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1 Seasonal drought limits tree species across the Neotropics

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74

ABSTRACT

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Within the tropics, the species richness of tree communities is strongly and positively associated with precipitation. Previous research has suggested that this macroecological pattern is driven by the negative effect of water-stress on the physiological processes of most tree species. This process implies that the range limits of taxa are defined by their ability to occur under dry conditions, and thus in terms of species distributions it predicts a nested pattern of taxa distribution from wet to dry areas. However, this ‘dry-tolerance’ hypothesis has yet to be adequately tested at large spatial and taxonomic scales. Here, using a dataset of 531 inventory plots of closed canopy forest distributed across the Western Neotropics we investigated how precipitation, evaluated both as mean annual precipitation and as the maximum climatological water deficit, influences the distribution of tropical tree species, genera and families. We find that the distributions of tree taxa are indeed nested along precipitation gradients in the western Neotropics. Taxa tolerant to seasonal drought are disproportionately widespread across the precipitation gradient, with most reaching even the wettest climates sampled; however, most taxa analysed are restricted to wet areas. Our results suggest that the ‘dry tolerance’ hypothesis has broad applicability in the world’s most species-rich forests. In addition, the large number of species restricted to wetter conditions strongly indicates that an increased frequency of drought could severely threaten biodiversity in this region. Overall, this study establishes a baseline for exploring how tropical forest tree composition may change in response to current and future environmental changes in this region.

96 **Introduction**

97 A central challenge for ecologists and biogeographers is to understand how climate
98 controls large-scale patterns of diversity and species composition. Climate-related gradients in
99 diversity observed by some of the earliest tropical biogeographers, including the global
100 latitudinal diversity gradient itself (e.g. von Humboldt 1808, Wallace 1878), are often
101 attributed to the physiological limitations of taxa imposed by climate conditions (e.g.
102 Dobzhansky 1950). This idea is expressed in the ‘physiological tolerance hypothesis’ (Currie
103 et al. 2004, Janzen 1967), which posits that species richness varies according to the tolerances
104 of individual species to different climatic conditions. Thus, species able to withstand extreme
105 conditions are expected to be widely distributed over climatic gradients, while intolerant
106 species would be constrained to less physiologically challenging locations and have narrower
107 geographical ranges. An implicit assumption of this hypothesis is that species’ realized niches
108 tend to reflect their fundamental niches, and a key implication of the hypothesis is that past,
109 present, and future distributions of species will tend to track changes in climate (Boucher-
110 Lalonde et al. 2014).

111 Within the tropics tree diversity varies considerably, possibly as a consequence of
112 variation in water supply (e.g. ter Steege et al. 2003). Water-stress is indeed one of the most
113 important physiological challenges for tropical tree species (Brenes-Arguedas et al. 2011,
114 Engelbrecht et al. 2007), and precipitation gradients correlate with patterns of species richness
115 at macroecological scales (Clinebell et al. 1995, ter Steege et al. 2003). In particular, tree
116 communities in wetter tropical forests tend to have a greater number of species than in drier
117 forests (Clinebell et al. 1995, Gentry 1988, ter Steege et al. 2003). If this pattern were driven
118 by variation among species in the degree of physiological tolerance to dry conditions, then we
119 would predict that all tropical tree species could occur in wet areas whilst communities at the

120 dry extremes would be made up of a less diverse, drought-tolerant subset. Thus, we would
121 expect a nested pattern of species' occurrences over precipitation gradients, characterised by
122 widespread dry-tolerant species and small-ranged species restricted to wet environments. In
123 this paper we refer to this scenario as the dry tolerance hypothesis (Fig. 1 a).

124 Alternatively, nestedness may not be the predominant pattern for tropical tree
125 metacommunities over precipitation gradients. Multiple studies have documented substantial
126 turnover in floristic composition over precipitation gradients in tropical forests (Condit et al.
127 2013, Engelbrecht et al. 2007, Pitman et al. 2002, Quesada et al. 2012). This pattern could be
128 driven by a trade-off between shade-tolerance and drought-tolerance (e.g. Brenes-Arguedas et
129 al. 2013, Markesteijn et al. 2011). Whilst drought-tolerant species tend to have a higher
130 capacity for water conductance and CO₂ assimilation under water-limiting conditions, they
131 grow more slowly in the scarce understory light of wet forests where shade-tolerant species
132 have a competitive advantage (Brenes-Arguedas et al. 2011, Brenes-Arguedas et al. 2013,
133 Gaviria and Engelbrecht 2015). Drought-tolerant species are also apparently more vulnerable
134 to pest damage in moist areas (Baltzer and Davies 2012, Spear et al. 2015). Thus, in less
135 physiologically stressful environments, tropical tree species' occurrences could be limited by
136 stronger biotic interactions, both with competitors and natural enemies (MacArthur 1972,
137 Normand et al. 2009). In a scenario in which both wet and dry limitations to species
138 distributions are equally important, we would expect progressive turnover of species' identities
139 along precipitation gradients (cf. Fig. 1b), rather than the nested pattern described above.

140 Both nested and turnover patterns have to some extent been documented in the tropics.
141 A nested pattern has been detected in the Thai-Malay peninsula where widespread species,
142 occurring across both seasonal and aseasonal regions, are more resistant to drought than species
143 restricted to aseasonal areas (Baltzer et al. 2008). Across the Isthmus of Panama, Engelbrecht
144 et al. (2007) found a direct influence of drought sensitivity on species' distributions, whilst

145 light requirements did not significantly limit where species occur, which is consistent with the
146 mechanisms underlying a nested pattern of species distributions. Also in Panama, another
147 experimental study found that pest pressure was similar for species regardless of their
148 distribution along a precipitation gradient (Brenes-Arguedas et al. 2009), indicating that the
149 distributions of taxa that occur in drier forests may not be constrained by pest pressure.
150 However, recent data from the same area show that drought-tolerant species are more likely to
151 die than drought-intolerant taxa when attacked by herbivores or pathogens (Spear et al. 2015).
152 Furthermore, when comparing two sites, an aseasonal (Yasuní; ca. 3200 mm y⁻¹ rainfall) and
153 seasonal (Manu; ca. 2300 ca. mm y⁻¹) forest in lowland western Amazonia, Pitman et al. (2002)
154 reported that similar proportion of species were unique to each (Yasuní, 300 exclusive species
155 out of 1017; Manu, 200 out of 693). The presence of a similar and large proportion of species
156 restricted to each site is consistent with species distributions showing a pattern of turnover
157 among sites. While there is thus evidence of both nestedness and turnover in tropical tree
158 species distributions, a comprehensive investigation at large scale is lacking.

