UNIVERSIDADE FEDERAL DE MINAS GERAIS
Instituto de Ciências Biológicas
Programa de Pós-graduação em Ecologia, Conservação e Manejo da Vida Silvestre

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HOW DOES ENVIRONMENTAL HETEROGENEITY AFFECT BIODIVERSITY IN FRESHWATER ECOSYSTEMS AND HOW DOES IT VARY?

Belo Horizonte
2022

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Versão final

Tese apresentada ao Programa de Pós-Graduação de Ecologia. Conservação e Manejo da Vida Silvestre, da Universidade Federal de Minas Gerais como requisito obrigatório para a obtenção do título de Doutora em Ecologia, Conservação e Manejo da Vida Silvestres.

Orientador: Prof. Dr. Marcos Callisto

Belo Horizonte
2022

043 Agra, Janaina Uchôa Medeiros.
How does environmental heterogeneity affect biodiversity in freshwater ecosystems and how does it vary? [manuscrito] / Janaina Uchôa Medeiros Agra. – 2022.
104 f. : il. ; 29,5 cm.

Orientador: Prof. Dr. Marcos Callisto.
Tese (doutorado) – Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas. Programa de Pós-Graduação em Ecologia Conservação e Manejo da Vida Silvestre.

1. Ecologia. 2. Biologia de Ecossistemas de Água Doce. 3. Biodiversidade. I. Pereira, Marcos Callisto de Faria. II. Universidade Federal de Minas Gerais. Instituto de Ciências Biológicas. III. Título.

CDU: 502.7

Ficha catalográfica elaborada pela bibliotecária Fabiane C M Reis - CRB: 6/2680

UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE

FOLHA DE APROVAÇÃO

"How does environmental heterogeneity affect biodiversity in freshwater ecosystems and how does it vary?"

JANAINA UCHÔA MEDEIROS AGRA

Tese de Doutorado defendida e aprovada, no dia **27 de outubro de 2022**, pela Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre da Universidade Federal de Minas Gerais constituída pelos seguintes professores:

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Esta tese está dedicada a todos os ecossistemas
de água doce do planeta Terra.

AGRADECIMENTOS

Não seria possível realizar esta tese sem que muitas outras pessoas antes de mim existissem. Para ser justa, os agradecimentos poderiam por si só compor uma longa lista de nomes e justificativas, e ainda assim não abarcariam tantas pessoas e outros seres que são necessários para fazer com que uma tese se conclua. Portanto, faço esta ressalva, por entender que palavras e textos possuem limites. Eu agradeço aqui apenas algumas das pessoas e instituições mais diretamente relacionadas à execução desta tese.

Agradeço a todas as pesquisadoras e pesquisadores pregressos, especialmente da área de ecologia aquática, pois sem eles meu trabalho não seria possível. Em mãos de seus artigos, eu pude aprender, gerar novos conhecimentos e propor soluções para os atuais desafios que vivemos frente às ameaças sobre os ecossistemas aquáticos. Agradeço a participação da minha banca de avaliação, pois são pessoas inspiradoras ao longo da minha trajetória acadêmica e cumprirão papel fundamental para que esta tese cumpra seus objetivos. Agradeço a colaboração fundamental do Prof. Rafael Ligeiro (UFPA), o Prof. Diego Macedo (UFMG), a Prof. Tatiana Cornelissen (UFMG), e dos pesquisadores Dr. Jani Heino (SUKE-Finlândia), Dr. Diego Castro e Dr. Marden Linares, em diferentes etapas como a concepção da pesquisa, a análise de dados e a escrita de capítulos. Aos membros do Laboratório de Ecologia de Bentos, coordenados pelo meu orientador, o prof. Marcos Callisto, eu tenho a máxima admiração e gratidão por todo o apoio que me deram durante os mais de seis anos em que me dediquei às atividades deste laboratório. O esforço conjunto dessas pessoas foi fundamental para que eu pudesse construir o conhecimento que apresento nesta tese. Dedico um agradecimento especial ao Laboratório de Ecologia de Peixes, coordenado pelo prof. Rafael Leitão, pela enorme parceria que fizemos ao longo da execução desta tese e o carinho que sempre me transmitiram.

Agradeço às instituições de fomento à ciência brasileira CAPES, CNPq e a empresa de energia elétrica CEMIG por tantos anos de investimento no Programa de Ecologia Conservação e Manejo da Vida Silvestre e no Laboratório de Ecologia de Bentos. Também, estas instituições financiaram meu projeto e bolsa de pesquisa ao longo do meu doutorado. Agradeço por ter tido acesso a todo o patrimônio que a Universidade Federal de Minas Gerais proporciona, desde os serviços gerais, a assistência estudantil, o apoio das técnicas e técnicos, e o conhecimento transmitido por cada uma das professoras e professores dessa Universidade. Toda essa rede de apoio foi fundamental para que eu conseguisse concluir todas as etapas do processo de formação de doutora. E deixo aqui o meu lamento pelas constantes ameaças que esses profissionais sofrem a cada corte orçamentário vindo de governos que não entendem a educação e a ciência como um dos maiores patrimônios de uma sociedade que se propõe a acabar com as desigualdades sociais.

Por fim, eu agradeço imensamente a minha ampla rede de apoio fora da Universidade. Familiares, amigos e amores foram fundamentais para atravessar esse momento, especialmente durante os dois anos de pandemia de COVID-19. Ao meu pai Virgílio, minha mãe Eliane, minha irmã Juliana agradeço por serem a base constituinte de tudo que posso ser hoje. Aos meus tios, em especial Márcia e Evaldo por terem me apoiado nos anos iniciais da minha formação como bióloga na UFPE. Agradeço em especial a todas as mulheres mais velhas que cuidaram de mim e rezaram por mim em diferentes momentos dessa caminhada. Gostaria de citar aqui algumas delas, como a minha avó Olivete Wanderley, minha mãe Eliane, minha sogra Rita Name, minha amiga Silvia Magalhães, e minha comadre Kele Firmiano. Agradeço ao meu companheiro Pedro pelo mais consistente amor e cuidado que já pude imaginar vir de um homem. E agradeço imensamente aos meus camaradas de capoeira, ao mestre Jurandir e a todos os mestres angoleiros, que juntos me ensinaram que “devagar também é pressa”.

“Assaz o senhor sabe: a gente quer passar um rio a nado, e passa; mas vai dar na outra banda é num ponto muito mais embaixo, bem diverso do em que primeiro se pensou. Viver nem não é muito perigoso?”

(Guimarães Rosa, Grandes Sertão: Veredas, 1956)

Resumo

A heterogeneidade ambiental (HA) é um dos fatores ambientais mais investigados em ecossistemas ecológicos de todo o mundo. É esperado que ecossistemas mais heterogêneos abriguem maior biodiversidade, porém efeitos negativos da HA sobre a biodiversidade também são observados. Variações na resposta de comunidades biológicas frente ao aumento da HA são atribuídas a diversos fatores, levantando dúvidas sobre o seu significado ecológico. Portanto, eu defini a seguinte pergunta norteadora para esta tese de doutorado: Como a HA afeta a biodiversidade em ecossistemas de água doce e como distúrbios antrópicos interferem nesse efeito? Para responder a esta pergunta, eu estabeleci dois objetivos principais: 1º) Sintetizar o conhecimento atual sobre a relação entre a HA e as múltiplas facetas da biodiversidade em ecossistemas de água doce, e estimar o tamanho do efeito geral 2º) Investigar o efeito de distúrbios antrópicos sobre a relação entre HA e as múltiplas facetas da biodiversidade de insetos aquáticos de riachos no Cerrado. No primeiro capítulo, eu apresento uma síntese de conceitos e metodologias de investigação da HA, com base em 98 artigos revisados. Utilizando ferramentas de meta-análise, pude demonstrar a existência de efeito geral positivo da HA sobre as diversidades alfa taxonômica e funcional de comunidades biológicas em ecossistemas de água doce. O efeito positivo da HA sobre a diversidade alfa taxonômica não variou entre comunidades biológicas de zonas temperadas e tropicais, entre comunidades de ecossistemas lênticos e lóticos, ou entre experimentos que controlaram o efeito de área e os que não controlaram. Não foi possível estimar efeitos significativos da HA sobre os respectivos componentes beta taxonômico e funcional da biodiversidade. No segundo capítulo, avalio como o efeito da HA varia em assembléias de insetos aquáticos, que foram submetidos a três diferentes níveis de distúrbios antrópicos. Por meio de uma abordagem de seleção de modelos identifiquei métricas de HA que possuem maior relevância ecológica para explicar o aumento das diversidades alfa taxonômica e funcional de insetos aquáticos, sendo elas: a diversidade de fluxo da água (em riachos sob mínimo distúrbio) e a variação na profundidade do canal (em riachos sob máximo distúrbio). Como conclusão desta tese, identifiquei que a HA é um fator ambiental fundamental para aumentar as diversidades alfa taxonômica e funcional em diferentes ecossistemas de águas doce em todo o mundo, porém seu efeito pode variar dependendo dos níveis de distúrbios antrópicos aos quais as comunidades de organismos aquáticos estão submetidas.

Palavras-chave: Complexidade de habitats, homogeneização ambiental, sínteses ecológicas, diversidade beta, diversidade funcional.

Abstract

Environmental heterogeneity (EH) is one of the most investigated environmental factors in freshwater ecosystems around the world. It is expected that more heterogeneous ecosystems harbor greater biodiversity, but negative effects of EH on biodiversity are also observed in nature. Variations in the response of biological communities to the increase in EH are attributed to several factors, raising doubts about its ecological significance. Therefore, I defined the following question for this thesis: How does environmental heterogeneity affect biodiversity in freshwater ecosystems and how can anthropogenic disturbance interfere with the effect? To answer this question, I established two main objectives: 1st) To synthesize the status of knowledge about the relationship between EH and the multiple facets of biodiversity in freshwater ecosystems and estimate the overall effect of EH over multiple facets of biodiversity; 2nd) To investigate the effect of anthropogenic disturbances on the relationship between EH and the multiple facets of the biodiversity of aquatic insects from streams in the Neotropical Savanna. In the first chapter, I systematically reviewed 98 articles and presented a synthesis of EH concepts and methodologies. Also, using a meta-analytical approach, I estimated the overall positive effect of EH over the taxonomic and functional alpha diversity of freshwater communities. The positive effect of EH on alpha taxonomic diversity did not vary between biological communities from temperate and tropical zones, from lentic and lotic ecosystems, or between experiments that controlled the area effect and those that did not. Nonetheless, it was not possible to estimate significant effects of EH over the respective taxonomic and functional beta components of biodiversity. In the second chapter, I demonstrate how the effect of EH varies in aquatic insect assemblages, which were submitted to three different levels of anthropogenic disturbances. Through a model selection approach, I identified EH metrics that have better ecological relevance to explain the increasing taxonomic and functional alpha diversity at each disturbance level, namely: the water flow diversity (in streams least-disturbed) and the variation in channel depth (in streams most-disturbed). As a general conclusion, it is possible to state that EH is a fundamental environmental factor to increase taxonomic and functional alpha diversity in different freshwater ecosystems around the world, but its effect varies depending on the levels of anthropogenic disturbances to which biological communities are submitted.

Key-words: Habitat complexity, environmental homogenization, ecological synthesis, beta diversity, functional diversity.

SUMÁRIO

General introduction

The seminal publication "On birds species diversity" (MACARTHUR, R H; MACARTHUR, 1961) identified heterogeneity as a relevant environmental factor in the structuring of biological communities. The authors observed that the increase in foliage height diversity (a *proxy* of environmental heterogeneity) was positively related to the increase in bird species diversity. The main mechanism evocated from past to nowadays is that a greater environmental heterogeneity would expand the gradients of resources and environmental conditions in a region, increasing the co-existence of a greater number of species with different ecological niches (HUTCHINSON, 1959) (Figure 1). This publication is considered a keystone of one of the main topics in ecology to date, being one of the ten most cited articles in the journal *Ecology* since 1945 (CUNHA *et al.*, 2012; FAGHIHINIA *et al.*, 2021). Around this topic, several questions were proposed, including: What is the ecological concept of environmental heterogeneity? How does environmental heterogeneity affect biodiversity? What are the ecological mechanisms behind this relationship? What factors may affect this relationship?

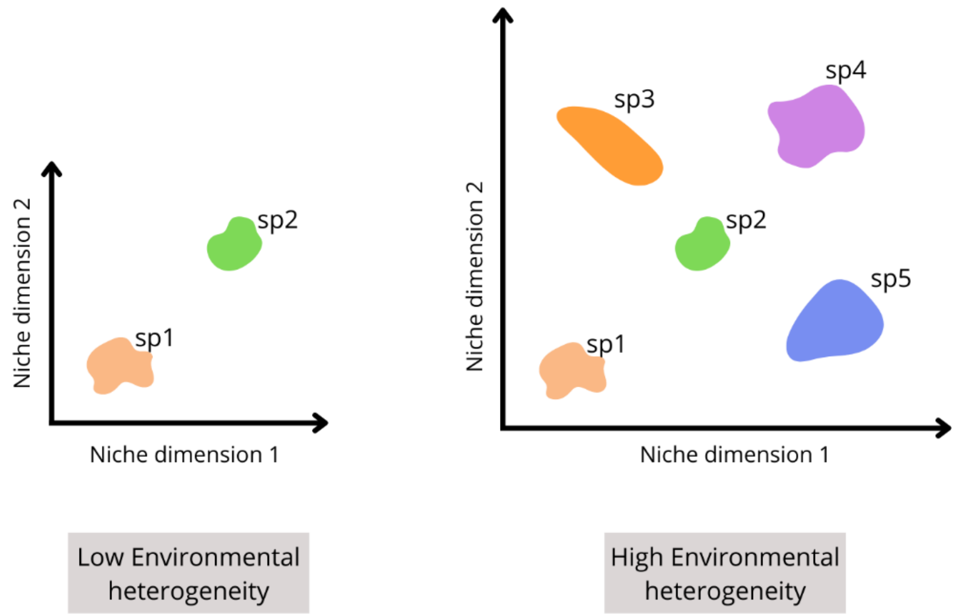

Figure 1: Theoretical example of a multidimensional space with two dimensions. Each axis represents one dimension that corresponds to one environmental gradient or resource. Species (sp1, sp2, sp3, sp4, sp5) occupy a particular space according to its ecological niche. A region with low environmental heterogeneity (left side) presents a shorter axis than a region with high environmental heterogeneity (right side). Thus, the increment of environmental heterogeneity expands the gradients of resources and environmental conditions in a region, which can be occupied for more species with different niches. Figure made by the author.

This thesis aims to provide contributions to fill some of those questions. For this, I stated the following question: How does environmental heterogeneity affect biodiversity in freshwater ecosystems and how can anthropogenic disturbance interfere with the effect? To answer this question, I established two general objectives:

1º) To synthesize the status of knowledge about the relationship between EH and the multiple facets (i.e., taxonomic and functional diversity, and their respective alpha and beta components) of biodiversity in freshwater ecosystems and estimate the overall effect of these relationships.

2º) To investigate the effect of anthropogenic disturbances on the relationship between EH and the multiple facets of biodiversity (i.e., taxonomic and functional diversity, and their respective alpha and beta components).

Along the following introduction sections (**1.1** and **1.2**), I present ecological concepts and bases to develop both objectives. **Chapter 1** encompasses a systematic review of 98 published articles from 1975 to 2020 that investigate the effect of EH over different biological communities of freshwater ecosystems around the world. In **Chapter 2**, I used a model selection approach to investigate the effect of anthropogenic disturbances on the relationship between EH and the biodiversity of aquatic insect assemblages in the Brazilian Neotropical Savanna headwater streams. This chapter was published in the *Ecological Indicators* Journal (2021). Finally, I present a **Thesis' General Conclusion** and propose **Future Perspectives** based on the results of this thesis.

1.1.The Environmental heterogeneity concept and its effects on biodiversity

Ecological studies about the relationship between environmental heterogeneity and biodiversity have been carried out for decades through observational studies, experimental studies and reviews of the published literature (see ALLOUCHE *et al.*, 2012; ORTEGA; THOMAZ; BINI, 2018; STEIN; GERSTNER; KREFT, 2014; STEIN; KREFT, 2015; TEWS *et al.*, 2004). More advances on the subject are seen for the ecology of terrestrial ecosystems, while studies in freshwater ecosystems still demand greater attention. Recent reviews and meta-analyses showed that EH has a positive overall effect on species richness (ORTEGA; THOMAZ; BINI, 2018; STEIN; GERSTNER; KREFT, 2014). For terrestrial ecosystems, the most invoked mechanisms to explain the species richness increase are coexistence, persistence, and species diversification (STEIN; KREFT, 2015). However, mechanisms are rarely tested through controlled experiments (ORTEGA; THOMAZ; BINI, 2018). Also, negative effects of

EH have also been reported in terrestrial and aquatic ecosystems (GRACO-ROZA *et al.*, 2020; KÄRNÄ *et al.*, 2018; TAMME *et al.*, 2010). To deal with that, Allouche et al. (2012) proposed an unimodal model, in which there is a trade-off between the EH and the species' occupancy area. Thus, high levels of EH would increase area fragmentation and the likelihood of stochastic extinctions, leading to the decreasing of species richness (ALLOUCHE *et al.*, 2012).

Since freshwater ecosystems have a wide variety of types (e.g., reservoirs, lakes, rivers, streams), which are hierarchically determined by factors ranging from the catchment scale to the local scale, the investigation of the EH - diversity relationship may vary in many aspects (FRISSELL *et al.*, 1986; MACEDO *et al.*, 2014) (Figure 2). For example, to understand the EH-biodiversity relationship in the whole catchment, factors such as geodiversity, land cover diversity or elevation variation must be considered (BÉJAR *et al.*, 2020; KÄRNÄ *et al.*, 2018). While investigating the effect of EH in the local scale has to encompass local environmental factors (e.g., habitat diversity, substrate and water flow variations) (MASSICOTTE *et al.*, 2014). Also, to get a wider picture of ecological mechanisms that govern the relationship between EH and biodiversity in freshwater ecosystems, the investigation of multiple facets of biological diversity (e.g., functional diversity and the beta component of diversity) are recommended but still rare (HEINO; MELO; BINI, 2015).

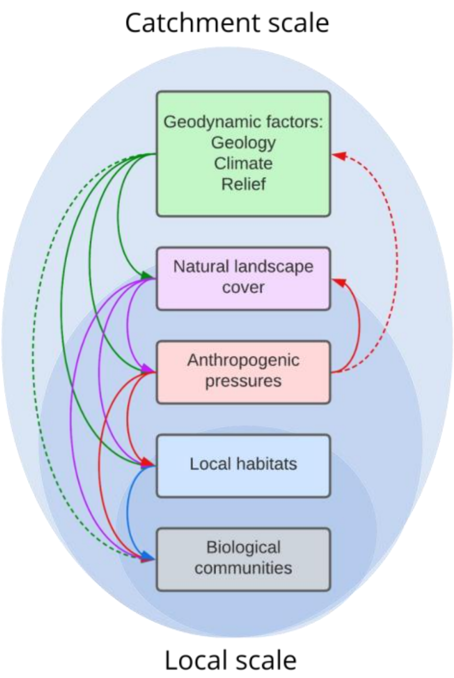

Figure 2: Freshwater ecosystems are hierarchically determined by factors from the catchment scale to the local scale. Anthropogenic factors may affect factors from scales above and below itself. Full arrows represent direct effect, and dashed arrows represent indirect effects. Figure was adapted from Macedo et al. (2014).

