



Empirical evaluations between beta-diversity, environmental heterogeneity, and spatial extent among multiple taxonomic groups

Testes empíricos das relações entre diversidade beta, heterogeneidade ambiental e extensão espacial entre múltiplos grupos taxonômicos

Carlos Henrique Lopes Liborio^{1*} 

¹Programa de Pós-graduação em Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Goiás – UFG, Av. Esperança, s/n, Chácaras de Recreio Samambaia, CEP 74690-900, Goiânia, GO, Brasil

*e-mail: carloshlibo@gmail.com

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Abstract: Aim: Beta diversity is expected to increase due to environmental heterogeneity and spatial extent. However, it remains unknown whether the response of beta diversity to these variables is consistent among different taxonomic groups. I investigated whether the beta diversity of lacustrine phytoplankton, zooplankton, and macroinvertebrate communities within nine ecoregions in the United States of America correlates with environmental heterogeneity and spatial extent. **Methods:** I used simple linear regression analyses to examine how the beta diversity of different communities was related to environmental heterogeneity and spatial extent. **Results:** Phytoplankton and macroinvertebrate community's beta diversity was positively related to environmental heterogeneity, while zooplankton and macroinvertebrates' beta diversity was significantly related to the spatial extent (within ecoregions). **Conclusions:** My results align with theoretical expectations that beta diversity increases due to environmental heterogeneity and spatial extent. These results contribute to a better understanding of processes structuring the composition of different aquatic communities in the United States.

Keywords: biodiversity patterns; environmental complexity; ecoregional diversity; aquatic communities.

Resumo: Objetivo: É esperado que a diversidade beta aumente devido à heterogeneidade ambiental e à extensão espacial. No entanto, ainda é incerto se a resposta da diversidade beta a estes fatores é consistente entre diferentes grupos taxonômicos. Eu investiguei se a diversidade beta de comunidades de fitoplâncton, zooplâncton e macroinvertebrados de lagos dentro de nove ecorregiões nos Estados Unidos da América se correlaciona com a heterogeneidade ambiental e extensão espacial. **Métodos:** Utilizei análises de regressão linear simples para examinar como a diversidade beta de diferentes assembleias estava relacionada com a heterogeneidade ambiental e extensão espacial. **Resultados:** A diversidade beta das assembleias de fitoplâncton e macroinvertebrados foi positivamente relacionada à heterogeneidade ambiental, enquanto a diversidade beta das assembleias zooplâncton e macroinvertebrados foi significativamente relacionada à extensão espacial (dentro das ecorregiões). **Conclusões:** Esses resultados estão alinhados com as expectativas teóricas de que a diversidade beta aumenta devido à heterogeneidade ambiental e à extensão espacial. Esses resultados contribuem para uma melhor compreensão dos processos que estruturaram a composição de diferentes assembleias aquáticas nos Estados Unidos.

Palavras-chave: padrões de biodiversidade; complexidade ambiental; diversidade ecorregional; comunidades aquáticas.



1. Introduction

Beta diversity, the variation in species composition among spatially distinct sites or within a given region, is a central concept in ecology as it relates to understanding various ecological theories that explain biodiversity patterns (Barton et al., 2013; Mori et al., 2018; Godsoe et al., 2022). Despite the increased interest in environmental and spatial influences on beta diversity, few studies have explicitly investigated the associations of beta diversity with environmental heterogeneity (henceforth, EH) and spatial extent (Agra et al., 2024). This scarcity of studies probably arises from the plurality of definitions of the concept of beta diversity itself (i.e., (Tuomisto 2010a, b), which makes it challenging to identify suitable scenarios for applying empirical tests (Anderson et al., 2011). To address this challenge, I examined beta diversity as variation in community structure among sites within ecoregions (see Figure 4 on Anderson et al., 2011), highlighting the ability of ecoregions to capture spatial turnover in species composition at a biogeographic scale.

