

The taxonomic distinctness of macroinvertebrate communities of Atlantic Forest streams cannot be predicted by landscape and climate variables, but traditional biodiversity indices can

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Abstract

Predicting how anthropogenic activities may influence the various components of biodiversity is essential for finding ways to reduce diversity loss. This challenge involves: a) understanding how environmental factors influence diversity across different spatial scales, and b) developing ways to measure these relationships in a way that is fast, economical, and easy to communicate. In this study, we investigate whether landscape and bioclimatic variables could explain variation in biodiversity indices in macroinvertebrate communities from 39 Atlantic Forest streams. In addition to traditional diversity measures, i.e., species richness, abundance and Shannon index, we used a taxonomic distinctness index that measures the degree of phylogenetic relationship among taxa. The amount of variation in the diversity measures that was explained by environmental and spatial variables was estimated using variation partitioning based on multiple regression. Our study demonstrates that taxonomic distinctness does not respond in the same way as the traditional used in biodiversity studies. We found no evidence that taxonomic distinctness responds predictably to variation in landscape metrics, indicating the need for the incorporation of predictors at multiple scales in this type of study. The lack of congruence between taxonomic distinctness and other indices and its low predictability may be related to the fact that this measure expresses long-term evolutionary adaptation to ecosystem conditions, while the other traditional biodiversity metrics respond to short-term environmental changes.

Keywords: biomonitoring, diversity indices, spatial structure, taxonomic diversity.

A distinção taxonômica de comunidades de macroinvertebrados de córregos da Mata Atlântica não pode ser previsto pela paisagem e por variáveis climáticas, mas os índices de biodiversidade tradicional podem

Resumo

Prever como as atividades antrópicas podem influenciar os vários componentes da biodiversidade é essencial para encontrar maneiras de reduzir a perda de diversidade. Este desafio envolve: a) a compreensão de como os fatores ambientais influenciam a diversidade em diferentes escalas espaciais e, b) desenvolver formas de medir essas relações de uma maneira rápida, econômica e de fácil comunicação. Neste estudo, nós investigamos se a paisagem e as variáveis bioclimáticas podem explicar a variação nos índices de biodiversidade em comunidades de macroinvertebrados de 39 riachos de Mata Atlântica. Adicionalmente às medidas tradicionais de diversidade, por ex.: riqueza de espécies, abundância e índice de Shannon, nos utilizamos índice de distinção taxonômica que mede o grau de relação filogenética dentre os *taxa*. A quantidade de variação nas medidas de diversidade que foi explicado por variáveis ambientais e espaciais foi estimada utilizando a variação particionada baseada em regressão múltipla. O presente estudo demonstra

que o índice de distinção taxonômica não responde da mesma maneira que os índices tradicionais utilizados em estudos de biodiversidade. Nós não encontramos nenhuma evidência de que a distinção taxonômica responde previsivelmente à variação métrica da paisagem, indicando a necessidade de incorporação de preditores em múltiplas escalas neste tipo de estudo. A falta de congruência entre a distinção taxonômica e outros índices e sua baixa previsibilidade pode estar relacionada com o fato de esta medida expressar adaptações evolutivas de longo prazo para as condições ambientais, enquanto as outras métricas tradicionais respondem às alterações ambientais de curto prazo.

Palavras-chave: biomonitoramento, índices de diversidade, estrutura espacial, diversidade taxonômica.

1. Introduction

Anthropogenic actions have drastically influenced ecosystems worldwide, resulting in modified biological communities, loss of species, and altered ecosystem services (Convention on Biological Diversity, 1992). Freshwater environments are among the most modified systems on Earth and require great effort to conserve and restore (Dudgeon et al., 2006). This is because: *i*) declines in biodiversity are far greater in freshwaters than in the most affected terrestrial ecosystems; and *ii*) freshwaters have been strongly affected by recent changes in climate, invasive species, habitat alteration and over-exploitation (Millennium Ecosystem Assessment, 2005). Many approaches have been developed aiming to evaluate the ecological effects of anthropogenic activities in freshwater ecosystems (Rosenberg and Resh, 1992; Bonada et al., 2006, Siqueira et al., 2012a). Part of the challenge involves understanding the large scale drivers of variation in biodiversity, and finding relationships between biological indicators and more easily measured predictor variables such as landscape metrics (Wiens, 2002; Johnson and Host, 2010).

