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**Efeitos espaciais e ambientais sobre diferentes  
medidas de diversidade beta em ecossistemas  
continentais**

Goiânia, GO  
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# **Efeitos espaciais e ambientais sobre diferentes medidas de diversidade beta em ecossistemas continentais**

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## ATA DE DEFESA DE TESE

Ata Nº 137 da sessão de Defesa de Tese de **Breno Laio Medeiros de Rezende**, que confere o título de Doutor em **Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução**.

Ao/s trinta dias do mês de outubro de dois mil e vinte e três (30/10/2023), a partir das 13h30 min, por vídeo conferência, seguindo Resolução CONSUNI/UFG Nº 141 de 13 de maio de 2022 e orientações do Ofício Circular no. 34/2022/PRPG/UFG (SEI 23070.030951/2022-07), realizou-se a sessão pública de Defesa de Tese intitulada "Efeitos espaciais e ambientais sobre diferentes medidas de diversidade beta em ecossistemas continentais". Os trabalhos foram instalados pelo Orientador **Prof. Dr. Adriano Sanches Melo (Depto Ecologia/IB/UFRGS)**, com a participação dos demais membros da Banca Examinadora: **Profa. Dra. Levi Carina Terribile (Depto Biologia/UFJ)**, membro interno, **Prof. Dr. Fabrício Barreto Teresa (RENAC/UEG)**, membro externo, **Prof. Dr. Fernando Gertum Becker (Depto Ecologia/IB/UFRGS)**, membro externo e **Profa. Dra. Rafaela Vendrametto Granzotti (ICB/UFG)**, membro externo. Durante a arguição os membros da banca não fizeram sugestão de alteração do título do trabalho. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da Tese tendo sido o candidato **aprovado** pelos seus membros. Proclamados os resultados pelo **Prof. Dr. Adriano Sanches Melo**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora, ao(s) trinta dias do mês de outubro de dois mil e vinte e três (30/10/2023).

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## **Apresentação da Tese**

A seguinte tese possui as seguintes partições: introdução geral, capítulo 1, capítulo 2, capítulo 3, e por fim considerações finais. Os capítulos seguem a formatação de artigos científicos, portanto contendo resumo, introdução, métodos, resultados e discussão. A tese possui temas variados, porém seu cerne é focado na diversidade beta de organismos de ambientes continentais. Mais especificamente, os dois primeiros capítulos abordam a diversidade beta de organismos de água doce enquanto o último trata da diversidade beta de mamíferos terrestres e aves. O primeiro capítulo é uma revisão sistemática que aborda o questionamento se a amplitude das diferenças das variáveis ambientais são responsáveis por determinar os tamanhos de efeito entre dissimilaridade beta e variáveis ambientais em ambientes de água doce. No segundo capítulo investigo efeitos de custos de dispersão sobre a diversidade beta de peixes de ambientes lóticos em quatro bacias hidrográficas do estado da Carolina do Norte, Estados Unidos da América. A justificativa para abordar determinada região se deve a natureza dos dados, que abrange inúmeras localidades em bacias hidrográficas com considerável tamanho de área e que, portanto, consegue capturar muito bem os efeitos de custos de dispersão em metacomunidades aquáticas. O terceiro e último capítulo é fruto de um questionamento concebido através da discussão dos resultados do primeiro capítulo, no qual investigo se o gradiente latitudinal é responsável por influenciar nossas interpretações das relações entre diferenças ambientais e diversidade beta em escala continental. Portanto, este último capítulo navega por temas mais associados a Biogeografia e Macroecologia, divergindo um pouco dos demais capítulos. A última seção finaliza a tese sintetizando as principais ideias em formato de conclusão.

## Resumo

Já faz muitos anos que o termo diversidade beta tem sido alvo de discussão e aplicação em estudos de Ecologia e, aparentemente, suas abordagens e aplicações parecem ser inesgotáveis uma vez que diferentes medidas de diversidade beta têm surgido com os anos. O primeiro capítulo desta tese trata-se de uma revisão sistemática na qual investiguei se a amplitude das diferenças ambientais são responsáveis por influenciar os tamanhos de efeito em estudos que avaliaram a relação entre diversidade beta e variáveis ambientais em ambientes de água doce. De acordo com os resultados obtidos, a amplitude parece não influenciar nos tamanhos de efeito. No segundo capítulo, investigo se efeitos de custos de dispersão em metacomunidade de ambientes lóticos são responsáveis por determinar a diversidade beta de peixes. Os resultados evidenciaram a influência de custos de dispersão associados a distâncias entre localidades ao longo de rios e riachos para três bacias hidrográficas, enquanto custos de dispersão representado pela combinação de efeitos entre distâncias entre localidade e declividade do canal somente foram observados em uma única bacia. Além disso, para uma das bacias hidrográficas, foi observado a influência dos custos de dispersão representados por efeitos mútuos da distância entre localidade e a área total de reservatórios formados por barragens. No terceiro capítulo investigo se o gradiente latitudinal é responsável por influenciar as relações entre diferenças ambientais e dissimilaridade beta obtidos em formato de células quadradas para todo o continente da América usando registros de distribuição de aves e mamíferos terrestres. A dissimilaridade beta tanto de aves e mamíferos terrestres foram explicados por variáveis ambientais, porém, somente a relação entre diferenças ambientais e diversidade beta de mamíferos parecem ser influenciados por padrões latitudinais.

**Palavras-chaves:** Diversidade beta; Meta-análise; Padrões de gradiente latitudinal; Diversidade funcional; Custos de dispersão; Amplitude de variáveis ambientais; Ambientes de água doce.

## **Abstract**

It has been many years since the term beta diversity has been the subject of discussion and application in Ecology studies, and apparently its methodological approaches and applications seems to be inexhaustible, as different measures of beta diversity have emerged over the years. The first chapter of this thesis is a systematic review in which I investigated whether the amplitude of environmental differences is responsible for influencing effect sizes in studies that assessed the relationship between beta dissimilarity and environmental variables in freshwater environments. According to the results obtained, the amplitude does not seem to influence effect sizes. In the second chapter I investigate whether dispersal costs effects in lotic metacommunities are responsible for determining the beta dissimilarity of fishes. The results revealed the influence of dispersal costs associated with distances between locations along rivers and streams for three basins, while dispersal costs represented by the combination of distances and channel slope were only observed in a single basin. Furthermore, for one of the river basins, the influence of dispersal costs was represented by mutual effects of the distance between locations and the total area of reservoirs formed by dams between locations. In the third chapter I investigate whether the latitudinal gradient is responsible for influencing the relationships between environmental differences and beta dissimilarity obtained in square cell format for the entire continent of America using records of distribution of terrestrial birds and mammals. Beta dissimilarity in both terrestrial birds and mammals was explained by environmental variables, but only the relationship between environmental differences and beta diversity of mammals appears to be influenced by latitudinal patterns.

**Keywords:** Beta diversity; Meta-analysis; Latitudinal gradient patterns; Functional diversity; Costs of dispersal; Environmental variables extent; Freshwater environments.

## Introdução Geral

A biodiversidade é um dos principais temas de estudo da Ecologia. As métricas mais tradicionais para avaliar a variação biológica são as diversidades alfa, beta e gama. Além disso, há uma quarta métrica de variação biológica com menor popularidade conhecida como zeta, que explora o particionamento de assembleias (Cang & McGeoch 2014). As medidas alfa, beta e gama têm como características em comum a capacidade de descrever a organização das espécies em comunidades; no entanto, elas diferem na perspectiva de como as espécies estão organizadas em relação a escalas espaciais (Jurasinski *et al.* 2009). A diversidade alfa mede a variação biológica nas localidades, enquanto a diversidade gama mede a variação em uma área maior que abrange muitas localidades. A diversidade beta é uma medida de comparação da variação biológica entre comunidades (pares de comunidades ou múltiplos-sítios) separadas pelo tempo ou espaço.

A definição e propagação do conceito de diversidade beta foi conduzido por Whittaker (1960) e, desde então, o conceito tem sido utilizado para avaliar a diversidade beta baseado na diferença entre a diversidade local (alfa) e a diversidade regional (gama). Além disso, a diversidade beta pode ser utilizada para medir o decaimento da similaridade ao longo de distâncias ou a taxa de substituição de espécies ao longo de gradientes espaciais e/ou ambientais. Em adição, existem diversas maneiras de estimar diversidade beta, o que inclui índices de dissimilaridade como por exemplo o tradicional índice de Jaccard e o índice de Sørensen. Koleff *et al.* (2003a) revisaram 24 índices de dissimilaridade que podem ser usados como estimadores de diversidade beta para dados de presença e ausência de espécies. Tuomisto (2010a, 2010b) realizou uma extensiva revisão sobre as medidas de diversidade beta, analisando suas aplicações, conceitos e propriedades matemáticas, um reflexo do uso extensivo do conceito de diversidade beta nas últimas décadas. Algumas medidas de diversidade beta podem ser particionadas em componentes de aninhamento (ou diferenças de riqueza de espécies) e de substituição de espécies (Baselga 2010). Atualmente, tem sido explorado diferentes abordagens de

quantificação de diversidade beta; como exemplos, temos o desenvolvimento de dispersão de escores de grupos de amostras em ordenação (PermDisp; Anderson *et al.* 2006), razões de índices de diversidade beta (Dobrovolski *et al.* 2012), contribuições locais para a diversidade beta (LCDB) (Legendre & De Cáceres 2013) e o índice de diversidade beta temporal (Legendre 2019).

As medidas de diversidade beta são influenciadas pela qualidade dos dados e o método de amostragem, como por exemplo, a posição espacial das unidades amostrais e o número de espécies amostradas por unidade (Beck 2013). Outros fatores importantes são a extensão espacial, que é o tamanho da unidade regional ou a maior distância/área/volume que abrange todas as unidades amostrais, e o tamanho do grão, que é o tamanho da unidade amostral (Wiens 1989, Barton *et al.* 2013). Isso se deve ao fato que unidades amostrais maiores possuem maior probabilidade de amostrar novas espécies, portanto, contribuindo no aumento de riqueza de espécies por localidade (Barton *et al.* 2013). Quanto mais espécies são abordadas em um estudo maior é a dificuldade de compreender os mecanismos responsáveis por gerar padrões de distribuição, pois as espécies respondem de forma distinta aos efeitos ambientais (*e.g.*, organismos endotérmicos e exotérmicos). Além disso, quanto maior o número de espécies investigadas em um estudo maior será o número de possíveis mecanismos responsáveis por gerar os padrões de distribuição de espécies (Marquet *et al.* 2004).

A quantificação mais clássica de diversidade beta é a taxonômica, no entanto, é possível obter medidas de diversidade beta usando traços funcionais e distâncias filogenéticas. Uma vantagem dessa abrangência de aplicação de medidas beta permite uma melhor investigação de processos e mecanismos em estruturas de comunidades (Verberk *et al.* 2013). Além disso, a diversidade beta filogenética e funcional possibilitam a investigação composicional de espécies influenciada por efeitos histórico-evolutivos (Cianciaruso 2011). Por exemplo, regiões de diversificação de clados podem ser detectados quando observados altos valores de substituição de espécies (diversidade beta taxonômica), em contraste a baixos valores de substituição de diversidade beta filogenética (*i.e.*, região composta por inúmeras espécies irmãs) (Cianciaruso 2011).

Minha tese inclui três estudos que abordam a diversidade beta. A primeira é revisão sistemática que aborda os efeitos da amplitude de variação do gradiente ambiental de múltiplas variáveis sobre a diversidade beta. Por muitos anos, os efeitos de fatores ambientais sobre a diversidade biológica têm sido investigados, como no caso de tendências de aumento ou diminuição da riqueza de espécies ou diversidade beta em relação ao gradiente ambiental. Por exemplo, sabe-se que a riqueza de espécies de aves diminui com o aumento da altitude, embora a diminuição da riqueza de espécies nem sempre seja monotônica (Rahbek 1995). No caso da relação entre altitude e diversidade beta de aves, a ausência de relações monotônicas entre as variáveis está associada a efeitos de microclima, cobertura vegetal e sombreamento em altitudes intermediárias. As altitudes intermediárias neste caso são responsáveis por criar pontos de alta diversidade quando comparado com os extremos do gradiente de altitude (Jankowski *et al.* 2009). Por outro lado, considerando especificamente ambientes lóticos, Specziár *et al.* (2018) observaram que a diversidade beta de mosquitos quironomídeos são determinados pelo gradiente ambiental, e a relação entre diversidade beta e gradiente é influenciado pela heterogeneidade ambiental. Conseqüentemente, a força e o sinal das correlações entre distância ambiental e a diversidade beta podem ser dependentes da amplitude do gradiente ambiental. Portanto, é esperado que estudos com gradiente extensos tenham maior probabilidade de detectar relações do que estudos com gradiente curtos.

O segundo capítulo aborda a influência de custos de dispersão na diversidade beta de diversos grupos funcionais de peixes de água doce. Os processos ecológicos são mais bem compreendidos quando a biodiversidade de grupos funcionais é analisada, pois assim é possível isolar as respostas específicas de cada grupo de espécies que compartilham alta afinidade a determinadas influências ambientais e espaciais (Lamouroux *et al.* 2002). Além disso, o uso de grupos funcionais permite uma compreensão adequada dos padrões ecológicos e seus mecanismos geradores. A diversidade beta vem sendo estudada há muitos anos sob a perspectiva dos grupos funcionais, o que inclui, por exemplo, a compreensão de condições ambientais determinantes da diversidade beta funcional (Villéger *et al.*

2012). Custos de dispersão são caracterizados por fatores que geram resistência ao movimento dos organismos entre localidades (Bonte *et al.* 2012). No caso de sistemas lóticos e especificamente para peixes, fatores que geram resistência à dispersão incluem características geomorfológicas dos rios tais como a declividade do canal, sinuosidade, presença de corredeiras e a distância entre localidades ao longo do canal (Camana *et al.* 2016, Mozzaquattro *et al.* 2020, Caetano *et al.* 2021). Portanto, neste capítulo investigo a influência de atributos geomorfológicos como custos de dispersão determinantes da diversidade beta taxonômica e funcional de peixes de rios e riachos de bacias hidrográficas dos Estados Unidos da América.

No terceiro capítulo investigo os efeitos das diferenças ambientais sobre a diversidade beta de espécies de mamíferos terrestres e aves do continente americano. Minha principal hipótese é que a relação entre a diversidade beta e a variação ambiental é dependente da latitude. Ao longo de várias décadas, tem sido detectado padrões do gradiente latitudinal tanto para a riqueza de espécies (Brown 2014, Field *et al.* 2008) como também para medidas de diversidade beta e seus componentes (Koleff *et al.* 2003b, Soininen *et al.* 2018). No entanto, ao longo dos últimos anos, muitos trabalhos têm relatado a não detecção do padrão latitudinal (Alahuhta *et al.* 2017, Heino & Alahuhta 2019, Xing & He 2019, Mruzek *et al.* 2022) como também divergências sobre quais seriam os principais mecanismos responsáveis por criar padrões latitudinais (Willig *et al.* 2003, Brown 2014, Nishizawa *et al.* 2022). Alguns autores argumentam que a falha da detecção de padrões latitudinais se deve por vieses associados a riqueza do *pool* de espécies (Kraft *et al.* 2011), ou devido aos métodos utilizados, ou simplesmente o padrão latitudinal não é válido para todos os grupos de espécies (Koleff *et al.* 2003). Portanto, neste capítulo utilizo o *Geographically Weighted Regression* (GWR) (Fotheringham *et al.* 2002) como uma abordagem que controla os efeitos de heterocedasticidade e de autocorrelação espacial que interferem nas relações lineares entre diversidade beta e diferenças ambientais. A autocorrelação espacial interfere na detecção de padrões latitudinais pois viola o pressuposto

estatístico de independência das amostras, enquanto a heterocedasticidade interfere no ajuste dos modelos. Nas próximas seções detalharei os três capítulos e seus desdobramentos.

