstract

1. Environmental gradients act as potent filters on species distributions driving compositional shifts across communities. Compositional shifts may reflect differences in physiological tolerances to a limiting resource that result in broad distributions for tolerant species and restricted distributions for intolerant species (i.e. a nested pattern). Alternatively, trade-offs in resource use or conflicting species' responses to multiple resources can result in complete turnover of species along gradients.

2. We combined trait (leaf area, leaf mass per area, wood density, and maximum height) and distribution data for 550 tree species to examine taxonomic and functional composition at 72 sites across strong gradients of soil phosphorus (P) and rainfall in central Panama.

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32 **3.** We determined whether functional and taxonomic composition were nested or turned over
33 completely and whether community mean traits and species composition were more strongly
34 driven by P or moisture.

35 **4.** Turnover characterized the functional composition of tree communities. Leaf traits
36 responded to both gradients, with species having larger and thinner leaves in drier and more
37 fertile sites than in wetter and less fertile sites. These leaf trait-moisture relationships
38 contradict predictions based on drought responses and suggest a greater role for differences
39 in light availability than in moisture. Shifts in wood density and maximum height were
40 weaker than for leaf traits with taller species dominating wet sites and low wood density
41 species dominating P-rich sites.

42 **5.** Turnover characterized the taxonomic composition of tree communities. Geographic
43 distances explained a larger fraction of variation for taxonomic composition than for
44 functional composition, and community mean traits were more strongly driven by P than
45 moisture.

46 **6. *Synthesis:*** Our results offer weak support for the tolerance hypothesis for tree communities
47 in central Panama. Instead, we observe functional and taxonomic turnover reflecting trade-
48 offs and conflicting species' responses to multiple abiotic factors including moisture, soil
49 phosphorus, and potentially other correlated variables (e.g. light).

50

51 **Keywords:** Leaf area, maximum height, meta-community analyses, nestedness, specific leaf
52 area, tree species distributions, turnover, wood density. **Introduction**

53 Tree community composition shifts along environmental gradients (Baldeck et al., 2013;
54 Gentry, 1988; Givnish, 1999; Wright, 1992), particularly with changes in precipitation and
55 soil fertility (Condit, Engelbrecht, Pino, Perez, & Turner, 2013; Esquivel-Muelbert et al.,
56 2016; Gentry, 1988; Katabuchi et al., 2017; Vitousek, Porder, Houlton, & Chadwick, 2010).
57 Although many studies have evaluated changes in taxonomic composition along
58 environmental gradients, this provides limited information concerning the strategies and life
59 histories that are optimal in different environments (Enquist et al., 2015; Grime, 2006;
60 McGill, Enquist, Weiher, & Westoby, 2006; Swenson et al., 2012). Examining how different
61 abiotic factors influence both ecological strategies and taxonomic composition of
62 communities offers a holistic approach for understanding the drivers of shifts in tree
63 communities along environmental gradients.

64 Changes in community composition in response to variation in abiotic conditions fall
65 along a continuum, with endpoints of completely nested species distributions or complete

66 turnover in species composition (Baselga, 2010, 2012; Harrison et al., 1992; Leibold &
67 Mikkelsen, 2002). Nested species composition emerges due to variation in physiological
68 tolerances among species. Specifically, the local environment operates as a filter sorting
69 species depending on their ability to withstand local abiotic conditions (Baltzer, Davies,
70 Bunyavejehwin, & Noor, 2008; Keddy, 1992). Thus, species able to tolerate a relatively
71 wide range of conditions would be broadly distributed, while less tolerant species would have
72 relatively restricted distributions, nested within the ranges of widely distributed species. This
73 physiological tolerance hypothesis (Janzen, 1967) predicts that local species richness and
74 functional composition will be determined by how many and which species can tolerate local
75 abiotic conditions. Thus, at the most stressful extreme of the gradient, species richness should
76 be low and functional variation should be small. In contrast, at the least stressful extreme,
77 species richness should be high and functional variation should be broad. This type of nested
78 pattern has been found at the taxonomic level for tropical tree communities distributed along
79 a gradient in drought seasonality in the Amazon (Esquivel-Muelbert et al., 2016). However,
80 studies testing for nested composition within a functional framework are largely lacking.