Studies analysing beta diversity across ecoregions often report positive associations with EH based on the premise that heterogeneous landscapes offer a broader array of ecological niches (Gómez et al., 2010; Astorga et al., 2014; Stewart & Schriever, 2023). Thus, ecoregions with high EH are expected to support higher species turnover, as distinct environmental conditions promote the establishment of different taxa in separate ecological compartments (Kotler & Brown, 1988; Heino et al., 2015a; Daleo et al., 2023). However, in some cases, high dispersal capacity (e.g., microbial taxa) combined with ecological plasticity may reduce the influence of environmental filtering, leading to weak or even non-significant associations between EH and beta diversity (Lopes et al., 2014; Diniz et al., 2021).

Similarly, several studies have reported positive relationships between spatial extent and beta diversity across ecoregions (Bini et al., 2014; Rodríguez-Alcalá et al., 2020; Reu et al., 2022). The expectation of an increase in beta diversity with an increase in spatial extent is based on the idea that larger geographic areas increase the dispersal limitation due to reduced habitat connectivity, promoting greater community differentiation (Heino et al., 2015b; Martín-Devasa et al., 2024). However, this relationship also appears to be context dependent. For instance, Godoy et al. (2025) showed that the influence of environmental drivers on macroinvertebrate beta diversity across the United States shifts with spatial extent: local

variables such as habitat structure and water quality were more relevant at finer scales, while climatic and watershed-level factors gained importance at broader spatial extents. These scale-dependent dynamics suggest that strong relationships between beta diversity and spatial extent or EH are likely to emerge under specific ecological conditions, depending on the dispersal traits and environmental sensitivity of the taxa involved.

Most investigations into EH and spatial extent effects on beta diversity have focused on smaller spatial scales (e.g., Carvalho et al., 2016; Kessler et al., 2009) and specific taxonomic groups, particularly plants and vertebrates (e.g., Melo et al., 2009; Steibl & Russell, 2024). Furthermore, more studies are needed to enable robust generalizations about the relationships of beta diversity, EH, and spatial extent in aquatic ecosystems (Agra et al., 2024). Expanding these studies to include vast geographic regions (e.g., biomes) and diverse taxa (e.g., micro and macro-organisms) has the potential to minimize taxonomic (i.e., the tendency to select only a few taxonomic groups) and spatial bias, providing thus a more comprehensive view of the influences of the environment and space on beta diversity (Mammola et al., 2023).

In freshwater ecosystems body size has been recognized as a functional attribute determining dispersal patterns and related beta-diversity patterns (Shurin et al., 2009). Smaller organisms (e.g., plankton) are expected to exhibit compositional variations more closely related to environmental gradients (Bie et al., 2012; Padial et al., 2014). In comparison, larger organisms tend to present a more apparent spatial structure due to dispersal restrictions and biogeographic history. For example, Potapova & Charles (2002) showed that diatom communities were strongly associated with a eutrophication gradient across the continental United States. In a complementary manner, Si et al. (2025) demonstrated that riverine macroinvertebrate communities can express strong beta diversity patterns mediated by spatial variables rather than environmental variables. Nevertheless, an empirical gap remains regarding the integrated assessment of multiple biological communities, divergent body size, and their respective relationships with EH and spatial extent.

Here, I investigate whether the beta diversity of phytoplankton, zooplankton, and macroinvertebrate communities increases in response to the EH and spatial extent of ecoregions across the United States of America (Figure 1). Specifically, I expect to (i) detect positive associations between beta

diversity and EH across all communities considered (ii) observe stronger relationships between beta diversity and EH in planktonic communities, given their higher sensitivity to environmental variation and (iii) identify weaker associations between beta diversity and spatial extent in planktonic communities compared to macroinvertebrates, due to their generally higher dispersal capacities.

2. Methods

I used an extensive collection of lake data covering the continental territorial extension of the United States of America (Figure 1). This data set was collected and systematized in 2012 through surveys conducted by the National Lakes Assessment (NLA) program. This data set comprises information about the communities of phytoplankton, zooplankton, and benthic macroinvertebrates, along with individual lake geographical coordinates and abiotic variables. Detailed instructions on collection procedures are available in field and laboratory manuals (USEPA, 2011, 2012), as well as the database accessible on the United States Environmental Protection Agency (USEPA, 2024).