Another challenge in investigating the effect of EH on biodiversity lies in the establishment of an EH common concept among researchers. More than 100 different terms have been used to refer to EH, and several authors established different conceptualizations for it (KOLASA; ROLLO, 1991; LI, H; REYNOLDS, 1995; STEIN; GERSTNER; KREFT, 2014). In a simple and direct sense, Heino et al. (2013) defined EH as the variation of abiotic factors between two or more locations within a region. To amplified this concept and include the biotic and abiotic resources aspect (e.g., habitats, shelter, and food), which are fundamental factors in the biological communities structuring (VELLEND, 2016), I propose that EH is the variation of environmental conditions and resources between two or more locations within a region. In the same way, the temporal EH is the variation of environmental conditions and resources in the same location over time (LI, H; REYNOLDS, 1995).

Beyond the EH concept, there is a wide variety of methodological approaches to investigate EH (STEIN; KREFT, 2015). The choice for a particular methodological approach should be guided by two main aspects: 1) the spatial scale of interest, and 2) the environmental elements that are considered *proxies* of EH (e.g., substrate, water flow, channel morphology, catchment land use) (TOKESHI; ARAKAKI, 2012). When the spatial scale of interest is delimited (i.e., region unit), variations of an EH *proxy* will be analyzed among locations within the region unit (Figure 3). Those *proxies* can be manipulated and measured in different ways. According to Tokeshi and Arakaki (2012), there are four main possibilities to manipulate and measure the features of an EH *proxy*: the size variation, the physical structure, the spatial arrangement, and abundance/density (Figure 4). Consequently, different calculation methods (e.g., indices, fractal dimensions, abundance, density, coefficients of variation and standard deviations) are used to quantify EH and test its effect over freshwater biodiversity (STEIN; KREFT, 2015).

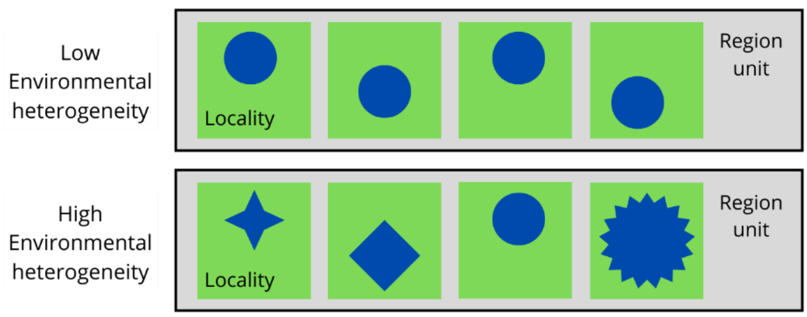

Figure 3: Environmental heterogeneity (EH) is evaluated among localities (green squares) within a region unit (gray rectangle). Blue symbols represent an EH *proxy* (e.g., substrate type, or channel morphology). A region with low EH region (above) presents low variability of EH *proxy* among localities. A region with high EH presents high variability of EH *proxy* among localities. Figure made by the author.

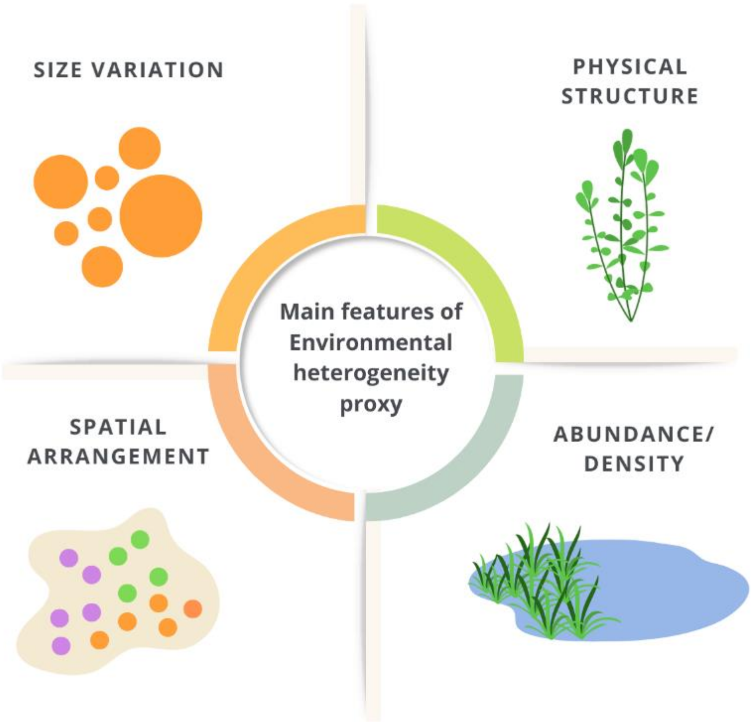

Figure 4: Environmental heterogeneity (EH) *proxies* can be evaluated through four main features in order to quantify EH and test its effect over freshwater biodiversity. Figure made by the author.

Because EH has become one of the most driving factors studied across freshwater ecosystems (FAGHIHINIA *et al.*, 2021), global synthesis is important to identify main ecological patterns over biodiversity and the sources of variation among studies. Previous reviews have focused on a specific point of the relationship between EH-biodiversity of freshwater ecosystems. For example, Cunha and co-authors (2012) analyzed publications on aquatic ecology (marine and freshwater ecosystems) that cited “On birds species diversity” of MacArthur and MacArthur (1961). Heino et al. (2015) reviewed publications that evaluated the effect of EH on freshwater beta diversity, proposing ecological concepts and predictions based on the spatial scale. Finally, Ortega et al. (2018) performed a meta-analytical study encompassing experimental and quasi-experimental studies of aquatic and terrestrial ecosystems, to estimate the overall effect size of EH over species richness.

Therefore, the first chapter of my thesis aims to broaden the understanding of the role of EH on freshwater biodiversity. I performed a global systematic review of all published literature that investigated the effect of EH on any biological metric of diversity (i.e., taxonomic and functional diversity, and their respective alpha and beta components), and estimate the magnitude of the overall effect of spatial EH over these multiple facets of freshwater biodiversity. Besides, I provided a global synthesis that elucidates a) how spatial EH is assessed across geographical locations, freshwater ecosystem types, biological groups, and their occurrence zone; b) which mechanisms are invoked to investigate the spatial EH-biodiversity relationship; c) which environmental variables are used as *proxy* of EH, as well as the methodological approach and calculation methods used to investigate and measure spatial EH in freshwater ecosystems. Lastly, I investigated possible sources of variation on the overall effect of EH over taxonomic alpha diversity.

1.2. Anthropogenic disturbances as an additional factor on the relationship between environmental heterogeneity and biodiversity

The pattern of community structure can be explained by a chain of factors and mechanisms from the regional to the local scale. Factors and mechanisms that limit the establishment and persistence of a species in an ecological community can be called environmental filters (VELLEND, 2016). From the regional scale, the dispersion filter acts as a barrier along a landscape (Figure 5a). Thus, only species which can overcome those barriers will colonize a local site (LEIBOLD, M. A. *et al.*, 2004). Resource availability and environmental conditions at the local scale are considered abiotic filters, affecting the persistence of those arriving species (LEIBOLD, MATHEW A., 1995). At the same time, interspecific competition excludes less competitive species, and this is called the biotic filter (VELLEND, 2016). Considering the environmental filter framework and incorporating the idea that spatial EH “expand the multiple dimensions of resources and environmental conditions in a region” (HUTCHINSON, 1959), it is predicted that spatial EH will loosen abiotic and biotic filters, allowing greater numbers of species to coexist in the same local (CASWELL; COHEN, 1991).

The effects of spatial EH in the environmental filter framework have been largely investigated, however the interference of human disturbance is rarely considered (YANG *et al.*, 2015). Anthropogenic disturbances interact with those environmental filters, often obscuring the EH-biodiversity relationship (ALLOUCHE *et al.*, 2012; FRISHKOFF *et al.*, 2019; PALMER; MENNINGER; BERNHARDT, 2010) (Figure 5b). Anthropogenic disturbances may reduce regional species pools or prevent some species from colonizing a site (GÁMEZ-VIRUÉS *et al.*, 2015; SUNDERMANN; STOLL; HAASE, 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; MCINTOSH; HARDING, 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 several species (CASTRO, DIEGO; DOLÉDEC; CALLISTO, 2018; OSORIO *et al.*, 2019; SOCOLAR *et al.*, 2016), EH may no longer be an important factor controlling variation in biodiversity, and it may even have a negative effect on some species (ALLOUCHE *et al.*, 2012; STOLL *et al.*, 2016).

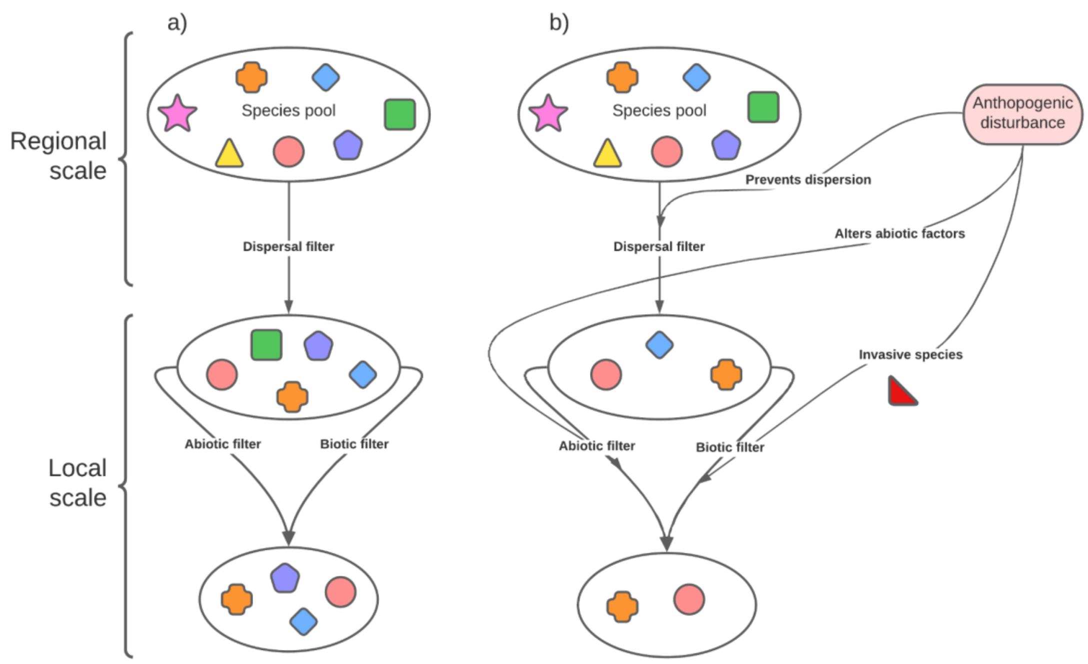

Figure 5: The environmental filter framework to explain the pattern of community structure. a) Without anthropogenic disturbance, a random subset of species in the regional scale can access a local site; and are submitted to biotic and abiotic filters. Only species that pass all filters will structure the local community. b) Anthropogenic disturbance may alter dispersal filter, abiotic and biotic filter, preventing potential species to colonize and survive in the local site. Figure made by the author.

The characteristics of freshwater ecosystems present both challenges and opportunities for understanding the mechanisms governing EH and biological diversity relationship (HEINO, 2013; POFF, 1997). Rivers and streams are among the most biodiverse ecosystems on the planet (REID *et al.*, 2019). However, these ecosystems are on average twice as threatened as terrestrial and marine ecosystems (GROOTEN; ALMOND, 2018). In the Brazilian Cerrado, a biome that encompasses three of the largest hydrographic basins in South America (Amazonian/Tocantins, São Francisco and Prata), the scenario is critical due to the historical suppression of native vegetation and replacement by agricultural areas (DASKALOVA *et al.*, 2020; MACEDO *et al.*, 2018). Forecasts indicate that by the year 2050 there will be a loss of 31-34% of native plant remnants, with these areas representing only 19.8% of the Cerrado (SOARES-FILHO *et al.*, 2016; STRASSBURG *et al.*, 2017). The suppression of native vegetation cover causes cascading effects on freshwater aquatic ecosystems (Allan, 2004), changing the physical structure and chemical dynamics of these ecosystems (e.g., silting and eutrophication) (BINI *et al.*, 2014; SILVA *et al.*, 2018). However, estimates of the consequences of these impacts are still difficult to make, especially among aquatic insects, due to the pronounced lack of information about this biological group in tropical zones (KLINK *et al.*, 2020).

Macroinvertebrates are responsible for an important part of the nutrient cycling that occurs in aquatic ecosystems. They compose the bottom of the food web of several fishes and birds (BOYERO *et al.*, 2012), playing a key role in ecological processes and in providing ecosystem services in rivers, streams and lakes (WALLACE; WEBSTER, 1996). These organisms. In particular, insect larvae of the orders Ephemeroptera, Plecoptera and Trichoptera (EPT) are effective ecological indicators of ecosystem health, as specific taxa respond to environmental stressors differently (FIRMIANO *et al.*, 2017). The use of EPT as ecological indicators have been validated and consolidated along the years (FIRMIANO *et al.*, 2021; LIGEIRO *et al.*, 2013; OLIVEIRA *et al.*, 2011; SILVA *et al.*, 2017). Also they are considered potential tools for temporal analysis of ecosystem health, as they respond more quickly to changes in land use when compared to vertebrates (DASKALOVA *et al.*, 2020).

Considering the lack of studies that explicitly attempt to examine how anthropogenic disturbance affects the relationship between biodiversity and EH in freshwater ecosystems, the second chapter of my thesis aims to assess how different levels of anthropogenic disturbance alter the relationship between EH biodiversity of EPT assemblages in the Neotropical Savanna. I used a model selection approach to test the following 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.

Chapter 1

“...
A água do rio não segue a mesma composição,
a cadência de ontem não é a mesma agora
E nem depois

A água não desassocia do rio,
o rio muda e a água também

Na beira a gente olha
E se a gente vê bem
Até escuta

O rio segue
E a água com sua sutil essência
Segue dando forma
a esse movimento

Esculpindo caminhos e
deixando margens por onde o rio passa,
É que a margem cuida de não deixar o rio só.

Oferece cor e vida pra que o rio não deixe de seguir
Cuidemos das margens,
as de fora e as de dentro.”
(Poema de Mayra Pontes, 2022)

Chapter 1: A global synthesis of the environmental heterogeneity effects on the freshwater biodiversity

Janaina Agra, Tatiana Cornelissen and Marcos Callisto

Abstract

The spatial Environmental Heterogeneity (EH) has been invoked as an important factor to explain biodiversity. It is expected that more spatial EH provides a wider range of resources and conditions for species with different requirements, leading to an increment of biodiversity. However, differences among geographical locations, ecosystem types, taxonomic group, their occurrence zone, and methodological approaches my reveals idiosyncrasy between studies. Thus, we aimed to synthesize the knowledge about the relationship between spatial EH and freshwater biodiversity (i.e., taxonomic and functional diversity, and their respective α and β components). We systematically reviewed 98 studies and presented an ecological synthesis of the role of spatial EH in freshwater ecosystems, regarding terminologies, EH *proxies* and methodological approaches. Through meta-analysis, we demonstrate that spatial EH has a positive effect over taxonomic and functional alpha diversity. Besides, we confirmed that the positive effect of spatial EH over taxonomic alpha diversity is consistent across geographical locations, ecosystem types, taxonomic groups, occurrence zones and between experiments with area controlled vs. not controlled. Nonetheless, there was not enough evidence to robustly estimate the overall effect of spatial EH over taxonomic and functional beta diversity. Further, we discuss the mechanisms addressed to explain spatial EH-biodiversity relationship, and implications for the management, conservation and restoration plans for freshwater ecosystems.

Key-words: Habitat heterogeneity, environmental complexity, functional diversity, beta diversity

1. Introduction

Since the publication of “On birds species diversity” (MACARTHUR, R H; MACARTHUR, 1961), ecologists from different areas have sought to understand the relationship between spatial environmental heterogeneity (EH) and biodiversity (FAGHIHINIA *et al.*, 2021; ORTEGA; THOMAZ; BINI, 2018). Heterogeneity encompasses several components and concepts (KOLASA; ROLLO, 1991) and spatial EH can be defined as any measurement of variation of abiotic factors between two or more locations within a region (HEINO; MELO; BINI, 2015). More heterogeneous environments present a larger range of food resources, refuge and a variety of environmental conditions for species with different requirements (MACARTHUR, R H; MACARTHUR, 1961). Thus, the main mechanism evocated from past to nowadays is that a greater environmental heterogeneity increases the co-existence of a greater number of species with different ecological niches in a given region, increasing therefore biodiversity (CARDINALE, 2011; CASWELL; COHEN, 1991; HUTCHINSON, 1959; WILLIS; WINEMILLER; LOPEZ-FERNANDEZ, 2005).

In freshwater ecosystems, spatial EH has been assessed through the measurement of several environmental factors such as water flow, channel morphology, bottom substrate composition and by the presence or the architecture of some structures (e.g., macrophytes, wood debris) (TOKESHI; ARAKAKI, 2012). The evidence of a positive relationship between spatial EH and species richness is well documented and, more recently, responses of multiple facets of biodiversity (i.e., taxonomic diversity, functional diversity, and the beta diversity component) have been investigated (AGRA *et al.*, 2021; LI, ZHENGFEI *et al.*, 2019; MILESI; DOLÉDEC; MELO, 2016). However, opposite or non-significant results have shown that this ecological pattern may not be universal (BOYERO; BOSCH, 2004; KÄRNÄ *et al.*, 2018; PALMER; MENNINGER; BERNHARDT, 2010) and the spatial EH – biodiversity relationship may depend on other factors such as spatial scale, biotic interactions (i.e., the strength of competition and predation) and gradients of disturbance (AGRA *et al.*, 2021; HEINO; MELO; BINI, 2015; YANG *et al.*, 2015).

The wide variety of methods used to manipulate EH *proxies* and test the effect of spatial EH may also explain idiosyncrasies in the results (STEIN; KREFT, 2015), because the way species perceive spatial EH is intrinsically associated with its ecological niche (CASWELL; COHEN, 1991). For instance, species that inhabits a river bottom responds to substrate heterogeneity (EH *proxy*) differently from a species that uses the water column (LUCENA-MOYA; DUGGAN, 2011; SCHNEIDER, KRISTAL N.; WINEMILLER, 2008). Thus, researchers employ different EH *proxies* and methodological approaches according to the taxonomic group investigated and aiming to capture the ecological meaning of the spatial EH on biodiversity (CASWELL; COHEN, 1991). Besides, several experiments do not control for the effects of area when spatial EH is increased, making it difficult to distinguish the effect of an increment of EH *per se* from the mere effects of increased area (ALLOUCHE *et al.*, 2012; THOMAZ *et al.*, 2008). Furthermore, a misuse of terminologies and concepts to describe spatial EH limits comparisons between studies, hampering generalizations and general implications of the effects of spatial EH over biological communities (CUNHA *et al.*, 2012; STEIN; KREFT, 2015).