81 In contrast to nested distributions, species and functional composition may show
82 complete turnover across environmental gradients, with species replaced by others from one
83 site to the next along the gradient (Engelbrecht et al., 2007; Pitman et al., 2002; Swenson,
84 Anglada-Cordero, & Barone, 2011). This pattern might emerge as a result of life-history
85 trade-offs, such as tolerance to low resource conditions versus competitive ability under high
86 resource conditions. For example, along light gradients, shade-tolerant species often survive
87 well under low light but are outcompeted by light-demanding species under high light
88 (Brokaw, 1987). Such trade-offs between performance at high vs. low levels of a single
89 resource can generate turnover in species composition along a resource gradient, as well as
90 turnover in functional traits that underlie differences in life-history strategies.

91 Turnover might also result from simultaneous variation in responses to several
92 resources. Abiotic variables often co-vary in space, creating contrasting gradients of resource
93 availability (e.g. sites having low availability of one resource, but high availability of another
94 resource). For example, in the tropics, sites with high rainfall tend to have low nutrient
95 availability due to leaching (Campo, Jaramillo, & Maass, 1998; Vitousek & Chadwick,
96 2013), which generates gradients from high nutrient/low rainfall to low nutrient/high rainfall
97 sites. When a species cannot tolerate both low nutrient and low water availability (i.e., the
98 two extremes of the gradient), conflicting stresses may select for trade-offs between the
99 ability to tolerate these two different low resource states. In this case, we may observe a

100 replacement of species along the gradient that is the outcome of some species being restricted
101 to dry sites and other species restricted to nutrient-poor sites. While turnover in species
102 composition is likely driven by whole plant responses to multiple resources, individual
103 functional traits are likely to enhance performance with respect to specific limiting resources.
104 This may lead to discrepancies between patterns of taxonomic and functional composition
105 along environmental gradients. Examining such discrepancies may provide a more
106 mechanistic understanding of how environmental variables drive spatial variation in plant
107 community composition.

108 Gradients in environmental variables can also lead to gradients in biotic variables. For
109 example, deciduousness declines with increasing rainfall intensifying competition for light in
110 the understory of wetter forests (Brenes-Arguedas, Broddy, Coley, & Kursar, 2011). Pest
111 pressure also varies with rainfall (e.g., Weissflog et al. 2018). Thus, shifts in functional
112 composition across environmental gradients may reflect responses not only to changes in
113 multiple abiotic variables but also to changes in biotic interactions.

114 In this study, we explore how taxonomic and functional composition changes over
115 two-fold moisture and 300-fold soil phosphorus (P) gradients extending over the 65 km
116 between the Pacific and Caribbean coasts of central Panama. There is a modest relationship
117 between local moisture and P availabilities ($r^2=0.30$), allowing us to disentangle the effects of
118 variation in these two critical resources (Condit et al., 2013). Both environmental factors
119 have significant effects on plant species distributions (Condit et al., 2013; Engelbrecht et al.,
120 2007; Prada et al., 2017; Turner, Brenes-arguedas, & Condit, 2018). We focus on four
121 functional traits that reflect resource acquisition strategies and have been linked to responses
122 to water and soil nutrient variation at the global scale: leaf mass per area (LMA), wood
123 density (WD), leaf area (LA), and maximum height MH) (Table 1). Using data on these four
124 functional traits, combined with data on the distribution of 550 lowland tropical tree species
125 across 72 plots spanning the regional-scale gradients in moisture and soil P in central
126 Panama, we ask:

127 (1) Are species' distributions nested along the moisture and soil P gradients or do species
128 exhibit turnover along these gradients? Do changes in functional composition across these
129 gradients follow the same pattern as taxonomic composition?

130 Given the observed strong species-level responses to both moisture and soil P
131 gradients in this system (Condit et al., 2013; Engelbrecht et al., 2007), we predicted that
132 species turnover should play a larger role in determining patterns of taxonomic beta diversity
133 in this system. For individual functional traits, we predicted that, if specific traits determine

134 species tolerances, then certain trait values would be filtered out at low resource sites (dry or
135 low-P sites), but not at less stressful sites (wet or rich-P sites). In this case, low resource sites
136 would possess a subset of the species with trait values that confer tolerance and therefore a
137 narrower range of functional trait values compared to higher resources sites, resulting in a
138 nested pattern of functional composition.

139 (2) Does moisture or soil P availability have a stronger influence on taxonomic and
140 functional composition?