159 There are various approaches to estimate the tolerance of taxa to water-stress. For
160 example, experimental studies of drought imposed on trees provide the clearest indicator of
161 sensitivity to water-stress and provide insight into the ecophysiological mechanisms involved.
162 Yet in the tropics, these are inevitably constrained to a minor proportion of tropical diversity,
163 limited by tiny sample sizes (e.g. da Costa et al. 2010, Nepstad et al. 2007) and practical
164 challenges of achieving any spatial replication and of integrating effects across multiple life
165 stages (e.g. Brenes-Arguedas et al. 2013). By contrast, observational approaches, which consist
166 of mapping species' distributions across precipitation gradients, could potentially indicate the
167 sensitivity of thousands of species to dry or wet conditions (e.g. Slatyer et al. 2013). Fixed-area
168 inventories of local communities from many locations, offer a particular advantage for this
169 kind of study as they avoid the bias towards more charismatic or accessible taxa that affects *ad*

170 *hoc* plant collection records (Nelson et al. 1990, Sastre and Lobo 2009). Inventory-based
171 attempts to classify tropical tree taxa by their affiliations to precipitation regimes have already
172 advanced the understanding of species precipitation niches (e.g. Butt et al. 2008, Condit et al.
173 2013, Fauset et al. 2012), but have been fairly limited in terms of spatial scale, number of
174 sample sites and taxa. In this paper we apply this inventory-based approach to investigate the
175 macroecological patterns of trees across the world's most species-rich tropical forests, those of
176 the Western Neotropics, an area of 3.5 million km² that encompasses Central America and
177 western South America. Because species richness in this region is so high, meaning that
178 individual species' identifications are often challenging, we also explore whether analyses at
179 the genus - or family - level offers a practical alternative for assessing the impacts of water-
180 stress on floristic composition.

181 We selected the Western Neotropics as our study area for two reasons. First, there is
182 substantial variability in climate at small spatial scales relative to that of the entire region,
183 meaning that associations between precipitation and floristic composition are less likely to be
184 the result of dispersal limitation and potential concomitant spatial autocorrelation in species'
185 distributions. The Andean Cordilleras block atmospheric moisture flow locally, maintaining
186 some areas with very low precipitation levels, whilst enhancing orographic rainfall in adjacent
187 localities (Lenters and Cook 1995). As a result, there are wetter patches surrounded by drier
188 areas across the region, such as the wet zones in central Bolivia and in South East Peru (Fig.
189 2). The inverse is also observed, such as the patches of drier forests south of Tarapoto in central
190 Peru. There is also a general tendency for precipitation to decline away from the equator in
191 both northward and southward directions (Fig. 2). Secondly, the western Neotropics is a
192 cohesive phylogeographic unit. Western Amazonian forests are floristically more similar to
193 forests in Central America than to those in the Eastern Amazon, despite the greater distances
194 involved and the presence of the world's second highest mountain range dividing Central

195 America from southern Peru (Gentry 1990). This floristic similarity between the western
196 Amazon and Central American forests is thought to be because: (1) the Andes are young
197 (~25Ma) so represent a recent phylogeographic barrier (Gentry 1982, Gentry 1990), and (2)
198 the soils of moist forests in western Amazonia and Central America are similar, being young,
199 relatively fertile, and often poorly structured, largely as a consequence of the Andean uplift
200 and associated Central American orogeny (Gentry 1982, Quesada et al. 2010).

201 Here, we use a unique, extensive forest plot dataset to investigate how precipitation
202 influences the distribution of tree taxa, at different taxonomic levels, across the Western
203 Neotropics. Using 531 tree plots that include 2570 species, we examine the climatic
204 macroecology of the region's tropical trees. Specifically, we 1) test the dry tolerance
205 hypothesis, which posits that tolerance to dry extremes explains taxa geographic ranges within
206 closed-canopy forests (Fig. 1a); and 2) quantify the affiliations of taxa to precipitation using
207 available data, in order to assess individual taxon-climate sensitivities and predict how tropical
208 trees may respond to potential future climatic changes.

209

210 **Methods**

211 **Precipitation in the Western Neotropics**

212 To investigate the effects of water-stress on the distribution of tropical forest taxa we
213 used the maximum climatological water deficit (CWD) (Chave et al. 2014). This metric
214 represents the sum of water deficit values (i.e. the difference between precipitation and
215 evapotranspiration) over consecutive months when evapotranspiration is greater than
216 precipitation. CWD values were extracted at a 2.5 arc-second resolution layer, based on
217 interpolations of precipitation measurements from weather stations between 1960 and 1990
218 and evapotranspiration calculated using the same data (New et al. 2002) (Supplementary

219 material Appendix 1). Additionally, we used mean annual precipitation (MAP) from the
220 WorldClim database (Hijmans et al. 2005) to quantify total annual precipitation. MAP values
221 are derived from interpolations of weather station data with monthly records between ca. 1950
222 and 2000 at a resolution equivalent to ca. 1 km². Although these datasets have different grain
223 sizes, the underlying data used in both interpolations have the same spatial scale (Chave et al.
224 2014, Hijmans et al. 2005).

