1 **Climate influences the response of community functional traits to local conditions**

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70 **Climate influences the response of community functional traits to local conditions**

75 **Abstract**

76 Functional traits determine an organism's performance in a given environment and as

77 such determine which organisms will be found where. Species respond to local

78 conditions, but also to larger scale gradients, such as climate. Trait ecology links these

79 responses of species to community composition and species distributions. Yet, we often

80 do not know which environmental gradients are most important in determining

81 community trait composition at either local or biogeographical scales, or their interaction.

82 Here we quantify the relative contribution of local and climatic conditions to the structure

83 and composition of functional traits found within bromeliad invertebrate communities. We

84 conclude that climate explains more variation in invertebrate trait composition within

85 bromeliads than does local conditions. Importantly, climate mediated the response of

86 traits to local conditions; for example, invertebrates with benthic life-history traits

87 increased with bromeliad water volume only under certain precipitation regimes. Our

88 ability to detect this and other patterns hinged on the compilation of multiple fine-grained

89 datasets, allowing us to contrast the effect of climate vs. local conditions. We suggest

90 that, in addition to sampling communities at local scales, we need to aggregate studies

91 that span large ranges in climate variation in order to fully understand trait filtering at

92 local, regional and global scales.

Introduction

Ecologists are reformulating long-held perspectives on biodiversity using functional traits. Since organisms interact with their environment through their traits, patterns in species distribution should be a direct function of their traits. Traits directly affect community assembly and species interactions, such that any snapshot of a community is the result of i) physiological tolerances (Winemiller et al. 2015, Pianka et al. 2017), ii) species interactions (Chesson 2000, Chase and Leibold 2004, Estes et al. 2011), iii) dispersal and priority effects (MacArthur and Wilson 1967, Diamond 1975, Hanski 1999), iv) demographic stochasticity (Lande et al. 2003, Hubbell 2011), and v) phylogenetic constraints (Vellend 2016, Pianka et al. 2017). Most of these mechanisms are, to some degree, driven by functional traits (mechanisms i-iii) or determine the distribution of traits (mechanism v), and their prevalence and diversity modulate the relationship between biodiversity and ecosystem function rather than species *per se* (Schmitz et al. 2015). Similarly, the redundancy of functional traits in a community can maintain ecosystem function and stability in the face of environmental change and species loss (Loreau et al. 2001). By shifting our focus away from taxonomic diversity to the diversity of functional traits within a community or metacommunity, we strengthen our ability to detect the mechanisms that underlie observed patterns in species distribution and biodiversity (McGill et al. 2006). In particular, functional traits have been associated with broad biogeographic patterns, such as the latitudinal gradient in biodiversity, leading to new insights into the processes and causes of global biodiversity (Chave et al. 2009, Ricklefs 2012, Lamanna et al. 2014).

114 This trait-based paradigm recasts community ecology's central question about species

115 diversity and coexistence as: which processes determine the functional trait composition

116 of ecological communities? Spatial scale is implicit in this question, as different processes

117 are expected to act at different scales (Levin 1992, Chave 2013). For example, species

118 interactions are expected to be strongest at small spatial scales, whereas environmental

119 filtering often occurs at spatial scales large enough for environmental gradients to

120 exceed physiological thresholds (Kraft and Ackerly 2010). Finally, processes like dispersal

121 limitation and biogeographical constraints to the species pool often operate at the

122 largest spatial scales (Ricklefs and Schluter 1993). The grand challenge of integrating

123 these multiple scale processes on traits can only be resolved by a synthesis of traditional

124 small-scale ecology with macroecology and biogeography (Violle et al. 2014).

125 Environmental conditions could have cross-scale effects on functional traits in several

126 ways. First, local factors (e.g. resource availability) could scale up to affect the geographic

127 distribution of functional traits, or, local conditions such as microclimate may compensate

128 apparently limiting climatic conditions. Second, climatic and biogeographic factors could

129 constrain the local distribution of functional traits and thereby impact local processes. A

130 practical difficulty of including large scale environmental factors or biogeography into

131 syntheses of local scale studies is that some variables will be spatially pseudo-replicated

132 and others will not. That is, several field studies that fall within a single climatic zone or

133 geographic region may not represent independent measures, yet a large number of

134 sampling units are needed to detect local effects on community functional trait

135 composition. These issues can be partially resolved by a spatially structured hierarchical

136 analysis.

137 The theory and motivation for our study could be applied to almost any ecological

138 community. Yet, the data required to test this theory requires extensive information on

139 species composition, functional traits, local conditions and climate for multiple

140 georeferenced occurrences of a defined community across a broad geographic range;

141 such data are rarely available for multitrophic communities. Here we use the aquatic

142 macroinvertebrates in tank bromeliads as a model system to understand community

143 structure. The invertebrate communities in tank bromeliads have proven to be useful

144 systems for testing ecological theory, as they are easily manipulated and censused and

145 are naturally highly replicated. Previous work has related ecosystem functions, trophic

146 structure and system resilience to a variety of invertebrate functional traits (Dézerald et

147 al. 2015, 2018, de Omena et al. 2019). To date, researchers of this system have primarily

148 focused on local-scale explanations for community composition and ecosystem function,

149 detailing how bromeliad size (volume of aquatic habitat), detrital inputs, and canopy

150 cover affect community composition (Petermann et al. 2015, Kratina et al. 2017). However,

151 much of the geographic variation in invertebrate composition remains unexplained, and

152 consequently begs for more explicit incorporation of broad-scale variables like climate.

153 For example, extreme rainfall events lead to an inversion of the trophic pyramid of

154 macroinvertebrates in bromeliads across seven study sites broadly distributed across the

155 neotropics (Romero et al. 2020).

156 Here, we used fine-grain data on the functional traits of aquatic macroinvertebrates

157 sampled in more than 1600 tank bromeliads across 18 climate zones throughout the

158 Neotropics to partition the separate and combined effects of local conditions and climate

159 on community trait composition. Based on previous studies of bromeliad

160 macroinvertebrate ecosystems, we expect that both local conditions and climatic

161 gradients affect trait composition (Céréghino et al. 2011, 2018, Dézerald et al. 2015). We

162 tested three hypotheses of how trait variation could be partitioned between local and

163 biogeographical environmental gradients: (i) Variation in trait composition is primarily

164 explained by variation in the environment at the biogeographic scale. This would occur

165 when climatic factors, which vary only at biogeographic scales, determine the cost and

166 benefits of different functional traits. For example, temperature determines development

167 rates (Damos and Savopoulou-Soultani 2012) and predation pressure (Romero et al.

168 2018), while precipitation determines the mortality rates due to desiccation (Amundrud

169 and Srivastava 2015). (ii) Variation in trait composition occurs primarily along regional

170 environmental gradients, or the interaction between local conditions and the climate at a

171 given region. This would occur when heterogeneity in local conditions determines life

172 history traits. For example, traits may vary as a response to the availability of resources

173 within a bromeliad (Srivastava et al. 2008) and the avoidance of negative species

174 interactions (Hammill et al. 2015). (iii) Neither local nor regional conditions determine trait

175 composition. This would occur at the regional scale if strong biogeographic constraints

176 dampen any effect climate may have on traits. For example, geographic dispersal

177 barriers on particular clades (Amundrud et al. 2018), coupled with deep phylogenetic

178 signal on some traits override the effects of climatic conditions. Similarly, at a local scale,

179 stochasticity in colonization coupled with noise added by a generalist predator can

180 overwhelm any signal caused by environmental gradients (Srivastava and Bell 2009). We

181 used hierarchical analyses to distinguish between these three hypotheses by testing the

182 effects of local conditions, climate, and their interaction on the community functional

183 traits of bromeliad invertebrates at local and bioclimatic scales.

