Anthropogenic disturbances alter the relationships between environmental heterogeneity and biodiversity of stream insects

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ABSTRACT

The effects of anthropogenic disturbance on multiple facets of biodiversity are poorly understood. In this study, we worked with the hypothesis that anthropogenic disturbances affect the relationship between environmental heterogeneity (EH) and biodiversity. We used a model selection approach to test three predictions. P1: The greater the level of anthropogenic disturbance, the weaker will be the relationship between EH and both taxonomic and functional alpha diversities. P2: The sign and strength of correlations between EH metrics and both taxonomic and functional alpha diversities will depend on the level of anthropogenic disturbance. P3: Taxonomic and functional beta diversities will not respond to the EH gradient. We sampled 76 stream sites in the Brazilian Neotropical savanna and collected insect of the orders Ephemeroptera, Plecoptera and Trichoptera to measure taxonomic and functional alpha and beta diversities. For P1, we did not find a trend of decreasing strength of this relationship with increasing disturbance. Results confirmed P2. Spatial flow diversity was positively correlated to taxonomic and functional alpha diversities in least-disturbed sites. Bankfull height variation was negatively correlated to taxonomic and functional alpha diversities in moderately-disturbed sites. Thalweg depth variation was positively correlated to taxonomic and functional alpha diversities in most-disturbed sites. Results partially confirmed P3 because taxonomic and functional beta diversities correlated with EH metrics in most-disturbed sites. We conclude that the biodiversity-EH relationship is not the same at all levels of anthropogenic disturbance, a finding that has implications for biomonitoring and ecosystem management.

1. Introduction

Biological diversity typically varies along major environmental gradients (Gaston, 2000). For example, the species richness-environmental heterogeneity relationship is a well-established pattern in ecology (Ortega et al., 2018; Stein et al., 2014). Studies over the last 50 years have shown that the greater the environmental heterogeneity (EH), the greater the species richness, both in terrestrial and aquatic ecosystems (Ortega et al., 2018). Recently, ecologists have also examined variation in measures of functional diversity (Graco-Roza et al., 2020; Heino and Grönroos, 2013; Milesi et al., 2016) and beta diversity (Fernández-Aláez et al., 2020; Heino et al., 2013; López-Delgado et al., 2020) along EH gradients, but the generality of these findings are still under debate. Clearly, a multi-faceted approach has become increasingly important to understand the mechanisms that govern the biodiversity-EH relationship and to predict impacts on biodiversity in various scenarios of habitat loss and environmental homogenization (Mouillot et al., 2013; Perez Rocha et al., 2019).

A mechanism commonly used to account for the positive effect of EH on biodiversity is the increased number of niche dimensions with increasing EH (MacArthur and MacArthur, 1961; Stein and Kreft, 2015). Within a riverscape (*sensu* Fausch et al., 2002; Wiens, 2002),

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heterogeneous environments offer a greater range of conditions (e.g., water pH, flow velocity) and variability of resources (e.g., coarse particulate organic matter, mosses), thereby increasing biodiversity (Boyero and Bosch, 2004; McCreadie and Bedwell, 2013). Nonetheless, the ways in which EH is perceived by an aquatic insect taxon varies according to its functional traits and concerning the spatial scales under study (Castro et al., 2020; Heino et al., 2015; Heino and Grönroos, 2013). For instance, compared to other guilds, the distributions of scrapers (a functional feeding group of freshwater macroinvertebrates; Cummins and Klug 1979) are more strongly correlated with variations in coarse substrates, moss cover and stream width (Heino and Grönroos, 2013).

Anthropogenic disturbances interact with environmental, ecological and biotic factors that shape biological communities, often obscuring the diversity-EH relationship and the variables driving it (Allouche et al., 2012; Palmer et al., 2010). Anthropogenic disturbances may reduce regional species pools or prevent some species from colonizing a site (Gámez-Virués et al., 2015; Sundermann et al., 2011). Also, they may alter environmental conditions so that they become unsuitable for some species (Bini et al., 2014; Graco-Roza et al., 2020), limit resource availability (Burdon et al., 2013; Silva et al., 2018), or facilitate the spread of invasive species that may increase competitive exclusion (Albano et al., 2018). Therefore, in a scenario where anthropogenic disturbances filter most of the functional traits and sensitive species (Castro et al., 2017; Silva et al., 2017), EH may no longer be a major factor controlling variation in biodiversity (Stoll et al., 2016), and it may even have a negative effect on some species (Allouche et al., 2012). Nonetheless, studies that have assessed the effect of anthropogenic disturbances on the biodiversity-EH relationship are scarce, making it difficult to predict this relationship for different scenarios of anthropogenic disturbance (Larsen and Ormerod, 2014; Yang et al., 2015).

