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Article:

1   Seasonal drought limits tree species across the Neotropics

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74

75   **ABSTRACT**

76   Within the tropics, the species richness of tree communities is strongly and positively

77   associated with precipitation. Previous research has suggested that this macroecological pattern

78   is driven by the negative effect of water-stress on the physiological processes of most tree

79   species. This process implies that the range limits of taxa are defined by their ability to occur

80   under dry conditions, and thus in terms of species distributions it predicts a nested pattern of

81   taxa distribution from wet to dry areas. However, this 'dry-tolerance' hypothesis has yet to be

82   adequately tested at large spatial and taxonomic scales. Here, using a dataset of 531 inventory

83   plots of closed canopy forest distributed across the Western Neotropics we investigated how

84   precipitation, evaluated both as mean annual precipitation and as the maximum climatological

85   water deficit, influences the distribution of tropical tree species, genera and families. We find

86   that the distributions of tree taxa are indeed nested along precipitation gradients in the western

87   Neotropics. Taxa tolerant to seasonal drought are disproportionally widespread across the

88   precipitation gradient, with most reaching even the wettest climates sampled; however, most

89   taxa analysed are restricted to wet areas. Our results suggest that the 'dry tolerance' hypothesis

90   has broad applicability in the world's most species-rich forests. In addition, the large number

91   of species restricted to wetter conditions strongly indicates that an increased frequency of

92   drought could severely threaten biodiversity in this region. Overall, this study establishes a

93   baseline for exploring how tropical forest tree composition may change in response to current

94   and future environmental changes in this region.

95

Introduction

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

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

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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 CO_2 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*

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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 km^2 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 phytogeographic 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 km^2. 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$^-$

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**

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 Mikkelson (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

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

Precipitation and taxa distribution

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

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

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

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

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

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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).

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

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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 τ = -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 τ = 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).

Discussion

371

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

15

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

16

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 CO_2 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).

18

Implications for climate change responses

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 CO_2 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.

483   **Acknowledgements**

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681

682

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

684   **1–9**

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
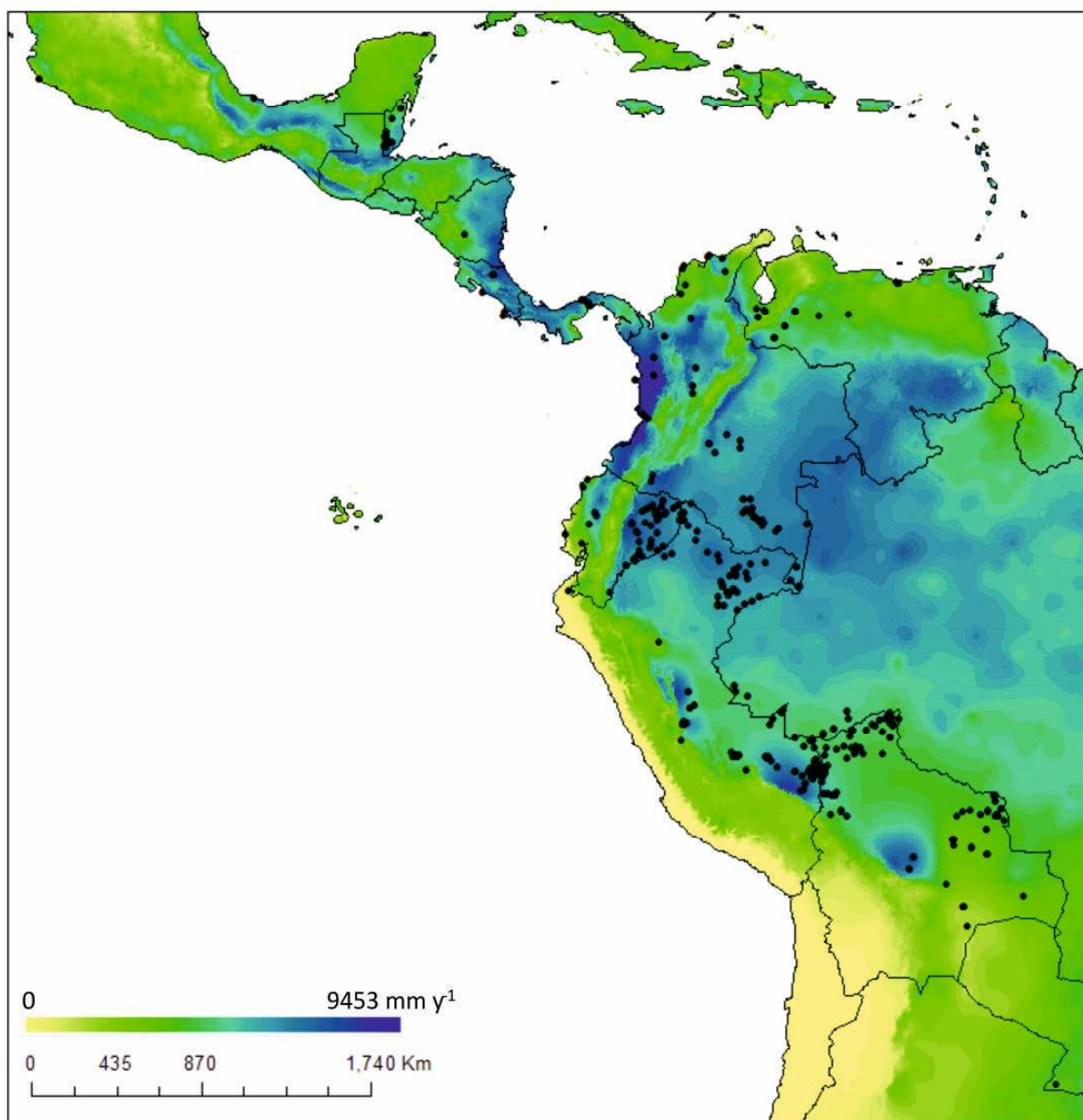
719   in plots with zero CWD.

