

Climatic effects on turnover of lowland forest bird communities across a precipitation gradient

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1 **Abstract**

2 One of the main goals of community ecology is to understand the influence
3 of the abiotic environment on the abundance and distribution of species. It has
4 been hypothesized that dry forests are harsher environments than wet forests,
5 which leads to the prediction that environmental filtering should be a more
6 important determinant of patterns of species abundance and composition than
7 in wet forest, where biotic interactions or random assembly should be more
8 important. We attempt to understand the influence of rainfall on the abun-
9 dance and distribution of bird species along a steep precipitation gradient in
1

10 an inter-Andean valley in Colombia. We gathered data on species distribu-
11 tions, abundance, morphological traits and phylogenetic relationships to deter-
12 mine the influence of rainfall on the taxonomic, functional and phylogenetic
13 turnover of species along the Magdalena Valley. We demonstrate that there is
14 a strong turnover of community composition at the limit of the dry forest. The
15 taxonomic turnover is steeper than the phylogenetic turnover, suggesting that
16 replacement of closely related species accounts for a disproportionate number
17 of changes along the gradient. We found evidence for environmental filtering
18 in dry forest as species tend to be more tolerant of higher temperature ranges,
19 stronger rainfall seasonality and lower minimum rainfall. On the other hand,
20 wet forest species tend to compete actively for nest space but not for the re-
21 sources associated with the axes we measured. Our results suggest that rainfall
22 is a strong determinant of community composition when comparing localities
23 above and below the 2400 mm rainfall isocline.

24 **1 Introduction**

25 Comparisons of species composition of different communities have long have been
26 used to infer the mechanisms underlying community assembly (Whittaker, 1960).
27 Environmental gradients are particularly useful for such purposes because they po-
28 tentially allow us to separate the influence of stochastic and niche-based processes
29 (Chase & Myers, 2011; Legendre *et al.*, 2005; Tuomisto & Ruokolainen, 2006) and to
30 predict the determinants of ecological communities (Whittaker, 1960; Terborgh, 1977;
31 Jankowski *et al.*, 2009, 2013; Condit *et al.*, 2002; Swenson *et al.*, 2011). In particular,
32 latitudinal and elevational gradients have been studied intensively to help identify the
33 roles of different biotic and abiotic variables in determining community composition
34 (Terborgh, 1977; Jankowski *et al.*, 2009, 2013; Swenson *et al.*, 2011; Qian & Ricklefs,
35 2007; Kraft *et al.*, 2011; Rodríguez & T Arita, 2004).

36 Environmental gradients are almost always associated with a change in the
37 harshness of the abiotic environment. At high elevations, for example, low temper-
38 atures and high temperature variability are thought to be analogous to the harsher
39 conditions at high latitudes. Such conditions should increase the influence of the
40 abiotic environment on the occurrence and abundance of species (Graham *et al.*,
41 2009; Qian & Ricklefs, 2007, but see Kraft *et al.*, 2011). At low elevations and lat-
42 itudes, where the environment becomes more stable, productivity increases, which
43 also increases the potential for intra- and inter-trophic biotic interactions to deter-
44 mine community composition (Jankowski *et al.*, 2012; Martin, 1988; Janzen, 1970).
45 Thus, the turnover of species along elevational and latitudinal gradients is hypoth-
46 esized to be the result of a change in the relative importance of abiotic and biotic
47 mechanisms that determine community assembly.

48 Rainfall gradients also potentially vary in climatic stability and harshness.
49 Along the rainfall gradient it is likely that water restricts the distribution of or-
50 ganisms at the dry end and biotic interactions potentially determining community
51 composition in the wet end (Engelbrecht *et al.*, 2007; Jabot *et al.*, 2008). Plant com-
52 munities along rainfall gradients, for example, are known to respond dramatically to
53 drought conditions (Condit *et al.*, 2002; Engelbrecht *et al.*, 2007; Jabot *et al.*, 2008).
54 Alternatively, within the same habitat, plants also show niche partitioning, a possi-
55 ble response to competition at different life stages. Pathogens, herbivores, and seed
56 predators also affect plant community composition.

57 Combining metrics of compositional, functional and phylogenetic beta diversity
58 could increase the power of studies of species turnover on gradients (Stegen & Hurl-
59 bert, 2011). Comparisons of functional traits and phylogenetic relationships among
60 species might give additional insights into the mechanisms underlying community
61 composition (McGill *et al.*, 2006; Petchey & Gaston, 2006; Graham & Fine, 2008;
62 Bryant *et al.*, 2008). The expectations of the functional and phylogenetic turnover

63 differ when the communities are assembled deterministically or stochastically along
64 gradients (Swenson *et al.*, 2011; Graham & Fine, 2008). Stochastic mechanisms such
65 as random colonization and extinction predict that while compositional turnover can
66 be high, functional turnover should be similar to that expected by chance (Swenson
67 *et al.*, 2011). In contrast, deterministic community assembly predicts high functional
68 turnover among habitat types and low turnover when comparing similar types of
69 habitats.

70 Both stochastic and deterministic turnover have been documented in plant and
71 animal communities at different geographic and environmental scales (Hubbell, 2001;
72 Gomez *et al.*, 2010; Qian & Ricklefs, 2007; Graham *et al.*, 2009). When functional
73 and compositional turnover are paired with phylogenetic turnover, the latter informs
74 us about the lability or conservatism of traits and the potential modes of speciation
75 and biogeographical process underlying species distributions (Graham & Fine, 2008).
76 Assuming that the environment plays an important role in determining the rate of
77 species and functional turnover along an environmental gradient, a high phylogenetic
78 turnover would be an indication that there is high niche conservatism that restricts
79 close relatives to particular environments. In contrast, low phylogenetic turnover
80 would be indicative of ecological speciation caused by local adaptation to different
81 environmental conditions. In this case, the replacement of species along the gradient
82 would happen mainly among close relatives, some of which may have originated in
83 situ (Graham & Fine, 2008)

84 Even though combining the three metrics (i.e. functional, phylogenetic and
85 compositional) of turnover provides a powerful test of niche versus stochastic pro-
86 cesses (Graham & Fine, 2008), the structure of traits within local communities should
87 further provide indications about the mechanisms underlying species turnover (McGill
88 *et al.*, 2006; Petchey & Gaston, 2002; Kraft *et al.*, 2008, 2015). Species are a collec-
89 tion of traits that could evolve at different rates and respond differently to selective

90 pressures (Ackerly & Cornwell, 2007). While some traits may vary stochastically
91 as a product of genetic drift, other traits may vary deterministically according to
92 different mechanisms (Ackerly & Cornwell, 2007). In addition, the scale at which
93 selection operates is likely to vary among species. In plants, for example, traits such
94 as rooting depth, leaf mass per area and the ability to fix nitrogen are traits that
95 should respond locally to competition; alternatively, the degree to which a plant is
96 deciduous and has compound or simple leaves is likely a response to climatic stres-
97 sors such as drought and high temperatures (Kraft *et al.*, 2015; Lebrija-Trejos *et al.*,
98 2010). In birds, Miles & Ricklefs (1984) and Ricklefs (2012) suggested that overall
99 morphology should respond to competitive interactions. Others have suggested that
100 physiological tolerances of adults and juveniles should reflect adaptations to the en-
101 vironment (Webb, 1987; Kearney & Porter, 2009). Therefore, a combination of the
102 measurement of trait turnover with the change in the structure of species traits along
103 environmental gradients should allow us to not only differentiate between stochastic
104 and deterministic community assembly, but could also reveal the mechanisms that
105 determine community composition (McGill *et al.*, 2006; Kraft *et al.*, 2008, 2015).

