

Comparing taxon- and trait-environment relationships in stream communities



Victor Satoru Saito^{a,*}, Tadeu Siqueira^b, Luis Mauricio Bini^c, Raul Costa-Pereira^d, Edineusa Pereira Santos^e, Sandrine Pavoine^f

^a Departamento de Ciências Ambientais, Universidade Federal de São Carlos, Rodovia Washington Luís, São Carlos 13565-905, Brazil

^b Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil

^c Departamento de Ecologia, Universidade Federal de Goiás, Goiânia, Brazil

^d Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, Brazil

^e Programa de Pós-Graduação em Ecologia e Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil

^f Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle (MNHN), Centre National de la Recherche Scientifique (CNRS), Sorbonne Université, CP135, 57 rue Cuvier, 75005 Paris, France

ARTICLE INFO

Keywords:

Distance-based redundancy analysis
Community weighted mean
Species trait
Mayflies
Tropical streams
Trait-environment relationship

ABSTRACT

Traits define how organisms interact with their surrounding environment and with other organisms. Thus, trait composition of biological communities is expected to change predictably along environmental gradients. Because organisms' traits, but not taxonomic identity, determine their fitness, trait-environment relationships should provide a better way to elucidate how biodiversity respond to environmental change. Here, we used data on tropical streams embedded in a landscape of intensive agriculture to investigate trait-environment and taxon-environment relationships in a set of 91 mayfly communities from southeastern Brazil. We expected that trait-environment relationships would be stronger than taxon-environment relationships and that the linkage between traits and environmental variables would provide mechanistic insights on environmental filtering. We found that variation in both species composition and traits were correlated to salinity, highlighting the influence of water salinization on mayfly communities due to agricultural practices. Surprisingly, using analogous statistical methods, in general, we found that the strengths of trait-environment relationships were lower than that of taxon-environment relationships. Further, (1) species responses to gradients were not correlated to similarity in their traits and (2) some species with different trait composition responded similarly to environmental variation, indicating that different suite of traits can cope with similar environmental contexts. Besides some cautionary results about trait-based approaches, results from taxon-based approaches indicated that variation in composition was more related to spatial variables, suggesting that dispersal limitation undermine its use for large scale assessments. Our results suggest that both taxon- and trait-based approaches have weakness and strengths and deciding between them for biomonitoring purposes will depend on spatial scales, trait interrelationships, and analytical methods.

1. Introduction

The 'habitat templet' concept is a major principle of modern trait-based approaches (Townsend and Hildrew, 1994; McGill et al., 2006; Dray and Legendre, 2008), which states that species evolve ecological strategies that "maximize the numbers of their descendants in their habitat" (Southwood, 1977). Accordingly, ecologists have sought for relationships between species' strategies and environmental variables under the assumption that this would reveal how the environment arranges natural communities (McGill et al., 2006; Dray and Legendre, 2008). A

prevalent approach to define species' strategies is to measure their functional traits, i.e., phenotypic characteristics of organisms that are expected to influence their fitness (McGill et al., 2006). Species with functional traits that maximize their population growth should be abundant, reflecting successful recruitment under a given environment (Tilman, 2004; Shipley, 2010; Shipley et al., 2016). Therefore, the relative representation of traits in local communities should change along environmental gradients, which have been called the trait-environment relationship (Townsend and Hildrew, 1994; Dray and Legendre, 2008).

Trait-based approaches are thought to have two main advantages

* Corresponding author.

E-mail address: victor.saito@gmail.com (V.S. Saito).

<https://doi.org/10.1016/j.ecolind.2020.106625>

Received 8 January 2020; Received in revised form 28 April 2020; Accepted 12 June 2020

Available online 23 June 2020

1470-160X/ © 2020 Elsevier Ltd. All rights reserved.

when compared to taxonomic approaches. First, variation in trait composition along environmental gradients have the potential to provide mechanistic understanding of community assembly, as traits should respond in predictable ways given their role in shaping individual fitness (Shipley, 2010). Second, trait-based approaches enable comparing biodiversity patterns along gradients (e.g. human pressures) at large spatial scales, while taxonomic analyses are contingent to the biogeographic context of the species pool because dispersal limitation also influences species distribution (McGill et al., 2006).

The potential advantages of trait-based approaches boosted their use in freshwater ecology in the last three decades. Morphological, ecological, and life-cycle traits have been traditionally used in biomonitoring protocols for diverse freshwater taxa (Resh et al., 1994; Townsend and Hildrew, 1994; Poff, 1997 Dolédec et al., 1999; Verberk et al., 2013). It has been suggested that using trait-based approaches would improve our ability to elucidate the sources of environmental change (e.g. organic pollution, flow alteration, salinization) (Dolédec et al., 1999, Aspin et al., 2019). However, although some studies have indeed found strong trait-environment relationships (e.g., macro-invertebrates: Dolédec et al., 1999; fishes: Leitão et al., 2016), many others have found weak or no relationship (e.g. Resh et al., 1994; Davies et al., 2000; Saito et al., 2016; see a review in Hamilton et al., 2019). Importantly, explanations for weak or absence of trait-environment relationships in freshwater communities are still unclear (Statzner et al., 2004). Thus, although trait-based approaches have been present in the literatures for decades, comparing their predictive performance against taxonomic approaches remains a challenge, especially in tropical regions where freshwater biomonitoring is still under development (Saito et al., 2015a).

