Constraints on the functional trait space of aquatic invertebrates in bromeliads

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Abstract

1. Functional traits are commonly used in predictive models that link environmental drivers and community structure to ecosystem functioning. A prerequisite is to identify robust sets of continuous axes of trait variation, and to understand the ecological and evolutionary constraints that result in the functional trait space occupied by interacting species. Despite their diversity and role in ecosystem functioning, little is known of the constraints on the functional trait space of invertebrate biotas of entire biogeographic regions.

2. We examined the ecological strategies and constraints underlying the realized trait space of aquatic invertebrates, using data on 12 functional traits of 852 taxa collected in tank bromeliads from Mexico to Argentina. Principal Component Analysis was used to reduce trait dimensionality to significant axes of trait variation, and the proportion of potential trait space that is actually occupied by all taxa was compared to null model expectations. Permutational Analyses of Variance were used to test whether trait combinations were clade-dependent.

3. The major axes of trait variation represented life history strategies optimizing resource use, and anti-predator adaptations. There was evidence for trophic, habitat, defence and life history niche axes. Bromeliad invertebrates only occupied 16-23% of the potential space within these dimensions, due to greater concentrations than predicted under uniform or normal distributions. Thus, despite high taxonomic diversity, invertebrates only utilized a small number of successful ecological strategies.

4. Empty areas in trait space represented gaps between major phyla that arose from biological innovations, and trait combinations that are unviable in the bromeliad ecosystem. Only a few phylogenetically-distant genera were neighbouring in trait space. Trait combinations aggregated taxa by family and then by order, suggesting that niche conservatism was a widespread mechanism in the diversification of ecological strategies.

Keywords: Aquatic invertebrates; ecological strategies; functional diversity; niche hypervolume; functional trait space

1. Introduction

Functional traits, the biological, physiological and ecological attributes of organisms, have been argued to be a universal currency in deciphering mechanisms of how organisms relate to the environment and each other, permitting generalization despite taxonomic differences across biogeographic regions and ecosystem types (Violle et al., 2014). The rationale for "*rebuilding community ecology from functional traits*" (McGill et al., 2006) is that traits predict how individuals respond to and affect their environment (Wilman et al., 2014). Hence, whilst environmental conditions and resources define Hutchinsonian niche dimensions (Hutchinson, 1959), functional traits predict organisms' performance in such multidimensional niche space. It is therefore necessary to identify major axes of trait variation that can be interpreted as proxies of niche dimensions (Winemiller et al., 2015), before we begin to understand the ecological and evolutionary constraints that result in the niche space occupied by a community.

Extending trait analyses to the functional space occupied by global species pools allows for the comparison of trait combinations among regions or ecosystem types (Pianka et al., 2017), so that constraints on the trait space occupied by co-evolved species can be interpreted in terms of evolutionary and ecological processes (Díaz et al., 2016). Trait combinations that define ecological strategies of animals and plants are often reduced to five fundamental niche dimensions: trophic position, habitat, life history, defence and metabolic type (Winemiller et al., 2015). Within the universe of possible ecological strategies, the trait space actually occupied by a species pool is restricted by trade-offs among traits, as well as phylogenetic and ecological constraints. First, life history trade-offs restrict trait spaces, for organisms cannot optimize their performance in all niche dimensions simultaneously (Leimar, 2001). Trade-offs between body form and physiological functions also limit the range of possible trait combinations. A well-known example is the scaling relationship between body shape and size (Raup, 1966) and its consequences on the physiology of invertebrates. For example, because aquatic invertebrates with cylindrical body shapes have low surface area:volume ratios, they have a maximum body size where respiration via gas exchange through the integument is still efficient (Barnes et al., 2009). Second, restrictions of the trait space can result from phylogenetic constraints. When diversification within lineages fills contiguous regions in trait space, species tend to concentrate in multidimensional space as many traits are conserved at genus-family level (Pianka et al., 2017). Third, assuming that habitat is a template for ecological strategies (Southwood, 1977), ecological constraints in any ecosystem type can prevent colonization by species with unsuitable trait combinations, resulting in empty areas in trait space. Evolutionary convergence (selection by the habitat) further tends to concentrate phylogenetically-distant species in trait space (Blonder, 2017), thus reducing overall occupancy.

Most of our current understanding of the constraints that shape the functional trait space of species pools has come from studies of plants (Dwyer & Laughlin, 2017). Despite recognition of their role in multi-trophic processes and ecosystem functioning (Moretti et al., 2017), little is known about the constraints on invertebrate trait spaces. Yet, invertebrates represent approximately 75% of all living species, and occur in virtually all habitats around the globe, denoting a highly successful adaptive radiation (Barnes et al., 2009). The tropics notably contain a disproportionate number of the world’s invertebrate species. The diversity of functional traits that is presumably associated with this speciose fauna provides an opportunity to improve our understanding of trait space occupancy. Assembling data on functional traits in species-rich macrocosms is challenging, however, because of their tremendous taxonomic diversity. Natural microcosms that host co-evolved species in small and contained habitats form relevant model systems to test ecological theory (Kitching, 2000; Srivastava et al., 2004). In this study, we focused on the aquatic invertebrates inhabiting tank bromeliads, a discrete ecosystem that is commonly found across a wide array of Neotropical environments. Bromeliads are flowering plants represented by 3403 species native to the Neotropics (Ulloa et al., 2017), some of which have rosettes of leaves that trap water, forming "freshwater islands" in a terrestrial matrix. Such tank bromeliads collect rainwater and detritus, providing a habitat for aquatic organisms. Detailed descriptions of the bromeliad biota, food-web structure and ecosystem can be found in Laessle (1961), Frank & Lounibos (2009), Petermann et al. (2015), among others.

We examine the strategies and constraints underlying the realized niche of aquatic invertebrates, using data collected from tank bromeliads. Over the past 20+ years, the bromeliad invertebrate fauna has been sampled by our teams of researchers at 22 Neotropical locations covering the latitudinal range of tank bromeliads, and we documented 12 functional traits for 852 taxa recorded. We use this data to address three research questions. First, what traits define the major axes of trait variation of bromeliad invertebrates? Assuming that environmental conditions and biotic interactions drive resource use and life history strategies (Townsend & Hildrew, 1994), we hypothesized that traits related to habitat, trophic position, life history and anti-predator defence would define significant ecological strategies in our study (Winemiller et al. 2015). Second, what proportion of potential trait space is filled? Recent research showed that the trait space occupied by vascular plants is only 2-28% that of null expectations (Díaz et al., 2016). We hypothesized that the realized trait space of bromeliad invertebrates is a similarly low percentage, especially as plants have more morphological plasticity than animals (Borges, 2008). Third, if not all trait space is occupied, what is the role of phylogeny in constraining trait space occupancy? Many traits seem to be conserved at family level in aquatic invertebrates (Dolédec, Statzner & Frainay, 1998), even if morphological-physiological attributes have stronger taxonomic affinities than ecological-behavioural attributes (Poff et al., 2006). We therefore hypothesized that species concentrations in functional trait space are mainly determined by taxonomic relatedness, denoting phylogenetic constraints. Alternatively, trait trade-offs and ecological filtering could play important roles in restricting occupancy of trait space.