Systematic reviews and meta-analysis emerged as fundamental tools to summarize research evidence and to seek for sources of variation in overall effects (GUREVITCH *et al.*, 2018) and may be particularly useful to evaluate the effects of spatial EH on species biodiversity. For terrestrial communities, a few reviews on EH-biodiversity have already synthesized concepts and methodologies (see TEWS *et al*., 2004, ALLOUCHE *et al*., 2012, STEIN and KREFT 2015), and meta-analyses have quantified the overall effect of spatial EH over species richness (see STEIN *et al*., 2014, ORTEGA *et al*., 2018). However, only one study has tested the effects of spatial EH on species richness (i.e., ORTEGA *et al*., 2018), including experimental or quasi-experimental studies carried out in both aquatic and terrestrial communities. Another caveat left by these studies is the focus on species richness only, and multiple facets of biological diversity (i.e., taxonomic and functional alpha and beta diversity) have been overlooked. We suggest the evaluation of these multiple components of biodiversity might aid to guide new approaches to unravel ecological mechanisms underlying spatial EH – biodiversity and the consequences on ecosystem functioning in a scenario of global change (HEINO; MELO; BINI, 2015; MOUILLOT *et al.*, 2013; ORTEGA; THOMAZ; BINI, 2018).

We synthesized the current status of knowledge regarding the study of spatial EH in freshwater ecosystems, elucidating a) how spatial EH is assessed across geographical locations, freshwater ecosystem types, taxonomic groups and their occurrence zone; b) which mechanisms are invoked to investigate the spatial EH-biodiversity relationship; and c) which environmental variables are used as *proxy* of spatial EH, as well as the methodological approach and calculation methods to manipulate and measure spatial EH in freshwater ecosystems. Using meta-analysis, we also aimed to d) estimate the magnitude of the overall effect of spatial EH over multiple facets of freshwater biodiversity (i.e., taxonomic and functional alpha and beta diversity); and e) test whether there is significant variation in the overall effect of spatial EH on taxonomic alpha diversity moderated by location (tropical vs. temperate); Ecosystem type (lotic vs. lentic ecosystems); Taxonomy (biological groups); occurrence zones (benthos, nekton, plankton and in the riparian meta-ecosystem); and experimental design (controlled or not for area). Based on the hypothesis that the increasing of spatial EH expands the partition of the ecological niche (HUTCHINSON, 1959; MACARTHUR, R H; MACARTHUR, 1961), we predict that the relationship of EH will be positive for taxonomic and functional alpha diversity. We did not predict beta components response, as it depends on the spatial scale design in each study (HEINO; MELO; BINI, 2015). Also, we expect that the strength of the spatial EH over taxonomic alpha diversity will be higher in experiments that did not control for surface area, because this factor is already known to increase resources for a greater number of species (MACARTHUR, ROBERT H; WILSON, 1967).

2. Methods

Data collection

We searched for studies that investigated the effect of EH over any metric of biological diversity (e.g., richness, taxonomic diversity indexes, functional diversity, or beta diversity). We applied three different approaches of data searching, aiming to detect as many studies as possible and, consequently, avoiding data bias (KORICHEVA; GUREVITCH; MENGERSEN, 2013). The first approach consisted of searching for terms in the three search engines ISI Web of Science, Scopus and Scielo, from 1945 to 2020. We used 46 terms that are frequently used to refer to EH (e.g., "habitat* heterogen*" OR "habitat* diversity" OR "habitat* complexity" OR "structural complexity" OR “fractal heterogen*” OR "biotop* heterogen*" OR "environment* complexity") (see complete syntax in Supplementary Material 1). The second approach consisted of a general search for studies on the Google Scholar webpage, using the four most used terms to refer to EH according to a previous study (see STEIN et al. 2015) (Supplementary Material 1). In this case we stablished a maximum of 600 articles to screen. The third approach consisted to search onto the references of previous reviews and opinion articles that included freshwater ecosystems in the central theme (i.e., CUNHA *et al*., 2012; KOVALENKO *et al*., 2012; ORTEGA *et al*., 2018; PALMER *et al*., 2010; TOKESHI and ARAKAKI 2012).

After duplicate exclusion we obtained 2,381 studies. Following PRISMA steps (Supplementary Material 2). To elect studies we considered the following criteria: (1) encompassed freshwater ecosystems and its associated organisms; (2) were either observational or experimental or both; (3) considered only spatial EH (temporal EH was not included); (4) explicitly investigated the relationship between EH and any biological metric of taxonomic and functional diversity; (5) were published in a peer reviewed journal. After the exclusion of 2,176 studies in the title and abstract screening stage, a total of 205 studies were fully read. After this second screening, we elected 98 studies to be included in our systematic review (Supplementary Material 3).

Because we aimed to test the overall effect size of EH over multiple facets of freshwater biodiversity, we conducted a second step of selection to elect studies suitable for a meta-analysis. Studies that did not provide any measurement of the effect of EH over a biological diversity metric or had fewer than five replicates were excluded (KORICHEVA; GUREVITCH; MENGERSEN, 2013). Also, studies that only informed results from multiple regressions, partial correlations and multivariate analysis were not included, because it was not possible to extract the single effect of EH over the biological metric. At the end, 74 studies were elected for a meta-analysis.

Qualitative data extraction

To conduct our systematic review we extracted information from the 98 studies about: 1) geographical location; 2) type of freshwater ecosystem; 3) study type (i.e., observational or experimental); 4) most cited term in the title and/or abstract to indicate EH (e.g., “habitat heterogeneity”, “environmental complexity”); 5) environmental variables used as *proxy* of EH (e.g., substrate, flow velocity); 6) methodological approaches to manipulated EH *proxies* (e.g., qualitative variation, roughness); 7) calculation methods to measure EH (e.g., indices, coefficient of variation); 8) biological group evaluated; 9) zone of communities’ occurrence (i.e., nekton, plankton, benthos or in the riparian meta-ecosystem); 10) type of biological metric considered as response variable (i.e., functional or taxonomic, and alpha or beta), 11) if experimental design controlled for the effect of surface area, and 12) the mechanisms invoked by authors to discuss patterns or used to test the relationship between EH and the biological metric response. We only considered the mechanisms that were explicitly cited by authors. Occasionally, studies encompassed more than one taxonomic group, at different occurrence zones, with different EH *proxies*, and using different methodological approaches and calculation methods. We incorporated this information in separate outcomes from the same study, which generated 276 comparisons.

EH *proxy* denotes the element that authors actually quantified in the ecosystem aiming to evaluate the effect of EH over biological metrics of diversity. During data extraction we identified several EH *proxies* used by authors, which was categorized into 12 categories: aquatic vegetation; artificial substrates; natural substrates; channel morphology; elevation; food resources; land cover; riparian vegetation; water flow; water chemistry; wood debris; and mixed. The mixed category included studies that used more than one category of *proxy* to manipulate EH in the experiments (Figure 6).

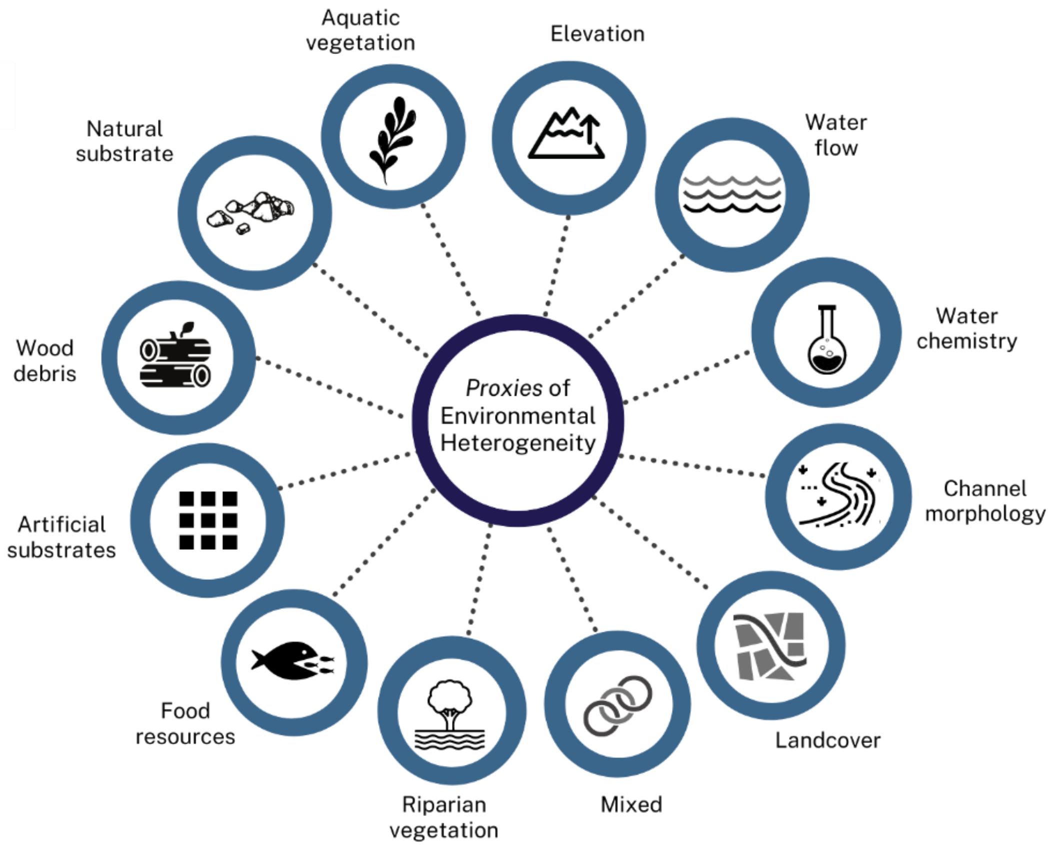

Figure 6: Categories of Environmental Heterogeneity (EH) *proxies* used to evaluate the effect of EH over biological metrics of diversity.

The methodological approach denotes the way authors manipulated the EH *proxies* to create EH gradients or EH levels, aiming to test the effect of spatial EH on a biological metric. In the same way, we created eight categories of methodological approach: density; mixed; presence vs. absence; qualitative variation; quantitative variation; roughness; structure; and size variation. For each category we present a conceptual definition and show some examples of the most frequent calculation methods to measure spatial EH *proxies* (Table 1).

Table 1. Glossary of methodological approaches to investigate spatial environmental heterogeneity, with its respective concepts, synonyms, and examples of calculation methods of measurement. Graphical abstract presents symbols with different shapes to represent distinct *proxies*, while different colors represent variations within the same *proxy*.

Methodological Approach	**Concept**	**Examples**	**Graphical Abstract** Homogeneous vs Heterogeneous
Size variation or size composition	Manipulation of particle sizes from an environmental proxy	Substrates with the same particle size vs substrate with different particles sizes; Standard deviation of particle size	
Structure or shape, fractal, architecture	Manipulation of the physical structure of an environmental proxy	Macrophytes with simple-shaped leaves vs intricately-shaped leaves	
Roughness or surface, topography, texture	Manipulation of the roughness of an environmental proxy	Smooth surface of a substrate vs grooved surface; Rugosity index	
Density or abundance	Manipulation of the density or abundance of an environmental proxy at a location	Number of macrophytes per area; Counting of large wood debris in a location	
Presence vs absence	Manipulation of addition or exclusion of an environmental proxy at a location	The presence of artificial substrates vs the lack of artificial substrates	
Qualitative variation or patchiness, ompositional variation	Manipulation of different qualities of the same environmental proxy	Richness of substrate types; Shannon diversity of water flow types	
Continuous variation	Manipulation of a environmental proxy which is continuous	Coeficient of variation of water flow velocity; Standard deviation of a river discharge	
Mixed	Manipulation different types of environmental proxies , including different types of the same proxy	Shannon diversity of different environmental proxies A PCA1 axis of several environmental proxies	

Quantitative data extraction

For meta-analysis, we used 74 studies that reported statistical results (e.g., correlation coefficient, mean and deviation values between treatments), variance and sample size which estimated the relationship between EH and any biological metric. With this information we calculated the individual effect size of each experiment or observation. When authors reported results in figures, we extracted information through the software Image J® (SCHNEIDER, CAROLINE A; RASBAND; ELICEIRI, 2012). When effects were not provided in the text, table, or figures, we obtained statistical results from the corresponding author.

From the 74 studies, we recorded 242 individual effect sizes. We separated effect sizes into four distinct categories according to the type of biological metric considered as the response variable: taxonomic alpha, taxonomic beta, functional alpha and functional beta (Supplementary Material 4). Among them, 200 refers to the effect size on taxonomic alpha, 20 on taxonomic beta, 16 on functional alpha and six on functional beta diversity.

Statistical analysis

To run meta-analysis and estimate the magnitude of the overall effect of EH on taxonomic alpha and beta diversity, we used the Fisher's *z* value as the measure of effect size. All statistical results provided by the authors were converted to the correlation coefficient (r), which was used to derive z by the formula: $z = 0.5 \text{ x } \ln[(1 + r)/(1 - r)]$ (KORICHEVA; GUREVITCH; MENGERSEN, 2013). For each z value, we calculate its respective variance (v_z) based on the sample size (n) of the test performed in the study: $v_z = 1/(n - 3)$ (KORICHEVA; GUREVITCH; MENGERSEN, 2013). Based on z variance and sample size, we calculated the 95% confidence intervals around each z value. Negative values of z represent a negative effect of the EH over the biological metric whereas positive z values represent a positive effect, and $z = 0$ represents no effect. If confidence intervals did not overlap zero, the estimate of the true effect size is considered significant.

Because many studies reported multiple effects sizes, we carried out a hierarchical meta-analysis that allowed us to take into account the dependence of multiple effect sizes within the same study (KORICHEVA; GUREVITCH; MENGERSEN, 2013). First, we runed random-effects meta-analysis models to calculate the overall mean effect size of EH on taxonomic alpha diversity (n = 200), on taxonomic beta diversity (n = 20), on functional alpha diversity (n = 16) and on functional beta diversity (n = 6). Second, we carried out random-effects meta-analysis models that incorporated moderators to investigate variations on the overall mean effect size of EH on taxonomic alpha diversity. It was not possible to incorporate moderators in other random-effects meta-analysis models (i.e., beta taxonomic, alpha functional and beta functional) because of the low sample size. We considered variation between geographical locations (tropical vs. temperate), ecosystem types (lentic vs. lotic), zone of communities' occurrence (i.e., nekton, plankton, benthos or in the riparian meta-ecosystem), taxonomic groups (i.e., algae, amphibian, birds, fish, macroinvertebrates and microfauna) and experimental design (controlled vs. not controlled for area). Since experiments in mesocosmos generated only six effect sizes, we did not include this class in the analysis with moderators of ecosystem types to avoid imprecision (KORICHEVA; GUREVITCH; MENGERSEN, 2013). The heterogeneity among categories of moderators were examined through p-values of Q statistics, which are weighted sums of squares tested against a χ^2 distribution (HEDGES; OLKIN, 2014). All analyses were run with the statistical software R (R Core Team 2016), using the "metafor" package (VIECHTBAUER, 2010).

Publication bias analysis

There is widespread evidence that studies are more likely to be published if their results are statistically significant, or confirm the initial hypothesis (MØLLERAND; JENNIONS, 2001). Thus, we analyzed publication biases for each random-effect model that was run to estimate the overall mean effect size. For this, we used two approaches: 1) visual inspections for a pattern of asymmetry in a funnel plot. When asymmetry was not explicit, we run a regression Egger's test (EGGER *et al.*, 1997); 2) calculation of the Rosenthal fail-safe number, which indicates the hypothetical number of missing unpublished evidence averaging a z-value of zero that, if added, would change our results from significant to non-significant effect (ROSENTHAL, 1979). Fail-safe numbers higher than 5n + 10 (n = number of independent comparisons), indicate that results are robust despite publication bias.

3. Results

Systematic Review

The 98 studies encompassed 33 countries, across all continents, except Antarctica (Figure 7). Studies carried out in the Palearctic region were the most frequent (32), followed by the Neotropical (29), Nearctic (19), Indomalaya (7), Australasia (6), and Afrotropical (4) regions. The first study that investigated the relationship between EH and freshwater diversity was conducted in the United States of America (see Allan 1975). Since then, the topic has been increasingly studied (Figure 8). The journals with the highest representation in our dataset are *Hydrobiologia* (18), *Freshwater Biology* (11), *Oecologia* (7) and *Oikos* (5).

Studies in lotic ecosystems (e.g., river, creek, stream) were more frequent (56), followed by lentic ecosystems (e.g., lake, pond, reservoir) (38), and in artificial structures such as mesocosms (4). There were more observational studies (69) than experimental ones (29).