In this study, we investigated trait- and taxon-environment relationships in tropical mayfly (Ephemeroptera) communities along a gradient of land use intensification. We focused on mayflies but not multiple insect orders because each taxonomic group is likely to have developed evolutionary solutions to environmental changes so that merging multiple groups could mask the responses of individual orders (Resh et al., 1994). We studied streams embedded in a landscape with different levels of forest cover and anthropogenic influence (mainly sugar cane plantations and pasture) in Brazil. We aimed to investigate two assumptions of trait-based approaches: (i) traits provide mechanistic explanations of environmental filtering that taxon-based approaches do not; (ii) taxon-environment relationships are dependent on the species pool given the influence of species dispersal for taxa distribution while trait approaches are not. Thus, we expected that (1) trait-environment relationships would be stronger than taxon-environment relationships. Because traits should allow a mechanistic explanation of the role of environmental filters, we expected that (2) gill traits (shape and number), which are strongly associated with osmoregulation and respiration in mayflies (Wingfield et al., 1939), would respond to salinity and dissolved oxygen levels; and (3) feeding strategies would change according to stream width and riparian forest cover because these variables determine the organic matter inputs in streams (Vannote et al., 1980). Finally, we expected that (4) variation in trait composition would be less constrained by the spatial structure of the landscape than the variation in taxonomic composition, since trait distribution should not be strongly associated to dispersal.

2. Methods

2.1. Sampling sites

We used data from 91 streams in the Corumbataí River Basin, state of São Paulo, Brazil (Fig. 1). The basin has an area of ~170,000 ha and deforestation was the primary impact in the beginning of the 1900s. After that, the region has been intensively used for sugarcane production and cattle ranching (Valente, 2001).

Sampled streams were distributed along a gradient of forest cover,

which is a major predictor of variation in stream insect communities in Brazil (Siqueira et al., 2012a,b, Siqueira et al., 2015; Saito et al., 2015a). We calculated the proportion of different land uses in the catchment area upstream the sampling sites. We calculated the area covered by pasture, sugar cane, and native forest using the software QGIS (Quantum GIS Development Team, 2019). Catchment forest cover ranged from 0 to 83% within the river catchment area.

We measured the following *in situ* stream variables to characterize local environmental variation: % of shading at the stream stretch (visually estimated), average stream width and depth (cm), flow velocity (m/s), water temperature (°C), pH, conductivity (µS/cm), salinity (mS cm⁻¹), turbidity (NTU), dissolved oxygen (mg/L) and substrate composition (sand, gravels, pebbles, cobbles, and boulders; %). Water characteristics were measured using a multiparameter sensor (Horiba device U-50). Additionally, water samples were taken from each stream for the laboratory analysis of total phosphorus (mg/L) and total nitrogen (mg/L) using methods described in Golterman, Clymo and Ohnstad (1978) and Mackereth, Heron and Talling (1978), respectively. Based on a correlation matrix between all variables, we decided to exclude the variables conductivity and % of pebbles from subsequent analysis due to collinearity (Pearson's correlations = 0.83 and -0.60 with salinity and % of boulders, respectively). We decided to keep salinity instead of conductivity given the alarming impact that freshwater salinization may have over mayflies and given our specific predictions about salinity and gill traits (Kaushal et al., 2005; Cañedo-Argüelles et al., 2016). To summarize the environmental data (standardized), we applied a Principal Component Analysis (PCA) to reduce the dimensionality of the environmental variables data (prior to standardization, continuous variables, except pH, were log-transformed and percentage variables – e.g., substrate composition – were transformed using the square root of arcsine).

2.2. Mayfly data

Between May and August (dry season) of 2015 we sampled mayflies using a two minutes kick-net procedure in each sampling site. We counted and identified all nymphs to the lowest possible taxonomic level (morphotype and species level). Based on previous studies and the natural history of Neotropical mayflies, we selected six key traits: feeding strategy, gills characteristics, body shape, locomotion strategy (all fuzzy coded trait), number of gills (quantitative discrete trait), and wing size (quantitative continuous traits). We compiled trait values from previous studies and databases (Tomanova et al., 2006; Colzani et al., 2013; Saito et al., 2015a). Additionally, for each species, we measured the mean body size (quantitative continuous trait) of nymphs (last instar, minimum of five individuals) under a stereomicroscope (Table S1).

2.3. Taxon- and trait-environment relationships

To describe trait syndromes in mayfly traits (i.e., trait combinations that are consistent among different species), we applied a PCA to the trait data after standardizing fuzzy and quantitative traits by zero mean and unit variance. We then compared taxon- and trait-environment relationships using the following multivariate methods (Kleyer et al., 2012):

- (1) Redundancy analysis (RDA) estimates the relationship between a multivariate explanatory matrix and a multivariate response matrix (Legendre and Legendre, 2008). We used the environmental variables (described above) as the explanatory matrix and the community composition dataset (Hellinger transformed) as the response matrix in the taxon-based approach (RDA-Composition). For the trait-based approach we used the community-weighted mean (CWM) values of traits as the response matrix (RDA-CWM). CWM is the mean value of a trait, weighted by species abundances,