2.1. Environmental variables

Within the variables available in the NLA database, I used the following environmental

variables: chlorophyll-a ($\mu\text{g/L}$), total nitrogen ($\mu\text{g/L}$), total phosphorus ($\mu\text{g/L}$), turbidity (NTU), pH, ammonia (mg/L), elevation (m), lake area (ha) and depth (m). These or comparable variables have been used in previous research examining community–environment relationships and are considered critical variables in structuring aquatic communities (e.g., García-Girón et al., 2020; Liborio & Loyola-Bartra, 2025). Pearson correlations among these variables were all less 0.5, indicating low collinearity.

2.2. Biological sampling

2.2.1. Phytoplankton

Phytoplankton was collected approximately 0.3 meters under the water surface, in areas of the lakes' littoral zone with approximately 1m (for more details, see USEPA, 2012; p. 76). Briefly, phytoplankton counts were conducted until reaching at least 400 natural units, and when possible, identification was taken to the species level. (see also USEPA, 2012, p. 28-29 for more information). In the original Lakes National Assessment (NLA) dataset, 841 taxonomic units were identified, representing organisms identified at different taxonomic levels.

2.2.2. Zooplankton

Two Wisconsin nets were used to collect zooplankton, one with a 50- μm and the other

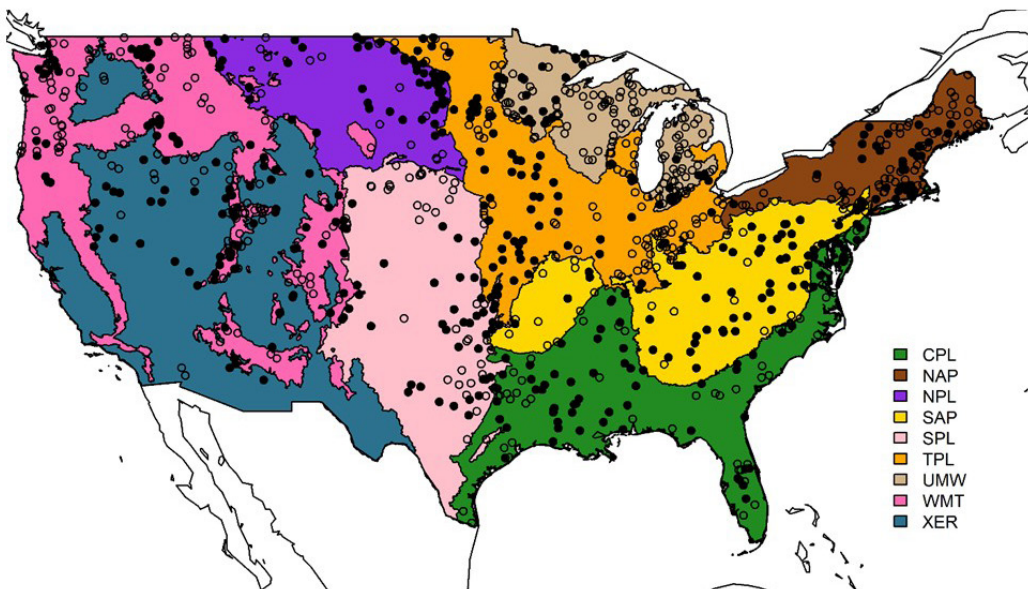


Figure 1. Ecoregions and 973 lakes sampled in the National Lakes Assessment (NLA) across the continental United States. Open circles represent lakes where only planktonic communities were sampled, while closed circles represent the 463 lakes where all assemblages (phytoplankton, zooplankton, and macroinvertebrates) were sampled. CPL = Coastal Plains; NAP = Northern Appalachians; NPL = Northern Plains; SAP = Southern Appalachians; SPL = Southern Plains; TPL = Temperate Plains; UMW = Upper Midwest; WMT = Western Mountains; XER = Xeric.

with a 150- μ m mesh, covering a cumulative length of 5 meters (see details in the USEPA manual; USEPA, 2012). The zooplankton count was conducted until reaching at least 400 individuals per sample (USEPA, 2012). In total, 327 zooplankton taxonomic units were collected and identified at different taxonomic levels. Detailed information on field sampling and zooplankton identification procedures can also be found in USEPA field and laboratory manuals (USEPA, 2011, 2012).