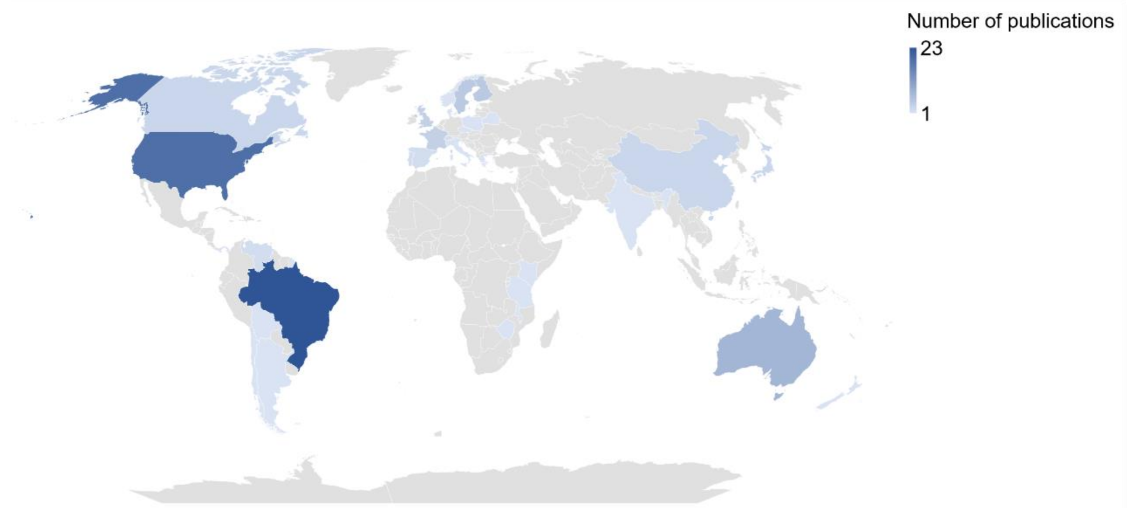

Figure 7: Geographic location of 98 studies that investigated the relationship between EH and freshwater biological diversity

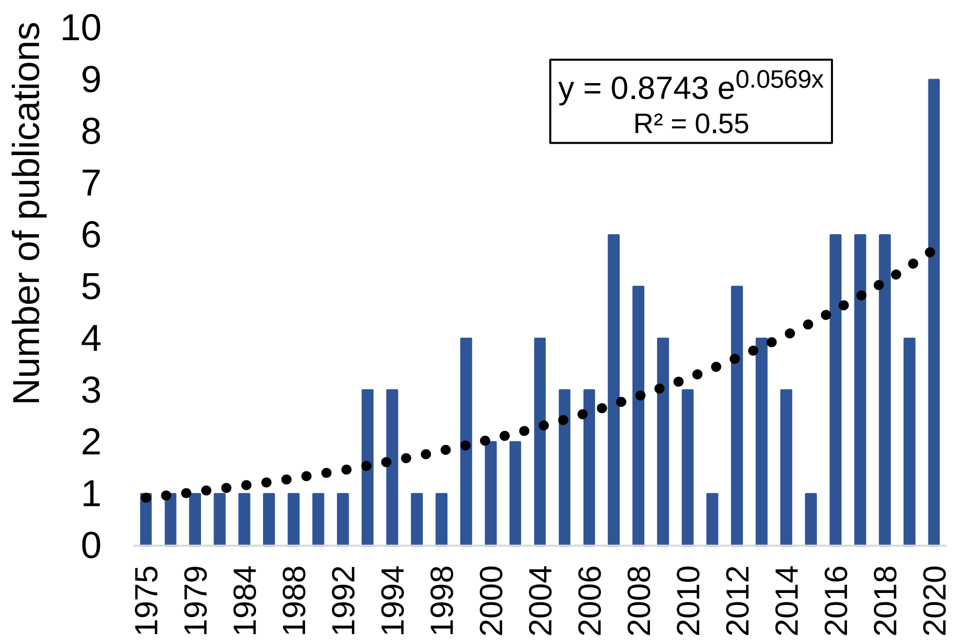

Figure 8: Number of published studies that investigated the relationship between environmental heterogeneity and freshwater biodiversity per year, from 1975 to 2020.

We identified 28 different terms to refer to the concept of spatial environmental heterogeneity in freshwater ecosystems, and 21 of them appeared only once in our dataset (Figure 9). Also, we observed some level of inconsistency in the use of terms within each study, because 42 % applied more than one term to refer to the spatial environmental heterogeneity along the text. The most used terms among all studies were “habitat complexity” (22), “habitat diversity” (14), “habitat heterogeneity” (12), “structural complexity” (9) and “environmental heterogeneity” (8).

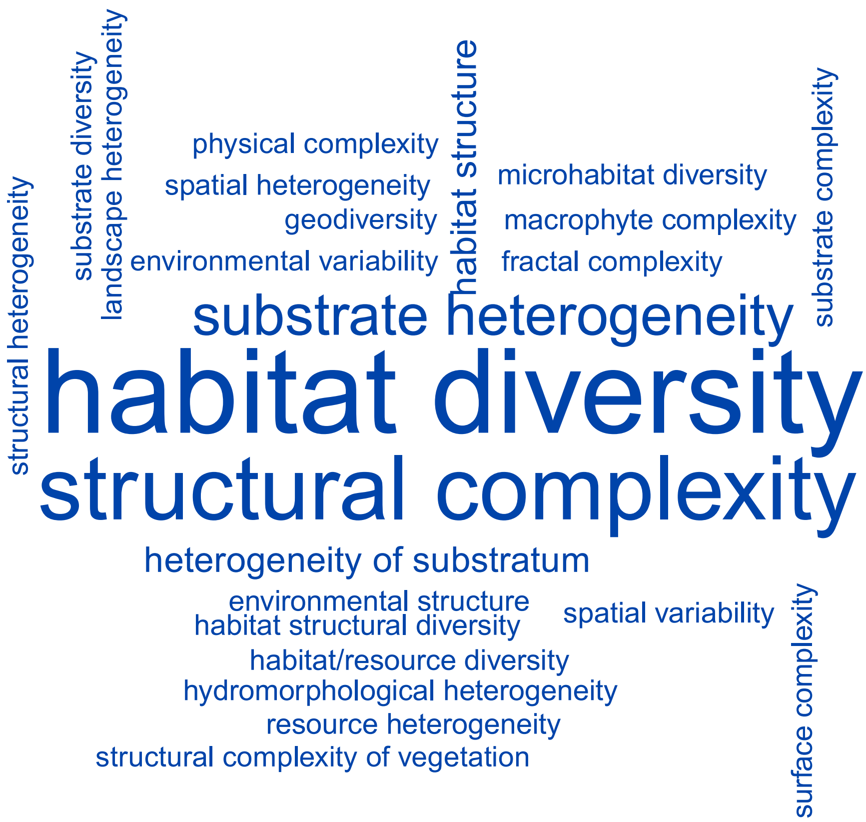

Figure 9: Wordle of terms used by authors that indicate measurements of environmental heterogeneity. Font size is proportional to the number of studies using each term in our database.

Most studies (71) did not explicitly invoke any mechanism to explain the relationship between spatial EH and the biological metric used in the discussion of results (Figure 10). Only 16 studies discussed possible mechanisms to explain the effect of EH, while 11 studies effectively predicted and tested mechanisms (i.e., niche partitioning, habitat resource, food resource, environmental resource, refuge and area increment).

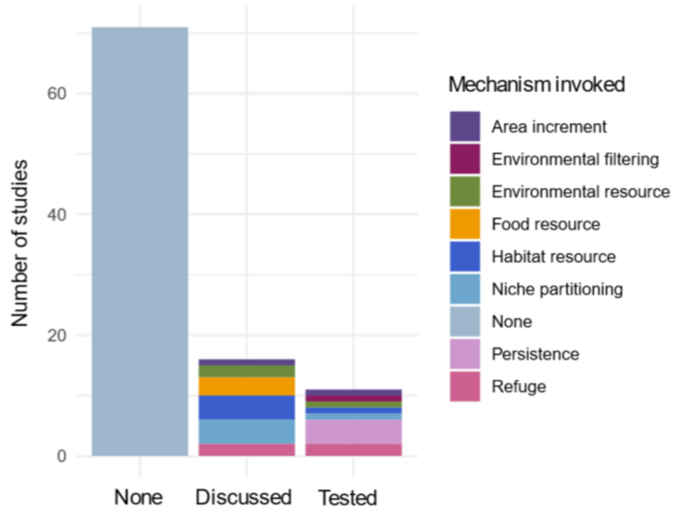

Figure 10: Number of studies by categories of mechanisms invoked to explain the relationship between spatial EH and the biological metric of response.

Authors manipulated several EH *proxies* to evaluate the effect of EH on biological metrics. Categories of EH proxies in order of frequency are: artificial substrates (54), natural substrate (53), aquatic vegetation (52), mixed (39), wood debris (18), channel morphology (18), land cover (17), water flow (14), elevation (4), riparian vegetation (4), water chemistry (2) and food resources (1). Categories of methodological approach in order of frequency are: qualitative variation (74), structure (65), mixed (45), roughness (25), presence vs. absence (25), size variation (21), density (13), and continuous variations (8).

The relationship between EH and biological diversity has been investigated mainly in macroinvertebrate (141) and fish (73) communities, and to a lesser extent in waterfowl (27), algae (13), microfauna (12) and amphibians (10). Concerning the aquatic zonation, studies investigated benthic (157), nektonic (77) and planktonic (9) communities, as well as communities that inhabit the riparian meta-ecosystem (e.g., waterfowl, frogs) (33).

Studies with macroinvertebrates and fishes were the ones that most used different types of EH proxies (Figure 11.a). Most studies that accessed the response of macroinvertebrates to spatial EH increment manipulated natural substrates (26%) and mixed environmental variables (11%). To evaluate the response of fishes, authors mostly used artificial substrates (25%), mixed elements (21%), and aquatic vegetation (18%). For waterfowl, most studies analyzed aquatic vegetation as a *proxy* for EH (85%). Artificial substrates were the most frequent EH *proxy* to assess the response of algae (61 %) and microfauna (67 %). Studies with amphibians used more mixed environmental variables (40%) and aquatic vegetation (30%).

To manipulate the spatial EH proxies, different methodological approaches were used (Figure 11.b). To increase heterogeneity in artificial substrates, most studies manipulated the structure (61%) or roughness (20%) of the substrate. Among the methodological approaches used to manipulate natural substrates, measures that considered qualitative variations (45%), size variations (27%) and roughness (18%) were the most frequent. In studies that used aquatic vegetation as a *proxy* of spatial EH, the methodological approach of qualitative variation was the most frequent (46%). For woody debris experiments, the "presence and absence" approach was the most used (66%).

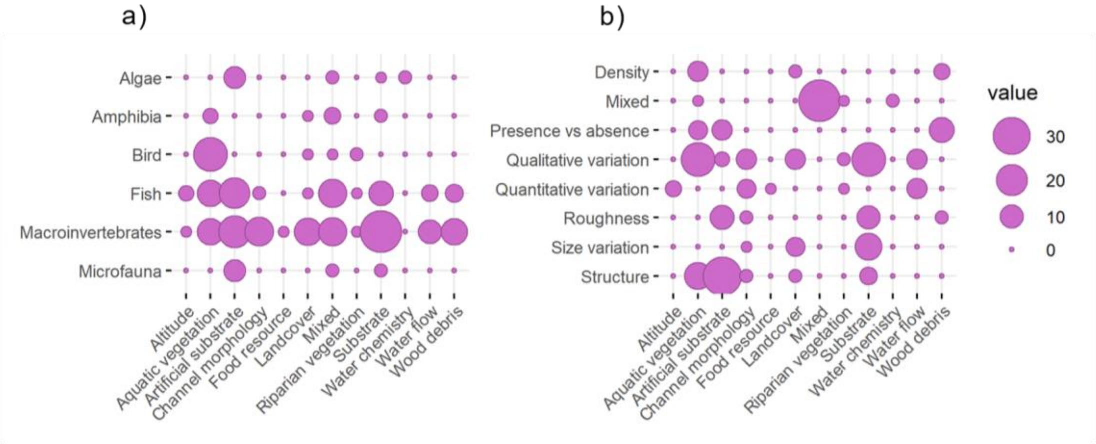

Figure 11: a) Relationship between categories of environmental heterogeneity proxies and biological groups in studies that evaluated the increase in environmental heterogeneity and freshwater biodiversity; b) Relationship between categories of environmental heterogeneity proxies and methodological approaches in studies that evaluated the increase in environmental heterogeneity and freshwater biodiversity. Bubble size is proportional to the number of observations in each study.

Meta-analysis

Overall, the spatial EH had a positive effect on taxonomic alpha diversity (z = 0.46, 95 % CI = 0.34 to 0.57, n = 200, Q_{199} = 1102,5, p-value < 0,0001) and functional alpha diversity (z = 0.54, 95 % CI = 0.23 to 0.85, n = 16, Q_{15} = 67,7, p-value < 0,0001). Also, spatial EH presented a positive effect on taxonomic beta diversity (z = 0.53, 95 % CI = 0.06 to 1.01, n = 20, Q_{19} = 232,8, p-value < 0,0001), but we did not observed effects on functional beta diversity (z = 0.39, 95 % CI = - 0.09 to 0.88, n = 6, Q_5 = 16,2, p-value = 0.0063) (Figure 12).

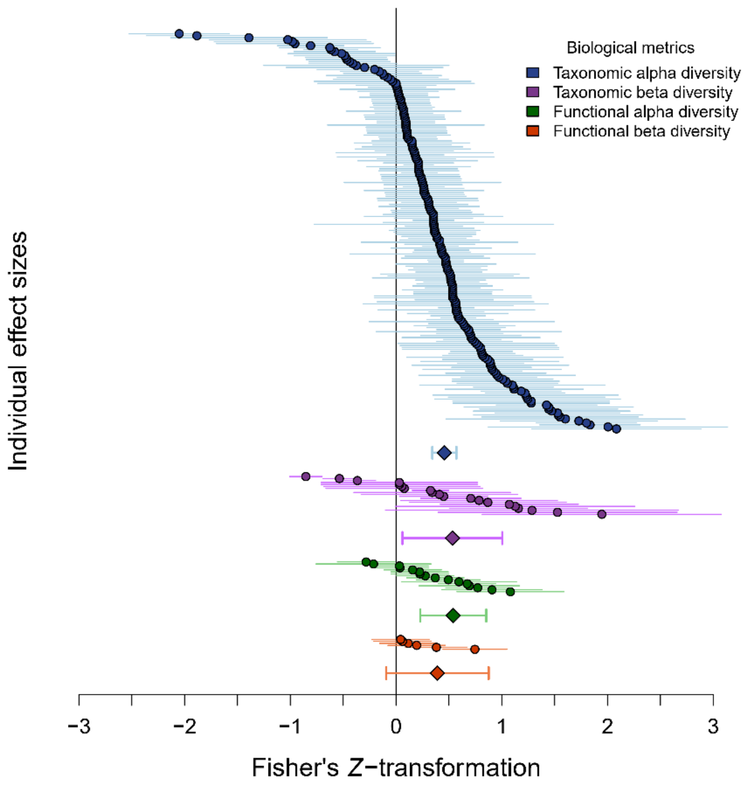

Figure 12: Forest plot showing effect size estimates of spatial EH effect over taxonomic alpha diversity (n = 200), taxonomic beta diversity (n = 20), functional alpha diversity (n = 16) and functional beta diversity (n = 6). Full dots are mean effect sizes with respective 95 % confidence intervals for each individual outcome. Diamonds and their respective lines represent the overall mean effect size estimate with its 95% CI for each biological metric.

The positive effect of spatial EH over taxonomic alpha diversity did not differ between tropical (z = 0.47, 95 % CI = 0.24 to 0.71) and temperate zones (z = 0.47, 95 % CI = 0.33 to 0.60) (Fig. 13.a). Also, there was no difference of spatial EH over taxonomic alpha diversity between lotic (z = 0.44, 95 % CI = 0.27 to 0.60) and lentic ecosystems (z = 0.53, 95 % CI = 0.35 to 0.71) (Fig. 13.b). Between experiments that controlled area (z = 0.50, 95 % CI = 0.27 to 0.74) and those that did not control area (z = 0.46, 95 % CI = 0.32 to 0.59), no difference was observed for the effect of spatial EH over taxonomic alpha diversity (Fig. 13.c).

The effect of spatial EH over taxonomic alpha diversity did not differ among those communities that live in the riparian meta-ecosystem (z = 0.51, 95 % CI = 0.18 to 0.85), the benthic zone (z = 0.50, 95 % CI = 0.34 to 0.66) and the nektonic zone (z = 0.45, 95 % CI = 0.25 to 0.66). There was no general effect of spatial EH over taxonomic alpha diversity of communities from the planktonic zone (z = - 0.21, 95 % CI = - 0.80 to 0.39) (Fig 13.d). There was a positive effect of spatial EH over taxonomic alpha diversity for amphibians (z = 0.67, 95 % CI = 0.15 to 1.19), macroinvertebrates (z = 0.49, 95 % CI = 0.32 to 0.67), birds (z = 0.49, 95 % CI = 0.10 to 0.89) and fish (z = 0.43, 95 % CI = 0.22 to 0.64), and this effect did not differ between these groups. Nonetheless, there was no general effect of spatial EH over the taxonomic alpha diversity of algae (z = 0.16, 95 % CI = - 0.53 to 0.84) and microfauna (z = 0.49, 95 % CI = -0.01 to 0.97) (Fig. 13.e).

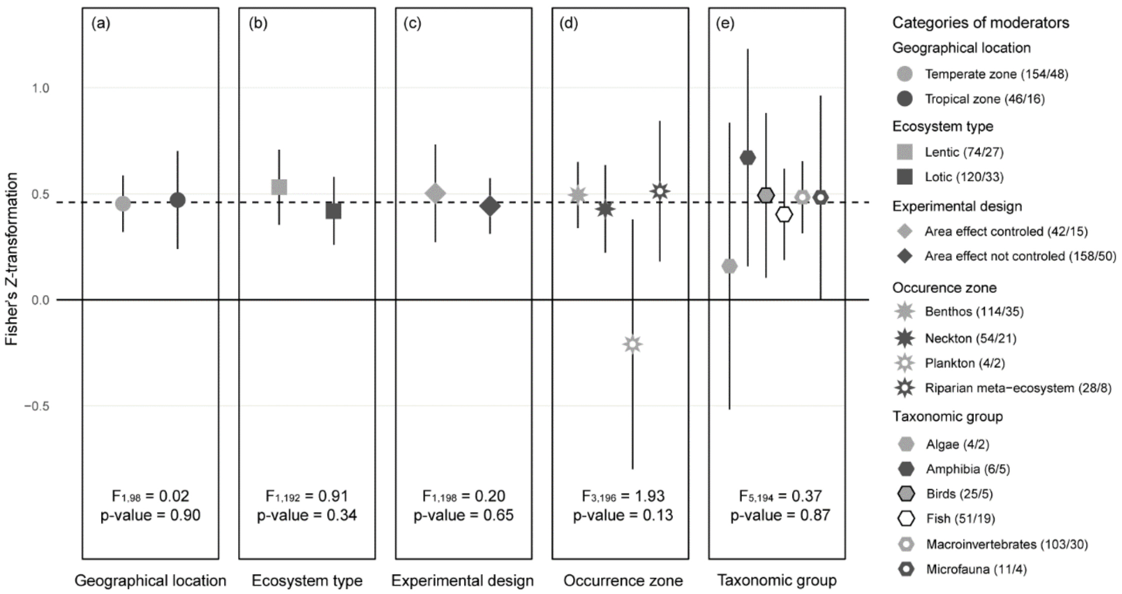

Figure 13: Mean effect size estimates over taxonomic alpha diversity, considering the following moderators: a) geographical location, b) ecosystem type, c) for experimental design controlled for the effect of surface area, d) occurrence zone, and e) taxonomic group. Full dots are mean effect sizes with respective 95 % confidence intervals for each category of moderator. Dashed line represents the overall mean effect size of spatial EH over taxonomic alpha diversity (Fisher's Z = 0.46). Numbers in parentheses give the respective numbers of outcomes/studies; note that one study can include multiple geographical locations, ecosystem types and experimental designs.

Publication bias

Funnel plots showed asymmetry of the residuals of the general random-effects meta-analysis models of taxonomic beta diversity and for functional alpha and beta diversity (Supplementary Material 5). Because the funnel plot of the taxonomic alpha diversity model was not explicit, we ran an Egger's regression, which confirmed publication bias (Intercept = 0.089, 95 % CI: - 0.1026, 0.2810, p = 0.001).

We observed that the overall effect of EH over taxonomic and functional alpha diversity were robust through the fail-safe numbers. For these biological metrics, it would be necessary to include 46,841 and 380 effects sizes averaging a z-value of zero respectively, to make the combined effect size nonsignificant. Nonetheless, more studies are needed to robustly describe the overall effect of spatial EH on the facets of taxonomic beta diversity (fail-safe number = 20) and functional beta diversity (fail-safe number = 34).