225 **Vegetation data set**

226 We used data from 531 floristic inventories from three plot networks: ATDN (ter Steege
227 et al. 2013, ter Steege et al. 2003), RAINFOR (Malhi et al. 2002) and Gentry and Phillips plots
228 (Gentry 1988, Phillips and Miller 2002, Phillips et al. 2003), distributed throughout the Western
229 Neotropics (see Supplementary material Appendix 2). Plot areas varied from 0.1 to 5.0 ha. We
230 included all trees with a diameter (D) ≥ 10 cm. Our analysis was restricted to lowland *terra*
231 *firme* forests below 1000 m.a.s.l., excluding all lianas. The RAINFOR and Gentry / Phillips
232 datasets were downloaded from ForestPlots.net (Lopez-Gonzalez et al. 2009, Lopez-Gonzalez
233 et al. 2011).

234 The plots in our dataset provide a largely representative sample of actual precipitation
235 values across all western neotropical lowland forests (see Supplementary material Appendix
236 3). However, the dataset only includes 18 plots in very wet environments (above 3500 mm y⁻¹
237 ¹, Fig. A3.2), which are largely confined to small pockets on both flanks of the Andes. Because
238 this sampling (3% of all plots) is insufficient to accurately determine species' occurrences and
239 ranges in the wettest forests, we restricted our precipitation and taxa distribution analyses (see
240 below) to the 513 plots with MAP ≤ 3500 mm y⁻¹.

241 **Analyses**

242 ***Precipitation and diversity***

243 If water supply broadly limits species' distributions, then community-level diversity
244 should also be controlled by precipitation regime. However, variation in local diversity is
245 nevertheless expected as a consequence of other factors (ter Steege et al. 2003). For example,
246 even under wet precipitation regimes, local edaphic conditions such as extremely porous soils
247 could lead to water stress and lower diversity. Therefore, we fitted a quantile regression
248 (Koenker and Bassett 1978), describing the role of precipitation in controlling the upper bound
249 of diversity. Diversity was quantified using Fisher's α because this metric is relatively
250 insensitive to variable stem numbers among plots. In addition, to assess whether the correlation
251 between diversity and precipitation is robust to the potential influence of spatial autocorrelation
252 we applied a Partial Mantel test (Fortin and Payette 2002), computing the relationship between
253 the Euclidian distances of diversity and precipitation, whilst controlling for the effect of
254 geographic distances. Lastly, we also used Kendal's τ non-parametric correlation coefficient to
255 assess the relationship between diversity and precipitation. We restricted all diversity analyses
256 to the 116 1-ha plots that had at least 80% of trees identified to species level.

257 ***Metacommunity structure***

258 We used the approach of Leibold and Mikkelsen (2002) to test whether the distribution
259 of taxa along the precipitation gradient follows a turnover or nested pattern. Our analysis was
260 performed by first sorting the plots within the community matrix by their precipitation regimes.
261 Then we assessed turnover by counting the number of times a taxon replaces another between
262 two climatologically adjacent sites and comparing this value to the average number of
263 replacements found when randomly sorting the matrix 1000 times. More replacements than
264 expected by chance indicate a turnover structure, whilst fewer imply that the metacommunity
265 follows a nested pattern (Presley et al. 2010) as predicted by the dry tolerance hypothesis. This

266 analysis was conducted applying the function *Turnover* from the R package *metacom* (Dallas
267 2014).

268 ***Precipitation and taxa distribution***

269 To explore the influence of precipitation on taxa distributions firstly, we simply plotted taxa
270 precipitation ranges, i.e. the range of precipitation conditions in which each taxon occurs, to
271 visually inspect the variation of precipitation ranges among taxa. According to the dry tolerance
272 hypothesis, for each taxon the precipitation range size should be positively associated with the
273 driest condition at which it is found, i.e. the more tolerant to dry conditions the taxon is, the
274 larger its climatic span should be. However, the predicted pattern could also arise artefactually
275 if taxa that occur under extreme regimes have on average bigger ranges regardless of whether
276 they are associated to dry or wet conditions. We therefore, secondly, used Kendall's τ
277 coefficient of correlation to explore analytically the relationship between taxon precipitation
278 range and both the driest and wettest CWD values at which each taxon occurs. If the dry
279 tolerance hypothesis holds we expect precipitation range size to be negatively correlated with
280 the driest precipitation condition where each taxon occurs and not correlated with wettest
281 precipitation where each taxon is found.

282 Thirdly, we compared taxa discovery curves, which represent the cumulative
283 percentage of taxa from the whole metacommunity that occur in each plot when following
284 opposite environmental sampling directions, i.e. from wet to dry and from dry to wet. The dry
285 tolerance hypothesis predicts that wet to dry discovery curves should be steeper initially than
286 dry to wet curves, as wet areas are expected to have more narrow-ranged taxa.

287 Finally, we examined the loss of taxa from extremely wet and from extremely dry plots
288 over the precipitation gradient. We tested whether tree taxa found at the driest conditions within
289 our sample can tolerate a larger range of precipitation conditions than taxa in the wettest plots.

290 We thus generated taxa loss curves to describe the decay of taxa along the precipitation gradient
291 within the 10% driest plots and the 10% wettest plots.

292 We compared discovery and loss curves in different directions of the precipitation
293 gradient (i.e. from wet to dry and from dry to wet) against each other and against null models
294 of no influence of precipitation on taxa discovery or loss. These null models represented the
295 mean and confidence intervals from 1000 taxa discovery and loss curves produced by randomly
296 shuffling the precipitation values attributed to each plot. Taxa recorded in 10 plots or fewer are
297 likely to be under-sampled within the metacommunity and were excluded from the analyses
298 regarding metacommunity structure and taxa distribution.

