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RESEARCH ARTICLE

Animal functional traits

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

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Abstract

1. It has been argued that the mechanisms structuring ecological communities may be more generalizable when based on traits than on species identities. If so, patterns in the assembly of community-level traits along environmental gradients should be similar in different places in the world. Alternatively, geographical change in the species pool and regional variation in climate might result in site-specific relationships between community traits and local environments. These competing hypotheses are particularly untested for animal communities.

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2. Here we test the geographical constancy of trait-based assembly patterns using a widespread multi-trophic community: aquatic macroinvertebrates within bromeliads. We used data on 615 invertebrate taxa from 1,656 bromeliads in 26 field sites from Mexico to Argentina. We summarized invertebrate traits with four orthogonal axes, and used these trait axes to examine trait convergence and divergence assembly patterns along three environmental gradients: detrital biomass and water volume in bromeliads, and canopy cover over bromeliads.
3. We found no overall signal of trait-based assembly patterns along any of the environmental gradients. However, individual sites did show trait convergence along detrital and water gradients, and we built predictive models to explore these site differences.
4. Sites that showed trait convergence along detrital gradients were all north of the Northern Andes. This geographical pattern may be related to phylogeographical differences in bromeliad morphology. Bromeliads with low detritus were dominated by detritivorous collectors and filter feeders, where those with high detritus had more sclerotized and predatory invertebrates.
5. Sites that showed the strongest trait convergence along gradients in bromeliad water were in regions with seasonal precipitation. In such sites, bromeliads with low water were dominated by soft-bodied, benthic invertebrates with simple life cycles. In less seasonal sites, traits associated with short-term desiccation resistance, such as hard exoskeletons, were more important.
6. In summary, we show that there are strong geographical effects on the trait-based assembly patterns of this invertebrate community, driven by the biogeography of their foundational plant species as well as by regional climate. We suggest that inclusion of biogeography and climate in trait-based community ecology could help make it a truly general theory.

KEYWORDS
bromeliad invertebrates, functional biogeography, habitat filtering, trait-based ecology

1 | 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 et al., 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 et al., 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, e.g., by habitat fragmentation: Zambrano et al., 2019) and micro-and macro-evolution (Denelle et al., 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 colonize 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 et al., 2019). In short, the geographical consistency of trait–environment coupling in communities could be influenced by both bioclimatic and biogeographical constraints (Barnagaud et al., 2019; Violle et al., 2014).

It has been argued that a mechanistic understanding of community trait patterns requires the underlying environmental drivers to be explicitly included in analyses (Pillar & Orlóci, 1993; Shipley et al., 2016). Traits integrated at the community level can change in two potential ways along environmental gradients (Figure 1). A trait-convergence assembly pattern (TCAP: Pillar et al., 2009) occurs when communities at similar positions on an environmental gradient converge on a common suite of traits. Such a pattern is often assumed to be underlain by strong habitat filtering at intraspecific or interspecific levels. A trait-divergence assembly pattern (TDAP: Pillar et al., 2009) occurs when trait dispersion within communities changes over the environmental gradient. For example, species coexistence in competitive communities may require sufficient dispersion of traits to minimize niche overlap, and the strength of the required niche differentiation may change systematically with environmental context (but see Mayfield & Levine, 2010). Trait-divergence patterns can also be generated when either the strength of habitat filtering or environmental heterogeneity changes systematically over the gradient in mean environmental conditions (Carlucci et al., 2012). Communities can simultaneously show trait convergence and divergence along environmental gradients, although different traits may be involved in each process (Pillar et al., 2009).

To date, studies that have examined the geographical consistency of community trait patterns have focused largely on trait convergence (but see Bruelheide et al., 2018). However, a complete understanding of community trait-based assembly requires examining both trait convergence and divergence along similar environmental gradients in multiple regions of the world. Furthermore, the majority of studies that have quantified trait-based assembly patterns have been conducted in plant communities (e.g. Carlucci et al., 2012; Mendes et al., 2016). Animal communities may differ from plant communities in trait-based assembly patterns for several reasons. It has been argued that animals show less phenotypic