141 We predicted that moisture and soil P would be similarly important for driving
142 taxonomic composition, given that individual species distributions have been shown to
143 respond strongly to both water and soil P availability in this region (Condit et al., 2013). For
144 functional composition, we predicted that moisture would be a stronger driver for wood
145 density and maximum height because species with lower wood density and larger maximum
146 size tend to be more susceptible to drought (Bennett, McDowell, Allen, & Anderson-
147 Teixeira, 2015; Falster & Westoby, 2005; Koch, Stillet, Jennings, & Davis, 2004; O'Brien et
148 al., 2017; Ryan & Yoder, 1997). For leaf traits, we expected that both moisture and soil P
149 should explain a high percentage of functional variation in LA and LMA (Shields, 1950;
150 Wright, Westoby, & Reich, 2002).

151 Addressing these questions reveals whether functional trait-environment relationships
152 underlie patterns of species distributions and changes in taxonomic community composition
153 along the moisture and soil P gradients spanning central Panama. Using four traits important
154 for different functions (see Table 1) offers new insights into the interplay of multiple
155 functions in response to complex resource gradients. More broadly, we seek a more
156 mechanistic understanding of species and community responses to shifts in abiotic conditions
157 along environmental gradients.

158

159 **Methods**

160 *Study area*

161 We used tree species occurrence data for individuals ≥ 1 cm DBH distributed across the
162 Isthmus of Panama. Forty sites contained 1-ha plots in which all individuals were tagged and
163 identified, yielding data on species presence/absence and abundance. At the remaining 32
164 sites, all species were recorded in 1-day surveys, but individuals were not counted and
165 therefore only presence/absence data were available. The sites are arranged along moisture
166 and soil P gradients that extend from the Caribbean Sea to the Pacific Ocean in forests near
167 the Panama Canal with a total range in mean annual temperature of 23.0 and 26.1°C (Condit

168 et al., 2013) (Figure 1). Of the 890 species recorded, 779 (87%) were identified to species, 88
169 to genus, and 23 remained unidentified. We used 550 species that were fully identified,
170 present in at least three of the 72 sites and that had data for at least one of the four functional
171 traits.

172

173 *Moisture and soil resin P predictors*

174 To estimate drought stress at each site, we used the dry-season moisture deficit index (D_m)
175 described by Condit et al. (2013), which is a measure of the difference between precipitation
176 and potential evapotranspiration. The precipitation information was obtained from 47 gauges
177 distributed along the Panama Canal. The evapotranspiration information was obtained from
178 Barro Colorado Island and corrected for elevation (Condit et al., 2013). For P, we used
179 information on soil resin P that quantifies the amount of inorganic phosphate available to
180 trees. Soil resin P (henceforth soil P) was determined for anion-exchange membranes placed
181 in the upper 10 cm of the soil profile during the wet season (Condit et al., 2013; Turner et al.,
182 2018; Turner & Romero, 2009). The dry-season moisture deficit index ranged from -579 mm
183 to -370 mm (Figure 1). Soil P ranged from 0.07 mg P kg⁻¹ to 22.80 mg P kg⁻¹ (Figure 1).

184

185 *Functional traits*

186 We measured LMA (g m⁻²) and LA (cm²) for leaves collected from adult individuals (~3
187 individuals per species) located close to the Barro Colorado Island (BCI) 50-ha forest
188 dynamics plot (9.15°, -79.85°) or to canopy cranes in the Bosque Protectora San Lorenzo
189 (9.27°, -79.98°) and the Parque Natural Metropolitano (8.99°, -79.54°). These three sites are
190 located near the center and the wet Caribbean and dry Pacific ends of the rainfall gradient,
191 respectively. Fully expanded and sun exposed leaves were collected from canopy branches.
192 Leaf area was calculated for entire leaves. MH (mm) was measured for up to the six largest
193 individuals of each species in the BCI 50-ha plot. WD (g cm⁻³) was measured from adult
194 individuals (~5 individuals per species) located within 15 km of the BCI 50-ha plot. Wright
195 et al. (2010) describe methods for all traits fully. We obtained WD for 58 species from a
196 global dataset (<http://wooddensity.univ-tlse3.fr/#about>). When species-level wood density
197 data were unavailable, we substituted genus or family means (20 and 7% of the species
198 respectively). Data were available for 67%, 65%, 76%, and 100% of the 550 species for
199 LMA, LA, MH, and WD, respectively. Table S1 lists the proportion of species for which data
200 were available for each site used in the analyses. Table S2 shows all pairwise correlations
201 between traits.