Considering the lack of studies that explicitly attempt to examine how anthropogenic disturbance affects the relationship between biodiversity and EH in freshwater ecosystems, we addressed the following question: How does increased anthropogenic disturbance alter the relationship between EH and taxonomic and functional alpha and beta diversities of aquatic insects? To answer this question, we analyzed biological and environmental data from 76 stream sites, representing three different levels of anthropogenic disturbance in the Brazilian Neotropical savanna. As biological response metrics, we analyzed the taxonomic and functional diversity of aquatic insects belonging to mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddisflies (Trichoptera), hereafter called EPT. Based on the importance of EH to assemblage structuring and the previous knowledge that anthropogenic disturbance interferes with one or more factors that shape biological communities, we tested three predictions. P1: The greater the level of anthropogenic disturbance, the weaker will be the relationship between EH and both taxonomic and functional alpha diversities. P2: The sign and strength of correlations between EH metrics and both taxonomic and functional alpha diversities will depend on the level of anthropogenic disturbance. P3: Taxonomic and functional beta diversities will not respond to the EH gradient at any level of disturbance because species dispersal rates among sampling stations within a stream site are assumed to be very high, potentially causing mass effects that homogenize assemblage compositional variation (Heino et al., 2015, 2013).

2. Methods

2.1. Study area

We used data from 76 stream sites from 1st to 3rd order (on 1:100,000 scale maps; Strahler, 1957) located in the Neotropical savanna (Cerrado biome, a hotspot of biodiversity; Myers et al., 2000) of southeastern Brazil. This biome covers 20% of the country, but less than 30% of its original area is currently covered by native vegetation (Strassburg et al., 2017). Agriculture and pasture land uses are the main

causes of loss of native vegetation, whereas hydropower dams, mining and urbanization are important secondary causes (Françoso et al., 2015; Strassburg et al., 2017).

Stream sites were distributed across four hydrological units, delimited by the contributing drainage area within 35 km upstream of four hydropower reservoirs: Três Marias (TM), Volta Grande (VG), São Simão (SS) and Nova Ponte (NP). We classified sites into three levels of disturbance (Fig. 1). All sites were selected through a probability-based procedure that considered a spatially-balanced design (Macedo et al., 2014; Olsen and Peck, 2008). Field samples were collected in 2010 to 2013 during September dry seasons with one visit per year at each aforementioned hydrological unit.

2.2. Anthropogenic disturbance categorization

We classified stream sites into three anthropogenic disturbance categories through the use of the Integrated Disturbance Index (IDI) (Ligeiro et al., 2013). This quantitative index integrates measures of anthropogenic disturbances at site and catchment scales into a single value.

The catchment disturbance index (CDI) corresponds to the formula (Rawer-Jost et al., 2004):

$$CDI = 4 \times \text{\% urban area} + 2 \times \text{\% agricultural area} + 1 \times \text{\% pasture area}$$

At the site scale, local site disturbance is based on the *w1_hall* metric which sums 11 types of anthropogenic disturbance (walls, dikes, revetments, riprap or dams, buildings, pavement or cleared lots, roads or railroads, inlet or outlet pipes, landfills or trash, parks or maintained lawns, row crops, pastures, rangelands, hay fields, or evidence of livestock, logging, and mining) observed in-channel and in the riparian zone of a stream site (Kaufmann et al., 1999).

The disturbance levels at both catchment and site scales were combined using the Euclidean distance between each site to the origin of the plane formed by the local and catchment axes. Therefore, the higher the IDI, the higher the level of anthropogenic disturbance at the stream sites (Ligeiro et al., 2013).

Stream sites categorization based on the IDI value has proven to be an effective means to analyze both taxonomic and functional diversity responses of stream macroinvertebrates to human disturbance in the Neotropics (Castro et al., 2017; Chen et al., 2017; Fierro et al., 2018; Martins et al., 2020). We separated stream sites into three categories of disturbance by visual inspection of ordered IDI values to detect natural breakpoints. We also considered cut-off values previously used for site categorization in Neotropical savanna streams as references to delimit our categories (e.g. Castro et al., 2018; Ligeiro et al., 2020; Macedo et al., 2016) (Supplementary Material 1). Guided by the breakpoints and considering a balanced number of stream sites in each category, we established the following categories: IDI less than 0.30 were considered as least-disturbed (n = 29); IDI values > 0.65 were considered as most-disturbed (n = 16); IDI values between these thresholds were considered as moderately-disturbed (n = 31).

