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1   **Abstract**

2

3   1.   It has been argued that the mechanisms structuring ecological communities may be more

4   generalizable when based on traits than on species identities. If so, patterns in the assembly of

5   community-level traits along environmental gradients should be similar in different places in the

6   world. Alternatively, geographic change in the species pool and regional variation in climate

7   might result in site-specific relationships between community traits and local environments. These

8   competing hypotheses are particularly untested for animal communities.

9   2.   Here we test the geographic constancy of trait-based assembly patterns using a widespread

10   multi-trophic community: aquatic macroinvertebrates within bromeliads. We used data on 615

11   invertebrate taxa from 1656 bromeliads in 26 field sites from Mexico to Argentina. We

12   summarized invertebrate traits with four orthogonal axes, and used these trait axes to examine

13   trait convergence and divergence assembly patterns along three environmental gradients: detrital

14   biomass and water volume in bromeliads, and canopy cover over bromeliads.

15   3.   We found no overall signal of trait-based assembly patterns along any of the environmental

16   gradients. However, individual sites did show trait convergence along detrital and water gradients,

17   and we built predictive models to explore these site differences.

18   4.   Sites that showed trait convergence along detrital gradients were all north of the Northern

19   Andes. This geographic pattern may be related to phylogeographic differences in bromeliad

20   morphology. Bromeliads with low detritus were dominated by detritivorous collectors and filter

21   feeders, where those with high detritus had more sclerotized and predatory invertebrates.

22   5.   Sites that showed the strongest trait convergence along gradients in bromeliad water were

23   in regions with seasonal precipitation. In such sites, bromeliads with low water were dominated

24   by soft-bodied, benthic invertebrates with simple life cycles. In less seasonal sites, traits

25   associated with short-term desiccation resistance, such as hard exoskeletons, were more

26   important.

27   6.   In summary, we show that there are strong geographic effects on the trait-based assembly

28   patterns of this invertebrate community, driven by the biogeography of their foundational plant

29   species as well as by regional climate. We suggest that inclusion of biogeography and climate in

30   trait-based community ecology could help make it a truly general theory.

31

33

34   **Resumen**

35   1.   Se ha argumentado que los mecanismos que estructuran las comunidades ecológicas pueden

36   ser más generalizados cuando se basan en los rasgos de las especies que en la identidad de

37   las especies. Si este es el caso, los patrones de ensamblaje de las comunidades a nivel de

38   rasgos a lo largo de gradientes ambientales deberían ser similares en distintos lugares en el

39   mundo. Alternativamente, los cambios en el grupo de especies y la variación climática a

40   nivel regional pueden resultar en una relación sitio-específica entre los rasgos de las

41   comunidades y los ambientes locales. Estas hipótesis contrastantes no han sido probadas

42   para las comunidades de animales.

43   2.   Aquí, probamos la constancia geográfica de los patrones de ensamblaje basados en rasgos

44   utilizando una comunidad multi trófica de amplia distribución: macroinvertebrados

45   acuáticos dentro de bromelias. Utilizamos datos de 615 taxones de invertebrados de 1656

46   bromelias en 26 áreas de estudio desde México hasta Argentina. Resuminos los rasgos de

47   los invertebrados dentro de cuatro ejes octagonal y utilizamos esos ejes para evaluar los

48   patrones de ensamblaje de convergencia y divergencia de rasgos a lo largo de tres

49   gradientes ambientales: biomasa de detritus y volumen de agua en las bromelias y cobertura

50   de dosel sobre las bromelias.

51   3.   No encontramos ninguna señal general de patrones de ensamblaje basados en rasgos a lo

52   largo de los gradientes ambientales. Sin embargo, sitios individuales mostraron

53   convergencia de rasgos a lo largo de los gradientes de detritus y agua, por lo que

54   construimos modelos predictivos para explorar estas diferencias entre sitios.

55   4.   Los sitios que mostraron convergencia de rasgos a lo largo del gradiente de detritus estaban

56   al norte de los Andes del Norte. Este modelo geográfico puede ser relacionado con

57   diferencias filogeográficas en la morfología de la bromelia. Las bromelias con bajo

58   contenido de detritus fueron dominadas por invertebrados detritívoros colectores y

59   filtradores mientras que bromelias con altos contenidos de detritus presentaron más

60   invertebrados predadores y con cuerpos esclerotizados.

61   5.   Los sitios que tuvieron alta convergencia de rasgos a lo largo del gradiente de agua de la

62   bromelia estuvieron en regiones con precipitaciones estacionales. En estos sitios, bromelias

63   con bajo cantidad de agua estuvieron dominados por invertebrados bentónicos con cuerpos

64   blandos y ciclos de vida simples. Los rasgos asociados con resistencia a la desecación a

65   corto plazo como exoesqueletos duro fueron más importantes en sitios con menos

66   estacionalidad.

67   6.   En síntesis, mostramos que hay efectos geográficos fuerte sobre los modelos de ensamblaje

68   basados en rasgos de esta comunidad de invertebrados impulsados por la biogeografía de

69   las especies de plantas fundacionales, así como por el clima regional. Sugerimos que la

70   inclusión de la biogeografía y el clima en la ecología de comunidades basada en rasgos

71   puede ayudar a hacer de esta una verdadera teoría general.

72   Palabras clave: ecología basada en rasgos, filtros de hábitat, biogeografía funcional,

73   invertebrados en bromelias

74

75

Introduction

Traits define the ways in which organisms interact with their surrounding environment and other species. As such, traits provide mechanistic links between species and the niche processes that may structure ecological communities (McGill, Enquist, Weiher, & Westoby, 2006). This presents the enticing possibility that ecological concepts based on traits may be more generalizable than those based on biological species. Shipley et al. (2016) argue that a "foundational claim" of trait-based ecology is that communities should show similar trait-based assembly patterns along environmental gradients, even if species composition differs among sites, asking: "Why, given the foundational importance of such patterns, do we have so few examples of generalizable and quantitative trait-based environmental gradients?". Certainly there are some relevant examples, including mesic grasslands where leaf traits change predictably with fire frequency (Forrestel, Donoghue, & Smith, 2014), and tropical forests where foliar chemistry changes consistently over elevation (Asner & Martin, 2016),

However, such geographically repeated patterns may not be the general rule for three reasons. First, these patterns require that the trait states favoured at different points along the environmental gradient must be present in all species pools, yet the traits of species pools may be constrained by dispersal (limited, for example, by habitat fragmentation: Zambrano et al., 2019) and micro-and macro-evolution (Denelle, Violle, & Munoz, 2019). For example, the trait space occupied by spider and beetle communities in native forests of the Azores archipelago is determined by the rate that exotic species colonise islands (Whittaker et al., 2014). Second, there may be multiple trait solutions to the challenges posed by environments (Warming, 1909), and the particular trait solution exhibited by a community may be constrained by the taxonomic composition of its species pool (Peet, 1978; Pillar & Orlóci, 1993). For example, the traits that desert plant communities use to survive aridity depend on which families are represented in the species pool (Peet, 1978). Third, large-scale bioclimatic factors determine how local environmental gradients filter traits. An example here is the shift in leaf nutrients over elevational gradients, which is accentuated in warmer regions (Midolo, De Frenne, Hölzel, & Wellstein, 2019). In short, the geographic consistency of trait-environment coupling in communities

103   could be influenced by both bioclimatic and biogeographic constraints (Barnagaud et al., 2019;

104   Violle, Reich, Pacala, Enquist, & Kattge, 2014).

105

106   It has been argued that a mechanistic understanding of community trait patterns requires the

107   underlying environmental drivers to be explicitly included in analyses (Pillar & Orlóci, 1993; Shipley

108   et al., 2016). Traits integrated at the community level can change in two potential ways along

109   environmental gradients (Figure 1). A trait-convergence assembly pattern (TCAP: Pillar, Duarte,

110   Sosinski, & Joner, 2009) occurs when communities at similar positions on an environmental gradient

111   converge on a common suite of traits. Such a pattern is often assumed to be underlain by strong

112   habitat filtering at intra- or interspecific levels. A trait-divergence assembly pattern (TDAP: Pillar et

113   al., 2009) occurs when trait dispersion within communities changes over the environmental gradient.

114   For example, species coexistence in competitive communities may require sufficient dispersion of

115   traits to minimize niche overlap, and the strength of the required niche differentiation may change

116   systematically with environmental context (but see Mayfield & Levine, 2010). Trait divergence

117   patterns can also be generated when either the strength of habitat filtering or environmental

118   heterogeneity changes systematically over the gradient in mean environmental conditions (Carlucci,

119   Streit, Duarte, & Pillar, 2012). Communities can simultaneously show trait convergence and

120   divergence along environmental gradients, although different traits may be involved in each process

121   (Pillar et al., 2009).

122

123   To date, studies that have examined the geographic consistency of community trait patterns have

124   focused largely on trait convergence (but see Bruelheide et al., 2018). However, a complete

125   understanding of community trait-based assembly requires examining both trait convergence and

126   divergence along similar environmental gradients in multiple regions of the world. Furthermore, the

127   majority of studies that have quantified trait-based assembly patterns have been conducted in plant

128   communities (e.g. Carlucci et al., 2012; Mendes et al., 2016). Animal communities may differ from

129   plant communities in trait-based assembly patterns for several reasons. It has been argued that animals

130   show less phenotypic plasticity than plants because animals have determinate growth and complete

organogenesis at the embryonic stage, as opposed to the indeterminate growth and lifelong production

of new organs (e.g. leaves) in plants (Borges, 2008). If so, we would expect weaker trait-assembly

patterns in animal than plant communities, at least when analyses considered intraspecific trait

variation. Alternatively, the behavioural traits of animals can be remarkably plastic and individualistic

which, when coupled with the ability of many animals to actively move, can lead to strong

associations of individual-level traits with environments (Dahirel, Dierick, De Cock, & Bonte, 2017).

Animal communities may also include a broader range of species interactions than plant communities,

such as predator-prey interactions in multi-trophic communities, complicating any theoretical

expectation that trait dispersion within communities aids coexistence. Although pairwise trophic

interactions can be predicted from traits (Brousseau, Gravel, & Handa, 2018), scaling these pairwise

patterns to community-level trait assembly patterns still remains elusive (Wong, Guénard, & Lewis,

2019). Finally, animal communities may not only experience environmental gradients directly, but

also indirectly via the traits of the plants that animals consume or use as foundational habitat (Abgrall

et al., 2017; Ohgushi, Craig, & Price, 2007; Pakeman & Stockan, 2014).

