

Meta-analysis

A global synthesis and meta-analysis of the environmental heterogeneity effects on the freshwater biodiversity

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The spatial environmental heterogeneity (EH) has been invoked as an important factor to explain biodiversity. It is expected that higher spatial EH provides a wider range of resources and conditions for species with different requirements, leading to an increase of biodiversity. However, differences among geographical locations, ecosystem types, taxonomic groups, their occurrence zone, and methodological approaches may reveal idiosyncrasy between studies. Thus, we aimed to synthesize the global knowledge about the relationship between spatial EH and freshwater biodiversity (i.e. taxonomic and functional diversity, and their respective α and β components). Through a systematic review, we integrated results from 98 studies, published in 33 different countries, about the role of spatial EH – biodiversity relationship in freshwater ecosystems. Through meta-analysis, we demonstrated 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 different methodological designs. 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.

Keywords: beta diversity, environmental complexity, functional diversity, habitat heterogeneity

Introduction

Since the publication of ‘On birds species diversity’ (MacArthur and MacArthur 1961), ecologists from different areas have sought to understand the relationship

between spatial environmental heterogeneity (EH) and biodiversity (Ortega et al. 2018, Faghihinia et al. 2021). Heterogeneity encompasses several components and concepts (Kolasa and 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 et al. 2015). More heterogeneous environments present a larger range of food resources, refuge and a variety of environmental conditions for species with different requirements (MacArthur and 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 (Hutchinson 1959, Caswell and Cohen 1991, Willis et al. 2005, Cardinale 2011).

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 structures such as macrophytes and wood debris (Tokeshi and 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 (Milesi et al. 2016, Li et al. 2019, Agra et al. 2021). However, opposite or non-significant results have shown that this ecological pattern may not be universal (Boyero and Bosch 2004, Palmer et al. 2010, Kärnä et al. 2018). 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). Also, the spatial EH – biodiversity relationship may depend upon other factors such as the spatial scale considered in the study, biotic interactions (i.e. the strength of competition and predation) and gradients of disturbance (Heino et al. 2015, Yang et al. 2015, Agra et al. 2021).

The wide variety of methods used to manipulate EH proxies and test the effects of spatial EH may also explain idiosyncrasies in the results (Stein and Krefl 2015), because the way species perceive spatial EH is intrinsically associated with its ecological niche (Caswell and Cohen 1991). For instance, species that inhabit a river bottom respond to substrate heterogeneity (EH proxy) differently from species that use the water column (Schneider and Winemiller 2008, Lucena-Moya and Duggan 2011). Thus, researchers employ different EH proxies and methodological approaches according to the taxonomic group investigated, aiming to capture the ecological meaning of the spatial EH on biodiversity (Caswell and 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 (Thomaz et al. 2008, Allouche et al. 2012). Furthermore, a misuse of terminologies and concepts to

describe spatial EH limits comparisons between studies, hampering generalizations and implications of the effects of spatial EH over biological communities (Cunha et al. 2012, Stein and Krefl 2015).

Systematic reviews and meta-analysis emerged as fundamental tools to summarize research evidence and to try explain variation sources 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 (Tews et al. 2004, Allouche et al. 2012, Stein and Krefl 2015), and meta-analyses have quantified the overall effect of spatial EH over species richness (Stein et al. 2014, Ortega et al. 2018). However, only one study has tested the effects of spatial EH on species richness (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, while 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 the relationship between spatial EH – biodiversity and the consequences on ecosystem functioning in a scenario of global change (Mouillot et al. 2013, Heino et al. 2015, Ortega et al. 2018).

We synthesized the current status of knowledge regarding the study of spatial EH in freshwater ecosystems, elucidating: 1) how spatial EH is assessed across geographical locations, freshwater ecosystem types, taxonomic groups and their occurrence zone; 2) which mechanisms are invoked to investigate the spatial EH-biodiversity relationship; and 3) 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 4) 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 5) test whether there is significant variation in the overall effect of spatial EH on taxonomic alpha diversity moderated by location (tropical versus temperate); ecosystem type (lotic versus 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 and 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 et al. 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 and Wilson 1967).