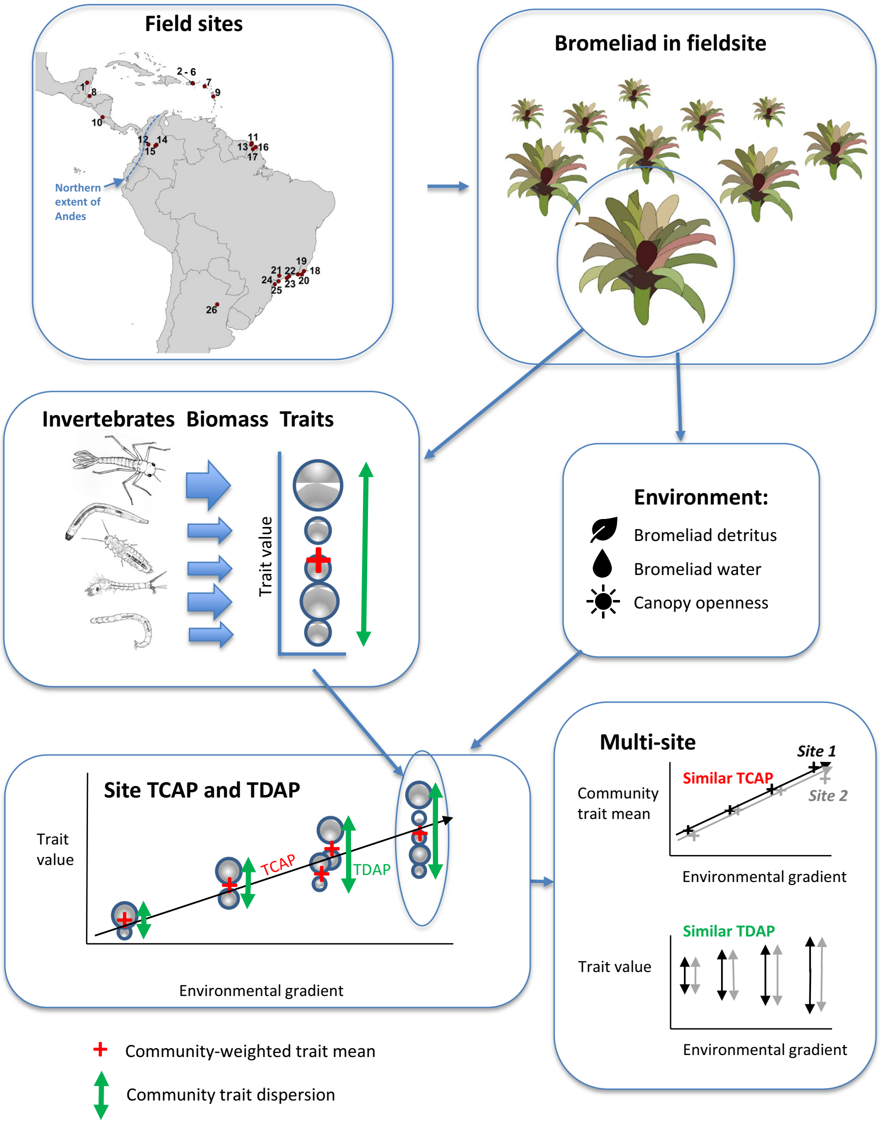

FIGURE 1 Study design for testing the geographical consistency of trait-assembly patterns. Bromeliads were sampled in 26 sites throughout the Neotropics ('Field sites' panel). In each site, bromeliads were sampled ('Bromeliad in field site' panel) for aquatic macroinvertebrates along environmental gradients ('Environment' panel). For each bromeliad, the traits of each invertebrate taxon were weighted by the taxon's total biomass (size of spheres and arrows in 'Invertebrates Biomass Traits' panel) to determine the community-weighted mean trait value (red cross) and the dispersion of the traits around this mean value (green arrow). A trait-based convergence assembly pattern (TCAP) occurred when the community-weighted mean changed consistently over environmental gradients; a trait-based divergence assembly pattern (TDAP) when dispersion changed consistently over environmental gradients ('Site TCAP and TDAP' panel). Note that TDAP includes both intertaxa variation in traits and variation in trait means between communities at similar points on the environmental gradient. Finally, TCAP and TDAP were compared among sites to determine whether trait-assembly patterns were geographically similar ('Multi-site' panel) or geographically different (not illustrated).

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 et al., 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 et al., 2018), scaling these pairwise patterns to community-level trait-assembly patterns still remains elusive (Wong et al., 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 et al., 2007; Pakeman & Stockan, 2014).

Here we examine the geographical 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; 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 dispersal barriers). Alternatively, differences in the sampling of sites (in terms of number or average size of bromeliads) could obscure a geographically general pattern.

2 | MATERIALS AND METHODS

2.1 | Field sampling

We compiled data on the aquatic macroinvertebrates in tank bromeliads previously sampled in 26 different sites (Figure 1; Table S1) throughout the natural distribution of the tank bromeliads (Bromeliaceae family). We obtained research permits for each of these field sites where required (Table S1b); in no field site was approval from an animal ethics board required. Field sites were distinct from each other in space, elevation and the species composition of invertebrate communities (Supporting Information). For every bromeliad, all water and detritus contained in the plant were removed, either by dissecting the plant or by pipetting. The water and detritus were examined for aquatic macroinvertebrates in small size-fractioned aliquots in white trays. Macroinvertebrates were identified to morphospecies in the field, and subsequently to the lowest possible taxonomic level. The detritus was oven-dried and weighed to determine dry mass. Bromeliads were sampled across a range of habitats, from exposed *restinga* (coastal sand-based shrub habitat) in Brazil to cloud forests on Caribbean mountaintops to rainforests in Central America. As no bromeliad genus was found in all field sites, we sampled the most common genera in sites. As this difference in bromeliad taxonomy between sites can lead to site differences in mean plant size, we explicitly test whether mean size drives site differences in trait-based assembly patterns in a post hoc test described later. In sum, the dataset consists of information on environmental attributes of bromeliads (n = 1,656), macroinvertebrate morphospecies ($n = 615$), macroinvertebrate traits ($n = 64$) and field sites ($n = 26$).