202

203 *Analyses*

204 Functional and taxonomic beta diversity – We implemented the framework of Baselga
205 (Baselga, 2010, 2012) to disentangle the contributions of turnover and nestedness for changes
206 in taxonomic and functional composition along the moisture and soil P gradients. Baselga
207 (2010) decomposed taxonomic beta diversity (β_{sor}) into two additive components due to
208 turnover (β_{sim}) (replacement) and nestedness (β_{nes}), such that $\beta_{\text{sor}} = \beta_{\text{sim}} + \beta_{\text{nes}}$. β_{sor} is calculated
209 as the Sørensen index and β_{sim} is calculated as the Simpson dissimilarity index.

210 We first assessed the turnover and nestedness components at the meta-community-
211 level calculating multiple-site dissimilarity using the functions ‘betapart.core’ and then ‘beta-
212 multi’ from package ‘betapart’ version 1.5.1 (Baselga & Orme, 2012). The meta-community-
213 level analysis reveals the relative contribution of turnover vs. nested to beta diversity across
214 this region, but not the degree to which such patterns are related to environmental gradients.
215 Therefore, we then examined if there was a relationship between the degree of turnover for a
216 given pair of plots and the difference in moisture, soil P, and geographic distance (pair-wise
217 environmental analysis). To do this we first calculated taxonomic dissimilarity (turnover)
218 between all pairs of plots along the gradients, again using the functions ‘betapart.core’ and
219 ‘beta.pair’. Next, we evaluated changes in taxonomic dissimilarity between pairs of plots
220 with moisture or soil P, accounting for geographic distance using partial Mantel tests, with
221 the function ‘mantel.partial’ in the package ‘vegan’ version 2.5-6 in R (Oksanen et al., 2019).

222 We extended this framework to functional beta diversity by decomposing the UniFrac
223 metric in turnover and nestedness components in the same way as described above (Baselga,
224 2010, 2012; Swenson, 2014). Unifrac is a distance-based metric that uses trait dendrograms
225 and quantifies the fraction of the dendrogram that is shared between two communities. To
226 calculate functional nestedness and turnover, we used a modification of the function
227 ‘betapart.core’ from package ‘betapart’ (see code in Supplementary Methods). Since
228 functional beta diversity and species richness might be correlated, we implemented a null
229 model to determine whether shifts in functional beta diversity were higher or lower than
230 expected given observed species richness (see Supplementary Methods for details). The
231 standardized values of beta diversity were then used to evaluate whether changes in
232 standardized beta diversity were related to dissimilarity in moisture and soil P accounting for
233 geographic distance, using partial Mantel tests as described above. We compared
234 standardized and non-standardized beta diversity results to examine whether the shifts in

235 functional dissimilarity along both gradients were mainly associated with shifts in species
236 richness.

237

238 Shifts in community mean trait values along the gradients – We used community mean trait
239 values (CM) to quantify community functional structure. We calculated CM with species
240 weighted equally for all 72 plots. We also calculated community weighted mean trait values
241 (CWM) with species weighted by their abundances for the 40 plots with abundance data.
242 However, we focus on the non-weighted metric to make our results comparable to Condit et
243 al. (2013).

244 To examine changes in CM values along the moisture and soil P gradients, we fit
245 separate linear models for each trait where the response variable was CM and the predictor
246 variables were D_m and soil P. We also fit models using CWM for the subset of sites that had
247 species abundance information.

248

249 Contribution of spatial and environmental factors – We used variance partitioning analyses
250 (Legendre, 2008; Legendre, Borcard, & Peres-Neto, 2005) to assess the relative contributions
251 of moisture, soil P, and space (i.e. the geographic distance between sites) to differences in
252 community mean trait values and taxonomic composition (see Supplementary Methods for
253 details).

254

255 All analyses were performed in R version 3.6.1 (R team project 2017).

256

257 **Results**

258 Taxonomic beta diversity – Meta-community level analyses showed that shifts in taxonomic
259 composition were mostly the result of turnover and less due to nestedness ($\beta_{sim} = 0.96$, $\beta_{nes} =$
260 0.014). In the pair-wise environmental analysis, we found a significant increase in taxonomic
261 turnover with dissimilarity in both moisture and soil P (Table 2).

262

263 Functional beta diversity – Meta-community level analyses showed that shifts in functional
264 composition were mostly determined by turnover and less by nestedness ($\beta_{simWD} = 0.97$,
265 $\beta_{nesWD} = 0.002$; $\beta_{simMH} = 0.97$, $\beta_{nesMH} = 0.002$; $\beta_{simLMA} = 0.97$, $\beta_{nesLMA} = 0.004$; $\beta_{simLA} = 0.97$,
266 $\beta_{nesLA} = 0.003$). For pair-wise environmental analysis, we found that comparisons for non-
267 standardized functional beta diversity showed that functional turnover increased with
268 moisture dissimilarity for WD and LMA and increased with soil P for WD and MH (Table

269 2). However, when using standardized values of functional turnover along the soil P and
270 moisture gradients, these relations were not significant (Table 2).