Material and 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 et al. 2013). The first approach consisted of searching for terms in the three searching 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 the Supporting information). 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 (Stein et al. 2014) (Supporting information). In this case we established a maximum of 677 articles to screen, because the number of results were excessive (1370) and overestimated. The third approach consisted to search onto the references of previous reviews and opinion articles that included freshwater ecosystems in the central theme (Palmer et al. 2010, Cunha et al. 2012, Kovalenko et al. 2012, Tokeshi and Arakaki 2012, Ortega et al. 2018). Through this, we added 29 studies that were not captured by the searching engines and Google Scholar.

After duplicate exclusion we obtained 2381 studies. The next steps of screening and selection process are described in the flowchart as recommended by the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) (O’Dea et al. 2021) (Supporting information). Also, we submitted all steps of our review and meta-analysis to the interactive PRISMA-EcoEvo Checklist (Supporting information). To select studies we considered the following criteria: 1) encompassed freshwater ecosystems and its associated organisms; 2) were either observational, 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. In the title and abstract screening stage 2176 studies were excluded, thus a total of 205 studies were fully read and evaluated. After this second screening, we selected 98 studies to be included in our systematic integrative review (Supporting information).

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 select 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 et al. 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 of diversity. At the end, 74 studies were selected for a meta-analysis.

Qualitative data extraction

To conduct our systematic integrative 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 used 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 a response variable (i.e. functional or taxonomic, and alpha or beta), 11) whether 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 used different methodological approaches and calculation methods. We incorporated this information in separate outcomes from the same study, which generated 276 comparisons or independent registers.

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 were then sorted 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 (Fig. 1).

The methodological approach denotes the way authors manipulated the EH proxies to create EH gradients or EH levels, aiming to test the effects of spatial EH on a biological metric. In the same way, we created eight categories of methodological approach: density; mixed; presence versus 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).

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. When authors reported results in figures, we extracted information using the software Image J (Schneider et al. 2012). When effects were not provided in the text, table, or figures, we requested data and/or statistical results from the corresponding author of the study.

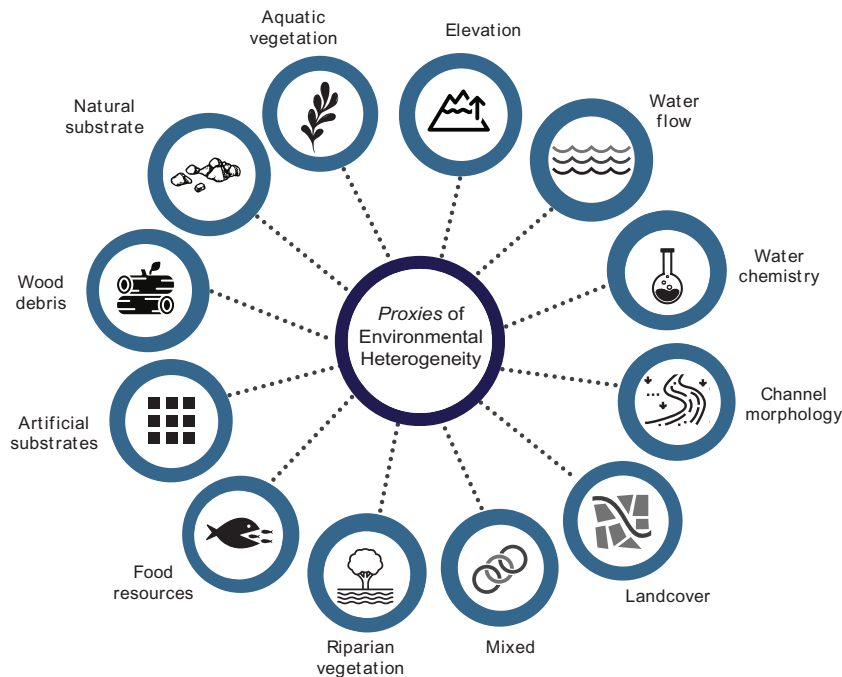


Figure 1. Categories of environmental heterogeneity (EH) proxies used to evaluate the effect of EH over biological metrics of diversity.