Historically many indices have been proposed to measure biological diversity across environmental gradients, e.g., species richness and the Shannon diversity index (Magurran, 2004). However, as measures of biological variability, these indices may provide inaccurate understanding, because taxonomy, phylogeny, and functional variability among species are not considered when a community is evaluated (Clarke and Warwick, 2001). To address this issue, Clarke and Warwick (1998) and Warwick and Clarke (1998) proposed a biodiversity index known as “taxonomic distinctness index - TDI”. This index measures the degree of relationship among taxa by incorporating information on the identity and taxonomic relationship among species through the analysis of a phylogenetic (or taxonomic) topology. Since its creation, the taxonomic distinctness index has been used and tested for several groups and habitats (Magurran, 2004). A bibliometric analysis using the key-words “taxonomic distinctness” in the Web of Science® (Thomson ISI) database retrieved a total of 279 results. Although there is an increasing number of studies focusing on taxonomic distinctness for macroinvertebrate stream communities (most studies still focus on marine communities), there is no previous study in Neotropical streams.

Here, we studied a gradient of land degradation, ranging from landscapes dominated by sugarcane plantations (low

vegetation cover ~10%) to well preserved landscapes (vegetation cover > 70%) within the Brazilian Atlantic Forest domain. First, we assessed the congruence between taxonomic distinctness and other traditional diversity indices (e.g., richness and the Shannon index). Second, we evaluated the use of landscape structure measures, such as vegetation cover area and climate variables to predict macroinvertebrate diversity. Considering the general expectations that anthropogenic impacts can reduce biodiversity (Barnosky et al., 2011) and that species sensitivities to disturbances may be phylogenetically conserved (Helmus et al., 2010), we hypothesized that taxonomic distinctness values would be higher in areas with higher environmental integrity (e.g., forested areas) than in degraded landscapes. Furthermore, we expected that regional bioclimatic variables (e.g., rainfall) would explain part of the variation in diversity indices, as observed in previous studies which focused on the importance of large-scale variables on macroinvertebrate distribution (Vinson and Hawkins, 1998; Heino, 2009). Finally, we discuss the implications of our results for incorporating taxonomic distinctness as a biodiversity metric for biomonitoring strategies in tropical streams.

2. Methods

2.1. Study area

We examined macroinvertebrate diversity–landscape relationships based on a data set from streams in the State of São Paulo, Brazil. São Paulo covers c.a. 248,800 km² and has a population of 40 million people, which comprises 22% of the Brazilian population. The Atlantic Forest is found at low and medium elevations (< 1.000 m above sea level) on the eastern foothills from the southern coast to the northeastern Brazil (Ribeiro et al., 2009, 2011). It is among the most threatened tropical biomes in the world, with its area reduced to less than 16% of the original coverage in São Paulo state (Ribeiro et al., 2009). The biome is considered as a global biodiversity hotspot (Myers et al., 2000). Most of the remnant fragments are located on the steep slopes of mountains (Ribeiro et al., 2011), and composed of small (<50 ha) and structurally isolated (mean distance 1 440 m) habitat patches that suffers from edge effects (Ribeiro et al., 2009). Twenty streams were located within protected areas and nineteen were located in regions occupied by extensive sugarcane monoculture, pastures, *Eucalyptus* plantations (L'Hér, Myrtaceae) and banana plantations (see: Suriano et al., 2011; Corbi et al., 2013).

2.2. Biological data

Macroinvertebrate community data were collected by the research group from the Laboratory of Aquatic Entomology at the Universidade Federal de São Carlos (Suriano et al., 2011; Siqueira et al., 2012b). We standardized the sampling procedure according the following criteria: i) samples were taken during the lowest rainfall period (May, June, September, and October); ii) all sampled streams were low order (first or second order) and their springs were located within the area of dominant land use (vegetation, sugarcane, pasture or *Eucalyptus*). A Surber sampler with a 30 x 40 cm open frame and 250 µm mesh was used to obtain six samples in each stream. This data set includes information on community composition and abundance of macroinvertebrates. Most of which were identified to genus level.