2.3. Sampling design

We settled the length of stream sites at 40 times their mean wetted widths, with a minimum length of 150 m (Peck et al., 2006; USEPA - United States Environmental Protection Agency, 2016). At each site, we marked 11 equidistant transects to sample EPT and environmental variables. Taxonomic and functional alpha diversities at each stream site corresponded to the sums of taxa and functional traits observed in the 11 transects, respectively. Taxonomic and functional beta diversities at each site corresponded to the taxonomic and functional traits dissimilarities among the 11 transects, respectively (Heino et al., 2015). Environmental heterogeneity at each site referred to environmental
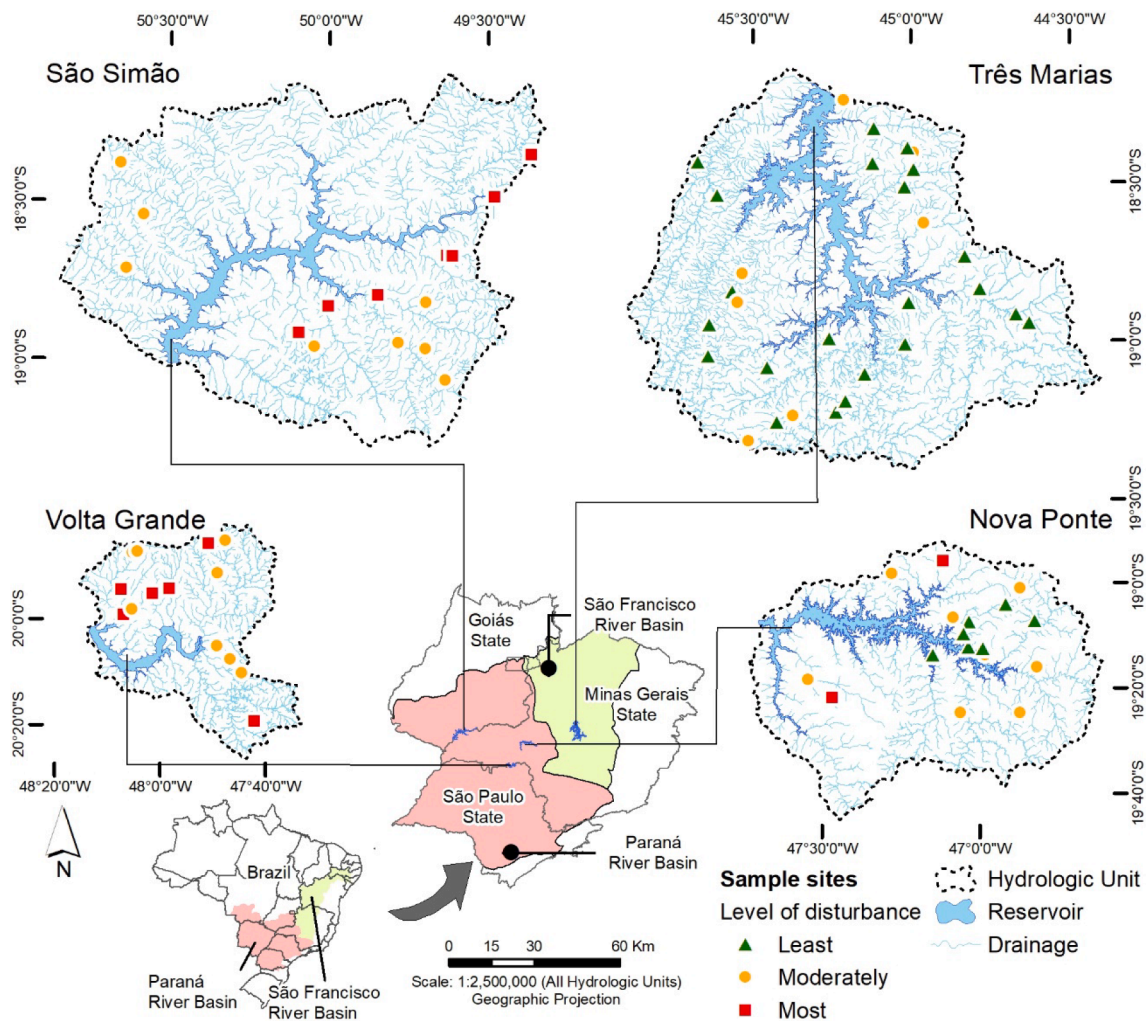
Fig. 1. Location of the stream sites sampled (n = 76) in the four hydrological units in the Neotropical Savanna, Minas Gerais state, southeastern Brazil.

differences among transects within each site (Anderson et al., 2006). Thus, we obtained a single value of each biological and EH metrics (taxonomic and functional alpha and beta diversities) per stream site.