271

272 Shifts in community mean trait values along the gradients – Relationships between moisture
273 availability and CM trait values were significantly positive for LMA and MH, significantly
274 negative for LA, and not significant for WD (Figure 2, Table S3). For the subset of plots with
275 species abundance data, relationships between moisture availability and CWM trait values
276 were significantly negative for LA and not significant for LMA, MH, and WD (Figure S1).

277 Relationships between soil P availability and CM trait values were significantly
278 negative for LMA and WD, significantly positive for MH and not significant for LA (Figure
279 2, Table S3). Relationships between soil P and CWM trait values were significantly negative
280 for LMA, significantly positive for MH and not significant for WD and LA (Figure S2).

281

282 Contribution of spatial and environmental factors – Soil P alone explained a larger percent of
283 variation than moisture availability for community means of WD, LMA, and MH, as well as
284 for taxonomic composition. In contrast, moisture availability explained more variation in
285 community mean LA. Space alone explained a smaller percentage of variation in functional
286 trait means (0-6%) compared to taxonomic composition (13%) (Figure 3). Table S4 gives the
287 total percentage of variation explained by each trait.

288

289 **Discussion**

290 We examined changes in taxonomic and functional composition of tree communities
291 distributed along moisture and soil P gradients in Panama. These changes are dominated by a
292 replacement of species and functional trait values (turnover) rather than nestedness. We
293 hypothesize that species are unable to tolerate the full range of both moisture availability and
294 soil P observed across our sites preventing nested taxonomic distributions. Likewise, we
295 hypothesize that functional tradeoffs prevent nested distributions of functional traits across
296 the moisture and soil P gradients. In addition, we observed significant shifts in community
297 mean traits along both gradients, with the strength of these functional responses varying
298 among traits (WD, LMA, LA, and MH) and resources (either moisture or soil P). Combined
299 these results suggest that shifts in species and functional composition are not dominated by a
300 single abiotic factor, but that instead, moisture, soil P, and possibly other factors generate
301 conflicting responses at both the individual trait and whole species levels.

302

303 *Dominance of taxonomic and functional turnover*

304 At the meta-community level, we found a prevalence of functional and taxonomic turnover
305 suggesting the simultaneous action of multiple environmental constraints generating
306 conflicting responses on species and their traits. This is consistent with results reported by
307 Condit et al. (2013), who found strong species-specific associations with both high and low
308 soil P and moisture levels, and provides further insights into the functional responses
309 underlying these compositional shifts. The integration of functional trait information
310 indicated that the extremes of the gradient that are either limiting in P or in water constrain
311 the number of species able to persist at those sites generating the observed functional
312 turnover. These results agree with the idea of environmental harshness as the main factor
313 limiting species richness via restrictions in species ranges (Kleidon & Mooney, 2000), with
314 restricted species distributions resulting from multiple environmental stressors.

315 Our results contrast with taxonomic nestedness along a pronounced seasonal drought
316 gradient in the Western Amazon (Esquivel-Muelbert et al., 2016) and with nested
317 distributions of plant growth forms with respect to soil fertility in lowland forests of South
318 America (Gentry & Emmons, 1987). We suggest that this discrepancy is related to variation
319 among study systems in the strength of abiotic filters and the length of the gradients, as well
320 as differences in the factors that co-vary with the environmental gradients being studied
321 (Ruokolainen et al., 2002). For example, the range of variation in soil P across the studied
322 gradient in Panama is larger than the range reported for the lowland Amazon forest (Quesada
323 et al., 2010). Also, in a tropical dry forest in Florida, temperature was detected as a major
324 factor driving nested taxonomic patterns for tree communities (Ross, Sah, Ruiz, Spitzig, &
325 Subedi, 2016).

326

327 *Functional turnover in response to moisture*

328 We examined whether the degree of functional turnover in pair-wise comparisons across all
329 plots was related to dissimilarity in environment (i.e., moisture or soil P) accounting for
330 spatial distance (pair-wise environmental analysis). We found evidence for functional
331 turnover of LMA and WD along the moisture gradient (Table 2). However, these patterns
332 disappear when we account for differences in species richness suggesting that a great part of
333 the observed directional trends in functional turnover along the moisture gradient are the
334 result of differences in species richness (Table 2).