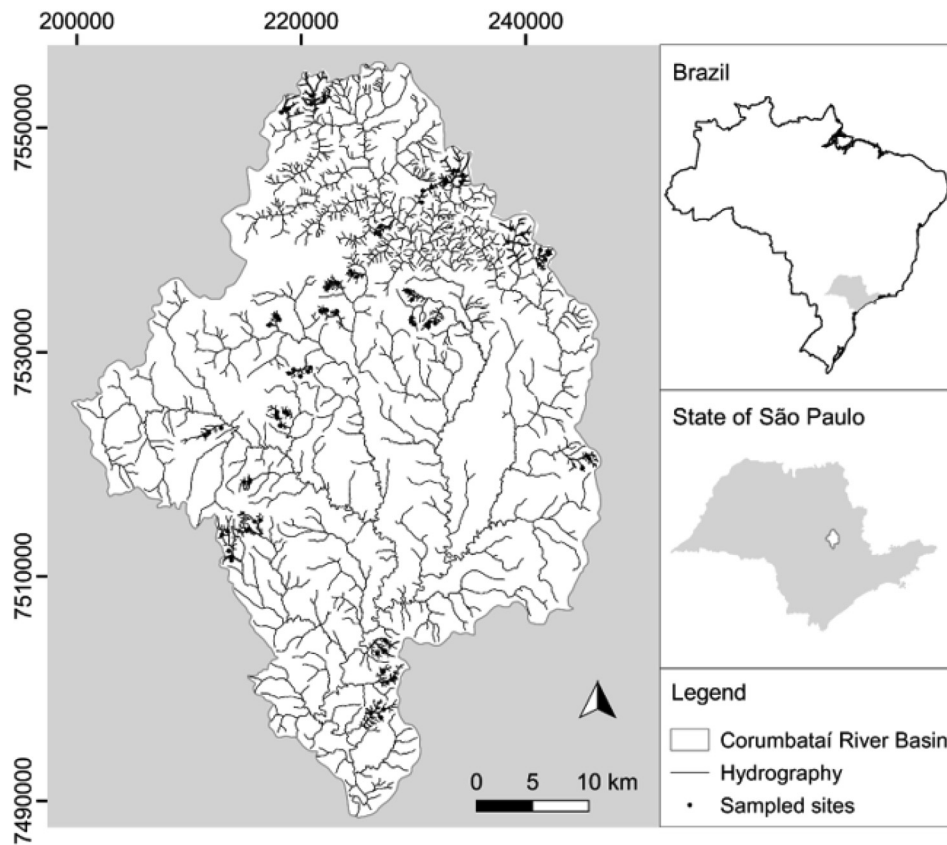


Fig. 1. Location of studied streams within the Corumbataí River Basin. Streams are represented by dots.

considering all species present at a site (Lavorel et al., 2008), being one of the most used metrics to test trait-environment relationships (Lavorel et al., 2008; Bruelheidet al., 2018, but see Peres-Neto et al., 2017). We applied a forward selection procedure with double stopping criterion (P-values and adjusted R^2 ; see Blanchet et al., 2008, Bauman et al., 2018) to select a subset of environmental variables to be used in the RDA. We used an ANOVA-like procedure with 999 permutations (Legendre et al., 2011) to test for the significance of RDA axes.

- (2) Distance based-RDA (db-RDA) is a variation of RDA to cope with dissimilarity matrices as response matrices (Legendre and Anderson, 1999). db-RDA finds linear relationships between all the Principal Coordinate Analysis (PCoA) axes (summarizing a dissimilarity matrix between sites) and environmental variables. We used the Bray-Curtis dissimilarity as response matrix in the taxon-based approach (db-RDA-Composition). For the trait-based approach, we used the trait dataset to calculate a dissimilarity matrix among sites that provides maximum dissimilarity between completely dissimilar communities (D_b coefficient - equation 12 in Pavoine and Ricotta, 2014) (hereafter the db-RDA-Traits approach). This coefficient relies on differences in traits between species, which were calculated using the modified Gower coefficient (Pavoine et al., 2009). We also used estimated P-values through an ANOVA-like procedure with 999 permutations (Legendre et al., 2011) to test for the significance of the axes. In all analyses described above, we used the adjusted coefficient of determination (Adj. R^2) to measure the strength of relationship between the response and explanatory matrices (Peres-Neto et al., 2006). We also added a constant to dissimilarities to avoid negative eigenvalues during ordination of matrices (Cailliez transformation, Legendre and Legendre, 2008).
- (3) In order to find a direct link between taxa, traits and the environment, we applied a RLQ analysis that simultaneously evaluate the relationships among sites, species, environmental variables and

traits using simultaneous ordination (Dolédec et al., 1996). RLQ relies on covariance measures between environmental variables and traits linked by the abundance of species in sites. For this approach, we considered the continuous traits number of gills, wing size and body size as fuzzy coded, separated in three distinct blocks with affinities sum to unity for a given species. We did that because the implemented RLQ statistical test cannot cope with the mixed type of data we used (feeding fuzzy-coded traits and body size; see also Thioulouse et al., 2018). Significance testing of the general relationships between species and the environment and between traits and the environment was based on a sequential test through a Monte-Carlo procedure with 9999 permutations that randomizes sites and species (model 6 in Dray et al., 2014, which combines in sequence the randomizations of model 2 and 4). Model 2 tests the relationship between species and the environment, while model 4 tests the relationship between traits and the environment. For this method, we used only the environmental variables selected by forward selection in the previous RDAs.

- (4) In order to find specific relationships between individual traits and environmental variables, we used the fourth-corner method (Dray and Legendre, 2008) to estimate the Pearson's correlation coefficient between each trait and each environmental variable. Again, significance levels were assessed by the model 6 described by Dray et al. (2014), which combines in sequence the randomizations of model 2 and 4.
- (5) We tested the association between the trait distance matrix (modified Gower distance) and the environmental response distance matrix (Euclidean distance matrix from the species scores along the first three axes of the RDA-Composition) using a Mantel test (9999 permutations). The first matrix describes the similarities between species in terms of traits composition, while the second matrix describes the similarities between species in terms of their responses to environmental gradients. We also applied a hierarchical

cluster analyses using the Unweighted arithmetic mean (UPGMA) method to the species trait distance and then compared it to a hierarchical cluster (UPGMA) based on the species environmental responses matrices.