2.2 | Environmental matrix

Our analysis included three environmental characteristics of each sampled bromeliad: (a) the dry mass of all detritus in the bromeliad (hereafter 'detritus', measured in grams); (b) the volume of standing water in each bromeliad on the day of sampling (hereafter 'water', measured in ml); and (c) the openness of the canopy above the bromeliad (hereafter 'canopy', a binary variable with 1 = open canopy and 0 = closed canopy). These variables were chosen because previous site-specific research had established that they were important environmental drivers of community structure and function (Montero et al., 2010; Petermann et al., 2015; Richardson, 1999; Romero et al., 2016), and because there was enough coverage within and among field sites to enable robust analyses (Figure S1). A final consideration was that the three environmental gradients were not collinear (pairwise Pearson correlations, $r = 0.31–0.36$). For example, we did not include bromeliad water-holding capacity, even though it is known to be an important driver of community composition, because it was tightly correlated ($r = 0.80$) with the volume of water on the day of sampling and we had much higher data coverage of the latter. Our environmental matrix ($\boldsymbol{E}$, sensu Pillar et al., 2009, see below) consists of the three environmental variables describing each of the sampled bromeliads.

2.3 | Community biomass matrix

We defined as our community all macroinvertebrates found in bromeliads that were macroscopic and either strictly aquatic or semi-aquatic. We organized the abundance data using the R package FWDATA (developed by A.A.M.M, https://github.com/SrivastavaLab/fwdata). We then converted abundances to biomass by multiplying abundance by the estimated per capita biomass of each morphospecies, based on taxon-specific allometric relationships, using the HELLOMETRY R package (provided courtesy of P. Rogy, https://github.com/pierrerogy/hellometry). We used biomass rather than abundance to weight traits as many large-bodied invertebrates in bromeliads (e.g. damselflies, tabanids and sometimes tipulids) are known to have strong consumptive effects on other species (Amundrud et al., 2019; Petermann et al., 2015) but have such low abundance as to be essentially invisible in abundance-weighted traits. Our ***W*** matrix (sensu Pillar et al., 2009, see below) describes the biomass of each morphospecies of macroinvertebrate as a proportion of the total macroinvertebrate biomass within each sampled bromeliad.

2.4 | Trait matrix

Our analysis considers interspecific, but not intraspecific, differences in traits. In Céréghino et al. (2018), each bromeliad invertebrate morphospecies was scored in terms of 12 traits: aquatic developmental stage, body form, maximum body size, cohort production interval, dispersal mode, food, feeding group, locomotion, morphological defence, reproduction mode, resistance forms and respiration mode. Each trait was represented by several modalities or categories (e.g. the modalities for the trait 'dispersal mode' were passive and active), and the affinity of the taxa for each modality was fuzzy coded. In total, the 12 traits were represented by 64 modalities. Céréghino et al. (2018) reduced these 64 trait modalities to four orthogonal axes using PCA. Since then, there have been modest updates to the trait data: some trait scores were improved, the number of missing values reduced, a few microscopic or terrestrial species were removed, and the taxonomic resolution of some species identifications was improved. We therefore reran the PCA analysis on the updated trait matrix, using the same R script as in Céréghino et al. (2018), and used the first four axes in our current study. Our ***B*** matrix (sensu Pillar et al., 2009, see below) describes the morphospecies of macroinvertebrates in terms of the four PCA trait axes.

2.5 | Site information

We collated information on biogeographical, bioclimatic and sampling characteristics of each field site to better contextualize differences among sites. Biogeographical characteristics included position north and north west versus south and southeast of the Northern Andes (simplified hereafter as north versus south of Andes; Figure 1). The Northern Andes are known to be a dispersal barrier for both bromeliads (Givnish et al., 2011) and bromeliad invertebrates (Amundrud et al., 2018). Although the Southern and Central Andes could be a potential barrier between the west coast and centre of South America, we have no bromeliad data from the former and so do not analyse these mountain ranges. We examined species pool richness, estimated with Chao's method (Chao, 1987; implemented in the VEGAN R package), to test if richer sites had stronger trait–environment matching. From the WorldClim database (Fick & Hijmans, 2017), we extracted site-specific estimates of four bioclimatic variables that a previous study (Guzman et al., 2020) found to underlie spatial variation in bromeliad macroinvertebrate traits: mean diurnal range in temperature (BC2), temperature annual seasonality (BC4), precipitation annual seasonality (BC15) and precipitation of the driest quarter (BC17). WorldClim data were extracted at the 1 km^2 scale; when field sites exceeded 1 km^2 in size we averaged data over the relevant 1 km^2 pixels. Finally, we examined sampling characteristics of each site, including the number of bromeliads sampled (which affects the power of tests) and the site mean of the focal environmental gradient (in case trait–environment relationships differ with site position on gradient).