2. Methods

2.1. Study sites and sampling

A total of 1762 tank bromeliads were sampled from 1993 to 2015, at 22 locations (Fig. 1) distributed in 10 countries from 18.42°N (Mexico) to 29.43°S (Argentina), with multiple years of data collection at many sites (Table S1). The spatial range for this study included important biogeographic features such as the epicentre of bromeliad radiation (the Guyana Shield; Benzing, 2000), the isolation effects of Caribbean islands, the dispersal barrier of the Andes, and the effects of the Great American Interchange on Central America.

Each bromeliad was dismantled and washed in a bucket to capture the invertebrates. Where plant dissection was not permitted by local regulation (395 bromeliads out of 1762), micropipettes were used to extract the water and invertebrates from the tanks (Brouard et al., 2012). All aquatic invertebrates were sorted and identified to species (13% of the taxa), or to morphospecies associated to a genus (37%), a family (45%), or an order (5%). In sum, 852 taxa were identified. Given the number of sampled bromeliads per site and repeated sampling of sites over the years, we have a high degree of confidence that we thoroughly sampled the species pool of aquatic invertebrates inhabiting tank bromeliads at these sites. Although the use of morphospecies remains a common and often inevitable practice in ecological studies on tropical insects, there is the potential of artificially inflating the actual number of taxa in the species pool, if two species or taxa are identified as separate when in fact they are the same. However, there are two reasons why we expect such bias to be limited to a very small fraction of the taxa in our study. First, taxonomists have been working at the scale of countries or large clusters of sites (Fig. 1), so that reference collections and repeated sampling over the years ensured within-site consistency and confidence in morphospecies identifications (see Table S1 for information on invertebrate reference libraries). Second, the geographic distance between sites suggests that taxonomic turnover is large enough to prevent assignment of a species to different morphospecies across countries. Moreover, species that occur throughout the range (e.g., the oligochaete *Dero superterrenus*) are well-known by taxonomists and bromeliad ecologists, and were consistently identified to species level.

2.2. Functional traits

Twelve functional traits were analysed: maximum body size (BS), aquatic developmental stage (AS), reproduction mode (RE), dispersal mode (DM), resistance forms (RF), respiration mode (RM), locomotion (LO), food (FD), feeding group (FG), cohort production interval (CP), morphological defence (MD), body form (BF). Each of these nominal traits had a number of modalities, or states (Table 1). Modalities for the first nine traits were based on Tachet et al. (2010), but the actual scores were determined by a survey of the literature on bromeliad invertebrate species, genera and families (Kitching, 2000; Frank & Lounibos, 2009; Céréghino et al., 2011; Amundrud & Srivastava 2015; Dézerald et al., 2013), as well as the broader literature on freshwater invertebrates for the few morphospecies assigned to an order (Bentley & Day, 1989; Armitage, Pinder & Cranston, 1995; Merritt & Cummins, 1996; Vinogradova, 2007; Brown et al., 2009). The CP scores were based on relevant life history studies (Oliver, 1971; Dézerald et al., 2017). Scores for MD and BF were based on our own observations of specimens. Traits were coded at genus or family level, a resolution known to capture the functional trait diversity of freshwater invertebrates (Dolédec, Statzner & Frainay, 1998), with subsequent analyses of phylogenetic constraint accounting for the level at which traits were coded (see *Data analysis* below). Information on the traits was structured using a fuzzy-coding technique (Chevenet, Dolédec & Chessel, 1994): scores ranged from "0" indicating "no affinity", to "3" indicating "high affinity" of the taxon for a given trait modality (see Céréghino et al., 2011 for a detailed example). Only 30 taxa out of 852 had missing data for up to 7 modalities. The fuzzy-coding technique allowed us to build a matrix of 852 invertebrate taxa in rows by 64 trait modalities in columns.

2.3. Data analysis

The data matrix of invertebrate taxa by trait modalities was analysed using a Principal Component Analysis (PCA), which accounts for the correlation matrix between trait modalities. Prior to the analysis, we transformed each column in the data matrix into ranks, treating ties as in the transformation used for Spearman's rank correlation (Legendre & Legendre, 2012; see Table S2). This transformation was essential, for affinities to some trait modalities based on expert knowledge may be imprecise, and therefore, their rank order is more reliable for further computations than their original values (Podani, 2005). With the rank-transformed matrix, we computed Spearman's rank correlations between trait modalities, which were then used for the PCA. Considering the low number of missing values (0.22% of the whole matrix), pairwise correlations between trait modalities were calculated by using only the taxa without missing data for the corresponding pairs of trait modalities (Dray & Josse, 2015).

Ordination stability was tested by bootstrap resampling (Pillar, 1999), allowing us to identify significant ordination axes. For each bootstrap sample, the algorithm measured the correlation (θ^*) between bootstrapped and original scores for the taxa (including Procrustes rotation; the higher the agreement, the more stable was the corresponding axis), and repeated the resampling in a parallel process to obtain the same correlation (θ^o) with randomly permuted data within trait modalities. After repeated bootstrap resampling 1000 times, the probability $P(\theta^o \geq \theta^*)$ for each axis was obtained. We retained the ordination axes with a P-value ≤ 0.05 for further interpretation.

The correlation strength between trait modalities and ordination axes was used to infer gradients in life history trade-offs along the main PCA axes, which we interpreted as niche dimensions. Because there were missing values, we computed the correlation by weighting (multiplying) the trait modality eigenvector values retrieved by the PCA by the square root of the corresponding eigenvalue (Legendre & Legendre, 2012). We retained for interpretation trait modalities with correlations > |0.5| with a given axis.

In order to assess what proportion of the potential trait space was actually occupied by invertebrate taxa, the volume of the observed multi-dimensional convex hull was computed in the selected ordination space (Cornwell, Schwilk & Ackerly, 2006). This hypervolume was then compared to three theoretical null models, following Díaz et al. (2016). These models represent null hypotheses that the taxa scores on the selected ordination axes are randomly distributed. Models 1 and 2 assume that simulated scores are uniformly and normally distributed in trait space, respectively. Model 3 assumes the observed scores are randomly and independently permuted in each axis. As the volume of the observed convex hull was based on independent trait dimensions (PCA axes 1-4), significant restrictions of the potential trait space would primarily indicate clustered distributions of traits (concentrations of species in niche space), rather than correlations between trait modality values. The use of convex hulls has been criticized (Podani, 2009), but limitations apply to the context of measuring habitat filtering and functional diversity of communities, which is not the case here.