106 In this study, we use compositional, functional and phylogenetic metrics of beta
107 diversity to determine if the distribution of bird species along a steep environmental
108 gradient in Colombia is deterministic or stochastic. Furthermore, we use ecological
109 and morphological traits to test the hypothesis that the turnover in bird communities
110 along the gradient is the product of a change in the mechanisms determining species
111 composition along the gradient. Specifically, we predict that because dry forests are
112 harsher and more stressful environments, the relative importance of species sorting
113 through environmental filtering should be highest in dry forests. Thus, we expect that
114 the trait space in physiological tolerances occupied by dry forest communities will be
115 smaller than the one occupied by wet forest ones. In contrast, because of higher
116 productivity and relaxed environmental filtering, wet forest communities should re-

117 spond more to biotic interactions such as competition and predation. In the par-
118 ticular case for competition, we expect wet forest communities to occupy broader
119 eco-morphological trait space than dry forest communities.

120 **2 Methods**

121 **2.1 Study Area**

122 The Magdalena is one of the two lowland inter-Andean valleys occurring in cen-
123 tral Colombia. The Magdalena River has been one of the most important rivers for
124 navigation in the history of Colombia and of high importance in the colonization of
125 northern South America. The river drops quickly from its headwaters to the lowlands
126 in the upper Magdalena Valley, which is characterized by low annual rainfall (1000
127 mm). The low rainfall in the upper Magdalena is the product of the rain shadow
128 of both the central and eastern Andes which rise above 4000 masl. About 200 km
129 down river, the central Andes drop considerably in elevation allowing rainfall from the
130 Pacific coast to pass over the Andes and fall in the mid Magdalena Valley increasing
131 mean annual precipitation to almost 6000 mm in the western foothills of the eastern
132 Andes. Because of its importance as a colonization route and as the connection for
133 the interior of South America with the Caribbean Sea, the Magdalena Valley has a
134 complex history of deforestation and fragmentation. The geological history of the
135 Magdalena is also complex, because the wet forest has contracted and expanded sev-
136 eral times during the last million years during glacial and interglacial periods. During
137 the glacial periods, the entire valley was dry, which provided connections among the
138 dry forest fauna and flora of the Caribbean region of Venezuela and Colombia and
139 the dry forests in the upper Magdalena Valley (Haffer, 1967). During these periods,
140 the wet forest fauna and flora were most likely restricted to refuges in the lowlands
141 north of the Andes, Choco and southern Central America (Haffer, 1967).

142 **2.2 Bird Sampling**

143 We selected at random 15 localities along the Magdalena Valley distributed to capture
144 the entire rainfall gradient (Table 1). In each locality we sampled birds using 50-m
145 fixed radius point counts (Hutto *et al.*, 1986) in which we counted all birds detected
146 both visually and aurally for a period of ten minutes at each point. Point counts
147 were repeated temporally a maximum of four times, although some of the points
148 where only counted once (Table 1). Points were separated from the edge of the forest
149 by a minimum distance of 75 m and were separated from each other by at least
150 200 m to ensure independence and minimize the sampling of species of the matrix
151 surrounding the patch (Blake & Loiselle, 2001). Each morning we conducted up
152 to ten point counts starting at dawn and until 10:00 AM or until activity dropped
153 considerably. We avoided censusing during windy and rainy days. For the analyses
154 we did not include Toucans, Parrots, Hummingbirds, Swallows, Swifts, water birds
155 or birds that flew over the point while censusing because it was difficult to determine
156 the independence of point counts for loud and highly mobile species. Because we did
157 not have a large enough sample size to estimate the density of birds while correcting
158 for detection probability, we estimated the abundance of bird species as the mean
159 number of counts per species per point count.

160 **2.3 Community Turnover**

161 We had two particular objectives in this study. The first was to test if there was
162 a difference among compositional, functional and phylogenetic turnovers in relation
163 to rainfall. In this analysis, we used three sources of information: abundance of
164 species in each locality (as described above - mean number of individuals per point
165 count), morphological and behavioral traits of each species and the phylogeny of all
166 of the species we detected in our study. In the sections below, we provide detailed
167 information about which traits we measured. For the phylogenetic comparisons, we

168 downloaded 1000 trees, to account for phylogenetic uncertainty, from BirdTree.org
169 using Hackett *et al.* (2008) as the back bone for the distribution of trees (see Jetz
170 *et al.*, 2012 for details on how the trees were constructed).

171 We calculated compositional turnover using the Chao index for assessing sim-
172 ilarity of composition among communities while taking into account both abundance
173 and sampling error (Chao *et al.*, 2005). The Chao index is an extension of the Jaccard
174 index, which incorporates a probabilistic framework to account for species abundances
175 and the chance that species might be shared but, because of their rarity in either com-
176 munity, they might be considered as absent from one of the communities because of
177 sampling limitations (Chao *et al.*, 2005). The index estimates the probability that
178 any two individuals sampled at random are shared by both communities while taking
179 into account that shared species might be present in the communities but not sam-
180 pled (Chao *et al.*, 2005). Phylogenetic turnover was calculated as the total length of
181 shared and unshared evolutionary history among any two communities denoted by
182 the length of the branches in the phylogenetic tree shared among communities and
183 unique to each community (Bryant *et al.*, 2008). Because we had a distribution of
184 phylogenetic trees we estimated phylogenetic turnover for each tree and report the
185 mean turnover for the set of 1000 trees.

186 We calculated functional turnover in a similar way to phylogenetic turnover,
187 but instead of using a molecular tree to determine relationships among species, we
188 used trait data to infer a dendrogram of similarity among species (Petchey & Gas-
189 ton, 2002). To construct the dendrogram, we used the total morphological matrix
190 using both continuous and categorical traits. A detailed description of the traits and
191 how they were measured is provided in the Trait Sampling section below. To allow
192 categorical traits in the calculation of the dissimilarity matrix we used the general
193 coefficient of similarity proposed by Gower (1971). Following the calculation of the
194 dissimilarity matrix we performed a hierarchical clustering using the UPGMA method

195 to construct the dendrogram, which performs better than other traditional methods
196 in estimating species clustering for functional diversity analysis (Podani & Schmera,
197 2006). We performed calculations of compositional and functional turnover using
198 *vegan* (Oksanen *et al.*, 2016) package and phylogenetic turnover using the *picante*
199 package (Kembel *et al.*, 2010) in R (R Core Team, 2013).

200 We determined the relationship between community similarity and rainfall by
201 performing a multidimensional scaling of the beta diversity and relating the first axis
202 of the scaling to rainfall. This methodology allowed us to determine if the turnover
203 happened linearly in relation to rainfall or had a logistic (stepwise) form, in which
204 case we could estimate the amount of rainfall at which the community turnover is
205 maximal. Additionally, using scaling of distance matrices or similar analyses such
206 as canonical correspondence analysis provides stronger statistical power to detect
207 the amount of community turnover that can be explained by the variation in the
208 environmental gradient (Legendre *et al.*, 2005). We compared the linear model with
209 a logistic function model in which scaled community similarity was the dependent
210 variable and rainfall the independent one. The logistic function was of the form

$$Community\ Similarity = \frac{a}{(1 + e^{(-b*(Rainfall-c)})})} - \frac{a}{2} \quad (1)$$

211 in which a determines the height of the curve and in this case the maximum
212 difference estimated between types of communities, b determines how fast the transi-
213 tion happens from one type of community to another, and c determines the inflection
214 point in which the community is expected to transition from type x to type y . To
215 estimate the parameters of the logistic function, we used least squares minimization
216 similar to a traditional linear regression. We then compared the models using Akaike
217 Information Criterion (AIC) and r^2 . We performed the least squares minimization of
218 the logistic function in R using the *optim* function.