Here we examine the geographic consistency of trait convergence and divergence assembly patterns

along local environmental gradients, using a community found throughout the Neotropics: the

freshwater macroinvertebrate community living in water impounded by bromeliad plants (Figure 1).

The aquatic food webs within bromeliads are fuelled by decaying detritus and algae and dominated by

macroinvertebrates, especially insect larvae. These invertebrates include detritivores which shred and

scrape detritus and its biofilm, collectors and filter feeders of fine particulate organic matter and algae,

and intermediate and top predators (Céréghino et al., 2018; Diane S. Srivastava et al., 2004). We test

two hypotheses: (H1) bromeliad invertebrate communities are structured by similar niche processes in

all sites ("Multi-site" panel in Figure 1), or alternatively (H2) sites differ in the strength or drivers of

trait-based assembly patterns. If H1 is true, we would expect (a) geographically general patterns in

trait-based assembly over local environmental gradients, and (b) these patterns to be driven by the

same traits in every site. If H2 is true, we would expect site differences in trait-based assembly

patterns to be related to climate (temperature and precipitation) or biogeography (species pool and

159   dispersal barriers). Alternatively, differences in the sampling of sites (in terms of number or average

160   size of bromeliads) could obscure a geographically general pattern.

161

162   **Materials and Methods**

163   *Field sampling.* We compiled data on the aquatic macroinvertebrates in tank bromeliads previously

164   sampled in 26 different sites (Figure 1; Table S1) throughout the natural distribution of the tank

165   bromeliads (Bromeliaceae family). We obtained research permits for each of these field sites where

166   required (Table S1b); in no field site was approval from an animal ethics board required. Field sites

167   were distinct from each other in space, elevation and the species composition of invertebrate

168   communities (Supplemental Material). For every bromeliad, all water and detritus contained in the

169   plant were removed, either by dissecting the plant or by pipetting. The water and detritus were

170   examined for aquatic macroinvertebrates in small size-fractioned aliquots in white trays.

171   Macroinvertebrates were identified to morphospecies in the field, and subsequently to the lowest

172   possible taxonomic level. The detritus was oven-dried and weighed to determine dry mass.

173   Bromeliads were sampled across a range of habitats, from exposed *restinga* (coastal sand-based shrub

174   habitat) in Brazil to cloud forests on Caribbean mountaintops to rainforests in Central America. As no

175   bromeliad genus was found in all field sites, we sampled the most common genera in sites. As this

176   difference in bromeliad taxonomy between sites can lead to site differences in mean plant size, we

177   explicitly test whether mean size drives site differences in trait-based assembly patterns in a *post hoc*

178   test described later. In sum, the dataset consists of information on environmental attributes of

179   bromeliads (n = 1656), macroinvertebrate morphospecies (n = 615), macroinvertebrate traits (n = 64)

180   and field sites (n = 26).

181

182   *Environmental matrix.* Our analysis included three environmental characteristics of each sampled

183   bromeliad: (1) the dry mass of all detritus in the bromeliad (hereafter "detritus", measured in grams);

184   (2) the volume of standing water in each bromeliad on the day of sampling (hereafter "water",

185   measured in mL); (3) the openness of the canopy above the bromeliad (hereafter "canopy", a binary

186   variable with 1 = open canopy and 0 = closed canopy). These variables were chosen because previous

187   site-specific research had established that they were important environmental drivers of community

188   structure and function (Montero, Feruglio, & Barberis, 2010; Petermann et al., 2015; Richardson,

189   1999; Romero, Piccoli, De Omena, & Gonçalves-Souza, 2016), and because there was enough

190   coverage within and amongst field sites to enable robust analyses (Figure S1). A final consideration

191   was that the three environmental gradients were not collinear (pairwise Pearson correlations, r = 0.31

192   to 0.36). For example, we did not include bromeliad water-holding capacity, even though it is known

193   to be an important driver of community composition, because it was tightly correlated (r = 0.80) with

194   the volume of water on the day of sampling and we had much higher data coverage of the latter. Our

195   environmental matrix (*E*, *sensu* Pillar et al. 2009, see below) consists of the three environmental

196   variables describing each of the sampled bromeliads.

197

198   *Community biomass matrix.* We defined as our community all macroinvertebrates found in

199   bromeliads that were macroscopic and either strictly aquatic or semi-aquatic. We organized the

200   abundance data using the R package *fwdata* (developed by A.A.M.M,

201   https://github.com/SrivastavaLab/fwdata). We then converted abundances to biomass by multiplying

202   abundance by the estimated per capita biomass of each morphospecies, based on taxon-specific

203   allometric relationships, using the *hellometry* R package (provided courtesy of P. Rogy,

204   https://github.com/pierrerogy/hellometry). We used biomass rather than abundance to weight traits as

205   many large-bodied invertebrates in bromeliads (e.g. damselflies, tabanids, and sometimes tipulids) are

206   known to have strong consumptive effects on other species (Amundrud et al., 2019; Petermann et al.,

207   2015) but have such low abundance as to be essentially invisible in abundance-weighted traits. Our *W*

208   matrix (*sensu* Pillar et al. 2009, see below) describes the biomass of each morphospecies of

209   macroinvertebrate as a proportion of the total macroinvertebrate biomass within each sampled

210   bromeliad.

211

212   *Trait matrix.* Our analysis considers interspecific, but not intraspecific, differences in traits. In

213   Céréghino et al. (2018), each bromeliad invertebrate morphospecies was scored in terms of twelve

214   traits: aquatic developmental stage, body form, maximum body size, cohort production interval,

215   dispersal mode, food, feeding group, locomotion, morphological defence, reproduction mode,

216   resistance forms and respiration mode. Each trait was represented by several modalities or categories

217   (e.g. the modalities for the trait "dispersal mode" were passive and active), and the affinity of the taxa

218   for each modality was fuzzy coded. In total, the 12 traits were represented by 64 modalities.

219   Céréghino et al. (2018) reduced these 64 trait modalities to four orthogonal axes using PCA. Since

220   then, there have been modest updates to the trait data: some trait scores were improved, the number of

221   missing values reduced, a few microscopic or terrestrial species were removed, and the taxonomic

222   resolution of some species identifications was improved. We therefore reran the PCA analysis on the

223   updated trait matrix, using the same R script as in Céréghino et al. (2018), and used the first four axes

224   in our current study. Our **B** matrix (*sensu* Pillar et al. 2009, see below) describes the morphospecies of

225   macroinvertebrates in terms of the four PCA trait axes.

226

227   *Site information.* We collated information on biogeographic, bioclimatic, and sampling characteristics

228   of each field site in order to better contextualize differences among sites. Biogeographic

229   characteristics included position north and north west versus south and southeast of the Northern

230   Andes (simplified hereafter as north versus south of Andes; Figure 1). The Northern Andes are known

231   to be a dispersal barrier for both bromeliads (Givnish et al., 2011) and bromeliad invertebrates

232   (Amundrud, Videla, & Srivastava, 2018). Although the Southern and Central Andes could be a

233   potential barrier between the west coast and center of South America, we have no bromeliad data

234   from the former and so do not analyse these mountain ranges. We examined species pool richness,

235   estimated with Chao's method (Chao, 1987; implemented in the vegan R package), to test if richer

236   sites had stronger trait-environment matching. From the WorldClim database (Fick & Hijmans, 2017),

237   we extracted site-specific estimates of four bioclimatic variables that a previous study (Guzman et al.,

238   2020) found to underlie spatial variation in bromeliad macroinvertebrate traits: mean diurnal range in

239   temperature (BC2), temperature annual seasonality (BC4), precipitation annual seasonality (BC15)

240   and precipitation of the driest quarter (BC17). WorldClim data was extracted at the $1km^2$ scale; when

241   field sites exceeded 1 km^2 in size we averaged data over the relevant 1 km^2 pixels. Finally, we

242   examined sampling characteristics of each site, including the number of bromeliads sampled (which

243   affects the power of tests) and the site mean of the focal environmental gradient (in case trait-

244   environment relationships differ with site position on gradient).

245

246   *Analysis of trait-based community assembly patterns*

247   Our analysis of trait-based community assembly patterns is based on the methodology developed by

248   Pillar et al. (2009) and implemented in the R package SYNCSA (Debastiani & Pillar, 2012). A trait-

249   convergence assembly pattern (TCAP) can be visualized as the multivariate correlation between the

250   average trait values of the community with the environment experienced by that community (Fig. 1).

251   The former is represented in the community-weighted trait mean (a new matrix, T), calculated by

252   multiplication of W (bromeliads by morphospecies in our data) and B (morphospecies by trait axes);

253   the latter is the environmental (E) matrix. TCAP is therefore simply the T-E correlation. Individual

254   taxa will differ in trait values from the mean of their community (i.e. be dispersed), and the trait-

255   divergence assembly pattern (TDAP) describes how this dispersion itself correlates with the

256   environmental gradient (Figure 1). Calculating TDAP requires first creating a new matrix X such that

257   the X-E correlation contains both TCAP and TDAP, and then partialling out the T-E correlation (i.e.

258   TCAP) to reveal TDAP (Pillar et al., 2009). In technical terms, the X matrix is created by weighting

259   the species in matrix W by their degree of belonging to fuzzy sets that describe similarities between

260   the species in traits (Duarte, Debastiani, Freitas, & Pillar, 2016; Pillar et al., 2009).

261

262   The significance of the matrix correlations that describe TCAP and TDAP must be tested through

263   permutations to ensure that traits, rather than the species that they are associated with, drive the

264   correlation. The SYNCSA method compares the observed correlation coefficient to those obtained

265   after repeatedly permuting row vectors of the B matrix. This permutation breaks up the association

266   between species and their traits while maintaining trait correlation structure, and is an appropriate null

267   model for trait-based assembly patterns (Pillar et al., 2009). In order to incorporate our field site

268   structure into the TDAP and TCAP analysis, we added a "strata" field to the SYNCSA R package,

269   which directs the permutations to be entirely within field sites so as to preserve the integrity of the

270   species pool in each site.