184 **Methods**

185 *Invertebrate traits*

186 We used as functional trait values the species scores on four main axes of invertebrate

187 trait variation identified by Cereghino et al. (2018), which represent life-history strategies

188 along trophic, habitat, defence and life-history niche axes describing ca. 852 aquatic

189 invertebrate taxa occurring in Neotropical tank bromeliads , mostly identified to species

190 or morphospecies (hereafter "species"). For completeness, in the following we explain

191 the method used by Cereghino et al. (2018) to identify such a synthetic traits: Each of

192 these species was characterized by 12 nominal traits: maximum body size, aquatic

193 developmental stage, reproduction mode, dispersal mode, resistance forms, respiration

194 mode, locomotion mode, food, feeding group, cohort production interval, morphological

195 defence, and body form. Each nominal trait had a number of modalities, or states. For

196 example, the states for the trait "feeding group" were "deposit feeder", "shredder",

197 "scraper", "filter-feeder", "piercer" and "predator". A full description of traits and states

198 can be found in Céréghino et al. (2018). Information on these traits was structured using a

199 fuzzy-coding technique (Chevenet et al. 1994): scores ranged from "0" indicating "no

200 affinity", to "3" indicating "high affinity" of the species for a given trait state. Scores were

201 based on observations of specimens (Dézerald et al. 2017), on the scientific literature

202 (e.g. Merritt and Cummins 1996, Céréghino et al. 2011) and expert opinion (see Céréghino

203 et al. 2018 for list of traits, modalities, and their definitions) the species x trait matrix is

204 available at https://doi.org/10.5281/ zenodo.1200194. Principal Component Analysis (PCA)

205 was used to reduce trait dimensionality to significant axes of trait variation. The

206 rank-transformed [species x trait] matrix was used to compute Spearman's rank

207 correlations between trait modalities, which then underwent PCA with bootstrap

208 resampling (Pillar, 1999). This procedure allowed us to test ordination stability and to

209 interpret the significant ordination axes in light of correlations with trait states. We

210 identified a robust set of four orthogonal and important axes of trait variation, namely

211 trophic position, habitat use, morphological defence, and life cycle complexity (Céréghino

212 et al. 2018). The species scores for these four PCA axes (available at

213 https://doi.org/10.5281/zenodo.1200194) thus represented continuous trait values, or

214 synthetic traits, which we then used in analyses of the processes underlying functional

215 diversity across different spatial scales in relation to environmental factors (this study).

216 *Site sampling*

217 The data for the present study consists of the abundance of macroinvertebrates found

218 within 1436 bromeliads in 18 field sites in 8 countries (Bromeliad Working Group BWG

219 database, Table A1). While the Bromeliad Working Group has sampled more countries

220 and field sites, we only use the sites where more than 15 bromeliads were sampled.

221 Some of these field sites were visited in multiple years (Table A1), while others were

222 visited only once. While we acknowledge there are temporal trends in community

223 abundance and composition, all of our sampling units (each sampled bromeliad) are a

224 snap-shot of the community structure, so we made the simplifying assumption to treat all

225 sampling units within a site the same, regardless of the year in which they were

226 collected. Examining temporal trends in trait composition, would be an interesting follow

227 up study.

228 The full suite of 19 bioclimatic variables was extracted from WorldClim using the latitude

229 and longitude of each sampled site (Fick and Hijmans 2017). Some of our sampling

230 locations were within 1 km^2 of one another. As such, these locations had the same

231 climatic conditions since this is the smallest resolution in WorldClim. We decided to group

232 the data collected from these locations, instead of attempting to downscale the climatic

233 conditions to a smaller resolution. After grouping the data from these locations, we

234 ended up with 18 sites, which we refer to as bioclimatic zones.

235 *Bromeliad sampling*

236 The following bromeliad genera were sampled across all sites: *Neoregelia*, *Quesnelia*,

237 *Tillandsia*, *Guzmania*, *Vriesea*, *Aechmea* and *Catopsis*. Each tank bromeliad was

238 exhaustively sampled either by dissecting the rosette, or by pipetting out all of its

239 contents. The bromeliad macroinvertebrate community is defined as all the aquatic

240   invertebrates found by the naked eye (> 0.5 mm) within a single plant. A total of 637

241   morpho-species were found.

242   Three local conditions were collected for each plant: water volume at time of sampling

243   (mL), total amount of detritus (mg), and canopy cover (either open or closed canopy). The

244   data on total amount of detritus and the water volume at the time of sampling were

245   log-transformed before the analyses. These variables are proxies of habitat size and

246   energy inputs, which are key drivers of food web structure (Oertli et al. 2002, Moore et

247   al. 2004). The total amount of detritus was calculated by adding the amount of small,

248   medium and large detritus. In 25.8% of bromeliads, total detritus was not measured

249   directly, instead we imputed total detritus with allometric relationships using other size

250   categories of detritus, and in a few cases with the number of leaves and the diameter of

251   the plant. In 50.4% of bromeliads, total water volume was not measured directly and

252   instead we imputed total water volume using leaf size, plant species, plant height, plant

253   diameter, and number of leaves. When either of these variables were missing, we used

254   generalized linear models with a Gaussian error distribution to impute missing values.

255   Thus, the dataset was a combination of directly measured and estimated values.

256   *Spatial scale of environmental variation*

257   To better understand the spatial scale of environmental variation, we partitioned the

258   variation in local environmental conditions of a bromeliad into site and bioclimatic scales

259   using three nested hierarchical models, one for each response. All three models used

260 the same structure of random effects, but different likelihoods according to the

261 environmental variable. The environmental variables partitioned in this way included log

262 detritus (normal likelihood) log water volume (normal) and canopy cover (binomial). By

263 using nested random effects, we can partition the variation of each local environmental

264 condition by spatial scale and determine at which spatial scale most of the variation is

265 explained. For each environmental variable, we estimated random effects for the field

266 visit (site by year combination) within bioclimatic zone, and bioclimatic zone. We also

267 calculated the correlation between all local conditions both within and across all

268 bioclimatic zones.

269 *Trait analysis*

270 Since our unit of analysis is the bromeliad invertebrate community, it was necessary to

271 quantify the presence and abundance of the animals and their traits for each bromeliad.

272 To do this, we calculated the community weighted means (CWM) of each synthetic trait

273 for each bromeliad (local scale analysis). Community weighted means (CWM) was given

274 by:

$$CWM \ = \ \sum_{i=1}^{n} p_i x_i \, , \tag{1}$$

276 where p_i is the proportion of species abundance, x_i is the trait value of that species and n

277 is the number of species in that community (Garnier et al. 2004, Swenson 2014). To

278 reduce the effect of highly abundant species on the analysis, we applied a square root

279 transformation of the proportional abundance of invertebrates within a bromeliad (i.e. a

280 Hellinger transformation). This transformation was necessary since we used abundance

281 and not biomass, and the most abundant species were orders of magnitude (up to 100s

282 of individuals) more abundant than the least abundant species (1 or 2 individuals)

283 (Legendre and Gallagher 2001). The square root transformation de-emphasizes

284 superabundant species (gave a more equal weight to rare species), and the community

285 weighted means (CWM) allowed us to characterize the relative abundance of traits in the

286 sampled bromeliad.

287 Community weighted means were obtained using the data version 0.7.7 extracted from

288 the BWG database in July 2017.