219 Because the rainfall gradient of the Magdalena Valley expands over two ecore-

220 gions (Olson *et al.*, 2001), we determined if the compositional, functional and phylo-
221 genetic turnover were higher than expected by chance between localities in different
222 ecoregions and lower within ecoregion. In particular, if environmental filtering op-
223 erates stronger in the dry forest than in wet forest we expected the turnover to be
224 lower in localities in the dry forest than in localities in the wet forest indicating lower
225 community variability. We constructed 1000 random communities using a swap algo-
226 rithm that maintains the species abundance distributions as well as the richness of the
227 communities (Hardy, 2008). For each of the 1000 random communities we calculated
228 the compositional, functional and phylogenetic metrics using the observed functional
229 dendrogram and phylogenetic tree. To determine if the turnover was higher or lower
230 than expected by chance we calculated a standardized effect size (SES) for each of
231 the metrics. The SES was computed as

$$SES = \frac{X_{obs} - \bar{X}_{null}}{SD X_{null}} \quad (2)$$

232 Overall, SES values higher than 1.96 or lower than -1.96 denote significantly
233 higher or lower turnover than expected by chance, respectively. Finally, we deter-
234 mined if turnover within types of forests was lower than expected by chance using a
235 t-test.

236 2.4 Climatic Description of Localities

237 To determine the influence of different environmental variables on the turnover of bird
238 communities along the Magdalena Valley, we obtained mean annual rainfall and tem-
239 perature variability from different sources. We obtained mean annual rainfall data
240 from the closest climatic station to each of the localities sampled (IDEAM; Table
241 1). Climatic stations are run by Instituto de Hidrologia, Meteorologia y Estudios
242 Ambientales (IDEAM) in Colombia. Mean rainfall for the period of 1981 - 2010 and

243 the location of each station are freely available for download from their website. We
244 determined the closest station to the locality by measuring geographic distance. Lo-
245 calities were all within 20 km of the closest station but most of them were much
246 closer (mean = 8.31 km; Table 1). To account for possible deviations in rainfall due
247 to distance from the station to the localities, we corroborated rainfall data from mean
248 annual rainfall layer from bioclim (Hijmans *et al.*, 2005). Because one way in which
249 dry forests might be stressful to birds is through its stronger seasonality than wet
250 forests, in addition to mean annual rainfall, we obtained information about rainfall
251 seasonality and rainfall in the driest quarter from bioclim (Hijmans *et al.*, 2005).
252 Mean annual temperature, mean maximum temperature and temperature range were
253 also obtained from bioclim (Hijmans *et al.*, 2005). Finally, to obtain temperature
254 variability, we used five Hobo U23 data loggers that were located in two dry forests
255 and three wet forests. The data loggers were set to measure temperature and relative
256 humidity each hour for an average of 662 days (Mana Dulce = 585 days, Jabiru =
257 233 days, Rio Manso = 730 days, San Juan = 659 days and Rio Claro = 1104 days).
258 Finally, we tested for significant differences in mean annual temperature, temperature
259 range, mean maximum temperature, temperature coefficient of variation, precipita-
260 tion seasonality and precipitation in driest month using a linear model relating each
261 of this variables to rainfall in each locality.

262 **2.5 Trait Sampling**

263 In order to determine the influence of different mechanisms that could determine
264 the rate of community turnover along the gradient, we constructed a database with
265 morphological and ecological traits hypothesized to vary according to environmen-
266 tal filtering and competition. Below, we will describe the traits and predictions of
267 how we expect the morphological trait space to vary depending on the mechanisms
268 hypothesized to operate in each locality.

269 **2.5.1 Environmental Filtering**

270 To test the hypothesis that the relative importance of environmental filtering is higher
271 in dry forests, we obtained data on species' climatic preferences. We specifically
272 wanted to test the hypothesis that species that occupy the dry forests in the Mag-
273 dalena Valley experience more stressful conditions throughout their ranges. By stress-
274 ful conditions we mean explicitly higher maximum temperatures, wider temperature
275 ranges, higher precipitation seasonality and lower precipitation during the dry sea-
276 sons. All four variables potentially affect species distributions directly or indirectly.
277 For example, wider temperature ranges and higher maximum temperatures might
278 be problematic for the eggs (Webb, 1987) and potentially the adults (McKechnie &
279 Wolf, 2009). Additionally, high precipitation seasonality and low precipitation dur-
280 ing dry season are problematic for water regulation in both adults and nests but
281 also might affect species through resource availability, which might be much lower
282 during the dry season for most (but not all e.g. nectarivores) foraging guilds. To
283 test the environmental filtering hypothesis, we obtained the mean values of diurnal
284 temperature range (bio2), maximum temperature in warmest month (bio5), precipi-
285 tation seasonality (bio15) and precipitation of driest quarter (bio17) for each species
286 throughout their range. We then computed community-wide environmental toler-
287 ances by computing the mean of the species present in the community weighted by
288 the abundance of each species. For the former analysis we assumed that climatic
289 variables are a good proxy for environmental stressors for species and thus for their
290 physiological tolerances. Environmental data were obtained from bioclim (Hijmans
291 *et al.*, 2005) and species distribution ranges from bird life international database
292 (Birdlife International & NatureServe, 2014). Another prediction of the environmen-
293 tal filtering hypothesis is that in communities with stressful environments the species
294 should have more similar environmental tolerances among them than species in more
295 benign environments. Therefore, communities in dry forests should occupy a smaller

296 trait space than wet forest communities. To test this prediction, we estimated func-
297 tional richness and dispersion using community-wide measurements of temperature
298 range, maximum temperature, rainfall seasonality and minimum rainfall. Functional
299 richness is defined as the volume of the convex hull polygon delimited by the values
300 of the n traits and s species present in the community (Cornwell *et al.*, 2006; Villéger
301 *et al.*, 2008). Functional Dispersion estimates the morphological centroid of the com-
302 munity in response to species abundances, and then estimates the spread of species
303 from the centroid of the community (Laliberté & Legendre, 2010). Finally, using
304 the same randomization procedure described previously to test for significance in the
305 turnover of communities, we constructed 1000 random communities, and calculated
306 a SES to determine if functional richness and dispersion of physiological tolerances
307 were smaller than expected by chance particularly in dry forests.

308 Additionally, we sought to test the hypothesis that dry forest species better
309 regulate the temperature of their nests than wet forest birds. Specifically, we wanted
310 to determine if dry forest birds had greater differences between maximum internal
311 and maximum external temperatures throughout their development to determine if
312 selection to avoid temperature extremes may be stronger in dry forests. Also, we
313 explored if dry forest nests had lower internal temperature variability relative to the
314 ambient temperature variability. We followed the development of 57 nests from 23
315 species in two localities, one in dry forest and one in wet forest (Dome = 6, Cup =
316 45, Platform = 6). We recorded temperature inside and 10 cm outside of the nest
317 with a Hobo USB data logger for the length of the entire development of the nest
318 or until it was either abandoned, depredated or nestlings died. We then calculated
319 the difference between the maximum ambient and nest temperatures and the ratio
320 between inside and outside temperature variance. As the ratio converges on one,
321 outside and inside temperature variance are similar. If the ratio is less than one, it
322 means that nest temperature variability is lower than ambient temperature variance

323 and thus the nests are able to dampen environmental variability. Thus, nests that are
324 adapted to avoid extreme changes in temperature that would affect the nest should
325 show a larger difference between inside and outside temperature and a lower than
326 one temperature variability ratio. We asked if there were differences in temperature
327 regulation within nest types among forest types using two sampled t-test. The p-value
328 of all of the t-tests performed were adjusted using bonferroni test correction.