Phylogenetic signal could not be directly tested because a phylogeny of bromeliad invertebrates is still lacking. Taxonomic signal was therefore used as a proxy. We used morphospecies' score on the relevant PCA axes in permutational analyses of variance (PERMANOVAs, Euclidean distance, 9999 permutations) to test whether taxa grouped by higher taxonomic levels in trait space were significantly more functionally dissimilar between groups than within groups. Two successive PERMANOVAs were applied, first on the PCA scores of morphospecies coded at genus level to test taxonomic signal at family level, and second on the scores of morphospecies coded at family or genus level to test signal at order level.

The analyses were conducted in MULTIV Software, which is available at http://ecoqua.ecologia.ufrgs.br/arquivos/software/MULTIV/. The procedure, except bootstrapped ordination, is also implemented in RStudio 3.4.2. using the SYNCSA package. The testing of hypervolume concentration was adapted from Díaz et al. (2016) and the R script available at ftp://pbil.univ-lyon1.fr/pub/datasets/dray/DiazNature/. PERMANOVAs were conducted using the adonis function in the R package Vegan. The R code and the morphospecies PCA scores are archived on Zenodo at http://doi.org/10.5281/zenodo.1200194 (Debastiani, Céréghino & Pillar, 2018).

3. Results

3.1. Bromeliad invertebrates

The aquatic invertebrate fauna of tank bromeliads comprised 852 taxa (Fig 2), distributed among 46 insect families and 11 non-insect taxa. Sixty percent of the insect taxa were represented by 6 Diptera families, Culicidae, Chironomidae, Ceratopogonidae, Tipulidae, Syrphidae and Psychodidae. The next 25% belonged to 22 other Diptera families. The remaining insects were Coleoptera (9.5%), Hemiptera (2.5%), Lepidoptera (1%), Odonata (1.5%), and Trichoptera (0.1%). Of the non-insect taxa, 45% were Annelida (Hirudinae, Aeolosomatidae, Naididae, Enchtraeida and Lumbricidae), 22% were Turbellaria (flatworms), 21% were Crustacea Ostracoda (Limnocytheridae, Cyprididae and Candonidae), and 10% were Acari. The remaining taxa (<1% each) were Mollusca (Planorbidae) and Crustacea (Chydoridae, Daphniidae, Cyclopidae and Camthocamptidae).

3.2. Functional traits and niche dimensions

The first four axes of the PCA were significant (P <0.001; bootstrapped ordination), and explained 45.4% of the total variance in species traits (Fig. 3). Although a fifth axis was just significant (P= 0.033, 6.6% of the total variance), it was not interpretable in terms of opposing trait modalities. We therefore interpreted the main axes of trait variation along the first four PCA axes, which revealed 4 niche dimensions: trophic, habitat, morphological defence, life cycle.

Axis 1 (15.4% of the explained variance in traits, Fig. 3) represented the trophic niche dimension, mostly characterized by trait modalities related to food acquisition and functional feeding groups. The trophic gradient contrasted predators (FD7, negative end of the axis) with deposit/filter-feeder detritivores (significant trait modalities at the positive end of the axis: FG1, FG4, FD1, FD2, FD4). Among secondary traits, detritivores had short development time (CP1), whereas predators had longer larval lifespans (CP3). Other significant trait modalities like circular-elongate body form (BF3), or the presence of hairs (MD3) were secondary attributes of small detritivores. Similarly, a sclerotized exoskeleton (MD6) or the absence of resistance form (RF4) characterised large predators.

Axis 2 (12.2% of the variance) accounted for the habitat niche dimension, contrasting pelagic invertebrates that breathe at the water surface with siphons or spiracles (bottom area of the scatterplot; RM4), to benthic forms that crawl or burrow in the bottom of the wells and breathe through their integument and/or with gills (top area; LO4, LO6, LO7, RM1). Benthic invertebrates showed a trend for asexual reproduction (RE8), whereas pelagic invertebrates were active dispersers (DM2).

Axis 3 (10%) accounted for morphological defence, contrasting armoured invertebrates (MD3, MD4, MD5) that lived close to the water surface (LO2; bottom of the scatterplot) to undefended taxa that lacked morphological defence (MD1).

Axis 4 (7.7%) represented a life history dimension, ranging from simple (bottom) to complex life cycles (top). The former taxa complete their entire life cycle in the water (AS4, LO3) and usually have a flat body (BF1). The latter disperse actively at the adult stage (DM2), and in addition, are predominantly detritivores (FG2, FD3).

3.3. Constraints on the niche space of bromeliad invertebrates

The realized hypervolume was only 16.29% (model 1; uniform distribution), 17.18% (model 2; normal distribution) and 23.35% (model 3; random permutations) of the hypervolume predicted under null expectations ($p < 0.001$ in all models). This reveals that the niche space currently occupied by bromeliad invertebrates is vastly smaller than the potential fundamental space available in the trophic, habitat, morphological defence and life cycle dimensions. Because the observed convex hull was based on independent trait dimensions, the significant concentration of bromeliad invertebrates in trait space (clumped distribution of species) could be explained by constraints on their niche space, rather than correlations between trait modality values. Groups of genera or families appeared concentrated in specific areas of the multi-dimensional trait space, e.g., Diptera Culicidae, Diptera Chironomidae, Heteroptera, Coleoptera, non-insects (Fig. 3). Functional trait combinations were significantly clade-dependent in trait space, i.e., genera differed significantly between families (PERMANOVA; df = 29, R^2= 0.83, p= 0.001), and families differed significantly between orders (df = 10, R^2= 0.28, p= 0.001).

4. Discussion

We demonstrate that: (1) the global pool of aquatic invertebrates inhabiting tank bromeliads can be characterized by four fundamental trait dimensions, which indicate four niche dimensions; (2) only a small fraction (~16-23%) of the potential trait space representing fundamental niche dimensions is filled; and (3) taxonomic relatedness, a proxy for phylogenetic signal, substantially constrains this trait space occupancy. We demonstrate these strategies and constraints at the level of a known, global pool of aquatic invertebrates within a broadly distributed ecosystem. Overall, fundamental trait dimensions of bromeliad invertebrates represent trophic and life history strategies to optimize resource use in space and time (Stearns, 1992), and anti-predator defences (Thorp & Rogers, 2014). Widespread taxonomic constraints on the diversification of trait combinations concentrated species in functional trait space, while empty areas represented “gaps” between major phyla (e.g., insects *vs* non-insects), as well as trait combinations that are unviable in the bromeliad ecosystem.