289 To determine the effects of environmental conditions on the CWM computed using the

290 species scores on the four synthetic traits, we used a permutational multivariate analysis

291 of variance - PERMANOVA (vegan R package; Anderson 2001). This method is based on

292 within- and between-group sums of squares computed on pairwise dissimilarities, in this

293 case, of bromeliad communities considering the CWM trait values. However, instead of

294 permuting the site matrix (bromeliads or bioclimatic zones), we adapted the method to

295 permute among the species vectors in the trait matrix and recomputed the CWMs, to

296 reduce the risk of type I error (Peres-Neto and Kembel 2015, Hawkins et al. 2017, Zelený

297 2018). Since each bioclimatic zone differs in the number of bromeliad communities

298 sampled (Table A1), and sample size may bias the relative amount of variance explained,

299 we devised a sub-sampling scheme where we randomly selected 15 bromeliads from a

300 randomly selected field visit within a bioclimatic zone (18 zones, Figure 1). Note that the

301 minimum number of bromeliads per site is 18 (Table A1), therefore for some sites, most

302 bromeliads are selected in every sub-sampling procedure. We found that 15 bromeliads

303 is the minimum number that still provides a comprehensive sample of the community

304 within a field visit. Every time we performed this sub-sampling procedure, we ran the

305 multivariate statistical analysis and compiled the main results (sum of squares). We

306 repeated this process 1000 times. We used the marginal sum of squares in the analysis

307 without interactions and the sequential sum of squares in the analysis with interactions to

308 the variation explained by the main effects. From these runs, we obtained a distribution

309 of P-values and sums of squares. We do not report P-values of individual runs, because

310 they do not represent valid independents tests, however, we do report the P-values of a

311 non-sub-sampled analysis in the appendix (Tables A3 and A4). Some of the distributions

312 of sums of squares were skewed, while some were normally distributed (Figure A5). To

313 summarize this variation, we first calculated the mean of the sum of squares explained by

314 each predictor across all sub-samplings, and then calculated the total contribution of

315 local conditions, climate variables, and their interaction. This procedure allowed us to

316 take advantage of the central limit theorem to ensure that the addition occurs on

317 normally distributed means.

318 We performed the multivariate analysis of variance for each spatial scale to replicate a

319 'fine-grained analysis' (Figure 1a), a 'coarse-grained analysis' (Figure 1b) and a

320 fine-grained analysis with resource-climate interactions (Figure 1c). Thus, we are able to

321 compare the explanatory power of these models to explain functional trait composition if

322 we only had local conditions, climate information or both. (i) For the fine-grained analysis,

323 we used each bromeliad as the sampling unit and only tested the effects of local

324 conditions (that is the environmental conditions that were measured for every bromeliad:

325 water level, detritus amount, and canopy cover). We restricted the sub-sampling to field

326 visits (site by year combination) to ensure that macroinvertebrate traits relating to species

327 that only occurred in a single bioclimatic zone (most species) were not mixed between

328 countries or years (Figure 1 - fine-grained analysis). Analysis using bromeliads as

329 sampling units and only climatic variables as predictors were used to filter the 19

330 bioclimatic variables to a smaller subset. We retained climatic variables that explained a

331 significant proportion of variation in at least 5% of the runs (BC2, 4, 15 and 17), and which

332 were then used in subsequent analyses. In 1000 randomizations we expect at least 5% of

333 runs to appear significant by chance (type I error), so we only report explanatory

334 variables that are significant in >5% of runs. (ii) For the coarse-grained analysis, we used

335 the 'bioclimatic zone' as units for which we calculated the species pool CWM by

336 summing the abundance of all the morphospecies across the sub-sampled 15 bromeliads

337 and only tested the effects of climatic variables (Figure 1 - coarse-grained analysis). (iii) To

338 test for the interactions between climate and local conditions, we used the bromeliad as

339 the sampling unit, and tested the effect of local conditions, climate and their interactions

340 (Figure 1 - fine-grained analysis with resource-climate interactions). We did not include

341 the interaction between canopy cover and climatic conditions because few bioclimatic

342 zones had both open and closed canopy, and consequently canopy cover would be

343 confounded with bioclimatic zone.

344 All multivariate analyses were performed using the vegan package (Oksanen et al. 2017).

345 Mixed effect models were performed using *lme4* R package (Bates et al. 2015) and all

346 analyses were done using the R programming language (R Core Team 2016). The code

347 for the sub-sampling and statistical analysis, as well as the adaptation of the

348 PERMANOVA can be found in: https://github.com/lmguzman/Climate_invertebrate_traits.
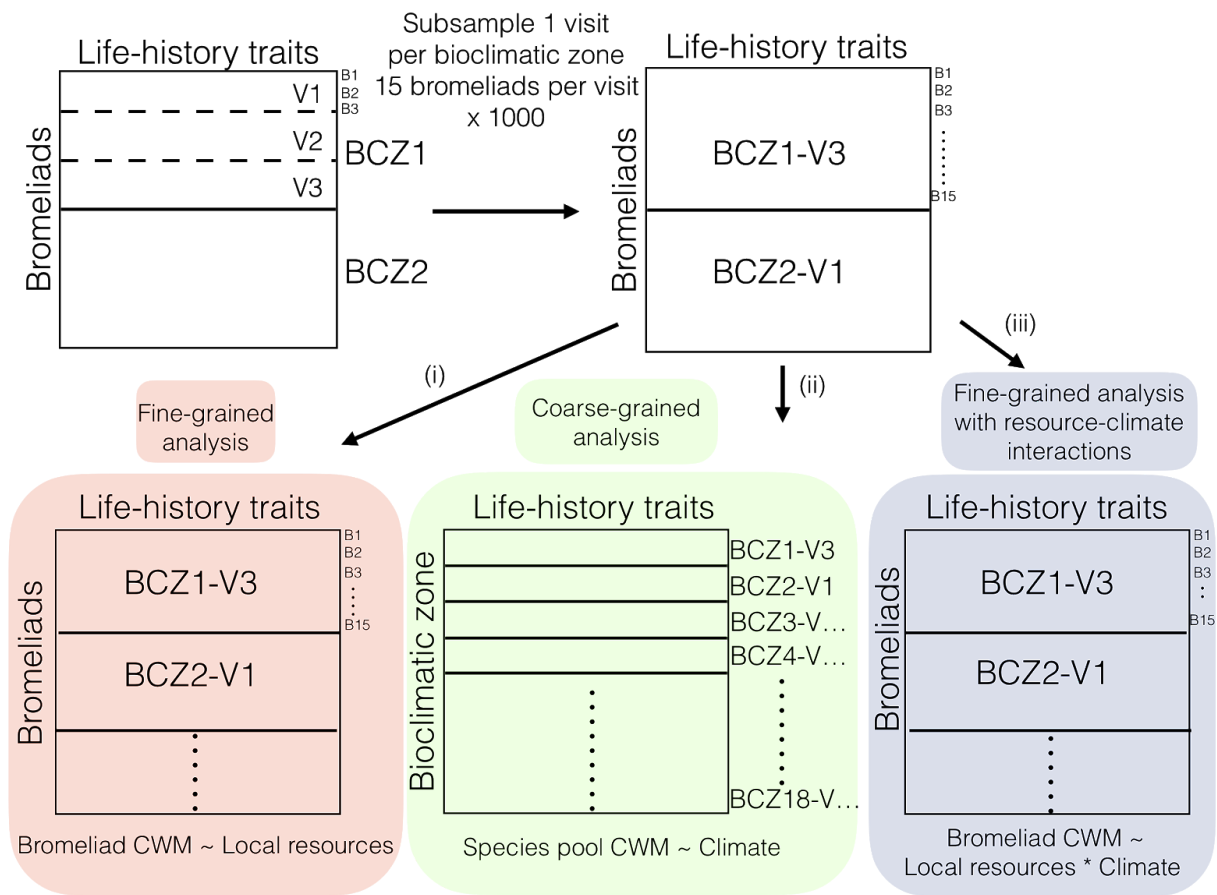
349   **Figure 1:** Schematic representation of the analysis. We tested for the effect of environmental conditions on

350   trait composition in three main analyses. BCZ1, BCZ2, BCZ... represent the bioclimatic zone, which can

351   contain multiple visits V1, V2, V3, V... We sampled one visit for each bioclimatic zone represented by

352   BCZ1-V3, that is, bioclimatic zone 1, visit 3. (i) At the fine grained (red area) analysis, we tested for the effect

353   of local conditions on bromeliad weighted means (CWM). (ii) At the coarse-grained analysis (green area),

354   we tested for the effect of climate on species pools CWM. (iii) We tested the interaction between climate

355   and local conditions in determining bromeliad CWM (blue-gray area).