271

272   All matrix correlations were based on Procrustes analysis (Peres-Neto & Jackson, 2001), which

273   describes the concordance between two superimposed matrices after optimizing their resizing,

274   reflection and rotation, with 0 = no concordance and 1 = perfect concordance. We chose Procrustes

275   analysis over the commonly used Mantel test, as it is more powerful (Peres-Neto & Jackson, 2001)

276   and less prone to spurious correlations (Dutilleul, Stockwell, Frigon, & Legendre, 2000).

277

278   *Analyses of across- and between-site patterns*

279   To test if trait-based assembly patterns are universal (hypothesis H1) or not (H2), we first conducted a

280   global test of either TCAP- and TDAP-environment associations, that is, considering all sites together

281   but restricting permutations within species pools. We included all four trait axes to capture the entire

282   multivariate trait space of the community. As sites differed substantially in their coverage of

283   environmental variables, we examined each environmental gradient separately. We log-transformed

284   both detritus and water data, as this improved correlations with TCAP and TDAP. Within each site,

285   we centered environmental gradients (i.e. subtracted the site mean, after any log transformation) to

286   ensure that our multi-site analysis only captured within-site correlations.

287

288   We further examined support for H1 by repeating the analysis (a) at the site level to determine if

289   many sites contributed to the overall pattern, and (b) for each trait axis individually, to determine if

290   the same specific trait axes drove associations in all sites. As the inclusion of uninformative traits

291   dilutes tests of trait-environment relationships, it is recommended to consider which traits (or in our

292   case, trait axes) optimize TCAP and TDAP as part of analyses (Debastiani & Pillar, 2012; Pillar,

293   Sabatini, Jandt, Camiz, & Bruelheide, 2021).

294

295   Where site differences in TCAP-and TDAP-environment associations existed, we tested hypothesis

296   H2 by using linear models to relate site differences in the strength of these associations to sampling

297   (sample size, mean bromeliad environment), bioclimatic (BC2, BC4, BC15, BC17) and biogeographic

298   (species pool size, location north and south of Northern Andes) characteristics of sites. We established

299   the significance of explanatory variables using ANOVA based on type II sums-of-squares to prevent

300   collinearity from influencing results. We only constructed linear models for gradients represented by

301   sufficient sites, namely gradients in detrital and water content. We visualized patterns in TCAP by

302   plotting community-weighted trait means for specific trait axes against the environmental gradient. As

303   TDAP patterns were largely not significant, we do not present visualizations.

304

305

Results

Our updated PCA of the functional traits of bromeliad invertebrate taxa (Figure S2, Table S2) can be interpreted in terms of the first four axes (which together represented 45.1% of the total inertia). The first axis can broadly be interpreted as separating flattened, sclerotized taxa, many of which are predators, from primary consumers that feed on algae, fine particulates and microorganisms. The second axis separates siphon or spiracle-respiring insects found in the water column from integument-respiring taxa that live in the benthos, often for their entire life cycle. The third axis separates taxa with dorsal plates or sclerotized spines from those with few morphological defences and simple, benthic life cycles. The fourth axis separates invertebrate taxa that spend their entire life cycle in bromeliads from insects, which generally only spend their larval stage in bromeliads. In general then, trait axes 1, 2, 3 and 4 can be simplified to trophic, habitat, defence and life cycle dimensions, respectively, as previously reported in Céréghino et al. (2018). We used these four orthogonal trait axes in all subsequent analyses of trait-assembly patterns (i.e. TCAP and TDAP).

Using these four trait axes, we then explored overall patterns in trait assembly. Considering all field sites together and all trait axes together, there were no overall trait-based assembly patterns (neither TCAP nor TDAP) along any of the environmental gradients (Figure 2). This contradicts hypothesis 1a. Site-level analyses of TDAP also support the regional analysis: hardly any sites (≤1 site per gradient) had significant dispersion patterns along environmental gradients when all trait axes were considered together (Figure 2b). However, site-level analyses of TCAP reveal a more nuanced pattern. Although no sites had significant TCAP over canopy cover gradients, several sites exhibited significant TCAP over bromeliad detrital or water gradients (five and six sites respectively: Figure 2a). When analyses are restricted to individual trait axes, TCAP are revealed in further sites, although the optimal trait axis sometimes differs between sites (contrary to hypothesis 1b). As a whole, the above analyses therefore show that there are not geographically general patterns in trait convergence or divergence driven by common traits.

333   Given that there is substantial difference between sites in the strength of TCAP patterns along

334   gradients in bromeliad detritus and water, we next tested whether these differences can be attributed

335   (hypothesis H2) to climate, biogeography, or site differences in sampling. In regression analyses, sites

336   north of the Northern Andes were more likely to have significant TCAP over detrital gradients (Table

337   S3). Indeed, all five sites where we detected trait convergence over gradients in detritus were located

338   in the Caribbean or Central America (Figure 2a). To confirm this effect of geography on TCAP, we

339   separated our sites into those north vs. south of the Northern Andes and re-ran all matrix analyses.

340   There was now an overall significant TCAP (p=0.04, rho = 0.18) driven by trait axis 1 (p=0.04, rho

341   =0.25) for the subset of sites north of the Andes, but not the subset of sites south of the Andes (p =

342   0.62, rho=0.10). Specifically, as detritus increased in northern sites, invertebrate communities shifted

343   from those dominated by detritivorous collectors and filter feeders to those dominated by sclerotized

344   and predatory invertebrates (Figure 3). By contrast, site differences in bioclimatic variables or

345   sampling characteristics (sample size, site mean of log detritus) did not affect either the significance

346   or strength of TCAP correlations in our regression analyses (Table S3).

347

348   Gradients in the amount of water in bromeliads were associated with convergence in community traits

349   in six sites. In four of the sites, this TCAP was driven by trait axis 3 (defence: Figure 4a), whereas in

350   the two other sites either trait axis 1(trophic) or 2 (habitat) were more important and inverse patterns

351   with trait axis 3 were observed (Figure 4a). The sites with significant water-based TCAP were

352   geographically scattered, unlike detrital-based TCAP results. Although site differences in the strength

353   of the TCAP were not explained by biogeographic or sampling attributes of sites, they could be

354   related to bioclimatic differences between sites (Table S3). Specifically, the strength of the TCAP

355   correlations was greatest in sites with more seasonal precipitation (bioclimatic variable BC15),

356   supporting H2, although not every site with seasonal precipitation had strong TCAP correlations

357   (Figure 4b).

358

359

Discussion

In general, we found little evidence for geographically consistent patterns in trait assembly. Overall patterns in TCAP and TDAP were not significant along any of our local environmental gradients, contrary to hypothesis H1. Supporting our alternative hypothesis H2, we were able to relate differences between sites in the strength of trait assembly patterns or dominant trait axis to biogeography (position relative to northern extent of Andes) and climate (precipitation seasonality). Our analysis of geographic variance in trait assembly patterns joins only a few other geographically-extensive studies of animal communities along environmental gradients, including those of fish (Lamouroux, Poff, & Angermeier, 2002; McLean et al., 2021), ants (Bishop et al., 2016; Gibb et al., 2018), bees (Moretti, De Bello, Roberts, & Potts, 2009) and birds (Barnagaud et al., 2019; Matthews et al., 2015). These studies show that geography can have a range of effects on community trait filtering by local environments, from minor effects of geographic location (McLean et al., 2021) to dominant effects of biogeography (Barnagaud et al., 2019) and bioclimatic context (Moretti et al., 2009).

In our study, local gradients in amounts of detritus were correlated with a shift in community-weighted traits in a number of sites, especially those north of the Northern Andes. In such sites, trait axis 1 (trophic) often underlies this TCAP-detritus relationship. For example, when we examined trait assembly patterns individually for each trait axis, only trait axis 1 resulted in significant TCAP patterns for most (five out of these eight) northern sites. This shift in trait axis 1 with increasing bromeliad detritus represents a community shift from dipteran detritivores to hard-bodied predators like dytiscid beetles and damselflies. There are several potential reasons for this shift in trophic traits. The first reason is a type of trophic sampling effect. Invertebrate abundance usually correlates positively with detrital quantity in tropical freshwaters (Benstead, Road, & El, 2010), and this is also true for the bromeliad fauna (Richardson, 1999; Diane S. Srivastava, Trzcinski, Richardson, & Gilbert, 2008). As predators have lower regional population sizes than detritivores, even random assembly would lead to the ratio of predator to detritivore taxa increasing with the amount of detritus (Diane S. Srivastava et al., 2008). A second possible reason is the energetic inefficiencies in trophic

388   transfer (Lindeman, 1942), leading to bottom-up limitation of the occurrence of large-bodied

389   predators when detritus is limiting (Wallace, Eggert, Meyer, & Webster, 1999). This hypothesis has

390   been tested by measuring the growth rate of predatory damselflies following relocation to bromeliads

391   with less detritus, and was not supported (Diane S. Srivastava, Ware, Ngai, Starzomski, & Amundrud,

392   2020). However, energetic limitation of other predatory taxa in this system remains unexplored. A

393   third possible reason is the often high covariance of bromeliad detritus with bromeliad capacity within

394   habitats (Diane S. Srivastava et al., 2008), coupled with the restriction of some large, long-lived

395   predators — such as the damselfly *Mecistogaster modesta* in Central America bromeliads — to high

396   capacity bromeliads that rarely dry out (Amundrud & Srivastava, 2015; Diane S. Srivastava et al.,

397   2020). Notably, both sampling effects and covariance with capacity are expected to influence trophic

398   structure most when the detrital gradient includes small bromeliads where the stochastic effects of

399   sampling or risk of drought are highest. Such bromeliads characterize the rainforests of Central

400   America and the Caribbean, and are in Tillandsioideae genera such as *Guzmania*, *Tillandsia, Vriesea*

401   and *Werauhia*. By contrast, phytotelm bromeliads south of the Andes are more often high-capacity

402   CAM species in Bromelioideae (Fig. S1, Table S1). This distinction reflects the historical

403   biogeography of bromeliads. The Tillandsioideae subfamily colonized the areas north of the Andes ca

404   8.7-14.2 million years ago, coinciding with rapid uplifting of the Northern Andes, whereas the

405   Bromelioideae subfamily evolved more recently, ca 5.5 million years ago, and radiated in the areas

406   south and east of the Andes (Givnish et al., 2011). Thus, the biogeography of the host plant may

407   contribute to the geographic signal in invertebrate trait-based assembly patterns.