335 At the same time, when examining community mean (CM) trait values, we found that
336 leaf traits and maximum stature (MH) respond significantly to dry-season severity. Species

337 with higher LMA, lower LA, and taller MH are more prevalent in wetter sites. While the
338 results for MH agree with our predictions, the leaf trends contradict the pattern expected by
339 environmental filtering due to drought (e.g. more conservative leaf traits in drier sites)
340 (Figure 2, Table S3). We believe this is due to additional factors that co-vary with moisture.
341 For example, in our study system, light availability varies along the moisture gradient, with
342 wet sites being more light-limited than dry sites due to more dense canopies, fewer drought-
343 deciduous species, and more cloudy days (Brenes-Arguedas, Roddy, & Kursar, 2013). This
344 variation in light should play an important role in determining photosynthetic strategies of
345 plants and, therefore, should influence traits involved in light-use strategies (Brenes-
346 Arguedas et al., 2013). Similarly, pest pressure might contribute to the observed shifts in leaf
347 traits given that pathogens and herbivores vary along environmental gradients and influence
348 species distributions and diversity (Brenes-Arguedas, Coley, & Kursar, 2009; Fine, Mesones,
349 & Coley, 2004; Gaviria & Engelbrecht, 2015). Pest pressure is also thought to be stronger in
350 wetter sites (Givnish, 1999; Leigh et al., 2004) (but see Weissflog, Markesteijn, Lewis,
351 Comita, & Engelbrecht, 2018) and should lead to leaves with higher LMA to deter herbivore
352 attack (Poorter et al., 2009). Thus, our results suggest that the observed functional turnover
353 along the rainfall gradient may be predominantly driven not by moisture directly but by
354 variation in light availability and/or pest pressure along the gradient. Given the modest
355 correlation between moisture and soil P ($r^2 = 0.30$), functional changes along the moisture
356 gradient may also be weakly influenced by soil P availability (see below).

357 An additional, but not mutually exclusive explanation for the observed trends in leaf
358 traits is that many species in dry sites respond via drought avoidance strategies such as
359 dropping their leaves during the dry season to minimize water loss (Brenes-Arguedas et al.,
360 2013; Comita & Engelbrecht, 2014; Markesteijn & Poorter, 2009). These deciduous species
361 tend to have thin leaves characterized by low LMA and are more dominant in dry sites
362 (Eamus, 1999). In fact, across our study sites, we find a higher predominance of deciduous
363 species at drier than at wetter sites (Figure S3), which may also contribute to the observed
364 trends in leaf traits.

365 366 *Functional turnover in response to soil P*

367 We found that functional turnover for WD and MH increases along the soil P gradient when
368 accounting for differences in spatial distance (Table 2). However, as with moisture, these
369 trends disappear when accounting for differences in species compositional turnover (Table

370 2). Combined, these results indicate that the directional changes in observed functional
371 turnover across the soil P gradient are largely due to changes in taxonomic richness.

372 We also examined if there were directional trends in community-level trait means
373 (CM) along the soil P gradient. We found significant shifts in community mean traits, with
374 species having more conservative resource-use strategies (i.e., high LMA high WD) at sites
375 with lower soil P (Figure 2). The decreasing trend of LMA towards high soil P sites may be
376 explained by the distribution of deciduous species, which tend to have acquisitive strategies,
377 and increased in proportion towards high soil P sites (Figure S4). Similar negative
378 relationships between LMA and soil P have been found in previous studies (Fyllas et al.,
379 2009; Hidaka & Kitayama, 2011; Reich, Uhl, Walters, & Ellsworth, 1991), but, in most
380 cases, the relationships reported are modest (reviewed by Poorter et al. 2009). We suggest
381 these differences in the responses to soil P are related to the variation in the magnitude of the
382 variation in soil P along gradients. In the case of the gradient in central Panama, soil P varies
383 300-fold across sites and is a key environmental factor influencing species distributions in
384 this region (Condit et al., 2013; Prada et al., 2017; Zalamea et al., 2016). Thus, soil P appears
385 to be a major factor determining ecological strategies of species related to LMA in this
386 system. Species with low LMA exhibit acquisitive resource-use strategies (Wright et al.,
387 2004) and may be at a competitive advantage over species with high LMA under high soil P
388 conditions.