2.4. Data collection

We measured 13 attributes of physical habitat structure, the variations of which were considered important predictors of aquatic macroinvertebrates assemblages (e.g. Boyero and Bosch, 2004; Heino and Grönroos, 2013; Kaufmann and Faustini, 2012) in each of the 11 transects and between them (Peck et al., 2006; USEPA - United States Environmental Protection Agency, 2016): wetted width (m); wetted depth (cm); wetted area (m^2); substrate embeddedness (%); canopy cover (%); thalweg depth (cm); flow velocity (m/s); bankfull width (m); bankfull height (m); bank angle (°); channel slope (cm); visual estimation of substrate types; and visual estimation of channel flow types.

We sampled macroinvertebrates by using a D-frame kick net (30 cm mouth width, 500 µm mesh size). Sampling followed a systematic zig-zag sequence along the 11 transects at each site (Peck et al., 2006; USEPA - United States Environmental Protection Agency, 2016). We preserved each of the 11 samples separately in 10% formalin and took them to the laboratory for further processing and identification.

In tropical regions, EPT taxonomy and functional traits are better known than those for other orders (Castro et al., 2017; Heino et al., 2018). We used the biological trait database for EPT genera summarized by Castro et al. (2017). This database encompasses seven trait

categories: body size, number of reproductive cycles per year, feeding habits, locomotion, body flexibility, body form, and association with the substrate. Body size categories were based on direct estimates of larval body length. The other categories were based on a literature specialized in Neotropical macroinvertebrates (Baptista et al., 2006; Dedieu et al., 2015; Reynaga and Dos Santos, 2012; Tomanova and Usseglio-Polatera, 2007). These functional traits were subsequently coded using the fuzzy coding approach (Chevenet et al., 1994), where each taxon gains an affinity score for each trait within a category (Castro et al., 2017).

2.5. Biological metrics

Taxonomic alpha diversity corresponded to all genera recorded at each single stream site. We measured taxonomic beta diversity through Permutational Analysis of Multivariate Dispersion (PERMDISP), which gives the average distance of individual samples to the group centroid (Anderson et al., 2006). Thus, the average distance of samples (each transect) to group centroid was considered the measure of beta diversity at each stream site. We applied the Jaccard coefficient to calculate dissimilarity based on the presence/absence of genera, and the modified Gower distance based on abundances using transformed data (log_2 X) + 1, with zeros not being transformed, instead remaining as zeros (Anderson et al., 2006).

To calculate functional alpha and beta diversities, we first computed taxon-by-taxon Gower distance from the fuzzy-coded trait matrix to generate a hierarchical tree cluster based on the group average method

(UPGMA) (following Cardoso et al. 2014). Alpha and beta functional diversity measurements were then based on the total branch length of the hierarchical tree that links all taxa represented in the stream site. We calculated these metrics using the package BAT in R program (Cardoso et al., 2015).

2.6. Environmental heterogeneity measures

Physical habitat differences among transects within each stream site were considered as the basis of EH metrics. For quantitative physical habitat measurements, we calculated the coefficient of variation (CV; standard deviation/mean), because it expresses a standardized measure of physical habitat variation among samples within each stream site. In contrast, qualitative (presence-absence) physical habitat measurements of substrate types (i.e., silt, sand, fine gravel, coarse gravel, small boulder, large boulder, concrete, rough bedrock, smooth bedrock, wood, and hardpan) and flow types (i.e., falls, cascade, rapid, riffle, glide and pool) were calculated using Simpson diversity index (1 – D), estimated across all 11 transects in the same stream site. The higher the value of Simpson diversity index, the greater the probability of observing the two different possible entities randomly pulling two samples within a dataset.

To avoid multicollinearity among the 13 EH metrics, we computed Variance Inflation Factors (VIFs). VIF scores that exceed 5 indicate high rates of multicollinearity with other metrics of the set (James et al., 2017) and should be eliminated from subsequent analytical steps. We identified high rates of multicollinearity for CV of channel wetted depth and CV of wetted area, and these metrics were thus excluded from the following analytical steps. Therefore, we ended up with 11 EH metrics.

2.7. Data analyses

We tested whether variations in biological metrics differed among categories of disturbance using an analysis of variance (one-way ANOVA; Supplementary Material 2). We used Levene's tests to evaluate differences in the variances of each EH metric among the categories of disturbance. Also, we performed Moran's I test to verify the spatial autocorrelation of all biological and EH metrics among stream sites. Tests were run in the R software using package spdep (Bivand and Wong, 2018). The results of the Moran's I test revealed a lack of spatial autocorrelation among stream sites (P-value > 0.05 for all Moran's I tests; Supplementary Material 3).