720

A	Sites					
	wet		dry			
	A	B	C	D	E	Occurrence
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	

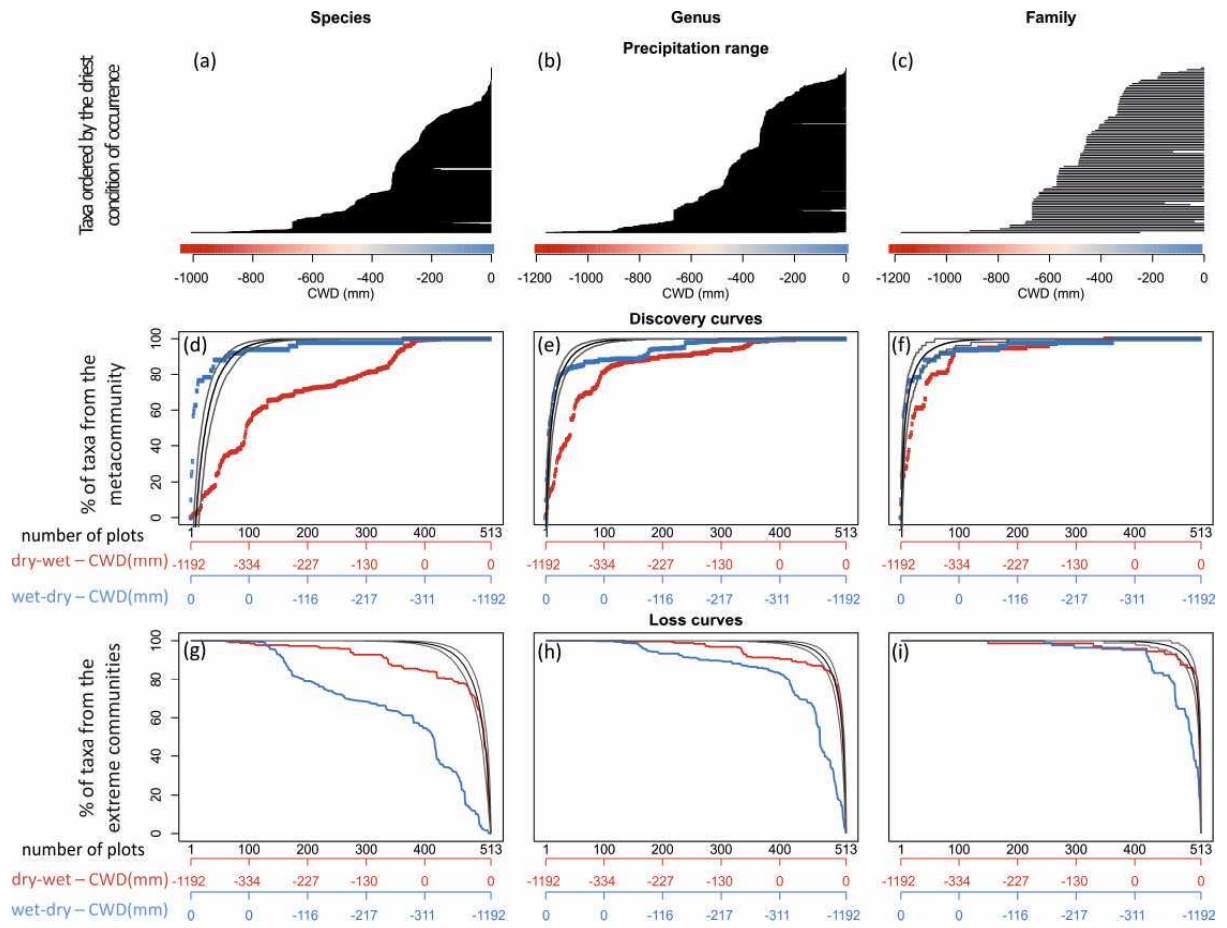| B	Sites					
	wet		dry			
	A	B	C	D	E	Occurrence
1			1	1	1	3
2			1	1	1	3
3			1	1		2
4		1	1			2
5	1	1				2
6	1	1				2
7	1	1				2
8	1	1				2
9	1					1
10	1					1
Richness	6	5	4	3	2	

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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 α = 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 & Mikkelson 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

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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 water deficit (mm) (CWD)		Mean annual precipitation (mm) (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