2.2.3. Macroinvertebrates

Macroinvertebrate sampling was conducted through a stratified sample approach encompassing diverse lake habitats (see USEPA, 2012, p. 77-78 for additional details). Each macroinvertebrate sample was counted to 300 individuals and identified at the most specific taxonomic level possible (up to genus when possible). The complete data set encompassed 516 taxonomic units identified at various levels, such as genus, family, order, class, or phylum. In all cases, we used the lowest possible taxonomic level as our community matrix (i.e., phytoplankton, zooplankton, and macroinvertebrate communities).

2.3. Biological and environmental similarity matrices

I used the log-chord distance to calculate the distance matrices between lakes individually for each taxonomic group. The log-chord coefficient mitigates skewness in abundance distribution and maintains essential Euclidean properties in linear multivariate approaches (Legendre & Borcard, 2018). I used previously standardized Euclidean distances to calculate the matrix of environmental distances between pairwise sites.

2.4. Estimating EH, spatial extent, and beta diversity

I accessed beta diversity through a multivariate dispersion homogeneity analysis (PERMDISP; Anderson et al., 2006). EH (of each ecoregion) was measured from standardized Euclidean distance matrices, following an approach previously used in beta diversity estimation (see Anderson et al., 2006).

I assessed spatial extent using two complementary approaches: (i) the total spatial area of each ecoregion (km^2) and (ii) the maximum Euclidean distance between two sites within each ecoregion. Both measures are commonly used in ecological studies (e.g., Godoy et al., 2025; Liborio & Bini, 2024) and capture different dimensions of spatial extent. They represent the physical scale over which ecological processes occur. This approach was informed by the selection of lakes sampled in the NLA 2012 dataset, ensuring spatial distribution across the nine

aggregated Omernik Level III ecoregions (Figure 1; see also USEPA, 2012, p. 2 for additional details). These aggregated ecoregions were derived from the original Omernik Level III (see Omernik, 1995) framework and specifically adapted to improve large-scale ecological assessments. The aggregation process aimed to maximize the similarity of streams of macroinvertebrate communities within each ecoregion while minimizing their differences (Herlihy et al., 2008). This approach ensured that each aggregated ecoregion represented a relatively homogeneous ecological unit, which is particularly important for establishing reference conditions and interpreting spatial patterns in aquatic biodiversity for diverse biological groups (Herlihy et al., 2008).

I also performed a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) using distance matrices to test with 999 permutations whether differences between ecoregions in community compositions and environmental conditions are greater than expected by chance.

I conducted simple linear regression analyses to explore whether distance to the centroid (representing beta diversity, as indicated by the previously mentioned PERMDISP; see Anderson et al., 2006) responds to EH and spatial extent. Linear regressions directly test whether community composition variation increases with increasing EH or spatial extent.

The analyses were performed using functions available for the R environment (R Core Team, 2023): log-chord distance (`dist.lcd` function from the `adespatial` package); PERMANOVA and PERMDISP (`adonis2` and `betadiver` functions, respectively, from the `Vegan` package); Regressions using the `lm` function from the `stats` package.

3. Results

Beta diversity and EH varied significantly between ecoregions (Table 1). The phytoplankton community had the highest beta diversity in all ecoregions. In general, the Northern Plains, Southern Plains, and Western Mountains ecoregions, were those that presented the highest values of EH (Table 2). Moreover, the Northern Appalachian and Upper Midwest ecoregions had the most minor EH (Table 2).

Beta diversity was correlated with ecoregions' spatial extent and EH (Figure 2). However, the magnitudes of the relationships varied considerably between taxonomic groups (Table 3). We detected significant relationships between EH and beta diversity for phytoplankton and macroinvertebrate communities but not for the zooplankton community

Table 1. Results of PERMANOVA tests evaluating differences in the dispersion of beta diversity and environmental heterogeneity (EH) between ecoregions.

	Taxonomic groups	R ²	F	p
Beta diversity	Phytoplankton	0.06	7.98	0.001
	Zooplankton	0.11	16.37	0.001
	Macroinvertebrates	0.09	5.70	0.001
EH	Plankton	0.12	16.30	0.001
	Macroinvertebrates	0.51	43.23	0.001

R² = coefficient of determination; F = F-test value; p = significance level.