299 *Taxa precipitation affiliation*

300 To describe the preferred precipitation conditions for each taxon we generated an index
301 of precipitation affiliation, or precipitation centre of gravity (PCG). We adopted a similar
302 approach to that used to estimate the elevation centre of gravity by Chen et al. (2009) (see also
303 Feeley et al. 2011), which consisted of calculating the mean of precipitation of locations where
304 each taxon occurs in, weighted by the taxon's relative abundance in each community (Equation
305 1).

$$306 \quad \text{PCG} = \frac{\sum_1^n P \times Ra}{\sum_1^n Ra} \quad (1)$$

307 Where: n = number of plots

308 P = precipitation

309 Ra = relative abundance based on number of individuals

310 The resulting taxon-level PCG values are in units of millimetres per year, the same
311 scale as the precipitation variables: CWD or MAP. We tested the null hypothesis of no
312 influence of precipitation on the distribution of each taxon by calculating the probability of an

313 observed PCG value being higher than a PCG generated by randomly shuffling the
314 precipitation records among the communities, following Manly (1997) (Supplementary
315 material Appendix 4). We also generated an alternative estimator of precipitation affiliation for
316 each taxon by correlating its plot-specific relative abundance and precipitation values using
317 Kendall's τ coefficient of correlation (following Butt et al. 2008). Here, a negative correlation
318 indicates affiliation to dry conditions, whilst a positive correlation indicates affiliation to wet
319 conditions (Supplementary material Appendix 6).

320 PCG values were calculated for each taxon recorded in at least three localities (1818
321 species, 544 genera and 104 families), and Kendall's τ values were calculated for each taxon
322 recorded in at least 20 localities (525 species, 327 genera and 78 families). We also calculated
323 the proportions of significantly dry- and wet-affiliated taxa. To verify that these proportions
324 were not merely a consequence of the number of taxa assessed, we compared our observed
325 proportions to 999 proportions calculated from random metacommunity structures where taxa
326 abundances were shuffled among plots (Supplementary material Appendix 5).

327 Each analysis was repeated at family, genus and species levels. All analyses were
328 performed for CWD, and precipitation affiliations were also calculated for MAP. Analyses
329 were carried out in R version 3.1.1 (R Core Team 2014).

330 **Results**

331 In the Western Neotropics, diversity was negatively related to water-stress at all
332 taxonomic levels, being strongly limited by more extreme negative values of maximum
333 climatological water deficit (CWD) (Fig. 3). This result remained after accounting for possible
334 spatial autocorrelation (Partial Mantel test significant at $\alpha = 0.05$ for all taxonomic levels: $r =$
335 0.31 for species; $r = 0.38$ for genera; $r = 0.37$ for families). The large increase in diversity

336 towards the wettest areas was most evident at the species level (around 200-fold), but was also
337 strong at genus (ca. 70-fold) and family levels (ca. 16-fold) (Fig. 3).

338 For all our analyses of taxa distributions it was evident that they follow a nested pattern
339 along the water-deficit gradient, as predicted by the dry tolerance hypothesis. Thus, firstly,
340 when investigating metacommunity structure, among any given pair of sites, the number of
341 times a taxon replaced another was significantly lower than expected by chance at all
342 taxonomic levels (Table 1). Secondly, compared to all taxa, those able to tolerate the dry
343 extremes were clearly distributed over a wider range of precipitation regimes (Fig. 4 a-c). This
344 was confirmed by precipitation ranges being very strongly and negatively correlated to the
345 driest condition where each taxon occurs (Kendall's $\tau = -0.93$ for species, -0.96 for genera and
346 -0.99 for families, one-tailed P values < 0.001) and not correlated to the wettest condition of
347 occurrence (Kendall's $\tau = 0.01$ for species, 0.05 for genera and -0.01 for families, P-values $>$
348 0.05).

349 Thirdly, nested patterns were evident in most taxa discovery curves, with the floristic
350 composition of dry plots being a subset of wet plots (Fig. 4 d-f). At species and genus levels,
351 the wet-dry cumulative discovery curves were steeper than the dry-wet curves, indicating more
352 taxa restricted to wet conditions. However, this distinction in the shape of the discovery curves
353 between the directions of the precipitation gradient (wet-dry vs. dry-wet) was much less evident
354 at the family level (Fig. 4 f). Finally, the loss curve analysis also showed that plots at the wet
355 extremes of the precipitation gradient have many more taxa restricted to wet conditions than
356 expected by chance (Fig. 4 g-i). Extreme dry plots also had a much greater proportion of species
357 with wide precipitation ranges than the wettest plots, with at least 80% of their species
358 persisting until all but the very wettest forests are reached (Fig. 4 g – red curve). Again, these
359 patterns were most clearly evident for species and genera.

360 For the 1818 species, 544 genera and 104 families assessed across the Western
361 Neotropics, we found a large proportion of taxa with significant values for rainfall affiliation
362 (Table 2 a, Supplementary Material, Appendix 9, tables A9.1, A9.2 and A9.3). Affiliations to
363 wet conditions were substantially more common than affiliations to dry conditions at all
364 taxonomic levels (Table 2 b) (see Supplementary material Appendix 5). Anacardiaceae and
365 Rutaceae are examples of the 10 most dry-affiliated families registered in 10 or more localities
366 and Lecythidaceae, Myrsinaceae and Solanaceae are amongst the most wet affiliated families
367 (see Supplementary material Appendix 7, Tables A7.1 and A7.2 for the most wet and dry
368 affiliated taxa). Lastly, the observed patterns persisted when repeating the analyses excluding
369 those species possibly affiliated to locally enhanced water supply (Supplementary material
370 Appendix 8).

371 **Discussion**

372 Our results demonstrate the influence of precipitation gradients on the patterns of
373 diversity and composition for families, genera and species of Neotropical trees. We confirm
374 that community diversity is much higher in wet than in drier forests, being as much as 200-fold
375 greater at the species level (Fig. 3). Additionally, our analyses indicate that the diversity decline
376 towards more seasonal forests is a consequence of increasingly drier conditions limiting species
377 distributions. To our knowledge this is the first time that the influence of precipitation
378 affiliation has been quantified at the level of individual Amazon tree species.