There was strong evidence for trophic, habitat, defence and life history niche axes in bromeliad invertebrates. The structure of the species × trait PCA was mostly driven by modalities related to food and feeding modes, lifespan, morphology (body size and form, defence), and locomotion-dispersion modes. The categorization of aquatic invertebrates into functional feeding groups based on morphological and behavioural adaptations to acquire food usually predicts the spatial distribution of aquatic invertebrates (Merritt & Cummins, 1996; Brouard et al., 2012), highlighting a strong coupling between trophic and habitat occupancy traits. Here, we show a gradient in the trophic × habitat dimensions, from benthic collector-gatherers (gather fine particulates of organic matter in the bottom of the wells, e.g., Chironomidae, Oligochaetes) to benthic (Odonata, Platyhelminthes) and then pelagic predators (Coleoptera Dytiscidae, Hemiptera Veliidae, predatory Culicidae). Filter-feeders (Culicidae) formed a distinct cluster of pelagic taxa. Predator-prey interactions also underlie the diversification of morphological anti-predator traits (Thorp & Rogers, 2014). Some taxa (annelids, flatworms and vermiform Diptera larvae) were devoid of morphological defence, but spines, thick exoskeletons, sclerotized plates, tubes or shells were conspicuous defences in most lineages, and these adaptations are not specific to bromeliad invertebrates (Peckarsky, 1982). Defensive structures effectively reduce predation risk of foraging invertebrates, but incur metabolic costs that imply trade-offs in the energy allocated to other aspects of organisms' biology or anatomy. For example, abdominal spines are formed to the detriment of cuticle thickness in less vital body parts, notably the legs (Flenner et al., 2009). We note that morphological defence traits (the third most important axis of trait variation) have not been documented in the vast majority of studies of aquatic invertebrate traits (e.g., Tomanova & Usseglio-Polatera, 2007), so the relevance of defence in the context of ecological strategies and invertebrate community assembly has probably been previously underestimated (but see Poff et al., 2006). In summary, significant PCA axes portrayed gradients predicted by life history and habitat template theories (Southwood, 1977; Townsend & Hildrew, 1994). Traits related to metabolic rates were not measured, so the relevance of a fifth metabolic dimension proposed by Winemiller et al. (2015) could not be tested in our study. Finally, we note that the cumulated inertia represented by the first four PCA axes (45.4%) may seem *a priori* low, but in fact it depends on the level of correlation between the trait modalities. The key issue here was to make sure that axes represented stable trends (this was tested by bootstrap resampling), and were interpretable (trait modalities × axis correlations > |0.5|).

Only 16 to 23% of the potential trait space of bromeliad invertebrates was occupied, a restriction similar to that of vascular plants worldwide (Díaz et al., 2016). A similar aggregation of bromeliad fauna has been found using elemental compositions (C, N, P in body tissues) instead of functional traits (González et al. 2017). Here the "stoichiometric niche space" of 40 invertebrate and vertebrate species (20 families) associated with bromeliads in Chile, Costa Rica and Brazil was only 26% of the potential space. It could be argued that in both our study and that of González et al. (2017), partial filling of potential hypervolumes represents incomplete sampling of the global pool. However, this is unlikely to be the full explanation. In a review of the bromeliad fauna, Frank & Lounibos (2009) listed 25 families of aquatic invertebrates, noting the dominance of Diptera with aquatic larvae (16 families reported), and to a lesser extent Coleoptera (3 families). With our geographically broader data set, we found more than 70 invertebrate families, including 30 Diptera and 10 Coleoptera families. We are therefore confident that, even though we did not sample *all* Neotropical ecoregions for bromeliad invertebrates, the discovery of new taxa would not add extreme trait combinations that would further influence our estimate of the non-random trait space (Brandl & Bellwood, 2014). The clade-dependent diversification of ecological strategies highlighted by our results further suggests that newly recorded taxa would fall within the space and even within the clusters of taxa delineated by our data.

The niche space of invertebrates must be constrained by the environmental conditions in the bromeliad ecosystem, which prevent colonization by taxa with unsuitable trait combinations for this system. This is also true of any other ecosystem type where environmental filtering (e.g., shear stress in running waters, water permanency in wetlands) excludes entire invertebrate families or even orders (Tachet et al., 2010). For example, entire aquatic insect orders commonly found in Neotropical freshwaters are missing (Ephemeroptera, Plecoptera, Megaloptera) or poorly represented in bromeliads (only one species of Trichoptera). Particular trait combinations that prevail in these groups are therefore absent from the bromeliad invertebrate fauna, leaving empty areas within continuous niche dimensions. With their benthic habitats and ability to swim in the water column, many Ephemeroptera could theoretically bridge the gap between benthic and pelagic detritivores, while predatory Plecoptera and Trichoptera would for instance fill the area of benthic predators within the habitat × trophic dimensions. The physical and chemical conditions in bromeliads (Richardson et al., 2000) exclude these invertebrates, which require well-oxygenated waters (something which makes them good indicators of nutrient pollution in rivers). We believe that similar constraints however apply in any other ecosystem type (e.g., water velocity in streams excludes or limits pelagic macroinvertebrates) so the corresponding habitat × trophic niche areas are probably similarly unevenly populated.

Both niche conservatism and convergence can theoretically clump taxa together in multi-dimensional trait space (Blonder, 2017). Here, trait combinations usually aggregated taxa by family and then by order. Similar findings were reported for North-American (Poff et al., 2006) and European river invertebrates (Usseglio-Polatera et al., 2000). Our results and the literature thus point to the idea of a phylogenetic signal in trait combinations, and suggest that niche conservatism is a widespread mechanism in the diversification of ecological strategies of freshwater invertebrates. There was a gap between insects and non-insects in all dimensions, and then between the various non-insect phyla. This is not surprising as major phyla arose from biological innovations (Wainwright & Price, 2016). For example, the cuticle represents a major innovation that underlies the diversification of body and appendage forms (legs, mouthparts) in arthropods (Gullan & Cranston, 2014), thereby supporting a variety of strategies related to food and habitat use. Most aquatic insects also have “complex”, cross-ecosystem life cycles with aquatic immature stages and a terrestrial adult (whereas non-insects have “simple”, entirely aquatic life cycles). Exceptions in bromeliads are Dytiscidae (Coleoptera) and Veliidae (Hemiptera), where adults are aquatic but kept an aerial respiration mode, interpreted as an evolutionary return to the aquatic life. Within any given lineage, concentrations of genera or families in niche space can then emerge from different ecological strategies in only one or two niche dimensions. For instance, Culicidae and Chironomidae form very distinct clusters in the habitat dimension, but occupy contiguous positions on the trophic, life history and defence dimensions. Evolutionary convergence was suggested in our PCA when phylogenetically-distant species were neighbouring in trait space. For instance, predatory *Toxorhynchites* departed from the majority of small, filter-feeding Culicidae to share traits found in other pelagic predators (Coleoptera, Hemiptera), including larger body size, long larval lifespan, and absence of a desiccation-resistant form (Dézerald et al., 2017). Such a pattern was, however, limited to a few genera only, suggesting that evolutionary convergence played a minor role in the functional diversification of bromeliad invertebrates.