356   **Results**

357   *Spatial scale of environmental variation*

358   We determined the spatial scale of variation in our three local conditions: total detritus,

359   water volume at time of sampling, and whether the canopy was open or closed. This

360   analysis gave some indication of the potential power of each variable to explain variation

361   in synthetic trait composition (i.e. little variation at a given scale indicates a lower

362   likelihood of a significant effect at that given scale). Variation in total detritus was greatest

363   at the level of the bioclimatic zone (39.2% of variation) but also was high at the local scale

364   of the field site (31%). Variation in water volume was greatest at the local scale of field

365   visits (42.6%) and minimal at the level of bioclimatic zone (2.7%). Finally, variation in

366   canopy cover was highest at the level of bioclimatic zone (73.5%) and lowest at the level

367   of field visit (26%) (Figure A3). We also found that these three local conditions were only

368   weakly correlated across and within zones. The correlation values across bioclimatic

369   zones ranged between -0.01 and 0.35, while the correlation values within bioclimatic

370   zones ranged between -0.32 and 0.28 (Table A2).

371 *Fine-grained analysis*

372 Invertebrate traits varied among every bromeliad within a field visit (Figure 2). We found

373 that only a small amount of trait variation in CWMs (6.1%) could be explained by local

374 conditions, and that no single local condition explained most of this variation. The

375 amount of variation explained ranged from zero to 19.7% depending on the subset of

376 bromeliads selected, and the distribution of variation explained was skewed (Figure A1,

377 Table 1 - Fine-grained analysis).
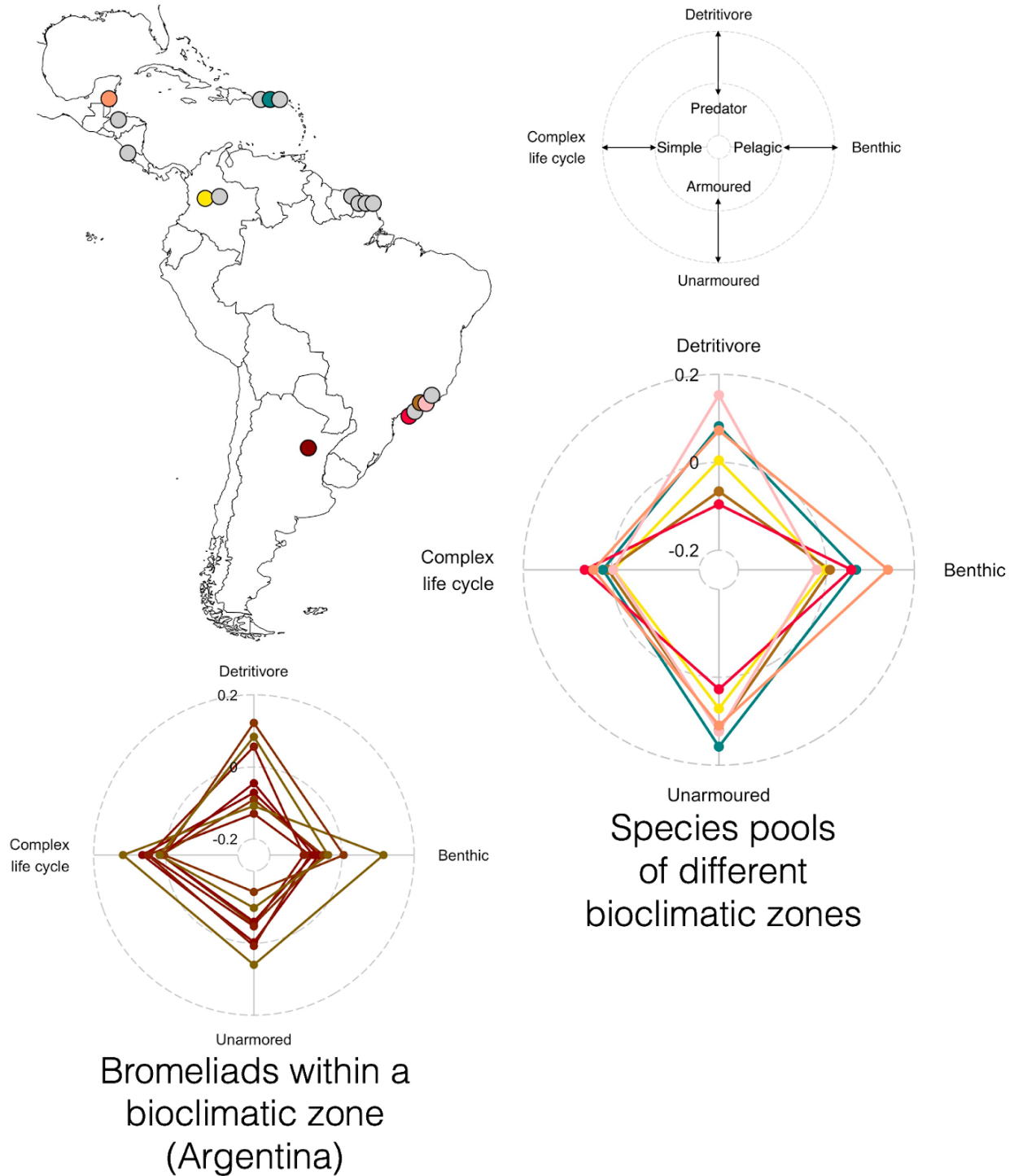
Figure 2: Invertebrate traits at the level of bromeliads and at the level of species pools, for bromeliads sampled in bioclimatic zones throughout the Neotropics (map, top left). Empty spider plot (top right) shows all the four trait axes and their directions, and forms a key for the two filled spider plots (bottom). Filled

381 spider plots summarize the CWM of the four trait axes in a single bromeliad (bottom left) and the CWM in

382 some example species pools (bottom right). Colours on spider plots correspond to bioclimatic zones on

383 map, with those zones not shown in spider plots indicated in grey on the map.

384 **Table 1.** Synthetic trait composition (CWM) explained by local conditions in the fine-grained analysis and by
385 climatic variables in the coarse-grained analysis. The analysis using the local conditions uses the CWM for
386 each bromeliad. This analysis is blocked within each bioclimatic zone. The analysis using the
387 biogeographic climatic variables uses the CWM for the species pool for each bioclimatic zone.

Fine-grained analysis		
Predictor	**Percentage of total sum of squares**	
	Mean	Median
Canopy cover	2.68	2.19
Detritus	2.30	1.92
Water volume	1.18	0.99
Full model	6.16	5.1
Coarse-grained analysis		
Mean Diurnal Temperature Range	14.7	14.7
Temperature Seasonality	10.2	10.1
Precipitation of Driest Quarter	7.64	7.69
Precipitation Seasonality	7.39	7.25
Full model	39.93	39.44

388 *Coarse-grained analysis*

389 Species pools differed in the relative proportions of invertebrate traits (Figure 2). In the

390 coarse-grained analysis we found that climatic variables explained on average 39.9% of

391 the variation in the trait composition of species pools (Table 1 - Coarse-grained analysis).

392 The range of explained variation was large (14 to 47%) depending on the subset of

393 bromeliads selected (Figure A2). The amount of variation explained in this analysis is not

394 necessarily directly comparable to that in the fine-grained analysis because the scale of

395 the response variable (CWMs) is different; for this analysis, we aggregated species at the

396 site rather than bromeliad level. This aggregation changes the mean by weighting

397 bromeliads with more individuals more heavily, and also reduces the number of

398 observations, which tends to raise the R2 values. Four out of 19 bioclimatic variables

399 explained substantial variation in trait composition of the macroinvertebrates across the

400 Neotropics: mean diurnal range in temperature (BC2), temperature annual seasonality

401 (BC4), precipitation annual seasonality (BC15), and precipitation of the driest quarter

402 (BC17) (Figure A4; Table 1). Species pools from zones with high mean diurnal temperature

403 range and high precipitation seasonality tended to be dominated by armoured

404 invertebrates (Figure A5d, A7d). These climatic variables also differed in their effect on

405 trophic traits: detritivores were favoured in zones with high precipitation in the driest

406 quarter (Figure A8c), whereas predators were favoured in zones with high precipitation

407 seasonality and mean diurnal range (Figures A5c, A7c).