Table 2. EH of each ecoregion and ecoregion size.

Ecoregions	EH (Plankton)	EH (Macroinvertebrates)	Ecoregion size (km ²)
CPL	1.89	1.9	1036836.8
NAP	1.29	1.3	356014
NPL	2.44	2.4	532465.1
SAP	1.22	1.41	841692
SPL	2.45	2.14	1081191.1
TPL	1.7	1.63	897025.2
UMW	1.1	1.18	404043.3
WMT	2.14	2.08	1044711.4
XER	1.9	2.02	1595756.6

EH was calculated based on all 973 sites where planktonic communities were sampled and the subset of 463 sites where macroinvertebrates were sampled. The abbreviations correspond to the ecoregions: CPL = Coastal Plains; NAP = Northern Appalachians; NPL = Northern Plains; SAP = Southern Appalachians; SPL = Southern Plains; TPL = Temperate Plains; UMW: Upper Midwest; WMT: Western Mountains; XER = Xeric, respectively (see also Figure 1).

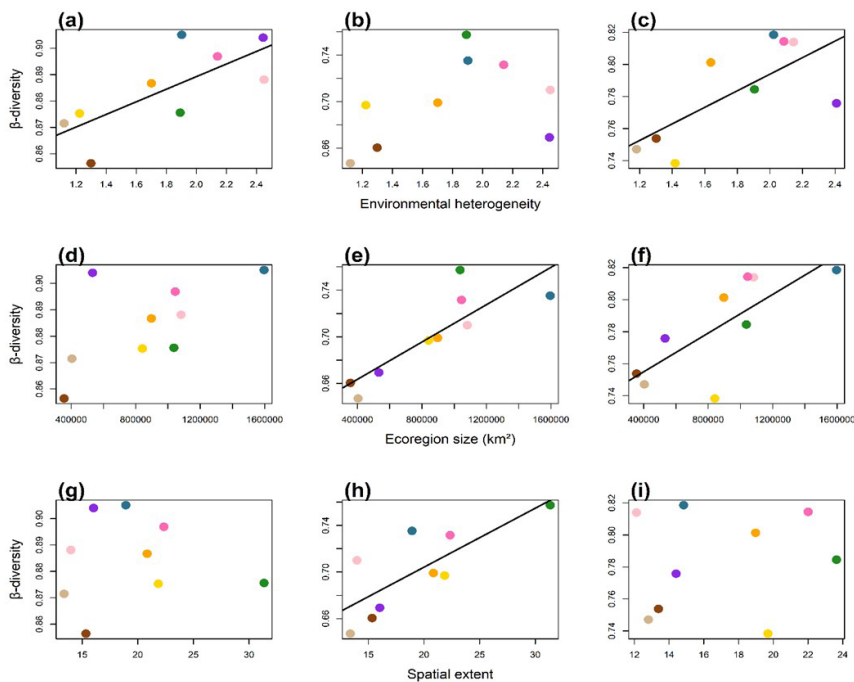


Figure 2. Relationships between beta diversity and explanatory variables across the nine ecoregions for the three aquatic communities studied. Panels (a), (b), and (c) show the relationships between beta diversity and EH for phytoplankton, zooplankton, and macroinvertebrates, respectively; Panels (d), (e), and (f) show the relationships between beta diversity and spatial extent measured as ecoregion area (km²) for phytoplankton, zooplankton, and macroinvertebrates, respectively; Panels (g), (h), and (i) depict the relationships between beta diversity and spatial extent measured as the maximum Euclidean distance between sites within each ecoregion for phytoplankton, zooplankton, and macroinvertebrates, respectively. Each point and its respective colors correspond to the ecoregions defined in Figure 1.

Table 3. Results of linear regressions between beta diversity and its ecoregional correlates. These variables were calculated for each taxonomic group.