The most compelling challenges of trait-based ecology include deciphering the processes that determine functional community composition at local to biogeographic scales, and predicting the response of communities and ecosystems to environmental changes from functional traits (Violle et al., 2014). Ecologists however lack the prerequisite of robust trait-environment relationships across major lineages. We reduced the dimensionality of the functional trait space of bromeliad invertebrates to four ecologically relevant and continuous dimensions. The scores of the 852 taxa for four main PCA axes represent continuous trait values, which can now be used in analyses of the processes underlying functional diversity across different spatial scales in relation to spatial, environmental and biotic factors. At the bromeliad to site scale, we expect that environmental gradients will determine the relative representation of these four trait axes (Dézerald et al., 2015). At much larger scales, encompassing marked differences in the species pool between sites, we can make two opposing predictions. On one hand, convergence in functional trait compositions between geographically-distinct sites would suggest a dominant role for niche processes in community assembly. Phylogenetic conservatism could be an evolutionary mechanism behind such functional convergence, as species in a genus or family could stand in for each other in terms of functional traits despite spatial turnover. On the other hand, very dissimilar trait compositions in geographically-distant communities could occur if entire taxonomic groups are absent in some areas (e.g., due to dispersal limitations) and if phylogenetic constraints prevent convergent evolution of distantly related taxa. These mechanisms would thus point to a strong role for historical contingency in functional community composition. Such large-scale analyses would allow us to determine whether functional diversity is largely determined by niche-based processes, or limited by dispersal, evolution, or biogeography (Vellend et al., 2014). These types of analyses are contingent on a robust set of orthogonal and important trait axes, such as those produced here.

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Authors' contributions

RC, VDP and DSS conceived the ideas, VDP designed methodology; VDP and VJD analysed the data; RC and VDP led the writing of the manuscript. All authors, except VDP and VJD, collected the data. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data available from the Knowledge Network for Biocomplexity repository at https://knb.ecoinformatics.org/#view/doi:10.5063/F1VD6WMF (Céréghino et al., 2018).

References

Amundrud, S. L. & Srivastava, D. S. (2015). Drought sensitivity predicts habitat size sensitivity in an aquatic ecosystem. *Ecology*, 96, 1957–1965.

Armitage, P. D., Pinder, L. C. & Cranston, P. (1995). The Chironomidae: biology and ecology of non-biting midges. Springer Netherlands.

Barnes, R. S. K., Calow, P. P., Olive, P. J. W., Golding, D. W., Spicer, J. I. (2009). *The invertebrates: a synthesis*, 3rd Edition. Wiley-Blackwell.

Bentley, M.D. & Day, J.F. (1989). Chemical ecology and behavioral aspects of mosquito oviposition. Annual Review of Entomology, 34, 401–421.

Benzing, D. H. (2000). *Bromeliaceae: profile of an adaptive radiation*. Cambridge University Press, Cambridge, U.K.

Blonder, B. (2017). Hypervolume concepts in niche- and trait-based ecology. *Ecography*, 40, 1-13.

Borges, R. M. (2008). Plasticity comparisons between plants and animals. *Plant Signaling and Behaviour*, 3, 367–375.

Brandl, S. J. & Bellwood, D. R. (2014). Individual-based analyses reveal limited functional overlap in a coral reef fish community. *Journal of Animal Ecology*, 83, 661–670.

Brouard, O., Céréghino, R., Corbara, B., Leroy, C., Pelozuelo, L., Dejean, A. & Carrias, J. F. (2012). Understory environments influence functional diversity in tank-bromeliad ecosystems. *Freshwater Biology*, 57, 815–823.

Brown, B. V., Borkent, A., Cumming, J. M., Wood, D. M., Woodley, N. E. & Zumbardo, M. A. (eds). (2009). *Manual of central american Diptera: volume 1*. NRC Research Press, Ottawa, Canada.

Céréghino, R., Leroy, C., Carrias, J. F., Pelozuelo, L., Ségura, C., Bosc, C., Dejean, A. & Corbara, B. (2011). Ant-plant mutualisms promote functional diversity in phytotelm communities. *Functional Ecology*, 25, 954–963.

Céréghino, R., Srivastava, D. S., de Omena, P. M., MacDonald A. A. M., Barberis I. M., Corbara, B., … Montero, G. (2018). Data from: Constraints on the functional trait space of aquatic invertebrates in bromeliads. *Knowledge Network for Biocomplexity*, https://knb.ecoinformatics.org/#view/doi:10.5063/F1VD6WMF

Chevenet, F., Dolédec, S. & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31, 295–309.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87, 1465–1471.

Debastiani, V. J., Céréghino, R., & Pillar V. D. (2018). Code and results for: Constraints on the functional trait space of aquatic invertebrates in bromeliads. *Zenodo*, http://doi.org/10.5281/zenodo.1200194

Dézerald, O., Céréghino, R., Corbara, B., Dejean, A., Leroy, C. (2015). Functional trait responses of aquatic macroinvertebrates to simulated drought in a neotropical bromeliad ecosystem. *Freshwater Biology*, 60, 1917–1929.

Dézerald, O., Leroy, C., Corbara, B., Carrias, J.-F., Pélozuelo, L., Dejean, A. & Céréghino, R. (2013). Food-web structure in relation to environmental gradients and predator-prey ratios in tank-bromeliad ecosystems. *Plos One*, 8, e71735.

Dézerald, O., Leroy, C., Corbara, B., Dejean, A., Talaga, S. & Céréghino, R. (2017). Environmental drivers of invertebrate population dynamics in neotropical tank bromeliads. *Freshwater Biology*, 62, 229–242.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I.J., Lavorel, S., Dray, S., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171.

Dolédec, S., Statzner, B. & Frainay, V. (1998). Accurate description of functional community structure: identifying stream invertebrates to species-level? *Bulletin of the North American Benthological Society*, 15, 154–155.

Dray, S. & Josse, J. (2015). Principal component analysis with missing values: a comparative survey of methods. *Plant Ecology*, 216, 657–667.

Dwyer, J.M. & Laughlin, D.C. (2017). Constraints on trait combinations explain climatic drivers of biodiversity: the importance of trait covariance in community assembly. *Ecology Letters*, 20, 872–882.

Flenner, I., Olne, K., Suhling, F., & Sahlén, G. (2009). Predator-induced spine length and exocuticle thickness in *Leucorhinia dubia* (Insecta: Odonata): a simple physiological trade-off? *Ecological Entomology*, 34, 735–740.

Frank, J.H. & Lounibos, L.P. (2009). Insects and allies associated with bromeliads: a review. *Terrestrial Arthropod Reviews*, 1, 125–153.

González, A. L., Dézerald, O., Marquet, P. A., Romero, G. Q. & Srivastava, D. (2017). The multidimensional stoichiometric niche. *Frontiers in Ecology and Evolution*, 5, 110, doi: 10.3389/fevo.2017.00110

Gullan, P. J. & Cranston, P. S. (2014). *The insects: an outline of entomology*, 5th Edition. Wiley-Blackwell.

Hutchinson, G. E . (1959). Homage to Santa Rosalia, or why are there so many kinds of animals*? The American Naturalist*, 93, 145–159.

Kitching, R. L. (2000). *Food webs and container habitats: the natural history and ecology of phytotelmata*. Cambridge University Press.