408

409   The strength of TCAP over gradients in bromeliad water also varied substantially between sites, with

410   the strongest TCAP in sites with high seasonality in precipitation. A similar bromeliad volume by

411   precipitation seasonality interaction was reported for invertebrate traits by Guzman et al. (2020) using

412   a different analytical method, pointing to the robustness of this conclusion. In sites with strongly

413   seasonal precipitation, bromeliads are likely to dry out completely during the dry season, posing

414   substantial challenges to their aquatic fauna (Céréghino et al., 2020; Dézerald, Céréghino, Corbara,

415   Dejean, & Leroy, 2015). Therefore, we would expect the strength of filtering by bromeliad water

volume to be greater in such seasonal sites. In seasonal sites, trait axis 3 (defence) was often

important: bromeliads with low water volume were dominated by small, soft-bodied benthic

invertebrates with simple life cycles, like leeches and oligochaete worms, whereas high water volume

plants included sclerotized, surface-swimming insects like predacious diving beetles (Dytiscidae) and

riffle bugs (Veliidae). This suggests that in seasonal sites, invertebrate communities persist even at

low water through population resistance (simple life cycles in benthos), similar to the conclusion from

a study that experimentally excluded rainfall from bromeliads for up to three months (Bonhomme et

al., 2021). By contrast, in regions with less seasonal rainfall, TCAP was underlain by a variety of

different trait axes and showed a reverse pattern on trait axis 3. Under less seasonal rainfall, short-

term desiccation resistance of organisms (i.e. LD_{50}) may be more important for surviving fluctuating

water levels (Amundrud & Srivastava, 2015). Desiccation LD_{50} is well predicted by traits like cuticle

thickness and body mass (Céréghino et al., 2020) that fall at the negative end of trait axis 1.

Invertebrate communities in low seasonality sites were also often positioned lower on trait axis 3, a

pattern that may be related to the absence of odonates from the species pool of the three Caribbean

islands we studied. In general, our findings complement studies from other freshwater systems that

show strong filtering effects of drought on the traits of aquatic invertebrate communities (Aspin et al.,

2019; Datry et al., 2014).

Given that the amount of detritus and water in bromeliads influences the trait composition of

invertebrates, at least in some sites, we can then ask: what underlies this variation between bromeliads

in water and detritus? Both bromeliad morphology (i.e. size and shape) and canopy cover are

important determinants of bromeliad detritus and water (Farjalla et al., 2016; Zotz, Leja, Aguilar-

Cruz, & Einzmann, 2020); however, canopy cover was not directly found to be a driver of trait-based

assembly patterns. This suggests a large role for the bromeliad plant itself in mediating the trait-based

assembly of the invertebrates it contains. Bromeliads are a foundation species for the invertebrate

community we study, much in the same way that kelp, corals and seagrass form critical structural

habitat for marine species or dominant tree species provide key microhabitats for forest species

(Ellison, 2019). Foundation species can have profound effects on the species that rely on them, even

though these interactions are non-trophic in nature (Ellison, 2019; Kéfi et al., 2012). Such interactions between animal traits and plant traits have largely been overlooked in tests of trait assembly patterns (but see Abgrall et al., 2017; Pakeman & Stockan, 2014). Future studies could incorporate intraspecific trait variation of both the bromeliads and the invertebrates in such analyses of animal-plant interactions. Certainly, one limitation of the current study was that trait data was restricted to the species level or higher.

In summary, we show here that, while trait-assembly patterns can exist at the local level, these patterns are not often constant over large geographic areas. There are several reasons for this geographic variation. First, the effect of the environmental gradients on ecological communities may depend on the regional climate context: hydrologic dynamics may be qualitatively different in regions with strong seasonal variation in precipitation (Boersma, Bogan, Henrichs, & Lytle, 2014). Second, trait assembly patterns may be affected by the historical biogeography of species, including both the invertebrates and the bromeliads. While biogeographic effects on community trait patterns have been shown before in terms of the species pool of the focal animal community (Barnagaud et al., 2019; Gorczynski et al., 2021; Whittaker et al., 2014), here we show biogeographic effects also operate via the plants that form the structural habitat for the animal communities. This suggests that the future development of animal functional ecology should not occur in isolation from plant functional ecology, given the myriad of ways that plants and animals influence each other via their functional traits. The geographic contingency that we found in trait-assembly patterns does not necessarily invalidate the potential of developing a mechanistic trait-based theory of community ecology applicable over large regions of the globe. However, our results suggest that such a theory must include processes operating at larger spatial and temporal scales, such as the effects of dispersal limitation and evolutionary history (Violle et al., 2014), as well as often overlooked effects of non-trophic interactions between animals and plants (Ohgushi et al., 2007).

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Authorship statement. DSS led the conceptualization, statistical analysis, manuscript writing, data curation and data visualization and contributed to trait scoring, funding, data collection, project administration. RC led the trait scoring and funding and administration of the CESAB project, and

497   contributed to conceptualization, data collection and manuscript writing. AAMM led software

498   development and invertebrate and trait data curation, and contributed to statistical analyses,

499   conceptualization and project administration. VDP made strong contributions to the conceptualization

500   and statistical analysis and contributed to manuscript writing. VJD led software development and

501   contributed to the conceptualization, statistical analysis and created a figure. LMG contributed to

502   conceptualization, data curation, data collection, statistical analysis, and manuscript editing. MKT

503   contributed to conceptualization, data curation, CESAB funding, and manuscript editing. OD and

504   IMB contributed to conceptualization, data curation, data collection, and manuscript editing. PMdeO,

505   GQR and FOB contributed to conceptualization, data curation, and data collection. MACM

506   contributed to conceptualization, data collection, statistical analysis and manuscript editing. CL, VFF,

507   AZG, BC contributed to conceptualization and data collection. BAR, JSB, MJR, MCM contributed to

508   data collection and manuscript editing. MJ, JTN, ST, GCOP, GM, BMS, KRK all contributed to

509   extensive field data collections and processing of this data. All authors have approved this manuscript

510   for publication. Authorship order is based on CRediT roles, with the second ranked author in the final

511   (senior) author position.

512   **Data accessibility.** All supporting data and R scripts for this study are available from the Dryad

513   Digital Repository: https://doi.org/10.5061/dryad.vt4b8gtv4 (D. S. Srivastava et al., 2022)

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710

711

Figure legends

713 **Figure 1.** Study design for testing the geographic consistency of trait assembly patterns. Bromeliads

714 were sampled in 26 sites throughout the Neotropics ("Field sites" panel). In each site, bromeliads

715 were sampled ("Bromeliad in field site" panel) for aquatic macroinvertebrates along environmental

716 gradients ("Environment" panel). For each bromeliad, the traits of each invertebrate taxon were

717 weighted by the taxon's total biomass (size of spheres and arrows in "Invertebrates Biomass Traits"

718 panel) to determine the community weighted mean trait value (red cross) and the dispersion of the

719 traits around this mean value (green arrow). A trait-based convergence assembly pattern (TCAP)

720 occurred when the community-weighted mean changed consistently over environmental gradients; a

721 trait-based divergence assembly pattern (TDAP) when dispersion changed consistently over

722 environmental gradients ("Site TCAP and TDAP" panel). Note that TDAP includes both intertaxa

723 variation in traits as well as variation in trait means between communities at similar points on the

724 environmental gradient. Finally, TCAP and TDAP were compared among sites to determine if trait

725 assembly patterns were geographically similar ("Multi-site" panel) or geographically different (not

726 illustrated).

727 **Figure 2**. (A) Trait-based convergence assembly patterns (TCAP) of bromeliad macroinvertebrate

728 communities along three local environmental gradients: detrital biomass ("detritus", on a log scale) or

729 standing water volume in bromeliads ("water", on a log scale), and openness of the canopy above

730 bromeliads ("canopy"). Sites are ordered from north to south, with red arrows indicating the northern

731 extent of the Andes. Sites with no data for a particular environmental gradient are indicated with

732 white space. The strength of TCAP along each environmental gradient is evaluated with Procrustes

733 correlations, and is based either on the four trait axes combined (bar graph) or assessed individually

734 (symbols; where multiple trait axes are significant, the order of symbols progresses left to right from

735 strongest correlation to weakest). (B) Trait convergence assembly patterns (TDAP) of bromeliad

736 macroinvertebrate communities along local environmental gradients, labelled and ordered as in (A).

737 **Figure 3.** The community weighted mean value of trait axis 1 (associated with trophic position) in

738 each bromeliad is plotted as a function of the mass (log grams, without scaling or centering) of

739 detritus in the bromeliad for each site, allowing a visualization of this particular TCAP-environmental

740 correlation. Trendlines are shown simply to aid visualization of site-specific patterns; trendlines

741 representing TCAP that were found by SYNCSA to be significant for trait axis 1 are shown with solid

742 lines, otherwise the lines are dashed. Sites are divided into those north (sites 1-10) and south (sites 11-

743 26) of the northern extent of the Andes.