Every statistical result reported in those studies were converted into a correlation coefficient (r). To estimate the magnitude of the overall effect of EH on taxonomic and functional alpha and beta diversity, we used the Fisher's z value as the metric of effect size. We derive z values using the formula: $z = 0.5 \times \ln [(1+r)/(1-r)]$ (Koricheva et al. 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 et al. 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.

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

Statistical analysis

















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 et al. 2013). First, we run a random-effect meta-analysis model 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 mixed-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 the metrics of beta taxonomic, alpha functional and beta functional due to low sample size. We considered variation between geographical locations (tropical versus temperate), ecosystem types (lentic versus 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 versus 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 et al. 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 and Olkin 2014). All analyses were run with the statistical software R ver. 4.2.2 (www.r-project.org, 2022-10-31 ucrt), using the 'metafor' package ver. 3.8-1 (Viechtbauer 2010). The full database supporting the results of this study are available from the Dryad digital repository <https://doi.org/10.5061/dryad.g4f4qrfw2> (Agra et al. 2023).

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 (Møller and Jennions 2001). Thus, we analyzed publication biases for each meta-analysis model

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, and different colors represent variations within the same proxy

Methodological approach	Concept	Examples	Graphical abstract Homogeneous versus heterogeneous	
Size variation or size composition	Manipulation of particle sizes from an environmental proxy	Substrates with the same particle size versus 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 versus intricately-shaped leaves		
Roughness or surface, topography, texture	Manipulation of the roughness of an environmental proxy	Smooth surface of a substrate versus 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 versus absence	Manipulation of addition or exclusion of an environmental proxy at a location	The presence of artificial substrates versus the lack of artificial substrates		
Qualitative variation or patchiness, compositional variation	Manipulation of different qualities of the same environmental proxy	Richness of substrate types; Shannon diversity of water flow types		
Continuous variation	Manipulation of an environmental proxy which is continuous	Coefficient of variation of water flow velocity; standard deviation of a river discharge		
Mixed	Manipulation of 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		

to examine possible publication bias as well as the strength of our significant models. For this, we used two approaches: 1) visual inspections of a pattern of asymmetry in a funnel plot (Supporting information). 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 are the number of hypothetical unpublished evidence averaging a z-value of zero that, if added to the dataset, would change our results from significant to non-significant (Rosenthal 1979). Fail-safe numbers higher than $5n + 10$ ($n = \text{number of independent comparisons}$), provides evidence for the strength of our results despite publication bias.

Results

Systematic review

The 98 studies encompassed 33 countries, across all continents, except Antarctica (Fig. 2). 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 (Allan 1975). Since then, the topic has been increasingly studied (Fig. 3). 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 studies (29).

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. 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



Figure 2. Geographic location of 98 studies that investigated the relationship between EH and freshwater biological diversity. Light blue indicates the smallest number of studies whereas darker blue indicates the largest number of studies.

heterogeneity' (12), 'structural complexity' (9) and 'environmental heterogeneity' (8).

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 (Fig. 4). 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).

Authors manipulated several EH proxies to evaluate the effect of EH on biological metrics. Categories of EH proxies ranked by frequency were: 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 were: qualitative variation (74), structure (65), mixed (45), roughness (25), presence versus 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 (Fig. 5a). Most studies that evaluated the response of macroinvertebrates to spatial EH 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 (Fig. 5b). 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%).