2.6 | Analysis of trait-based community assembly patterns

Our analysis of trait-based community assembly patterns is based on the methodology developed by Pillar et al. (2009) and implemented in the R package SYNCSA (Debastiani & Pillar, 2012). A trait-convergence assembly pattern (TCAP) can be visualized as the multivariate correlation between the average trait values of the community with the environment experienced by that community (Figure 1). The former is represented in the community-weighted trait mean (a new matrix, ***T***), calculated by multiplication of ***W*** (bromeliads by morphospecies in our data) and ***B*** (morphospecies by trait axes); the latter is the environmental (***E***) matrix. TCAP is therefore simply the ***T–E*** correlation. Individual taxa will differ in trait values from the mean of their community (i.e. be dispersed), and the trait-divergence assembly pattern (TDAP) describes how this dispersion itself correlates with the environmental gradient (Figure 1). Calculating TDAP requires first creating a new matrix ***X*** such that the ***X–E*** correlation contains both TCAP and TDAP, and then partialing out the ***T–E*** correlation (i.e. TCAP) to reveal TDAP (Pillar et al., 2009). In technical terms, the ***X*** matrix is created by weighting the species in matrix ***W*** by their degree of belonging to fuzzy sets that describe similarities between the species in traits (Duarte et al., 2016; Pillar et al., 2009).

The significance of the matrix correlations that describe TCAP and TDAP must be tested through permutations to ensure that traits, rather than the species that they are associated with, drive the correlation. The SYNCSA method compares the observed correlation coefficient to those obtained after repeatedly permuting row vectors of the ***B*** matrix. This permutation breaks up the association between species and their traits while maintaining trait correlation structure, and is an appropriate null model for trait-based assembly patterns (Pillar et al., 2009). To incorporate our field site structure into the TDAP and TCAP analyses, we added a 'strata' field to the SYNCSA R package, which directs the permutations to be entirely within field sites so as to preserve the integrity of the species pool in each site.

All matrix correlations were based on Procrustes analysis (Peres-Neto & Jackson, 2001), which describes the concordance between two superimposed matrices after optimizing their resizing, reflection and rotation, with 0 = no concordance and 1 = perfect concordance. We chose Procrustes analysis over the commonly used Mantel test, as it is more powerful (Peres-Neto & Jackson, 2001) and less prone to spurious correlations (Dutilleul et al., 2000).

2.7 | Analyses of across- and between-site patterns

To test if trait-based assembly patterns are universal (hypothesis H1) or not (H2), we first conducted a global test of either TCAP- and TDAP-environment associations, that is, considering all sites together but restricting permutations within species pools. We included all four trait axes to capture the entire multivariate trait space of the community. As sites differed substantially in their coverage of environmental variables, we examined each environmental gradient separately. We log-transformed both detritus and water data, as this improved correlations with TCAP and TDAP. Within each site, we centred environmental gradients (i.e. subtracted the site mean, after any log transformation) to ensure that our multi-site analysis only captured within-site correlations.

We further examined support for H1 by repeating the analysis (a) at the site level to determine whether many sites contributed to the overall pattern and (b) for each trait axis individually, to determine whether the same specific trait axes drove associations in all sites. As the inclusion of uninformative traits dilutes tests of trait–environment relationships, it is recommended to consider which traits (or in our case, trait axes) optimize TCAP and TDAP as part of analyses (Debastiani & Pillar, 2012; Pillar et al., 2021).

Where site differences in TCAP- and TDAP-environment associations existed, we tested hypothesis H2 using linear models to relate site differences in the strength of these associations to sampling (sample size, mean bromeliad environment), bioclimatic (BC2, BC4, BC15 and BC17) and biogeographical (species pool size, location north and south of Northern Andes) characteristics of sites. We established the significance of explanatory variables using ANOVA based on type II sums-of-squares to prevent collinearity from influencing results. We only constructed linear models for gradients represented by sufficient sites, namely gradients in detrital and water content. We visualized patterns in TCAP by plotting community-weighted trait means for specific trait axes against the environmental gradient. As TDAP patterns were largely not significant, we do not present visualizations.

3 | 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.

Given that there is substantial difference between sites in the strength of TCAP patterns along gradients in bromeliad detritus and water, we next tested whether these differences can be attributed (hypothesis H2) to climate, biogeography or site differences in sampling. In regression analyses, sites north of the Northern Andes were more likely to have significant TCAP over detrital gradients (Table S3). Indeed, all five sites where we detected trait convergence over gradients in detritus were located in the Caribbean or Central America (Figure 2a). To confirm this effect of geography on TCAP, we separated our sites into those north vs. south of the Northern Andes and re-ran all matrix analyses. There was now an overall significant TCAP ($p = 0.04$, rho = 0.18) driven by trait axis 1 ($p = 0.04$, rho = 0.25) for the subset of sites north of the Andes, but not the subset of sites south of the Andes ($p = 0.62$, rho = 0.10). Specifically, as detritus increased in northern sites, invertebrate communities shifted from those dominated by detritivorous collectors and filter feeders to those dominated by sclerotized and predatory invertebrates (Figure 3). By contrast, site differences in bioclimatic variables or sampling characteristics (sample size, site mean of log detritus) did not affect either the significance or strength of TCAP correlations in our regression analyses (Table S3).