744 **Figure 4.** (a) The community weighted mean value of trait axis 3 (associated with defence traits) in

745 each bromeliad is plotted as a function of the volume (log ml, without scaling or centering) of water in

746 the bromeliad for each site, allowing a visualization of this particular TCAP-environmental

747 correlation. Trendlines are shown simply to aid visualization of site-specific patterns; trendlines

748 representing TCAP that were found by SYNCSA to be significant for trait axis 3 are shown with solid

749 lines, otherwise the lines are dashed. Sites are divided into those with low (bio15 ≤ 40) and high

750 (bio15 > 40) seasonality in precipitation as indicated in (b). (b) When considering all four trait axes,

751 the strength of TCAP correlations increases with seasonality in precipitation, as represented by the

752 bioclimatic variable bio15, with weak TCAP in low seasonality sites and often stronger TCAP in high

753 seasonality sites. The predicted effect of seasonality was extracted as the partial residuals from a

754 multiple regression model, conditioned on the mean effects of other site-level explanatory variables

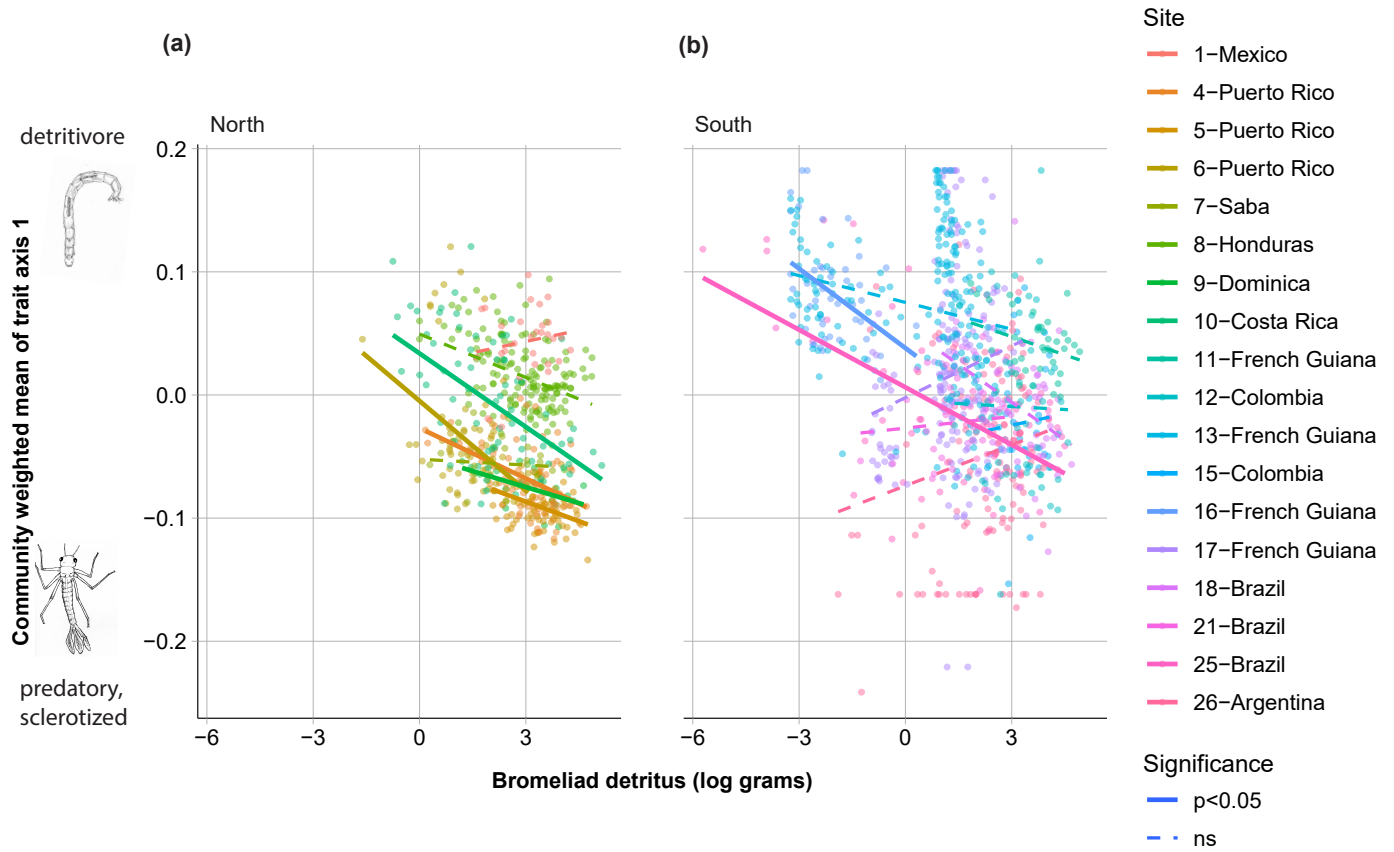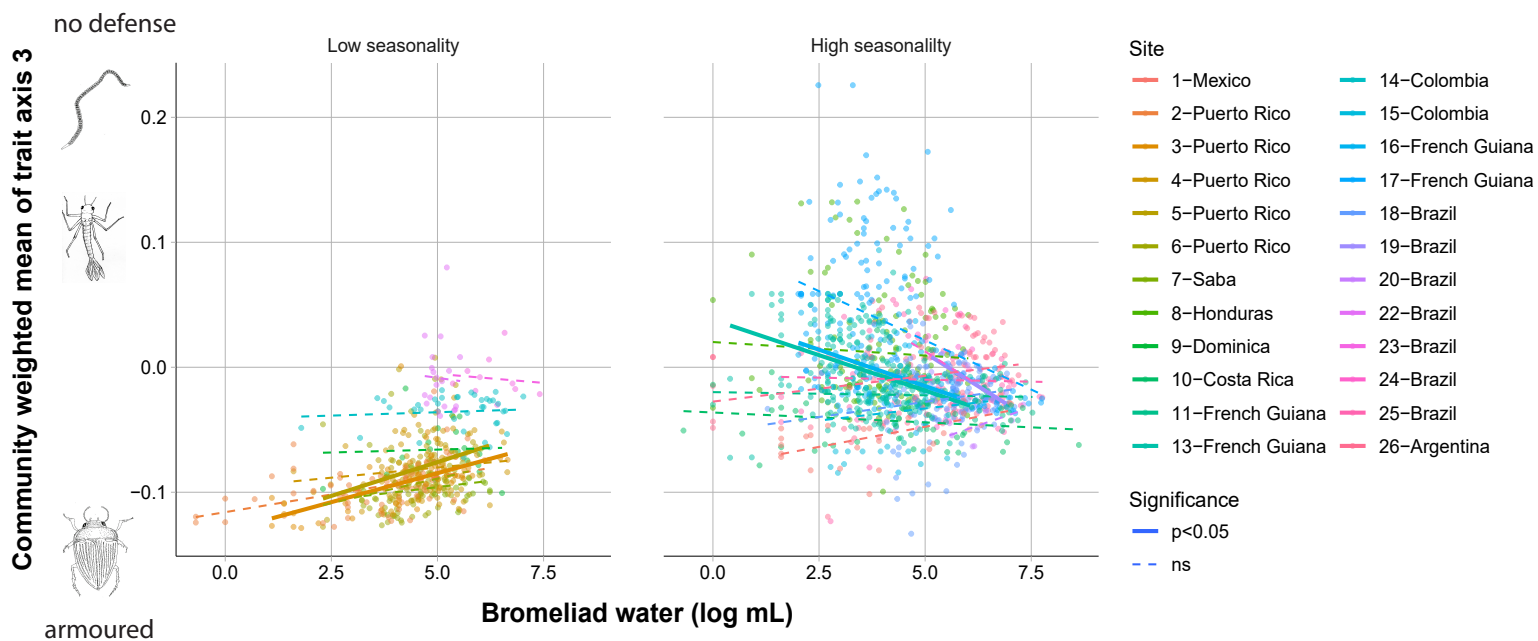755 (Table S3). The shaded area represents the 95% CI around the predicted effect.
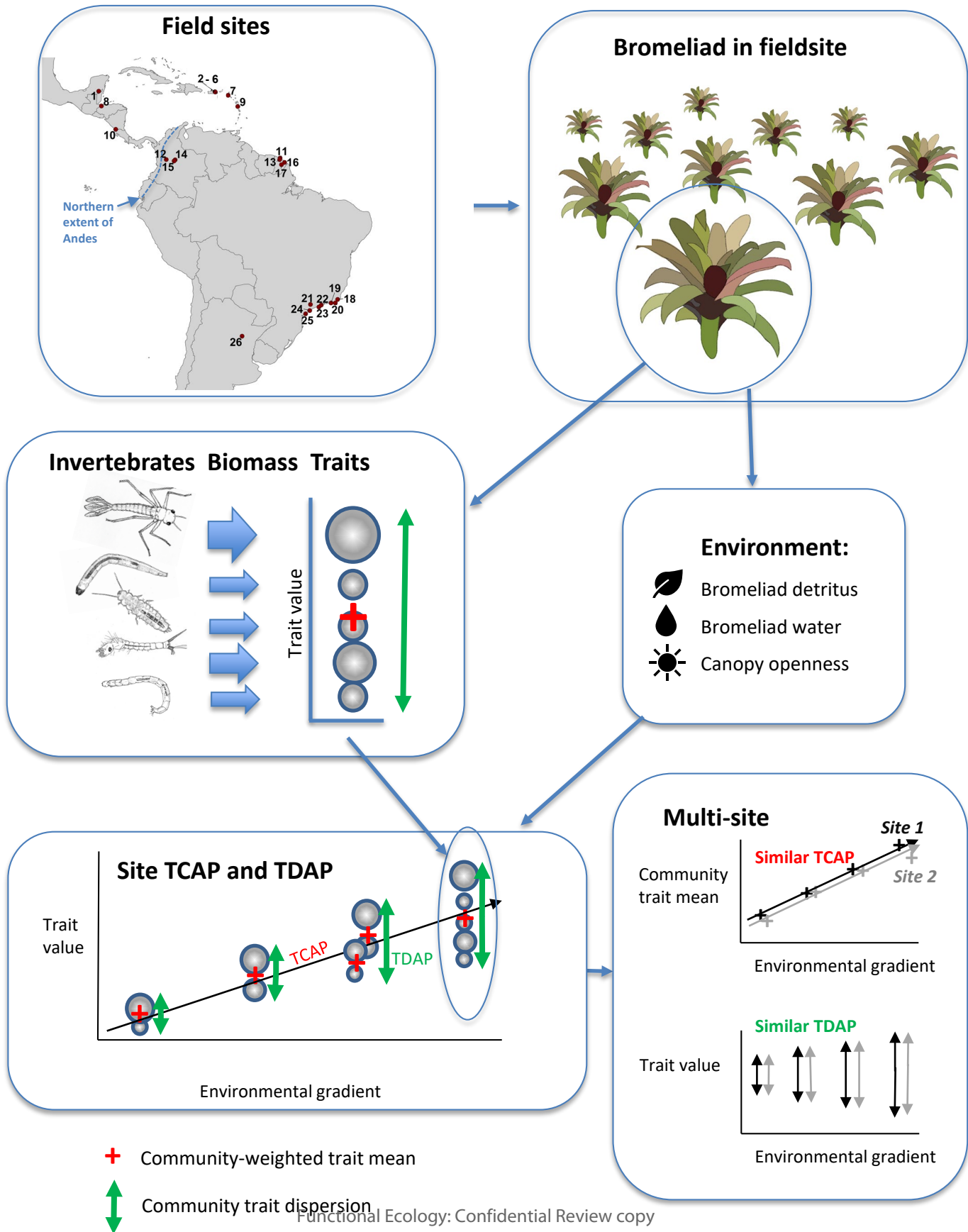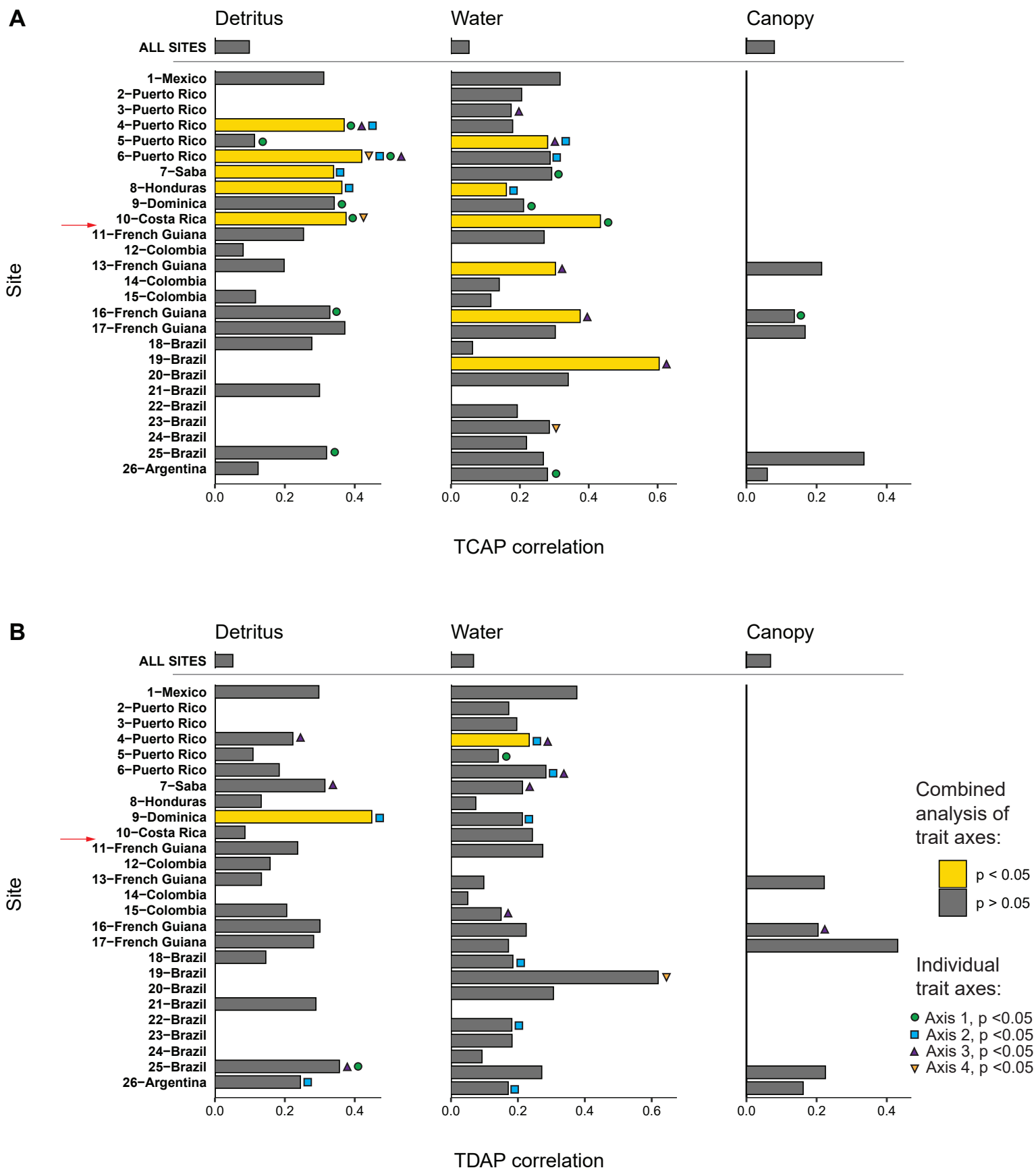
Figure 2