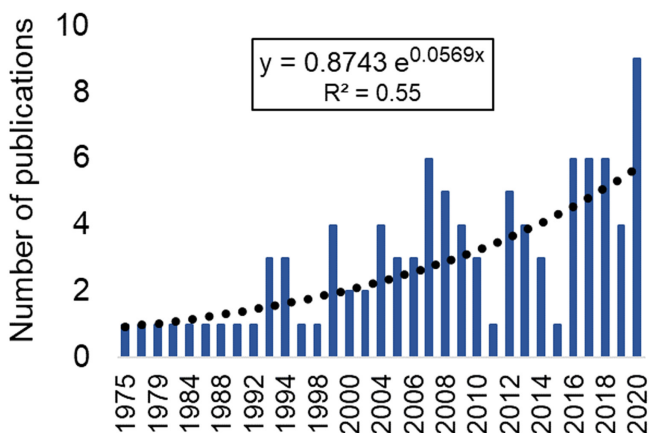


Figure 3. Number of published studies that investigated the relationship between environmental heterogeneity and freshwater biodiversity per year, from 1975 to 2020.

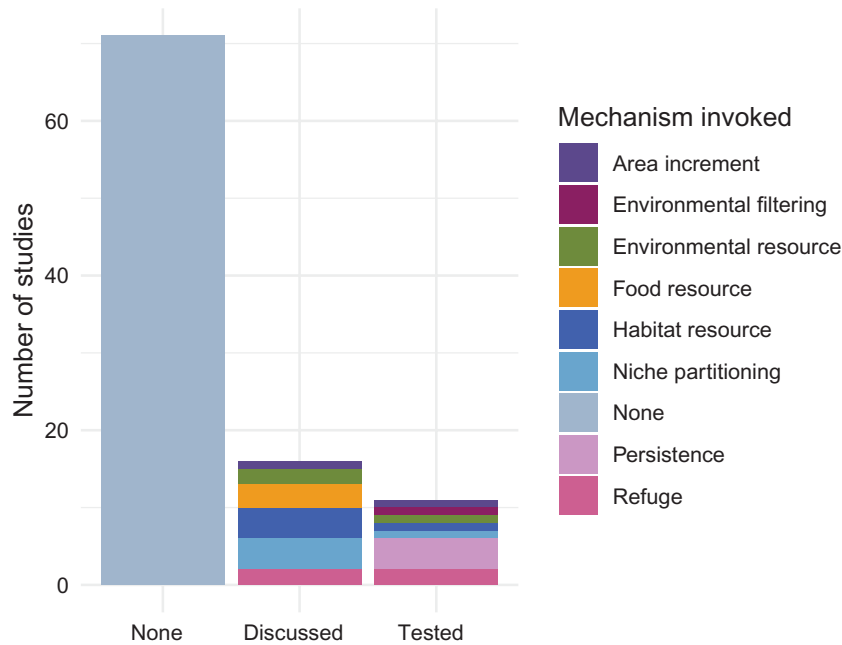


Figure 4. Number of studies by categories of mechanisms invoked to explain the relationship between spatial EH and the biological metric of response.

Meta-analysis

Overall, the spatial EH had a positive effect on taxonomic alpha diversity ($z=0.46$, 95% CI=0.34–0.57, $n=200$ individual effect size: 64 study numbers, $Q_{199}=1102.5$, $p\text{-value} < 0.0001$) and functional alpha diversity ($z=0.54$, 95% CI=0.23–0.85, $n=16$: 6, $Q_{15}=67.7$, $p\text{-value} < 0.0001$). Also, spatial EH had a significant and positive effect on taxonomic beta diversity ($z=0.53$, 95% CI=0.06–1.01, $n=20$: 10, $Q_{19}=232.8$, $p\text{-value} < 0.0001$), but we did not observe effects on functional beta diversity ($z=0.39$, 95% CI=–0.09–0.88, $n=6$: 3, $Q_5=16.2$, $p\text{-value}=0.0063$) (Fig. 6).