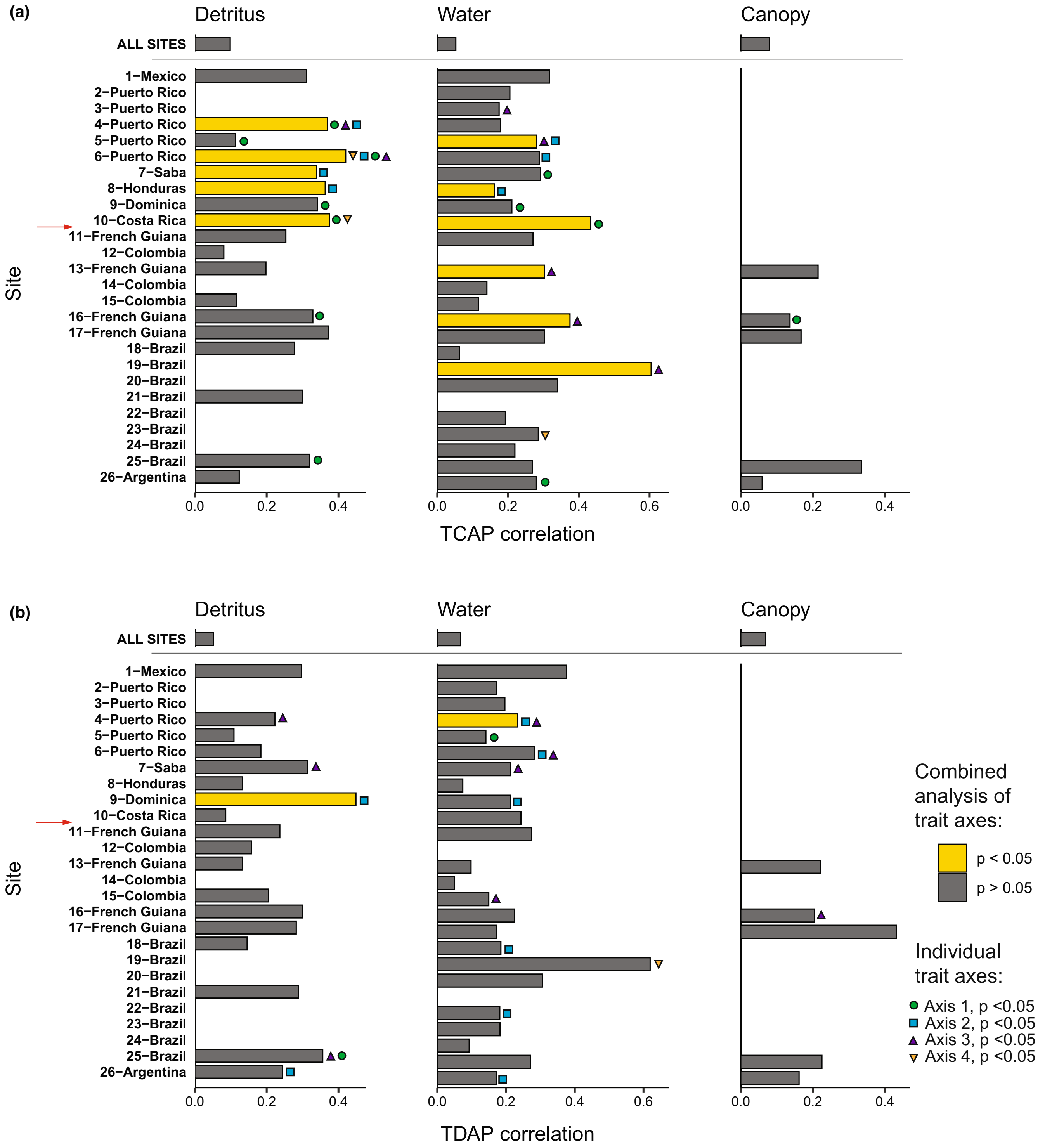

FIGURE 2 (a) Trait-based convergence assembly patterns (TCAP) of bromeliad macroinvertebrate communities along three local environmental gradients: detrital biomass (‘detritus’, on a log scale) or standing water volume in bromeliads (‘water’, on a log scale), and openness of the canopy above bromeliads (‘canopy’). Sites are ordered from north to south, with red arrows indicating the northern extent of the Andes. Sites with no data for a particular environmental gradient are indicated with white space. The strength of TCAP along each environmental gradient is evaluated with Procrustes correlations, and is based either on the four trait axes combined (bar graph) or assessed individually (symbols; where multiple trait axes are significant, the order of symbols progresses left to right from strongest correlation to weakest). (b) Trait convergence assembly patterns (TDAP) of bromeliad macroinvertebrate communities along local environmental gradients, labelled and ordered as in (a).