408 *Fine-grained analysis with resource-climate interactions*

409 The full model - using both the climatic and local resource environmental gradients to

410 explain traits within individual bromeliads - explained between 27.2 and 44.1% of trait

411 variation, when all the explanatory variables were included, with an average of 36.5% of

412 the variation explained (Figure A9). We found that the local conditions explained 8.7%,

413 climate explained 17.7%, and their interaction explained 10% of the variation in community

414 weighted functional traits (CWMs) on average across all runs. Among the local conditions

415 tested, detritus explained more variation than canopy cover or water volume. Of the

416 climatic conditions tested, mean diurnal range in temperature (BC2) explained more

417 variation than did the other climatic variables. Bromeliads with high mean diurnal range in

418 temperature typically had more complex and unarmoured invertebrates (Figure A10). The

419 cross-scale interaction that explained the most variation was detritus amount and

420 temperature seasonality (BC4; Figure 3-4, Figures A11, Table 2). Specifically, detritus-rich

421 bromeliads in zones with seasonal temperatures tended to contain more unarmoured

422 invertebrates, predators, and invertebrates with complex life cycles (Figure 4). No single

423 explanatory variable consistently explained the most variation in CWMs, rather, each

424 variable contributed a small amount to the total amount of variation explained by the full

425 model, which taken together explained more than a third of the variation in functional

426 traits.

427 **Table 2:** Synthetic trait composition explained by local conditions, biogeographic climatic variables and
428 their interactions. This analysis used the CWM for each bromeliad. We did not include the interaction
429 between canopy cover and climatic conditions because few bioclimatic zones had both open and closed
430 canopy, therefore canopy cover would be confounded with bioclimatic zone.

	Percentage of total sum of squares	
	Mean	Median
Local conditions		

Canopy cover	2.43	1.86
Detritus	4.95	4.86
Water volume	1.35	1.09
Climatic variables		
Mean Diurnal Temperature Range	5.55	5.55
Temperature Seasonality	3.55	3.31
Precipitation of Driest Quarter	4.66	4.57
Precipitation Seasonality	3.97	3.99
Interactions between local conditions and climatic variables		
Detritus : Mean Diurnal Temperature Range	1.23	1.0
Detritus : Temperature Seasonality	2.22	2.12
Detritus : Precipitation of Driest Quarter	1.33	1.25
Detritus : Precipitation Seasonality	1.56	1.39
Water volume: Mean Diurnal Temperature Range	0.84	0.68
Water volume: Temperature Seasonality	0.95	0.86
Water volume: Precipitation of Driest Quarter	1.37	1.20
Water volume: Precipitation Seasonality	0.52	0.44
Total sum of squares		
Full model	36.49	36.62
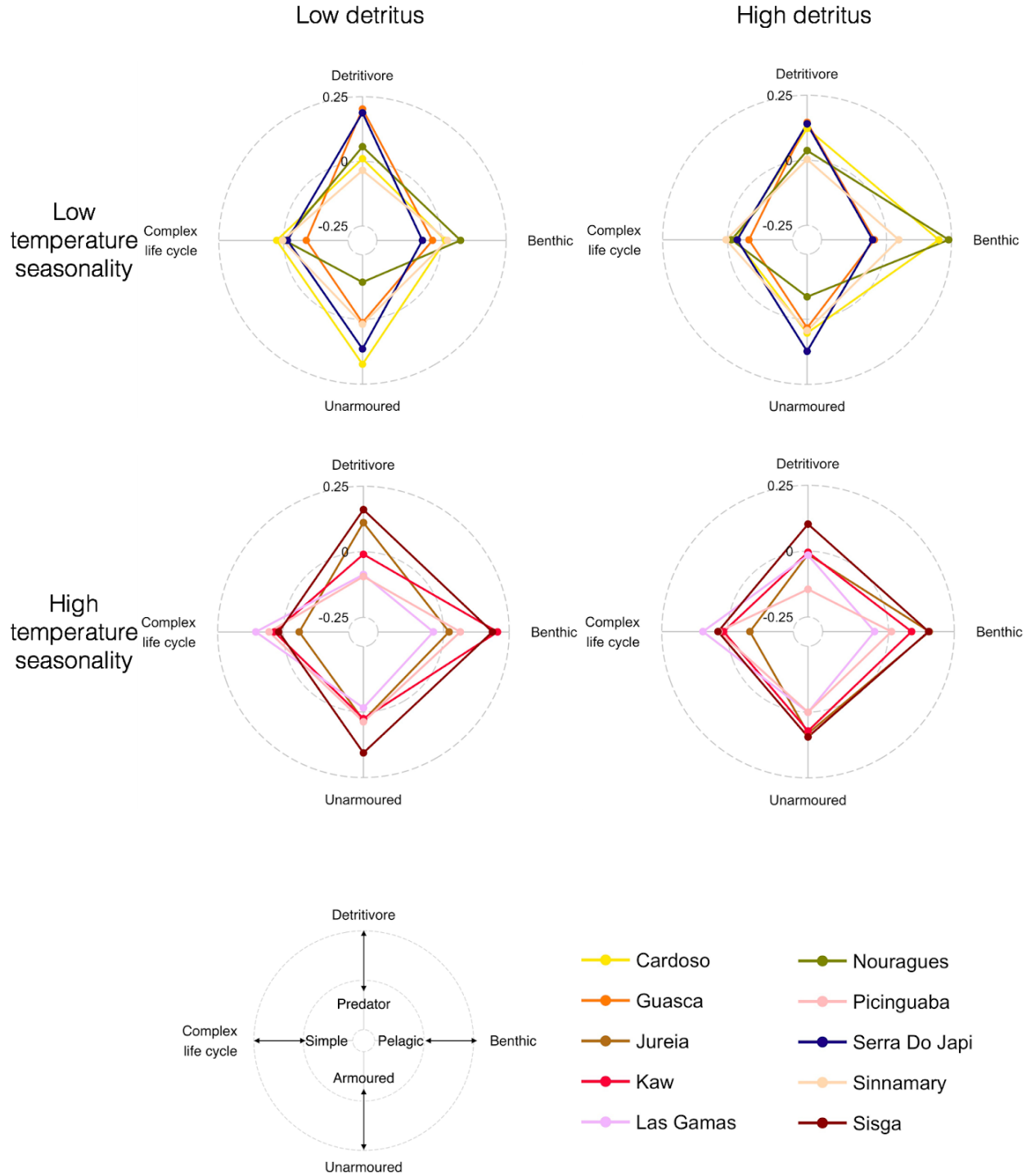
Figure 3: Bromeliads are characterized by their community-weighted mean traits for bioclimatic zones with low and high detritus, and high and low temperature seasonality. Detritus affects particularly the

433   Benthic-Pelagic axis: bromeliads with high detritus have more benthic organisms (i.e. high Benthic-Pelagic

434   axis values). Bioclimatic zones with high temperature seasonality have more organisms with complex life