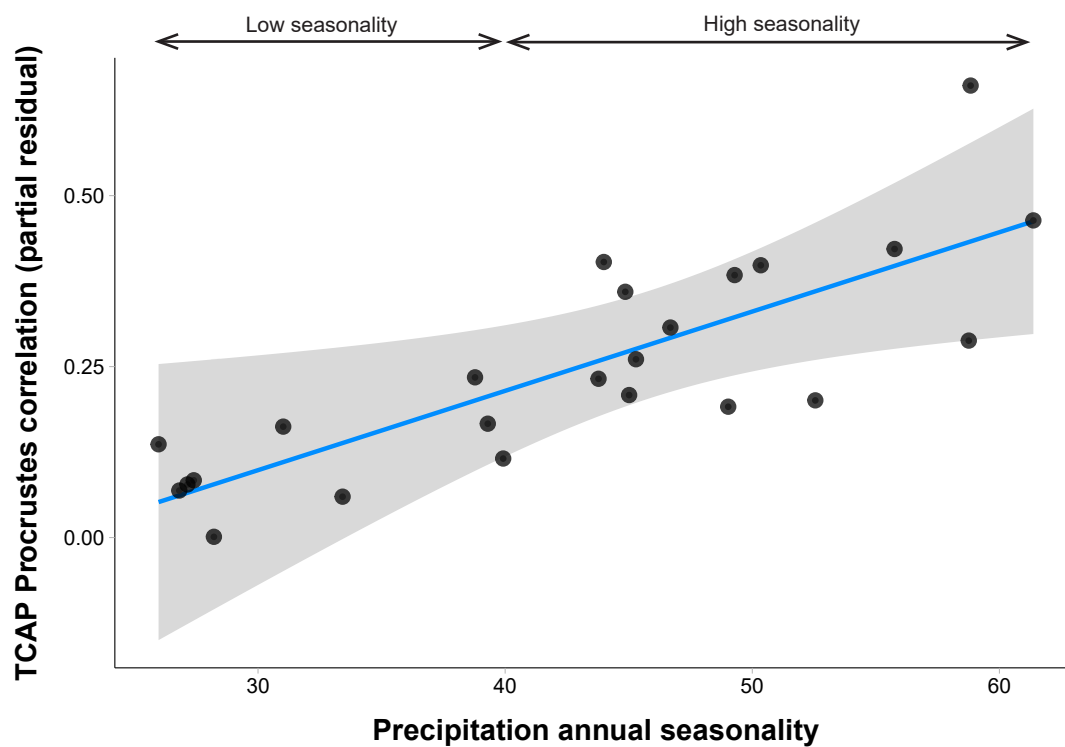Figure 3

(a)

(b)

Figure 4

Geographical variation in the trait-based assembly patterns of multitrophic invertebrate communities

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Supplemental material

Contents:

Appendix S1. Supplemental methods.

Table S1. (a) Site locations and characteristics. **(b)** Sample years and research permits

Table S2. Correlation of trait modalities with the first four axes of a PCA analysis of 64 traits of bromeliad macroinvertebrates.

Table S3. Regression analyses of potential drivers of site variation in Procrustes correlations between TCAP along gradients in either bromeliad detritus or bromeliad water volume.

Figure S1. Distribution of bromeliads in each site along the studied environmental gradients.

Figure S2. A replotting of Figure 3 from Céréghino et al. 2018.

Appendix S1

Supplemental methods. We defined a distinct "site" as one that was distinct in terms of: space, elevation and taxonomic identity of its species pool. All bromeliads surveyed within a site must occur in an area <3.5 km in linear dimension and within a 300 m range of elevation. The invertebrate species pool should also be >50% dissimilar (Jaccard dissimilarity, based on presence-absence) between adjacent sites. For example, bromeliads surveyed along a transect covering an elevation gradient (Sonadora transect, Puerto Rico) are assigned to a low elevation (400-700m) and high elevation (750-1000m) site based on differences in elevation and dissimilarity in the invertebrate species.

Table S1. (a) Site locations and characteristics

Site code	Field site name and location (latitude, longitude)	Sample size (no. bromeliads)	Species pool diversity (Chao estimate ± SE)	Bromeliad genera (B = Bromelioideae subfamily, T = Tillandsioideae)
1 Mexico	Kohunlich, Quintana Roo (18.427, -88.804)	29	18.1 ± 0.4	*Aechmea bracteata* (B)
2 Puerto Rico	Luquillo Experimental Forest, Sonadora transect (400-700m) (18.321, -65.817)	67	36.9 ± 6.4	*Guzmania* spp.(T)
3 Puerto Rico	Luquillo Experimental Forest, Sonadora transect (750-1000m) (18.315, -65.798)	58	37.9 ± 6.4	*Guzmania* and *Werauhia* spp.(T)
4 Puerto Rico	El Verde Biological Station, Tabonuco forest (<600m) (18.321, -65.817)	79	70.8 ± 23	*Guzmania lingulata , G. berteroniana* (T)
5 Puerto Rico	El Verde Biological Station, Palo Colorado forest (600-900m) (18.296, -65.798)	70	53.2 ± 6.8	*Guzmania lingulata , G. berteroniana* (T)
6 Puerto Rico	Pico del Este, Dwarf forest (900-1050m) (18.265, -65.760)	70	27.5 ± 2.9	*Guzmania berteroniana, Werauhia sintenisii* (T)
7 Saba	Saba 650-840m (17.638, -63.235)	20	23.8 ± 5.0	*Tillandsia utriculata, Guzmania plumieri, Vriesea antillana, Werauhia ringens* (T)
8 Honduras	Cusuco National Park (15.542, -88.264)	155	39.5 ± 7.1	*Tillandsia guatemalensis* (T)