Finally, to compare how taxon- and trait-environment relationships were constrained by the spatial structure of the sampling sites, we used a variation partitioning approach (Peres-Neto et al., 2006). First, we applied distance-based Moran's Eigenvector Maps (db-MEM, Dray et al., 2006) to the geographic coordinates of sampling sites, which transforms spatial distances into a rectangular matrix, where orthogonal vectors describe the various forms of spatial variation among sites. The first vectors represent the largest scale of spatial variation, whereas the last represent fine scale spatial variation. Then, we partitioned the variation in community response matrices among two explanatory matrices – environmental (all environmental variables) and spatial (db-MEM vectors) (Peres-Neto et al., 2006). We used the strength of partial relationships (Adj. R²; Peres-Neto et al., 2006) to measure the relative importance of the environmental and spatial variables in explaining the variation in the response matrices. Significance levels were assessed with an ANOVA like permutation (999 permutations, as explained above). We used this technique to partition variation of four response matrices in the redundancy approaches described above (i.e., RDA-Composition, RDA-CWM, db-RDA-Composition and db-RDA-Traits).

3. Results

We identified 18,803 nymphs distributed into 23 morphotypes/species. The PCA depicted complex environmental gradients in the studied region, with the first two axes explaining 33% of the environmental variation across sites (Fig. 2). Along the first PCA axis (PCA1), streams in catchments dominated by sugarcane cultivation were, in general, deeper, wider, with a predominance of cobbles, and higher streamflow. In turn, streams in catchments dominated by pasturelands presented substrates dominated by sand and gravel, with lower depth and flow velocity. Along the second axis (PC2), the streams were mainly differentiated according to shading; streams positively related to

Table 1

Results of trait-environment and taxon-environment relationships in mayfly communities from Corumbataí River basin. NS = non-significant. * Adjusted P-value. **S.E.S. = Standardized effect size.

Method	Association statistics	Value	P-value
RDA-Composition	Adj. R ²	0.141	0.001
RDA-CWM	Adj. R ²	0.088	0.015
db-RDA-Composition	Adj. R ²	0.173	0.001
db-RDA-Trait	Adj. R ²	0.216	0.003
RLQ	Model 2 S.E.S.**	6.219	0.001
	Model 4 S.E.S.	1.476	0.082
	Model 6 S.E.S.	–	0.084
Fourth-Corner method	Pearson correlation	All < 0.10	all NS*

shading and high dissolved oxygen concentration in forested catchments were negatively related to pH and salinity. The trait-PCA depicted a phylogenetic constraint pattern in species trait as species of the same family were tended to be grouped together. Along the first axis, we found a separation between Baetidae (with negative scores) and Leptophlebiidae (with positive scores), while Caenidae and Leptohyphidae were separated from the other families along the second axis (Fig. 2).

RDA-Composition and RDA-CWM detected weak relationships between species abundance and environmental variables and between abundance-weighted trait mean (CWM) and environmental variables, respectively (Table 1). However, the strength of the relationship detected by the RDA-Composition (Adj. R² = 0.14, P = 0.001) was higher than that detected by the RDA-CWM (Adj. R² = 0.08, P = 0.015). Forward selection indicated that the best set of variables to explain variation in species composition included salinity (F = 8.93, P = 0.002), stream width (F = 3.02, P = 0.008), and percentage of sand (F = 2.22, P = 0.046). Forward selection applied to RDA-CWM indicated that the best set of variables to explain variation in CWM included stream width (F = 3.97, P = 0.012), salinity (F = 3.49, P = 0.012) and water temperature (F = 2.61, P = 0.032). The db-RDA-Composition also showed slightly higher explanatory power (all axes used, Adj. R² = 0.17, P = 0.001) than simple RDA-Composition, but

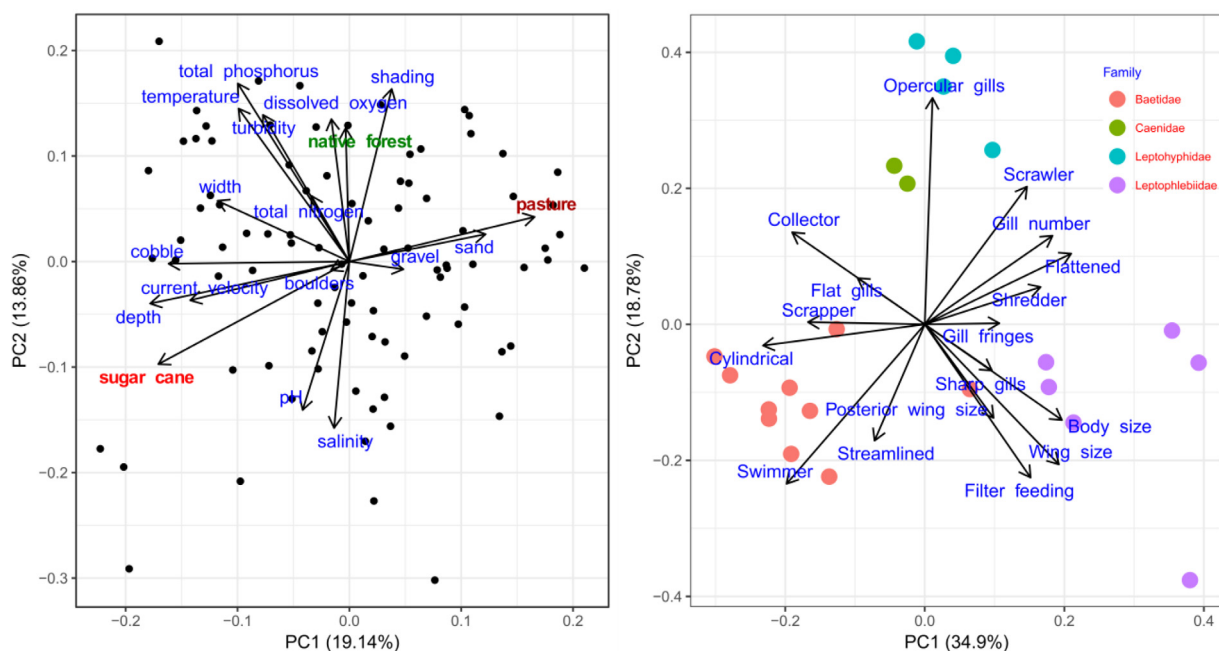


Fig. 2. Principal component analysis biplots of the environmental (left panel) gradient and trait (right panel) datasets. Left: Ordination of environmental variables using Principal Components Analysis (PCA) in the Corumbataí River Basin. Right: PCA depicting the trait syndromes in mayfly species from four different families. Black and colored dots represent streams and taxonomic units (species or morphospecies), respectively.