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## **Chapter 1 – Is the environmental extent crucial to our interpretation of the relationship between environmental distances and beta diversity in freshwater ecosystems?**

### **Abstract**

Currently, great attention has been devoted to certain ecological factors that contribute to the species distribution patterns, such as climate, latitudinal gradient, productivity, and spatial extent. On the other hand, little attention has been given to the influence of the environmental extent on the relationship between environmental dissimilarity and beta diversity. One likely explanation for the lack of studies investigating the influence of environmental extent is that, in many cases, the environmental extent is correlated with other factors, such as spatial extent. Therefore, I conducted a meta-analysis on the relationship between environmental dissimilarity and beta diversity in freshwater ecosystems, including 34 studies. Thus, I tested the influence of environmental extent, using several proxy variables (76), on the effect size of the relationship between beta diversity and environmental dissimilarity. Additionally, organism groups, types of freshwater ecosystems (lotic or lentic), and spatial extent were analyzed as moderators, along with their interactions with environmental extent variables. The results do not indicate any influence of environmental extent or other moderators on effect sizes. These findings may be associated with other random effects that were not detected during the review, including latitudinal effects, species niche width, and specific methodological characteristics of the selected studies (choice of statistical methods, selection of environmental variables, and connectivity).

**Keywords:** Systematic review; Environmental distance; Freshwater; Beta diversity.

## Introduction

Recent studies have advanced the understanding of how patterns of biodiversity in aquatic ecosystems and their interpretations have been influenced by differences in spatial or environmental scales (*e.g.*, Rahbek 2005, Estes *et al.* 2018, Jarzyna & Jetz 2018, Chase *et al.* 2019, Keil & Chase 2019, Viana & Chase 2019). One aspect of scale is its extent, or the maximum difference between two units (or grains) encompassed by the study. This may refer to variation of the geographical extensions, known as spatial extensions (Viana & Chase 2019), climate, productivity, environmental heterogeneity (Field *et al.* 2008), altitudinal (Rahbek 2005) and latitudinal gradients (Soininen *et al.* 2018). However, the influence of environmental gradient length over the beta diversity of freshwater organisms has not been investigated yet in a systematic review. A possible explanation for the absence of studies addressing the importance of environmental extensions is the assumption that environmental extent is correlated with other extensions, such as spatial extension (Nekola & White 1999, Soininen *et al.* 2007). Consequently, the other extensions (particularly the spatial) assume the role of surrogates for the environmental extension.

Except for the case that dispersal limitation is important, beta diversity should respond directly to environmental conditions and resources, not to spatial extents *per se*. Although in many cases the spatial extent and environmental extent are correlated, there are situations where they are not (Heino 2009, Virtanen & Soininen 2012, Heino & Tolonen 2017), such as in watersheds that have suffered historical processes (*e.g.*, glaciation) that are characterized by high beta diversity in relation to distances between locations, but with low environmental variation (Heino 2009). The effect of environmental extent on the detection of important relationships in ecological studies follows the basic statistical advice that we should include as much variation of our explanatory variable as possible (Rahbek 1995, Leibold *et al.* 2004). Thus, the commonly opposing results found by different authors, and usually associated with local contingencies, may result from distinct environmental extents. Despite this concern regarding environmental extents, there are no studies that evaluated the

effects of the amplitude of environmental factors (*e.g.*, pH, conductivity, dissolved oxygen) on the beta diversity of freshwater ecosystems. The lentic and lotic ecosystems are diverse and each one includes distinct characteristics related to environmental conditions (Heino 2009, Heino *et al.* 2015b) even at short spatial scales such as mesohabitats (*e.g.*, riffles and pools in lotic ecosystems) (Costa & Melo 2008). Thus, the environmental dissimilarity can be high at short spatial scales, such as between adjacent riffle and pool habitats, or low when only riffle reaches kilometers apart are studied (Costa & Melo 2008, Heino *et al.* 2013).

The investigation of the environmental extension is crucial, as it influences the interpretations of correlations between environmental dissimilarity and beta diversity (Heino *et al.* 2015a). Usually, beta diversity between communities has been found to be positively correlated to environmental dissimilarity, yet this association may depend on environmental extent (Vinson & Hawkins 1998, Heino *et al.* 2015a). Also, the well-known positive correlation between beta diversity and geographic distance may depend on the mechanisms acting on communities such as dispersal. The dispersal can blur the detection of environmental effects because some species cannot reach suitable locations, or some species are present in unfavorable locations because of mass effects.

Species have distinct environmental niches and respond differently to changes in the environmental gradient (Wellborn *et al.* 1996, Heino 2005, Lappalainen & Soininen 2006). Thus, the species turnover along the environmental gradient is related to differences in their niches (Wellborn *et al.* 1996). Long environmental extensions include more diverse habitats and, in consequence, more environmental heterogeneity, which in turn is positively correlated with increased variation of species composition (Perez-Rocha *et al.* 2018). Therefore, it can be expected that studies including relatively large environmental extents enhance the likelihood to best represent the species composition in the studied sites (Nishizawa *et al.* 2021). Thus, species sorting should be strongly detected in large environmental extents (Heino *et al.* 2015a).

I conducted a systematic review and employed meta-analyses to assess the influence of environmental extent (range of variables related to habitat, physical and chemical features) on the beta diversity of freshwater organisms. I hypothesize that the explanatory power of environmental variables is dependent on their extent used in the study. The greater the environmental extent, the greater should be their strength to explain beta diversity. Consequently, studies that have low environmental extents should likely fail to observe important relationships between environment and beta diversity, whereas those that incorporate wide environmental extensions should present strong relationships. Additionally, response to environmental factors may depend on the biological group because each group has distinct niche requirement and dispersal capabilities; therefore, I evaluated the effect of the environmental extent on the relationship of beta diversity with environmental variables for each biological group separately (*e.g.*, aquatic insects, zooplankton, and fish). Furthermore, I tested whether the environmental extent is more important in the context of lotic or lentic ecosystems and the spatial extent of studies.

## **Methods**

### *1. Selection of articles*

I followed the suggested standards of PRISMA (*Preferred Reporting Items for Systematic Reviews and Meta-analysis*; Moher *et al.* 2009) to standardize the meta-analysis steps. The data was obtained from a screening of studies in the databases of the *ISI Web of Science* and *Scopus*. The screening of the studies was carried out in *Scopus* in May 2021 and the *ISI Web of Science* in June 2021. The search key was (“*environment\* filtering*” OR “*environment\* variables*” OR “*environment\* heterogeneity*” OR “*environment\* gradient*”) AND (“*beta diversity*” OR “*\*similarity*”

OR “*species turnover*” OR “*nested\**” OR “*β-diversity*”) AND (“*stream\**” OR “*river\**” OR “*lotic\**” OR “*lentic\**” OR “*pond\**” OR “*freshwater*”).

The studies found were included in the screening stage, where the abstracts were read, and the complete reading of the article was done in case of doubts about the information present in the abstract. Then, I retained those that included analyzes that applied environmental variables as predictors of the beta diversity in freshwater ecosystems. In addition, the articles retained were those that included the range of the environmental variables (the environmental extent) and effect size values associated with the statistics used to assess the relationship between environmental variable(s) and beta diversity. To avoid pseudoreplication, I retained the oldest study among those that employed the same dataset.

Due to the limited number of eligible studies to conduct the meta-analysis, I supplemented my dataset with effect sizes calculated from raw data. The raw data were obtained from the online database repository *Dryad* (Fig. 1). I searched for the raw data in June 2021 using the terms “*environment\**” and “*freshwater*” (Fig. 1). The species data were log-transformed (Melo 2021), and matrices of beta diversity were obtained using the Sørensen (presence-absence data) and Bray-Curtis (abundance) indices. Subsequently, Mantel correlations using the Pearson method were applied to beta diversity matrices and environmental distances matrices (Euclidean method) to obtain the effect sizes. The criterion for choosing the Mantel method and beta diversity indices (Sørensen and Bray-Curtis) was the large number of studies obtained in the screening of the literature that employed these analysis and indices.

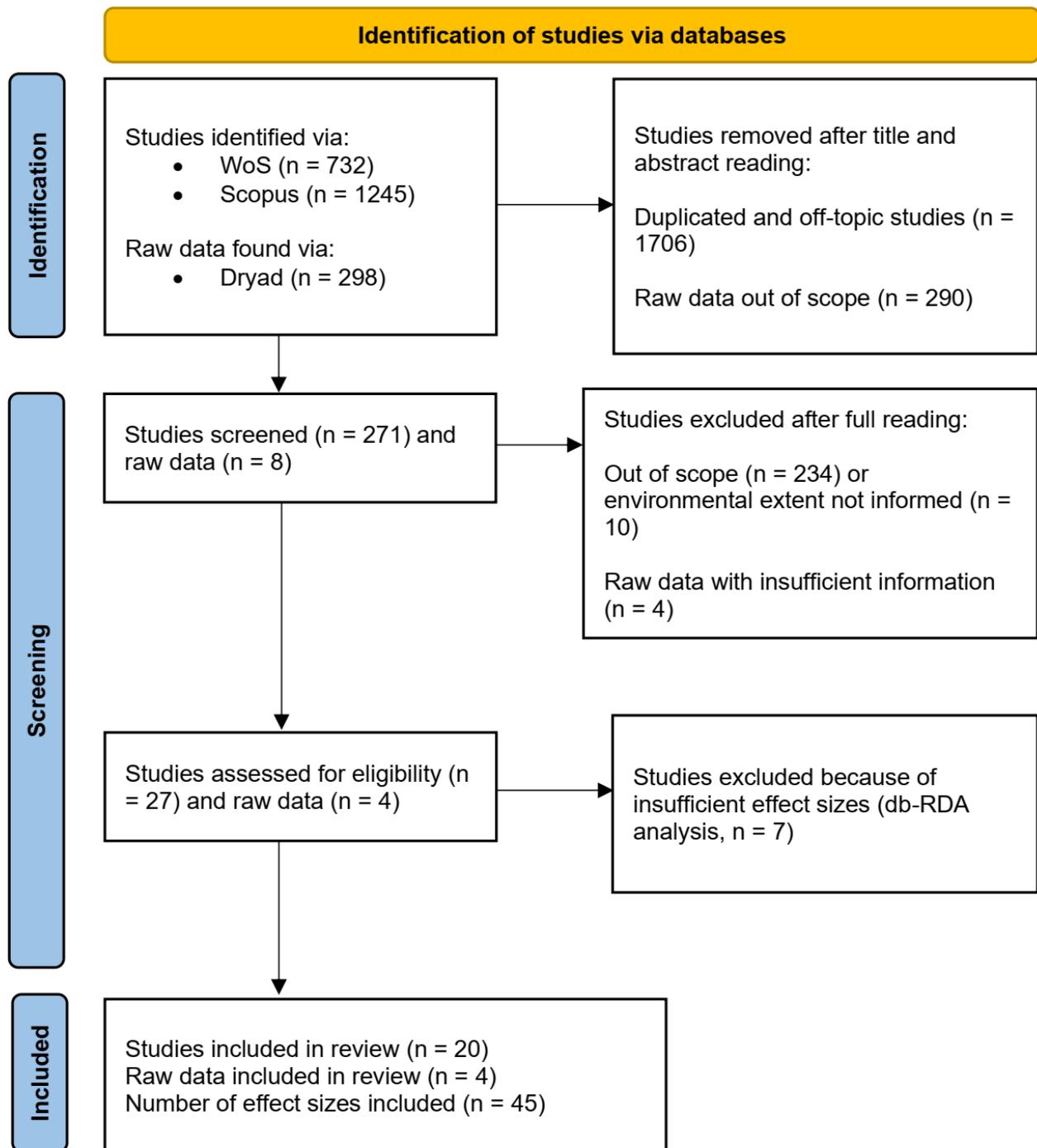


Figure 1. Flowchart summarizing each step of the procedure to select studies to be used in the meta-analysis, following the Preferred Reporting Items for Systematic Reviews and Meta-analysis (PRISMA, Moher *et al.* 2009).

In the screening stage, studies that estimated beta diversity between a focal community and the remaining samples, such as the LCBD (local contribution to beta diversity) or PermDisp (permutational analysis of multivariate dispersions) were considered as out of scope (Fig. 1). In addition, I disregarded studies that included semi-aquatic organisms such as aquatic birds and marginal vegetation (helophytes). The db-RDA effect sizes were excluded because they did not represent sufficient replicate effort to conduct a meta-analysis apart and the effect sizes are not comparable with Mantel correlations according to Legendre & Fortin (2010), and Legendre *et al.* (2015) (Fig. 1). During the selection of raw data, four datasets were excluded because the author did not inform the measurement system associated with environmental variables or informed it incompletely (Fig. 1). Furthermore, studies that reported more than one effect size associated with more than one organism collected in the same sampling locations or more than one independent region were included in the meta-analysis as non-independent effects (random effect). After the identification and selection stages, the total of effect sizes considered eligible to conduct the meta-analysis was 45 and the total of studies and raw data analyzed was 24 (Fig. 1) (Table 1).

Table 1. Summary of the selected publications and datasets included in the meta-analysis. The autotrophic group includes macrophyte, diatoms, and phytoplankton.

Taxon	Ecosystem	Data source	Author
autotrophic / macroinvertebrate	lotic	published	Rocha <i>et al.</i> (2019)
autotrophic	lentic	published	Bertuzzi <i>et al.</i> (2018)
autotrophic	lentic	published	Fernández-Aláez <i>et al.</i> (2020)
autotrophic	lentic	published	Zhang <i>et al.</i> (2018)
autotrophic	lotic	published	Wu <i>et al.</i> (2018)
autotrophic	lotic	published	Virtanen & Soininen (2012)
autotrophic	lentic	published	Nistal-Garcia <i>et al.</i> (2021)

autotrophic / fish / macroinvertebrate	lotic	published	Grenouillet <i>et al.</i> (2008)
bacterioplankton	lotic	published	Ren & Gao (2019)
fish	lotic	published	Huang <i>et al.</i> (2019)
fish	lotic	published	Benone <i>et al.</i> (2018)
fish	lotic	published	Eros <i>et al.</i> (2017)
macroinvertebrate	lotic	published	Ongaratto <i>et al.</i> (2018)
macroinvertebrate	lentic	published	Cai <i>et al.</i> (2017)
macroinvertebrate	lentic	published	Heino & Tolonen (2017)
macroinvertebrate	lotic	published	Gauthier <i>et al.</i> (2021)
macroinvertebrate	lentic	published	Kotzian <i>et al.</i> (2020)
macroinvertebrate	lotic	published	Hepp & Melo (2013)
macroinvertebrate	lotic	published	Breda <i>et al.</i> (2020)
zooplankton	lotic	published	Le Coz <i>et al.</i> (2018)
autotrophic	lotic	raw data	Virta <i>et al.</i> (2020)
bacterioplankton	lotic	raw data	Mykrä <i>et al.</i> (2017)
macroinvertebrate	lotic	raw data	Elo <i>et al.</i> (2021)
zooplankton	lentic	raw data	Sinclair <i>et al.</i> (2020)

## 2. Moderators

The environmental extent was represented by the mean of the range values of the environment variables. The range of values were obtained from the subtraction of the maximum and minimum of each environmental variable in each study and standardized using the standard deviation for all differences obtained (function *scale* from the R environment). The standardization of the environmental extent values was applied because each environmental variable presents distinct measurement units (*e.g.*, Celsius, centimeters, meters per second). Posteriorly, I analyzed the environmental extent as a continuous moderator (fixed effect) in a meta-regression. Additionally, I calculated the environmental extent using the mean of the range values of the four most frequent environmental variables (pH, temperature, conductivity, and total phosphorus), and for each of these four variables separately.