The positive effect of spatial EH over taxonomic alpha diversity did not differ between tropical ($z=0.47$, 95% CI=0.24–0.71) and temperate zones ($z=0.47$, 95% CI=0.33–0.60). Also, there was no difference of spatial EH over taxonomic alpha diversity between lotic ($z=0.44$, 95% CI=0.27–0.60) and lentic ecosystems ($z=0.53$, 95% CI=0.35–0.71). Between experiments that controlled for area ($z=0.50$, 95% CI=0.27–0.74) and those that did not control for area ($z=0.46$, 95% CI=0.32–0.59), no difference was observed for the effect of spatial EH over taxonomic alpha diversity. 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=0.18–0.85), the benthic zone ($z=0.50$, 95% CI=0.34–0.66) and the nektonic zone ($z=0.45$, 95% CI=0.25–0.66). There was no general effect of spatial EH over taxonomic alpha diversity of communities from the planktonic zone ($z=-0.21$, 95% CI=–0.80–0.39). There was a positive effect of spatial EH over taxonomic alpha diversity for amphibians ($z=0.67$, 95% CI=0.15–1.19), macroinvertebrates ($z=0.49$, 95% CI=0.32–0.67), birds ($z=0.49$, 95% CI=0.10–0.89) and

fish ($z=0.43$, 95% CI=0.22–0.64), 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=–0.53–0.84) and microfauna ($z=0.49$, 95% CI=–0.01–0.97) (Fig. 7).

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 (Supporting information). Because the funnel plot of the taxonomic alpha diversity model was not explicit, we ran an Egger's regression, which provided evidence for publication bias (Intercept=0.089, 95% CI: –0.1026, 0.2810, $p=0.001$).

Calculation of fail-safe numbers indicated that the overall effect of EH over taxonomic and functional alpha diversity provides evidence of robustness, despite the bias. 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 non-significant, respectively. Nonetheless, more studies are needed to improve the strength of describe the overall effect of spatial EH on the facets of taxonomic beta diversity (fail-safe number=20). No bias analysis was done for the model of EH effect over functional beta diversity, since it was not a significant model.

Discussion

Through an integrative and systematic review of 98 studies, we mapped a wide range of terminologies and methodological approaches globally used to investigate the effects of