4. Discussion

Through a systematic review of 98 studies, we mapped a wide range of terminologies and methodological approaches to investigate the effects of spatial EH over freshwater biodiversity. Our meta-analytical approach confirmed our first prediction of a positive effect of spatial EH over taxonomic and functional alpha diversity. More specifically, we demonstrated that the positive effect of spatial EH over taxonomic alpha diversity is consistent across geographical zones, ecosystem types, taxonomic groups, occurrence zones and between experimental designs (area controlled vs. not controlled). Nonetheless, there was not enough evidence to robustly estimate the overall effect of spatial EH over taxonomic and functional beta diversity. Next, we discuss a synthesis of terminology and methodological approaches to investigate the effects of the spatial EH over freshwater biodiversity, the general ecological patterns, and mechanisms addressed to explain those ecological patterns. Additionally, we present implications for the management, conservation and restoration plans for freshwater ecosystems.

Synthesis of terms and methods

We considered spatial "Environmental Heterogeneity" any measurement of variation in environmental conditions and resources between locations in the same region, and we identified 28 distinct terms associated with this concept. The same was done by Stein and Kreft (2015), who covered studies on terrestrial ecosystems, and found 2.2 times more terms associated with spatial EH. Besides, 42% of authors applied interchangeable terms as synonyms within the same study, generating inconsistencies and misleading spatial EH concepts. Interestingly, those inconsistencies are common in ecological studies. For example, there are several efforts to gather and synthetize ecological concepts of terms around functional ecology, beta diversity, ecological invasions and metacommunity (BASTOS-PEREIRA *et al.*, 2022; FALK-PETERSEN; BØHN; SANDLUND, 2006; LEIBOLD, M. A. *et al.*, 2004; TUOMISTO, 2010). In this review, we systematically collect and present a set of terms associated with the most used methodological approaches and link these methods to spatial EH proxies and taxonomic groups, providing a more comprehensive framework for future research on the topic (see Table 1).

The "habitat complexity", "habitat heterogeneity", "habitat diversity", "structural complexity" were, in fact, the most frequent terms associated with the concept of "environmental heterogeneity". Nonetheless, we emphasize that these terms are restricted to just one aspect of heterogeneity, such as the availability of resources (e.g., habitat heterogeneity) or their spatial arrangement (e.g., habitat complexity). Therefore, we support the idea that the term "Environmental Heterogeneity" remains as an umbrella that encompasses any condition and/or resources that vary spatially and may affect the community composition in a region (STEIN; KREFT, 2015). Still, wherever possible we encourage authors to stick with one single term with a clear conceptualization. In the methods section we suggest authors should explain which methodological approach was used to manipulate heterogeneity aiming therefore to have a concept that is transparent, a method that is replicable, and results that are comparable among studies.

The variety of methodological approaches access different features of the spatial EH (e.g., interstitial space, surface convolution, spatial arrangement of elements) and has played an important role in advancing the spatial EH concept (CUNHA *et al.*, 2012). We separated methodological approaches into eight categories, according to the way authors manipulated environmental elements to create differences of heterogeneity between control and treatment groups or gradients of spatial EH. Historically, the most used approach comprise the manipulation of a single environmental element, such as the qualitative variation approach (27%), mainly using different types of aquatic vegetation or substrates (BOYERO; BOSCH, 2004; GUADAGNIN; MALTCHIK; FONSECA, 2009), and the structure approach (20%), mainly manipulating the structure of artificial substrates and aquatic plants (BENSON; MAGNUSON, 1992; OSORIO *et al.*, 2019). Third, the mixed approach has been increasingly used in ecological studies (16%), in which the authors bring a more holistic view, including multiple elements to evaluate spatial EH (e.g., water quality, substrate, riparian cover, channel morphology) (ARUNACHALAM, 2000; KÄRNÄ *et al.*, 2018). Regardless of how the methodological approach is conducted, we highlight that the calculation methods of the spatial EH can affect the detection of the statistical relationship between the spatial EH and the biological metric (AGRA *et al.*, 2021; KÄRNÄ *et al.*, 2018). Therefore, we argue that experiments should consider different elements of the environment. Preferably, measurements should be continuous (e.g., centroid distance, coefficient of variation, standard deviation or EH indexes), since comparisons by categories (e.g., low complexity vs high complexity) do not always show concordance with the perception of organisms (SHUMWAY; HOFMANN; DOBBERFUHL, 2007). Besides, continuous measurements provide an understanding of the effects of spatial EH along an environmental continuum, given tools for modeling predictions in scenarios of spatial EH loss.

The spatial EH – biodiversity relationship

Our estimation of the overall effect of spatial EH over taxonomic alpha diversity is in line with previous meta-analysis carried out by Stein et al. (2014), which encompassed studies in terrestrial ecosystems, and by Ortega et al. (2018), whose surveyed experimental and quasi-experimental studies in all realms (marine, freshwater and terrestrial). Furthermore, we showed that the positive effect of spatial EH extends to the functional alpha diversity. Through the evaluation of functional alpha diversity we bring out an insight that spatial EH is contributing not only to the persistence of different species, but is indeed governing niche partitioning processes, as the functional component of biodiversity reflects how different are species requirements (LI, ZHENGFEI *et al.*, 2019; WILLIS; WINEMILLER; LOPEZ-FERNANDEZ, 2005). However, we emphasize that the understanding of the spatial EH over the functional facet of diversity is just in the beginning. Given the high heterogeneity among studies in community ecology, the low number of publications that considered the functional alpha diversity facet (n = 16) exposes the fragility of the overall effect size estimate (KORICHEVA; GUREVITCH; MENGERSEN, 2013).

The positive spatial EH – taxonomic alpha diversity relationship is consistent and independent of geographic zones (temperate or tropical), ecosystem types (lotic or lentic), and between experimental designs that control or not for the surface area. Our expectation that the strength of the relationship between spatial EH and taxonomic alpha diversity would be higher in experiments that did not control the surface area was not confirmed. This result suggests that there is an interaction between area and the spatial EH (BÁLDI, 2008; TRIANTIS *et al.*, 2003), where the increasing of spatial EH plays a fundamental role over niche partitioning while area may affect species diversity through the events of immigration and extinction (MACARTHUR, ROBERT H; WILSON, 1967; UDY *et al.*, 2021). Thus, both drivers should be considered in biological community modeling (TRIANTIS *et al.*, 2003). Regarding taxonomic groups, the spatial EH effect over taxonomic alpha diversity is positive and did not differ between macroinvertebrates, fish, birds, and amphibians. However, the overall effect of spatial over microfauna and algae did not differ from zero. The same was observed in planktonic communities, while a positive effect was observed for communities that inhabit benthonic, nektonic and the meta-ecosystem zone. The low number of evidence for the microfauna, algae and planktonic categories (n = 4, 3 and 2, respectively) may account for the lack of statistical significance. But difficulties associated with manipulating the spatial EH to make them ecologically significant for organisms are also under discussion, especially for small size organisms (CASWELL; COHEN, 1991).

According to the fail-safe number analysis, we could not robustly test our second prediction, concerning the relationship between spatial EH over taxonomic and functional beta diversity. Thus, we highlight the literature gap related to these ecological patterns. Furthermore, studies involving beta diversity have an additional difficulty on pattern definitions, because beta diversity is strongly dependent on a dispersal-environmental control model (HEINO; MELO; BINI, 2015). When the region scale extent is small, the mass effect can mask species sorting (AGRA *et al.*, 2021; HEINO; GRÖNROOS, 2013), whereas on a large scale, dispersion limitation can hamper the interpretation of processes that would lead beta diversity along environmental gradients (BINI *et al.*, 2014; CASTRO, DIEGO *et al.*, 2020). In our meta-analysis, most experiments that considered the beta diversity component (around 58 %) were not even explicit about the spatial extent of the regional scale, evidencing the challenge to include metacommunity approach and macroecology aspects to understand processes behind compositional variation (HEINO, 2011). In any case, the implications regarding a possible increase in beta diversity due to the increase in spatial EH are not straightforward. For example, the increment of beta diversity in a region can be associated with a negative process, such as non-native species establishment or localized species losses, which result in more dissimilarities between localities within a region (SOCOLAR *et al.*, 2016).

Mechanisms driving EH – biological diversity relationships

The mechanisms that possibly explain the effect of spatial EH over freshwater biological diversity have been rarely discussed (~ 17 %) nor effectively tested (~ 16 %). Similar to studies on terrestrial ecosystems (see STEIN and KREFT, 2015), the most invoked ecological processes are ecological niche partitioning (e.g., OSORIO *et al*., 2019; WILLIS *et al*., 2005), resource availability (e.g., BURDETT and WATTS, 2009; MILESI *et al*., 2016) (BURDETT; WATTS, 2009; DUDLEY, 1988; MILESI; DOLÉDEC; MELO, 2016) and persistence (SCHNECK; MELO, 2013). In general, the authors simulate an increase in the spatial EH by creating roughness and cavities in a landscape that can directly affect the community of interest. In practice, those invoked mechanisms are interconnected, as niche partitioning occurs when a greater variety of resources is provided (e.g., habitat, food, shelter) or different conditions area created (e.g., variation in luminosity, oxygen concentration, water flow velocity), allowing the establishment of organisms with different ecological requirements (DUDLEY, 1988; MILESI; DOLÉDEC; MELO, 2016). Also, the heterogeneity increment creates more space for refuge and retention, ensuring the individuals persistence when under pressure from predators or disturbances (SCHNECK; MELO, 2013; YANG *et al.*, 2015).

Since there is consistent evidence that spatial EH has a positive effect on the alpha diversity of communities, it is necessary to move towards new frontiers of ecological knowledge. We advocate a shift in the question on this topic from “how” to “why does environmental heterogeneity positively affect alpha biodiversity?”. The use of mesocosms to investigate the effect of spatial EH over biodiversity is still rare (see JEFFRIES 1993, BURDETT and WATTS 2009, SCHULER *et al*., 2017, BROWN *et al*., 2018), but should be encouraged as a tool to control for other confounding factors (area, dispersion and migration), and include other factors to test the mechanisms of persistence (e.g., including predators or disturbances) (ORTEGA; THOMAZ; BINI, 2018).

Management implications

Environmental homogenization is one of the persistent threats to global freshwater biodiversity (e.g., silting, canalization and regulation of water flow) (REID *et al.*, 2019). Thus, this scenario demands a broad knowledge about the spatial EH - biodiversity relationship and the interrelated factors to support conservation policy and environmental restoration practices (PALMER; MENNINGER; BERNHARDT, 2010; PALMER; BERNHARDT; ALLAN, 2005). We conclude that biological communities can respond to different elements of a landscape, thus there is not only one way or mechanisms by which spatial EH can act. This is why it would not be possible to elect a single or a few “keystone structures" to manage these ecosystems, as suggested by Tews *et al*. (2004).

We observed that the current knowledge on the spatial EH effect over freshwater biodiversity is concentrated on macroinvertebrate, fish, and waterfowl communities. Thus, these taxonomic groups have greater scientific support for management, which increases the chances of successful management. Also, the distance from a source of colonization, anthropogenic disturbances, the presence of invasive species, and the area size are factors that interfere in the relationship between spatial EH and alpha diversity (ARRINGTON; WINEMILLER; LAYMAN, 2005; SUNDERMANN; STOLL; HAASE, 2011; YANG *et al.*, 2015). Therefore, actions to increase spatial EH in a freshwater ecosystem need to be associated with i) recovering of areas that are source of species colonization (regional pool), ii) creating connection between regional pool and the areas managed, and iii) reducing anthropogenic disturbances.

5. Acknowledgements

We are grateful for financial support from P&D Aneel-Cemig GT-599, the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance Code 001. JA received a PhD scholarship from the Conselho Nacional de Pesquisa e Desenvolvimento (grant No. 140364/2021-8), MC was awarded CNPq research productivity grant 304060/2020-8 and FAPEMIG research grant PPM 00104-18. We also thank Arleu Viana for statistical and graphical advice, and Julian Agra for design support.

Chapter 2

"Definitivamente não somo iguais, e é maravilhoso saber que cada um de nós que está aqui é diferente um do outro, como constelações. O fato de podermos compartilhar esse espaço, de estarmos juntos viajando não significa que somos iguais; significa exatamente que somos capazes de atrair uns aos outros pelas nossas diferenças, que deveriam guiar nosso roteiro de vida. Ter diversidade, não isso de uma humanidade com o mesmo protocolo. Porque isso foi até agora só uma maneira de homogeneizar e tirar nossa alegria de estar vivo."

(Ailton Krenak, Ideias para adiar o fim do mundo, 2019)

Chapter 2: Anthropogenic disturbances alter the relationships between environmental heterogeneity and biodiversity of stream insects

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https://doi.org/10.1016/j.ecolind.2020.107079

Highlights

- EH[1] plays a more important role in biodiversity when disturbance is high
- Within a stream site, EH does not affect beta diversity
- Model selection approach pinpointed ecologically meaningful EH metrics
- Managing EH requires knowledge of how disturbances drive biological indicators

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 insects of the order 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

[1] EH – Environmental Heterogeneity abbreviation

the biodiversity-EH relationship is not the same at all levels of anthropogenic disturbance, a finding that has implications for biomonitoring and ecosystem management.

Key-words: habitat heterogeneity, beta diversity, taxonomic diversity, functional diversity, Neotropical savanna.

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; THOMAZ; BINI, 2018; STEIN; GERSTNER; KREFT, 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; THOMAZ; BINI, 2018). Recently, ecologists have also examined variation in measures of functional diversity (GRACO-ROZA *et al.*, 2020; HEINO; GRÖNROOS, 2013; MILESI; DOLÉDEC; MELO, 2016) and beta diversity (FERNÁNDEZ-ALÁEZ *et al.*, 2020; HEINO *et al.*, 2013; LÓPEZ-DELGADO; WINEMILLER; VILLA-NAVARRO, 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, R H; MACARTHUR, 1961; STEIN; KREFT, 2015). Within a riverscape (*sensu* Fausch et al., 2002; Wiens, 2002), 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; BOSCH, 2004; MCCREADIE; 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, DIEGO *et al.*, 2020; HEINO; GRÖNROOS, 2013; HEINO; MELO; BINI, 2015). 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; 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; MENNINGER; BERNHARDT, 2010). Anthropogenic disturbances may reduce regional species pools or prevent some species from colonizing a site (GÁMEZ-VIRUÉS *et al.*, 2015; SUNDERMANN; STOLL; HAASE, 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; MCINTOSH; HARDING, 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, DIEGO; DOLÉDEC; CALLISTO, 2018; 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; 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.*, 2013; HEINO; MELO; BINI, 2015).

2. Methods

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 (Figure 14). All sites were selected through a probability-based procedure that considered a spatially-balanced design (MACEDO *et al.*, 2014; OLSEN; PECK, 2008). Field samples were collected in 2010 to 2013 during September dry seasons with one visit per year at each aforementioned hydrological unit.

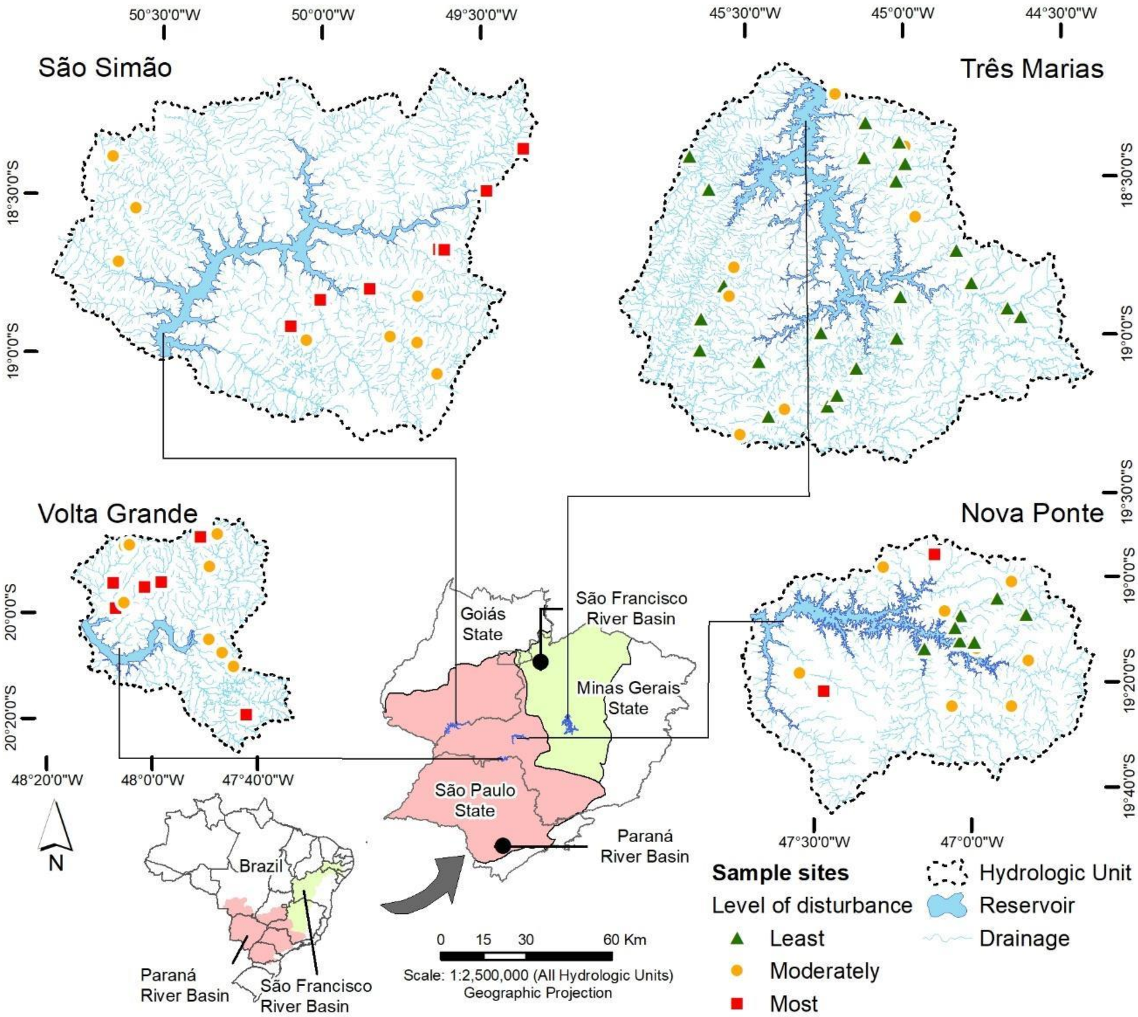


Figure 14: Location of the stream sites sampled (n = 76) in the four hydrological units in the Neotropical Savanna, Minas Gerais state, southeastern Brazil

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; ZENKER; BÖHMER, 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, DIEGO; DOLÉDEC; CALLISTO, 2018; 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 6). Guided by the breakpoints and considering a balanced number of stream sites in each category, we established the following categories: IDI < 0.30 were least-disturbed (n= 29); IDI values > 0.65 were most-disturbed (n=16); IDI values between these thresholds were moderately-disturbed (n = 31).