The interaction of environmental extent including the range of all environmental variables was tested together with the other moderators such as groups of organisms (autotrophic, bacterioplankton, fish, macroinvertebrates, zooplankton), ecosystems (lentic and lotic) and spatial extent (logarithm of watershed area reported in studies, km<sup>2</sup>). The interactions of moderators of environmental extent, ecosystems, groups of organisms, and spatial extent were analyzed using multi-factor meta-regressions.

### 3. Multi-level meta-analysis models

Because one work can provide more than one effect size, I applied the method of multi-level meta-analysis that considers the non-independence between the effects sizes (Nakagawa & Santos 2012). Most of the effect sizes were related to Mantel correlations that present distinct methods of correlation such as Pearson and Spearman. Thus, I standardized the correlation effect sizes of Spearman to Pearson product-moment correlation coefficient ( $r$ ) and transformed them into Fisher's Z scores (Lajeunesse 2013). The Spearman correlation ( $\rho$ ) was standardized using the equation:

$$r = 2 \times \sin\left(\frac{\pi \times \rho}{6}\right), \text{ if } n < 90 \text{ or } r = \rho, \text{ if } n \geq 90$$

Where  $n$  represents the sample size. The Fisher's Z score was obtained using the following equation (Borenstein *et al.* 2009):

$$z = 0.5 \times \left(\frac{1 + r}{1 - r}\right)$$

Finally, the multi-level analysis was weighted by the sample size of the studies. The meta-analyses were done in the statistical environment R (R Development Core Team 2019) using the

package “metafor” (Viechtbauer 2010) and the package “robumeta” (Fisher & Tipton 2015) following the directions of Bishop & Nakagawa (2021) and Nakagawa *et al.* (2020).

#### 4. Publication bias

The scientific literature may be biased as studies with non-significant statistical effects may be discontinued by authors or have higher rejection rates than those presenting statistically significant effects. Assessment of publication bias was done using Orwin’s Fail Safe Number (Orwin 1983), which estimates the number of unpublished studies with insignificant results needed to make the pooled effect of the meta-analysis equal to zero. I did not evaluate the effects of time-lag publication bias as it is unable to estimate the variance of Mantel tests (de Oliveira Jr. *et al.* 2020). The Orwin’s Fail Safe Number was estimated using the *fsn* function from the package “metafor” (Viechtbauer 2010).

## Results

The 24 studies compiled used a total of 76 predictor environmental variables and 34 of them were used in at least two studies (Table S1). The most frequent variables used were pH, followed by conductivity, temperature, and total phosphorus (Table S1). Many of the effect sizes were positive, appearing in 39 out of the total 45 effect sizes. The lowest effect size value detected was -0.187, meanwhile the highest effect size value was 0.62. The number of sampling units varied among studies; the study with the lowest number of sampling units had 10, while the study with the highest number had 240.

I found no evidence that environmental extent influences the correlation between environmental distances and beta diversity ( $Q = 0.037$ ,  $p = 0.846$ ). The meta-analysis model including environmental extent using only the pH, conductivity, temperature, and phosphorus variables (the four most common variables) revealed no influence of the moderator on the correlations ( $Q = 0.047$ ,  $p = 0.828$ ). The pH extent had no influence on the effect sizes ( $Q = 0.119$ ,  $p = 0.729$ ) and the same was observed for conductivity extent ( $Q < 0.001$ ,  $p = 0.992$ ), temperature extent ( $Q < 0.001$ ,  $p = 0.973$ ) and phosphorus total extent ( $Q = 0.191$ ,  $p = 0.662$ ). Likewise, no influence of interactions between moderators of environmental extents and ecosystems was detected (Table 2). The same results were observed for the interactions between environmental extents and group of organisms, and between environmental extent and spatial extent as well (Table 2).

Table 2. Multi-factor meta-analysis results, including the interactions of moderators of environmental extent, ecosystem type, organisms, and spatial extent.

	C.I (Low)	Estimate	C.I. (Up)	P-Valor
<b>Ecosystem</b>				
Intercept	-0.796	0.546	1.889	0.425
Environmental Extent	-1.958	-0.251	1.456	0.773
Lotic	-2.063	-0.287	1.489	0.751
Env. Extent*Lotic	-2.255	0.182	2.620	0.883
<b>Organisms</b>				
Intercept	-1.510	0.153	1.817	0.856
Environmental Extent	-1.664	0.086	1.836	0.922
Bacterioplankton	-3.545	0.668	4.883	0.756
Fish	-2.475	0.370	3.216	0.798
Macroinvertebrate	-1.845	0.288	2.422	0.791
Zooplankton	-6.516	0.577	7.671	0.873
Env.Extent*Bacterioplankton	-11.217	-0.559	10.094	0.918
Env.Extent*Fish	-4.030	-0.497	3.035	0.782
Env.Extent*Macroinvertebrate	-2.989	-0.274	2.440	0.842
Env.Extent*Zooplankton	-10.686	-0.899	8.888	0.857
<b>Spatial</b>				
Intercept	-0.622	0.252	1.126	0.572

Env. Extent*Spatial Extent	-0.135	0.009	0.154	0.154
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Note: C.I. = Confidence Interval.

The Orwin's fail safe number indicates the absence of publication bias ( $fsn = 45$  studies), considering the target effect size of 0.121 (average effect size = 0.243). In other words, it would be necessary to find more than 45 studies to the meta-analysis for the cumulative effect to become non-robust.

## Discussion

I conducted a systematic review to investigate the effects of environmental extent on the correlation between beta diversity and environmental dissimilarity. My results demonstrate that environmental extent does not influence the correlations between environmental dissimilarity and beta diversity in freshwater realms. Therefore, my hypothesis that explanatory strength of environmental dissimilarity is dependent on the extent of its composing variables was not verified. Furthermore, I detected no effects of the interactions of environmental extent for lentic or lotic ecosystems, groups of organisms, and spatial extent.

The intuitive hypothesis that studies with high amplitude of environmental variables result in a better correlation between compositional dissimilarity and environmental dissimilarity was not supported by the meta-analysis. This result may have arisen from factors not investigated in this assessment. Observational studies vary regarding many other factors, including biogeographic realm and latitudinal position (Soininen *et al.* 2018, Nishizawa *et al.* 2022). Latitudinal zones are significant determinants of niche characteristics of species, such as niche width. Species in lower latitudes tend to have small distribution ranges compared to high-latitude species (Rapoport's rule), consequently,

variations in beta diversity should be more sensitive to environmental changes in low-latitude regions (Qian *et al.* 2009). Furthermore, the niche breadth of species is not always unimodal and symmetrically distributed along the environmental gradient (Oksanen & Minchin 2002, Heino 2005). In addition, ecological effects such as biotic interactions or disturbances are responsible for removing species from locations with adequate environmental conditions (*i.e.*, realized niche) (Heino 2005). Consequently, mechanisms that are related to patch colonization and dispersal such as priority and mass effects, respectively, obscure the detection of species niches along the gradient (Heino *et al.* 2013, Nishizawa *et al.* 2022). Dispersal limitations would explain the discrepancy of effect sizes between studies with similar environmental extensions as well, as isolated communities may differ in species composition not because of environmental dissimilarity but lack of connectivity.

Correlations between environmental dissimilarities and beta diversity are thought to depend on at least three factors: the statistics applied to assess the correlations, the environmental extent, and the spatial extent (Heino *et al.* 2015). Among the three factors mentioned, my results do not support the influence of the environmental extent and spatial extent, but it is likely that the analyzed effect sizes were influenced by the statistics and methodological particularities from the studies that were not investigated in the systematic review. The effect size of the Mantel test is sensitive to variations in environmental extent that extrapolates the assumption that the correlations follow a linear relationship model. Beta diversity studies using linear methods fail to detect non-linear turnover composition rates across broad gradients (Adler & Levine 2007, Ferrier *et al.* 2007, Guerin *et al.* 2013). The lack of monotonicity (absence of linearity) is due to the intrinsic characteristics of beta diversity metrics that are restricted to values from zero to one and is especially important when analyzing broad environmental gradients. Alternatively, curvilinear relationships have been observed between the environmental gradient of precipitation and tropical forest tree diversity (Ferrier *et al.* 2007), as well as between the elevation gradient and the beta diversity of freshwater fish (Herrera-Pérez *et al.* 2019). Furthermore, ecological studies present low rates of replicability as they are very

divergent in terms of methods, and innumerable studies with low number of sampling units have been reported large effect sizes, indicating the possibility of time-lag publication bias (Yang *et al.* 2023).

The lack of effect of environmental extent on the result of the relationship of beta diversity and environmental dissimilarity may also results from the failure of studies to include important environmental factors perceived by the organisms (Heino 2011, Heino *et al.* 2013). Furthermore, the evaluated studies included a considerable number of variables that are considered environmental predictors (75 variables). From an operational perspective, Heino *et al.* (2015) point out that the results of correlations between beta diversity and environmental variables are dependent on the identity and quantity of variables analyzed in the studies. Therefore, the comparison of environmental extent effects should be interpreted with caution because obtaining comparable environmental extents is not a trivial task as variables used to estimate extents are mostly distinct across studies. Finally, environmental variables that are fundamental to determine species composition in one region may not be relevant for another region (Alahuhta *et al.* 2017).

The present study evidenced that the environmental extent is not relevant to determine the strength of the correlations between beta diversity and environmental dissimilarity. Even restricted analyses for groups of organisms and different freshwater ecosystems did not reveal effects of environmental extent. Explanations for the absence of the environmental extent effect are based on many other effects such as dispersal limitation, mass effects, priority effects, and disturbances. Consequently, even if there is some supposed effect of the environmental extent, it is possible that it is associated with the effects of other extensions such as latitudinal, biogeographical, and spatial. A possible caveat for my meta-analysis is that due to the large number of environmental variables and heterogeneities of studies in evaluating the same environmental variables, the effect of environmental extension may have not been effectively assessed between studies. However, this review pioneered the gathering of information from scientific literature to empirically investigate the effects of environmental extents, as much importance has been given to its effects even though it has not been

properly investigated. Future studies are needed to disentangle the shared effects of numerous known mechanisms and extensions on relationship of the beta diversity of aquatic organisms and environmental dissimilarity.

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## Supplementary Material

Table S1. Summary of the environmental variables found as predictor of beta diversity dissimilarity in the selected studies used to calculate environmental extents.

Variable name	Studies	Extents	Maximum	Minimum	Mean	SD
pH	19	37	5.72	0.41	1.61	1.03
Conductivity ( $\mu\text{s}/\text{cm}$ )	16	34	1217.60	17.60	332.43	301.15
Temperature ( $^{\circ}\text{C}$ )	14	29	17.00	1.59	8.24	4.26
Phosphorus (mg/L)	13	22	0.78	0.01	0.33	0.25
Dissolved oxygen (mg/L)	9	16	15.33	1.13	5.99	3.31
Stream width (m)	6	16	149.20	0.84	26.03	39.99
Water depth (cm)	5	14	846.70	0.37	143.02	245.08
Nitrite (mg/L)	6	13	0.38	0.01	0.11	0.11
Nitrogen (mg/L)	7	13	14.72	0.20	3.77	4.08
Nitrate (mg/L)	5	12	21.00	0.61	5.24	6.85
Phosphate (mg/L)	6	13	2.50	0.08	0.95	1.06
Altitude (m)	4	11	100.00	50.00	85.47	20.69
Ammonium (mg/L)	5	11	99.88	0.06	20.09	35.26
Shading or canopy cover (%)	4	10	100.00	50.00	85.47	20.69
Water current velocity (m/s)	4	10	1.13	0.25	0.67	0.28
Chlorophyll a ( $\mu\text{g}/\text{L}$ )	3	9	56490.00	41.34	15081.01	19751.29
Turbidity (NTU)	5	9	501.95	3.70	146.19	157.71
Calcium (mg/L)	3	8	400.00	42.12	227.89	184.33
Gravel (%)	2	7	100.00	40.00	72.86	26.12

Sand (%)	2	7	100.00	25.00	74.97	33.10
Total dissolved solids (mg/L)	3	7	6.00	0.08	0.98	2.21
Chlorine (mg/L)	3	6	102.88	7.97	37.55	45.02
Colour (mg Pt L)	4	5	360.00	40.00	175.00	136.84
Pebble (%)	1	4	70.00	10.00	44.68	29.64
Riparian vegetation (%)	2	4	99.50	15.90	78.60	41.80
Potassium (mg/L)	2	3	7.71	5.05	6.49	1.34
Sulphate (mg/L)	2	3	186.48	60.20	130.42	64.32
Alkalinity (meq/L)	1	2	6.10	0.25	3.18	4.14
Area (km <sup>2</sup> )	2	2	8.89	0.92	4.90	5.64
Carbon (mg/L)	2	2	44.80	2.37	23.59	5.38
Dissolved organic carbon (mg/L)	2	2	8.00	2.76	5.38	3.70
Magnesium (mg/L)	1	2	12.01	5.05	8.53	4.92
Sodium (mg/L)	1	2	70.73	43.03	56.88	19.57
Soluble reactive phosphorus (mg/L)	1	2	0.51	0.01	0.26	0.35

Note: SD = Standard deviation.

## **Chapter 2 – The influence of dispersal costs on the functional beta diversity of freshwater fish from large basins in North America**

### **Abstract**

Freshwater fish species can be organized into at least three functional groups (equilibrium, opportunistic, and periodic) based on morphological, reproductive, and behavioral characteristics. Some geomorphological features of rivers and streams represent resistances to fish dispersal, known as dispersal costs, and some of the functional groups appear to be more responsive to dispersal costs than others. The aim of this chapter is to test the effects of dispersal costs associated with distances along watercourses, channel slope, and some physical attributes of dams on the beta diversity and functional groups of freshwater fish. Therefore, we analyzed the beta taxonomical and functional dissimilarity of fish in four watersheds in North Carolina (United States of America) using reproductive and dispersal traits. Three out of the four watersheds supported that dispersal costs are important for determining both taxonomic and functional beta dissimilarity. Furthermore, the results revealed that the beta diversity of periodic species and, to a lesser extent, equilibrium species are influenced by dispersal costs. Periodic species are more dependent on dispersal processes to inhabit locations throughout river basins, which would explain a greater percentage of explanation for dispersal cost variables. Meanwhile, dams appear to reduce species dissimilarity of equilibrium species because some species can adapt to the lentic environments imposed by reservoirs and are less dependent on dispersal.

**Keywords:** Functional beta diversity, Dispersal cost, Dams, Freshwater fish, Dendritic Network.

## Introduction

There are many processes that act in metacommunities, which turns the comprehension of metacommunities into a hard task for ecologists (Vellend 2010). Furthermore, the metacommunity mechanisms must be known to understand the determinant factors that shape species diversity. Metacommunities of lotic environments are highly dependent on dendritic networks, which influence the dispersal dynamics of organisms, mostly those restricted to aquatic dispersal (Altermatt 2013, Tonkin *et al.* 2018). This is due to specific features of dendritic network connectivity that create a series of dispersal limitations for organisms, consequently resulting in different species distribution patterns (Carrara *et al.* 2012, 2014).

Species can be organized and studied according to their evolutionary history and functional traits. Evolutionary theories based on traits have been studied for many years, and the first examples are the establishment of the concept of semelparity and iteroparity (Schaffer 1974), and *r* and K species (Pianka 1970). The *r* species are characterized by a reproductive strategy aimed at producing many offspring in a short period of time, while K species tend to produce fewer offspring, investing more time and resources in parental care and the growth of offspring. Winemiller & Rose (1992) expanded the *r* and K concept using freshwater fish by defining three functional groups (equilibrium, periodic and opportunistic) based on their evolutionary and reproductive histories. The main characteristics of periodic species are late maturation, high longevity, low juvenile survivorship, small-eggs size, large body size, and the breeding season usually short and synchronized. On the other hand, the opportunistic species have small-body size, low longevity, small eggs, prolonged breeding seasons and high resistance to disturbances. The opportunistic species have similar traits to the *r*-strategist species, although with reduced egg-

laying. Therefore, opportunistic species specialize in recolonization processes to persist in the metacommunity. Finally, the equilibrium species are characterized by intermediate traits compared to the opportunistic and periodic species, with body size varying between small and medium and an intermediate number of eggs. Most equilibrium species have parental care behavior, low fecundity, high juvenile survivorship, and the eggs are bigger compared to the other groups and are favored in lentic and stable environments.