329 **2.5.2 Biotic interactions: Competition**

330 To test the competition hypothesis, which predicts that competitively structured
331 communities will be more overdispersed in morphological trait space, we measured
332 eight morphological traits and one ecological trait that have been suggested to be
333 correlated with the ecology of species (Pigot *et al.*, 2016; Ricklefs, 2012; Miles &
334 Ricklefs, 1984). The traits were: body mass, wing length, tail length, bill width,
335 depth and height and tarsus length and foraging strata. The morphological traits were
336 collected in the field using mistnets to capture birds. Tarsus and bill measurements
337 were collected using a caliper with 0.01 precision and tail and wing length were
338 measured using a wing ruler. Morphological data were available for 123 of the 213
339 species accounted in the analysis. For most of the species we used the mean of
340 at least two individuals but some were represented by only one specimen (n=1225
341 individuals, mean number of individuals per species = 10, Number of species with
342 two or more individuals = 92, Number of species represented by one individual =
343 31). We are aware that the species represented by one individual can potentially bias
344 our analysis, but it is likely that in all of the species within the Magdalena Valley,
345 intraspecific trait variation is smaller than interspecific variation. We estimated body
346 mass for the species that we did not have morphological measurements using the CRC
347 hand book of avian body masses (Dunning Jr, 1992). For foraging strata, we used
348 a recently published database for all the bird species of the world (Wilman *et al.*,

2014). The database separates foraging strata into five separate categories; ground, understory, mid story, canopy and aerial and for each category assigns a proportion of time that the species spends in each stratum. In that way, foraging stratum can be treated as a quantitative trait instead of a categorical one. To maintain foraging stratum as a single trait we coded the stratum from 1 - 5 sequentially from the ground to aerial foraging. Subsequently, we obtained the weighted average for each species, with weights determined by the percent use of each strata. For example, if a species forages 20% of the time in the ground, 40% in the understory and 40% in the mid story the foraging strata value for that particular species was calculated as $Foraging\ Stratum = 0.2 \times 1 + 0.4 \times 2 + 0.4 \times 3 + 0 \times 4 + 0 \times 5 = 2.2$.

Using the nine eco-morphological traits, we performed a principal components analysis (PCA) to reduce collinearity among variables. Because the variables ranged over several orders of magnitude, all of the variables were centered to have a mean of zero and scaled to have variance of one prior to the PCA analysis. We used the rotated scores from the first five PCs (the first five components explained 99.5% of the variation) to calculate functional richness and dispersion indices (i.e. eco-morphological richness and evenness). In competitively structured communities, the prediction is that ecomorphological richness and dispersion are higher than in communities structured by environmental filtering. Given the previous definitions of the metrics of functional diversity, the competition hypothesis predicts that there should be an increase in both functional richness and dispersion with rainfall along the gradient (Pigot *et al.*, 2016; Kraft *et al.*, 2008). The significance of the relationship between eco-morphological richness and rainfall was assessed using a least squares linear regression.

Additionally, to determine if eco-morphological richness and dispersion were higher in wet forest than expected by chance, we constructed 1000 random communities for each of the 15 localities using the entire source pool of the Magdalena Valley,

376 but maintaining both the frequency of each species and the richness of communities.
377 To assemble the random communities we used the independent swap algorithm over
378 1000 iterations (Gotelli, 2000; Hardy, 2008). For each of the 15000 communities, we
379 then calculated eco-morphological richness and dispersion. Finally, we calculated a
380 SES richness and dispersion for each community with the expectation that wet forest
381 communities would have SES values of richness and evenness greater than 1.96.

382 In addition to the competition for food resources, species might also compete
383 for nest space (Martin, 1988). This hypothesis predicts that species in the wet for-
384 est would have more diversified nesting strategies than in dry forests. To test the
385 latter prediction, we calculated nest diversity and dispersion among communities in
386 a similar way than for eco-morphological traits. In this case, because the trait is
387 categorical, functional richness was measured as the number of unique trait combi-
388 nations in the locality (i.e. number of nest types, Villéger *et al.*, 2008). Functional
389 dispersion was calculated in a similar way as described above. Because in the case of
390 nest richness the data are counts of species with the same type of nest, we tested the
391 significance of the functional richness and rainfall relationship using Poisson regres-
392 sions. The relationship between nesting dispersion and rainfall was assessed using a
393 beta regression. Functional dispersion and richness metrics were calculated using the
394 FD package (Laliberté & Legendre, 2010; Laliberté *et al.*, 2014) in R.

395 **3 Results**

396 **3.1 Compositional, Functional and Phylogenetic Turnover**

397 We found support for a stepwise turnover pattern in composition, function and phy-
398 logeny. In all of the cases, the logistic model fit the data better than a simple linear
399 model even though it had at least one more parameter (Table 2, Figure 1). Rainfall
400 explained on average 88% of the variance in community similarity along the gradient

401 (Table 2). The maximum turnover of the communities occurred around the 2300 - 2400
402 mm isocline consistently for the three types of turnover measurements. Communities
403 above and below the 2300 mm isocline are on average 75% different according to the
404 compositional turnover, 64% to the functional turnover and 58% to the phylogenetic.

405 Thirty-seven percent, 71% and 61% of the communities had higher composi-
406 tional, functional and phylogenetic turnover, respectively, than expected by chance
407 between types of forests (Figure 1). Within the dry forest all of the comparisons were
408 smaller than expected by chance according to the compositional turnover. Functional
409 and phylogenetic turnover showed that 71% and 67% of the comparisons respectively
410 had smaller turnover than expected by chance, respectively. Within wet forest, on the
411 other hand, the rates of compositional, functional and phylogenetic turnover showed
412 that 67%, 52% and 19% of the comparisons were significantly smaller than expected
413 by chance. Finally, the dry forests were significantly less variable than the wet forests,
414 as suggested by a lower mean compositional, functional and phylogenetic SES (Com-
415 positional; mean dry = -5.4, mean wet = -2.92, $t = 3.9$, $df = 38.8$, $p > 0.01$; Functional;
416 mean dry = -2.6, mean wet = -1.6, $t = -3.5$, $df = 38.5$, $p = 0.001$; Phylogenetic; mean
417 dry = -2.19, mean wet = -1.1, $t = 3.29$, $df = 39.2$, $p > 0.01$).

418 3.2 Environmental Variables

419 We found that while mean annual temperature was constant among localities ($Temperature =$
420 $27.7 - 3.8 \times 10^{-4} \times Rainfall$; $p = 0.16$), both temperature range ($Temperature Range =$
421 $11.9 - 6.8 \times 10^{-4} \times Rainfall$; $p < 0.01$, $r^2 = 0.57$) and mean maximum temperature
422 ($Max Temperature = 35.9 - 1.1 \times 10^{-3} \times Rainfall$; $p < 0.01$, $r^2 = 0.53$) decreased
423 with rainfall. Also, the coefficient of variation of hourly temperature decreased signif-
424 icantly with rainfall ($Temperature CV = 18.19 - 3 \times 10^{-3} \times Rainfall$; $p < 0.01$, $r^2 =$
425 0.93), suggesting that temperature is significantly less variable as rainfall increases.
426 Finally, rainfall seasonality and rainfall in the driest month significantly increased

427 along the gradient ($Seasonality = 58.4 - 5 \times 10^{-3} \times Rainfall, p < 0.01; r^2 =$
428 $0.45; Min\ Rainfall = 39.7 + 0.09 \times Rainfall, p < 0.01; r^2 = 0.62$)

429 **3.3 Environmental Filtering**

430 We found that community temperature range and rainfall seasonality decreased signif-
431 icantly ($Temperature\ Range = 15.05 + Rainfall^{(-0.054)}; r^2 = 0.59; Rainfall\ Seasonality =$
432 $68 - 4.6^{-3} \times Rainfall; p < 0.01; r^2 = 0.85$) and community minimum rainfall to in-
433 crease with annual rainfall in each locality ($Minimum\ Rainfall = 66.3 + 0.05 \times$
434 $Rainfall, p < 0.01; r^2 = 0.82$; Figure 2). We found no relationship between rainfall
435 and community maximum temperature ($Maximum\ Temperature = 31.9 - 1 \times 10^{-4} \times$
436 $Rainfall, p = 13; r^2 = 0.15$; Figure 2). Physiological trait structure did not follow
437 our predictions. The trait space in physiological tolerances was not smaller or less
438 dispersed in dry forests as expected. This is shown by the non-significant relation-
439 ship between community physiological richness or dispersion and rainfall ($Richness =$
440 $20.4 + 6.8 \times 10^{-4} \times Rainfall, p = 0.8; Dispersion = 1.44 + 6.5 \times 10^{-6} \times Rainfall, p =$
441 0.9). Finally, neither physiological richness nor dispersion of dry forest communities
442 was lower than expected by chance.