Sampling design

We settled the length of stream sites at 40 times their mean wetted widths, with a minimum length of 150 m (PECK; LAZORCHAK; KLEMM, 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; MELO; BINI, 2015). Environmental heterogeneity at each site referred to environmental differences among transects within each site (ANDERSON; ELLINGSEN; MCARDLE, 2006). Thus, we obtained a single value of each biological and EH metrics (taxonomic and functional alpha and beta diversities) per stream site.

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; BOSCH, 2004; HEINO; GRÖNROOS, 2013; KAUFMANN; FAUSTINI, 2012) in each of the 11 transects and between them (PECK; LAZORCHAK; KLEMM, 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 mm mesh size). Sampling followed a systematic zig-zag sequence among the 11 transects each site (PECK; LAZORCHAK; KLEMM, 2006; USEPA - UNITED STATES ENVIRONMENTAL PROTECTION AGENCY, 2016). We fixed 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, DIEGO M.P.; DOLÉDEC; CALLISTO, 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 the literature for exclusively Neotropical macroinvertebrates (BAPTISTA et al., 2006; DEDIEU et al., 2015; REYNAGA; DOS SANTOS, 2012; TOMANOVA; USSEGLIO-POLATERA, 2007). These functional traits were subsequently coded using the fuzzy coding approach (CHEVENET; DOLÉDEC; CHESSEL, 1994), where each taxon gains an affinity score for each trait within a category (CASTRO, DIEGO M.P.; DOLÉDEC; CALLISTO, 2017).

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; ELLINGSEN; MCARDLE, 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_2X) + 1, with zeros not being transformed, instead remaining as zeros (ANDERSON; ELLINGSEN; MCARDLE, 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; RIGAL; CARVALHO, 2015).

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 the 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. Thus, we ended up with 11 EH metrics.

Data analyses

We tested whether variations in biological metrics differ among categories of disturbance using an analysis of variance (one-way ANOVA; Supplementary Material 7). 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; 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 8).

To test if the relationship between the EH metrics and the biological metrics change with anthropogenic disturbance, we used a model selection approach (BURNHAM; ANDERSON, 2002). The model selection is based on all possible additive combinations of all EH metrics (i.e., predictor variables) to explain each biological metric (i.e., response variables) at each category of anthropogenic disturbance (Figure 15). This analysis results in a set of balanced models (DOHERTY; WHITE; BURNHAM, 2012), which allows calculation of the cumulative AICc (w+) weights for each EH metric (BURNHAM; 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 predictive 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).

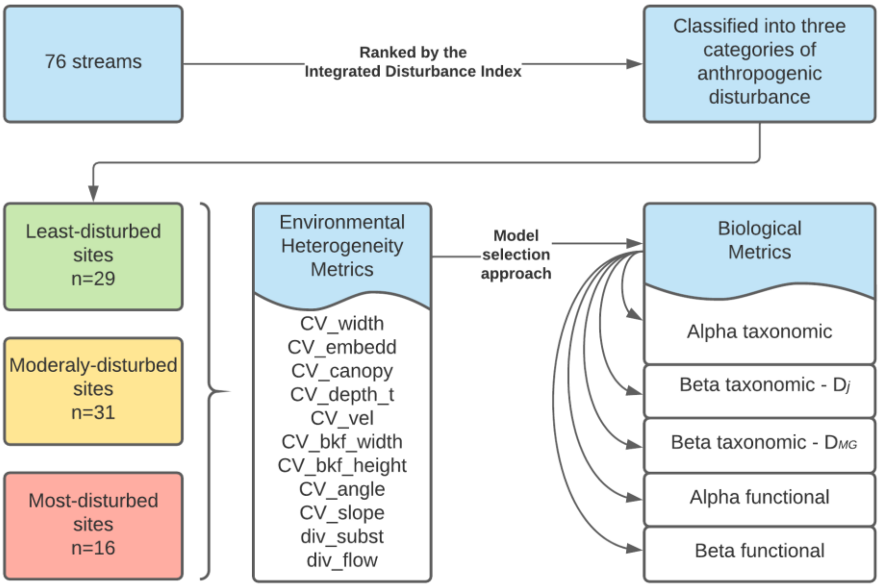


Figure 15: A schematic diagram presenting the analytical approach based on model selection. Modeling was performed by category of disturbance, based on all metrics of environmental heterogeneity against each of the biological metrics.

3. Results

We counted 24,874 individuals and found 77 EPT genera. Moderately and least-disturbed sites had similar mean abundances (n = 366.7 and 365.9, respectively), whereas most-disturbed sites had lower abundances (n = 180.7). Taxonomic and functional metrics' means did not differ among disturbance categories (Table 2).

Table 2: 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 – (dj) corresponds to Jaccard coefficient dissimilarity measure. Beta taxonomic – (dMG) 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

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

The model selection algorithm chose four EH metrics that were important variables accounting for variation in biological metrics across categories of anthropogenic disturbance (Table 4). 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.

Table 3: 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

Table 4: 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				
				Estimate	Lower 95% CI	Upper 95% CI	R^2	p-value
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	-	-	-	-	-	-	-

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 understanding 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 better understand the causes and consequences of anthropogenic disturbances on the biodiversity and potential functioning of stream ecosystems (MORI; ISBELL; SEIDL, 2018; MOUILLOT *et al.*, 2013).

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 is. 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 relationship (STEIN; 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; 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; LAZORCHAK; KLEMM, 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 lead us to conclude 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; PROULX; WIRTH, 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; 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; 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; FAUSTINI, 2012), which ultimately lead to effects similar to those caused by spatial flow diversity.

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; MELO; BINI, 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, DIEGO; DOLÉDEC; CALLISTO, 2018; LARSEN; ORMEROD, 2014; SIQUEIRA; LACERDA; SAITO, 2015).

Beta diversity patterns in freshwater ecosystems are typically strongly scale dependent (HEINO; MELO; BINI, 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; 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, B. L.; SWAN, 2010). In this case, individuals may be randomly distributed in space, and they do not exhibit a specific relationship with the environment (BROWN, BRYAN L.; WAHL; SWAN, 2017; HEINO *et al.*, 2013).

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; 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; MENNINGER; BERNHARDT, 2010). The factors that may influence the biodiversity-EH relationship include: (i) the absence of suitable species in the regional species pool (SUNDERMANN; STOLL; HAASE, 2011); (ii) the ongoing effects of anthropogenic stressors on the biota (BROWN, BRYAN L.; WAHL; SWAN, 2017; STOLL *et al.*, 2016); (iii) focus on the wrong spatial scale; (iv) the wrong perception of increased EH by the biota (POLVI; NILSSON; HASSELQUIST, 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.

5. Acknowledgments

The authors are grateful to Programa Peixe-Vivo of Companhia Energética de Minas Gerais (CEMIG) and P&D Aneel-Cemig GT-487, GT-599 and GT-611, for scholarships and financial support. MC received a research grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 303380/2015-2) and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (PPM 00104-18). DRM received a research grant from Pró-Reitoria de Pesquisa (PRPq) -UFMG (ADRC-05/2016) and a research project grant from CNPq (402907/2016–7). DMPC and MSL received postdoctoral scholarships from P&D Aneel-Cemig GT-611 and GT-599, respectively. We are grateful for colleagues from Universidade Federal de Minas Gerais (UFMG), Universidade Federal de Lavras (UFLA), Centro Federal de Educação Tecnológica de Minas Gerais (CEFET-MG) and Pontifícia Universidade Católica de Minas Gerais (PUC-MG) who helped with field sampling and sample processing. We thank R. Massara and C. Alberto for statistical advice, and R. M. Hughes and P. R. Kaufmann for a critical manuscript review and English editing. We also thank the two anonymous reviewers for all comments.

Thesis' General Conclusion

Based on the results of this two chapters, it was possible to establish the following conclusions for this thesis:

1. Spatial Environmental Heterogeneity (EH) plays an important role in the structure of communities in freshwater ecosystems across the world, increasing taxonomic and functional alpha diversity.
2. The positive effect of spatial EH over taxonomic alpha diversity is consistent and did not differ among:
   a) tropical and temperate zones,
   b) lentic and lotic ecosystems,
   c) amphibia, birds, fishes, macroinvertebrates, and microfauna,
   d) benthos, nekton, and communities that lives in the riparian meta-ecosystem,
   e) experimental designs that controlled and did not control the area.
3. There is insufficient evidence to consistently estimate the overall effect of EH on taxonomic and functional beta diversity.
4. Anthropogenic disturbances interfere the relationship between spatial EH and taxonomic and functional alpha diversities.
5. There is no well-defined pattern or direction for estimating the interference caused by anthropogenic disturbances on the spatial EH-biodiversity relationship.
6. In headwater streams of the Brazilian Neotropical Savanna, the positive effect of spatial EH was stronger for aquatic insect assemblages that lived in streams most impacted by anthropogenic disturbances.
7. There was no relationship between spatial EH and taxonomic and functional beta diversity of aquatic insect assemblages at the local scale.
8. The model selection approach can be an effective tool to pinpoint ecologically meaningful spatial EH metrics.

   In headwater streams of the Brazilian Neotropical Savanna, I identify two important spatial EH metrics that positively affect taxonomic and functional alpha diversity of aquatic insect assemblages:

- Water flow diversity
- Variation on channel morphology (i.e., thalveg depth).

9. Managing spatial EH to recover biodiversity in freshwater ecosystems requires knowledge of how this environmental factor disturbances drive biological communities.

Future Perspectives

In the current scenario of rapid global changes caused by anthropogenic disturbances, which is called the Anthropocene Era (CRUTZEN, 2002), it is urgent to understand ecological relationships in order to conserve biodiversity and ecosystem processes. In my thesis, I aimed to contribute to the long debate about the effect of environmental heterogeneity on aquatic biodiversity. I argue that it is essential to understand the relationship between EH and biodiversity, so we can predict the possible impacts on aquatic biodiversity in current and future scenarios of environmental homogenization (MOUILLOT *et al.*, 2013). Furthermore, understanding how environmental heterogeneity, at multiple spatial scales, affects biodiversity in different freshwater ecosystems around the world is critical for managing these ecosystems, preserve biodiversity, and maintaining ecosystem processes.

In addition to the results obtained through this thesis, I was able to identify several gaps on the subject. These gaps can guide future research so that we have a more robust and detailed knowledge about HE and its ecological relationships with the biodiversity of freshwater ecosystems in the world.

As main future perspectives I point out:

- The effects of HE on the taxonomic groups of algae, amphibians and microfauna, in addition to the organisms that inhabit the planktonic zone, are poorly represented throughout the published literature. This raises doubts about the effects of HE at the ecosystem scale. Therefore, I suggest that a greater number of studies focusing on these underrepresented groups will be fundamental to understand how the chain of ecological factors may be being affected by EH at the ecosystem scale;
- Investment in experimental studies, such as the use of mesocosms, to better control the possible mechanisms that explain the positive effects of HE on biodiversity. In addition, experimental studies can bring significant contributions in testing the effectiveness of different methods of increasing environmental heterogeneity, serving as a guide for future management and river restoration actions.

Supplementary Material

Supplementary Material 1: Search protocol with the terms and combinations used

Online Resource 1 – Web of Science

We conducted a systematic search at the Web of Science database in using the 46 following terms and Boolean operators:

ts = ("habitat* heterogen*" OR "habitat* diversity" OR "habitat* complexity" OR "habitat* number*" OR "biotop* heterogen*" OR "biotop* diversity" OR "biotop* complexity" OR "biotop* number*" OR "structural heterogen*" OR "structural diversity" OR "structural complexity" OR “fractal heterogen*” OR “fractal diversity” OR “fractal complexity” OR “substrate* heterogen*” OR “substrate* diversity” OR “substrate* complexity” OR “substrate* variation*” OR “flow heterogen*” OR “flow diversity” OR “flow complexity” OR “flow variation*” OR "spatial heterogen*" OR "spatial complexity" OR "enviroment* heterogen*" OR "environment* diversity" OR "environment* complexity" OR "climat* heterogen*" OR "climat* diversity" OR "climat* complexity" OR "geoheterogen*" OR "geodiversity" OR "geocomplexity" OR "landscape heterogen*" OR "landscape diversity" OR "landscape complexity")

AND

ts = ("species diversity" OR "species richness" OR "species number*" OR "species density" OR “alpha diversity” OR “beta diversity” OR “spatial beta diversity” OR “temporal beta diversity” OR “functional diversity” OR “functional richness”)

NOT

ts = (terrestrial* OR plant* OR marine OR pelagic OR coral$ OR “coral reef$” OR “deep sea” OR “seafloor” OR “sea floor” OR bacteri* OR virus* OR viral OR archaea* OR microbe* OR microbiol* OR microbial*)

We applied these terms and operators in the "Topic" field and we considered all years (since 1945). We excluded non-English language and refined results by research area: “Ecology”, “Environmental Sciences”, “Biodiversity Conservation”, “Marine Freshwater Biology”, “Forestry”, “Geography Physical”, “Zoology”, “Entomology”, “Multidisciplinary Sciences”, “Plant Sciences”, “Evolutionary Biology”, “Geosciences Multidisciplinary”, “Limnology”, “Agriculture Multidisciplinary”, “Fisheries”, “Biology”, “Water resources”, “Ornithology”, “Environmental Studies”, “Urban studies”, “Remote sensing”, “Geography”, “Soil science”, “Engineering Environment”, “Imaging Science Photography Technology”, “Regional Urban planning” and “Green sustainable science technology”.

Online Resource 2 – Scopus

We conducted a systematic search at the Scopus database in using the 46 following terms and Boolean operators:

TITLE-ABS-KEY = ("habitat* heterogen*" OR "habitat* diversity" OR "habitat* complexity" OR "habitat* number*" OR "biotop* heterogen*" OR "biotop* diversity" OR "biotop* complexity" OR "biotop* number*" OR "structural heterogen*" OR "structural diversity" OR "structural complexity" OR “fractal heterogen*” OR “fractal diversity” OR “fractal complexity” OR “substrate* heterogen*” OR “substrate* diversity” OR “substrate* complexity” OR “substrate* variation*” OR “flow heterogen*” OR “flow diversity” OR “flow complexity” OR “flow variation*” OR "spatial heterogen*" OR "spatial complexity" OR "enviroment* heterogen*" OR "environment* diversity" OR "environment* complexity" OR "climat* heterogen*" OR "climat* diversity" OR "climat* complexity" OR "geoheterogen*" OR "geodiversity" OR "geocomplexity" OR "landscape heterogen*" OR "landscape diversity" OR "landscape complexity")

AND

TITLE-ABS-KEY = ("species diversity" OR "species richness" OR "species number*" OR "species density" OR “alpha diversity” OR “beta diversity” OR “spatial beta diversity” OR “temporal beta diversity” OR “functional diversity” OR “functional richness”)

AND NOT

TITLE-ABS-KEY = (terrestrial* OR plant* OR marine OR pelagic OR coral$ OR “coral reef$” OR “deep sea” OR “seafloor” OR “sea floor” OR bacteri* OR virus* OR viral OR archaea* OR microbe* OR microbiol* OR microbial*)

We applied these terms and operators in the "Title, abstract, key-words" field and we considered all years (since 1960). We excluded articles in non-English language and refined the results by research area: “Agriculture and Biological Science”, “Environmental Science”, “Earth and Planetary Sciences”, “Multidisciplinary” and “Decision Science”.

Online Resource 3 – Scielo

We conducted a systematic search at the Scielo database using the 46 following terms and Boolean operators:

TITLE-ABS-KEY = ("habitat* heterogen*" OR "habitat* diversity" OR "habitat* complexity" OR "habitat* number*" OR "biotop* heterogen*" OR "biotop* diversity" OR "biotop* complexity" OR "biotop* number*" OR "structural heterogen*" OR "structural diversity" OR "structural complexity" OR “fractal heterogen*” OR “fractal diversity” OR “fractal complexity” OR “substrate* heterogen*” OR “substrate* diversity” OR “substrate* complexity” OR “substrate* variation*” OR “flow heterogen*” OR “flow diversity” OR “flow complexity” OR “flow variation*” OR "spatial heterogen*" OR "spatial complexity" OR "enviroment* heterogen*" OR "environment* diversity" OR "environment* complexity" OR "climat* heterogen*" OR "climat* diversity" OR "climat* complexity" OR "geoheterogen*" OR "geodiversity" OR "geocomplexity" OR "landscape heterogen*" OR "landscape diversity" OR "landscape complexity")

AND

TITLE-ABS-KEY = ("species diversity" OR "species richness" OR "species number*" OR "species density" OR “alpha diversity” OR “beta diversity” OR “spatial beta diversity” OR “temporal beta diversity” OR “functional diversity” OR “functional richness”)

AND NOT

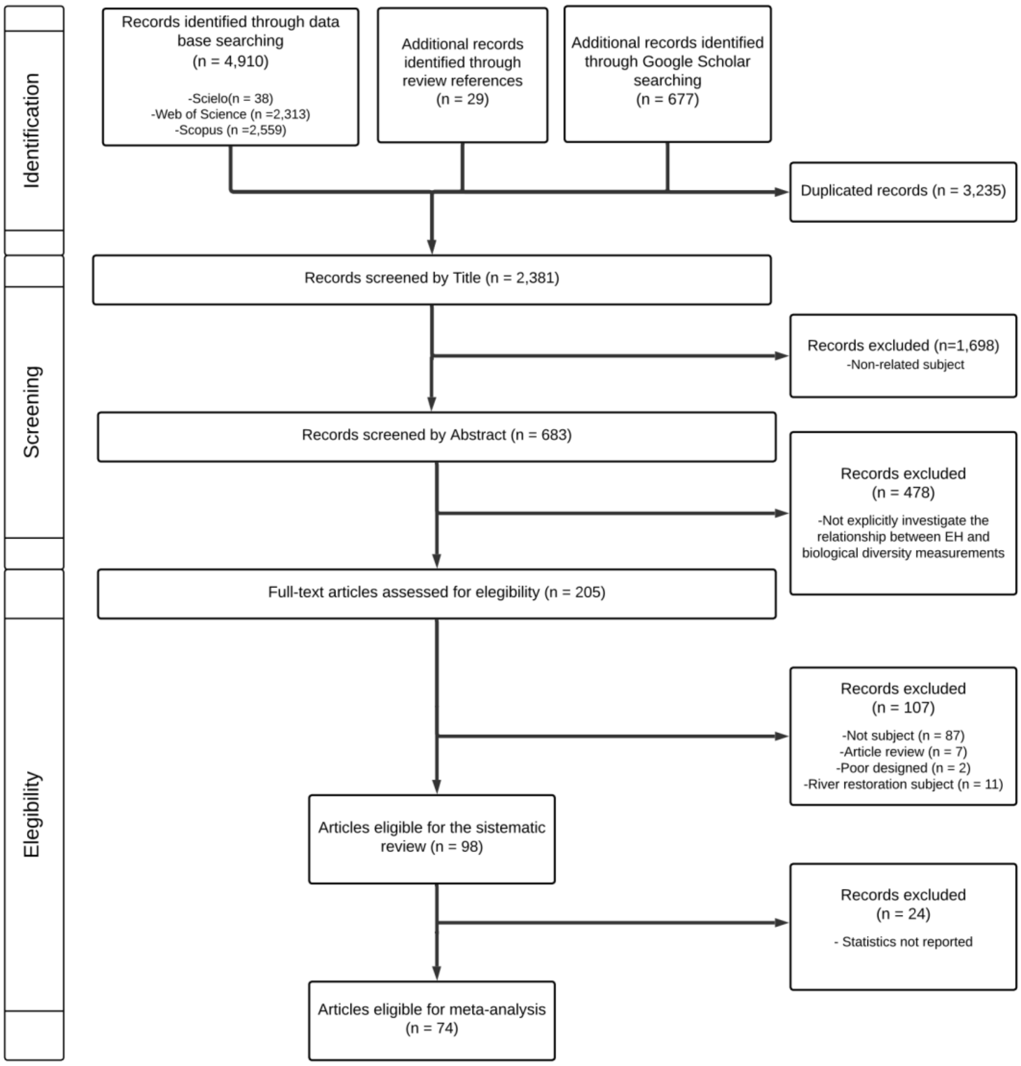
TITLE-ABS-KEY = (terrestrial* OR plant* OR marine OR pelagic OR coral$ OR “coral reef$” OR “deep sea” OR “seafloor” OR “sea floor” OR bacteri* OR virus* OR viral OR archaea* OR microbe* OR microbiol* OR microbial*)