389 In addition to the results for leaf traits, we found that CM for WD and MH were also
390 related to the soil P gradient, with harder wooded and shorter species characterizing less
391 fertile sites. This result agrees with our predictions and with previous studies across other
392 Neotropical lowland forests that found negative correlations between WD and soil fertility
393 (Muller-Landau, 2004; Patiño et al., 2009). Low soil fertility may favor species exhibiting
394 resource conservative life-history strategies (i.e., high WD) that are more tolerant to adverse
395 conditions.

396

397 *Explained variation in taxonomic and community mean functional composition along the*
398 *environmental gradient*

399 Among all traits analyzed, CM leaf traits showed the strongest responses to both moisture
400 and soil P gradients, with variation in LA mainly associated with the moisture gradient and
401 LMA mainly associated with soil P. These results were also reflected in the variance
402 partitioning analyses where variation in CM LMA was better explained by the soil P
403 gradient, and variation in CM LA was better explained by the moisture gradient (Figure 3).

404 WD and MH showed less dramatic shifts in our study system and had lower percentages of
405 variance explained by both gradients (between 0 to 10%). Combined, our results indicate that
406 variation among sites in mean functional traits is more strongly driven by deterministic
407 factors associated with moisture and soil P than by spatial location of plots alone (Figure 3).
408 This indicates that functional composition of tree communities in central Panama is strongly
409 determined by environmental filters that change over space. In terms of taxonomic
410 composition, we found that soil P explained a higher percentage of variance (5%) than
411 moisture (1%). Condit et al. (2013) found that moisture was a stronger predictor of species
412 distributions than soil P in central Panama, but this discrepancy may be due to differences in
413 statistical approaches (e.g. community vs. individual species level analyses). Also, space
414 explained a larger percentage of variance in taxonomic composition than for functional trait
415 composition, suggesting that there are additional factors, such as dispersal limitation, that
416 drive shifts in species composition but that may be less important for shaping functional
417 composition. Ultimately, we found that soil P and moisture explained relatively small
418 amounts of taxonomic variation (~ 13% combined) (Figure 3 and Table S4), suggesting that
419 additional environmental factors likely also contribute to the observed taxonomic turnover.

420

421 *Caveats*

422 While the present study offers a comprehensive examination of the effects of resource
423 gradients on functional composition of tree communities in central Panama, there are several
424 caveats. First, although the trait data used in the study represent the most complete dataset
425 available, information is missing for ~35 % of species for at least one trait. Most of the
426 species missing trait information are rare, with restricted distributions in wet and infertile
427 sites (Figure S5). This missing information could have a sizeable effect on community-level
428 and functional turnover results obtained, particularly given that previous studies have shown
429 that rare species can make an important contribution to local functional diversity (Leitaõ et
430 al., 2016; Umaña et al., 2017). For example, functional turnover results were mostly
431 significant for WD (Table 2), which was the only trait with information for all species in the
432 dataset. However, CM trait relationships remained consistent when we excluded plots with
433 leaf trait data for less than 30% of species (Table S5). Nonetheless, collecting trait data for
434 rare species at wet and infertile sites along these gradients should be a priority for future
435 studies of functional composition and diversity. Further, we only considered a handful of
436 aboveground traits that might not represent the multifunctional nature of tree species. Root
437 traits should provide further insights into species and functional responses to belowground

438 resources (Zemunik, Turner, Lambers, & Laliberté, 2015). Finally, we did not consider
439 intraspecific trait variation, even though trait variation within species can be substantial
440 (Albert et al., 2010; Messier, McGill, & Lechowicz, 2010; Siefert et al., 2015; Umaña,
441 Zhang, Cao, Lin, & Swenson, 2018).

442

443 *Conclusion*

444 Changes in functional and taxonomic composition of tree communities along environmental
445 gradients result from the simultaneous influence of multiple factors on tree species. Our
446 results reveal that shifts in species composition over these gradients are dominated by a
447 replacement of species and functional trait values instead of nestedness, which suggests
448 conflicting responses of species and their traits to different factors. In addition, we found that
449 despite considerable variation in rainfall and previously documented strong species'
450 responses to seasonal drought (Condit et al., 2013; Engelbrecht et al., 2007), community-
451 level responses in leaf traits did not match the expected patterns. Instead, soil P appears to be
452 a main determinant of community mean leaf trait distributions. Finally, variation in moisture
453 and soil P explained a higher percentage of variation for CM leaf traits than for WD and MH,
454 suggesting that leaf traits are more strongly shaped by these gradients than the other traits. A
455 full understanding of the underlying mechanisms driving shifts in tree community
456 composition along gradients will require accounting for multi-dimensional responses of
457 species to multiple factors that simultaneously co-vary along gradients and exert potent
458 selective forces.