9 Dominica	Dominica 800-830m (15.362, -61.325)	20	54.4 ± 37.6	*Guzmania plumieri, G. megastachya* (T)
10 Costa Rica	Pitilla (10.983, -85.433)	73	50.4 ± 10.1	*Guzmania* and *Werauhia* spp. (T)
11 French Guiana	Sinnamary (4.083, -52.683)	39	24.9 ± 3.7	*Aechmea aquilega* (B)
12 Colombia	Rio Blanco (5.047, -74.579)	51	30.8 ± 11.4	*Guzmania multiflora* (T)
13 French Guiana	PetitSaut (4.736, -52.925)	199	59.0 ± 10.1	*Vriesea* sp (T), *Aechmea mertensii* (B)
14 Colombia	Sisga (5.017, -73.700)	37	21.5 ± 1.3	*Tillandsia turneri* (T)
15 Colombia	Guasca (4.767, -74.167)	35	28.1 ± 16.7	*Tillandsia turneri, T. complanata* (T)
16 French Guiana	Kaw (4.083, -52.683)	47	23.1 ± 4.8	*Aechmea mertensii* (B)
17 French Guiana	Nouragues (4.083, -52.683)	171	64.6 ± 6.8	*Catopsis berteroniana, Guzmania lingulata, , Vriesea pleiosticha, Vriesea* sp. (T), *Aechmea melinonii, A. aquilega* (B)
18 Brazil	Macae (-22.216, -41.507)	133	65.5 ± 4.2	*Aechmea nudicaulis, A. lingulata, Neoregelia cruenta* (B), *Vriesea neoglutinosa* (T)
19 Brazil	Marica (-22.947, -42.888)	10	32.1 ± 9.2	*Neoregelia* sp. (B)
20 Brazil	Arraial do Cabo (-22.951, -42.043)	10	15.4 ± 1.2	*Neoregelia* sp. (B)
21 Brazil	Serra do Japi (-23.233, -46.967)	29	37.7 ± 7.3	*Vriesea carinata* (T)

22 Brazil	Picinguaba (-23.339, -44.781)	20	44.4 ± 11.9	*Vriesea procera* (T)
23 Brazil	Ilha Bella (-23.738, -45.291)	10	31.2 ± 6.8	*Neoregelia* sp. (B)
24 Brazil	Jureia (-24.431, -47.109)	20	94.4 ± 18.1	*Vriesea procera* (T)
25 Brazil	Cardoso (-25.084, -47.940)	66	119.5 ± 18.7	*Quesnelia arvensis* (B)
26 Argentina	Las Gamas (-29.433, -60.467)	137	57.3 ± 30.9	*Aechmea distichantha* (B)

Table S1. (b) Sample years and research permit information. NA = not applicable.

Site code	Years sampled	Permit organization	Permit number	Permit holder
1 Mexico	2011	No permit required at the time of sampling	NA	NA
2 Puerto Rico	2004	No permit required at time of sampling for Long Term Ecological Research (LTER) research areas of Luquillo Experimental Forest (LEF)	NA	NA
3 Puerto Rico	2004	No permit required at time of sampling for LTER research areas of LEF	NA	NA
4 Puerto Rico	1993,1994, 1996,1997, 2010	No permit required at time of sampling for LTER research areas of LEF	NA	NA
5 Puerto Rico	1993,1994, 1996,1997, 2010	No permit required at time of sampling for LTER research areas of LEF	NA	NA

6 Puerto Rico	1993,1994, 1996, 2010	No permit required at time of sampling for LTER research areas of LEF	NA	NA
7 Saba	2009	Executive Council of the Island Territory of Saba, Netherlands Antilles	1218/09	Barbara A. Richardson
8 Honduras	2006, 2007	La Administración Forestal del Estado – Corporación Hondureña de Desarrollo Forestal (AFE- COHDEFOR)	#7691	Merlijn Jocque, Jose Nuñez Miño
9 Dominica	2002	Dominica Dept. of Forestry and Wildlife	Permit not numbered	Barbara A. Richardson
10 Costa Rica	1997, 2000, 2002, 2004, 2010	1997-2004:Ministerio del Ambiente y Energia (MINAE); 2010: Ministerio del Ambiente, Energia y Telecomunicaciones (MINAET), Costa Rica	163-97-OFAU, 243-2000-OFAU, 296-2002-OFAU, ACG-PI-023-2004, ACG-PI-028-2010	Diane S. Srivastava 1997-2004, Jana S. Petermann 2010
11 French Guiana	2011	No permit required at the time of sampling	NA	NA
12 Colombia	2012, 2014	No permit required at the time of sampling	NA	NA
13 French Guiana	2014	No permit required at the time of sampling	NA	NA
14 Colombia	2000	No permit required at the time of sampling for private farms	NA	NA
15 Colombia	2001	No permit required at the time of sampling for private farms	NA	NA
16 French Guiana	2008	No permit required at the time of sampling	NA	NA
17 French Guiana	2006	No permit required at the time of sampling	NA	NA

18 Brazil	2008, 2015	Ministério do Meio Ambiente (MMA), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) Sistema de Autorização e Informação em Biodiversidade(SISBIO)	2008 permit not numbered, 2015 permit: 47164-1	Vinicius Fortes Farjalla, L. Melissa Guzman Uribe
19 Brazil	2015	MMA-ICMBio - SISBIO	47164-1	L. Melissa Guzman Uribe
20 Brazil	2015	MMA-ICMBio - SISBIO	47164-1	L. Melissa Guzman Uribe
21 Brazil	2011	MMA-ICMBio - SISBIO	23689-1	Gustavo Quevedo Romero
22 Brazil	2011	Secretaria do Meio Ambiente (SMA) and MMA	12.429/2011 and 29738-3	Ana Zangirolame Gonçalves
23 Brazil	2015	MMA-ICMBio - SISBIO	47164-1	L. Melissa Guzman Uribe
24 Brazil	2013	SMA and MMA	12.429/2011 and 29738-3	Ana Zangirolame Gonçalves
25 Brazil	2008, 2011	MMA-ICMBio – SISBIO, Instituto Forestal	23689-1, COTEC N° 804/2011 D85/07 M	Gustavo Quevedo Romero
26 Argentina	2004-2005, 2010, 2012, 2013	"Specific Collaboration Agreement" between the Faculty of Agricultural Sciences of the National University of Rosario and the Ministry of Production of the Province of Santa Fe, Argentina	Not numbered	Guillermo Montero

Table S2. Correlation of trait modalities with the first four axes of a PCA analysis of 64 traits of bromeliad macroinvertebrates. Only traits with strong negative or positive correlations with the axis are listed, with the correlation coefficient in parentheses; a full list of the 64 traits is provided in Table 1 of Cereghino et al. (2018). The 64 traits in the PCA include those that characterize aquatic stage (traits starting with "AQ"), body form ("BF"), cohort production interval ("CPI"), dispersal mode ("DM"), food ("FD"), feeding group ("FG"), locomotion ("LO"), morphological defence ("MD"), reproduction ("RE"), resistance form ("RF"), respiration mode ("RM"), as well as traits on maximum body size.

	Trait Axis 1	Trait Axis 2	Trait Axis 3	Trait Axis 4
% inertia	15.1	12.5	9.9	7.6
Interpretation	Trophic: predators -> detritivores	Habitat: pelagic -> benthic	Defence: armoured -> none	Life cycle: simple -> complex
Traits negatively correlated with axis (r ≤ -0.5)	**RF4**: No resting stage (-0.67) **BF2:** Flat ovoid body (-0.57) **MD6:** Sclerotized exoskeleton (-0.54) **LO1**: Flier (-0.50)	**RM4**: Siphon/spiracle respiration (-0.69) **DM2:** Active dispersal (-0.65)	**MD4:** Sclerotized spines (0.75) **LO2:** Surface swimmer (0.63) **MD5:** Dorsal plates (0.59) **RE2:** Isolated eggs, free (0.52)	**LO3:** Full water swimmer (0.60) **AS4:** Adults aquatic (0.59) **BF1:** Flat elongate (0.58)
Traits positively correlated with axis (r ≥ 0.5)	**FD4:** Consumes living microphytes (0.75) **AS3:** Nymphs aquatic (0.73) **RF3:** Diapause or dormancy (0.70) **CP1:** Cohort production interval<21 days (0.69) **FG1:** Deposit feeder (0.61) **MD3:** Hairs on body (0.59) **FD1:** Consumes micro-organisms	**LO7:** tube builder (0.81) **MD8:** case or tube defence (0.81) **RE8:** Asexual reproduction (0.72) **LO6:** Interstitial use (0.72) **RM1:** Integument respiration (0.72) **FG3:** Scraper (0.64) **DM1:** Passive dispersal (0.54)	No correlations less than -0.42	**FD3:** Consumes dead plant litter (-0.67) **FG2**: Shredder (-0.51)

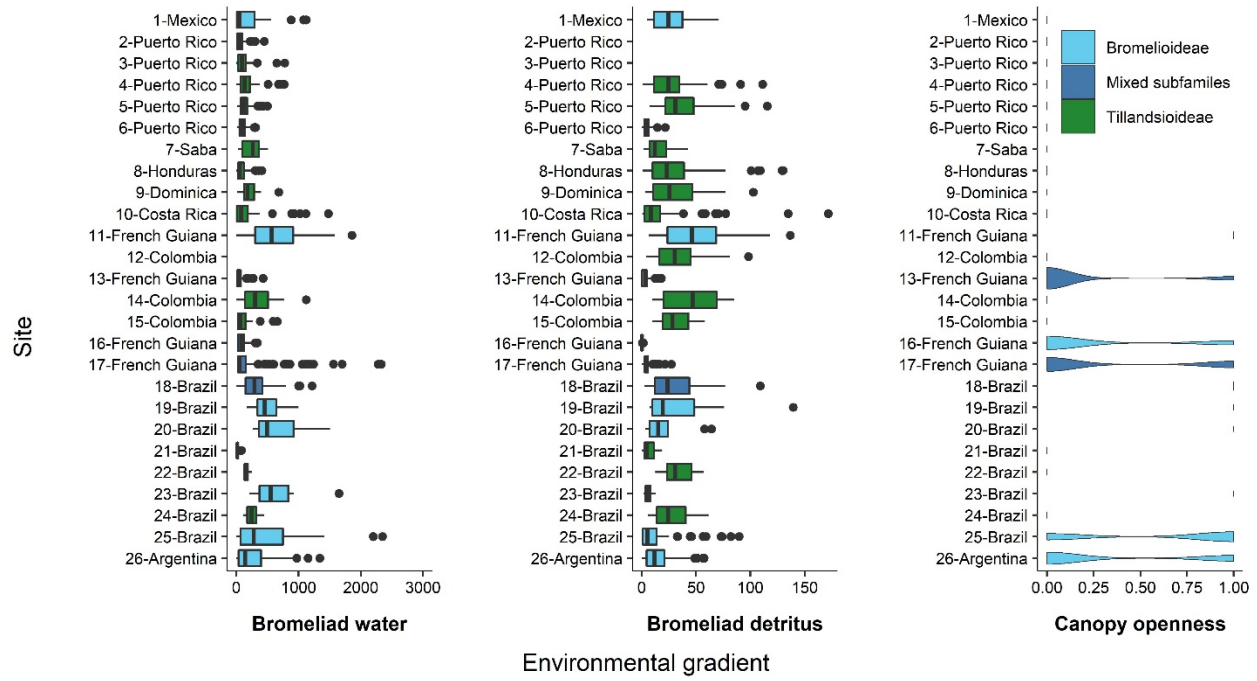|	(0.58)			
	FG4: Filter-feeder (0.52)			
	FD2: Consumes detritus <1 mm (0.51)			