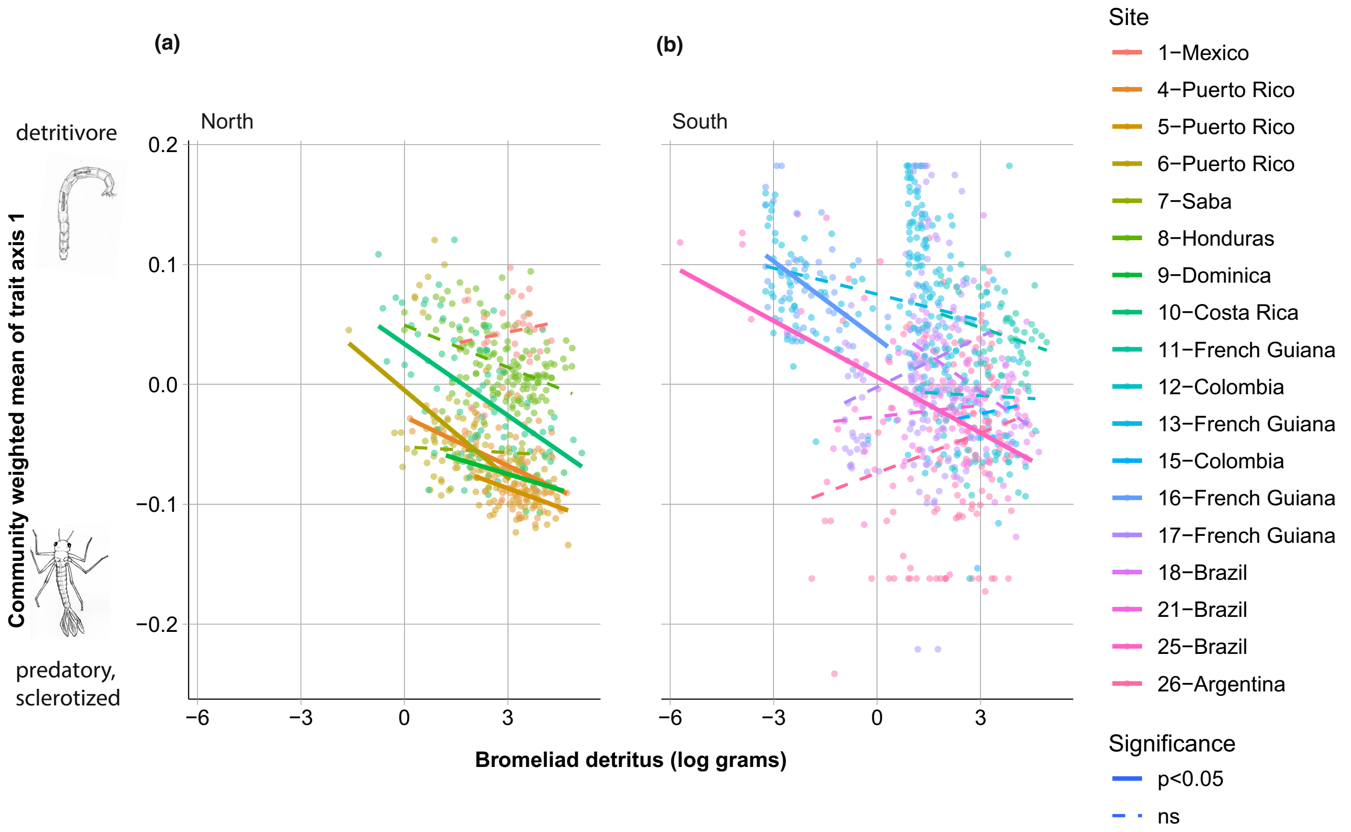

FIGURE 3 The community-weighted mean value of trait axis 1 (associated with trophic position) in each bromeliad is plotted as a function of the mass (log grams, without scaling or centring) of detritus in the bromeliad for each site, allowing a visualization of this particular TCAP-environmental correlation. Trendlines are shown simply to aid visualization of site-specific patterns; trendlines representing TCAP that were found by SYNCSA to be significant for trait axis 1 are shown with solid lines, otherwise the lines are dashed. Sites are divided into those north (sites 1–10) and south (sites 11–26) of the northern extent of the Andes.

Gradients in the amount of water in bromeliads were associated with convergence in community traits in six sites. In four of the sites, this TCAP was driven by trait axis 3 (defence: Figure 4a), whereas in the two other sites either trait axis 1(trophic) or 2 (habitat) were more important and inverse patterns with trait axis 3 were observed (Figure 4a). The sites with significant water-based TCAP were geographically scattered, unlike detrital-based TCAP results. Although site differences in the strength of the TCAP were not explained by biogeographical or sampling attributes of sites, they could be related to bioclimatic differences between sites (Table S3). Specifically, the strength of the TCAP correlations was greatest in sites with more seasonal precipitation (bioclimatic variable BC15), supporting H2, although not every site with seasonal precipitation had strong TCAP correlations (Figure 4b).