Laessle, A. M. (1961). A micro-limnological study of Jamaican bromeliads. *Ecology*, 42, 499–517.

Legendre, P. & Legendre, L. (2012). *Numerical Ecology*. Elsevier.

Leimar, O. (2001). Evolutionary change and Darwinian demons. *Selection*, 2, 65–72.

McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185.

Merritt, R. W. & Cummins, K. W. (1996). *An introduction to the aquatic insects of North America*. 3rd edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Moretti, M., Dias, A. T. C., de Bello, F., Altermatt, F., Chown, S. L., Azcarate, F. M., … Berg, M. P. (2017). Handook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, 31, 558-567.

Oliver, D. R. (1971). Life history of the Chironomidae. *Annual Review of Entomology*, 16, 211–230.

Peckarsky, B. L. (1982). Insect predator-prey relations. *BioScience*, 32, 261–266.

Petermann, J. S., Farjalla,V. F., Jocqué, M., Kratina, P., MacDonald, A. A. M., Marino, N. A. C., … Srivastava, D. S. (2015). Dominant predators mediate the impact of habitat size on trophic structure in bromeliad invertebrate communities. *Ecology*, 96, 428-439.

Pianka, E. R., Vitt, L. J., Pelegrin, N., Fitzgerald, D. B. & Winemiller, K. O. (2017). Toward a periodic table of niches, or exploring the lizard niche hypervolume. *The American Naturalist*, 190, DOI: 10.1086/693781

Pillar, V. D. (1999). The bootstrapped ordination re-examined. *Journal of Vegetation Science*, 10, 895–902.

Podani, J. (2005). Multivariate exploratory analysis of ordinal data in ecology: Pitfalls, problems and solutions. *Journal of Vegetation Science*, 16, 497–510.

Podani, J. (2009). Convex hulls, habitat filtering, and functional diversity: mathematical elegance versus ecological interpretability. *Community Ecology*, 10, 244–250.

Poff, N. L., Olden, J. D., Viera, N. K. M., Finn, D.S., Simmons, M. P. & Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: traits based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, 25, 730–755.

Raup, D. M. (1966). Geometrical analysis of shell coiling: general problems. *Journal of Palaeontology*, 40, 1178–1190.

Richardson, B. A., Richardson, M.J., Scatena, F. N. & McDowell, W. H. (2000). Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Tropical Ecology*, 16, 167-188.

Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, 46, 337–365.

Srivastava, D. S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S. P., Miller, T. E., Munguia, P., Romanuk, T., Schneider, D. C. & Trzcinski, M. K. (2004). Are natural microcosms useful model systems for ecology? *Trends in Ecology and Evolution*, 19, 379–384.

Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.

Tachet, H., Richoux, P., Bournaud, M. & Usseglio-Polatera, P. (2010). *Invertébrés d'eau douce. Systématique, biologie, écologie*. CNRS editions, Paris.

Thorp, J. H. & Rogers, D. C. (2014). *Thorp and Covich's freshwater invertebrates: ecology and general biology*. 4th Edition, Elsevier.

Tomanova, S. & Usseglio-Polatera, P. (2007). Patterns of benthic community traits in neotropical streams: relationship to mesoscale spatial variability. *Fundamental and Applied Limnology*, 170, 243–255.

Townsend, C. R. & Hildrew, A. G. (1994). Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, 31, 265–275.

Ulloa, C. U., Acevedo-Rodríguez, P., Beck, S., Belgrano, M. J., Bernal, R., Berry P. E., … Jørgensen, P. M. (2017). An integrated assessment of the vascular plant species of the Americas. *Science*, 358, 1614-1617.

Usseglio-Polatera, P., Bournaud, M., Richoux, P. & Tachet, H. (2000). Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology*, 43, 175–205.

Vellend, M., Srivastava, D. S., Anderson, K. M., Brown, C. D., Jankowski, J. E., Kleynhans, E. J., … Xue, X. (2014). Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos*, 123, 1420-1430.

Vinogradova, E. B. (2007). *Diapause in aquatic insects, with emphasis on mosquitoes*. Pages 83–113 in Alekseev V.R. et al. (eds.), Diapause in aquatic invertebrates, Springer.

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J. & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13690–13696.

Wainwright, P. C. & Price, S.A. (2016). The impact of organismal innovation on functional and ecological diversification. *Integrative and Comparative Biology*, 56, 479–488.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M. & Jetz, W. (2014). Elton traits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027–2027.

Winemiller, K.O., Fitzgerald D.B., Bower L. & Pianka E.R. (2015). Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, 18, 737–751.

Table 1. Functional traits and their modalities. Cohort production interval is the time from hatching to adult emergence (days). Abbreviations as in Fig. 3.

Traits	Modality	Abbreviation	Functional interpretation
Maximum body size	≤0.25 cm	BS1	Energetic demands increase with body size
	0.25-0.5 cm	BS2	
	0.5-1 cm	BS3	
	1-2 cm	BS4	
	>2 cm	BS5	
Aquatic stage	egg	AS1	Cross-ecosystem life cycles reduce competition among developmental stages
	larva	AS2	
	nymph	AS3	
	adult	AS4	
Reproduction	ovoviviparity	RE1	Egg care increase survival and hatching success
	isolated eggs, free	RE2	
	isolated eggs, cemented	RE3	
	clutches, cemented	RE4	
	clutches, free	RE5	
	clutches in vegetation	RE6	
	clutches, terrestrial	RE7	
	asexual reproduction	RE8	
Dispersal mode	passive	DM1	Dispersal ability influences species range and access to new resources
	active	DM2	
Resistance form	eggs, statoblasts	RF1	Resting stages allow populations to persist through the duration of unfavourable periods
	cocoons	RF2	
	diapause or dormancy	RF3	
	none	RF4	
Respiration mode	integument	RM1	Adaptations relate to dissolved oxygen availability. Siphons and spiracles permit to live underwater while using aerial oxygen, so dominate in anoxic waters. Other adaptations allow to use dissolved oxygen in oxygenated waters
	gill	RM2	
	plastron	RM3	
	siphon/spiracle	RM4	
	hydrostatic vesicle	RM5	
Locomotion	flier	LO1	Use and partition of micro- to mesohabitats; potential interactions
	surface swimmer	LO2	
	full water swimmer	LO3	
	crawler	LO4	
	burrower	LO5	
	interstitial	LO6	
	tube builder	LO7	
Food	microorganisms	FD1	Use and partition of food resource
	detritus (< 1mm)	FD2	
	dead plant (litter)	FD3	
	living microphytes	FD4	
	living leaf tissue	FD5	
	dead animals (> 1mm)	FD6	