Taxonomic groups	Correlates	F	R ²	Slope
Phytoplankton	EH	8.57	0.55	0.02
	Region Size	4.01	0.36	2.49
	Spatial Extent	0.001	0.01	3.1
Zooplankton	EH	1.58	0.18	0.03
	Region Size	17.9	0.71	8.01
	Spatial Extent	10.2	0.59	0.005
Macroinvertebrates	EH	8.89	0.49	0.05
	Region Size	9.56	0.72	6.03
	Spatial Extent	0.1	0.01	0.001

R² = coefficient of determination; F = F-test value. Values in bold are significant.

(Figures 2a-c). On the other hand, the beta diversity of zooplankton and macroinvertebrate communities was significantly and positively related to ecoregion size (Figures 2e and 2f). This relationship was not significant for the phytoplankton community (Figure 2d). The zooplankton community was the only one that showed a significant association with spatial extent based on the maximum distance between lakes (Figure 2h; see also Table 3).

4. Discussion

The initial expectation was to identify positive relationships between beta diversity and EH for the three taxonomic groups. I observed positive and significant correlations between the beta diversity of the phytoplankton and macroinvertebrates with EH. However, I did not observe this relationship when evaluating the zooplankton community. Thus, the hypothesis that planktonic communities would be better predicted by EH than spatial extent was only partially confirmed. On the other hand, the beta diversity of the zooplankton community was correlated with the spatial extent. The regression slope coefficients comparing ecoregion size and spatial extent with beta diversity were higher for the zooplankton community than phytoplankton and macroinvertebrates. Therefore, the expectation of a stronger relationship between macroinvertebrate communities and spatial extent, compared to planktonic communities, was only partially confirmed.

Understanding the mechanisms that structure beta diversity at large geographic scales has advanced by incorporating ecoregional approaches (Smith et al., 2018, 2020). Although many studies have focused on local or regional scales, relatively few explicitly address how EH and spatial extent influence beta diversity patterns across ecoregions. However, this study points to a consistent trend that

environmental and spatial factors simultaneously influence compositional variation among communities on a continental scale. This trend is corroborated by other studies, for example, by Veech & Crist (2007), who identified a positive relationship between bird beta diversity and spatial extent, highlighting the importance of considering environmental variation across ecoregions and its spatial effects to understand the structure of beta diversity. In this same context, Siegloch et al. (2018) highlighted the relevance of local EH in maintaining the ecoregional diversity of aquatic insects. However, by simultaneously analyzing the relationships between environment and space in steams macroinvertebrates, Bini et al. (2014) found positive relationships between invertebrate beta diversity, EH, and spatial extent in ecoregions of the United States.

Meta-analytic studies have shown that EH is a consistent predictor of both alpha diversity (see Stein et al., 2014; Ortega et al., 2018) and beta diversity (Agra et al., 2024). I found positive relationships between EH and beta diversity of phytoplankton and macroinvertebrate communities. This result aligns with most existing observations that address the topic in similar studies (Bini et al., 2014; Astorga et al., 2014; Mondal & Bhat, 2022). The association between EH and beta diversity of phytoplankton and macroinvertebrate communities can be attributed to the high sensitivity of these organisms to local environmental conditions. Phytoplankton, for example, have a high turnover rate and respond rapidly to eutrophication gradients (Cai et al., 2017; Salk et al., 2022). Similarly, benthic macroinvertebrates are structurally dependent on microhabitats (e.g., substrate type, water flow, refuge availability) and, therefore, highly susceptible to physicochemical variations (Šorfová et al., 2022). These factors reinforce the idea that environmental heterogeneity acts as an important ecological filter for these communities, even at large geographic scales.

Unexpectedly, I did not detect this relationship between beta diversity and EH when considering the zooplankton community, which contradicts most of the results reported in the literature (Beaver et al., 2014; Galir Balkić et al., 2018; Rizo et al., 2020; Ramos et al., 2023). However, similar results have been reported in other contexts. For instance, Lopes et al. (2014) also failed to detect such a relationship for zooplankton communities in continental aquatic environments in Brazil. Similarly, Diniz et al. (2021), analyzing zooplankton communities in arid and semi-arid regions of Brazil, found no significant compositional differences between these two ecoregions. Overall, this lack of a clear pattern can be attributed to at least two non-mutually exclusive mechanisms: (i) the dominance of generalist species with broad geographic distributions (Brown, 1984; Slatyer et al., 2013), and (ii) high ecological plasticity, which enables these species to persist across a wide range of environmental conditions (Yampolsky et al., 2013). Furthermore, other studies have detected a negative or non-significant relationship between beta diversity and EH, considering other taxonomic groups (e.g., macroinvertebrates as in Heino et al., 2013). These results and those described above suggest that the role of EH may depend on the taxonomic group studied or the environmental context.