443 Among nest types, we found that cup and platform nests in dry forests had
444 significantly lower differences between internal and external max temperatures. Only
445 cup nests in dry forests had significantly lower internal variance relative to the en-
446 vironmental variance when compared to wet forests (Table 3). In fact, the tem-
447 perature variance in cup nests of dry forests was significantly lower than ambient
448 temperature ($Mean = 0.5, df = 3, p = 0.03$). This result means that variance in
449 temperature of cup nests in dry forests was 50% lower than the variance in ambi-
450 ent temperature. The variance in nest temperature of platform nests in dry forests
451 was also 45% lower than ambient variance, but this difference was not significant
452 ($Mean = 0.55, df = 1, p = 0.06$)

453 **3.4 Biotic Interactions: Competition**

454 As rainfall increases, the strength of environmental filtering should decrease and
455 thus competition for resources should be more important in determining commu-
456 nity structure. The competition hypothesis predicts that species co-occurring locally
457 should be ecologically and consequently morphologically more diverse to avoid com-
458 petition (MacArthur & Levins, 1967), but we found no evidence for change in eco-
459 morphological richness or dispersion with increasing rainfall (*Functional Richness* =
460 $86.7 - 2 \times 10^{-4} \times \text{Rainfall}$, $p = 0.99$; *Functional Dispersion* = $1.45 - 9.8 \times 10^{-6} \times$
461 Rainfall , $p = 0.9$). Furthermore, only one site in the wet forest (Barbacoas) had eco-
462 morphological richness higher than expected by chance (Figure 3). We found no rela-
463 tionship between nest richness and rainfall (*Nest Richness* = $5.25 + 3.9^{-4} \text{Rainfall}$, $p =$
464 0.26), but nest dispersion increased with rainfall as predicted (*Nest Dispersion* =
465 $0.23 + 2.99 \times 10^{-5} \text{Rainfall}$, $p < 0.01$; $r^2 = 0.58$).

466 **4 Discussion**

467 Our results suggest that there is deterministic bird community turnover around the
468 2400 mm annual rainfall isocline in the Magdalena Valley in Colombia. The rainfall
469 gradient promoted a strong compositional, morphological and phylogenetic turnover
470 in which almost the entire community was replaced in a short geographic distance.
471 The models are strongly consistent with a stepwise function replacement of the com-
472 munities (Table 1). Around the 2400 mm isocline there is up to a 75% change in the
473 community, whereas in more than 200 km of dry or wet forest spanning a rainfall
474 gradient of more than 1000mm on either side of this transitional zone, the average
475 turnover among communities within the same type of forest was only 41%. Further-
476 more, our results partially suggest that environmental filtering might be of higher
477 importance for structuring communities in the dry end of the Valley. Not only did

478 dry forest communities have significantly less turnover than expected by chance, they
479 also had lower turnover rates than wet forest communities (Figure 1). Species in the
480 dry forests were also better adapted to higher rainfall seasonality and stronger dry
481 seasons (Figure 2). In wet forests, we found evidence that competition for nest sites
482 is stronger than in dry forests and the lower phylogenetic turnover compared with
483 compositional turnover might be an indication of replacements among closely related
484 ecologically similar species that do not coexist because of competition (Robinson &
485 Terborgh, 1995). Nevertheless, there was little evidence that the communities were
486 more dispersed in traits in wet forests than in dry forests suggesting that competi-
487 tively structured niches are not necessarily more likely in wet than in dry forests.

488 Differences in temperature regulation within nest types between types of forests
489 also point to the possibility that climate might be a determinant of community com-
490 position in dry forests. Cup and platform nests in the dry forests dampen the high
491 environmental variability of the habitat whereas they do not in wet forests (Table 3).
492 Our data also show that the difference in maximum inner and outer nest temperature
493 is lower in cup and platform nests of dry forests, suggesting that that species might be
494 more selective of the microclimates of nest sites in the dry than in the wet forests (Ta-
495 ble 3). Such patterns might also result from higher nesting seasonality in dry forest
496 birds, which may only nest during the wet season when temperature variation is less
497 extreme. Thus, an alternative prediction that arises from the environmental filtering
498 hypothesis is that there should be a decrease in nesting seasonality with increasing
499 rainfall. Some studies suggest that in Amazonian wet forests birds nest throughout
500 the year, ignoring rainfall seasonality (Stouffer *et al.*, 2013). In dry forests, however,
501 we have no comparable data on the nesting phenology that could potentially support
502 our hypothesis and predictions.

503 One caveat that rises against the environmental filtering hypothesis is the
504 low support for the prediction that dry forest species should be exposed to higher

505 temperatures throughout their ranges and that physiological trait space in dry forest
506 communities should be smaller and less dispersed compared to wet forest communities
507 (Figure 2). On average species in the dry forests are not exposed to higher temper-
508 atures throughout their ranges than wet forest species and there was no relationship
509 between physiological trait richness and dispersion and rainfall. Also, even though
510 the relationship between mean temperature range of species in the community and
511 rainfall differed significantly, the magnitude of the decrease was less than in 0.5°C,
512 which might not necessarily represent a strong selective agent. It is possible that the
513 resolution of the environmental layers used to collect the data throughout the ranges
514 of the species was not high enough to capture the real strength of the environmental
515 filtering in dry forest. First, our data logger captured hourly and daily variability that
516 were not represented in the broad-scale data. The data obtained across the ranges
517 of species were rough estimates of mean maximum annual temperature and monthly
518 temperature ranges. The hypothesis specifically deals with daily temperature in a
519 few hours in a portion of the days of the year were temperature rises above 40°C.

520 Birds can potentially compete for nest resources, which might influence commu-
521 nity assembly (Martin, 1988). We found support for this hypothesis as the dispersion
522 in nesting types increased significantly with rainfall. Such patterns further support a
523 shift in the mechanisms that drive community composition along the gradient. One of
524 the ways that environmental filtering may be operating in the dry forests is through
525 high variability and extreme high temperatures in the dry forests. Such mechanisms
526 would predict lower functional dispersion of nesting types as the nests that better
527 regulate temperature should be selectively favored in this type of forest. We provide
528 some evidence that cup and platform nests in dry forests better regulate temperature
529 than the same types of nest in wet forests, in which temperature extremes may not
530 be great enough to require regulation of the microclimate. Nevertheless, our results
531 indicate that temperature is a potential determinant of species composition and/or

532 behavior. The increase in rainfall was associated with a decrease in temperature
533 variability and maximum temperature. If temperature regulation is not a problem
534 in wet forests, it opens the possibility of a diversification in nest types to decrease
535 the impact of competition. In dry forests, however, the reduction in nest types could
536 increase competition as it is more critical for species to select for the best places to
537 locate nests and avoid high temperatures. Thus, environmental filtering may increase
538 competition for a potentially limiting resource (i.e., nest sites), which could further
539 constrain which species can occur in a community.