2.3. Environmental predictors

We considered landscape vegetation cover and bioclimatic variables (WorldClim 1.3 map database; Hijmans et al., 2005) as environmental predictors in the statistical analysis.

Here, we used the percentage of vegetation to represent landscape structure. This metric was selected because it has been indicated as one of the main landscape properties influencing species distribution at varying scales for a number of groups, e.g., mammals (Pardini et al., 2010; Jorge et al., 2013), and mosquitoes (Laporta et al., 2011). A 200 m radius was used to delimit the virtual landscape around the sampling points. Within these landscapes, we estimated the percentage of vegetation cover. It is important to note that we have no previous information to determine the best design (radius area or catchment area) or scale to calculate landscape metrics because we do not have information about dispersal patterns and biology of aquatic insects in the Neotropical region to makes this approach more functional. Moreover, studies that have examined patterns of macroinvertebrates under a variety of measures of stream conditions in relation to land use at multiple scales report mixed influences (Allan, 2004). Thus, given the absence of specific information, we consider our exploratory approach an appropriate option for our purpose of estimating the effect of landscape processes on the structure of the macroinvertebrate community (see Roque et al., 2010; Siqueira et al., 2009, 2012b for a similar approach).

The São Paulo Forest Institute provided the land cover maps for 2005 (Kronka et al., 2005; Metzger et al., 2008). Cover classes were obtained through visual interpretation of Landsat/TM images at a scale of 1:50,000 with a spatial resolution of 30 m. Albers projection and Sad69 datum were used. Although the original map had five classes of vegetation cover (dense humid forest, mixed humid forest, semi-deciduous forest, savanna formations and restinga/mangrove), we grouped all of them into a single class (vegetation). Since other classes (e.g., pasture, reforestation, agriculture, water and urban area) were correlated with each other and with vegetation cover, we grouped them

into a generic class defined as matrix (Metzger et al., 2008) to avoid multicollinearity problems in our analysis.

Bioclimatic variables have been intensively used in studies using species distribution models (Hijmans et al., 2005; Loiselle et al., 2010; Laporta et al., 2011). Such models search for biogeographic patterns associated with the occurrence of species, which can be based on presence/absence records, and through ecological niches concepts (Elith and Graham, 2009; Loiselle et al., 2010). WorldClim is a recognized project in the scientific community and it offers a set of 19 bioclimatic variables for species distribution modeling (<http://biogeog.berkeley.edu>; Hijmans et al., 2005). The bioclimatic maps of WorldClim were generated from the interpolation of a historical series of monthly average temperatures from around the globe. These data are from a 30-year period, have a spatial resolution of 900 x 900m, and are available in geographic coordinates in the WGS84 datum. Three bioclimatic variables that we consider to be most influential to aquatic macroinvertebrates occurrence were selected: 1. minimum temperature of the coldest month (TEMP) was selected for its potential in influencing population dynamic in aquatic insects; 2. annual precipitation (APREC) was selected because previous studies have demonstrated the importance of rain in the dynamics of macroinvertebrates in tropical streams (e.g., Bispo et al., 2001); and 3. seasonal precipitation (SPREC), which can be considered an indirect measure of hydrological environmental variability at the regional scale.

When both response variables and predictors are spatially structured, it is necessary to avoid inflated Type I error rates (see Peres-Neto and Legendre, 2010). We used a spatial eigenfunction approach (Thioulouse et al., 1995; Griffith and Peres-Neto, 2006) to generate spatial variables, through the Principal Coordinates of Neighbor Matrices technique (PCNM; Borcard and Legendre, 2002), with the aim of representing spatial structures generated by environmental autocorrelation and potential biotic processes, such as dispersal (Dray et al., 2006). These spatial variables were used as spatial explanatory variables in our regression analyses together with a variation partitioning technique (Borcard and Legendre, 2002). By running this analysis, we filtered out the effects of spatial correlation when testing for the importance of ecological factors, such as environmental predictors (Peres-Neto and Legendre, 2010). PCNM is similar to other spatial eigenfunction analyses, such as Distance-based Eigenvectors Maps and Moran's Eigenvector Maps (these are actually all variations on the same theme; see Dray et al., 2006). PCNM was based on a Euclidean distance matrix between streams. This distance matrix was then submitted to a Principal Coordinate Analysis in which the axes (eigenvectors) represent distinct spatial patterns that are both mutually orthogonal and linearly uncorrelated (Griffith and Peres-Neto, 2006). PCNMs with high eigenvalues (e.g., the first eigenvector or axis, which we designate PCNM-1) represent broad-scale patterns of relationships among sampling sites, whereas those associated with low eigenvalues (e.g., PCNM-20) represent fine-scale patterns (Griffith and Peres-Neto, 2006). From