Online Resource 4 – Google Scholar

We conducted a systematic search at the Google Scholar database using the 46 following terms:

“Habitat" "environmental" "spatial" "heterogeneity" "diversity” "complexity" "freshwater" "river" "lake" "stream" "richness" "functional" "beta"

Supplementary Material 2: PRISMA protocol



Supplementary material 3: List of articles included in the systematic review

Study ID	Included in meta-analysis	Authors	Year	Title	Journal
1	no	J. D. Allan	1975	The Distributional Ecology and Diversity of Benthic Insects in Cement Creek, Colorado	Ecology
2	yes	B. Sillen; C. Solbreck	1977	Effects of Area and Habitat Diversity on Bird Species Richness in Lakes	Oikos
3	no	D. H. Wise; M. C. Molles	1979	Colonization of artificial substrates by stream insects: influence of substrate size and diversity	Hydrobiologia
4	yes	D. D. Williams	1980	Some Relationships Between Stream Benthos and Substrate Heterogeneity	Limnology and oceanography
5	yes	D. C. Erman; N. A. Erman	1984	The response of stream macroinvertebrates to substrate size and heterogeneity	Hydrobiologia
179	yes	C. Bronmark	1985	Freshwater snail diversity: effects of pond area, habitat heterogeneity and isolation	Oecologia
12	yes	T. L. Dudley	1988	The roles of plant complexity and epiphyton in colonization of macrophytes by stream insects	Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen
6	no	N. A. O'Connor	1991	The Effects of Habitat Complexity on the Macroinvertebrates Colonising Wood Substrates in a Lowland Stream	Oecologia
7	yes	B. J. Benson; J. J. Magnuson	1992	Spatial heterogeneity of littoral fish assemblages in lakes - relation to species-diversity and habitat structure	Canadian Journal of Fisheries and Aquatic Sciences
9	yes	C. Celada; G. Bogliani	1993	Breeding bird communities in fragmented wetlands	Bolletino di zoologia

11	yes	J. Elmberg; P. Nummi; H. Poysa; K. Sjoberg	1993	Factors affecting species number and density of dabbling duck guilds in North Europe	Ecography
14	yes	M. Jeffries	1993	Invertebrate colonization of artificial pondweeds of differing fractal dimension	Oikos
13	yes	J. Elmberg; P. Nummi; H. Poysa; K. Sjoberg	1994	Relationships between species number, lake size and resource diversity in assemblages of breeding waterfowl	Journal of Biogeography
15	yes	A. N. Nilsson; J. Elmberg; K. Sjoberg	1994	Abundance and species richness patterns of predaceous diving beetles (Coleoptera, Dytiscidae) in swedish lakes	Journal of Biogeography
16	yes	M. Douglas; P. S. Lake	1994	Species richness of stream stones: an investigation of the mechanisms generating the species-area relationship	Oikos
19	no	A. Kirchhofer	1995	Morphological variability in the ecotone - an important factor for the conservation of fish species richness in Swiss rivers	Hydrobiologia
26	no	J. N. Beisel; P. Usseglio-Polatera; S. Thomas; J. C. Moreteau	1998	Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics	Hydrobiologia
31	yes	J. Belliard; R. B. D. Thomas; D. Monnier	1999	Fish communities and river alteration in the Seine Basin and nearby coastal streams	Hydrobiologia
32	yes	E. Franquet	1999	Chironomid assemblage of a Lower-Rhone dike field: Relationships between substratum and biodiversity	Hydrobiologia
33	yes	S. Merigoux; B. Hugueny; D. Ponton; B. Statzner; P. Vauchel	1999	Predicting diversity of juvenile neotropical fish communities: patch dynamics versus habitat state in floodplain creeks	Oecologia

34	yes	B. J. Robson; E. T. Chester	1999	Spatial patterns of invertebrate species richness in a river: The relationship between riffles and microhabitats	Australian Journal of Ecology
35	yes	M. Arunachalam	2000	Assemblage structure of stream fishes in the Western Ghats (India)	Hydrobiologia
37	yes	B. J. Downes; P. S. Lake; E. S. G. Schreiber; A. Glaister	2000	Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates	Oecologia
44	no	H. Taniguchi; S. Nakano; M. Tokeshi	2003	Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants	Freshwater Biology
45	no	P. Petry; P. B. Bayley; D. F. Markle	2003	Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain	Journal of Fish Biology
46	no	J. G. Rae	2004	The colonization response of lotic chironomid larvae to substrate size and heterogeneity	Hydrobiologia
48	yes	T. M. Koel	2004	Spatial variation in fish species richness of the upper Mississippi River system	Transactions of the American Fisheries Society
50	yes	L. Boyero; J. Bosch	2004	The effect of riffle-scale environmental variability on macroinvertebrate assemblages in a tropical stream	Hydrobiologia
52	yes	H. Taniguchi; M. Tokeshi	2004	Effects of habitat complexity on benthic assemblages in a variable environment	Freshwater Biology
53	yes	D. A. Arrington; K. O. Winemiller; C. A. Layman	2005	Community assembly at the patch scale in a species rich tropical river	Oecologia
57	yes	S. C. Willis; K. O. Winemiller; H. Lopez-Fernandez	2005	Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river	Oecologia

193	yes	L. McAbendroth; P. M. Ramsay; A. Foggo; S. D. Rundle; D. T. Bilton	2005	Does macrophyte fractal complexity drive invertebrate diversity, biomass and body size distributions?	Oikos
59	no	D. M. Warfe; L. A. Barmuta	2006	Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community	Oecologia
60	yes	A. L. Robertson; A. M. Milner	2006	The influence of stream age and environmental variables in structuring meiofaunal assemblages in recently deglaciated streams	Limnology and oceanography
67	yes	W. T. Kadye; B. E. Marshall	2006	Habitat diversity and fish assemblages in an African river basin (Nyagui River, Zimbabwe)	African Journal of Ecology
61	yes	L. G. Afonso; P. C. Eterovick	2007	Spatial and temporal distribution of breeding anurans in streams in southeastern Brazil	Journal of Natural History
62	yes	A. A. Agostinho; S. M. Thomaz; L. C. Gomes; S. Baltar	2007	Influence of the macrophyte Eichhornia azurea on fish assemblage of the Upper Parana River floodplain (Brazil)	Aquatic Ecology
63	yes	A. Barnett; B. E. Beisner	2007	Zooplankton biodiversity and lake trophic state: Explanations invoking resource abundance and distribution	Ecology
64	yes	C. A. Shumway; H. A. Hofmann; A. P. Dobberfuhl	2007	Quantifying habitat complexity in aquatic ecosystems	Freshwater Biology
68	yes	E. Tales; R. Berrebi	2007	Controls of local young-of-the-year fish species richness in flood plain water bodies: Potential effects of habitat heterogeneity, productivity and colonisation-extinction events	Ecology of Freshwater Fish
70	yes	L. C. G. Vieira; L. M. Bini; L. F. M. Velho; G. R. Mazao	2007	Influence of spatial complexity on the density and diversity of periphytic rotifers, microcrustaceans and testate amoebae	Fundamental and Applied Limnology

66	yes	D. M. Warfe; L. A. Barmuta; S. Wotherspoon	2008	Quantifying habitat structure: surface convolution and living space for species in complex environments	Oikos
69	yes	S. M. Thomaz; E. D. Dibble; L. R. Evangelista; J. Higuti; L. M. Bini	2008	Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons	Freshwater Biology
71	yes	D. J. McGarvey; R. M. Hughes	2008	Longitudinal zonation of Pacific Northwest (USA) fish assemblages and the species-discharge relationship	The American Society of Ichthyologists and Herpetologists
72	yes	D. J. McGarvey; G. M. Ward	2008	Scale dependence in the species-discharge relationship for fishes of the southeastern U.S.A.	Freshwater Biology
73	yes	K. N. Schneider; K. O. Winemiller	2008	Structural complexity of woody debris patches influences fish and macroinvertebrate species richness in a temperate floodplain-river system	Hydrobiologia
74	yes	A. Burdett; R. Watts	2009	Modifying living space: an experimental study of the influences of vegetation on aquatic invertebrate community structure	Hydrobiologia
75	yes	E. G. Drakou; D. C. Bobori; A. S. Kallimanis; A. D. Mazaris; S. P. Sgardelis; J. D. Pantis	2009	Freshwater fish community structured more by dispersal limitation than by environmental heterogeneity	Ecology of Freshwater Fish
76	yes	D. L. Guadagnin; L. Maltchik; C. R. Fonseca	2009	Species-area relationship and environmental predictors of fish communities in coastal freshwater wetlands of southern Brazil	Diversity and Distributions
78	no	A. Keller; M. O. Rodel; K. E. Linsenmair; T. U. Grafe	2009	The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs	Journal of Animal Ecology

80	yes	D. M. Dehling; C. Hof; M. Brandle; R. Brandl	2010	Habitat availability does not explain the species richness patterns of European lentic and lotic freshwater animals	Journal of Biogeography
82	no	L. Maltchik; L. E. K. Lanes; C. Stenert; E. S. F. Medeiros	2010	Species-area relationship and environmental predictors of fish communities in coastal freshwater wetlands of southern Brazil	Environmental Biology of Fishes
83	no	L. F. B. Moreira; I. F. Machado; T. V. Garcia; L. Maltchik	2010	Factors influencing anuran distribution in coastal dune wetlands in southern Brazil	Journal of Natural History
89	yes	P. Lucena-Moya; I. C. Duggan	2011	Macrophyte architecture affects the abundance and diversity of littoral microfauna	Aquatic Ecology
95	no	K. S. Gois; R. R. Antonio; L. C. Gomes; F. M. Pelicice; A. A. Agostinho	2012	The role of submerged trees in structuring fish assemblages in reservoirs: Two case studies in South America	Hydrobiologia
92	yes	L. E. Burlakova; A. Y. Karatayev; V. A. Karatayev	2012	Invasive mussels induce community changes by increasing habitat complexity	Hydrobiologia
93	no	F. R. da Silva; C. P. Candeira; D. D. Rossa-Feres	2012	Dependence of anuran diversity on environmental descriptors in farmland ponds	Biodiversity and Conservation
96	yes	L. U. Hepp; V. L. Landeiro; A. S. Melo	2012	Tropical fishes as biological bulldozers: Density effects on resource heterogeneity and species diversity	Ecology
97	no	M. Kratochvil; T. Mrkvicka; M. Vasek; J. Peterka; M. Cech; V. Drastik; T. Juza; J. Matena; M. Muska; J. Sed'a; P. Znachor; J. Kubecka	2012	Littoral age 0+ fish distribution in relation to multi-scale spatial heterogeneity of a deep-valley reservoir	Hydrobiologia

103	yes	J. B. Barnes; I. P. Vaughan; S. J. Ormerod	2013	Reappraising the effects of habitat structure on river macroinvertebrates	Freshwater Biology
104	yes	J. Heino; M. Gronroos; J. Ilmonen; T. Karhu; M. Niva; L. Paasivirta	2013	Environmental heterogeneity and b diversity of stream macroinvertebrate communities at intermediate spatial scales	Freshwater Biology
197	yes	J. Heino; M. Gronroos	2013	Does environmental heterogeneity affect species co-occurrence in ecological guilds across stream macroinvertebrate metacommunities?	Ecography
106	yes	F. Schneck; A. S. Melo	2013	High assemblage persistence in heterogeneous habitats: na experimental test with stream benthic algae	Freshwater biology
111	yes	M. L. Pedersen; K. K. Kristensen; N. Friberg	2014	Re-Meandering of Lowland Streams: Will Disobeying the Laws of Geomorphology Have Ecological Consequences?	Plos One
113	yes	J. I. St Pierre; K. E. Kovalenko	2014	Effect of habitat complexity attributes on species richness	Ecosphere
121	no	B. Q. Ding; J. Curole; M. Husemann; P. D. Danley	2014	Habitat complexity predicts the community diversity of rock-dwelling cichlid fish in Lake Malawi, East Africa	Hydrobiologia
120	yes	M. Delatorre; N. Cunha; J. Raizer; V. L. Ferreira	2015	Evidence of stochasticity driving anuran metacommunity structure in the Pantanal wetlands	Freshwater Biology
127	yes	X. Li; Y. R. Li; L. Chu; R. Zhu; L. Z. Wang; Y. Z. Yan	2016	Influences of local habitat, tributary position, and dam characteristics on fish assemblages within impoundments of low-head dams in the tributaries of the Qingyi River, China	Zoological Research

129	yes	S. V. Milesi; S. Doledec; A. S. Melo	2016	Substrate heterogeneity influences the trait composition of stream insect communities: an experimental in situ study	Freshwater Science
130	yes	F. Pilotto; G. L. Harvey; G. Wharton; M. T. Pusch	2016	Simple large wood structures promote hydromorphological heterogeneity and benthic macroinvertebrate diversity in low-gradient rivers	Aquatic Sciences
133	yes	A. Terui; Y. Miyazaki	2016	Three ecological factors influencing riverine fish diversity in the Shubuto River system, Japan: habitat capacity, habitat heterogeneity and immigration	Limnology
134	yes	J. D. Walrath; D. C. Dauwalter; D. Reinke	2016	Influence of Stream Condition on Habitat Diversity and Fish Assemblages in an Impaired Upper Snake River Basin Watershed	Transactions of the American Fisheries Society
139	yes	D. K. Petsch; F. Schneck; A. S. Melo	2016	Substratum simplification reduces beta diversity of stream algal communities	Freshwater Biology
136	yes	A. P. Couto; E. Ferreira; R. T. Torres; C. Fonseca	2017	Local and landscape drivers of pond-breeding amphibian diversity at the northern edge of the mediterranean	Herpetologica
137	yes	R. M. Dias; J. C. B. da Silva; L. C. Gomes; A. A. Agostinho	2017	Effects of macrophyte complexity and hydrometric level on fish assemblages in a Neotropical floodplain	Environmental Biology of Fishes
140	yes	M. S. Schuler; J. M. Chase; T. M. Knight	2017	Habitat size modulates the influence of heterogeneity on species richness patterns in a model zooplankton community	Ecology
143	yes	B. L. Brown; C. Wahl; C. M. Swan	2017	Experimentally disentangling the influence of dispersal and habitat filtering on benthic invertebrate community structure	Freshwater Biology

144	yes	M. R. Casartelli; C. Ferragut	2017	The effects of habitat complexity on periphyton biomass accumulation and taxonomic structure during colonization	Hydrobiologia
155	no	G. P. Servat; R. Alcocer; M. V. Larico; M. E. Olarte; R. Linares-Palomino; A. Alonso; K. Ledesma	2017	The Effects of Area and Habitat Heterogeneity on Bird Richness and Composition in High Elevation Wetlands (BBofedales^) of the Central Andes of Peru	Wetlands
147	no	M. I. Ilarri; L. Amorim; A. T. Souza; R. Sousa	2018	Physical legacy of freshwater bivalves: Effects of habitat complexity on the taxonomical and functional diversity of invertebrates	Science of the Total Environment
148	yes	J. Jyrkankallio-Mikkola; M. Siljander; V. Heikinheimo; P. Pellikka; J. Soininen	2018	Tropical stream diatom communities - The importance of headwater streams for regional diversity	Ecological Indicators
149	yes	O. M. Karna; J. Heino; M. Gronroos; J. Hjort	2018	The added value of geodiversity indices in explaining variation of stream macroinvertebrate diversity	Ecological Indicators
150	yes	B. Li; W. Zhang; X. X. Shu; E. L. Pei; X. Yuan; T. H. Wang; Z. H. Wang	2018	Influence of breeding habitat characteristics and landscape heterogeneity on anuran species richness and abundance in urban parks of Shanghai, China	Urban Forestry & Urban Greening
151	no	J. W. McCreadie; P. H. Adler	2018	Patterns of regional beta diversity in a widespread group of North American aquatic insects	Freshwater Science
152	no	J. W. McCreadie; R. H. Williams; S. Stutsman; D. S. Finn; P. H. Adler	2018	The influence of habitat heterogeneity and latitude on gamma diversity of the Nearctic Simuliidae, a ubiquitous group of stream-dwelling insects	Insect Science

159	yes	E. R. Cunha; K. O. Winemiller; J. C. B. da Silva; T. M. Lopes; L. C. Gomes; S. M. Thomaz; A. A. Agostinho	2019	α and β diversity of fishes in relation to a gradient of habitat structural complexity supports the role of environmental filtering in community assembly	Aquatic Sciences
161	no	H. R. Hatcher; L. E. Miranda; M. E. Colvin; G. Coppola; M. A. Lashley	2019	Fish assemblages in a Mississippi reservoir mudflat with low structural complexity	Hydrobiologia
164	yes	Z. F. Li; X. M. Jiang; J. Wang; X. L. Meng; J. N. Heino; Z. C. Xie	2019	Multiple facets of stream macroinvertebrate alpha diversity are driven by different ecological factors across an extensive altitudinal gradient	Ecology and Evolution
166	yes	N. C. Osorio; E. R. Cunha; R. P. Tramonte; R. P. Mormul; L. Rodrigues	2019	Habitat complexity drives the turnover and nestedness patterns in a periphytic algae community	Limnology
167	yes	M. Bejar; C. Gibbins; D. Vericat; R. J. Batalla	2020	Influence of habitat heterogeneity and bed surface complexity on benthic invertebrate diversity in a gravel-bed river	River Research and Applications
168	no	L. H. Elliott; L. D. Igl; D. H. Johnson	2020	The relative importance of wetland area versus habitat heterogeneity for promoting species richness and abundance of wetland birds in the Prairie Pothole Region, USA	The Condor: Ornithological Applications
170	yes	C. Junior; E. M. Eskinazi-Sant'Anna; M. R. S. Pires	2020	Environmental drivers of tadpole community structure in temporary and permanent ponds	Limnologica
171	no	L. Taxbock; D. N. Karger; M. Kessler; D. Spitale; M. Cantonati	2020	Diatom Species Richness in Swiss Springs Increases with Habitat Complexity and Elevation	Water

173	yes	A. P. T. Costa; L. O. Crossetti; S. M. Hartz; F. G. Becker; L. U. Hepp; J. E. Bohnenberger; M. S. Lima; T. Guimarães; F. Schneck	2020	Land cover is the main correlate of phytoplankton beta diversity in subtropical coastal shallow lakes	Aquatic Ecology
176	no	J. Y. White; C. J. Walsh	2020	Catchment-scale urbanization diminishes effects of habitat complexity on instream macroinvertebrate assemblages	Ecological Applications
182	yes	K. J. Gething et al	2020	The influence of substrate type on macroinvertebrate assemblages within agricultural drainage ditches	Hydrobiologia
189	yes	C. Graco-Roza; J. B. O. Santos; V. L. M. Huszar; P. Domingos; J. Soininen; M. M. Marinho	2020	Downstream transport processes modulate the effects of environmental heterogeneity on riverine phytoplankton	Science of the Total Environment
192	yes	A. R. Manzotti; M. Ceneviva-Bastos; F. B. Teresa; L. Casatti	2020	Short-term response of fish assemblages to instream habitat restoration in heavily impacted streams	Neotropical Ichthyology

Supplementary material 4: Biological metrics used as response variables in the meta-analysis

Categories	Biological metrics
Alpha taxonomic	Species richness (S), Rarefied richness, Log(S+1), Mean of S, Density of S, Shannon-Wiener index, Simpson index, Evenness, Species density, Chao richness and Berger Parker dominance
Beta taxonomic	Bray-curtis dissimilarity index, Sorensen dissimilarity index, Gower dissimilarity index, Jaccard dissimilarity index, Distance of Hellinger considering abundance and presence, and the Raup crick distance
Alpha functional	Maximum morphological distance, Mean morphological distance, Functional richness, Functional diversity and Functional evenness
Beta functional	Standard deviation of morphological distance, Functional dispersion and Variation standard length.