with the same variables retained by forward selection. Interestingly, db-RDA-Traits contrasted the general trend and had the highest adjusted coefficient of determination (all axes used, adj. $R^2 = 0.21$, $P = 0.003$) of all methods, and with the same variables retained in db-RDA-Composition (salinity, stream width and percentage of sand) (Table 1).

The RLQ analysis, which was computed considering only salinity, stream width, water temperature and percentage of sand as environmental variables (i.e., retained by forward selection in RDAs), did not detect a general relationship between the three data (i.e., species abundances, species traits and environmental variables; model 6 combining results of model 2 and 4; see Dray et al., 2014). However, model 2 indicated a relationship between species abundances and environmental variables, while model 4, which tests the null hypothesis of a random distribution of traits along environmental axes, did not. Fourth-Corner correlations also did not detect relationships between specific traits and specific environmental variables (Table 1); thus, the specific predictions regarding gill traits and feeding habits were not supported.

We found a lack of relationship between dissimilarity in species traits and dissimilarity in species' environmental responses (Mantel's $r = -0.02$, $P = 0.522$). The comparison of the two hierarchical clusters also demonstrated a lack of association between similarity in species traits and similarity in environmental responses (Fig. 3). The high number of crossing lines when comparing the two clusters depicts how species with very distinct trait composition can respond in similar ways to the environment. For example, – e.g. the trait composition of *Baetodes* sp.1 differed from that of *Thraulodes* sp. and yet both taxa responded similarly to the environmental gradients (Fig. 3). The opposite pattern can also be seen, as *Baetodes* sp.1 and *Zelus* sp. were similar in trait composition and yet responded differently to the environmental gradients (Fig. 3).

Variation partitioning indicated that taxonomic composition was more related to spatial variables than traits, supporting our expectations. Environmental and spatial variables explained 16% ($F = 1.58$, $P = 0.004$) and 11% ($F = 1.26$, $P = 0.059$) of the variation in species composition and 9% ($F = 1.28$, $P = 0.120$) and 1% ($F = 1.02$, $P = 0.452$) of the variation in CWM, respectively. Using db-RDA the results were similar. For db-RDA-Composition, 15% ($F = 1.57$, $P = 0.010$) of variation was explained by the environment, 10% explained by db-MEM axes ($F = 1.24$, $P = 0.097$) and 4% of shared explanation. As for the trait-based approach (db-RDA-Traits), the

environmental and the spatial variables explained 22% ($F = 10.65$, $P = 0.028$) and 5% of the variation ($F = 9.87$, $P = 0.005$), respectively (Fig. S1).

4. Discussion

By applying diverse multivariate methods, we found that mayfly trait-based approaches do not provide a better and clearer understanding of community assembly along environmental gradients in comparison to a taxonomic-based approach based on species identities and abundances. While trait-based approaches have provided valuable insights about biodiversity variation that would not be possible using species identities alone (McGill et al., 2006; Pavoine and Bonsall, 2011), they often have limited explanatory power on how communities respond to environmental variation (Davies et al., 2000; Horrigan and Baird, 2008).

Trait-based approaches rely on multiple methodological choices that are still under debate in comparison to compositional approaches. For instance, the decision about which traits to measure and how is discussed in the literature (Ackerly and Cornwell, 2007; Saito et al., 2016), as well as the organization level needed to measure them (e.g., species vs. individual level, Cianciaruso et al., 2009). In this regard, weak trait-environment relationships in empirical studies may emerge due to methodological aspects. First, a weak relationship between traits and environmental conditions may arise simply due to the use of imprecise data gathered from the literature – as opposed to the use of precise measurements of traits from locally sampled organisms (Cano-Barbacid et al., 2020). Second, we usually cannot be sure whether all traits are relevant to determine community assembly and, so, using irrelevant traits could obscure the detection of environmental filtering (Colwell and Winkler, 1984; Saito et al., 2016). Third, in general, we do not know the best resolution and scale to measure traits in order to detect trait-environment relationships (Violle et al., 2012). Fourth, trait measurements have trade-offs of information quality and time/resources costs (Saito et al., 2016). For example, while we have considered wing length, what explains species flight ability is the whole design of the wing, a very challenging and time-consuming trait to measure. Thus, because trait-based approaches are dependent on a higher number of methodological steps and decisions, when compared to taxonomic-based approaches, they are also more prone to