the entire set of eigenvectors, we selected those associated with positive eigenvalues and with significant Moran's *I* because they represent positive spatial autocorrelation (Griffith and Peres-Neto, 2006).

2.4. Data analysis

The taxonomic distinctness index (Δ^*) was calculated according to Warwick and Clarke (1995) and Clarke and Warwick (1998) following the formula:

$$\Delta^* = [\sum \sum_i \omega_{ij} x_i x_j] / [\sum \sum_i x_i x_j]$$

Where x_i denote the abundance of *i*th of species *s*; *n* ($=\sum_i x_i$) is the total number of individuals in a sample, and ω_{ij} is the weight given to the length of the path which joins the species *i* and *j* in the taxonomy.

Other commonly used biodiversity measures, such as the Shannon diversity index (Shannon and Weaver, 1949), species richness, and total abundance were calculated. All indices were calculated using the PAST program (Hammer, 2002).

Pearson's correlation analysis was used to assess the congruence between diversity measures. Considering that spatial data are generally correlated (Legendre and Legendre, 1998), and that the degrees of freedom could be inflated, we calculated the effective number of degrees of freedom for each correlation and reported adjusted *P* values based on the Dutilleul method (Dutilleul et al., 1993).

We estimated the amount of variation in each diversity measure that was explained by environmental and spatial variables through a variation partitioning technique based on multiple regression (Legendre and Legendre, 1998). The analysis measured the amount of variation in diversity indices that could be attributed exclusively to environmental (E) or spatial (S) variables. The different components of variation were as follows: total explained variation [a+b+c], environmental variation [a+b], spatial variation [b+c], environmental variation without the spatial component [a], spatial variation without the environmental component [c], the common fraction of variation [b]

shared by E and S, and the residual fraction of variation not explained by E and S [d] (Peres-Neto et al., 2006). The results of variation partitioning were based on adjusted *R* squared (Peres-Neto et al., 2006). Analyses were performed in the R-language environment (R Development Core Team, 2011).

3. Results

Our data set included a total of 18024 individuals in 240 taxonomic units in all of the 39 Atlantic Forest streams. We found that species richness and the Shannon index were positively correlated with each other. The other correlation values, including those referring to the taxonomic distinctness index, were lower than 0.7, which indicates a moderate or weak correlation (see Table 1).

Of the six PCNMs extracted from the geographic distance matrix among sampling sites, PCNM-1 accounted for the highest level of spatial autocorrelation.

Variation in the taxonomic distinctness index was not related to variation in environmental or spatial predictors (Table 2). Species richness, on the other hand, had a positive relationship with annual precipitation (Bio 2), seasonal precipitation (Bio 3), and PCNM-1. Annual precipitation (Bio 2) had a significant effect on variation of the Shannon diversity index, while Bio 2 and PCNM-1 influenced abundance (Table 3). Variance partitioning analysis showed that environmental variables explained most variability in the richness, abundance and Shannon diversity data, although PCNM-1 also explained some variation (Table 4).

4. Discussion

Diversity indices have been widely used in programs of environmental assessment and studies of biodiversity patterns (Magurran, 2004; Green and Chapman, 2011). The correlation between the different indices and their responses to environmental variables is crucial in the selection of metrics for environmental assessment, biomonitoring,

Table 1. Pearson's correlation between the five diversity indices used to measure Atlantic Forest stream macroinvertebrate diversity.

Indices	Pearson's <i>r</i>	P*
Taxonomic distinctness x Richness	0.502	0.019
Taxonomic distinctness x Shannon	0.526	0.008
Taxonomic distinctness x Abundance	0.188	0.320
Richness x Shannon	0.748	<0.001
Richness x Abundance	0.584	0.002
Shannon x Abundance	0.078	0.672

*Corrected Probability based on the Dutilleul method (Dutilleul et al., 1993).