379 Water-stress during the dry season, represented here by the climatological water-deficit
380 (CWD), limits tree species distributions across the Western Neotropics (Fig. 4). In areas with
381 a very negative CWD, forest composition is a subset of those communities that do not suffer
382 water-stress (Fig. 4). These findings are consistent with results from studies at much smaller
383 scales (Baltzer et al. 2008, Engelbrecht et al. 2007). The physiological challenges in dry areas

384 require species to have specific characteristics in order to recruit and persist. For example,
385 certain species have the capacity to maintain turgor pressure and living tissues under more
386 negative water potentials at the seedling stage, which allow them to obtain water from dry soils
387 (Baltzer et al. 2008, Brenes-Arguedas et al. 2013). At the wet extreme of the gradient, more
388 favourable conditions may allow a wider range of functional strategies to coexist (Spasojevic
389 et al. 2014). Consistent with this, most taxa in our data set occur in the wet areas, with only a
390 small proportion restricted to dry conditions (Fig. 4). Furthermore, our results indicate that
391 other factors such as pests and pathogens (Spear et al. 2015) or tolerance to shaded
392 environments (Brenes-Arguedas et al. 2013), are much less important in determining the
393 distribution of taxa. In some cases these may restrict the abundance of dry affiliated taxa but
394 generally appear not to limit their occurrence. Geomorphology and dispersal limitation can
395 impact species' distributions, and these drivers likely account for some of the unexplained
396 variation in the relationship between diversity and precipitation shown here (Dexter et al. 2012,
397 Higgins et al. 2011). The scarcity of plots from the very wettest forests (Supplementary
398 material Appendix 3, Fig. A3.2) may also have limited our ability to fully document patterns
399 of species turnover. Nevertheless, our analysis shows that more than 90% of the species
400 occurring in the driest 10% of the neotropical forest samples are also registered in at least one
401 forest with zero mean annual CWD (Fig. 4 g). It could be argued that such widespread taxa
402 may not necessarily tolerate dry conditions, but instead be sustained by locally enhanced water
403 supply due to particular conditions such as the presence of streams. However, our results were
404 robust even after excluding taxa potentially affiliated to such local water availability
405 (Supplementary material Appendix 8). Thus, our findings, together with those from Asian and
406 Central American tropical forests (Baltzer et al. 2008, Brenes-Arguedas et al. 2009), suggest
407 that the limitation of most tree species' distributions by water-stress may represent a general
408 macroecological rule across the tropics. This has obvious parallels to the well-known pattern

409 for temperate forest tree species, for which frost tolerance substantially governs species'
410 geographical ranges (e.g. Morin and Lechowicz 2013, Pither 2003).

411 Affiliations to specific precipitation regimes are strongest at the species level, but
412 climate sensitivity can still be clearly detected with genus-level analyses (Fig. 4 d-i). The
413 stronger relationship between species and precipitation when compared to other taxonomic
414 levels could be a consequence of a relatively stronger influence of climate on recent
415 diversification. In particular, massive changes in precipitation regimes took place in the
416 Neogene and Quaternary due to Andean uplift and glacial cycles (Hoorn et al. 2010). During
417 this period, global fluctuations in climate and atmospheric CO₂ concentrations, which affect
418 water-use efficiency (Brienen et al. 2011), are thought to have influenced speciation (cf. Erkens
419 et al. 2007, Richardson et al. 2001 although see Hoorn et al. 2010). Climate sensitivity was also
420 clearly evident at the genus level (Fig. 4), which has relevant practical implications for tropical
421 community and ecosystem ecology. Because of the challenges of achieving sufficient sample
422 size and accurate identification in hyperdiverse tropical forests (Martinez and Phillips 2000),
423 ecosystem process and community ecological studies in this ecosystem often rely on the
424 simplifying assumption that the genus-level represents a sufficiently functionally-coherent unit
425 to address the question at hand (e.g. Butt et al. 2014, Harley et al. 2004, Laurance et al. 2004).
426 Our results suggests that analysis at the genus-level could be used to assess, for instance, the
427 impacts of climate change on diversity, but that nevertheless such impacts would be
428 underestimated without a species-level analysis.

429 In addition to the physiological tolerance to dry conditions, other, underlying
430 geographical and evolutionary processes could conceivably drive the patterns we observe in
431 this study. These are, notably, (1) a greater extent of wet areas (Fine 2001, Terborgh 1973), (2)
432 greater stability of wet areas through time leading to lower extinction rates (Jablonski et al.

433 2006, Jansson 2003, Klopfer 1959), and (3) faster rates of speciation in wet forests (Allen et
434 al. 2002, Jablonski et al. 2006, Rohde 1992). The first alternative (Rosenzweig 1992) requires
435 that species-area relationships govern the climate-diversity associations that we find. Within
436 our region, the areas that do not suffer water-stress (i.e. CWD = 0) are where the great majority
437 of the species (90%) can be found (Fig. 4), yet they occupy a relatively small area (25% of the
438 Western Neotropics and 31% of plots). Thus, the area hypothesis appears unlikely to be driving
439 the precipitation-diversity relationship.

440 The other two alternative hypotheses could more plausibly be contributing to the
441 patterns observed here. Climate stability is indeed associated with diversity throughout the
442 Neotropics (Morueta-Holme et al. 2013). In contrast with most of the Amazon basin, the
443 lowland forests close to the Andes and in Central America apparently had relatively stable
444 climates, with only moderate changes during the Quaternary/Neogene (Hoorn et al. 2010),
445 which could have reduced extinction rates (Jablonski et al. 2006, Klopfer 1959). The diversity
446 gradient may also be a consequence of more diverse areas having higher diversification rates
447 (Jablonski et al. 2006, Jansson 2003, Rohde 1992). While both lower extinction rates and
448 higher speciation rates in wet forest might contribute to explaining the climate-diversity
449 gradient, their influence does not invalidate the idea that wet-affiliated species are drought-
450 intolerant. Indeed, the mechanisms that might have favoured lower extinction rates in wetter
451 forests are related to the inability of many taxa to survive environmental fluctuations such as
452 droughts. Experiments showing that seedlings of species from wet tropical environments have
453 higher mortality under water-stress than dry-distributed taxa (Baltzer et al. 2008, Engelbrecht
454 et al. 2007, Poorter and Markesteijn 2008) indicate that water stress can have direct impacts on
455 species survival and distribution. As ever, untangling ecological and historical explanations of
456 patterns of diversity is difficult with data solely on species distributions (Ricklefs 2004).