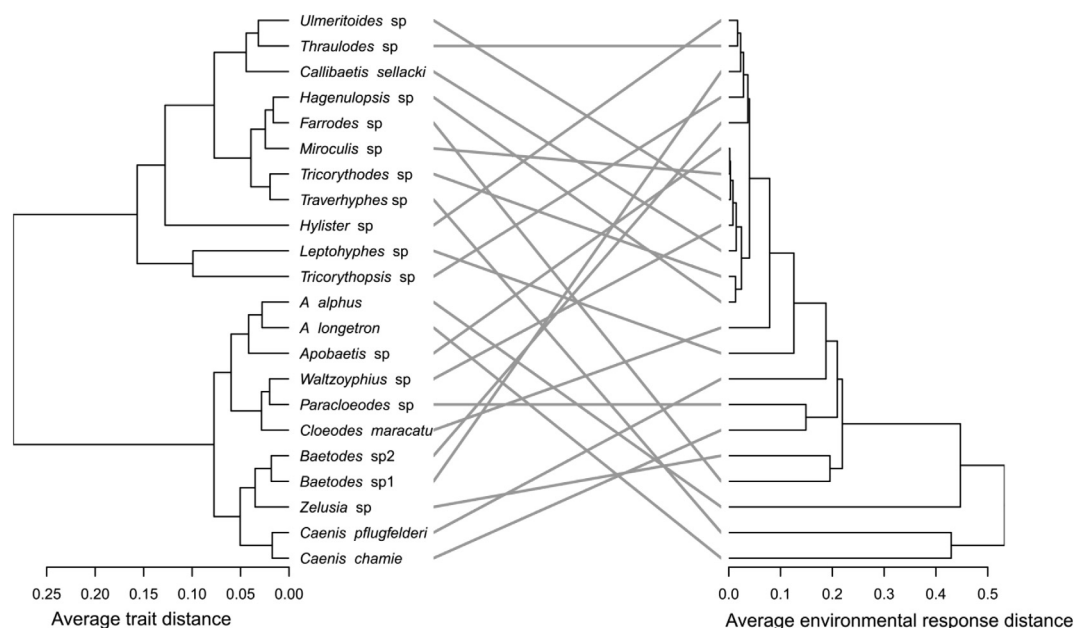


Fig. 3. UPGMA clustering based on species traits (left panel) and on their responses to environmental gradients (left panel). The cophenetic correlation coefficients were 0.94 and 0.95, respectively. The species *A. alphas* and *A. longetron* are from the genus *Americabaetis* (Baetidae).

methodological issues that will ultimately affect our ability to detect trait-environment relationships.

We expected that some traits would respond specifically to some environmental variables (e.g., gill traits to dissolved oxygen). However, we did not find clear single-trait vs. single-environmental characteristic relationship to support the mechanistic assumption of trait-based approaches. In this sense, it is likely that trait composition, rather than individual traits, affects individual fitness (Resh et al., 1994; Verberk et al., 2013; Laughlin, 2014; Pilière et al., 2016). In general, from an evolutionary perspective, traits do not evolve independently in response to environmental pressures but as specific combinations of traits that enable spin-offs (combination of traits maximizing fitness) and trade-offs (investments in one trait reducing investments in another traits) (Verberk et al., 2013). The strength of such evolutionary constraint was exemplified by the phylogenetic signal pattern in the PCA of the trait data, where genera from the same family shared similar suite of traits. While these ideas address the importance of trait combinations, one should also argue that there are different suites of traits able to maximize species abundances in a given environment (Resh et al., 1994). For example, water-penny beetles with flattened bodies, caddisflies with strong anal claws, and blackfly larvae using glues to attach to the substrate all use different strategies to deal with the same environmental filter, high streamflow. Our results support these ideas, since we found that genera with distinct trait composition (suite of traits) can respond similarly along the same environmental gradient (e.g., *Farrodos* and *Leptohyphes*).

Both trait-based and taxon-based approaches revealed a clear relationship between mayfly communities and salinity. Our results suggest that even a small variation in salinity (from 0.01 to 0.05 mS cm⁻¹) may indicate impacts able to modify mayfly communities, which in our case is related to land use practices in the study area. Salinity was present in streams surrounded by sugarcane plantations but not in forested streams, suggesting that agricultural practices are driving freshwater salinization. This salinization process is currently a major concern in aquatic ecology (Kaushal et al., 2005; Cañedo-Argüelles et al., 2016; Kefford, 2018) and our findings suggest that small increases in salinity can modify the taxonomic and trait composition of mayfly communities. This environmental filter has been hypothesized to be important because of the probable interference in pH regulation and osmoregulation costs that are mediated by gill traits (Kefford, 2018). However, the specific effects over gill traits at the community level were not evidenced given the lack of a relationship between salinity and gill traits in fourth-corner correlations.

Compared to species, trait variation should be less related to spatial variables and this is a key assumption to the generalized use of trait-based approaches. We found some support to this assumption as variation in taxonomic composition was more related to db-MEM vectors. Pure spatial signals in partial constrained ordination have been commonly associated with both the effect of unmeasured spatially structured environmental variables and dispersal on species composition (Diniz-Filho et al., 2012, Siqueira et al., 2012b, Saito et al., 2015b). Because we measured a high number of environmental variables that has been previously shown to drive the distribution of mayflies, we suggest the first explanation is less likely (effect of unmeasured spatially structured environmental variables). In contrast, mayflies tend to disperse over short distances because adults usually live only hours or few days and are considered weak fliers in comparison to other taxa (e.g., Odonata) with low ability to direct their trajectories, making them prone to have limited geographic distribution (Malmqvist, 2000). For example, Caudill (2003) showed that most females emerging from one lake lay their eggs in the same lake, despite the occurrence of several other lakes in the vicinity (~250 m). The stronger spatial structure detected in composition data, as compared to trait data, adds support to the use of trait-based approaches for large scale assessments.