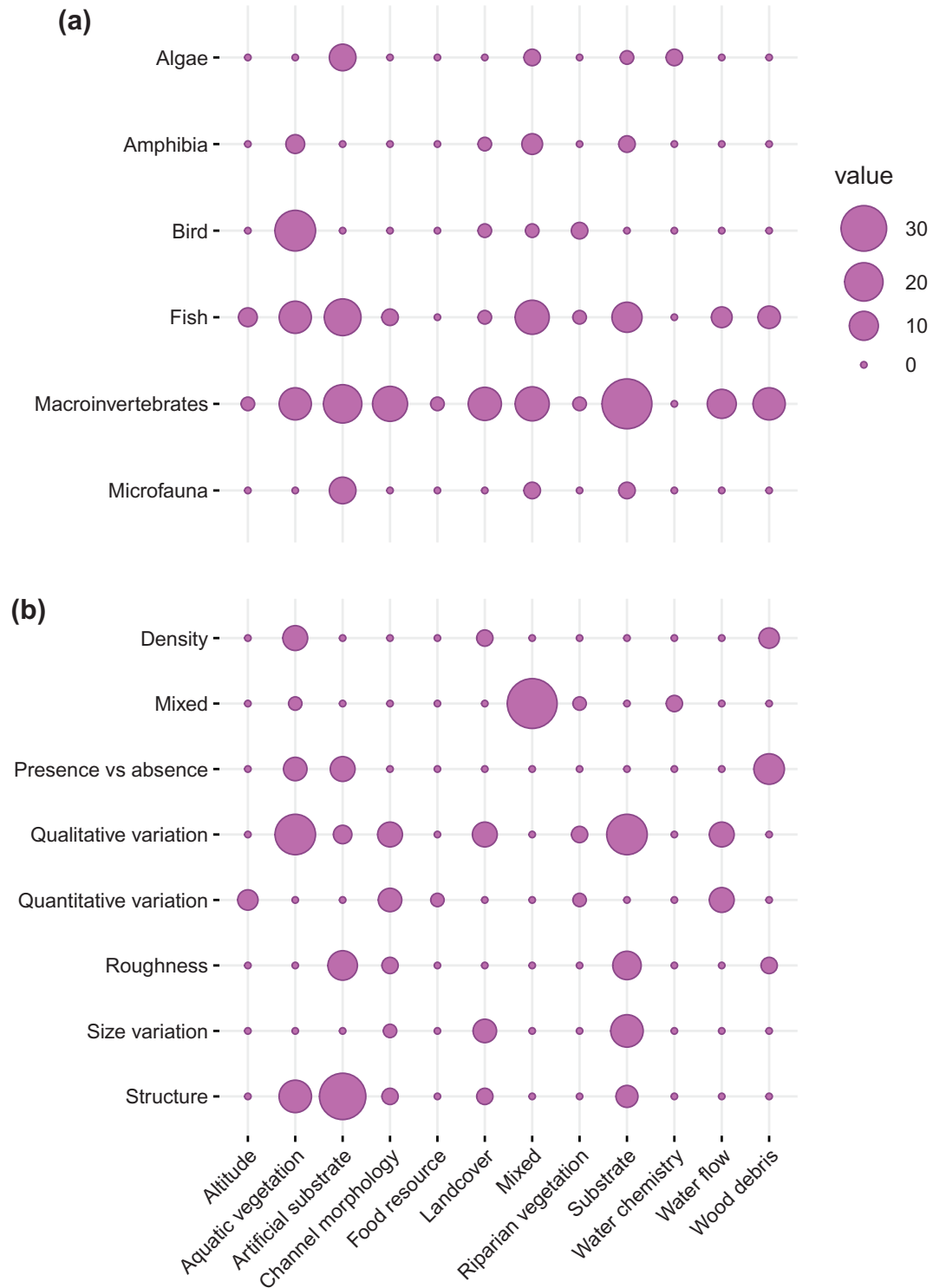


Figure 5. (a) Relationship between categories of environmental heterogeneity proxies and biological groups in studies that evaluated the increase in environmental heterogeneity and freshwater biodiversity. (b) Relationship between categories of environmental heterogeneity proxies and methodological approaches in studies that evaluated the increase in environmental heterogeneity and freshwater biodiversity. Bubble size is proportional to the number of observations in each study.