To test if the relationship between the EH metrics and the biological metrics change with anthropogenic disturbance, we used a model selection approach (Burnham and Anderson, 2002). The model selection is based on all possible additive combinations among EH metrics (i.e., predictor variables) to explain each biological metric (i.e., response variables) at each category of anthropogenic disturbance (Fig. 2). This analysis results in a set of balanced models (Doherty et al., 2012), which allows calculation of the cumulative AICc (w +) weights for each EH metric (Burnham and Anderson, 2002). Thus, we selected the EH metrics that were the most likely (w+ $\geq$ 0.50) to explain the variation in our response variables at each category of disturbance (least-, moderately- and most-disturbed). Each model selected provides the regression β parameters and significance value (*p*-value). The explanatory strength of each model is given by the coefficient of determination (R^2), calculated as 1 - (sums square of residual deviance/sums square of null deviance). Model selection was run in the R software using the package MuMIn (Bartón, 2019).

3. Results

We counted 24,874 individuals and found 77 EPT genera. Moderately and least-disturbed sites had similar mean abundances (366.7 and 365.9, respectively), whereas most-disturbed sites had lower abundances (180.7). Taxonomic and functional metrics' means did not differ among disturbance categories (Table 1).

In most cases, the variances of the EH metrics did not differ among disturbance categories, except for CV of substrate embeddedness (CV_embedd) ($F_{2,73} = 3.264$, p = 0.032) (Table 2). CV_embedd at least-
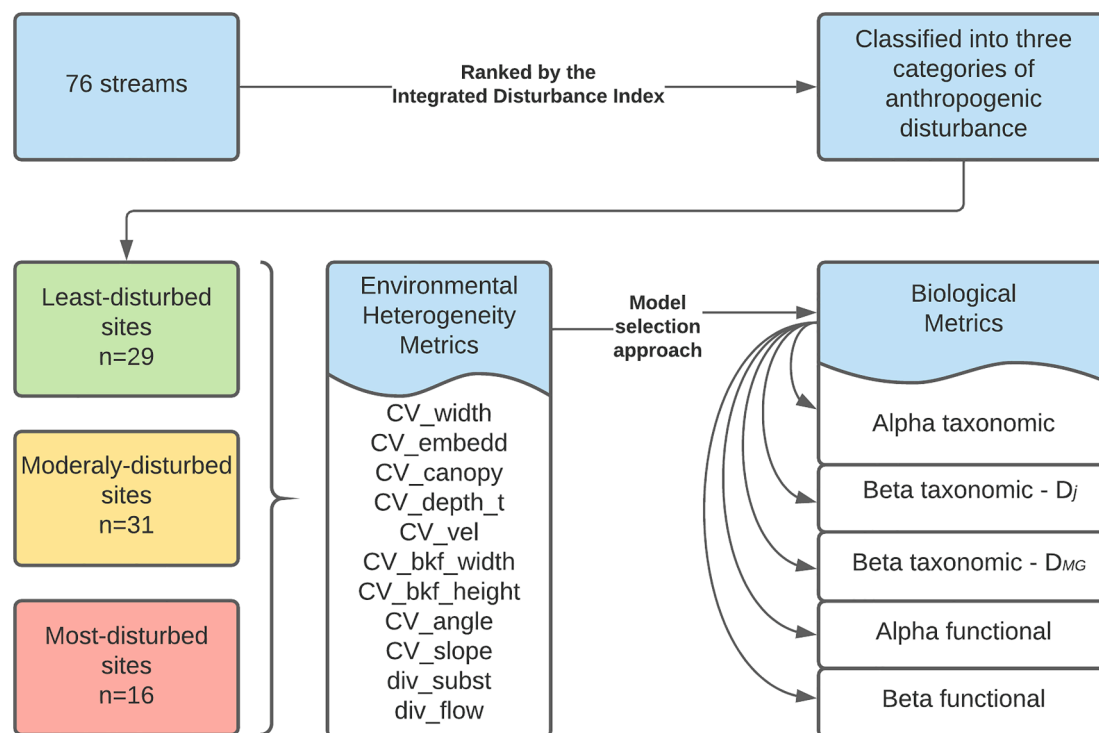

Fig. 2. A schematic diagram presenting the analytical approach based on model selection. Modeling was performed by category of disturbance, based on all metrics of environmental heterogeneity against each of the biological metrics.

Table 1

Mean values of taxonomic and functional diversity metrics (standard deviation in parentheses) representing biological response in different categories of disturbance: least-, moderate- and most-disturbed sites. Beta taxonomic – (d_J) corresponds to Jaccard coefficient dissimilarity measure. Beta taxonomic – (d_{MG}) corresponds to modified Gower distance-based measure. P-values of ANOVA's test between disturbance categories are presented.