458 Understanding how floristic composition is distributed along precipitation gradients is
459 critical to better predict outcomes for the rich biodiversity of the region in the face of climatic
460 changes. The observed small precipitation ranges of wet-affiliated taxa (Fig. 4 a-c) together
461 with the rareness of extremely wet areas (Fig. A3.2) indicate high potential vulnerability to
462 changes in climate. So far, while total precipitation has recently increased in Amazonia (Gloor
463 et al. 2013), much of Amazonia and Central America have also seen an increase in drought
464 frequency, and more generally in the frequency of extreme dry and wet events (Aguilar et al.
465 2005, Li et al. 2008, Malhi and Wright 2004, Marengo et al. 2011). These neotropical trends
466 toward similar or greater annual precipitation, but a greater frequency and intensity of dry
467 events, are expected to continue, albeit with important regional differences (IPCC 2013). While
468 elevated atmospheric CO₂ concentrations may alleviate physiological impacts of water-stress
469 on plants by increasing water-use efficiency (Brienen et al. 2011, van der Sleen et al. 2015),
470 warming will have the opposite impact. Temperatures have increased markedly in Amazonia
471 since 1970 (Jiménez-Muñoz et al. 2013) and this trend is highly likely to continue (IPCC 2013)
472 so that plants will experience increased water-stress throughout Amazonia (Malhi et al. 2009)
473 with thermally-enhanced dry season water-stress challenging trees even in wetter
474 environments. The restriction of most tree taxa in the Western Neotropics to wetter areas
475 indicates widespread low tolerance to dry conditions and low capacity to acclimate to them.
476 Together with the anticipated climate changes this suggests that floristic composition may
477 change substantially, potentially with the loss of many wet forest specialists and compensatory
478 gains by the fewer, more climatologically-generalist dry tolerant species. While research is
479 clearly needed to track and analyse ecological monitoring sites to examine where and how
480 tropical forest composition responds to anthropogenic climate changes, protecting the

481 remaining ever-wet forests and coherent up-slope migration routes will be essential if most
482 neotropical diversity is to survive into the next century.

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682

683 **Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix**
684 **1-9**

685 **Figure Legends**

686 **Figure 1** Two conceptual models of how species' distributions may be arrayed along a
687 precipitation gradient, with presence/absence matrices where rows represent taxa and columns
688 represent communities, ordered from wet to dry. **A.** Nested pattern expected by the dry
689 tolerance hypothesis. Nestedness (*sensu* Leibold and Mikkelson 2002) is represented by
690 gradual disappearance of taxa along the precipitation gradient from wet to dry. **B.** Turnover of
691 taxa along the precipitation gradient. This pattern is characterized by the substitution of taxa
692 from site to site, resulting in communities at opposite sides of the precipitation gradient being
693 completely different in composition (Leibold and Mikkelson 2002).

694 **Figure 2** Mean annual precipitation in the Western Neotropics and distribution of the 531
695 forest inventory plots (black dots) analysed in this study. Precipitation data come from
696 WorldClim (Hijmans *et al.*, 2005). Note the spatial complexity of precipitation patterns within
697 the study area.

698 **Figure 3** Tree alpha diversity (evaluated with Fisher's alpha parameter) as a function of
699 precipitation, represented by maximum climatological water-deficit (CWD) for 1 ha plots
700 across the Western Neotropics. Solid curves represent the 90% upper quantile regression. Note
701 that more negative values of CWD limit alpha diversity and that the diversity vs. CWD
702 correlation is stronger for finer taxonomic levels – Kendall's $\tau = 0.66$ for species, 0.60 for
703 genus and 0.51 for family level, P values < 0.001.

704 **Figure 4** The influence of precipitation on the distribution of taxa in Western neotropics. **a-c**
705 Range of water-deficit conditions (black horizontal lines) over which each **(a)** species, **(b)**
706 genus, and **(c)** family occurs. The x-axes express the water-deficit gradient in mm of maximum
707 climatological water-deficit (CWD) from dry (red) to wet (blue), while taxa are stacked and
708 ordered along y-axes by the most negative value of CWD of occurrence. **d-f** Discovery curves

709 showing the cumulative percentage (y-axes) of **(d)** species, **(e)** genera, and **(f)** families from
710 the whole region found in each plot when moving along the CWD gradient (x-axes). **g-i** Loss
711 curves giving the percentage of **(g)** species, **(h)** genera, and **(i)** families from the 10% of plots
712 under the most extreme precipitation regimes that drop out when moving to the opposite
713 extreme of the gradient. In **d-i** x-axes show the number of plots, ordered from wet to dry (blue
714 axis labels and blue curves) and from dry to wet (red axis labels and red curves). Black and
715 grey curves represent respectively, the mean and 95% confidence limits of loss and discovery
716 curves generated by shuffling values of precipitation within the plots 1000 times. Taxa
717 restricted to 10 or fewer localities were excluded from analyses. Note that of the taxa from the
718 10% driest communities, 86% of species, 91% of genera and 96% of families are also recorded
719 in plots with zero CWD.

