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

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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.

93 Introduction

94 Ecologists are reformulating long-held perspectives on biodiversity using functional traits.
 95 Since organisms interact with their environment through their traits, patterns in species
 96 distribution should be a direct function of their traits. Traits directly affect community
 97 assembly and species interactions, such that any snapshot of a community is the result of
 98 i) physiological tolerances (Winemiller et al. 2015, Pianka et al. 2017), ii) species
 99 interactions (Chesson 2000, Chase and Leibold 2004, Estes et al. 2011), iii) dispersal and
 100 priority effects (MacArthur and Wilson 1967, Diamond 1975, Hanski 1999), iv) demographic
 101 stochasticity (Lande et al. 2003, Hubbell 2011), and v) phylogenetic constraints (Vellend
 102 2016, Pianka et al. 2017). Most of these mechanisms are, to some degree, driven by
 103 functional traits (mechanisms i-iii) or determine the distribution of traits (mechanism v),
 104 and their prevalence and diversity modulate the relationship between biodiversity and
 105 ecosystem function rather than species *per se* (Schmitz et al. 2015). Similarly, the
 106 redundancy of functional traits in a community can maintain ecosystem function and
 107 stability in the face of environmental change and species loss (Loreau et al. 2001). By
 108 shifting our focus away from taxonomic diversity to the diversity of functional traits within
 109 a community or metacommunity, we strengthen our ability to detect the mechanisms that
 110 underlie observed patterns in species distribution and biodiversity (McGill et al. 2006). In
 111 particular, functional traits have been associated with broad biogeographic patterns, such
 112 as the latitudinal gradient in biodiversity, leading to new insights into the processes and
 113 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

fuzzy-coding technique (Chevenet et al. 1994): scores ranged from “0” indicating “no affinity”, to “3” indicating “high affinity” of the species for a given trait state. Scores were based on observations of specimens (Dézerald et al. 2017), on the scientific literature (e.g. Merritt and Cummins 1996, Céréghino et al. 2011) and expert opinion (see Céréghino et al. 2018 for list of traits, modalities, and their definitions) the species x trait matrix is available at <https://doi.org/10.5281/zenodo.1200194>. Principal Component Analysis (PCA) was used to reduce trait dimensionality to significant axes of trait variation. The rank-transformed [species x trait] matrix was used to compute Spearman’s rank correlations between trait modalities, which then underwent PCA with bootstrap resampling (Pillar, 1999). This procedure allowed us to test ordination stability and to interpret the significant ordination axes in light of correlations with trait states. We identified a robust set of four orthogonal and important axes of trait variation, namely trophic position, habitat use, morphological defence, and life cycle complexity (Céréghino et al. 2018). The species scores for these four PCA axes (available at <https://doi.org/10.5281/zenodo.1200194>) thus represented continuous trait values, or synthetic traits, which we then used in analyses of the processes underlying functional diversity across different spatial scales in relation to environmental factors (this study).

Site sampling

The data for the present study consists of the abundance of macroinvertebrates found within 1436 bromeliads in 18 field sites in 8 countries (Bromeliad Working Group BWG 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 km² 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

the same structure of random effects, but different likelihoods according to the environmental variable. The environmental variables partitioned in this way included log detritus (normal likelihood) log water volume (normal) and canopy cover (binomial). By using nested random effects, we can partition the variation of each local environmental condition by spatial scale and determine at which spatial scale most of the variation is explained. For each environmental variable, we estimated random effects for the field visit (site by year combination) within bioclimatic zone, and bioclimatic zone. We also calculated the correlation between all local conditions both within and across all bioclimatic zones.

Trait analysis

Since our unit of analysis is the bromeliad invertebrate community, it was necessary to quantify the presence and abundance of the animals and their traits for each bromeliad. To do this, we calculated the community weighted means (CWM) of each synthetic trait for each bromeliad (local scale analysis). Community weighted means (CWM) was given by:

$$CWM = \sum_{i=1}^n p_i x_i, \quad (1)$$

where p_i is the proportion of species abundance, x_i is the trait value of that species and n is the number of species in that community (Garnier et al. 2004, Swenson 2014). To 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 independent 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.

Figure 1: Schematic representation of the analysis. We tested for the effect of environmental conditions on trait composition in three main analyses. BCZ1, BCZ2, BCZ... represent the bioclimatic zone, which can contain multiple visits V1, V2, V3, V... We sampled one visit for each bioclimatic zone represented by BCZ1-V3, that is, bioclimatic zone 1, visit 3. (i) At the fine grained (red area) analysis, we tested for the effect of local conditions on bromeliad weighted means (CWM). (ii) At the coarse-grained analysis (green area), we tested for the effect of climate on species pools CWM. (iii) We tested the interaction between climate and local conditions in determining bromeliad CWM (blue-gray area).