540 Our functional trait data do not support the hypothesis that there is stronger
541 competition for resources in the wet forests as there was no difference in the trait
542 space of wet and dry forests. Alternatively, competition for resources in the dry forest
543 may occur at similar levels in both communities. Many studies have inferred that
544 competition is an important determinant of bird species distributions and abundance
545 (Jankowski *et al.*, 2012), but few of these studies were conducted in dry forests, which
546 have been historically understudied (Oswald *et al.*, 2016). Thus, our data suggest
547 that in addition to the environmental filtering, competition for resources might also
548 influence dry forest communities. However, neither eco-morphological richness nor
549 dispersion was higher than expected by chance in any of the localities. The other
550 potential explanation is that the morphological traits are not related to the niche
551 axes that experience competition (Miles & Ricklefs, 1984; Ricklefs, 2012) or that the
552 relationship between ecology and morphology is much more complex than previously
553 thought (Pigot *et al.*, 2016). Thus, it is also possible that that competition happens
554 through other niche axes that we were unable to detect in this study.

555 One hypothesis that remains to be tested is the possibility that predation is
556 stronger in wet forests, influencing community assembly (Martin, 1988; Jankowski
557 *et al.*, 2012). Many of the most important nest predators were only found in the wet
558 forest. Preliminary data suggest that the three toucan species exclusively found in

559 wet forest during my study (unpublished Data) are strong nest predators in these
560 forests of the Magdalena Valley (G. Londono, unpublished data). In addition to the
561 toucans, the number of forest raptors also increases as well as the richness of primates
562 (Gomez et al unpublished data) in wet forests. While it has been hypothesized that
563 cavity nests might protect the eggs and nestlings from heavy rainfall (Oniki, 1985),
564 there is more evidence to suggest that this type of nest provides protection against
565 predators (Oniki, 1979, 1985). Thus, increased predation pressure in wet forests might
566 select for the observed increase in cavity nesters and a decrease in cup nesters with
567 rainfall. Our data support this prediction (Figure 4) but the main assumption –that
568 nest predation in dry forests is significantly lower than in wet forest– remains to be
569 tested. Thus, our data are inconclusive about this hypothesis which we believe might
570 be an interesting one to test in the future.

571 In our study functional and phylogenetic turnover were lower than composi-
572 tional turnover. A lower functional than compositional turnover suggests that there
573 are some similar niches to be filled in both wet and dry forests, even though the
574 niches are filled by different species with the same functional traits. This scenario
575 would support a turnover mediated by interspecific competition (Robinson & Ter-
576 borgh, 1995). In their work, Robinson & Terborgh (1995) report that intrageneric
577 replacements along a productivity gradient in lowland Amazonia responded to inter-
578 specific aggression between ecologically similar species. The heavier congener almost
579 always actively displaced the smaller congener from the sites with higher produc-
580 tivity. We found several examples of replacement among ecologically similar species
581 along the Magdalena Valley that fit this scenario. For example, white-bellied antbird
582 (*Myrmeciza longipes*) in the dry forest is replaced by the chestnut-backed antbird
583 (*Myrmeciza exsul*) in the wet forest. Both forage in similar habitats, close to the
584 ground and potentially searching for similar insect items. An other example is the
585 replacement of the endemic Apical flycatcher (*Myiarchus apicalis*) with its close rela-

586 tive dusky-capped flycatcher (*Myiarchus tuberculifer*). Both of these examples as well
587 as some other ones occur among close relatives most likely in the same genus. Such
588 patterns would lead to lower phylogenetic turnover. The functional and phylogenetic
589 turnover, however, are still higher than expected by chance between forests and lower
590 than expected by chance within forests suggesting a high change in function and
591 evolutionary history of these communities with rainfall (Figure 1).

592 Even though we found a mismatch in the amount of turnover among composi-
593 tional, functional and phylogenetic metrics, there is a spatial congruence in where the
594 turnover happens (Table 2, Figure 1). The three metrics predict that the community
595 shift happens at the boundary delimiting the Magdalena dry forests and Magdalena-
596 Uraba moist forests ecoregions (Olson *et al.*, 2001). Provided that the ecoregions
597 of northern South America were delimited by vegetation data (Olson *et al.*, 2001),
598 this suggests a spatial match in the turnover of bird and plant communities along the
599 rainfall gradient. Others have found strong associations between the turnover of plant
600 and bird communities (Jankowski *et al.*, 2013), suggesting that vegetation might have
601 a very strong influence on the structuring of tropical bird communities. There might
602 be direct and indirect effects of vegetation on bird communities but we hypothesize
603 that in the case of the Magdalena Valley the effects are direct. The dry forest tree
604 community is mainly deciduous, such that in the dry season, the entire forest loses
605 its canopy over, potentially increasing temperatures inside the forest, at least during
606 the day. In the wet forest, the canopy is more permanent throughout the year, which
607 stabilizes temperature and eliminates the strong filtering by high temperatures. This
608 hypothesis predicts that the limits of the dry and wet forest are associated with a
609 strong change in the proportion of deciduous trees that compose the canopy.

610 In conclusion, we provide evidence that suggests that the mechanisms driving
611 community assembly along the Magdalena Valley in Colombia change with precipita-
612 tion. In localities with low rainfall (<2400 mm), we found evidence for environmental

613 filtering, whereas in localities above the 2400 mm isocline we found only partial evi-
614 dence supporting stronger biotic interactions (e. g., predation and nest site use). This
615 change in mechanisms can potentially explain the strong compositional, functional
616 and phylogenetic turnover that happens abruptly over a short geographic distance.
617 The Magdalena River has been one of the major centers for development in Colombia
618 since colonial times. The high within-forest community variability might reflect this
619 long history of fragmentation and deforestation (Harrison, 1997; Pardini *et al.*, 2005).
620 We report here that the Magdalena Valley bird communities might be two separate
621 entities with high functional and phylogenetic diversity. Despite its high diversity
622 and high levels of fragmentation and deforestation, there are no protected areas in
623 the region. Our data suggest that the upper and middle Magdalena Valley must be
624 treated separately in conservation strategies.

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799 **6 Tables**

Locality	Elev	Bio12	Dist	Bio1	Bio2	Bio5	Bio15	Bio17	Points	Reps
Bateas	429	1193.5	3.29	27.5	11.7	35.1	60	78	36	3
El Triunfo	196	1281.8	8.40	27.3	10.4	34	51	217	7	2
Potosi	400	1330.5	1.47	27.4	11.3	35	58	102	30	2
ManaDulce	490	1456	5.04	27	11.2	33.8	46	176	32	4
Venadillo	335	1599.7	10.39	27.5	11.3	34.5	45	174	20	2
Jabiru	341	1623.5	4.77	27.2	10.4	33.9	48	216	27	4
Boqueron	650	2249.6	6.37	26.2	10.8	32.6	44	219	13	1
Mariquita	475	2263	0.00	26.2	9.8	32.5	43	334	11	2
Maceo	639	2554	17.67	25.9	9.9	31.5	43	265	13	2
Barbacoas	138	2675.2	6.16	27.8	9.9	33.6	45	245	34	3
Rio Manso	160	2697.1	9.22	27.4	10.2	33.6	47	325	26	4
La Perla	300	2714.7	16.79	27.1	9.6	32.5	35	399	9	1
San Juan	168	2888.5	11.07	28.1	9.7	33.8	44	254	20	4
Remedios	718	2906.3	20.22	25.4	9.7	31.1	44	272	20	3
Rio Claro	449	3775.9	3.88	26.1	10.1	32	43	347	15	4