Biological metrics	least n = 29		moderately n = 31		most n = 16		p-value
Alpha taxonomic	19.13	(7.50)	20.14	(8.30)	16.31	(8.30)	0.306
Beta taxonomic - d_J	0.53	(0.06)	0.52	(0.07)	0.49	(0.08)	0.246
Beta taxonomic - d_{MG}	1.26	(0.22)	1.24	(0.28)	1.24	(0.21)	0.931
Alpha functional	8.42	(2.56)	9.38	(3.19)	7.30	(2.88)	0.072
Beta functional	0.59	(0.08)	0.62	(0.07)	0.61	(0.10)	0.551

Table 2

Mean values of EH metrics (standard deviation in parentheses) representing environmental heterogeneity among sites in different categories of disturbance: least-, moderately- and most-disturbed sites. P-values of Levene's test between disturbance categories are presented.

Environmental heterogeneity metric	code	least n = 29	moderately n = 31	most n = 16	p-value
Coefficient of variation of channel wetted width (m)	CV_width	0.37 (0.12)	0.35 (0.14)	0.31 (0.08)	0.063
Coefficient of variation of substrate embeddedness (%)	CV_embedd	0.61 (0.35)	0.40 (0.22)	0.41 (0.18)	0.032
Coefficient of variation of canopy cover (%)	CV_canopy	0.22 (0.20)	0.23 (0.30)	0.21 (0.18)	0.864
Coefficient of variation of thalweg depth (cm)	CV_depth_t	0.64 (0.15)	0.50 (0.18)	0.44 (0.08)	0.081
Coefficient of variation of flow velocity (m/s)	CV_vel	0.94 (0.65)	0.75 (0.52)	0.49 (0.27)	0.145
Coefficient of variation of bankfull width (m)	CV_bkf_width	0.29 (0.10)	0.35 (0.15)	0.27 (0.10)	0.064
Coefficient of variation of bankfull height (m)	CV_bkf_height	0.37 (0.33)	0.29 (0.18)	0.28 (0.20)	0.626
Coefficient of variation of margin angle (°)	CV_angle	0.64 (0.20)	0.51 (0.18)	0.42 (0.16)	0.445
Coefficient of variation of channel slope (cm)	CV_slope	1.21 (0.50)	1.23 (0.62)	0.93 (0.33)	0.318
Simpson's diversity of substrate types	div_subst	0.44 (0.14)	0.44 (0.15)	0.44 (0.18)	0.633
Simpson's diversity of spatial flow types	div_flow	0.21 (0.14)	0.18 (0.12)	0.22 (0.12)	0.772

disturbed sites presented variance ($s^2 = 0.1225$) 3.8 times greater than in most-disturbed sites ($s^2 = 0.0324$).

The model selection algorithm indicated four EH metrics that were important variables accounting for variation in biological metrics across categories of anthropogenic disturbance (Table 3). At least-disturbed streams, spatial flow diversity (div_flow) was positively correlated to taxonomic ($w+ = 0.91$) and functional ($w+ = 0.97$) alpha diversities. At moderately-disturbed streams, CV of bankfull height (CV_bkf_hight) negatively correlated with taxonomic ($w+ = 0.60$) and functional ($w+ = 0.81$) alpha diversities. In most-disturbed streams, CV of thalweg depth (CV_depth_t) was positively correlated to taxonomic ($w+ = 0.93$) and functional ($w+ = 0.96$) alpha diversities, while the CV of flow velocity (CV_vel) had a positive effect on taxonomic beta diversity based on modified Gower distance.

The model strengths did not decrease as the level of anthropogenic disturbance increased. In most-disturbed streams, the models that explained the increasing trend of taxonomic and functional alpha diversities as a function of CV_depth_t showed the highest R^2 values (0.52 and 0.59, respectively). In contrast, streams with moderate disturbance showed weaker explanatory power for the taxonomic alpha diversity model ($R^2 = 0.10$) and functional alpha diversity model ($R^2 = 0.18$). In least-disturbed streams, div_flow metric showed intermediate percentage of explanation for taxonomic ($R^2 = 0.22$) and functional ($R^2 = 0.30$) alpha diversities.

4. Discussion

Our results showed that anthropogenic disturbances at multiple spatial scales affected the relationship between EH and taxonomic and functional alpha diversities at the site scale. However, the increase in anthropogenic disturbances did not lead to the weakening of these relationships in a unidirectional way. Also, EH did not affect beta diversity between transects at each stream site, as we predicted.