Aspects of the evolutionary history of freshwater fish are associated with dispersal capabilities, and evolutionary selection pressures contribute to the trade-off between dispersal traits and reproductive traits (Bonte & Doherty 2017). For example, species that invest in parental care demand energy for reproduction, disfavoring the selection of traits that allow efficient dispersal over long distances (Bonte *et al.* 2012). On the other hand, some species may invest in dispersal as a reproductive strategy because they rely on dispersal to reach suitable habitats for egg deposition (periodical fish); however, it is important to point out they do not exhibit parental care behavior (Mims *et al.* 2010). Furthermore, species that disperse over short distances require more specific local environmental conditions, while generalists can disperse over long distances and track locations with suitable conditions (Comte & Olden 2018).

Fish body size, body shape, and aspect ratio of the caudal fin (ratio between caudal fin depth and caudal peduncle depth) are recognized as traits associated with dispersal ability (Radinger & Wolter 2014). Furthermore, Comte & Olden (2018) verified that these morphological characteristics are indicative of the dispersal capacity of fish, which is mainly associated with evolutionary history. The aspect ratio of the caudal fin represents the efficiency of swimming ability (Radinger & Wolter 2014), in other words, it is an evolutionarily selected trait that allows

organisms to disperse over considerable distances with energy cost efficiency (Comte & Olden 2018). The body size of active dispersers, such as freshwater fish species, is well-established as a dispersal proxy in the scientific literature (Rosenfield 2002, De Bie *et al.* 2012, Radinger & Wolter 2014, Comte & Olden 2018, Cote *et al.* 2021, Cote *et al.* 2022). Thus, it is classified as an organismal-based proxy in contrast to other proxies such as geographical or network distances (Heino *et al.* 2017). In addition, large-bodied species are known to be more widely distributed than small-bodied species (Rosenfield 2002, De Bie *et al.* 2012). Body shape is fundamental in determining swimming efficiency as it influences the amount of drag resistance during body movement (Pettersson & Hedenström 2000, Ohlberger *et al.* 2006).

Life history and functional traits have been identified as important features to investigate the effects of metacommunity dispersal processes on the beta diversity of freshwater fishes (Vitorino Junior *et al.* 2016, Peláez & Pavanelli 2019, Ma *et al.* 2020). Spatial factors (*i.e.*, connectivity) and dispersal costs (*e.g.*, barriers) contribute to the selection of species that share similar dispersal strategies, consequently forming patterns of species distribution in metacommunities. Reduced streamflow and fragmentation reduce dispersal rates of species (Driver & Hoeinghaus 2016, Hubbel *et al.* 2020). Furthermore, alteration of hydrologic connectivity, for instance by dams, enhances the effects of dispersal costs, affecting the beta diversity of aquatic communities (Pelicice *et al.* 2015, Rolls *et al.* 2016). Recently, it has been recognized that dispersal costs such as physical barriers play crucial roles in determining the composition of freshwater fishes (Perkin *et al.* 2017, Mozzaquattro *et al.* 2020, Rezende *et al.* 2023). In addition, the spatial attribute of channel slope has emerged as an important factor to species richness and trait diversity in freshwater dendritic systems (Camana *et al.* 2016, Caetano *et al.* 2021). Lamouroux *et al.* (2002) claimed that fish biological traits are selected by geomorphic

and hydraulic gradients; however, those gradients were tested as predictor variables of local communities and not as dispersal costs between communities. Therefore, this study brings novelty in investigating the effects of different dispersal costs on the functional diversity of fish associated with reproductive and dispersal attributes.

Dams are anthropogenic structures that contribute most to preventing the dispersal of freshwater fish species along basins, regardless of the direction of dispersal (upstream or downstream). The construction of dams prevents dispersal of freshwater fish species along river courses, while also fragmenting habitats, altering streamflow and local environmental conditions (Barbarossa *et al.* 2020, Freeman *et al.* 2022). The effects of dams on fish are not solely linked to their physical structure that interrupts upstream dispersal, but also to other factors such the formation of upstream reservoirs that prevent juvenile fishes to disperse downstream (Agostinho *et al.* 2007, Pelicice *et al.* 2015). The dispersal costs associated with dam construction affect the diversity of functional characteristics in fish species communities. For instance, species with traits associated with high current flow are extirpated from areas impacted by reservoir formation (Agostinho *et al.* 2016, Arantes *et al.* 2019). Another example includes the effect of the prevention of periodic fishes from reaching upstream locations to reproduce. Therefore, metacommunity studies should investigate the effects of dams as dispersal costs in freshwater metacommunities to understand fish distribution patterns.

The goal of this work is to test distinct effects of dispersal costs (watercourse distances, channel slopes and dams) on the taxonomic and functional beta diversity of freshwater fishes, which includes morphometric traits associated with dispersal capacity and reproduction. I assume that dispersal cost contributes to increasing beta diversity of functional traits related to both

reproductive and morphometric traits because some species invest more in dispersal strategies meanwhile some species are more sedentary and invest in parental care. Furthermore, freshwater fish metacommunities are spatially structured because of the effects of dispersal limitations and associated factors such as streamflow, productivity, biotic interactions, disturbance, and abiotic conditions (Driver & Hoeinghaus 2016, King *et al.* 2016, Chen & Olden 2017). I expect equilibrium species to be more influenced by watercourse distance and channel slope dispersal costs (compared to opportunistic and periodic species) due to their lower dispersal capability and specialization in parental care and sedentary behavior (Mims *et al.* 2010, Arantes *et al.* 2019). On the other hand, I expect dams to have a greater effect on periodic species, since these species are specialized in life strategies associated with long-distance dispersal, which allows them to occupy distinct locations throughout the river basins (Arantes *et al.* 2019).

## **Methods**

### *Study area and data source*

The data was obtained from the database of the North Carolina Department of Environment and Natural Resources – Division of Water Resources (<https://deq.nc.gov/>). The state of North Carolina is composed of 17 major river basins, and I selected the four largest basins (Cape Fear, Neuse, Tar-Pamlico, Yadkin-Pee Dee). The data consists of freshwater fish species presence-absence matrices converted from a format list (long format) containing species presence. The fish were sampled by two-pass electrofishing depletion technique, conducted by a team of two groups, one responsible for the backpack electrofishing and the other for netting the stunned fishes. The collected fishes

were surveyed between the years of 1990 and 2021 from distinct macro and microhabitats including pools, riffles, runs and snags (North Carolina Department of Environment and Natural Resources 2013). Synonyms and the validity of scientific species names were checked using the FishBase database information, and the checklist name was accessed using the *rfishbase* package (Boeting *et al.* 2012) in the R programming environment (R Development Core Team 2021). Information of dams present in the studied river basins was accessed from the National Inventory of Dams (USACE 2018, <https://nid.sec.usace.army.mil>) and the USGS ScienceBase Catalog (<https://www.sciencebase.gov/catalog>) (Tables S1-S4). The extracted information from the dams included the sum of the height of the dams (m), the sum of the area of the reservoirs (km<sup>2</sup>), and the age of the oldest dam (years) along the watercourse distance between locations. The extracted information was used as dispersal costs for fishes (more details in dispersal cost distances section).

### *Cape Fear River Basin*

The Cape Fear River Basin is the largest basin in the state of North Carolina (approximately 23,622 km<sup>2</sup>) covering 17% of the state, and it is formed from the confluence of the Haw River and Deep River (Fig. 1). The main channel and its tributaries are approximately 320 km, crossing the North Carolina piedmont into the Cape Fear Estuary and Atlantic Ocean. A total of 103 locations were sampled, and a total number of 81 freshwater fish species were recorded.

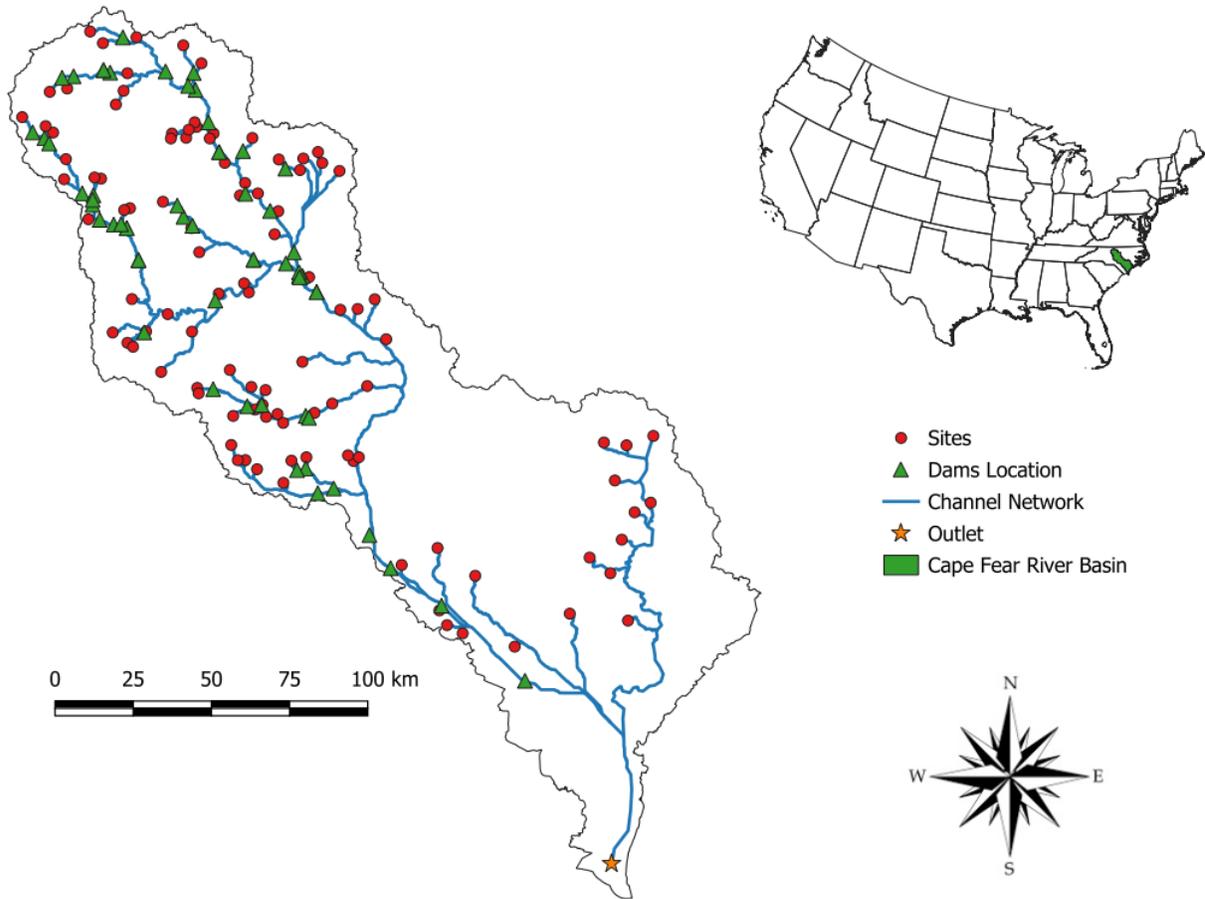


Figure 1. Map of the Cape Fear River Basin. The map contains the location of the basin in the North Carolina state (USA), the 103 sampled sites, the representation of the channel network connecting the sites, and the location of the dams.

### *Neuse River Basin*

The Neuse River originates in the headwaters of the Piedmont of North Carolina state and the waters flow into the Atlantic Ocean forming the Pamlico Sound, an estuarine lagoon formed with the contribution of the waters of the Neuse River and Tar-Pamlico River (Fig. 2). The Neuse River

is formed by the confluence of the Eno and Flat Rivers, and its main channel network is 443 km long. The Neuse watershed is the largest in the state and corresponds to approximately 16,000 km<sup>2</sup> (Christian *et al.* 1991). A total of 73 locations were sampled, and a total of 74 freshwater fish species were recorded.

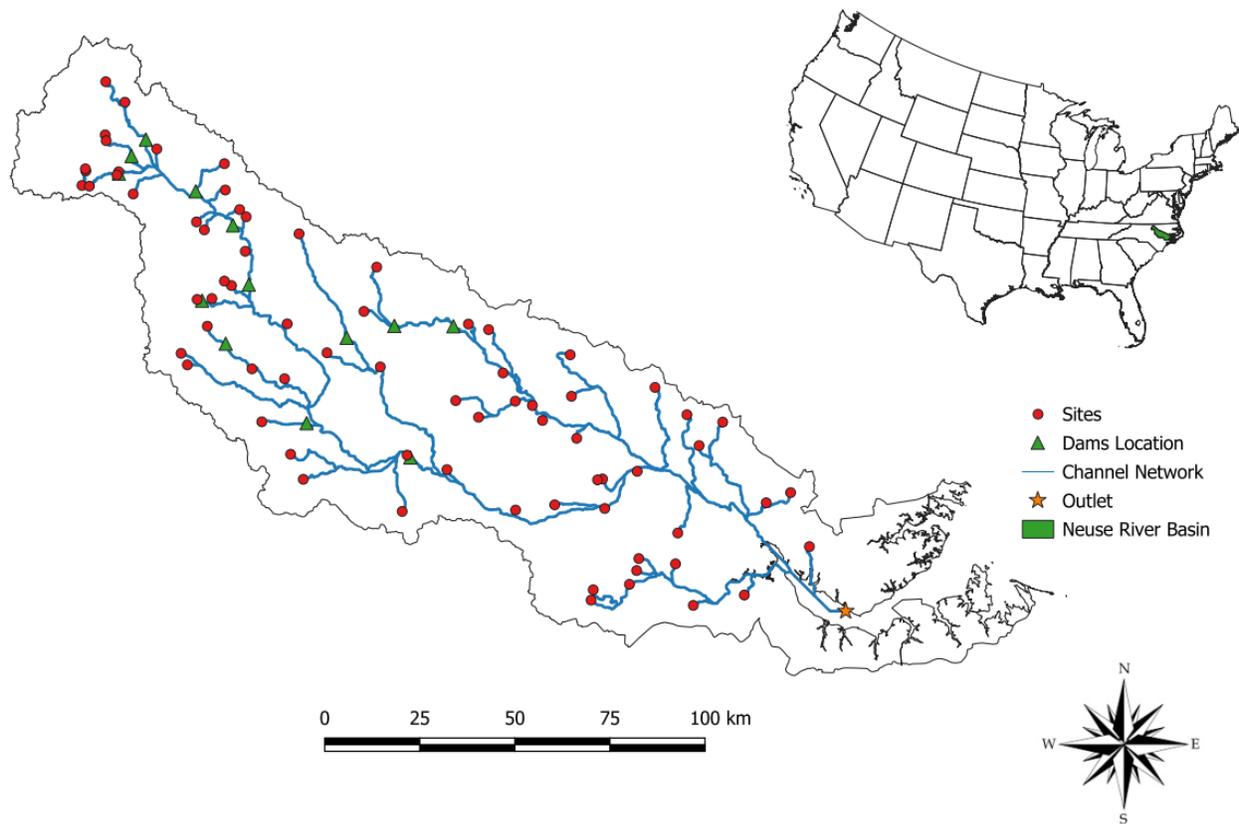


Figure 2. Map of the Neuse River Basin. The map contains the location of the basin in the North Carolina state (USA), the 73 sampled sites, the representation of the channel network connecting the sites, and the location of the dams.