The positive relationship between beta diversity and spatial extent observed mainly for the zooplankton highlights the role of dispersal limitation in structuring these communities. Furthermore, compared to macroinvertebrates and phytoplankton, zooplankton was the group that showed the most pronounced response to spatial extent. This result indicates that differences in dispersal capacity may play a central role in shaping the observed patterns. In particular, the lack of spatial relationship for phytoplankton may reflect this group's wide distribution and high dispersal capacity, supporting the hypothesis that "[...] everything is everywhere, but the environment selects" (de Wit & Bouvier, 2006). In contrast, the stronger spatial responses observed for zooplankton suggest more pronounced dispersal limitations for this group. These findings highlight the need for future studies that investigate the relative contributions of dispersal limitation among different taxonomic groups and across various spatial scales (e.g., Lansac-Tôha et al., 2019, 2021; Liborio & Bini, 2025).

Macroinvertebrates, in turn, exhibited a mixed pattern: they did not respond to maximum distance between sites, but showed an increase in beta diversity

with ecoregion size. This finding (i.e., increased beta diversity with ecoregion size) aligns with the expectation that organisms with comparatively more limited dispersal capacity tend to exhibit greater compositional differentiation as the size of the sampled regions increases (Hepp & Melo, 2013). However, because macroinvertebrates comprise taxa with contrasting dispersal strategies (e.g., flying and non-flying macroinvertebrates; see Tolonen et al., 2018), the observed increase in beta diversity with ecoregion size may reflect both limited dispersal of less mobile taxa and species turnover driven by environmental gradients across large areas, thus making it difficult, for example, to detect a positive relationship between beta diversity and maximum distance between sites. Furthermore, these results suggest that the two spatial metrics capture distinct aspects of spatial processes: maximum distance may be less relevant for taxa strongly dependent on local habitat conditions. At the same time, ecoregion size may better reflect broader habitat heterogeneity and potential dispersal barriers. Future studies incorporating trait-based or species-level information (e.g., dispersal mode, habitat specialization) may help identify which subgroups drive these patterns and elucidate how dispersal limitation operates within such a diverse taxonomic group.

The differences observed in the correlation patterns between beta diversity, EH and spatial extent among biological groups indicate that these organisms respond differently to the same environmental and spatial gradients. This divergence in responses was corroborated by Liborio & Bini (2024), who identified low compositional concordance among planktonic and macroinvertebrate communities in United States lentic ecosystems. Such differences have relevant implications for biomonitoring and conservation of aquatic biodiversity, as they suggest that management strategies based on a single taxonomic group may not adequately capture regional biological diversity nor faithfully reflect the responses to environmental disturbances that these ecosystems have been experiencing (Dudgeon et al., 2006). In this context, adopting multi-taxonomic approaches has the potential to broaden the understanding of the effects of environmental changes on the structure of biological communities, in addition to allowing the formulation of conservation strategies more representative of the ecological complexity of continental aquatic ecosystems.

In summary, this study reinforces that beta diversity in continental ecoregions is shaped by the interaction between environmental filters and spatial processes, whose effects are modulated by

the ecological characteristics of different taxonomic groups. The detection of positive associations between EH and beta diversity of phytoplankton and macroinvertebrates highlights the deterministic role of the environment in structuring these communities. In contrast, the absence of this relationship for zooplankton raises relevant questions about the mechanisms that govern the assembly of this community. The use of different metrics to represent spatial extent—such as ecoregion area and maximum distance between sites—allowed us to capture other dimensions of dispersal limitation, especially in the case of macroinvertebrates. Analysing how different dimensions of spatial extent can capture complementary variations in beta diversity may be a promising avenue for future research.

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Data availability

The original data is freely available from the US EPA websites, at <https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys>.

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