In general, biomonitoring tools in the Neotropics are still under development and our results raise a question on whether we should

focus on trait-based approaches. Previous studies found relationships between functional diversity, trait composition, and environmental change (Saito et al., 2015a; Castro et al., 2017). However, our findings indicate that both trait and taxonomic composition responded to the same environmental variables, indicating the importance of the same environmental gradients (e.g., salinity) in structuring the local communities. We highlight that traits are inherently interrelated and therefore may not respond monotonically and invariably to environmental variation, but instead present complex responses depending on the set of traits a species has (Resh et al., 1994). Also, trait-based approaches indicated a weaker spatial signal on trait composition variation, potentially being more appropriate for large scale assessments, a desirable attribute for biomonitoring tools. For biomonitoring purposes, choosing between approaches remains a challenge as trait- and taxonomic-based approaches have advantages and disadvantages and could, in practice, give similar information regarding community response to environmental change.

CRedit authorship contribution statement

Victor Satoru Saito: Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Visualization, Writing - original draft, Writing - review & editing. **Tadeu Siqueira:** Conceptualization, Methodology, Investigation, Resources, Supervision, Visualization, Project administration, Funding acquisition, Writing - review & editing. **Luis Mauricio Bini:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Supervision, Writing - review & editing. **Raul Costa-Pereira:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Edineusa Pereira Santos:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Visualization, Project administration, Writing - review & editing. **Sandrine Pavoine:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank many colleagues who stimulated interesting discussions during the elaboration of this study at the Brazilian Symposium of Limnology in 2017, as well as colleagues from the Conference of the Iberian Association of Limnology in 2018. We also thank two anonymous reviewers that helped us during the preparation of this manuscript. The study was partly funded by grants #13/50424-1, #18/02074-5 and #19/04033-7, São Paulo Research Foundation (FAPESP). Work by LMB has been supported by CNPq (304314/2014-5) and the National Institute for Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation (proc. 465610/2014-5 MCTIC/CNPq and FAPEG).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106625>.

References

- Ackerly, D.D., Cornwell, W.K., 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol. Lett.* 10 (2), 135–145.
- Aspin, T.W., Khamis, K., Matthews, T.J., Milner, A.M., O'Callaghan, M.J., Trimmer, M.,