*Tar-Pamlico River Basin*

The Tar-Pamlico is the fourth longest river in North Carolina state, and the region of the Piedmont concentrates most of the rivers and streams of the basin (the Tar). The water in the Pamlico region is characterized by the influence of salt water of the Atlantic Ocean, therefore, the basin has considerable number of brackish areas, and the main channel river is approximately 346 km long. A total of 56 locations were sampled, and a total number of 64 freshwater fish species were recorded.

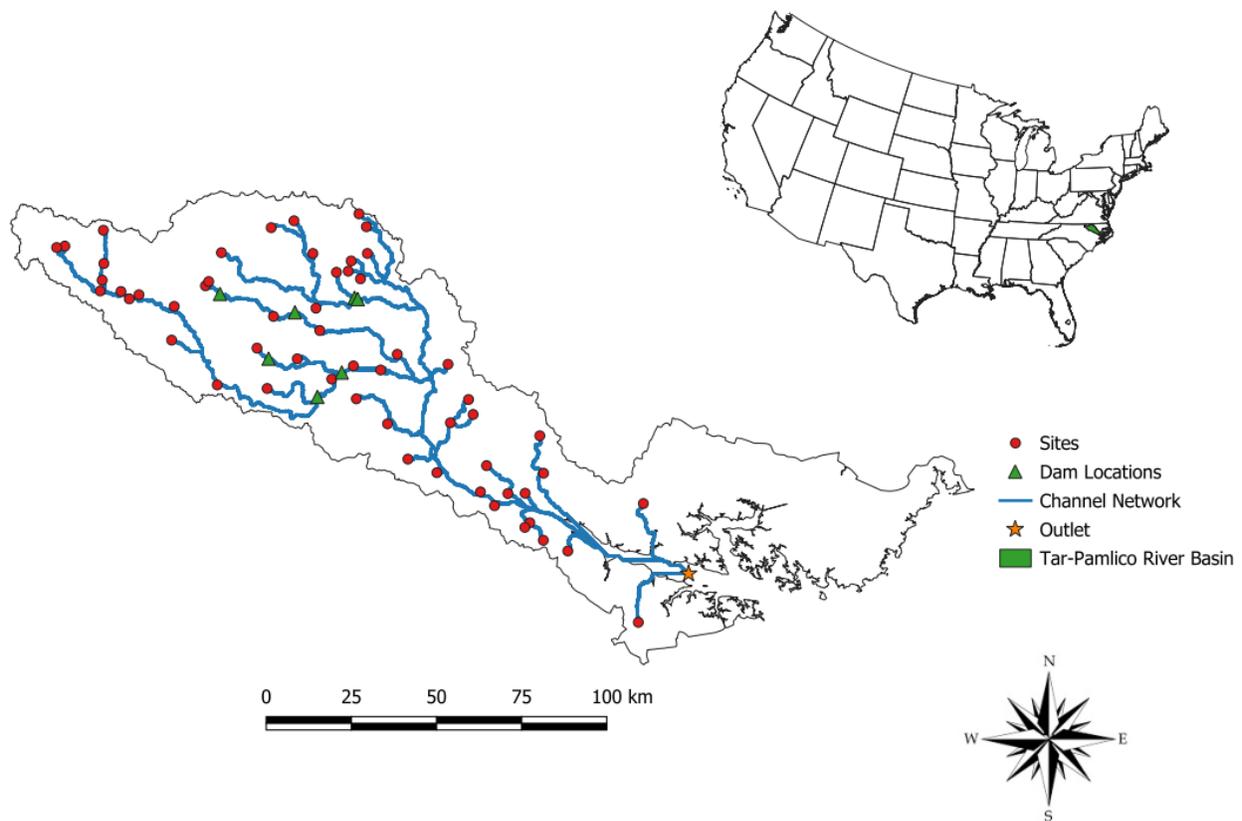


Figure 3. Map of the Tar-Pamlico River Basin. The map contains the location of the basin in the North Carolina state (USA), the 56 sampled sites, the representation of the channel network connecting the sites, and the location of the dams.

### *Yadkin – Pee Dee River Basin*

The Yadkin – Pee Dee River is approximately 378 km long and its topography is formed of igneous and metamorphic rocks (Fig. 4). The waters of the Yadkin River flow into the South Carolina state, and posteriorly to the Atlantic Ocean. The database includes samples from the upper river segment restricted to the North Carolina territory state. A total of 110 locations were sampled, and a total of 80 freshwater fish species were registered.

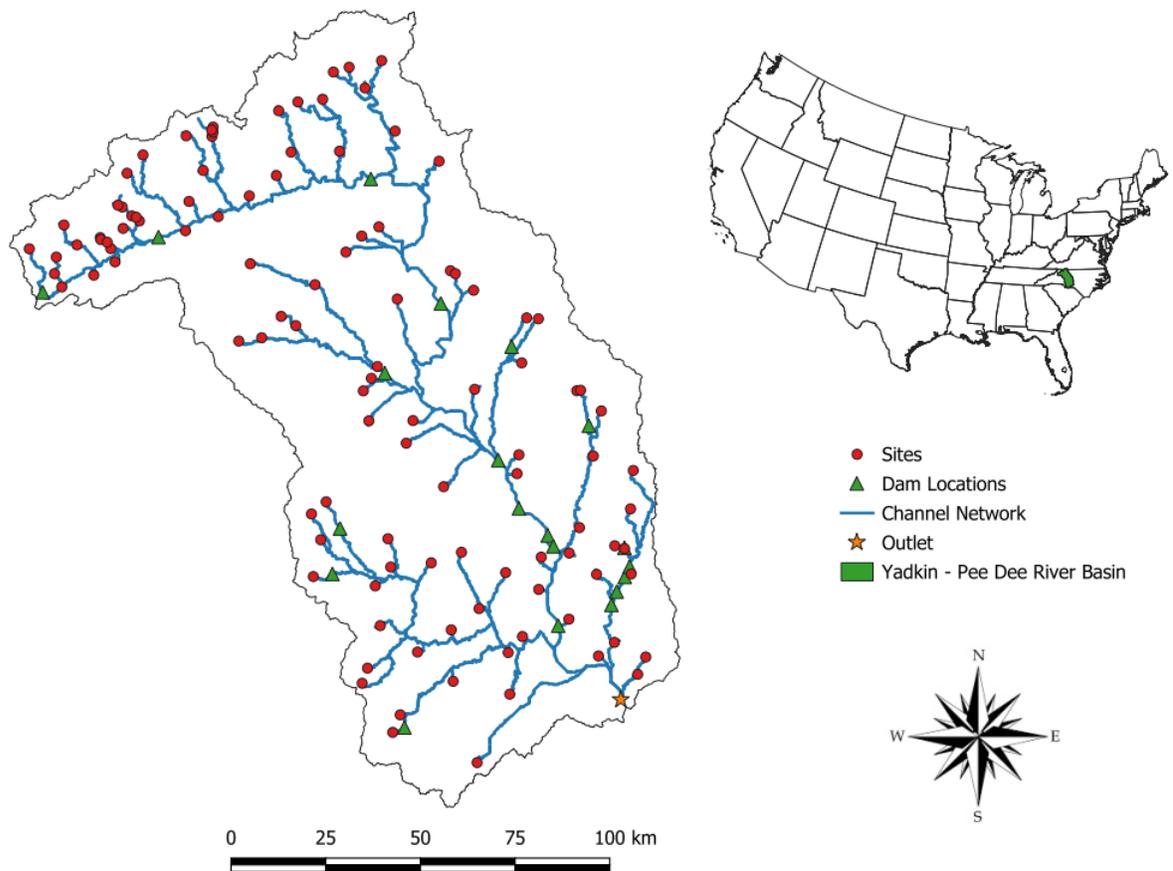


Figure 4. Yadkin - Pee Dee River Basin. The map contains the location of the basin in the North Carolina state (USA), the 110 sampled sites, the representation of the channel network connecting the sites, and the location of the dams.

### *Functional beta diversity*

I obtained morphological traits from the Fishmorph database repository (Brosse *et al.* 2021) and reproductive traits from the Fishtraits (Frimpong & Angermeier 2009). The morphological traits, used as a proxy for dispersal capacity, included were: (1) maximum body size (cm), (2) body elongation measured as the ratio between body length and body depth, and (3) caudal peduncle throttling measured as the ratio between caudal fin depth and caudal peduncle depth. The reproductive traits included were: (1) median, mean or modal age at maturity in years for females, (2) longevity in years based on life in the wild, (3) fecundity, and (4) presence/absence of parental care. Due to the differences in the scale units, the continuous traits were scaled using the centered mean and standardized by the standard deviation using the *scale* function. I calculated Gower distances using the scaled traits matrices and binary distance matrix of parental care and obtained a functional dendrogram using hierarchical clustering method (UPGMA algorithm). The continuous traits and the binary distance matrix (parental care) were estimated by the average of the dissimilarity matrices (De Bello *et al.* 2021). The functional beta diversity matrices were obtained using the Sørensen index and the branches of the functional dendrogram. In addition, I obtained taxonomic beta diversity using the Sørensen index. All the steps to obtain the functional beta diversity were done using the package *BAT* (Cardoso *et al.* 2015), and the taxonomic beta diversity was obtained by using the package *betapart* (Baselga & Orme 2012).

### *Functional groups*

Three functional groups of fish (opportunistic, periodic and equilibrium) were estimated using the functional distances obtained in the previous step combined with phylogenetic distances estimated using the *FishPhyloMaker* package (Nakamura *et al.* 2021). The functional trait distances and phylogenetic distances (phylogenetic-functional distance) were combined using the decouple function (De Bello *et al.* 2017), which consists of the summed phylogenetic and functional trait differences (covariance or joint dissimilarity). Subsequently, the functional groups were classified based on hierarchical clustering method (UPGMA algorithm) and used to obtain species presence-absence matrices for each functional group. Three species lacked sufficient information on morphological or reproductive traits for their classification into functional groups; consequently, they were removed from the hierarchical clustering analysis. These species are *Etheostoma brevispinum*, *Lampetra aepyptera*, and *Petromyzon marinus*. Furthermore, I compared my classification results with other classifications available in the literature.

### *Dispersal cost distances*

I calculated dispersal costs based on the channel network of the river basins. To delineate the channel networks, I used global 1 arc second SRTM digital elevation models (30 m tiles) from EarthData (<https://www.earthdata.nasa.gov>) (NASA Jet Propulsion Laboratory 2013) using the software of geoprocessing QGIS (QGIS.org 2022). The channel network shapefiles were overlaid with raster containing slope values for each 30 m tile and dams' information (point shapefiles). Consequently, the shapefiles of lines (delineated channel networks) were transformed into shapefiles of points containing identification number of the point, identification of the segment which the point belongs, the identification number of the next segment connected down-river, and

slope value assigned to the tile. The matrices containing the segments information were transported to R software (R Core Team 2021) and transformed into graphs in which the nodes were represented by the confluences and sampled sites, and the edges represented by river or stream segments. The channel network shapefiles were used to obtain the watercourse distances between the sampled sites using the package *shp2graph* (Lu *et al.* 2018). The graphs were used to obtain the mean slope, standard deviation slope, maximum slope, sum of the height of the dams, sum of the area of the reservoirs, and the oldest age of the dams between the sampled sites. The standard deviation represents variation in slope within segments while the maximum slope value was assumed to represent the most effective barrier in the segment. The criterion for choosing the sum of reservoir areas and dam heights is that the effects accumulate over distances and the age of the oldest dam represents the primary effect on communities' diversity based on the temporal effect scale. All the dispersal costs matrices associated with channel slopes and dams' attributes were multiplied by the watercourse distances and used in the next step of the analysis.

### *Data analysis*

The dispersal cost distance matrices were converted into eigenfunction spatial models using the method of distance-based Moran's eigenvector map (db-MEM) (Bocard & Legendre 2002, Dray *et al.* 2006). Posteriorly, I only selected spatial variables with significant positive spatial correlation using the Moran's I coefficient (Blanchet *et al.* 2011) and I performed a global db-RDA test using the positive correlation eigenvectors. The  $R^2$  adjusted values of the global db-RDA test were used to reduce the number of spatial variables with the forward selection procedure. The eigenfunction spatial models were obtained by applying the function *dbmem* in the *adespatial*

package (Dray *et al.* 2023). The selected positive eigenvalues were used as predictors of functional and taxonomic beta diversity in a distance-based redundancy analysis (db-RDA) using the package *vegan* (Oksanen *et al.* 2022). Each dispersal cost was analyzed in independent analyses and the same procedure was applied for the beta diversity of each functional group matrix (periodic, opportunistic and equilibrium species).

## Results

The most frequent fish species in the Cape Fear Basin was *Lepomis auritus*, observed in 94 out of the 103 sampled locations (91.26%). Within the Neuse Basin, *Lepomis macrochirus* was the most frequent species, found in 68 out of 73 locations (93.15%). In the Tar-Pamlico Basin, the species with the highest frequency was *Aphredoderus sayanus*, recorded in 54 out of 56 (96.42%) sampled locations. Lastly, the most frequent species in the Yadkin-Pee Dee Basin was *Nocomis leptocephalus*, identified in 106 out of 111 (95.49%) sampled locations.

The results of the hierarchical clustering analysis revealed the presence of three functional groups and one group of non-classified species derived from 113 fish species (Fig. 5). Species that were not classified into any of the three functional groups were classified according to information from other studies in the literature, they are *Amia calva*, *Anguilla rostrata*, *Ctenopharyngodon idella*, *Cyprinus carpio*, *Lepisosteus osseus* and *Pylodictis olivaris* (Table S5). In general, the classification of species into functional groups was in accordance with the literature (82.45% of agreement with at least one study), although the literature showed some divergence in classifications. The total number of fish species included in the opportunistic group was 23, in the equilibrium group was 44, and in the periodic group was 40 (Fig. 5).



In general, the watercourse distance was an important factor in determining both the taxonomic and functional beta dissimilarity among freshwater fish species in at least three basins—Cape Fear, Tar-Pamlico, and Yadkin-Pee Dee (Table 1). The beta dissimilarity in the Tar-Pamlico and Yadkin Basins was best explained by the effects of watercourse distances when compared to other combined dispersal effects (Table 1). Conversely, the Cape Fear Basin demonstrated an enhancement in the impact of watercourse distances when weighted by maximum slope (accounting for 26% and 25% of taxonomic and functional beta dissimilarity, respectively) and the sum of reservoirs’ surface area (contributing to 25% and 26% of taxonomic and functional beta dissimilarity, respectively) (Table 1). On the other hand, the Yadkin-Pee Dee Basin showed the highest percentage of beta dissimilarity predicted by watercourse distances, accounting for 40% of taxonomic beta diversity and 35% of functional beta dissimilarity (Table 1). Furthermore, it is worth noting that the effects of dispersal costs had a more pronounced impact on taxonomic beta dissimilarity when compared to their influence on functional beta diversity.

Table 1. Results of db-RDA analyses (adjusted R<sup>2</sup>) using the db-MEM axes from dispersal costs, taxonomic and functional beta dissimilarity based on reproductive and swimming ability traits. Zero values correspond to analysis in which no eigenvectors were selected by the forward procedure. No eigenvectors were selected for the Neuse River.