In a scenario where freshwater ecosystems are strongly threatened by anthropogenic disturbances (Collen et al., 2014), our results contribute to understand how tropical stream insect (EPT) assemblages respond to key gradients of EH at three levels of anthropogenic disturbance. Following a multi-faceted approach that encompassed alpha and beta components of taxonomic and functional diversities, we can better understand the causes and consequences of anthropogenic disturbances on the biodiversity and potential functioning of stream ecosystems (Mori et al., 2018; Mouillot et al., 2013).

4.1. The responses of taxonomic and functional alpha diversities to the EH gradient

For the first prediction (P1), we expected that the higher the level of anthropogenic disturbance, the weaker would be the strength of the relationship between EH and taxonomic and functional alpha diversities. Contrary to our expectations, as the anthropogenic disturbance increased, the strength of this relationship did not decrease. In the most-disturbed stream category, thalweg depth variation was a stronger predictor of taxonomic and functional alpha diversities compared to spatial flow diversity in the least-disturbed streams. On the other hand, bankfull height variations negatively affected taxonomic and functional alpha diversities in moderately-disturbed stream sites. The absence of a unidirectional pattern of biological responses along the EH gradient with the disturbance increase has also been reported in the literature. Using a theoretical model, Yang et al. (2015) predicted that plant species richness increases along the EH gradient when plants are subjected to low or high environmental severity, but the pattern becomes unimodal at moderate levels. In contrast, benthic communities did not respond to a local habitat quality gradient when regional disturbance levels were low or high, but they did when regional disturbance levels are moderate (Stoll et al., 2016). Based on these results, we can conclude that the sign and strength of the biodiversity-EH relationship is not universal in stream insect assemblages and that it depends on the level of anthropogenic disturbance.

Different mechanisms may explain the diversity-heterogeneity

Table 3

Environmental heterogeneity metrics selected to the model of biological metrics of the EPT assemblages. All models are separated according to the category of anthropogenic disturbance to which the assemblages are subjected: Least-, moderate- and most-disturbed. The estimates of the effects of the environmental heterogeneity metrics (β parameters) are given for the model built with meaningful environmental heterogeneity metrics based on criteria of cumulative AICc weights > 0.50. Beta taxonomic (d_J) corresponds to Jaccard coefficient dissimilarity measure. Beta taxonomic (d_{MG}) corresponds to modified Gower distance- based measure.

Category of disturbance	Biological metric	Physical habitat metric	Cumulative AICc Weights	β parameters			R^2	p-value
				Estimate	Lower 95% CI	Upper 95% CI		
Least	Alpha taxonomic	div_flow	0.91	26.64	7.54	45.74	0.22	0.011
	Beta taxonomic - d_J	–	–	–	–	–	–	–
	Beta taxonomic - d_{MG}	–	–	–	–	–	–	–
	Alpha functional	div_flow	0.97	12.18	5.22	19.14	0.30	0.002
	Beta functional	–	–	–	–	–	–	–
Moderately	Alpha taxonomic	CV_bkf_hight	0.60	−13.18	−27.36	1.00	0.10	0.079
	Beta taxonomic - d_J	–	–	–	–	–	–	–
	Beta taxonomic - d_{MG}	–	–	–	–	–	–	–
	Alpha functional	CV_bkf_hight	0.81	−5.99	−10.59	−1.39	0.18	0.016
	Beta functional	–	–	–	–	–	–	–
Most	Alpha taxonomic	CV_depth_t	0.93	70.40	34.75	106.05	0.52	0.002
	Beta taxonomic - d_J	–	–	–	–	–	–	–
	Beta taxonomic - d_{MG}	CV_vel	0.55	0.43	0.09	0.77	0.30	0.028
	Alpha functional	CV_depth_t	0.96	26.07	14.64	37.50	0.59	0.001
	Beta functional	–	–	–	–	–	–	–

relationship (Stein and Kreft, 2015). It is possible that many ecological factors (e.g., large-scale factors, competition, stochastic events) other than environmental heterogeneity affect the structure of biological assemblages (McCabe and Gotelli, 2000; Perez Rocha et al., 2018). Therefore, the lower explanatory power may have been attributed to EH in our dataset response under least-disturbed conditions ($R^2 = 0.22$ for taxonomic alpha diversity; $R^2 = 0.30$, functional alpha diversity). On the other hand, EH may play a major role in maintaining diversity in streams subject to high levels of anthropogenic disturbance, where a single metric of heterogeneity explained 52% of the variation in taxonomic diversity and 59% of the variation in functional diversity. We also observed that bankfull height heterogeneity can have a weak negative effect on aquatic insect diversity in moderately-disturbed streams, a pattern usually reported in studies conducted at small scales (Tamme et al., 2010; Tews et al., 2004). In this case, an increase in EH can lead to habitat fragmentation, making organisms more susceptible to stochastic events (Allouche et al., 2012). In fact, bankfull height heterogeneity provides a measure of channel form heterogeneity (Peck et al., 2006), which suggests that the increment of the selected metrics might be causing habitat fragmentation for EPT assemblages. Since both biological metrics (taxonomic and funcional alpha diversity) responded in the same direction (positively) and with a similar percentage of explained variation (R^2), these patterns suggest that the taxonomic and functional alpha diversity respond similarly to EH gradients in any category of disturbance.