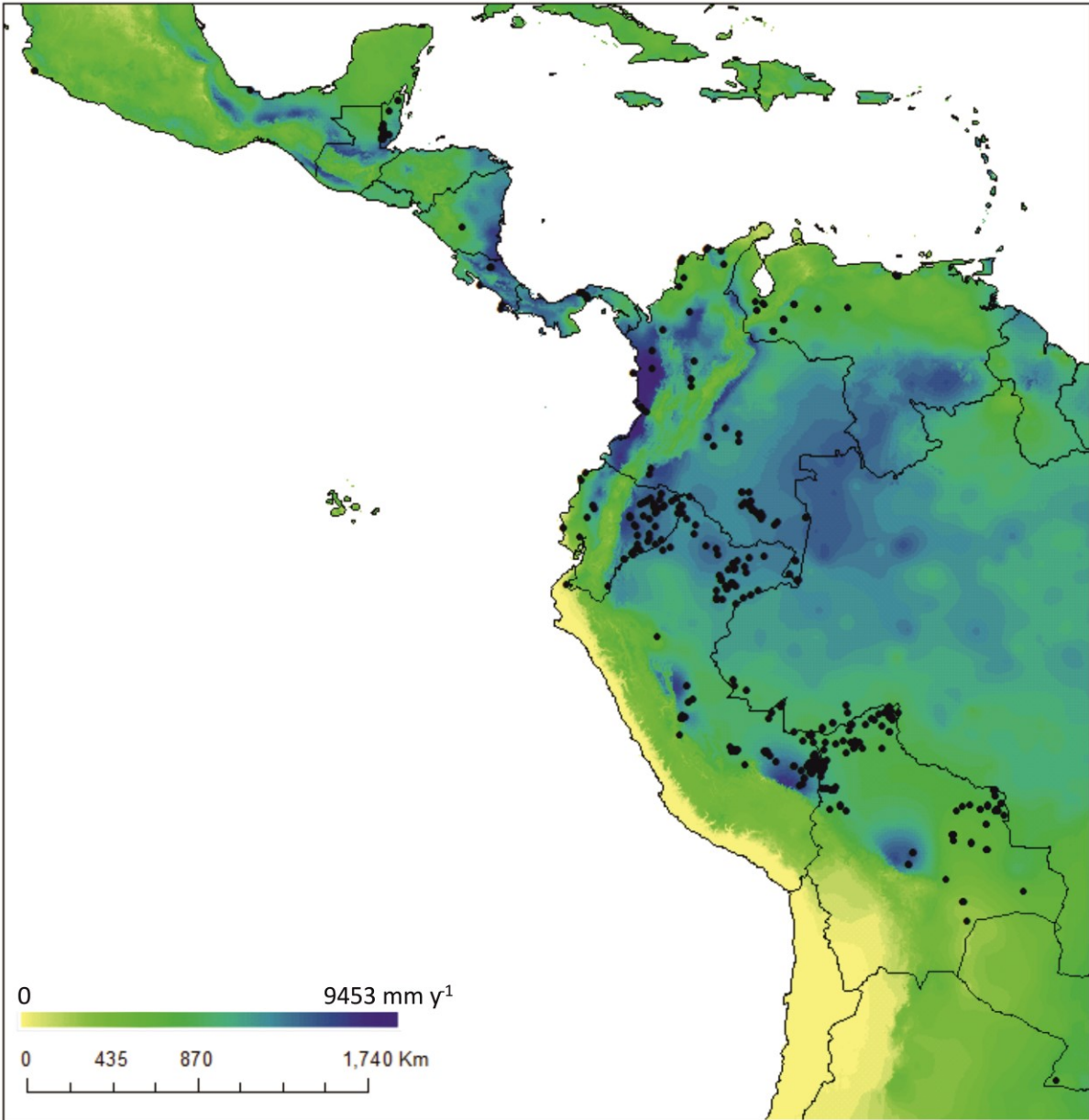
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| | Sites | | | | | Occurrence |
|----------|-------|---|-----|---|---|------------|
| | wet | | dry | | | |
| | A | B | C | D | E | |
| 1 | 1 | 1 | 1 | 1 | 1 | 5 |
| 2 | 1 | 1 | 1 | 1 | 1 | 5 |
| 3 | 1 | 1 | 1 | 1 | | 4 |
| 4 | 1 | 1 | 1 | 1 | | 4 |
| 5 | 1 | 1 | 1 | | | 3 |
| 6 | 1 | 1 | 1 | | | 3 |
| 7 | 1 | 1 | | | | 2 |
| 8 | 1 | 1 | | | | 2 |
| 9 | 1 | | | | | 1 |
| 10 | 1 | | | | | 1 |
| Richness | 10 | 8 | 6 | 4 | 2 | |

| | Sites | | | | | Occurrence |
|----------|-------|---|-----|---|---|------------|
| | wet | | dry | | | |
| | A | B | C | D | E | |
| 1 | | | 1 | 1 | 1 | 3 |
| 2 | | | 1 | 1 | 1 | 3 |
| 3 | | | 1 | 1 | | 2 |
| 4 | | 1 | 1 | | | 2 |
| 5 | 1 | 1 | | | | 2 |
| 6 | 1 | 1 | | | | 2 |
| 7 | 1 | 1 | | | | 2 |
| 8 | 1 | 1 | | | | 2 |
| 9 | 1 | | | | | 1 |
| 10 | 1 | | | | | 1 |
| Richness | 6 | 5 | 4 | 3 | 2 | |