Dispersal costs	Watersheds		
	Cape Fear	Tar-Pamlico	Yadkin - Pee Dee
<b>Taxonomic Beta Diversity</b>			
Watercourse distance	0.25	0.27	0.40
W. dist. * Maximum slope	0.26	0.27	0.37
W. dist.* Standard deviation slope	0.17	0.18	0.35

W. dist. * Mean slope	0.23	0.00	0.32
W. dist. * Sum of heights of dams	0.16	0.00	0.22
W. dist. * Sum of reservoirs surfaces	0.26	0.24	0.37
W. dist. * Maximum age of dams	0.21	0.21	0.34
<b>Functional Beta Diversity</b>			
Watercourse distance	0.24	0.33	0.35
W. dist. * Maximum slope	0.25	0.00	0.31
W. dist. * Standard deviation slope	0.24	0.00	0.31
W. dist. * Mean slope	0.19	0.00	0.26
W. dist. * Sum of heights of dams	0.17	0.00	0.14
W. dist. * Sum of reservoirs surfaces	0.26	0.31	0.32
W. dist. * Maximum age of dams	0.19	0.31	0.23

The influence of dispersal costs on beta diversity of functional groups was only observed for periodic and equilibrium species, mostly related to the species in the Cape Fear Basin. In the Yadkin-Pee Dee basin, dispersal costs only accounted for the diversity of periodic species, with dispersal costs associated with watercourse distances (41%) and combined effects of watercourse distances and maximum slope (42%). Interestingly, the results revealed that periodic species in the Cape Fear were more influenced by dispersal costs than equilibrium species (Table 2). Furthermore, the greater effect associated with dispersal costs for Cape Fear equilibrium species was observed for the combined effect between watercourse distances and standard deviations of channel slopes (Table 2). Meanwhile, for periodic species, it was noted that the best model explaining beta dissimilarity of periodic species was associated with combined effects between watercourse distances, mean slope, and maximum slope (Table 2).

Table 2. Results of db-RDA analyses (adjusted  $r^2$ ) using the db-MEM axes from dispersal costs and beta dissimilarity for each functional group analyzed in the Cape Fear Basin. Beta diversity of

opportunistic species was not associated to dispersal costs. Zero values correspond to analysis in which no eigenvector was selected by the forward procedure.

Dispersal Costs	Equilibrium Species	Periodic Species
Watercourse distance	0.18	0.28
W. dist * Maximum slope	0.00	0.30
W. dist * Standard deviation slope	0.19	0.28
W. dist. * Mean slope	0.00	0.30
W. dist * Sum of heights of dams	0.12	0.26
W. dist. * Sum of reservoirs surfaces	0.00	0.00
W. dist. * Maximum age of dams	0.00	0.24

## Discussion

This study provides evidence that watercourse distances are an important dispersal cost for freshwater fish species as well as relevant predictor to determine the differences in composition of freshwater fish traits along the river basins. In addition, my results included investigation of different dispersal costs that enhanced the effects of the watercourse distances for large-scale catchments of the Appalachian Piedmont freshwater ecoregion. Moreover, I detected variation in the explained percentages of taxonomic and functional beta dissimilarity by the dispersal costs despite the basins being adjacent and located in the same ecoregion. Therefore, the results corroborate in part my assumption that dispersal costs are important to determine the functional and taxonomic beta dissimilarity, although their magnitude varied among basins. Periodic species were more affected by dispersal cost effects than other fish species groups, regardless of whether the effects are associated with dam effects or channel slope.

Although the importance of the spatial effects of watercourse distances are widely recognized (Vitorino Júnior *et al.* 2016, Zbinden & Matthews 2017, Zbinden *et al.* 2022), it is

important to point out that innumerable mechanisms act in parallel to the effects of dispersal limitation such as streamflow, biotic interactions, and disturbance (Driver & Hoeninghaus 2016, King *et al.* 2016, Chen & Olden 2017). Furthermore, the distances between the assemblages seem to reflect the dynamic effects of river structures such as the longitudinal organization (Zhang *et al.* 2020), and the spatial differentiation of main rivers and headwaters (Xia *et al.* 2022). In other words, the differentiation of spatial and environmental structure of headwaters and main rivers contributes to the taxonomic and functional diversity organization pattern (Zhang *et al.* 2020, Carvalho *et al.* 2021). In fact, Zbinden *et al.* (2022) obtained similar results with multiple large-scale basins in which adjacent basins presented distinct percentage of beta diversity explained by spatial factors, and the authors claimed it was due to the varying aspects of hydrology and physiography.

The explanation of functional and taxonomic beta diversities was not concordant as it was observed variation in the amount of explained percentage of functional and taxonomic beta dissimilarity in the same basin. A possible explanation for this pattern is due to the replacement of species with redundant functional traits (Campbell & Mandrak 2020). Considering the effects of environmental filtering, the replacement of species with similar traits is expected because the environmental selection pressure is responsible to select certain species traits in relation to others (Pool *et al.* 2014, Campbell & Mandrak 2020).

Many fluvial geomorphological attributes such channel slopes are crucial to determine the movement of individuals of freshwater fishes (Carvajal-Quintero *et al.* 2015, Dunn & Paukert 2021). However, the effects of channel slope on functional and taxonomic beta dissimilarity were only observed for the Cape Fear River basin. One possible explanation for the observed pattern

variation could be the presence of intrinsic variations within the river basins, with some of these variations being related to the presence of waterfalls or gentle slopes in montane regions (Herrera-Pérez *et al.* 2019). Furthermore, low slope segments are not sufficient to create hydraulic harshness able to limit fish dispersal compared to steep channel slopes (Camana *et al.* 2016). The Cape Fear River functional and taxonomic beta dissimilarities may respond to channel slopes resistances because of the high variation in mean and standard deviation slopes compared to other basins located in plain locations.

A possible explanation for the absence of beta dissimilarity patterns explained by dispersal costs may be associated with the presence of other unexamined effects, such as increased connectivity caused by river and stream channel diversions. The increase in connectivity due to anthropogenic effects contributes to the homogenization of assemblages (Strecker & Brittain 2017) and influences dispersal costs estimates. Additionally, the presence of alternative dispersal routes between locations may allow species to access some areas using routes with lower dispersal costs resistance that was not investigated in this study. Another relevant factor, at least for functional dissimilarity patterns, is that downstream regions of the Cape Fear, Neuse, and Tar-Pamlico River basins are influenced by marine ecosystems (brackish regions), thus explaining the absence of spatial patterns of functional beta dissimilarity.

Species with periodic life strategies are better predicted by dispersal cost effects than other species groups. This is due to the life history strategy employed by these species, which rely on dispersal to inhabit different assemblages along the river basins. When migratory periodic species encounter unfavorable local conditions, they tend to disperse throughout the river basin in search of favorable conditions for feeding or reproduction (Winemiller & Rose 1992, Arantes *et al.* 2019).

On the other hand, the absence of beta dissimilarity patterns for opportunistic species may be explained by the low number of identified species, resulting in highly reduced species matrices, as well as the resilience characteristics of these species in adverse conditions associated with dams (Winemiller & Rose 1992). Despite the hypothesis that equilibrium species would be more affected by the effects of watercourse distances and channel slopes, it is important to note that the standard deviation of slope combined with watercourse distances explained 19% of equilibrium species dissimilarity. A possible factor that reduced the percentage of explanation of dispersal effects for equilibrium species is that many of them adapt to changes from lotic to lentic environments (presence of reservoirs) (Miyazono *et al.* 2010, Arantes *et al.* 2019). It is important to emphasize that strict classifications of functional groups can obscure some results of functional studies, as there are many species with intermediate traits, as observed in other studies that obtained functional group classifications for freshwater fish (Table S5).

Dams impose a series of effects that influence the distribution of freshwater fish species, including dispersal cost effects; therefore, these effects should be considered in decisions involving restoration efforts and fisheries management. Furthermore, advanced studies are needed to investigate fish dispersal accurately, as distances between locations along river and stream courses only serve as proxies for dispersal estimates (Heino *et al.* 2017), and the same applies to dispersal cost measures. The results of this study suggest that dispersal cost effects are important in determining the taxonomic and functional beta dissimilarity of fish, although some river basins did not exhibit spatial patterns associated with dispersal costs. Some functional groups are more sensitive to changes in slope and the presence of dams along channels, such as periodic species.

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### Supplementary Material

Table S1. Information of the dams located in watercourse distances between sampled sites in the Cape Fear River Basin.

Name	Height (m)	Surface Area (km <sup>2</sup> )	Age (years)	Latitude	Longitude
B. Everett Jordan Dam	34.747	56.413	49	35.654	-79.066
Baldwin Millpond Dam	3.657	0.074	203	35.826	-79.235
Buckhorn Lake Dam	9.448	0.028	108	35.539	-78.990
Camp Nawaka Lake Dam	3.657	0.060	103	35.829	-79.774
Cane Creek Reservoir Dam	21.945	Undetermined	34	35.950	-79.241
Charles L. Turner Reservoir Dam	3.657	3.237	14	35.763	-79.456
Carbonton Dam	5.791	0.469	101	35.519	-79.348
City Lake Dam	15.240	1.161	95	35.995	-79.944
Coleridge	3.657	0.040	110	35.639	-79.617
Cox Lake	7.315	0.210	105	35.757	-79.752
Glen Raven Altamahaw	5.334	0.101	Undetermined	36.182	-79.511
Hackney Millpond Dam	3.657	Undetermined	192	35.736	-79.424
Hardys Millpond Dam	3.962	0.101	104	36.182	-79.709
Hedrick Lake Dam	4.572	0.084	69	35.214	-79.243
Hope Mills Dam	10.058	0.275	102	34.972	-78.945
Lake Brandt Dam	12.009	3.306	63	36.170	-79.837
Lake Cammack Dam	18.440	3.063	Undetermined	36.177	-79.411
Lake Higgins Dam	10.607	0.914	67	36.168	-79.879
Lake Rim Dam	6.096	0.141	103	35.031	-79.041
Lake Williams Dam	4.876	0.040	73	35.027	-79.072
Lockville Hydro Dam	3.657	Undetermined	193	35.623	-79.096
Oak Hollow Lake Dam	16.306	2.792	52	36.012	-79.985
Oakdale Cotten Mills Dam	7.254	0.048	Undetermined	35.980	-79.928

Odell Lake Dam	3.048	0.404	143	35.776	-79.149
Old Stony Creek Dam	11.277	0.485	95	36.128	-79.406
Phillips Creek Dam	5.913	0.016	Undetermined	34.738	-78.751
Raeford Dam and Fuseplug	8.534	0.849	109	35.815	-79.776
Ramseur Water Supply Dam	13.716	0.364	173	35.743	-79.677
Randleman Dam	31.089	12.423	96	35.834	-79.813
Randolph Mill Lake Dam	5.486	0.020	143	35.744	-79.703
Reeves Lake	7.620	Undetermined	173	35.636	-79.211
Robbins Raw Water Reservoir	7.620	0.141	43	35.431	-79.600
Rocky River Power Plant	9.144	0.404	62	35.795	-79.477
Saxapahaw	7.924	1.315	85	35.947	-79.325
Siler City Water Supply Lower Dam	3.657	0.048	83	35.762	-79.455
Thaggards Lake Dam	6.401	0.853	59	35.264	-79.360
Townsend Lake Dam	12.466	6.616	54	36.189	-79.732
Troublesome Creek Dam	14.203	2.751	49	36.282	-79.661
University Lake Dam	11.856	0.861	91	35.897	-79.092
William O. Huske Lock and Dam	6.705	2.630	88	34.835	-78.823
Woodlake Dam	7.010	0.064	50	35.217	-79.191
Worthville Dam	6.096	0.089	103	35.801	-79.776

Table S2. Information of the dams located in watercourse distances between sampled sites in Neuse River Basin.

Name	Height (m)	Surface Area (km <sup>2</sup> )	Age (years)	Latitude	Longitude
Atkinson Millpond Dam	3.658	Undetermined	93	35.668	-78.260
Beaverdam Creek Lake Dam	12.192	Undetermined	49	36.024	-78.688
Buckhorn Lake	6.096	Undetermined	Undetermined	35.691	-78.120
Eno West Point Dam	3.048	Undetermined	Undetermined	36.071	-78.911

Falls Lake Dam	28.042	45.770	42	35.942	-78.583
Hf Lee Cooling Lake Dam	5.182	2.274	68	35.381	-78.085
Holt Lake Dam	6.096	0.243	123	35.468	-78.383
Lake Benson Dam	7.925	1.874	71	35.662	-78.611
Lake Michie Dam	28.042	1.862	97	36.151	-78.830
Lake Raleigh Dam	6.706	0.267	109	35.765	-78.677
Wiggins Millpond	5.182	Undetermined	Undetermined	35.688	-77.949

Table S3. Information of the dams located in watercourse distances between sampled sites in Tar-Pamlico River Basin.

Name	Height (m)	Surface Area (km <sup>2</sup> )	Age (years)	Latitude	Longitude
Allen Dam	9.144	0.019	Undetermined	36.179	-78.191
Bellamy Lake Dam	6.096	0.283	83	36.158	-77.753
Bodies Millpond Dam	4.572	0.405	90	36.004	-78.039
Fishing Creek Millpond Dam	3.048	Undetermined	223	36.154	-77.743
Rocky Mount Millpond Dam	4.572	0.156	100	35.961	-77.803
Scott Braswell Dam	4.877	Undetermined	Undetermined	36.124	-77.950
Tar River Reservoir Dam	10.668	4.047	52	35.899	-77.885

Table S4. Information of the dams located in watercourse distances between sampled sites in Yadkin-Pee Dee River Basin.

Name	Height (m)	Surface Area (km <sup>2</sup> )	Age (years)	Latitude	Longitude
Lake Lee Dam	11.887	0.445	98	34.966	-80.511

Smitherman Millpond Dam	3.048	0.142	123	35.344	-79.853
Troy Town Reservoir Dam	5.486	0.036	91	35.390	-79.870
Bruton Millpond Dam	12.192	0.055	123	35.284	-79.894
Eury	14.630	0.113	107	35.254	-79.909
Tillery	26.213	21.286	95	35.206	-80.067
Lake Tom-A-Lex Dam	13.106	2.630	66	35.871	-80.193
High Rock	19.812	61.431	96	35.601	-80.235
Tuckertown	19.202	10.360	61	35.485	-80.177
Yadkin Narrows	59.741	21.671	106	35.420	-80.093
Yadkin Falls	22.555	0.826	104	35.395	-80.075
Coolemee	4.267	0.081	121	35.810	-80.563
W. Kerr Scott Dam	Undetermined	5.969	60	36.134	-81.226
Idols Reservoir Dam	4.572	0.170	126	35.975	-80.399
Lake Don T. Howell Dam	16.764	5.261	90	35.438	-80.699
Heritage Pointe Dam	3.475	0.001	Undetermined	35.332	-80.718
Little River	7.010	0.198	104	35.285	-79.893
Robert L. Reece Lake Dam	13.716	2.428	40	35.681	-79.970
Deer Pond Ltd. Dam	7.833	0.009	Undetermined	36.274	-80.602
Blue Ridge Tissue Dam	5.486	Undetermined	Undetermined	36.002	-81.564
Capelsie Lake Dam	4.572	0.121	134	35.320	-79.868

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Table S5. Classification of freshwater fishes in functional groups from the North Carolina basins using phylogenetic-functional distances. The second column represents the results of the functional groups classification estimated in this study and the third column represents functional groups classifications from scientific literature.