435   cycles (i.e. higher values in the Complex life cycle – Simple axis).
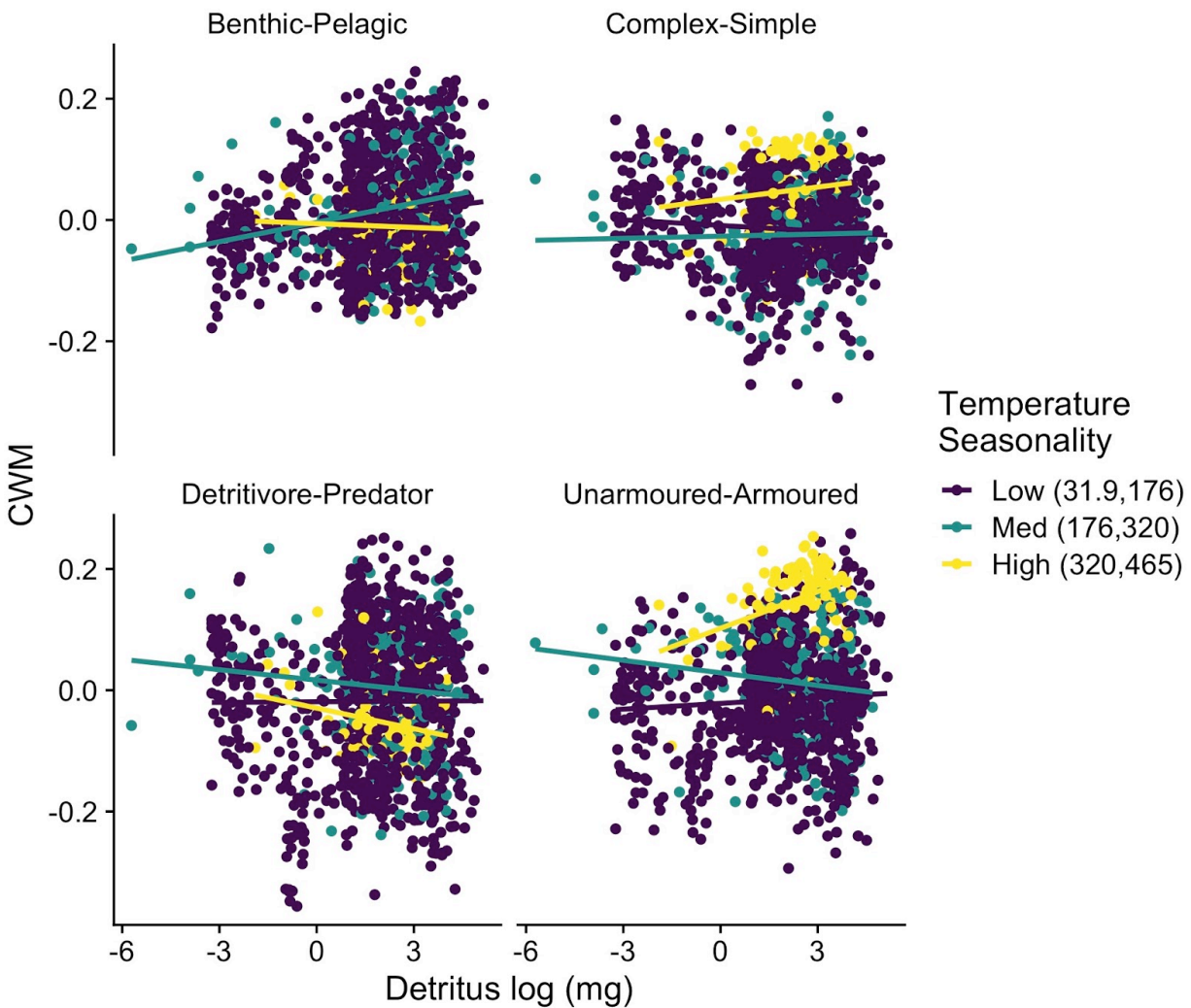
436   **Figure 4:** The four trait axes differ in their relationship with the total amount of detritus which is also

437   mediated by temperature seasonality. Each point is the community weighted mean of a single bromeliad.

438   The coloured lines are simple linear regressions intended only to improve the visualization of the data and

439   not meant to be used for formal analysis since the CWM are multivariate.

440 **Discussion**

441 Our analyses demonstrate the importance of climate and cross-scale interactions of

442 climate with local conditions on the functional traits of macroinvertebrate communities.

443 Climate explained 40% of the trait variation in regional species pools, corroborating the

444 hypothesis that trait composition is primarily explained by the environment at the

445 biogeographic scale. Climate also explained a substantial amount (28%) of trait variation

446 at the scale of individual bromeliads, both directly (18%), and by modifying the response

447 of traits to local conditions in cross-scale interactions (10%) (Figure A9). By contrast, local

448 conditions of bromeliads, by themselves, explained only 6-9% of trait variation depending

449 on the model used. The fact that we were able to explain trait variation with both climate

450 and local conditions means that functional traits are not entirely determined by stochastic

451 factors, historical contingency and phylogenetic constraints. Although stochastic and

452 biogeographic factors no doubt affect trait distribution, they are not strong enough to

453 completely overwhelm or erase the effects that climate and local conditions have on the

454 functional traits of bromeliad macroinvertebrate communities. The implication is that local

455 adaptation and/or filtering occurs in response to both local and climatic conditions, and

456 ultimately shapes the ecological communities of bromeliad macroinvertebrates and their

457 suite of traits.

458 The most important climatic factor in explaining trait variation was mean diurnal range of

459 temperature. Combinations of precipitation and temperature were also important.

460 Detritus and canopy cover were the most important local conditions, but only explained

461 6.1 % of the variation in invertebrate trait composition. In general, not a single predictor

462 (either local conditions or climate) explained very large amounts of variation in trait

463 composition. Instead, the aggregated effects of each predictor contributed to the total

464 variation explained.

465 Our fine-grained analysis with cross-scale interactions allowed us to conclude that

466 climate explains more variation in macroinvertebrate trait composition than local

467 conditions. There are several possible explanations for this pattern. First, our synthetic

468 trait axes may have captured fundamental differences in the strategies of species for

469 tolerating climate-related stress, but not for exploiting local habitat heterogeneity. One of

470 the most important stresses in the bromeliad system is hydrologic variability, including

471 periods of drought. Some species are able to withstand drought with drought-resistant

472 eggs (e.g. Wyeomyia spp.: Dézerald et al. 2015), whereas others have drought-tolerant

473 larvae (e.g. Tipulidae larvae: Amundrud and Srivastava 2015). Many mosquito larvae are

474 sensitive to drought because their legless larvae require water to move (e.g. Culex spp.:

475 Amundrud and Srivastava 2015). However, odonates – a dominant predator in the food

476 web – are vulnerable to drought because of their long larval stage (Guzman et al. 2019,

477 Srivastava et al. 2020a). Therefore, multiple trait axes, as used in our study, are needed

478 to capture traits relevant to drought tolerance, including resistant life forms, larval

479 duration (i.e. cohort production interval), and pelagic requirements. Geographic patterns

480 in drought predict the distribution of invertebrate families that comprise the species pool

481 of bromeliad invertebrates (Srivastava et al. 2020b) and families often have unique

482 functional traits (Céréghino et al. 2018). Climate is likely a better predictor of such

483 geographic patterns in drought prevalence than bromeliad water volume, as water

484 volume is only measured on the particular day of sampling and is very dynamic between

485 days. Invertebrate mortality rarely follows a single day of drought; instead mortality

486 ranges from 11-73% after 18 days without water (Amundrud and Srivastava 2015). Similarly,

487 experimental exclusion of rainfall from French Guiana bromeliads led to changes in

488 functional trait composition of invertebrates only after six weeks without rain (Dézerald et

489 al. 2015). Although no single climate variable dominated the effects on traits, many of the

490 top climate variables were related to variation (daily or seasonal) in temperature and

491 precipitation as might be anticipated if climate affected traits via drought prevalence.

492 Our conclusion that temperature seasonality was an important determinant of trait

493 composition is similar to Swenson et al. (2012).

494 A second explanation is that deterministic filtering by local conditions is largely

495 overwhelmed by stochasticity in the colonization and emergence rates of invertebrates

496 from bromeliads. The majority of invertebrates in bromeliads are insects and thus have

497 complex life cycles, meaning that only the egg to larval or pupal stages are aquatic.

498 Larval development can be as fast as two weeks for mosquitoes, and the majority of

499 insects (except odonates) have cohort production intervals of less than 30 days (Dézerald

500 et al. 2017). This is a relatively short period for the amount of detritus, water or light to

501 limit their abundances, and suggests that abundances may be more affected by

502 oviposition and predation – both of which have an important stochastic component.