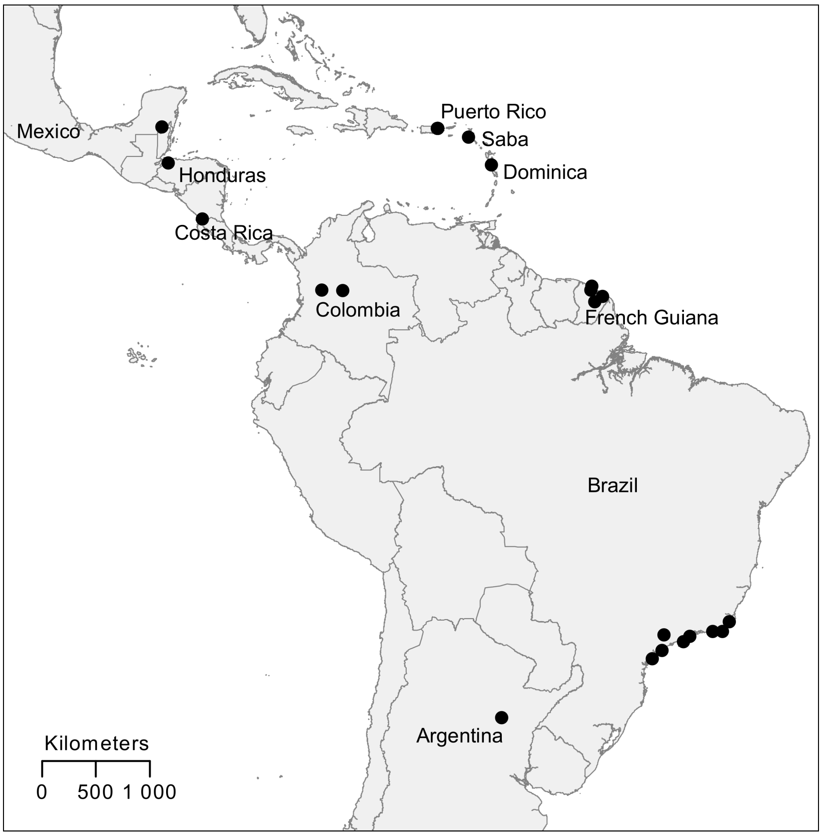
	living microinvertebrates	FD7	
	living macroinvertebrates	FD8	
Feeding group	deposit feeder	FG1	Morphological and behavioural adaptations to acquire food determine particle size ingestion, and how energy is processed
	shredder	FG2	
	scraper	FG3	
	filter-feeder	FG4	
	piercer	FG5	
	predator	FG6	
Cohort production interval	<21 days	CP1	Growth and reproductive strategies
	21-60 days	CP2	
	>60 days	CP3	
Morphological defence	none	MD1	Defensive structures reduce predation risk and favour survival
	elongate tubercle	MD2	
	hairs	MD3	
	sclerotized spines	MD4	
	dorsal plates	MD5	
	sclerotized exoskeleton	MD6	
	shell	MD7	
	case or tube	MD8	
Body form	flat elongate	BF1	Body form relates to physiological functions, as invertebrates interact with their environment at surfaces
	flat ovoid	BF2	
	cylindrical elongate	BF3	
	cylindrical ovoid	BF4	

Figure legends

Figure 1. Map of Central and South America illustrating the distribution of sampling locations. See Table S1 for details.

Figure 2. The bromeliad invertebrate families (insects) or higher taxa (non-insects as inset), ranked from top to bottom by decreasing number of morphospecies.

Figure 3. Principal components analysis (PCA) ordination of aquatic taxa (left) according to their functional traits (right). The first four PCA axes are depicted pairwise and only trait modalities with correlations $r > |0.5|$ with at least one axis are shown. Grey arrows are interpretations of ecological strategies based on changes in trait combinations along the axes (see text). Abbreviations for trait modalities as in Table 1.