Table S3: Regression analyses of potential drivers of site variation in Procrustes correlations between TCAP along gradients in either bromeliad detritus or bromeliad water volume. For each environmental gradient, we built models that explain either the strength ("size of correlation coefficient") or significance ("log(p value of correlation)" of the TCAP Procrustes correlation. Bioclimatic variables include BC2 (mean diurnal range temperature), BC4 (temperature seasonality), BC15 (precipitation seasonality), and BC17 (precipitation of driest quarter). The site mean in the environmental gradient refers to either the site mean of log detritus per bromeliad (units = log grams) as an explanatory variable for Procrustes correlation for detritus-based TCAP, or the site mean of log water volume per bromeliad (units = log ml) as an explanatory variable for Procrustes correlation for water-based TCAP. Significance ("p") of potential drivers is evaluated using type II ANOVAs (likelihood ratio = "LR") which conservatively evaluate the partial effects of explanatory variables. * = significant variables ($p < 0.05$)

	Procrustes correlation for detritus-based TCAP				Procrustes correlation for water-based TCAP			
	Size of correlation coefficient		Log(p value of correlation)		Size of correlation coefficient		Log(p value of correlation)	
	LR χ^2	p	LR χ^2	p	LR χ^2	p	LR χ^2	p
Sample size	0.00	0.96	0.16	0.69	0.00	0.99	0.66	0.42
Site mean in the environmental gradient	1.02	0.31	0.47	0.49	0.34	0.56	0.04	0.85
BC2	0.66	0.42	0.13	0.72	1.75	0.19	0.61	0.44
BC4	0.19	0.67	0.00	0.99	2.00	0.16	0.29	0.59
BC15	1.03	0.31	0.05	0.83	**5.92**	**0.015***	1.45	0.23
BC17	0.28	0.60	0.02	0.89	3.18	0.07	0.62	0.43
Species pool (Chao)	0.04	0.83	0.00	0.99	1.46	0.22	0.04	0.84
North or south of Andes (binary)	**6.20**	**0.01***	**6.20**	**0.01***	1.44	0.23	0.29	0.59

Figure S1. Distribution of bromeliads in each site along the studied environmental gradients in either (a) a linear scale, in the case of bromeliad water and bromeliad detritus, or (b) log transformed scale. TCAP and TDAP analyses were conducted with a linear scale for canopy cover and a log scale for bromeliad water and detritus. Canopy cover is binary data, and so its distribution is displayed with a violin plot, where the shape represents the estimated density in either open (1) or closed (0) canopy. Bromeliad water and detritus are continuous data, and so their distribution is displayed with box plots, with the box bounded by the first and third quartiles, the median indicated with the central line in the box, and whiskers and dots indicating estimated range and potential outliers respectively.

Figure S2. A replotting of Figure 3 from Céréghino et al. 2018 (doi: 10.1111/1365-2435.13141) using updated matrices. Only traits with an absolute correlation ≥ 0.5 with one of the PCA axes are included in the biplot, and the alphanumeric trait codes for these traits are provided in Table S2. Species positions are shown on biplots, and the taxonomic affinity of species is indicated by different symbols.
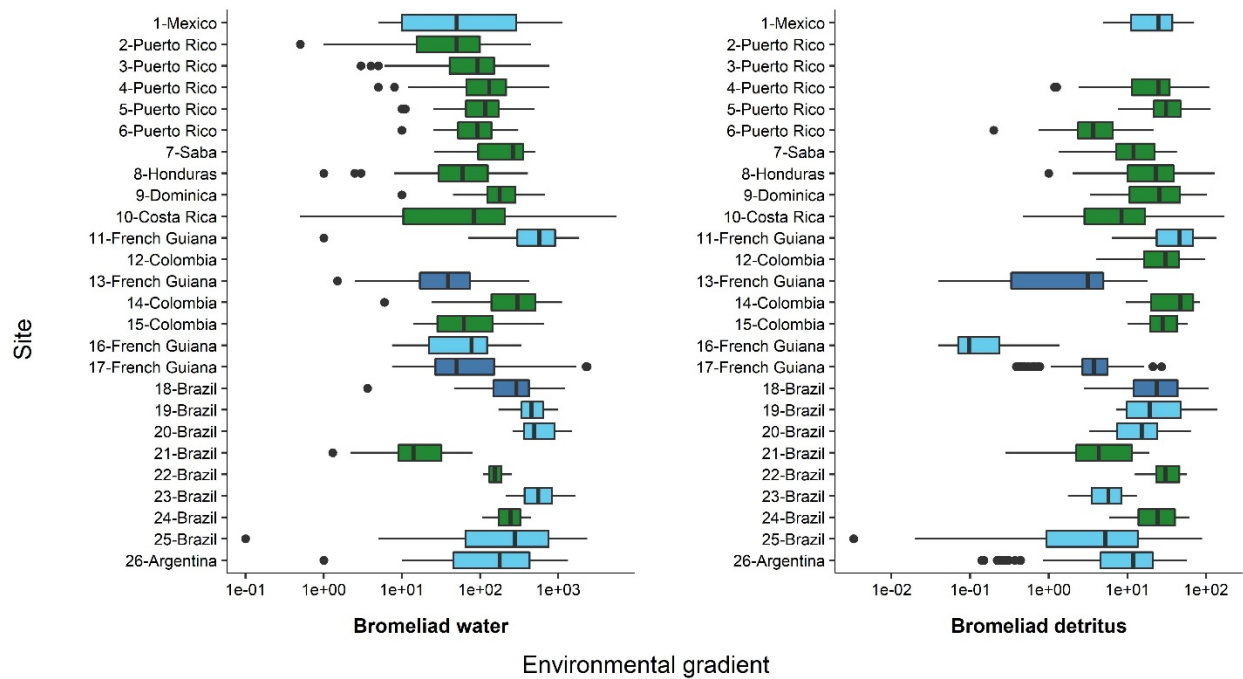
(a)

(b)

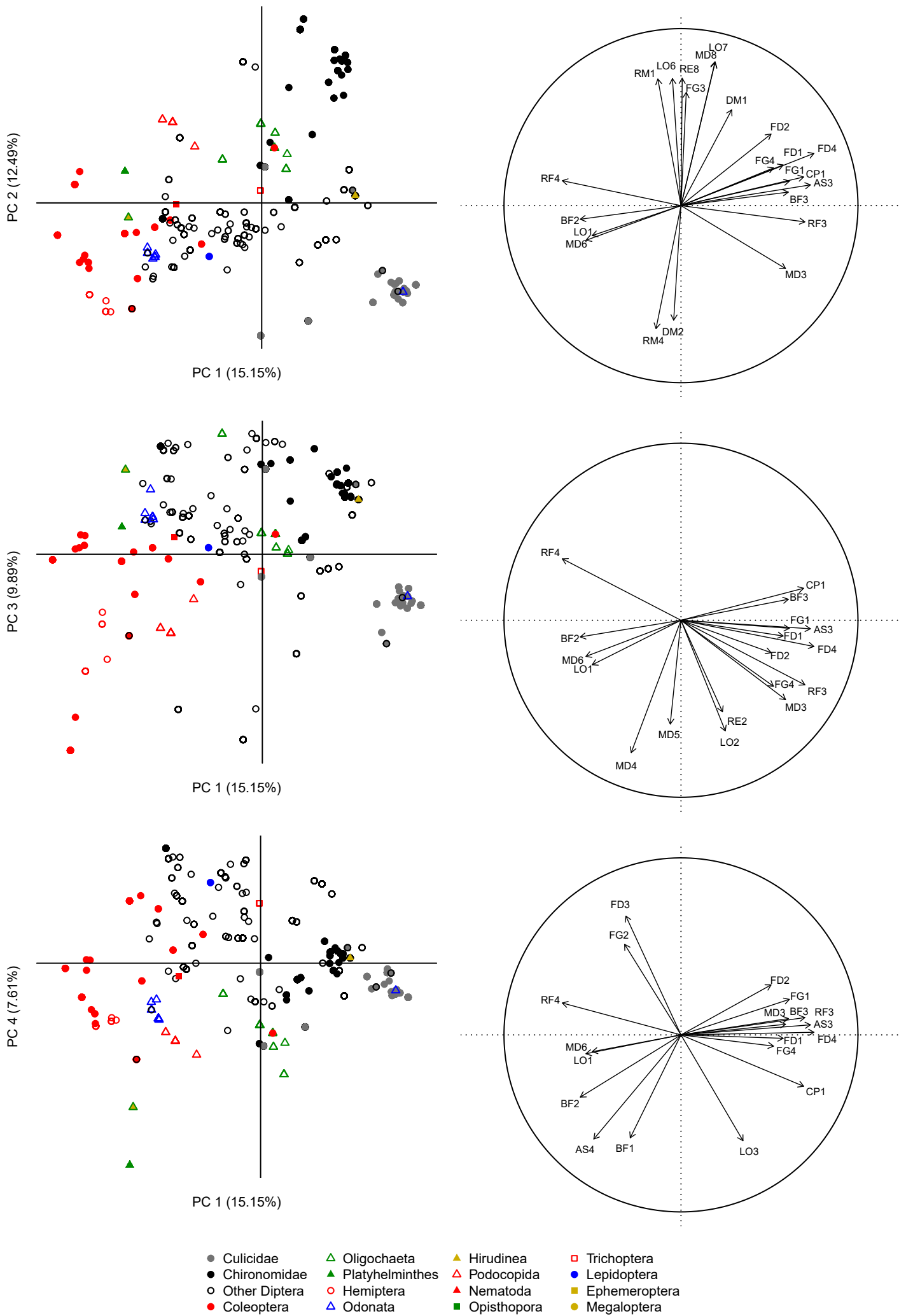**Figure S1**.

Figure S2