Table 2. Summary of multiple regressions (full models) between diversity indices and environmental and spatial variables as predictors.

	Distinctness	Richness	Shannon	Abundance
<i>R</i> ²	0.207	0.608	0.486	0.486
F	1.392	8.260	5.033	5.033
P	0.248	<0.001	<0.001	<0.001

Table 3. Multiple regression analysis results for diversity indices (with significant full models) using environmental and spatial variables as predictors. TEMP. minimum temperature of the coldest month; APREC. annual precipitation; SPREC. seasonal precipitation.

	Constant	TEMP	APREC	SPREC	% of vegetation	Altitude	PCNM-1
Richness							
Std. coefficient	0	-0.29	0.91	-1.47	0.16	-0.06	-1.82
t	3.06	-0.87	4.32	-2.78	0.81	-0.15	-3.89
P	0.01	0.39	<.001	0.01	0.43	0.88	<.001
Shannon							
Std. coefficient	0	-0.04	0.89	-0.54	0.19	0.02	-0.93
t	1.076	-0.118	3.675	-0.89	0.847	0.047	-1.735
P	0.29	0.91	<.001	0.38	0.4	0.96	0.09
Abundance							
Std. coefficient	0	-0.04	0.89	-0.54	0.19	0.02	-0.93
t	1.08	-0.12	3.68	-0.89	0.85	0.05	-1.74
P	0.29	0.91	<.001	0.38	0.4	0.96	0.09

Table 4. Results of variance partitioning analysis for diversity indices with environmental [E] and spatial [S] analysis as predictors, and their combinations (E:S - environmental independent of space, and [1-(E+S)] - residual fraction of variation not explained by E and S).

	Richness	Shannon	Abundance
[E]	0.61	0.48	0.33
[E:S]	-0.19	-0.04	0.06
[S]	0.19	0.05	0.11
[1-(E+S)]	0.39	0.51	0.62

and conservation of priority areas (Hering et al., 2004). In this context, our study has two main results: i) the taxonomic distinctness of stream macroinvertebrates of the Atlantic Forest responds differently from other metrics that have been widely used in biodiversity studies, such as species richness, the Shannon index, and abundance; ii) the taxonomic distinctness of macroinvertebrates cannot discriminate landscape structure (percentage of vegetation) in Atlantic Forest streams.

Many diversity indices show low consistency in their responses to environmental gradients and their use has been suggested as a complementary method (Heino et al., 2007; Gallardo et al., 2011). In our study, although the low correlation between taxonomic distinctness and the other indices supports the possibility of complementary methods, we suggest that the performance of the distinctness index should be intensively tested under several types of diffuse anthropogenic impacts in streams before being applied to biomonitoring, because in our study it does not respond to environmental variables in a predictable way. The lack of congruence between taxonomic distinctness and other indices can be related to its characteristic of expressing long-term evolutionary adaptation to ecosystem conditions, while the other metrics respond to short-term environmental

changes (Gallardo et al., 2011). With the data set used in this study, we cannot distinguish the role of short-term vs. long-term environmental changes in the response of these indices. However, we can say that the variation in taxonomic distinctness does not respond to simple landscape metrics (vegetation cover) or the response of the taxonomic distinctness to landscape predictors should be more complex (or less predictable) than the responses of abundance and species richness.

The Shannon index, species richness and abundance responded to bioclimatic and spatial variables. This supports the results of recent studies that have shown a relationship between these biodiversity indices and environmental gradients in the Neotropical region (e.g., Suriano et al., 2011). It has been generally argued that a significant relationship between community-based response variables and spatial variables indicates that factors other than the environmental predictors are important, such as colonization processes, unmeasured local environmental variables that are spatially autocorrelated, and dispersal pathways among habitat patches (Peres-Neto and Legendre, 2010). However, there has also been recent criticism on the use of spatial variables in variation partitioning, especially regarding using them as a direct representation of dispersal limitation (Gilbert and Bennett, 2010; Smith and Lundholm, 2010). These authors showed with simulations that the strength of dispersal limitation can affect the explanatory power of both the spatial and environmental predictors. Thus, although we estimated both pure environmental and spatial components in variation partitioning, our main intention was to use spatial variables as a way to control for inflated Type I error in assessing the environmental component. Together with previous studies about Atlantic Forest streams, these results indicate that by using local, landscape and spatial predictors (or a combination of them), we are usually able to explain around 40% or

less of the of variation in macroinvertebrate abundance and distribution (Siqueira et al., 2009), taxa associations (Roque et al., 2010), diversity metrics (Suriano et al., 2011), common and rare taxa (Siqueira et al., 2012b) and functional diversity metrics (Colzani et al., 2013).