Table 1: Location and description of localities sampled along the rainfall gradient of the Magdalena Valley. We show environmental variables as well as number of point counts and replicates per point count performed in each forest patch. Elev = Elevation (m), Bio12 = Annual Rainfall (mm), Dist = Distance to climatic station (Km), Bio2 = Mean Diurnal Temperature Range ($^{\circ}$ C), Bio5 = Max Temperature of Warmest Month ($^{\circ}$ C), Bio15 = Precipitation Seasonality (Coefficient of Variation), Bio17 = Precipitation of Driest Quarter (mm), Points = Number of census points for birds, Reps = Number of Replicates each point was censused

Model	Intercept	m	a	b	c	R^2	AIC
Logistic							
Compositional			0.61(0.23,97)	210.4(8.59,478.4)	2425.2(1840,3772.5)	0.88	-15.32
Functional			0.44(0.08,0.68)	362.7(64,507.8)	2457.5(1899.9,5810.3.8)	0.87	-24.33
Phylogenetic			0.32(-0.03,0.5)	409.24(75.14,625.4)	2317(1987.9,6453.1)	0.91	-38.81
Linear							
Compositional	-0.87(-1.15,-0.59)	4e-04(3e-04,5e-04)				0.79	-8.55
Functional	-0.6(-0.84,-0.42)	3e-04(1.9e-04,3.7e-04)				0.79	-17.7
Phylogenetic	-0.46(-0.59,-0.32)	2e-04(1.5e-04,2.6e-04)				0.81	-29.8

Table 2: Results of model selection for the relationship between community similarity and rainfall. Intercept and m are the parameters of the linear model and a, b and c are the parameters estimated for the logistic model. The best model is the one with the lowest AIC and significant differences among models are determined by differences greater than 2 in their AIC.

Type of Nest	Dry	Wet	df	p
Max Difference				
Cup	4.69	9.6	8.5	> 0.01
Dome	5.93	4.17	2.96	1
Platform	3.65	9.12	2.99	0.02
Variance Ratio				
Cup	0.5	3.57	36.5	> 0.01
Dome	1.63	1.87	3.71	1
Platform	0.55	1.46	2.07	1

Table 3: Results of t-tests comparing max difference and variance ratio between nest and ambient temperature among nests in dry and wet forests. The results are product of multiple t-tests comparing types of nests and each type of nest between localities. For comparison among types of nests the objective was to determine if the difference between nest and ambient temperature was less than zero and less than one in the case of the ratio of variances.

800 **7** Figures

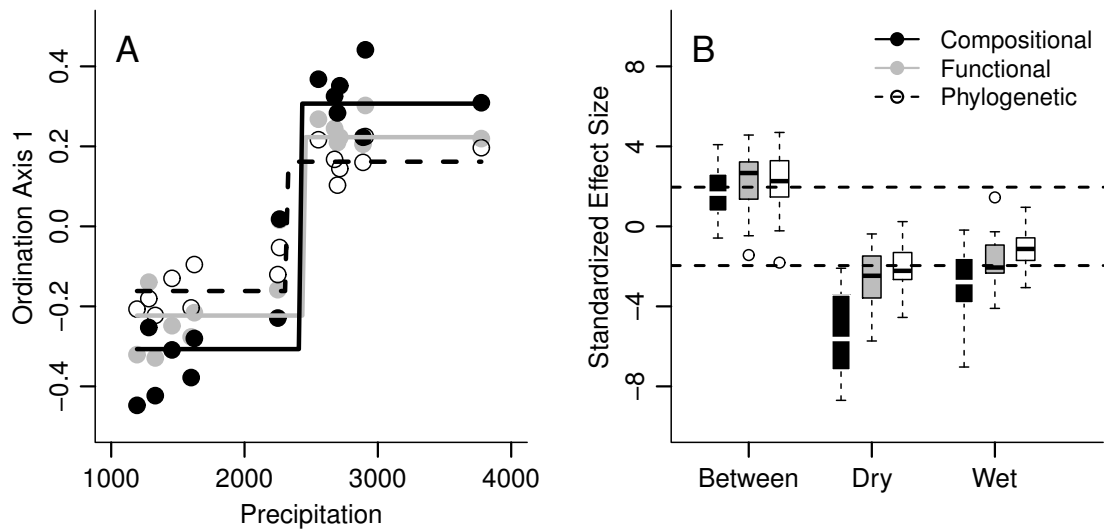


Figure 1: Compositional, functional and phylogenetic turnover of lowland bird communities along the rainfall gradient of the Magdalena Valley, showing (A) a step turnover around the 2300 mm rainfall isocline that is consistent among the measurements, but the measurements decrease in strength of turnover from compositional to phylogenetic, and (B) shows the distribution of the Standardized Effect Sizes for three types of comparisons: between and within wet and dry forests, showing higher than expected by chance turnover between types of forest and lower than expected by chance turnover within dry forests.