Supplementary material 5: Funnel plots

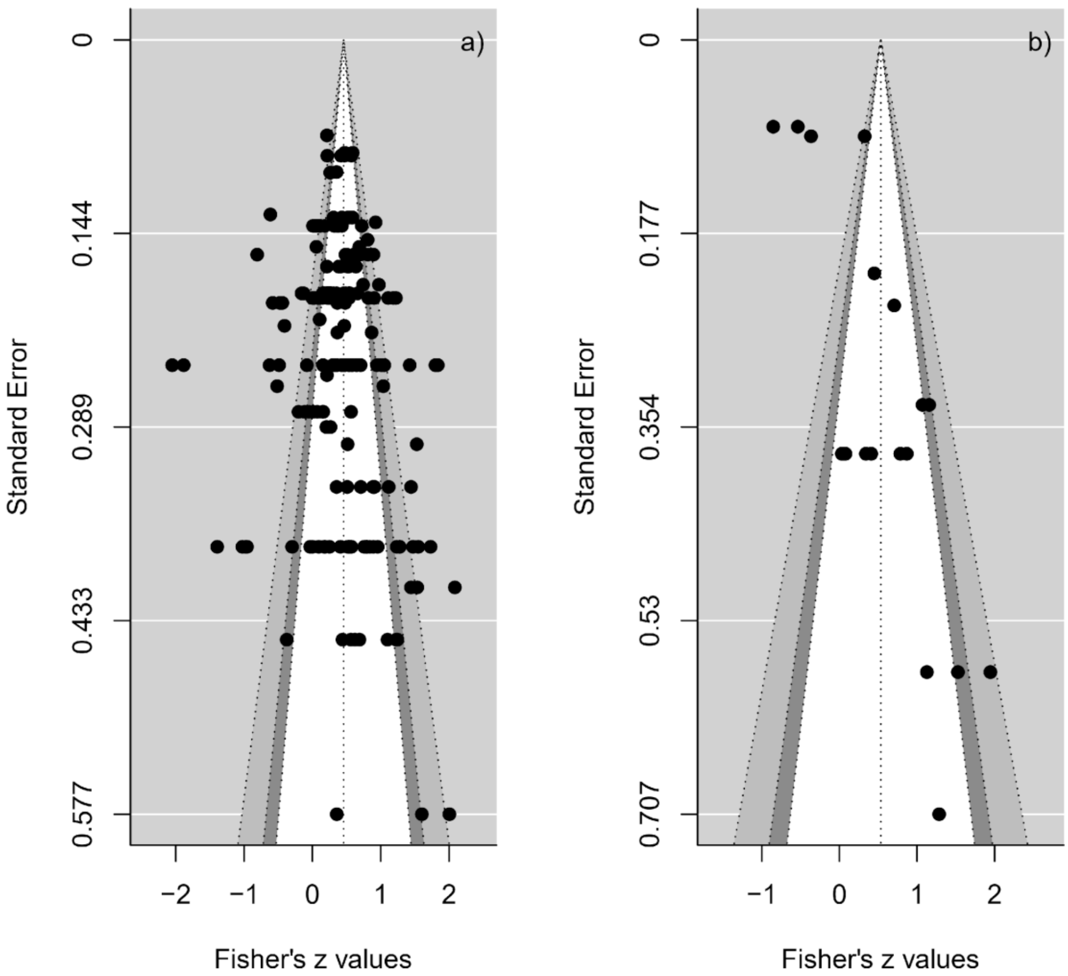


Figure S16: Funnel plots showing the relationship between effect size and standard error of (a) the EH effect on taxonomic alpha diversity and (b) the EH effect on taxonomic beta diversity. Fail safe numbers for taxonomic alpha diversity model is equals to 46,841 and taxonomic beta diversity model is equals to 20.

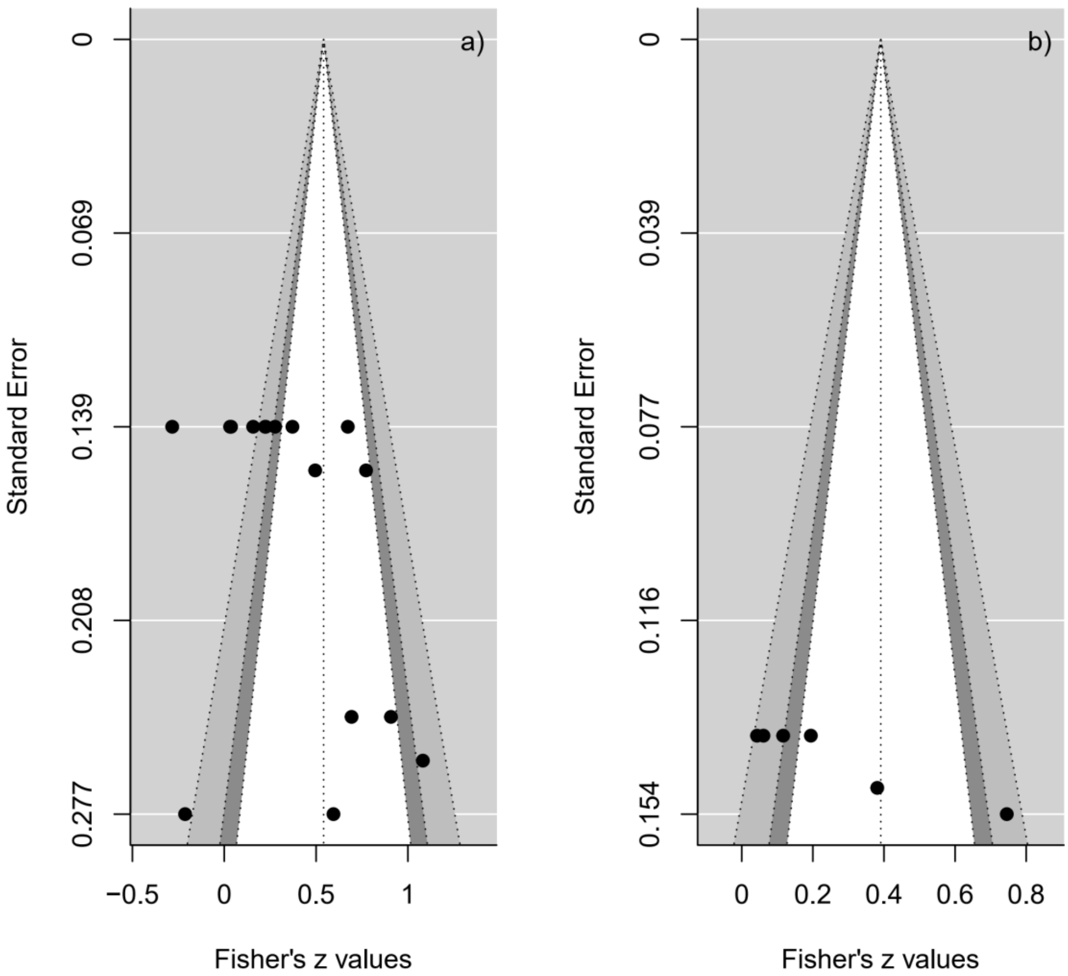
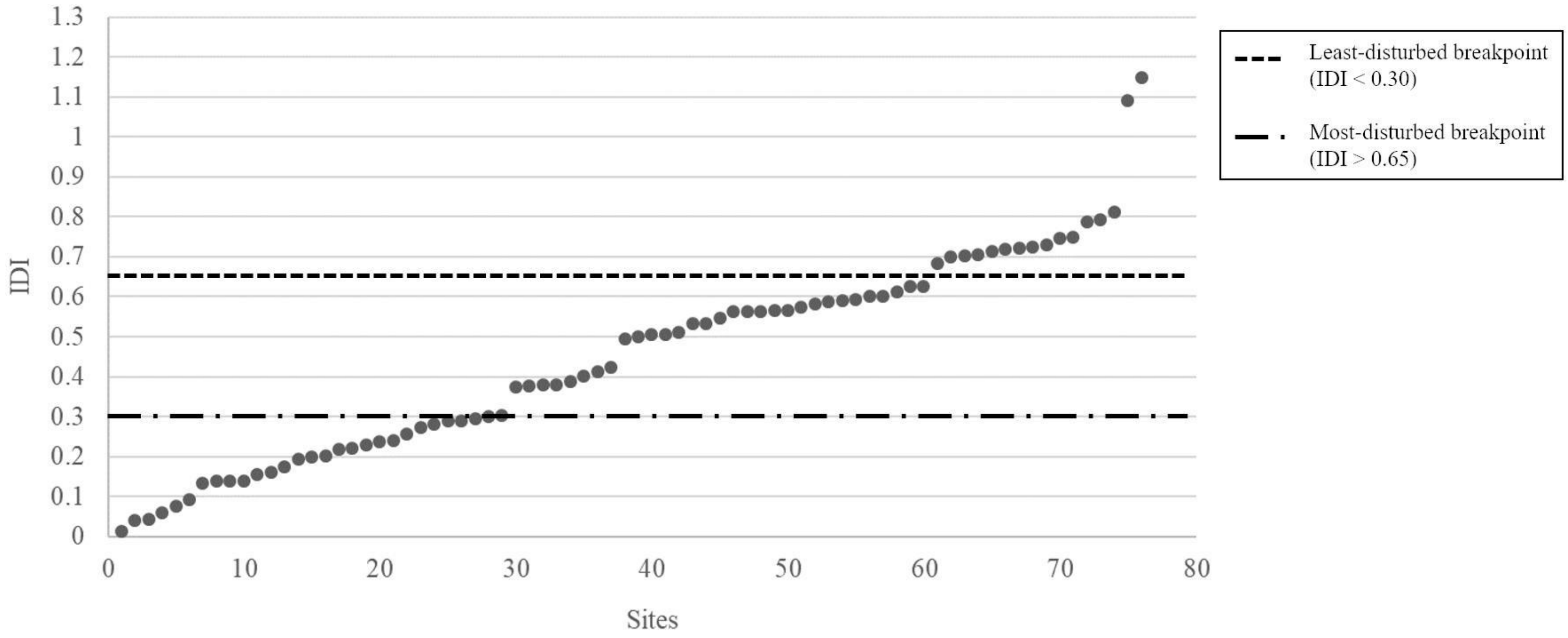


Figure S17: Funnel plots showing the relationship between effect size and standard error of the EH effect on functional alpha diversity (a) and the EH effect on functional beta diversity (b). Fail safe numbers for functional alpha diversity model is equals to 380 and functional beta diversity model is equals to 34.

Supplementary Material 6: Stream sites ranked by the Integrated Disturbance Index (IDI).



Supplementary Material 7: Results of analysis of variance (ANOVA) for each biological metric compared among categories of disturbance (Least-disturbed; (ii) moderately-disturbed; (iii) most-disturbed).

1. ANOVA test calculated for taxonomic alpha diversity. The null hypothesis of this test was calculated under the assumption of non-different mean values of taxonomic alpha diversity among categories. There were no differences of taxonomic alpha diversity among categories ($F_{2,73}$ = 1.02; p = 0.306).
2. ANOVA test calculated for taxonomic beta diversity (considering Jaccard coefficient). The null hypothesis of this test was calculated under the assumption of randomization mean values of taxonomic beta diversity among categories. There were no differences of taxonomic beta diversity among categories ($F_{2,73}$ = 1.429; p = 0.2461).
3. ANOVA test calculated for taxonomic beta diversity (considering modified Gower distance). The null hypothesis of this test was calculated under the assumption of non-different mean values of taxonomic beta diversity among categories. There were no differences of taxonomic beta diversity among categories ($F_{2,73}$ = 0.07137; p = 0.9312).
4. ANOVA test calculated for functional alpha diversity. The null hypothesis of this test was calculated under the assumption of non-different mean values of functional alpha diversity among categories. There were no differences of functional alpha diversity among categories ($F_{2,73}$ = 2.731; p = 0.07179).
5. ANOVA test calculated for functional beta diversity. The null hypothesis of this test was calculated under the assumption of non-different mean values of functional beta diversity among categories. There were no differences of functional beta diversity among categories ($F_{2,73}$ = 0.6002; p = 0.5514).

Supplementary Material 8: Results of the Moran's I test for each biological and environmental heterogeneity metric.

1. Moran's I test calculated for taxonomic alpha diversity as response variable. The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = 0.0055494, p-value =
0.4978
alternative hypothesis: greater
sample estimates:

Moran I statistic	*Expectation*	*Variance*
-0.012886606	*-0.013333333*	*0.006480369*

2. Moran's I test calculated for taxonomic beta diversity (Jaccard coefficient) as response variable. The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

Moran I test under randomisation
data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -0.66929, p-value =
0.7483
alternative hypothesis: greater
sample estimates:

Moran I statistic	*Expectation*	*Variance*
-0.070046727	*-0.013333333*	*0.007180398*

3. Moran's I test calculated for taxonomic beta diversity (modified Gower distance) as response variable. The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -1.5617, p-value = 0.9408
alternative hypothesis: greater
sample estimates:

Moran I statistic	*Expectation*	*Variance*
-0.145656373	*-0.013333333*	*0.007178886*

4. Moran's I test calculated for functional alpha diversity as response variable. The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -0.96866, p-value =
0.8336
alternative hypothesis: greater
sample estimates:

Moran I statistic	*Expectation*	*Variance*
-0.092930679	*-0.013333333*	*0.006752382*

5. Moran's I test calculated for functional beta diversity as response variable. The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -0.96866, p-value =
0.8336
alternative hypothesis: greater
sample estimates:

Moran I statistic	Expectation	Variance
-0.092930679	-0.013333333	0.006752382

6. Moran's I test calculated for coefficient of variation of channel wetted width as response variable (CV_width). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -0.70194, p-value =
0.7586
alternative hypothesis: greater
sample estimates:

Moran I statistic	Expectation	Variance
-0.072862277	-0.013333333	0.007192101

7. Moran's I test calculated for coefficient of variation of substrate embeddedness (CV_embedd). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -0.96862, p-value =
0.8336
alternative hypothesis: greater
sample estimates:

Moran I statistic	Expectation	Variance
-0.095714850	-0.013333333	0.007233565

8. Moran's I test calculated for coefficient of variation of canopy cover (CV_canopy). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)

weights: lstw

Moran I statistic standard deviate = -1.5188, p-value = 0.9356

alternative hypothesis: greater

sample estimates:

Moran I statistic	Expectation	Variance
-0.14262995	-0.01333333	0.00724742

9. Moran's I test calculated for coefficient of variation of thalweg depth (CV_depth_t). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)

weights: lstw

Moran I statistic standard deviate = -1.2456, p-value = 0.8935

alternative hypothesis: greater

sample estimates:

Moran I statistic	Expectation	Variance
-0.118531125	-0.013333333	0.007133085

10. Moran's I test calculated for coefficient of variation of flow velocity (CV_vel). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)

weights: lstw

Moran I statistic standard deviate = 0.0054582, p-value =
0.4978
alternative hypothesis: greater
sample estimates:

Moran I statistic	Expectation	Variance
-0.012873973	-0.013333333	0.007082946

11. Moran's I test calculated for coefficient of variation of bankfull width (CV_bkf_width). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -0.058564, p-value =
0.5234
alternative hypothesis: greater
sample estimates:

Moran I statistic	Expectation	Variance
-0.01830922	-0.01333333	0.00721905

12. Moran's I test calculated for coefficient of variation of bankfull height (CV_bkf_height). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -0.85711, p-value =
0.8043
alternative hypothesis: greater
sample estimates:

Moran I statistic   Expectation   Variance

-0.086059407   -0.013333333   0.007199499

13. Moran’s I test calculated for coefficient of variation of margin angle (CV_angle). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)

weights: lstw

Moran I statistic standard deviate = -0.81397, p-value =

0.7922

alternative hypothesis: greater

sample estimates:

Moran I statistic   Expectation   Variance

-0.082525609   -0.013333333   0.007226047

14. Moran’s I test calculated for coefficient of variation of channel slope (CV_slope). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)

weights: lstw

Moran I statistic standard deviate = -0.57541, p-value =

0.7175

alternative hypothesis: greater

sample estimates:

Moran I statistic   Expectation   Variance

-0.061894087   -0.013333333   0.007122248

15. Moran's I test calculated for Simpson's diversity of substrate types (div_subst). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = 0.56647, p-value = 0.2855
alternative hypothesis: greater
sample estimates:

Moran I statistic	Expectation	Variance
0.034221109	*-0.013333333*	*0.007047401*

16. Moran's I test calculated for Simpson's diversity of spatial flow types (div_flow). The null hypothesis of this test was calculated under the assumption of random spatial patterns of sites (i.e., lack of spatial autocorrelation).

data: residuals.glm(model)
weights: lstw

Moran I statistic standard deviate = -1.7312, p-value = 0.9583
alternative hypothesis: greater
sample estimates:

Moran I statistic	Expectation	Variance
-0.160267617	*-0.013333333*	*0.007203322*

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