4 | 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 geographical variance in trait-assembly patterns joins only a few other geographically extensive studies of animal communities along environmental gradients, including those of fish (Lamouroux et al., 2002; McLean et al., 2021), ants (Bishop et al., 2016; Gibb et al., 2018), bees (Moretti et al., 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 geographical 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

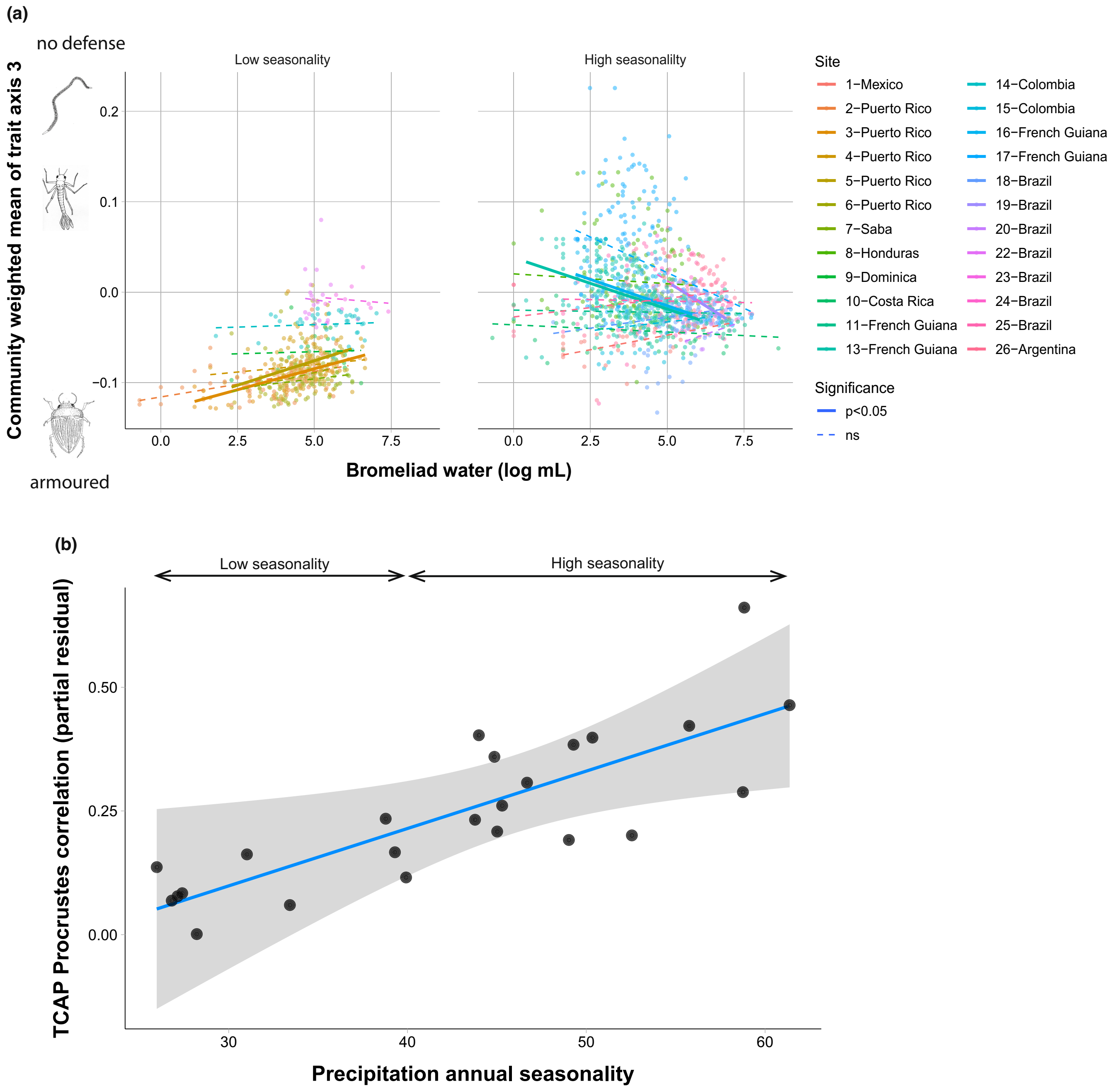

FIGURE 4 (a) The community-weighted mean value of trait axis 3 (associated with defence traits) in each bromeliad is plotted as a function of the volume (log ml, without scaling or centring) of water in the bromeliad for each site, allowing a visualization of this particular TCAP-environmental correlation. Trendlines are shown simply to aid visualization of site-specific patterns; trendlines representing TCAP that were found by SYNCSA to be significant for trait axis 3 are shown with solid lines, otherwise the lines are dashed. Sites are divided into those with low ($bio15 \leq 40$) and high ($bio15 > 40$) seasonality in precipitation as indicated in (b). (b) When considering all four trait axes, the strength of TCAP correlations increases with seasonality in precipitation, as represented by the bioclimatic variable bio15, with weak TCAP in low seasonality sites and often stronger TCAP in high seasonality sites. The predicted effect of seasonality was extracted as the partial residuals from a multiple regression model, conditioned on the mean effects of other site-level explanatory variables (Table S3). The shaded area represents the 95% CI around the predicted effect.