We confirmed our second prediction (P2) because different features of EH affected aquatic insect assemblages at different levels of anthropogenic disturbance. Because anthropogenic disturbances interact with natural ecological conditions (Seiferling et al., 2014), one EH metric could be ecologically relevant in the context of least anthropogenic disturbance category, but other ones would become more relevant when disturbances increase. Our observations point to the importance of measuring a wide range of environmental factors to identify those that are ecologically important for the biological assemblage studied (Heino and Grönroos, 2013). In our dataset encompassing stream sites (~150 m) in least-disturbed conditions, the positive effect of spatial flow diversity on taxonomic and functional alpha diversities corroborated previous studies (Kärnä et al., 2018; Silva et al., 2014). A higher level of spatial flow diversity increases the range of environmental conditions suitable for species with different functional traits (Bouckaert, 1995). Flow diversity is directly related to substrate diversity (Boyero, 2003), and the interaction of these factors results in a riverine landscape with distinct habitat patches that are perceived differently by aquatic insect species (Boyero and Bosch, 2004; Wiens, 2002). Thalweg depth

variations may also play a role similar to spatial flow diversity in most-disturbed streams. This metric is associated with changes in the water flow velocity and direction (Kaufmann and Faustini, 2012), which ultimately lead to effects similar to those caused by spatial flow diversity.

4.2. The responses of taxonomic and functional beta diversities to the EH gradient

For the third prediction (P3), we expected that taxonomic and functional beta diversities would not respond to the gradient of EH in any disturbance category, because mass effects are a major factor structuring biological assemblages at small scales in streams (Heino et al., 2015). We found that in almost all categories of anthropogenic disturbance, no EH metric was correlated with the taxonomic and functional dissimilarities among samples within a given stream. Only in the most-disturbed streams, taxonomic beta diversity increased with increasing variation in water velocity, which is surprising given that anthropogenic disturbances have contributed to the biotic homogenization of freshwater ecosystems (Castro et al., 2017; Larsen and Ormerod, 2014; Siqueira et al., 2015).

Beta diversity patterns in freshwater ecosystems are typically strongly scale dependent (Heino et al., 2015). Our results reinforce the idea that EH measured within streams does not strongly affect the distributions of organisms among samples within each stream site (Heino et al., 2013; Heino and Grönroos, 2013). In our sampling design, transects within the stream site are 15 to 25 m apart, and dispersal limitations are thus likely to be minimal as organisms can easily access different habitat patches (Brown and Swan, 2010). In this case, individuals may be randomly distributed in space, and they do not exhibit a specific relationship with the environment (Brown et al., 2018; Heino et al., 2013).

4.3. Implications for management

Ecosystem management aiming to increase EH to re-establish biodiversity must take into account the relevant factors for the organisms studied at a given spatio-temporal scale (Kolasa and Rollo, 1991). We provided insights into how aquatic insects may perceive EH in a set of tropical streams classified into different levels of anthropogenic disturbance. Maintaining spatial flow diversity in preserved streams seems to be an effective means to increase local alpha diversity, whereas the increment in thalweg depth variations potentially results in an increase of local taxonomic and functional alpha diversity in most-disturbed streams. On the other hand, we suggest that efforts to

increase beta diversity should also be tested at broader spatial scales.

A high number of restoration projects that have aimed to increase EH in streams have not achieved a significant increase in biodiversity (Palmer et al., 2010). The factors that may influence the biodiversity-EH relationship include: (i) the absence of suitable species in the regional species pool (Sundermann et al., 2011); (ii) the ongoing effects of anthropogenic stressors on the biota (Brown et al., 2018; Stoll et al., 2016); (iii) focus on the wrong spatial scale; (iv) the wrong perception of increased EH by the biota (Polvi et al., 2014). We propose that there are often two or more factors interacting, depending on a given case. The model selection approach used in our study identified ecologically meaningful EH metrics accounting for variation in the taxonomic and functional alpha diversities in each disturbance category. Finally, we recommend the use of a model selection approach to pinpoint the most important EH metrics that should be managed for the preservation of stream biodiversity.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107079.

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