Results

Spatial scale of environmental variation

We determined the spatial scale of variation in our three local conditions: total detritus, water volume at time of sampling, and whether the canopy was open or closed. This analysis gave some indication of the potential power of each variable to explain variation in synthetic trait composition (i.e. little variation at a given scale indicates a lower likelihood of a significant effect at that given scale). Variation in total detritus was greatest at the level of the bioclimatic zone (39.2% of variation) but also was high at the local scale of the field site (31%). Variation in water volume was greatest at the local scale of field visits (42.6%) and minimal at the level of bioclimatic zone (2.7%). Finally, variation in canopy cover was highest at the level of bioclimatic zone (73.5%) and lowest at the level of field visit (26%) (Figure A3). We also found that these three local conditions were only weakly correlated across and within zones. The correlation values across bioclimatic zones ranged between -0.01 and 0.35, while the correlation values within bioclimatic 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).

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

spider plots summarize the CWM of the four trait axes in a single bromeliad (bottom left) and the CWM in some example species pools (bottom right). Colours on spider plots correspond to bioclimatic zones on map, with those zones not shown in spider plots indicated in grey on the map.

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

Coarse-grained analysis

Species pools differed in the relative proportions of invertebrate traits (Figure 2). In the coarse-grained analysis we found that climatic variables explained on average 39.9% of the variation in the trait composition of species pools (Table 1 - Coarse-grained analysis). The range of explained variation was large (14 to 47%) depending on the subset of bromeliads selected (Figure A2). The amount of variation explained in this analysis is not necessarily directly comparable to that in the fine-grained analysis because the scale of the response variable (CWMs) is different; for this analysis, we aggregated species at the site rather than bromeliad level. This aggregation changes the mean by weighting bromeliads with more individuals more heavily, and also reduces the number of observations, which tends to raise the R² values. Four out of 19 bioclimatic variables explained substantial variation in trait composition of the macroinvertebrates across the Neotropics: mean diurnal range in temperature (BC2), temperature annual seasonality (BC4), precipitation annual seasonality (BC15), and precipitation of the driest quarter (BC17) (Figure A4; Table 1). Species pools from zones with high mean diurnal temperature range and high precipitation seasonality tended to be dominated by armoured invertebrates (Figure A5d, A7d). These climatic variables also differed in their effect on trophic traits: detritivores were favoured in zones with high precipitation in the driest quarter (Figure A8c), whereas predators were favoured in zones with high precipitation seasonality and mean diurnal range (Figures A5c, A7c).

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
<i>Local conditions</i>		

Canopy cover	2.43	1.86
Detritus	4.95	4.86
Water volume	1.35	1.09
<i>Climatic variables</i>		
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
<i>Interactions between local conditions and climatic variables</i>		
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
<i>Total sum of squares</i>		
Full model	36.49	36.62

431 **Figure 3:** Bromeliads are characterized by their community-weighted mean traits for bioclimatic zones with
 432 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

ecological strategies we studied here, have previously been identified as basic niche dimensions in other systems and in other clades (Winemiller et al. 2015), suggesting that they may be general across different types of communities, and perhaps, broadly applicable to aquatic invertebrates in other ecosystems. Extensive research on bromeliad communities has demonstrated that local conditions such as water volume, detrital amount and canopy cover affects bromeliad community structure, including predator:prey ratios and species richness in bromeliads (Richardson et al. 2000, Srivastava et al. 2008, Dézerald et al. 2014). There are well-known mechanistic reasons behind these relationships. The amount of light available to a bromeliad (i.e. canopy cover) determines algal productivity, and therefore, the relative importance of detritus versus algae in the diet of different macroinvertebrates (Farjalla et al. 2016). In general, detritus is the main source of nutrients in the bromeliad food web, and its quantity is related to overall macroinvertebrate biomass (Richardson et al. 2000). The amount of water found in a bromeliad at the time of sampling is related to the amount of habitat available to invertebrates, the risk of drought, and whether it is colonized by predators, and as such, habitat size is an important predictor of species richness, species composition and trophic structure (Srivastava et al. 2008, Amundrud and Srivastava 2015, Petermann et al. 2015). In an experiment where many of these factors were controlled for, local variation in rainfall impacted the community structure of bromeliad macroinvertebrates (Srivastava 2020b), and in extreme cases, caused an inversion of the trophic pyramid (Romero et al. 2020). So a combination of local conditions will have 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.

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