sampling effect. Invertebrate abundance usually correlates positively with detrital quantity in tropical freshwaters (Benstead et al., 2010), and this is also true for the bromeliad fauna (Richardson, 1999; Srivastava et al., 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 (Srivastava et al., 2008). A second possible reason is the energetic inefficiencies in trophic transfer (Lindeman, 1942), leading to bottom-up limitation of the occurrence of large-bodied predators when detritus is limiting (Wallace et al., 1999). This hypothesis has been tested by measuring the growth rate of predatory damselflies following relocation to bromeliads with less detritus, and was not supported (Srivastava et al., 2020). However, energetic limitation of other predatory taxa in this system remains unexplored. A third possible reason is the often high covariance of bromeliad detritus with bromeliad capacity within habitats (Srivastava et al., 2008), coupled with the restriction of some large, long-lived predators—such as the damselfly *Mecistogaster modesta* in Central America bromeliads—to high capacity bromeliads that rarely dry out (Amundrud & Srivastava, 2015; Srivastava et al., 2020). Notably, both sampling effects and covariance with capacity are expected to influence trophic structure most when the detrital gradient includes small bromeliads where the stochastic effects of sampling or risk of drought are highest. Such bromeliads characterize the rainforests of Central America and the Caribbean, and are in Tillandsioideae genera such as *Guzmania*, *Tillandsia*, *Vriesea* and *Werauhia*. By contrast, phytotelm bromeliads south of the Andes are more often high-capacity CAM species in Bromelioideae (Figure S1, Table S1). This distinction reflects the historical biogeography of bromeliads. The Tillandsioideae subfamily colonized the areas north of the Andes *c*. 8.7–14.2 million years ago, coinciding with rapid uplifting of the Northern Andes, whereas the Bromelioideae subfamily evolved more recently, *c*. 5.5 million years ago, and radiated in the areas south and east of the Andes (Givnish et al., 2011). Thus, the biogeography of the host plant may contribute to the geographical signal in invertebrate trait-based assembly patterns.

The strength of TCAP over gradients in bromeliad water also varied substantially between sites, with the strongest TCAP in sites with high seasonality in precipitation. A similar bromeliad volume by precipitation seasonality interaction was reported for invertebrate traits by Guzman et al. (2020) using a different analytical method, pointing to the robustness of this conclusion. In sites with strongly seasonal precipitation, bromeliads are likely to dry out completely during the dry season, posing substantial challenges to their aquatic fauna (Céréghino et al., 2020; Dézerald et al., 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, such as 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 3 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 et al., 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 were 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 geographical areas. There are several reasons for this geographical 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 et al., 2014). Second, trait-assembly patterns may be affected by the historical biogeography of species, including both the invertebrates and the bromeliads. While biogeographical 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 biogeographical 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 geographical 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).

AUTHORS' CONTRIBUTIONS

D.S.S. led the conceptualization, statistical analysis, manuscript writing, data curation and data visualization and contributed to trait scoring, funding, data collection, project administration; R.C. led the trait scoring and funding and administration of the CESAB project, and contributed to conceptualization, data collection and manuscript writing; A.A.M.M. led software development and invertebrate and trait data curation, and contributed to statistical analyses, conceptualization and project administration; V.D.P. made strong contributions to the conceptualization and statistical analysis and contributed to manuscript writing; V.J.D. led software development and contributed to the conceptualization, statistical analysis and created a figure; L.M.G. contributed to conceptualization, data curation, data collection, statistical analysis and manuscript editing; M.K.T. contributed to conceptualization, data curation, CESAB funding and manuscript editing; O.D. and I.M.B. contributed to conceptualization, data curation, data collection and manuscript editing; P.M.d.O., G.Q.R. and F.O.-B. contributed to conceptualization, data curation and data collection; M.A.C.M. contributed to conceptualization, data collection, statistical analysis and manuscript editing; C.L., V.F.F., A.Z.G. and B.C. contributed to conceptualization and data collection; B.A.R., J.S.B., M.J.R. and M.C.M. contributed to data collection and manuscript editing; M.J., J.T.N., S.T., G.C.O.P., G.M., B.M.S. and K.R.K. all contributed to extensive field data collections and processing of this data. All authors have approved this manuscript for publication. Authorship order is based on CRediT roles, with the second ranked author in the final (senior) author position.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All supporting data and R scripts for this study are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.vt4b8gtv4 (Srivastava et al., 2022).

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