- Ledger, M.E., 2019. Extreme drought pushes stream invertebrate communities over functional thresholds. *Glob. Change Biol.* 25 (1), 230–244.
- Bauman, D., Drouet, T., Dray, S., Vlemminck, J., 2018. Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography* 41 (10), 1638–1649.
- Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. *Ecology* 89 (9), 2623–2632.
- Cañedo-Argüelles, M., Hawkins, C.P., Kefford, B.J., Schäfer, R.B., Dyack, B.J., Brucet, S., Coring, E., 2016. Saving freshwater from salts. *Science* 351 (6276), 914–916.
- Cano-Barbacid, C., Radinger, J., & García-Berthou, E. Reliability analysis of fish traits reveals discrepancies among databases. *Freshwater Biology*. In press.
- Castro, D.M., Dolédec, S., Callisto, M., 2017. Landscape variables influence taxonomic and trait composition of insect assemblages in Neotropical savanna streams. *Freshw. Biol.* 62 (8), 1472–1486.
- Caudill, C.C., 2003. Measuring dispersal in a metapopulation using stable isotope enrichment: high rates of sex-biased dispersal between patches in a mayfly metapopulation. *Oikos* 101 (3), 624–630.
- Cianciaruso, M.V., Batalha, M.A., Gaston, K.J., Petchey, O.L., 2009. Including intraspecific variability in functional diversity. *Ecology* 90 (1), 81–89.
- Colwell, R.K., Winkler, D.W., 1984. A null model for null models in biogeography. *Ecolog. Communities: Conceptual Issues Evidence* 344–359.
- Colzani, E., Siqueira, T., Suriano, M.T., Roque, F.O., 2013. Responses of aquatic insect functional diversity to landscape changes in Atlantic Forest. *Biotropica* 45 (3), 343–350.
- Davies, K.F., Margules, C.R., Lawrence, J.F., 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81 (5), 1450–1461.
- Diniz-Filho, J.A.F., Siqueira, T., Padiá, A.A., Rangel, T.F., Landeiro, V.L., Bini, L.M., 2012. Spatial autocorrelation analysis allows disentangling the balance between neutral and niche processes in metacommunities. *Oikos* 121 (2), 201–210.
- Dolédec, S., Chessel, D., Ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environ. Ecol. Stat.* 3 (2), 143–166.
- Dolédec, S., Statzner, B., Bournaud, M., 1999. Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshw. Biol.* 42 (4), 737–758.
- Dray, S., Legendre, P., 2008. Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology* 89 (12), 3400–3412.
- Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecology* 87 (3–4), 483–493.
- Dray, S., Choler, P., Doledec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95 (1), 14–21.
- Golterman, H.L., Clymo, R.S., Ohnstad, M.A.M., 1978. *Methods for Physical and Chemical analysis of freshwater*. IBP. Hand book NO. 8. Black well Scientific Publications. Osney Mead.
- Hamilton, A.T., Schäfer, R.B., Pyne, M.I., Chessman, B., Kakouie, K., Boersma, K.S., Bierwagen, B., 2019. Limitations of Trait-Based Approaches for Stressor Assessment: the Case of Freshwater Invertebrates and Climate Drivers. *Glob. Change Biol.*
- Horrihan, N., Baird, D.J., 2008. Trait patterns of aquatic insects across gradients of flow-related factors: a multivariate analysis of Canadian national data. *Can. J. Fish. Aquat. Sci.* 65 (4), 670–680.
- Kaushal, S.S., Groffman, P.M., Likens, G.E., Belt, K.T., Stack, W.P., Kelly, V.R., Fisher, G.T., 2005. Increased salinization of fresh water in the northeastern United States. *Proc. Natl. Acad. Sci.* 102 (38), 13517–13520.
- Kefford, B.J., 2018. Why are mayflies (Ephemeroptera) lost following small increases in salinity? Three conceptual osmophysiological hypotheses. *Philos. Trans. R. Soc. B* 374 (1764) 20180021.
- Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Lavorel, S., 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? *J. Veg. Sci.* 23 (5), 805–821.
- Laughlin, D.C., 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. *J. Ecol.* 102 (1), 186–193.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S., Garden, D., Dorrrough, J., Bonis, A., 2008. Assessing functional diversity in the field—methodology matters!. *Funct. Ecol.* 22 (1), 134–147.
- Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multi-species responses in multifactorial ecological experiments. *Ecol. Monogr.* 69 (1), 1–24.
- Legendre, P., Legendre, L.F., 2008. *Numerical ecology*. Elsevier.
- Legendre, P., Oksanen, J., ter Braak, C.J., 2011. Testing the significance of canonical axes in redundancy analysis. *Methods Ecol. Evol.* 2 (3), 269–277.
- Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., Moullot, D., 2016. Rare species contribute disproportionately to the functional structure of species assemblages. *Proc. R. Soc. B: Biol. Sci.* 283 (1828), 20160084.
- Mackereth, F.J.H., Heron, J., Talling, J.F., 1978. *Water Analysis of Freshwater*. Biological Assessment Publications 36, 120.
- Malmqvist, B., 2000. How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? *Biol. Conserv.* 93 (2), 271–276.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21 (4), 178–185.
- Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biol. Rev.* 86 (4), 792–812.
- Pavoine, S., Ricotta, C., 2014. Functional and phylogenetic similarity among communities. *Methods Ecol. Evol.* 5 (7), 666–675.
- Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118 (3), 391–402.
- Peres-Neto, P.R., Dray, S., ter Braak, C.J., 2017. Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography* 40 (7), 806–816.
- Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87 (10), 2614–2625.
- Pilière, A.F.H., Verberk, W.C.E.P., Gräwe, M., Breure, A.M., Dyer, S.D., Posthuma, L., Schipper, A.M., 2016. On the importance of trait interrelationships for understanding environmental responses of stream macroinvertebrates. *Freshw. Biol.* 61 (2), 181–194.
- Poff, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. North Am. Benthol. Soc.* 16 (2), 391–409.
- Quantum GIS Development Team. 2019. *Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project*. <http://qgis.osgeo.org>.
- Resh, V.H., Hildrew, A.G., Statzner, B., Townsend, C.R., 1994. Theoretical habitat templates, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. *Freshw. Biol.* 31 (3), 539–554.
- Saito, V.S., Siqueira, T., Fonseca-Gessner, A.A., 2015a. Should phylogenetic and functional diversity metrics compose macroinvertebrate multimetric indices for stream biomonitoring? *Hydrobiologia* 745 (1), 167–179.
- Saito, V.S., Soininen, J., Fonseca-Gessner, A.A., Siqueira, T., 2015b. Dispersal traits drive the phylogenetic distance decay of similarity in Neotropical stream metacommunities. *J. Biogeogr.* 42 (11), 2101–2111.
- Saito, V.S., Cianciaruso, M.V., Siqueira, T., Fonseca-Gessner, A.A., Pavoine, S., 2016. Phylogenies and traits provide distinct insights about the historical and contemporary assembly of aquatic insect communities. *Ecol. Evol.* 6 (9), 2925–2937.
- Shipley, B., 2010. Community assembly, natural selection and maximum entropy models. *Oikos* 119 (4), 604–609.
- Shipley, B., De Bello, F., Cornelissen, J.H.C., Laliberté, E., Laughlin, D.C., Reich, P.B., 2016. Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* 180 (4), 923–931.
- Siqueira, T., Bini, L.M., Roque, F.O., Cottenie, K., 2012a. A metacommunity framework for enhancing the effectiveness of biological monitoring strategies. *PLoS ONE* 7 (8), e43626.
- Siqueira, T., Bini, L.M., Roque, F.O., Marques Couceiro, S.R., Trivinho-Strixino, S., Cottenie, K., 2012b. Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography* 35 (2), 183–192.
- Siqueira, T., Lacerda, C.G.L.T., Saito, V.S., 2015. How does landscape modification induce biological homogenization in tropical stream metacommunities? *Biotropica* 47 (4), 509–516.
- Southwood, T.R., 1977. Habitat, the templet for ecological strategies? *J. Anim. Ecol.* 46 (2), 337–365.
- Statzner, B., Dolédec, S., Huguency, B., 2004. Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography* 27 (4), 470–488.
- Thioulouse, J., Dray, S., Dufour, A.B., Siberchicot, A., Jombart, T., Pavoine, S., 2018. Relating Species Traits to Environment. In: *Multivariate Analysis of Ecological Data with ade4*. Springer, New York, NY, pp. 223–237.
- Tilman, D., 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci.* 101 (30), 10854–10861.
- Tomanova, S., Goitia, E., Helešic, J., 2006. Trophic levels and functional feeding groups of macroinvertebrates in neotropical streams. *Hydrobiologia* 556 (1), 251–264.
- Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat templet for river systems. *Freshw. Biol.* 31 (3), 265–275.
- Valente, R.D.O.A., 2001. *Análise da estrutura da paisagem na bacia do rio Corumbataí, São Paulo, Brazil*, Master thesis – São Paulo University.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37 (1), 130–137.
- Verberk, W.C., Van Noordwijk, C.G.E., Hildrew, A.G., 2013. Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Sci.* 32 (2), 531–547.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L.L.N., Albert, C.H., Hulshof, C., Messier, J., 2012. The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* 27 (4), 244–252.
- Wingfield, C.A., 1939. The function of the gills of mayfly nymphs from different habitats. *J. Exp. Biol.* 16 (3), 363–373.