459

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467

468 **Authors' contributions**

469 MNU and LSC conceived the idea. RC, RP, BT, SJW collected the data. MNU analyzed and
470 wrote the first draft of the manuscript with input from LSC. All authors contributed critical
471 comments on drafts.

472

473 **Data accessibility**

474 Survey and census data are available from Dryad: Condit, Richard; Pérez, Rolando; Aguilar,
475 Salomón; Lao, Suzanne (2019), Census data from 65 tree plots in Panama, 1994-2015,
476 DataONE, Dataset, <https://doi.org/10.15146/mdpr-pm59>. Condit, Richard et al. (2019), BCI
477 50-ha Plot Taxonomy, v4, DataONE, Dataset, <https://doi.org/10.15146/R3FH61>

478

479 Trait data is available from Dryad and TRY or through previously published archives:
480 maximum height (Dryad, <https://doi.org/10.5061/dryad.85k53v8>), wood density and LMA
481 (supplementary files from Wright et al, 2010), and LA (from try-db.org, Panama trait
482 databased by S.J. Wright, database ID 112).

483

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704 TABLES

705 Table 1. Functional trait descriptions and expected functional responses to moisture and soil
706 P gradients.

Trait	General description	Expected response for drier sites	Expected response for infertile sites	References
WD: Wood density (g cm ⁻³)	Trade-offs between mechanical stability and transport efficiency and safety	High wood density trees are less susceptible to drought	High wood density trees display conservative resource use strategies that allow them to succeed in infertile conditions	(Chave et al. 2009, Heineman et al. 2016)
MH: maximum height (m)	Competitive ability for light	Taller trees are more susceptible to drought	Maximum tree height increases with nutrient supply	(Ryan and Yoder 1997b, Koch et al. 2004, Givnish et al. 2014, Bennett et al. 2015)
LMA: leaf mass per area (g m ⁻²)	Trade-off between carbon acquisition and conservation	Species with high LMA are more conservative in carbon use and better tolerate drought	Species with high LMA survive better in infertile soils	(Wright et al. 2002, 2004, Greenwood et al. 2017)
LA: Leaf area (cm ²)	Display area for capturing light and transpiration.	Smaller LA and transpirational	Unknown	(Shields 1950, Ashenden

area are 1978,
 advantageous Poorter and
 in dry Rozendaal
 conditions 2008)

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Table 2. Partial mantel tests to evaluate relationships between taxonomic or functional turnover (β_{sim}) and dissimilarity in moisture, or soil P while controlling for geographic distance. Bold numbers indicate significant relationships ($\alpha = 0.05$). WD – wood density, MH – maximum height, LMA – leaf mass per area, LA – leaf area, SES – standardized effect size.

	Turnover	
	Moisture	P(resin)
Taxonomic	0.329	0.204
WD	0.205	0.181
MH	-0.007	0.232
LMA	0.307	0.105
LA	-0.098	0.141
SES WD	0.043	0.090
SES MH	0.001	-0.018
SES LMA	-0.012	-0.002
SES LA	0.016	0.003

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FIGURE LEGENDS

Figure 1. Map of Panama showing the distribution of sites along the moisture and soil resin P gradients. A) Shows the study site location in Panama. B) shows a regional map where dark blue represents wetter sites, while red represents drier sites. C) shows a regional map where red represents sites rich in soil resin P, while yellow represents sites poor in soil resin P. Triangles indicate plots with abundance data and circles indicate plots with occurrence data.

Figure 2. Relationships between community mean (CM) trait values and dry-season moisture deficit (D_m) (top row) and soil resin P (bottom row) across 72 sites in Panama. Units are g

725 cm^{-3} for wood density, m for maximum height, g m^{-2} for leaf mass per area, and cm^2 for leaf
726 area. The lines show significant relationships and the shaded area represents the 95%
727 confidence intervals ($\alpha = 0.05$).

728

729 **Figure 3.** Percentages of variation in community mean trait values (WD, wood density; MH,
730 maximum height; LMA, leaf mass per area; LA, leaf area) and taxonomic composition (SP)
731 explained by soil resin P, dry season moisture deficit index (D_m) and space (Spatial). The
732 combined effects of soil resin P, D_m and/or space explain percentages enclosed by two or
733 three circles.

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