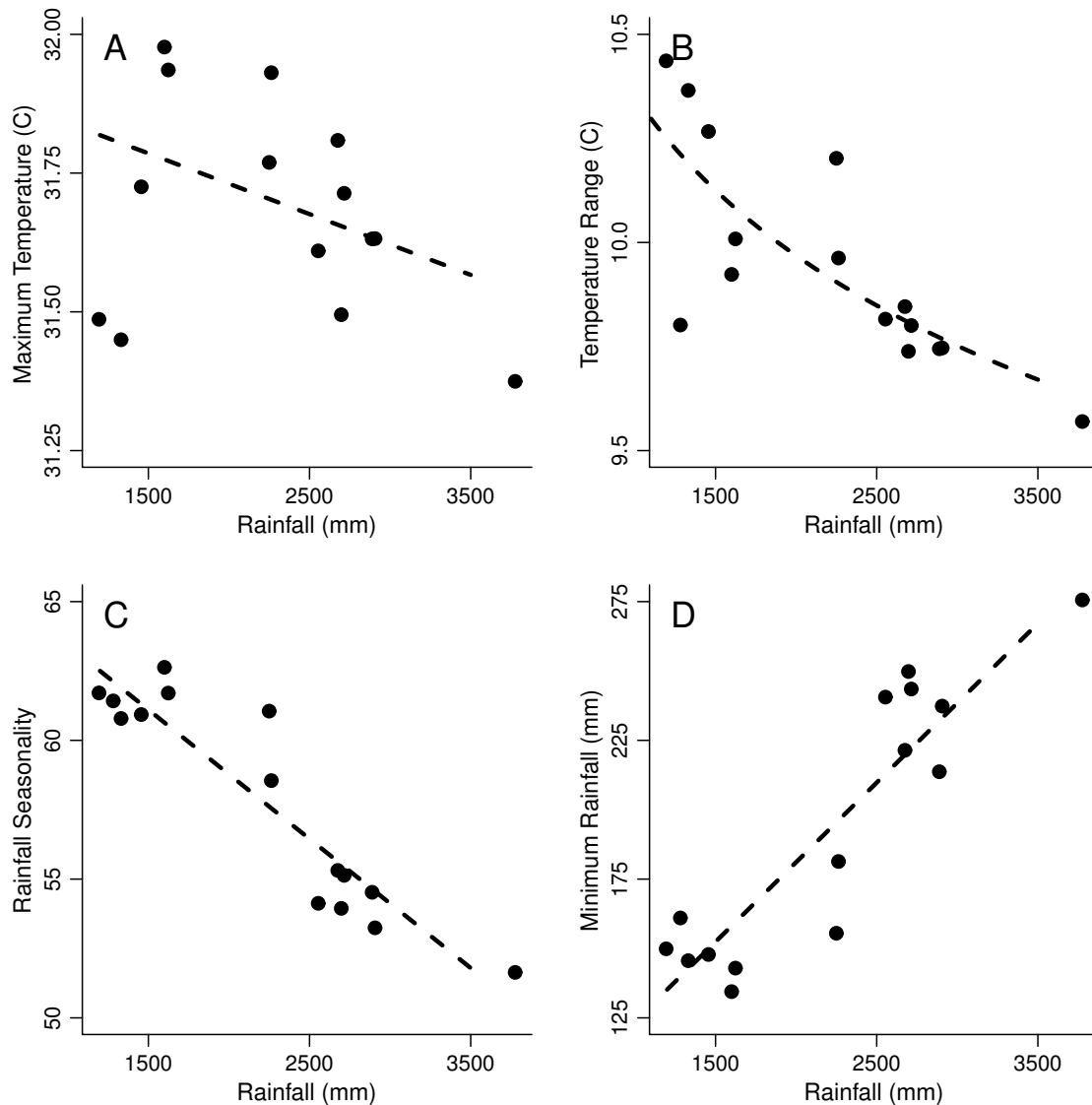


Figure 2: Relationship between average community physiological tolerances and rainfall, showing, (A) no relationship between community average maximum temperature tolerance; (B) a negative relationship between average community temperature range and rainfall; (C), a decrease in mean community rainfall seasonality with locality rainfall and; (D) an increase in the minimum rainfall that species experience throughout their ranges.

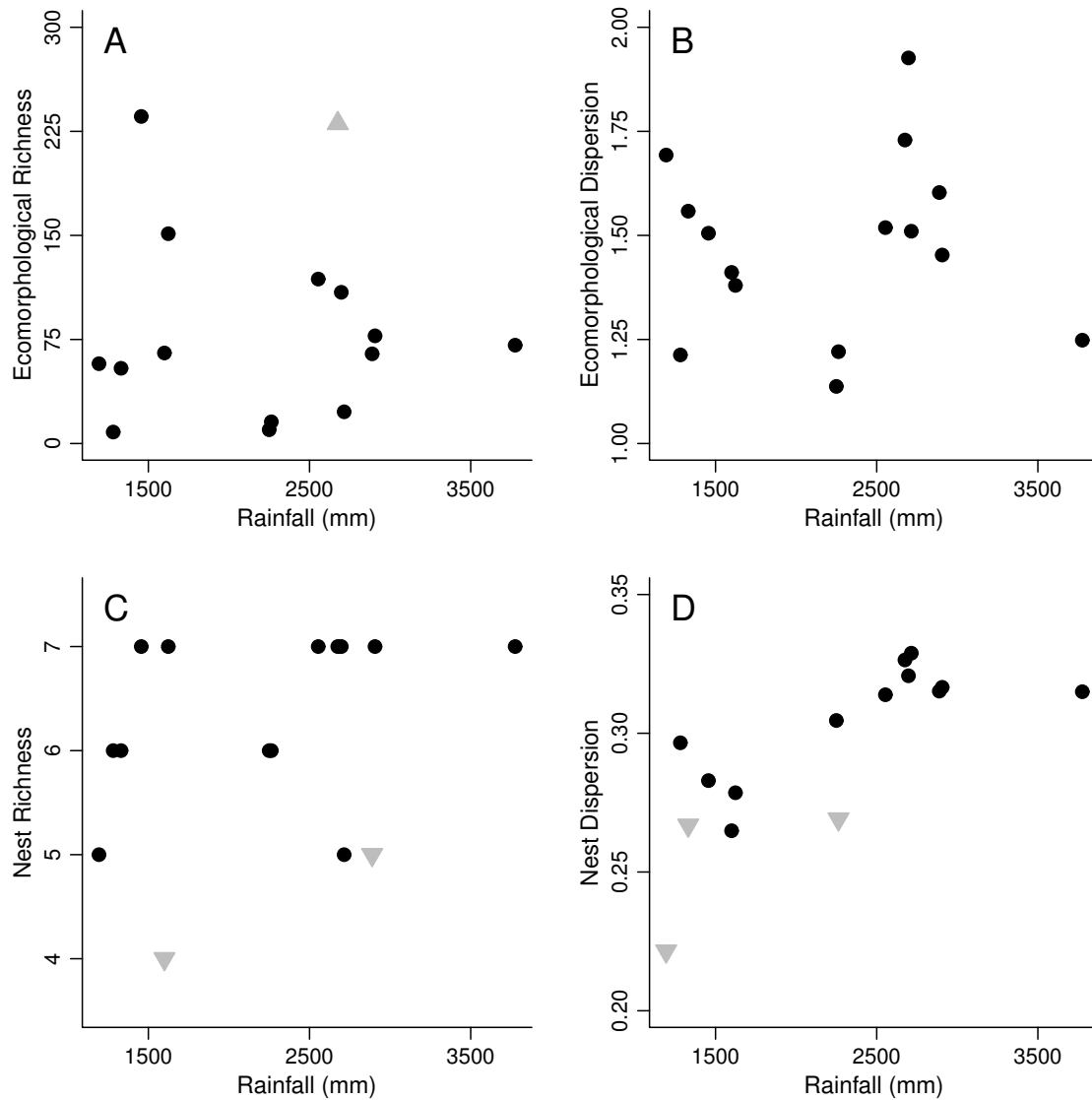


Figure 3: Eco-morphological and nest structure of communities along the rainfall gradient of the Magdalena Valley. A and B show no relationship between ecomorphological richness and dispersion and rainfall. C shows a slight but not significant increase in nest richness with rainfall and D shows a significant increase in nest dispersion throughout the gradient. Grey triangles indicate localities in which functional richness or dispersion was higher (triangles pointing up) or lower (triangles pointing down) than expected by chance

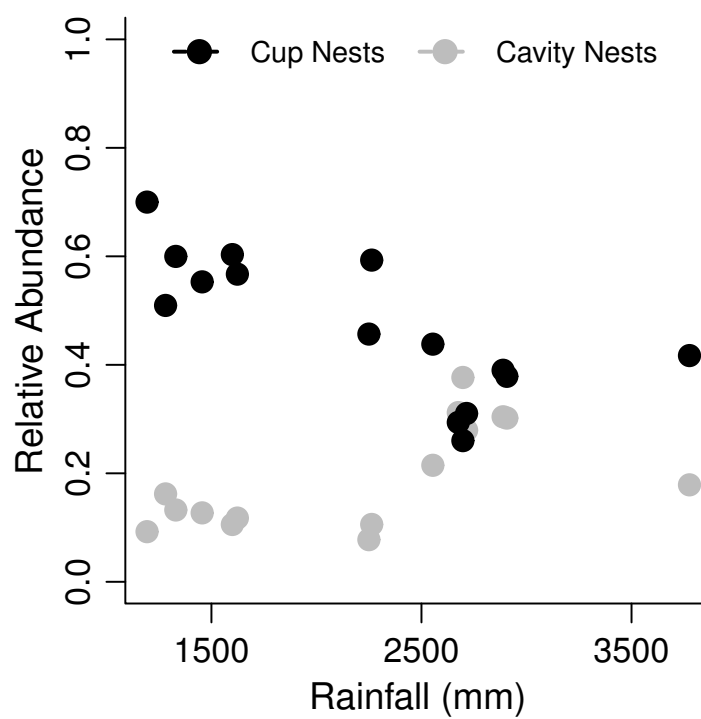


Figure 4: Relative abundance of Cavity and Cup nests along the rainfall gradient of the Magdalena Valley. Gray and black dotted lines are the fitted lines from a beta regression for the relationship between cup and cavity nests and rainfall.