Species	Strategy (Estimated)	Strategy (Literature)
<i>Acantharchus pomotis</i>	Equilibrium	N/A
<i>Alosa sapidissima</i>	Opportunistic	N/A
<i>Ambloplites cavifrons</i>	Equilibrium	N/A
<i>Ambloplites rupestris</i>	Equilibrium	Periodic-Equilibrium <sup>1</sup> , Intermediate <sup>3</sup>
<i>Ameiurus brunneus</i>	Equilibrium	Periodic-Equilibrium <sup>1</sup>
<i>Ameiurus catus</i>	Equilibrium	Equilibrium <sup>2</sup>
<i>Ameiurus melas</i>	Equilibrium	Equilibrium <sup>1,3,6</sup> , Periodic <sup>4</sup>
<i>Ameiurus natalis</i>	Equilibrium	Equilibrium <sup>2,3,4,6</sup> , Periodic-Equilibrium <sup>1</sup>
<i>Ameiurus nebulosus</i>	Equilibrium	Equilibrium <sup>2</sup>
<i>Ameiurus platycephalus</i>	Equilibrium	N/A
<i>Amia calva</i>	?	Equilibrium <sup>2,6</sup>
<i>Anguilla rostrata</i>	?	Opportunistic <sup>2</sup> , Periodic <sup>6</sup> Equilibrium <sup>3</sup> , Opportunistic-Periodic <sup>1</sup> , Opportunistic <sup>5</sup> , Intermediate <sup>2</sup> , Opportunistic <sup>6</sup>
<i>Aphredoderus sayanus</i>	Equilibrium	Opportunistic <sup>6</sup>
<i>Campostoma anomalum</i>	Periodic	Periodic <sup>3</sup> , Opportunistic-Periodic <sup>1</sup> , Opportunistic <sup>2,4</sup>
<i>Carassius auratus</i>	Opportunistic	N/A
<i>Catostomus commersonii</i>	Opportunistic	Opportunistic <sup>2</sup> , Periodic <sup>1,4</sup>
<i>Centrarchus macropterus</i>	Equilibrium	N/A
<i>Chologaster cornuta</i>	Equilibrium	N/A
<i>Chrosomus oreas</i>	Periodic	N/A
<i>Clinostomus funduloides</i>	Periodic	N/A

<i>Ctenopharyngodon idella</i>	?	Periodic <sup>2,6</sup>
<i>Cyprinella analostana</i>	Periodic	N/A
<i>Cyprinella chloristia</i>	Periodic	N/A
<i>Cyprinella labrosa</i>	Periodic	N/A
<i>Cyprinella lutrensis</i>	Periodic	Opportunistic-Periodic <sup>3</sup> , Opportunistic-Equilibrium <sup>1</sup> , Opportunistic <sup>4,5</sup>
<i>Cyprinella nivea</i>	Periodic	N/A
<i>Cyprinella pyrrhomelas</i>	Periodic	N/A
<i>Cyprinus carpio</i>	?	Periodic <sup>3,6</sup> , Intermediate <sup>2</sup>
<i>Dorosoma cepedianum</i>	Periodic	Periodic <sup>1,3,4,5,6</sup> , Opportunistic <sup>2</sup>
<i>Dorosoma petenense</i>	Periodic	Opportunistic <sup>2,3,6</sup> , Intermediate <sup>5</sup>
<i>Elassoma zonatum</i>	Equilibrium	Opportunistic-Equilibrium <sup>3</sup>
<i>Enneacanthus chaetodon</i>	Equilibrium	N/A
<i>Enneacanthus gloriosus</i>	Equilibrium	N/A
<i>Enneacanthus obesus</i>	Equilibrium	N/A
<i>Erimyzon oblongus</i>	Opportunistic	Periodic-Equilibrium <sup>1</sup> , Periodic <sup>6</sup>
<i>Erimyzon sucetta</i>	Opportunistic	N/A
<i>Esox americanus</i>	Opportunistic	Opportunistic-Equilibrium <sup>3</sup>
<i>Esox niger</i>	Opportunistic	Periodic <sup>1,6</sup>
<i>Etheostoma brevispinum</i>	Not included	N/A
<i>Etheostoma collis</i>	Equilibrium	N/A
<i>Etheostoma flabellare</i>	Equilibrium	Opportunistic-Equilibrium <sup>1</sup> , Intermediate <sup>2</sup>
<i>Etheostoma fusiforme</i>	Equilibrium	Opportunistic-Equilibrium <sup>3</sup> , Opportunistic <sup>6</sup>
<i>Etheostoma nigrum</i>	Equilibrium	Opportunistic-Equilibrium <sup>1</sup> , Intermediate <sup>2</sup>
<i>Etheostoma olmstedi</i>	Equilibrium	Opportunistic-Equilibrium <sup>1</sup>
<i>Etheostoma serrifer</i>	Equilibrium	N/A
<i>Etheostoma vitreum</i>	Equilibrium	N/A
<i>Fundulus lineolatus</i>	Periodic	N/A

<i>Fundulus rathbuni</i>	Periodic	N/A
<i>Gambusia holbrooki</i>	Periodic	N/A
<i>Hybognathus regius</i>	Periodic	N/A
<i>Hybopsis hypsinotus</i>	Periodic	N/A
<i>Hypentelium nigricans</i>	Opportunistic	Periodic <sup>1</sup> , Opportunistic <sup>2</sup>
<i>Hypentelium roanokense</i>	Opportunistic	N/A
<i>Ictalurus punctatus</i>	Equilibrium	Periodic-Equilibrium <sup>1,3</sup> , Equilibrium <sup>2,4,5</sup>
<i>Lampetra aepyptera</i>	Not included	N/A
<i>Lepisosteus osseus</i>	?	Periodic <sup>1,3</sup> , Intermediate <sup>2</sup> , Equilibrium <sup>6</sup>
<i>Lepomis auritus</i>	Equilibrium	Equilibrium <sup>3</sup> , Periodic-Equilibrium <sup>1</sup>
<i>Lepomis cyanellus</i>	Equilibrium	Equilibrium <sup>3,5,6</sup> , Periodic-Equilibrium <sup>1</sup> , Intermediate <sup>2</sup>
<i>Lepomis gibbosus</i>	Equilibrium	Periodic-Equilibrium <sup>1</sup> , Intermediate <sup>2</sup>
<i>Lepomis gulosus</i>	Equilibrium	Equilibrium <sup>3,6</sup> , Periodic-Equilibrium <sup>1</sup> , Intermediate <sup>2,5</sup>
<i>Lepomis macrochirus</i>	Equilibrium	Equilibrium <sup>3,4,6</sup> , Periodic-Equilibrium <sup>1</sup> , Intermediate <sup>2,5</sup>
<i>Lepomis marginatus</i>	Equilibrium	Equilibrium <sup>3</sup>
<i>Lepomis microlophus</i>	Equilibrium	Equilibrium <sup>3,6</sup> , Periodic-Equilibrium <sup>1</sup> , Intermediate <sup>2,5</sup>
<i>Lepomis punctatus</i>	Equilibrium	Equilibrium <sup>3</sup> , Periodic-Equilibrium <sup>1</sup>
<i>Luxilus albeolus</i>	Periodic	N/A
<i>Luxilus cerasinus</i>	Periodic	N/A
<i>Luxilus coccogenis</i>	Periodic	Opportunistic-Periodic <sup>1</sup>
<i>Lythrurus ardens</i>	Periodic	N/A
<i>Lythrurus matutinus</i>	Periodic	N/A
<i>Micropterus dolomieu</i>	Equilibrium	Periodic-Equilibrium <sup>1,3</sup> , Equilibrium <sup>2</sup>
<i>Micropterus punctulatus</i>	Equilibrium	Periodic-Equilibrium <sup>1,3,6</sup> , Intermediate <sup>5</sup> , Equilibrium <sup>2</sup>
<i>Micropterus salmoides</i>	Equilibrium	Periodic-Equilibrium <sup>1,3</sup> , Intermediate <sup>5</sup> , Equilibrium <sup>3,4,6</sup>
<i>Minytrema melanops</i>	Opportunistic	Periodic <sup>1,3,5,6</sup> , Opportunistic <sup>2</sup>

<i>Misgurnus anguillicaudatus</i>	Opportunistic	N/A
<i>Morone americana</i>	Opportunistic	Opportunistic <sup>2</sup>
<i>Moxostoma cervinum</i>	Opportunistic	N/A
<i>Moxostoma collapsum</i>	Opportunistic	N/A
<i>Moxostoma erythrurum</i>	Opportunistic	Periodic <sup>1</sup> , Opportunistic <sup>2</sup>
<i>Moxostoma lachneri</i>	Opportunistic	N/A
<i>Moxostoma macrolepidotum</i>	Opportunistic	Periodic <sup>1,4</sup> , Opportunistic <sup>2</sup>
<i>Moxostoma pappillosum</i>	Opportunistic	N/A
<i>Moxostoma rupiscartes</i>	Opportunistic	N/A
<i>Nocomis leptcephalus</i>	Equilibrium	Opportunistic-Periodic <sup>1</sup>
<i>Nocomis raneyi</i>	Equilibrium	N/A
<i>Notemigonus crysoleucas</i>	Periodic	Periodic <sup>3,6</sup> , Intermediate <sup>5</sup> , Opportunistic <sup>2</sup>
<i>Notropis alborus</i>	Periodic	N/A
<i>Notropis altipinnis</i>	Periodic	N/A
<i>Notropis amoenus</i>	Periodic	N/A
<i>Notropis chalybaeus</i>	Periodic	N/A
<i>Notropis chiliticus</i>	Periodic	N/A
<i>Notropis cummingsae</i>	Periodic	N/A
<i>Notropis hudsonius</i>	Periodic	Opportunistic-Periodic <sup>1</sup> , Opportunistic <sup>2</sup>
<i>Notropis mekistocholas</i>	Periodic	N/A
<i>Notropis petersoni</i>	Periodic	N/A
<i>Notropis procne</i>	Periodic	N/A
<i>Notropis szepticus</i>	Periodic	N/A
<i>Notropis volucellus</i>	Periodic	Opportunistic-Periodic <sup>3</sup> , Opportunistic-Equilibrium <sup>1</sup> , Opportunistic <sup>5</sup>
<i>Noturus furiosus</i>	Equilibrium	N/A
<i>Noturus gyrinus</i>	Equilibrium	Opportunistic-Equilibrium <sup>3</sup> , Opportunistic-Periodic <sup>1</sup> , Intermediate <sup>2</sup> , Opportunistic <sup>6</sup>
<i>Noturus insignis</i>	Equilibrium	Opportunistic-Periodic <sup>1</sup>

<i>Oncorhynchus mykiss</i>	Opportunistic	Opportunistic <sup>2</sup>
<i>Perca flavescens</i>	Opportunistic	Opportunistic <sup>2</sup>
<i>Percina crassa</i>	Periodic	N/A
<i>Percina nevisense</i>	Periodic	N/A
<i>Percina roanoka</i>	Periodic	N/A
<i>Petromyzon marinus</i>	Not included	N/A
<i>Pimephales promelas</i>	Equilibrium	Opportunistic-Equilibrium <sup>1</sup> , Intermediate <sup>2</sup> , Equilibrium <sup>3</sup>
<i>Pomoxis annularis</i>	Equilibrium	Periodic-Equilibrium <sup>3</sup> , Intermediate <sup>2,5</sup> , Equilibrium <sup>4,6</sup>
<i>Pomoxis nigromaculatus</i>	Equilibrium	Intermediate <sup>2,5</sup> , Equilibrium <sup>6</sup>
<i>Pylodictis olivaris</i>	?	Equilibrium <sup>6</sup>
<i>Rhinichthys obtusus</i>	Periodic	Intermediate <sup>2</sup>
<i>Salmo trutta</i>	Opportunistic	N/A
<i>Salvelinus fontinalis</i>	Opportunistic	N/A
<i>Semotilus atromaculatus</i>	Periodic	Opportunistic-Periodic <sup>1</sup> , Intermediate <sup>2</sup> , Opportunistic <sup>4</sup>
<i>Semotilus lumbee</i>	Periodic	N/A
<i>Umbra pygmaea</i>	Equilibrium	N/A

Note: information obtained from the studies of <sup>1</sup>Meador & Brown 2015, <sup>2</sup>Pyron *et al.* 2019, <sup>3</sup>Hoeinghaus *et al.* 2007, <sup>4</sup>Kirk *et al.* 2022,

<sup>5</sup>Perkin *et al.* 2016, <sup>6</sup>Miyazono *et al.* 2010.

### **Chapter 3 – Latitudinal gradient modulates the environment-beta diversity relationship for mammals but not for birds in the America continent**

#### **Abstract**

The pattern of the latitudinal gradient of species richness and distribution is a well-known phenomenon. Many candidate theories and explanations are advocated to explain the spatial latitudinal patterns, which includes productivity, elevation, climate, biotic interactions, niche breadth and historical processes of evolution and dispersal. However, little is known about the influence of latitude on the relationship between beta diversity and the environmental variables at continental scales. Therefore, my main goal was to investigate the latitudinal effects on the relationship between beta diversity and environmental differences in the American continent controlling the effect of non-stationarity, commonly observed over large areas. My hypothesis is that the beta diversity between adjacent cells is determined by differences of elevation and bioclimatic variables, but the strength of the association is dependent on the latitude. My results indicated that beta diversity is determined by elevation and bioclimatic variables for both birds and terrestrial mammals. However, the association between beta diversity and environmental differences was only modulated by latitude considering terrestrial mammal species. This finding should be due to several factors, including time since historical divergence of the two clades or physiological differences between of the two groups of vertebrates.

**Keywords:** Beta diversity, Latitudinal environmental gradients, Elevation, Distinctiveness.

## Introduction

The distribution of biodiversity along latitudinal gradients is one of the main patterns studied in Ecology and Biogeography. However, the spatial species richness patterns are often incongruent, and currently there is a heated debate about the mechanisms generating the observed patterns. In addition, the patterns of latitudinal gradient distribution have received greater attention concerning alpha diversity, whereas studies addressing large scale beta diversity patterns are more recent and less numerous. Some authors argue that beta diversity varies according to latitude, with the highest rates of change found in regions at lower latitudes (Koleff *et al.* 2003, Gaston *et al.* 2007, Qian *et al.* 2009, Soininen *et al.* 2018). Additionally, it has been observed that correlations between beta diversity and environmental variables are stronger in regions near the equator (Qian & Ricklefs 2007, Qian *et al.* 2009, Nishizawa *et al.* 2022).

Numerous factors have been suggested as responsible for creating latitudinal patterns, such as productivity, elevation, climate, or intrinsic species characteristics like niche breadth and origin of the group (Mittelbach *et al.* 2001, Beck *et al.* 2017, Nishizawa *et al.* 2021). According to Rapoport's rule, latitudinal patterns are influenced by the niche characteristics of species, where species with broader niches are more frequently present in regions at higher latitudes, and species with narrower niche breadth are common in regions at lower latitudes. This is because species with greater niche breadth are favored by their tolerance to environmental variations and dispersal capacity (with exceptions for migratory species) (Stevens 1992). Many tropical regions include areas of high productivity, which is responsible for generating habitat and resource diversity and, consequently, high species richness (Andrew *et al.* 2012). On the other hand, latitudinal patterns

can reflect historical evolutionary events (Qian *et al.* 2009, Dobrovolski *et al.* 2012), such as glaciations (Qian & Ricklefs 2007).

From a mechanistic perspective, one could hypothesize that latitudinal patterns are also the result of temperature effects, influencing physiological responses of organisms or increasing speciation rates (Willig *et al.* 2003). The other two important mechanisms are dispersal limitation and ecological drift (Ford & Roberts 2018). Mruzek *et al.* (2022) found that the variation in the latitudinal gradient concerning dispersal limitation and niche effects would be relevant for alpha diversity but not for beta diversity. Additionally, ecological transition zones and biogeographic region borders also exhibit substantial variation in species composition, thus explaining changes in species composition along the latitudinal gradient (Tang *et al.* 2012). Furthermore, latitudinal patterns of beta diversity may vary among groups of organisms, as some may exhibit positive, negative, or even null correlations (Koleff *et al.* 2003, Alahuhta *et al.* 2017; Heino & Alahuhta, 2019, Xing & He 2019, Mruzek *et al.* 2022).

In recent decades, the importance of environmental variables in determining beta diversity along the latitudinal gradient has been extensively discussed. Among the main environmental variables, it is well-known that differences in elevation have a considerable influence on biodiversity differences at a continental scale (Melo *et al.* 2009, Bogoni *et al.* 2021). The influence of elevation on biodiversity follows an expected pattern according to the Stevens' extension, as elevation is associated with fast change in various abiotic factors such as temperature, humidity, precipitation, and evapotranspiration (Stevens 1989, 1992). Additionally, bioclimatic variables have demonstrated significant relevance as predictors of beta diversity in numerous organism groups (Qian *et al.* 2009, Xing & He 2019, Zhang *et al.* 2020). Indeed, bioclimatic variables such

as temperature, precipitation, and humidity are thought to be the causal factors behind latitudinal distribution patterns, with latitude serving as a proxy for these variables (Hawkins & Diniz-Filho 2004).