Recent studies have tested the performance of taxonomic diversity and taxonomic distinctness in several systems and taxonomic groups. In general, in marine environments, these indices respond well to human disturbances (Hall and Greenstreet, 1998; Warwick and Clarke, 1998; Warwick and Light, 2002; Leonard et al., 2006), whereas in freshwater environments different results have emerged. For example, Abellán et al. (2005) demonstrated that taxonomic distinctness does not show any signal of anthropogenic degradation in aquatic beetles in many types of aquatic environments. Bhat and Magurran (2006) did not detect predictable responses in fish communities experiencing gradients of anthropogenic impact. Heino et al. (2007, 2008) demonstrated that taxonomic distinctness was weakly related to landscape metrics. On the other hand, Mouillot et al. (2005) and Gallardo et al. (2011) found a clear relationship between taxonomic distinctness and organic enrichment.

We found no evidence that taxonomic distinctness responded predictably to vegetation cover. Our study extends the known pattern of weak predictive and explanatory power of some landscape variables in understanding macroinvertebrate community structure in streams to the Neotropical region (Heino et al., 2007; Pyne et al., 2007). There are many explanations for the low performance of taxonomic diversity and distinctness indices in terms of landscape environmental gradients in freshwater habitats: *i-* natural environmental gradients can mask disturbance effects in biodiversity (Heino et al., 2007); *ii-* some environmental gradients may not be strong enough to elicit responses by diversity indices (Heino et al., 2007); *iii-* studies evaluating multiple anthropogenic impacts categorically (e.g., division of environments into reference vs. impact) may express environmental simplifications resulting in a low response of indices (Heino et al., 2007); *iv-* the predictor variables used may not represent important processes and mechanisms (at an appropriate scale) of the assessed community (Heino et al., 2007; Pyne et al., 2007); *v-* the structure of macroinvertebrate communities may respond to multiple factors at different scales, including local ones; *vi-* the assessed taxonomic groups may not respond predictably in terms of taxonomic and phylogenetic variability to environmental gradients of anthropogenic disturbance; and *vii-* the taxonomic resolution used may not be appropriate to detect patterns in community structure in relation to some types of environmental gradients.

Among the potential reasons listed above, we think that explanations *ii*, *iii* and *vi* do not explain our results. We included a strong environmental gradient that covered areas with high vegetation cover to areas strongly dominated by sugarcane plantations and pasture. Moreover, the measures of environmental characterization used do not express discrete *a priori* characterization of the areas (e.g., reference areas vs. impacted areas). In relation to

the taxonomic resolution (explanation *iv*), we believe that our identification, most at genus level, is enough to detect responses of macroinvertebrate to ecological patterns within the same pool of species (see Melo, 2005).

Regarding explanation *i*, we might expect that spatial or large-scale variables, such as the minimum temperature of the coldest month and annual precipitation, could have explained some variability in taxonomic diversity and taxonomic distinctness; however, our results indicate no relationship between these indices and natural environmental gradients on a large scale, supporting the results of Heino et al. (2007). The remaining explanations require empirical tests and we emphasize that hypotheses *iv* and *vi*, which have some support from studies conducted in temperate regions (Heino et al., 2007; Pyne et al., 2007), are also candidates for explaining a portion of the results in tropical regions.

Despite the need for simple diversity measurements to assess environmental integrity in a decision-making context at landscape scale, our results, together with other evidence (Heino et al., 2007; Pyne et al., 2007), indicate no clear relationship between biodiversity indices and vegetation cover, which is generally used as a surrogate of anthropogenic impacts. Overall, our results indicate that we need a better understanding of the relative role of natural and human related disturbance on distributional patterns of stream macroinvertebrates, particularly the information provided by different indices, before using this information in a decision-making context.

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