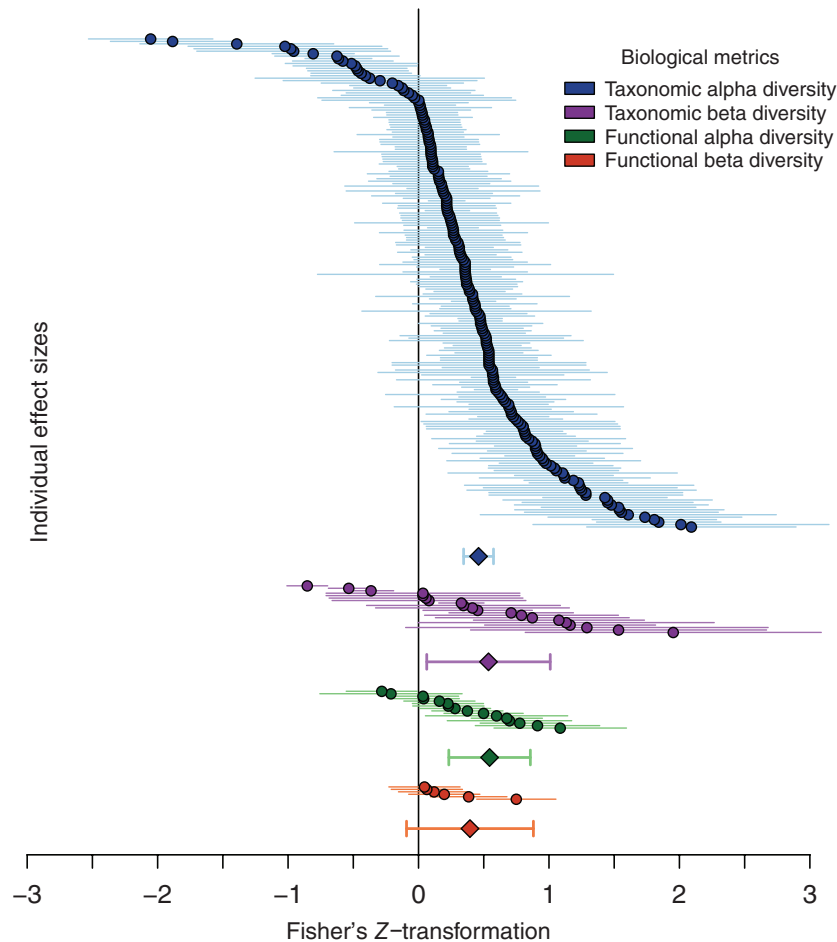


Figure 6. Forest plot showing effect size estimates of spatial EH effect over taxonomic alpha diversity ($n=200$), taxonomic beta diversity ($n=20$), functional alpha diversity ($n=16$) and functional beta diversity ($n=6$). Filled dots are individual effect sizes with respective 95% confidence intervals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

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 importantly, 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 (controlled area versus 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 as spatial EH 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. For terrestrial ecosystems, several terms have also been used to describe EH (Stein and Kreft 2015). Besides, 42% of authors here reviewed, 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 synthesize ecological concepts of terms around functional ecology, beta diversity, ecological invasions and metacommunity (Leibold et al. 2004, Falk-Petersen et al. 2006, Tuomisto 2010, Bastos-Pereira et al. 2022). In our 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 (Table 1).

The terms 'habitat complexity', 'habitat heterogeneity', 'habitat diversity', 'structural complexity' were, in fact, the most frequent expressions associated with the concept of EH. Nonetheless, we emphasize that these terms are restricted to