Puerto Rico
Mexico
Saba
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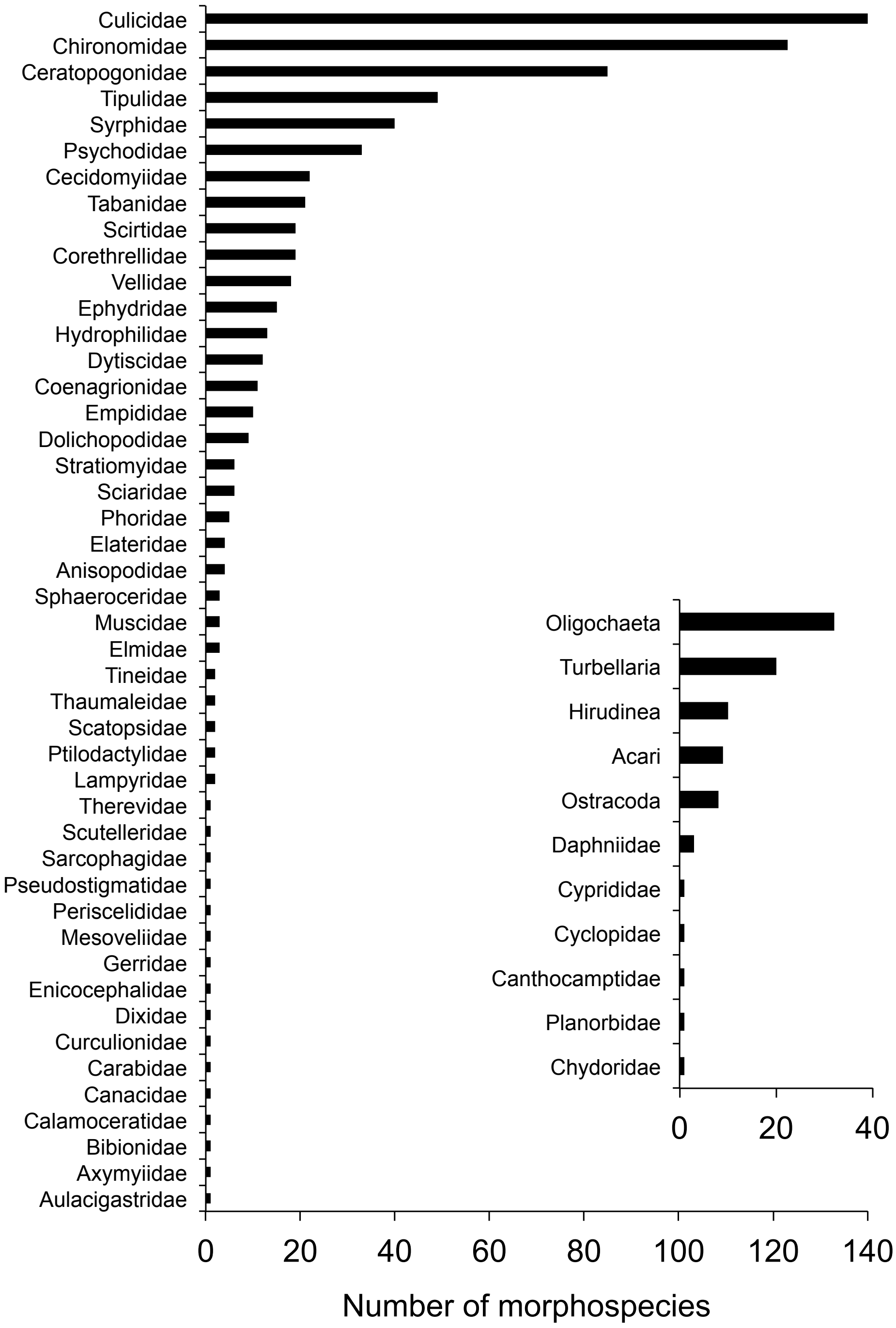
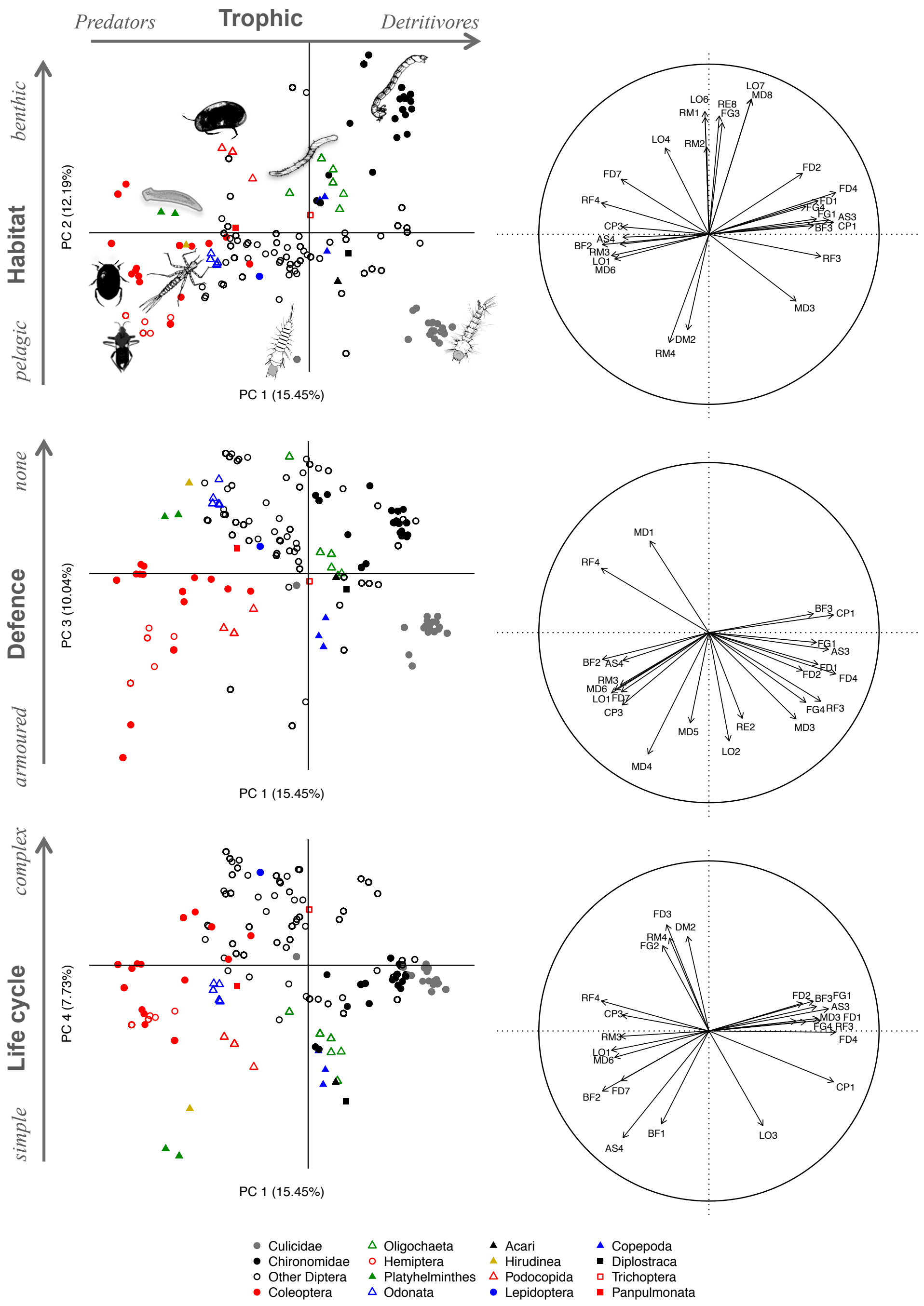
Dominica
Costa Rica
Colombia
French Guiana
Brazil
Argentina
Kilometers
0
500
1 000


Culicidae
Chironomidae
Ceratopogonidae
Tipulidae
Syrphidae
Psychodidae
Cecidomyiidae
Tabanidae
Scirtidae
Corethrellidae
Vellidae
Ephydridae
Hydrophilidae
Dytiscidae
Coenagrionidae
Empididae
Dolichopodidae
Stratiomyidae
Sciaridae
Phoridae
Elateridae
Anisopodidae
Sphaeroceridae
Muscidae
Elmidae
Tineidae
Thaumaleidae
Scatopsidae
Ptilodactylidae
Lampyridae
Therevidae
Scutelleridae
Sarcophagidae
Pseudostigmatidae
Periscelididae
Mesoveliidae
Gerridae
Enicocephalidae
Dixidae
Curculionidae
Carabidae
Canacidae
Calamoceratidae
Bibionidae
Axymyiidae
Aulacigastridae
0
20
40
60
80
100
120
140
Number of morphospecies
Oligochaeta
Turbellaria
Hirudinea
Acari
Ostracoda
Daphniidae
Cyprididae
Cyclopidae
Canthocamptidae
Planorbidae
Chydoridae
0
20
40


Predators
Trophic
Detritivores
benthic
Habitat
pelagic
PC 2 (12.19%)
PC 1 (15.45%)
LO7
MD8
LO6
RE8
RM1
FG3
LO4
RM2
FD7
FD2
RF4
FD4
FD1
FG4
FG1
AS3
CP3
BF3
CP1
AS4
BF2
RM3
LO1
MD6
RF3
MD3
DM2
RM4
none
Defence
armoured
PC 3 (10.04%)
PC 1 (15.45%)
MD1
RF4
BF3
CP1
FG1
AS3
BF2
AS4
FD1
FD2
FD4
RM3
MD6
LO1
FD7
CP3
FG4
RF3
MD5
RE2
MD3
LO2
MD4
complex
Life cycle
simple
PC 4 (7.73%)
PC 1 (15.45%)
FD3
DM2
RM4
FG2
RF4
FD2
BF3
FG1
AS3
CP3
MD3
FD1
FG4
RF3
RM3
FD4
LO1
MD6
BF2
FD7
CP1
BF1
LO3
AS4
● Culicidae
● Chironomidae
○ Other Diptera
● Coleoptera
△ Oligochaeta
○ Hemiptera
▲ Platyhelminthes
△ Odonata
▲ Acari
▲ Hirudinea
△ Podocopida
● Lepidoptera
▲ Copepoda
■ Diplostraca
□ Trichoptera
■ Panpulmonata