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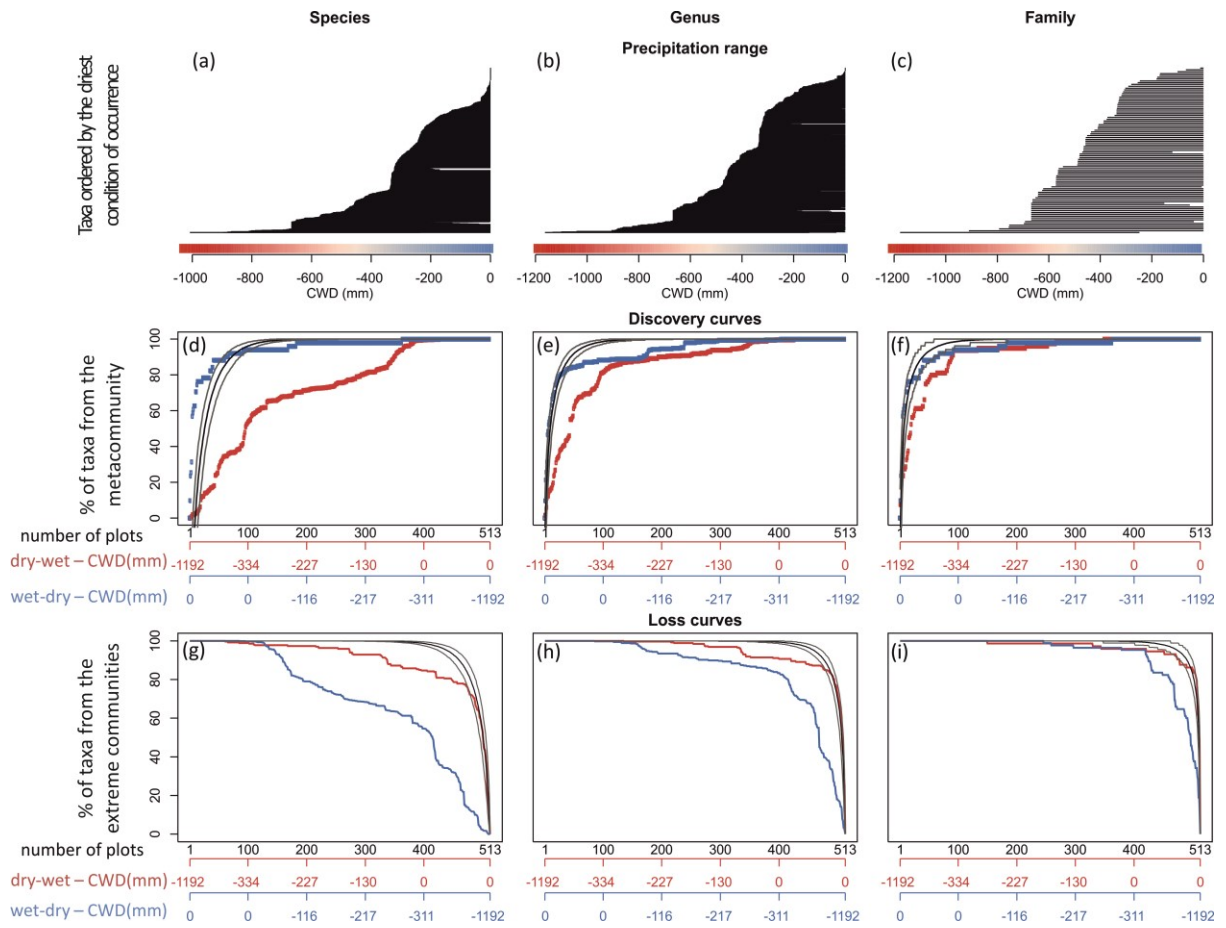
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728 **Tables**

729 **Table 1** Observed and expected turnover of taxa along the precipitation gradient. Turnover was
 730 measured by the number of times a taxon replaces another between two sites. Expected values
 731 represent the average turnover when randomly sorting the matrix 1000 times. P-values test the
 732 null hypothesis that replacement of taxa along the precipitation gradient does not differ from
 733 random expectations considering $\alpha = 0.05$. Note that observed taxa turnover is significantly
 734 lower than the expected, which indicates that the distributions of taxa follows a nested pattern
 735 along the precipitation gradient (Leibold & Mikkelsen 2002, Presley et al. 2010).

| | Observed turnover | Expected turnover | P |
|----------|----------------------|----------------------|--------|
| Families | 0 | 755,226 | 0.01 |
| Genera | 2,061 | 3,529,527 | < 0.01 |
| Species | 0 | 25,592,113 | < 0.01 |

736

737

738 **Table 2a.** Number of taxa significantly affiliated to wet or dry precipitation regimes, based on
739 their precipitation centre of gravity (PCG) and Kendall's τ coefficient of correlation between
740 relative abundance and precipitation. Taxa with significant PCG are more dry or wet-affiliated
741 than expected by chance, at $\alpha < 0.05$. Significant values of Kendall's τ indicate that the
742 probability of observing a correlation between relative abundance and precipitation by chance
743 is lower than 5%. Affiliations calculated for two precipitation variables: maximum
744 climatological water deficit (CWD) and mean annual precipitation (MAP). Values in brackets
745 show the proportions of significant values of precipitation affiliations in relation to the total
746 number of taxa in the analyses. We tested the influence of the sample size on the proportion of
747 significant values by comparing the observed proportion against 1000 random proportions
748 generated by shuffling precipitation values across communities. The null hypothesis that
749 proportions are an artefact of the number of taxa analysed was rejected considering $\alpha = 0.001$
750 in all cases (see Supplementary material Appendix 5 for details).

| | Total | | Significant PCG | | Total | | Significant Kendall's τ | |
|----------|-------|------------|-----------------|-----|-------|-----------|------------------------------|-----|
| | | | CWD | MAP | | | CWD | MAP |
| Species | 1818 | 1065 (58%) | 615 (34%) | | 525 | 426 (81%) | 398 (76%) | |
| Genera | 544 | 291 (53%) | 236 (43%) | | 327 | 259 (79%) | 242 (74%) | |
| Families | 104 | 60 (58%) | 46 (44%) | | 78 | 60 (77%) | 59 (76%) | |

751

752 **Table 2b.** As in Table 2a, but giving a breakdown by affiliations to wet and dry conditions. As
 753 for table 2a the influence of the sample size on the proportion of significant values was assessed
 754 by comparing the observed proportion against 1000 random proportions generated by shuffling
 755 precipitation values across communities (see Supplementary material Appendix 5 for details).
 756 P-values test the null hypothesis that proportions are an artefact of the number of taxa.

| | | Maximum climatological | | Mean annual precipitation (mm) | |
|---------------------------------|----------|--------------------------|------------|--------------------------------|------------|
| | | water deficit (mm) (CWD) | | (MAP) | |
| | | dry | wet | dry | wet |
| Significant PCG | Species | 112 (6%)* | 953 (52%)* | 153 (8%)* | 462 (25%)* |
| | Genera | 67 (12%)* | 224 (41%)* | 94 (17%)* | 142 (26%)* |
| | Families | 13 (12%)* | 47 (45%)* | 18 (17%)* | 28 (27%)* |
| Significant Kendall's τ | Species | 59 (11%)* | 367 (70%)* | 52 (10%)* | 346 (66%)* |
| | Genera | 49 (15%)* | 210 (64%)* | 48 (15%)* | 194 (59%)* |
| | Families | 6 (8%) | 54 (69%)* | 8 (10%)* | 51 (65%)* |

757 * P < 0.05