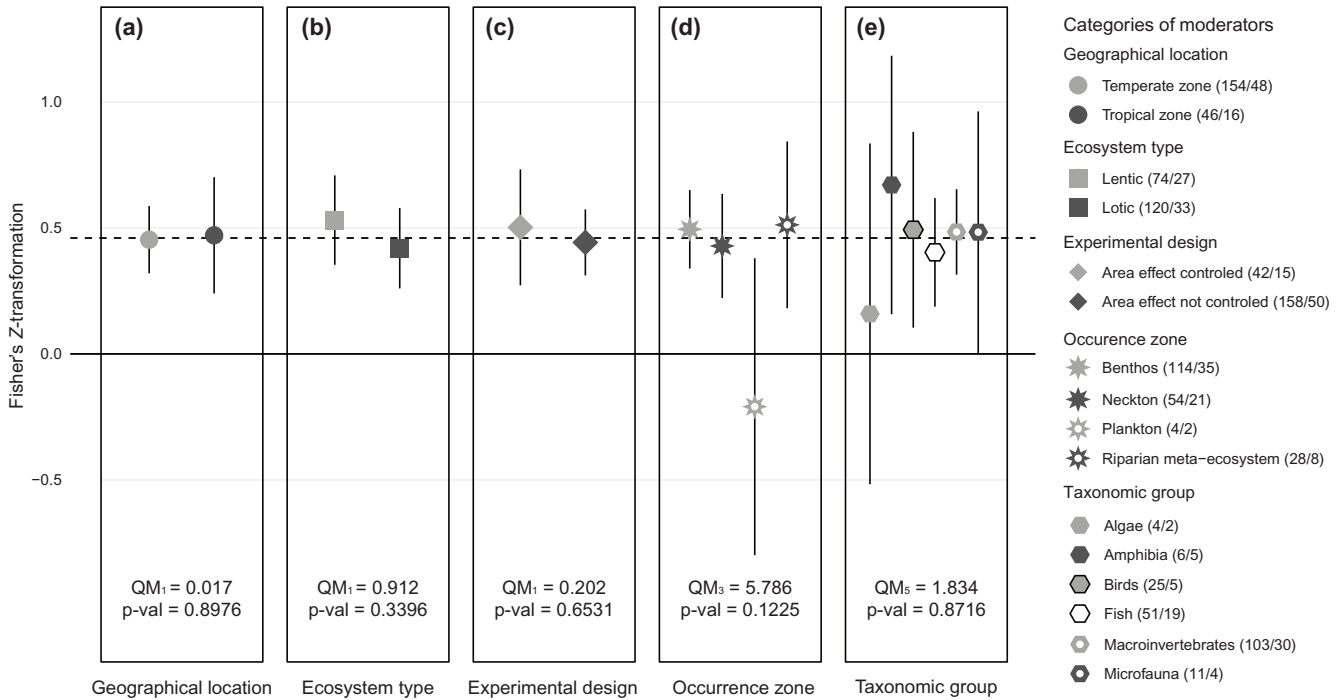


Figure 7. Mean effect size estimates over taxonomic alpha diversity, considering the following moderators: (a) geographical location, (b) ecosystem type, (c) for experimental design controlled for the effect of surface area, (d) occurrence zone and (e) taxonomic group. Full dots are mean effect sizes 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.

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 and Kreft 2015). Still, wherever possible we encourage authors to stick with one single term with a clear conceptualization. In the methods section of the study, 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 evaluate 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 (used in 27% of the studies), mainly using different types of aquatic vegetation or substrates (Boyer et al. 2009, Guadagnin et al. 2009), and the structure approach (20% of the studies), mainly manipulating the structure of artificial substrates and

aquatic plants (Benson and Magnuson 1992, Osório et al. 2019). Third, the mixed approach has been increasingly used in ecological studies (16% of the studies), 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 (Kärnä et al. 2018, Agra et al. 2021). 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 versus high complexity) do not always show concordance with the perception of organisms (Shumway et al. 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), which

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 (Willis et al. 2005, Li et al. 2019). 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 freshwater 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 et al. 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 (Triantis et al. 2003, Báldi 2008), 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 and 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 EH 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 and Cohen 1991).

There was insufficient number of studies to test our second prediction, concerning the relationship between spatial EH over taxonomic and functional beta diversity. Even in the model that showed a significant positive relationship between EH and taxonomic beta diversity, the fail-safe number analysis showed the lack of strength of the model due to the low number of evidence. Thus, we here highlight this important literature gap and suggest the importance of data collection for these variables to be able to test the influence of EH on such metrics of biodiversity. Studies involving beta diversity have an additional difficulty on pattern definitions, because beta diversity is strongly dependent on a dispersal–environmental

control model (Heino et al. 2015). When the region scale extent is small, the mass effect can mask species sorting (Heino and Grönroos 2013, Agra et al. 2021), 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 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% of the studies) and not effectively tested (~16% of the studies). Similar to studies on terrestrial ecosystems (Stein and Kreft 2015), the most invoked ecological processes are ecological niche partitioning (Willis et al. 2005, Osório et al. 2019), resource availability (Burdett and Watts 2009, Milesi et al. 2016) and persistence (Schneck and 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 community dynamics. 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 et al. 2016). Also, the heterogeneity increment creates more space for refuge and retention, ensuring the individuals persistence when under pressure from predators or disturbances (Schneck and Melo 2013, Yang et al. 2015).

Since there is consistent evidence that spatial EH has a positive effect on the alpha diversity of freshwater 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 (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 et al. 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 et al. 2005, 2010). We conclude that biological communities can respond to different elements of a landscape, thus there is not a simple one way or mechanisms by which spatial EH can act to shape communities. 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 et al. 2005, Sundermann et al. 2011, Yang et al. 2015). Therefore, actions to increase spatial EH in a freshwater ecosystem need to be associated with 1) recovering of areas that are source of species colonization (regional pool), 2) creating connection between regional pool and the areas managed, and 3) reducing anthropogenic disturbances.

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Author contributions

Janaina Agra: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Writing – original draft (lead). **Tatiana Cornelissen:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (lead); Writing – review and editing (lead). **Arleu Barbosa Viana-Junior:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Validation (equal). **Marcos Callisto:** Conceptualization (supporting); Funding acquisition (lead); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.g4f4qrfw2> (Agra et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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