503 Furthermore, because low abundances of species in bromeliads can indicate either

504 insufficient oviposition, successful completion of the larval stage and emergence, or

505 larval mortality, even deterministic effects of local factors may result in a complex array of

506 positive and negative effects on abundance. Given that the population dynamics of

507 species with complex life cycles (i.e. insects) occurs at scales larger than the bromeliad

508 (LeCraw et al. 2014), we might expect stronger trait-environment correlations to be found

509 at these larger scales, scales which are based on the bioclimatic zone and /or the

510 species pool.

511 A third possibility is that the suite of synthetic trait axes and local variables we used for

512 analysis somehow pre-determined greater matching of traits with climatic variables than

513 with local conditions. However, both the traits and local conditions used in this study

514 have been identified in previous studies as important factors determining community

515 composition (Richardson 1999, Usseglio–Polatera et al. 2000, Dézerald et al. 2014). The

516 four synthetic trait axes represent major fundamental niche dimensions such as trophic

517 position, habitat, life history and defence (Céréghino et al. 2018), and explained 45% of

518 the total variance in species traits from the 12 traits we assembled. Although the main

519 goal of this study was to explain variations in those four main ecological strategies or four

520 PCA axes, other important ecological strategies (PCA5, PCA6, PCA7, . . .) could also be

521 influenced by local and bioclimatic conditions, however, these other axes were not

522 significant in (Céréghino et al. 2018)) and did not have biological interpretations. The four

523 ecological strategies we studied here, have previously been identified as basic niche

524 dimensions in other systems and in other clades (Winemiller et al. 2015), suggesting that

525 they may be general across different types of communities, and perhaps, broadly

526 applicable to aquatic invertebrates in other ecosystems. Extensive research on bromeliad

527 communities has demonstrated that local conditions such as water volume, detrital

528 amount and canopy cover affects bromeliad community structure, including

529 predator:prey ratios and species richness in bromeliads (Richardson et al. 2000,

530 Srivastava et al. 2008, Dézerald et al. 2014). There are well-known mechanistic reasons

531 behind these relationships. The amount of light available to a bromeliad (i.e. canopy

532 cover) determines algal productivity, and therefore, the relative importance of detritus

533 versus algae in the diet of different macroinvertebrates (Farjalla et al. 2016). In general,

534 detritus is the main source of nutrients in the bromeliad food web, and its quantity is

535 related to overall macroinvertebrate biomass (Richardson et al. 2000). The amount of

536 water found in a bromeliad at the time of sampling is related to the amount of habitat

537 available to invertebrates, the risk of drought, and whether it is colonized by predators,

538 and as such, habitat size is an important predictor of species richness, species

539 composition and trophic structure (Srivastava et al. 2008, Amundrud and Srivastava

540 2015, Petermann et al. 2015). In an experiment where many of these factors were

541 controlled for, local variation in rainfall impacted the community structure of bromeliad

542 macroinvertebrates (Srivastava 2020b), and in extreme cases, caused an inversion of the

543 trophic pyramid (Romero et al. 2020). So a combination of local conditions will have

544 some effect on community dynamics and the distribution of traits.

545 Our conclusion that climate overwhelms local conditions in driving community trait

546 structure contrasts to studies on plant communities by Bruelheide et al. (2018) who found

547 that micro-environmental gradients were more influential than climate. This may be

548 because two of the three local scale factors we analyzed varied more at biogeographical

549 than local scales (Table A2).

550 An important conclusion of our analysis is that there are cross-scale interactions between

551 environmental drivers of trait composition. That is, the effect of local conditions depends

552 on the regional climate. Specifically, the effect of either detrital amount or water volume

553 depended on temporal variation in precipitation and temperature at the field site. This

554 may reflect the ability of large detrital-filled bromeliads to buffer the effects of climate

555 variation on drought prevalence (Srivastava et al. 2020a). Studies of functional traits that

556 use coarse-grained data such as range maps or remote sensing data cannot test for such

557 cross-scale effects of the response of the community to local and climatic conditions.

558 However, there is a growing number of fine-grained datasets with a complete census of

559 the community for which interactions between local conditions and larger scale

560 environmental constraints can be tested. Such datasets are particularly well represented

561 by plants (e.g. Blonder 2018, Bruelheide et al. 2018), but also freshwater invertebrates

562 (e.g. Aspin et al. 2019), fish (e.g. Winemiller et al. 2015), intertidal organisms (e.g. Menge

563 et al. 1999) and marine coastal fishes (e.g. Hemingson and Bellwood 2018). The

564 challenge for analyzing cross-scale effects in these studies is not the large-scale climatic

565 data, but rather the fine-grained environmental data that matters for resource acquisition,

566 competition, predation and facilitation. Fine-grained microenvironmental data, only some

567 of which was available in our study, is likely to be critical in determining the relative

568 importance of environmental filtering and biotic interactions as well as the degree of

569 context dependence (Blonder 2018). A particular advantage of our study was that we

570 were able to measure the entire aquatic macroinvertebrate community at a fine scale at

571 multiple locations across a wide biogeographic range, which then were assembled into a

572 large database, through the support of the French data synthesis centre, CESAB. The

573 randomized sub-sampling procedure was used to control for uneven sampling effort

574 between sites, and gave robust estimates of variance explained between sites. Although

575 sub-sampling reduces statistical power, we gained confidence in our among site

576 comparisons.

577 Overall, we found that climate explained more variation than local conditions, and that

578 the two scales interactively determine the functional traits of bromeliad

579 macroinvertebrate communities across their Neotropical range. Our ability to contrast the

580 effects of climatic vs. local conditions hinged on the compilation of multiple fine-grained

581 datasets. We argue that in addition to sampling communities at local scales, ecologists

582 should aggregate studies that span large ranges in climate variation in order to fully

583 understand trait filtering at local, regional and global scales.

584 **References**

585 Amundrud, S. L. and Srivastava, D. S. 2015. Drought sensitivity predicts habitat size
586   sensitivity in an aquatic ecosystem. - Ecology 96: 1957–1965.

587 Amundrud, S. L. et al. 2018. Dispersal barriers and climate determine the geographic
588   distribution of the helicopter damselfly Mecistogaster modesta. - Freshwater Biology
589   63: 214–223.

590 Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance.
591   - Austral Ecology 26: 32–46.

592 Aspin, T. W. H. et al. 2019. Extreme drought pushes stream invertebrate communities over
593   functional thresholds. - Glob. Chang. Biol. 25: 230–244.

594 Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. - J. Stat. Softw. 67:
595   1–48.

596 Blonder, B. 2018. Hypervolume concepts in niche- and trait-based ecology. - Ecography
597   41: 1441–1455.

598 Bruelheide, H. et al. 2018. Global trait-environment relationships of plant communities. -
599   Nat Ecol Evol 2: 1906–1917.

600 Céréghino, R. et al. 2011. Ant-plant mutualisms promote functional diversity in phytotelm
601   communities. - Functional Ecology 25: 954–963.

602 Céréghino, R. et al. 2018. Constraints on the functional trait space of aquatic
603   invertebrates in bromeliads. - Functional Ecology 32: 2435–2447.

604 Chase, J. M. and Leibold, M. A. 2004. Ecological niches: linking classical and
605   contemporary approaches. - Biodivers. Conserv. 13: 1791–1793.

606 Chave, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20
607   years? - Ecol. Lett. 16: 4–16.

608 Chave, J. et al. 2009. Towards a worldwide wood economics spectrum. - Ecol. Lett. 12:
609   351–366.

610 Chesson, P. 2000. Mechanisms of maintenance of species diversity. - Annu. Rev. Ecol.
611   Syst. 31: 343–366.

612 Damos, P. and Savopoulou-Soultani, M. 2012. Temperature-driven models for insect
613   development and vital thermal requirements. - Psyche: A Journal of Entomology
614   2012: 1–13.

615 de Omena, P. M. et al. 2019. Consumptive effects and mismatch in predator–prey
616   turnover rates cause inversion of biomass pyramids. - Oecologia 190: 159–168.

617   Dézerald, O. et al. 2014. Environmental determinants of macroinvertebrate diversity in
618   small water bodies: insights from tank-bromeliads. - Hydrobiologia 723: 77–86.

619   Dézerald, O. et al. 2015. Functional trait responses of aquatic macroinvertebrates to
620   simulated drought in a Neotropical bromeliad ecosystem. - Freshwater Biology 60:
621   1917–1929.

622   Dézerald, O. et al. 2017. Environmental drivers of invertebrate population dynamics in
623   Neotropical tank bromeliads. - Freshwater Biology 62: 229–242.

624   Dézerald, O. et al. 2018. Functional traits and environmental conditions predict
625   community isotopic niches and energy pathways across spatial scales. - Functional
626   Ecology 32: 2423–2434.

627   Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for
628   the design of natural reserves. - Biol. Conserv. 7: 129–146.

629   Estes, J. A. et al. 2011. Trophic downgrading of planet Earth. - Science 333: 301–306.

630   Farjalla, V. F. et al. 2016. Terrestrial support of aquatic food webs depends on light inputs:
631   a geographically-replicated test using tank bromeliads. - Ecology 97: 2147–2156.

632   Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate
633   surfaces for global land areas. - Int. J. Climatol. 37: 4302–4315.

634   Garnier, E. et al. 2004. Plant functional markers capture ecosystem properties during
635   secondary succession. - Ecology 85: 2630–2637.

636   Guzman, L. M. et al. 2019. Towards a multi–trophic extension of metacommunity ecology.
637   - Ecology Letters 22: 19–33.

638   Hammill, E. et al. 2015. Behavioural responses to predation may explain shifts in
639   community structure. - Freshwater Biology 60: 125–135.

640   Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic
641   landscapes. - Oikos 87: 209–219.

642   Hawkins, B. A. et al. 2017. Structural bias in aggregated species-level variables driven by
643   repeated species co-occurrences: a pervasive problem in community and
644   assemblage data. - Journal of Biogeography 44: 1199–1211.

645   Hemingson, C. R. and Bellwood, D. R. 2018. Biogeographic patterns in major marine
646   realms: function not taxonomy unites fish assemblages in reef, seagrass and
647   mangrove systems. - Ecography 41: 174–182.

648   Hubbell, S. P. 2011. The unified neutral theory of biodiversity and biogeography (MPB-32).

649   - Princeton University Press.

650 Kraft, N. J. B. and Ackerly, D. D. 2010. Functional trait and phylogenetic tests of
651   community assembly across spatial scales in an Amazonian forest. - Ecological
652   Monographs 80: 401–422.

653 Kratina, P. et al. 2017. Environmental control of the microfaunal community structure in
654   tropical bromeliads. - Ecol. Evol. 7: 1627–1634.

655 Lamanna, C. et al. 2014. Functional trait space and the latitudinal diversity gradient. -
656   Proc. Natl. Acad. Sci. U. S. A. 111: 13745–13750.

657 Lande, R. et al. 2003. Stochastic population dynamics in ecology and conservation. -
658   Oxford University Press.

659 LeCraw, R. M. et al. 2014. Metacommunity size influences aquatic community composition
660   in a natural mesocosm landscape. - Oikos 123: 903–911.

661 Legendre, P. and Gallagher, E. D. 2001. Ecologically meaningful transformations for
662   ordination of species data. - Oecologia 129: 271–280.

663 Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur
664   Award Lecture. - Ecology 73: 1943–1967.

665 Loreau, M. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and
666   future challenges. - Science 294: 804–808.

667 MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. - Princeton
668   University Press.

669 McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. - Trends
670   Ecol. Evol. 21: 178–185.

671 Menge, B. A. et al. 1999. Top-down and bottom-up regulation of New Zealand rocky
672   intertidal communities. - Ecological Monographs 69: 297.

673 Merritt, R. W. and Cummins, K. W. 1996. An Introduction to the Aquatic Insects of North
674   America. - Kendall Hunt.

675 Moore, J. C. et al. 2004. Detritus, trophic dynamics and biodiversity. - Ecology Letters 7:
676   584–600.

677 Oertli, B. et al. 2002. Does size matter? the relationship between pond area and
678   biodiversity. - Biological Conservation 104: 59–70.

679 Oksanen, J. et al. 2017. Vegan: Community Ecology Package.

680 Peres-Neto, P. R. and Kembel, S. W. 2015. Phylogenetic gradient analysis: environmental

681   drivers of phylogenetic variation across ecological communities. - Plant Ecology 216:
682   709–724.

683 Petermann, J. S. et al. 2015. Dominant predators mediate the impact of habitat size on
684   trophic structure in bromeliad invertebrate communities. - Ecology 96: 428–439.

685 Pianka, E. R. et al. 2017. Toward a periodic table of niches, or exploring the lizard niche
686   hypervolume. - Am. Nat. 190: 601–616.

687 R Core Team 2016. R: A Language and Environment for Statistical Computing. R
688   Foundation for Statistical Computing, Vienna, Austria.

689 Richardson, B. A. 1999. The bromeliad microcosm and the assessment of faunal diversity
690   in a neotropical forest. - Biotropica 31: 321–336.

691 Richardson, B. A. et al. 2000. Effects of nutrient availability and other elevational changes
692   on bromeliad populations and their invertebrate communities in a humid tropical
693   forest in Puerto Rico. - Journal of Tropical Ecology 16: 167–188.

694 Ricklefs, R. E. 2012. Species richness and morphological diversity of passerine birds. -
695   Proc. Natl. Acad. Sci. U. S. A. 109: 14482–14487.

696 Ricklefs, R. E. and Schluter, D. 1993. Species diversity in ecological communities:
697   historical and geographical perspectives. - University of Chicago Press.

698 Romero, G. Q. et al. 2018. Global predation pressure redistribution under future climate
699   change. - Nature Climate Change 8: 1087–1091.

700 Romero, G. Q. et al. 2020. Extreme rainfall events alter the trophic structure in bromeliad
701   tanks across the Neotropics. - Nat. Commun. 11: 3215.

702 Schmitz, O. J. et al. 2015. Functional traits and trait-mediated interactions: connecting
703   community-level interactions with ecosystem functioning. - In: Pawar, S. et al. (eds),
704   Trait-based ecology - from structure to function. Advances in ecological research.
705   Academic Press, pp. 319–343.

706 Srivastava, D. S. and Bell, T. 2009. Reducing horizontal and vertical diversity in a foodweb
707   triggers extinctions and impacts functions. - Ecology Letters 12: 1016–1028.

708 Srivastava, D. S. et al. 2008. Why are predators more sensitive to habitat size than their
709   prey? insights from bromeliad insect food webs. - Am. Nat. 172: 761–771.

710 Srivastava, D. S. et al. 2020a. Habitat size thresholds for predators: why damselflies only
711   occur in large bromeliads. - Biotropica in press.

712 Srivastava, D. S. et al. 2020b. Ecological response to altered rainfall differs across the

713   Neotropics. - Ecology in press.

714 Swenson, N. G. 2014. Functional and phylogenetic ecology in R. - Use R! in press.

715 Swenson, N. G. et al. 2012. The biogeography and filtering of woody plant functional
716   diversity in North and South America. - Global Ecology and Biogeography 21:
717   798–808.

718 Usseglio–Polatera, P. et al. 2000. Biological and ecological traits of benthic freshwater
719   macroinvertebrates: relationships and definition of groups with similar traits. -
720   Freshwater Biology 43: 175–205.

721 Vellend, M. 2016. The theory of ecological communities (MPB-57). - Princeton University
722   Press.

723 Violle, C. et al. 2014. The emergence and promise of functional biogeography. - Proc.
724   Natl. Acad. Sci. U. S. A. 111: 13690–13696.

725 Winemiller, K. O. et al. 2015. Functional traits, convergent evolution, and periodic tables of
726   niches. - Ecol. Lett. 18: 737–751.

727 Zelený, D. 2018. Which results of the standard test for community-weighted mean
728   approach are too optimistic? - Journal of Vegetation Science 29: 953–966.