In contrast to previous studies, this study contributes new features by investigating the latitudinal influence on the environmental-beta diversity relationship strength controlling the effects of non-stationarity. Therefore, I used the Geographically Weighted Regression (GWR) approach and compared local r-squared values across latitudes. One of the main features of the Geographically Weighted Regression method is the ability to recognize non-stationary spatial effects (Fotheringham *et al.* 2002), as it is known that variations in beta diversity over space follow non-monotonic patterns (*i.e.*, non-constant linear coefficient regressions) (Zhang *et al.* 2020). Hence, I investigated the hypotheses: (1) that beta diversity (estimated using dissimilarity among square grid cells) is determined by bioclimatic and elevation differences, and (2) that correlation is latitude-dependent, with low latitudes showing higher correlation values as it is assumed that latitude is responsible for moderating local environmental effects (Hawkins & Diniz-Filho 2004).

## Methods

### *1. Obtaining data*

I obtained species distribution records for terrestrial mammals and birds in shapefile format from the IUCN Red List online database (IUCN 2023, <https://www.iucnredlist.org/resources/spatial-data-download>). I projected the species distributions onto the American continent grid cell of 1.0° x 1.0° spatial resolution to obtain species incidence matrices. I excluded isolated cells (*i.e.*, without any adjacent neighbor cell), cells located on islands and archipelagos (*e.g.*, Galápagos Islands,

America Central Islands), and cells covering less than 50% of land area. Cells located in islands and archipelagos were excluded because insular systems are weakly influenced by climatic variables compared to continental systems (Field *et al.* 2008). The species incidence matrices were used to obtain the beta diversity (distinctiveness) using the mean of pairwise Sørensen index for each squared grid cell compared to all adjacent neighbor cells (see Koleff *et al.* 2003, Melo *et al.* 2009).

## 2. Environmental variables

I obtained a total of 20 environmental variables in raster data format with a spatial resolution of 10 minutes or approximately 340 km<sup>2</sup> from the WorldClim database (Hijmans *et al.* 2005, [www.worldclim.org](http://www.worldclim.org)) (Table 1). I adjusted the resolution of the raster files compatible with the spatial resolution of the grid shapefiles and I estimated the mean values of the overlaid raster cells. Subsequently, I measured the environmental difference of each focal cell compared to each neighboring cell (in pairs) and obtained a mean value of the differences (this procedure was applied for each environmental variable independently). To avoid the collinearity between the predictor variables, I tested the correlation between environmental differences (Table S1) and excluded one of them when correlation value was higher than 0.7 or lower than -0.7 (Table 1).

Table 1. Elevation and bioclimatic environmental variables obtained from the WorldClim database with description and respective abbreviation code. Variables marked with an asterisk were selected for the next analysis stage.

Abbreviation	Environmental Variables
Elev.	Elevation *
BIO-1	Annual Mean Temperature
BIO-2	Mean Diurnal Range (Mean of monthly (max temp – min temp.)) *
BIO-3	Isothermality (BIO2/BIO7) *
BIO-4	Temperature Seasonality (standard deviation x 100) *
BIO-5	Max. Temperature of Warmest Month
BIO-6	Min. Temperature of Coldest Month
BIO-7	Temperature Annual Range (BIO5-BIO6) *
BIO-8	Mean Temperature of Wettest Quarter *
BIO-9	Mean Temperature of Driest Quarter *
BIO-10	Mean Temperature of Warmest Quarter
BIO-11	Mean Temperature of Coldest Quarter
BIO-12	Annual Precipitation
BIO-13	Precipitation of Wettest Month *
BIO-14	Precipitation of Driest Month
BIO-15	Precipitation Seasonality (coefficient of variation) *
BIO-16	Precipitation of Wettest Quarter
BIO-17	Precipitation of Driest Quarter *
BIO-18	Precipitation of Warmest Quarter
BIO-19	Precipitation of Coldest Quarter *

### 3. Geographically Weighted Regressions (GWR)

I employed the environmental differences as predictors of beta diversity obtained between adjacent cells using the GWR analysis. GWR is a statistical tool that accounts for non-stationary effects in the regressions data (Fotheringham *et al.* 2002). Non-stationary effects are common in large spatial data because large areas encompass distinct amounts of variation in different parts of the territory, which may result in heteroscedasticity when the data is analyzed using a global linear regression model. The GWR approach fits regression parameters based on local slopes (for each cell) and the values are weighted according to a kernel bandwidth function (Fotheringham *et al.* 2002). Bandwidth is a moving regression window that defines a region and a centered point that is used to weigh other points (points closer to the centered point receive greater weight, while distant

points receive less weight). The next step includes calibrating the local regression with all data, and the process is repeated for all regression points. Therefore, bandwidth is essential to detect and overcome problems associated with spatial autocorrelation. Here, the method chosen to determine the bandwidth was based on the Akaike Information Criterion. Finally, I investigated the correlation between local r-squared values and latitude using the Pearson's correlation method to test my second hypothesis. All the analysis was performed using the R environment (R Development Core Team 2023), and the GWR analysis was performed using the R package GWmodel (Lu *et al.* 2014, Gollini *et al.* 2015).

## Results

The total number of grid cells obtained from the continent of America was 4,107, and the total number of terrestrial mammal species analyzed was 1,897, while the total number of bird species was 4,361. The bird species with the highest presence value in the grid cells was *Tringa flavipes* that was present in 3,692 cells, while for terrestrial mammal species was *Lasiurus cinereus* that was present in 2,459 cells. Beta diversity values showed heterogeneous and sparse spatial distribution across the map, with some regions with high dissimilarity in the Andean region, the southwest coast of North America and the Central American region (Figs 1-2). The highest value of beta diversity was found for the bird species (0.507) compared to the terrestrial mammal species (0.436). Moreover, the bird map showed large areas of low dissimilarity located in the central and southeast region of North America (Fig. 1).

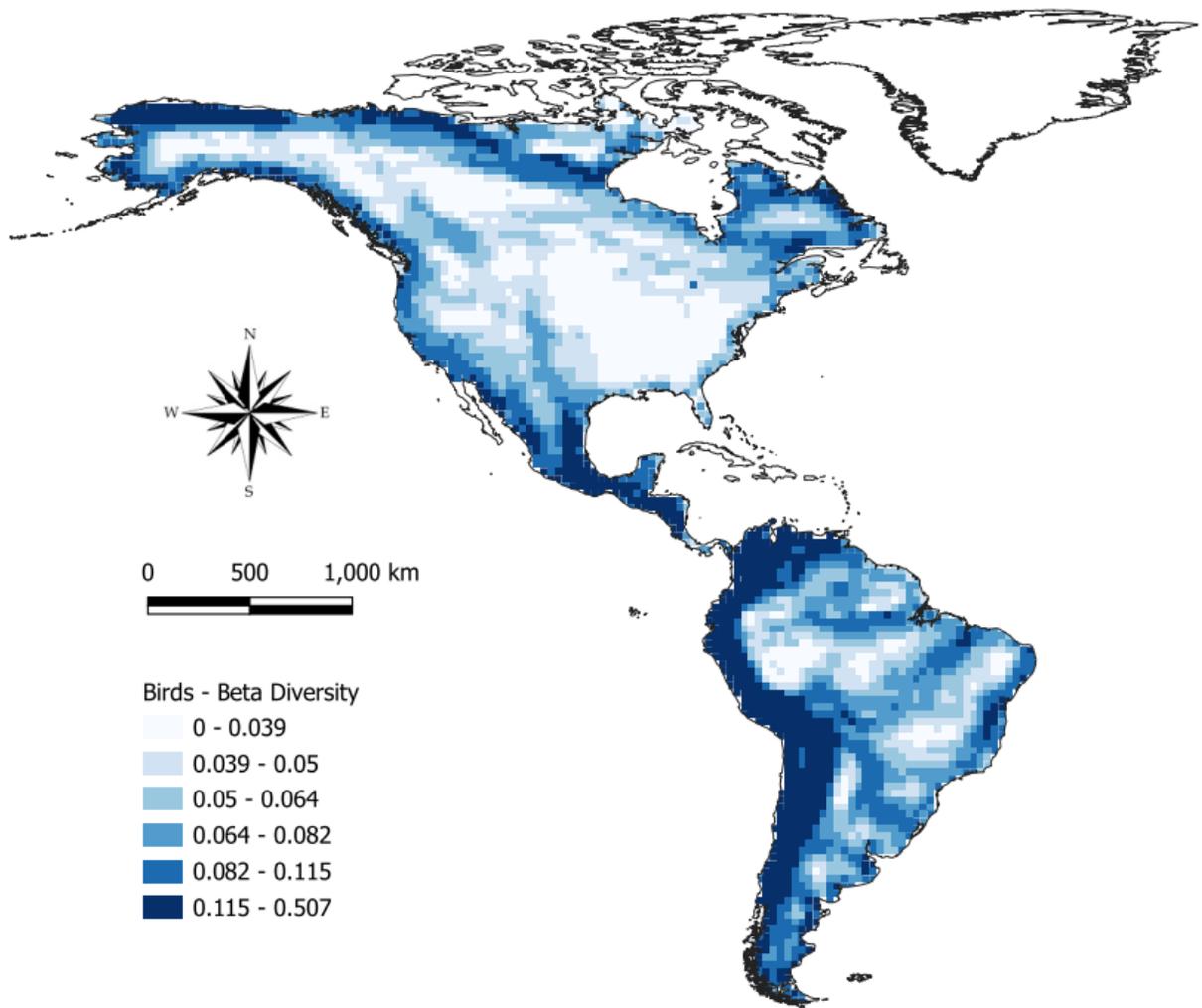


Figure 1. Grid map containing cells of 1.0° x 1.0° spatial resolution representing the obtained values of beta diversity of birds recorded for the continent of America.

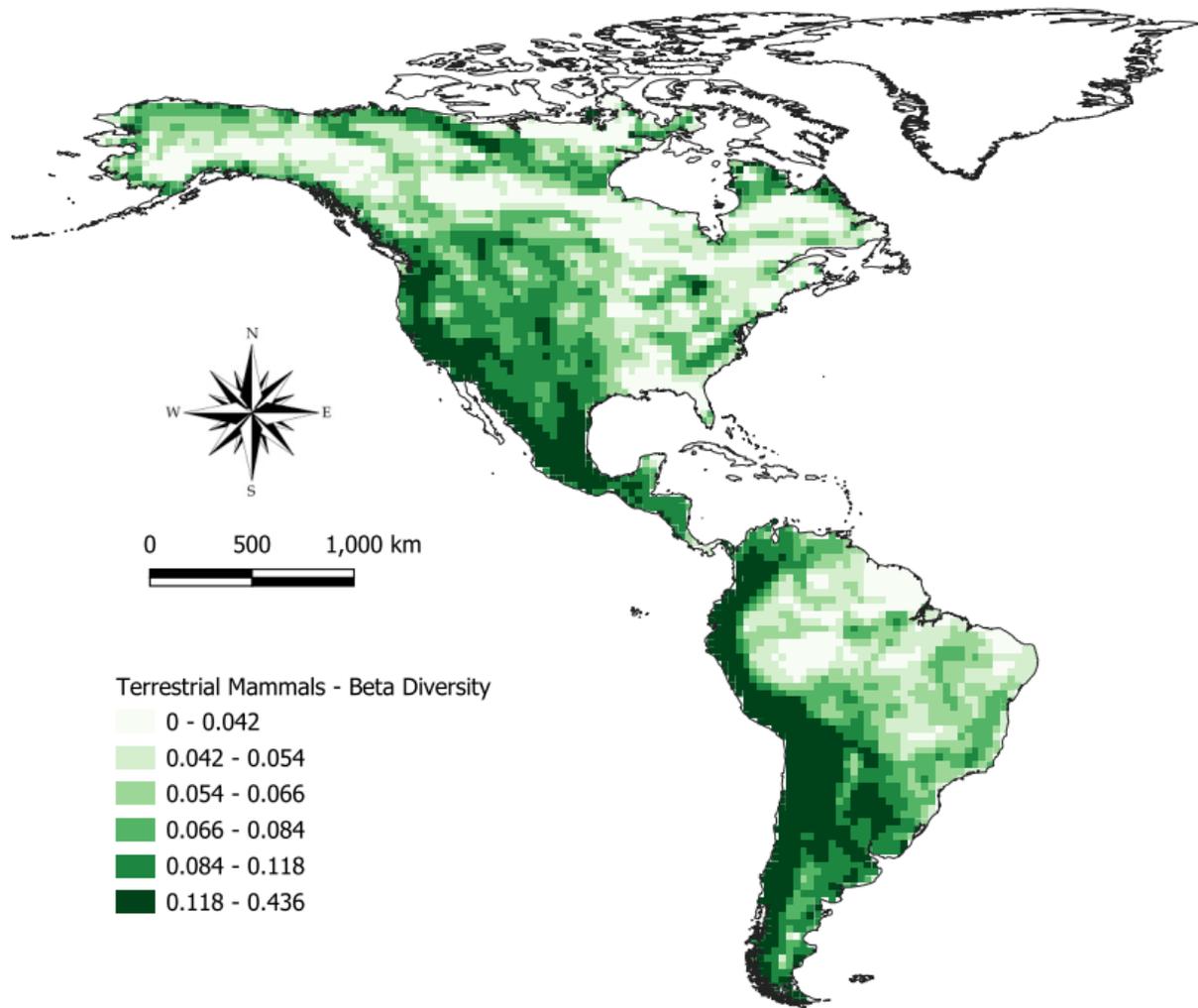


Figure 2. Grid map containing cells of  $1.0^{\circ} \times 1.0^{\circ}$  spatial resolution representing the obtained values of beta diversity of terrestrial mammals recorded for the continent of America.

The GWR analysis revealed that beta diversity was largely determined by the environmental differences between cells, both for birds (Adjusted r-squared = 0.93, bandwidth selected = 71, AICc = -21834.9) and for mammals (Adjusted r-squared = 0.92, bandwidth selected = 71, AICc = -21724.1). In the global regression, the bird beta diversity was predicted by

differences of all selected non-colinear variables (Table 1). On the other hand, the terrestrial mammal dissimilarities were predicted by the differences of the variables of Elevation, Mean Diurnal Range, Temperature Seasonality, Precipitation of Wettest Month, Precipitation Seasonality, and Precipitation of Coldest Quarter.

The local r-squared values varied between 0.578 and 0.999 for birds (Fig. 3) and between 0.487 and 0.999 for mammals (Fig. 4). The highest local r-squared values were observed in the Andean regions for both birds and terrestrial mammals. However, birds and mammals differed in the distribution of the highest local r-squared values in other regions, such as the central region of North America for birds and the northern part of the South American continent for terrestrial mammals. As expected, the Pearson's correlation between local r-squared and latitude was negative for terrestrial mammals ( $r = -0.35$ ,  $t = -24.22$ ,  $p < 0.001$ ), indicating stronger associations of beta diversity and environmental dissimilarity at low latitudes. On the other hand, there was no correlation between latitudinal gradient and the environmental-beta diversity relationship for birds ( $r = -0.01$ ,  $t = -0.04$ ,  $p = 0.962$ ). Furthermore, the latitudinal structure of the correlations did not reflect a clear gradient, with certain regions exhibiting high values of local r-squared far from the equator, indicating the presence of local spatial structuring factors, such as the Andean region, Ontario and north British Columbia regions (Canada) for terrestrial mammals. For birds, high values of local r-squared were found for a wide range of central North America. The opposite pattern can be notice for regions near to equator with low values of local r-squared, represented by cells in the Central America (*e.g.*, territories of Nicaragua, Guatemala, and Costa Rica) for both birds and terrestrial mammals.

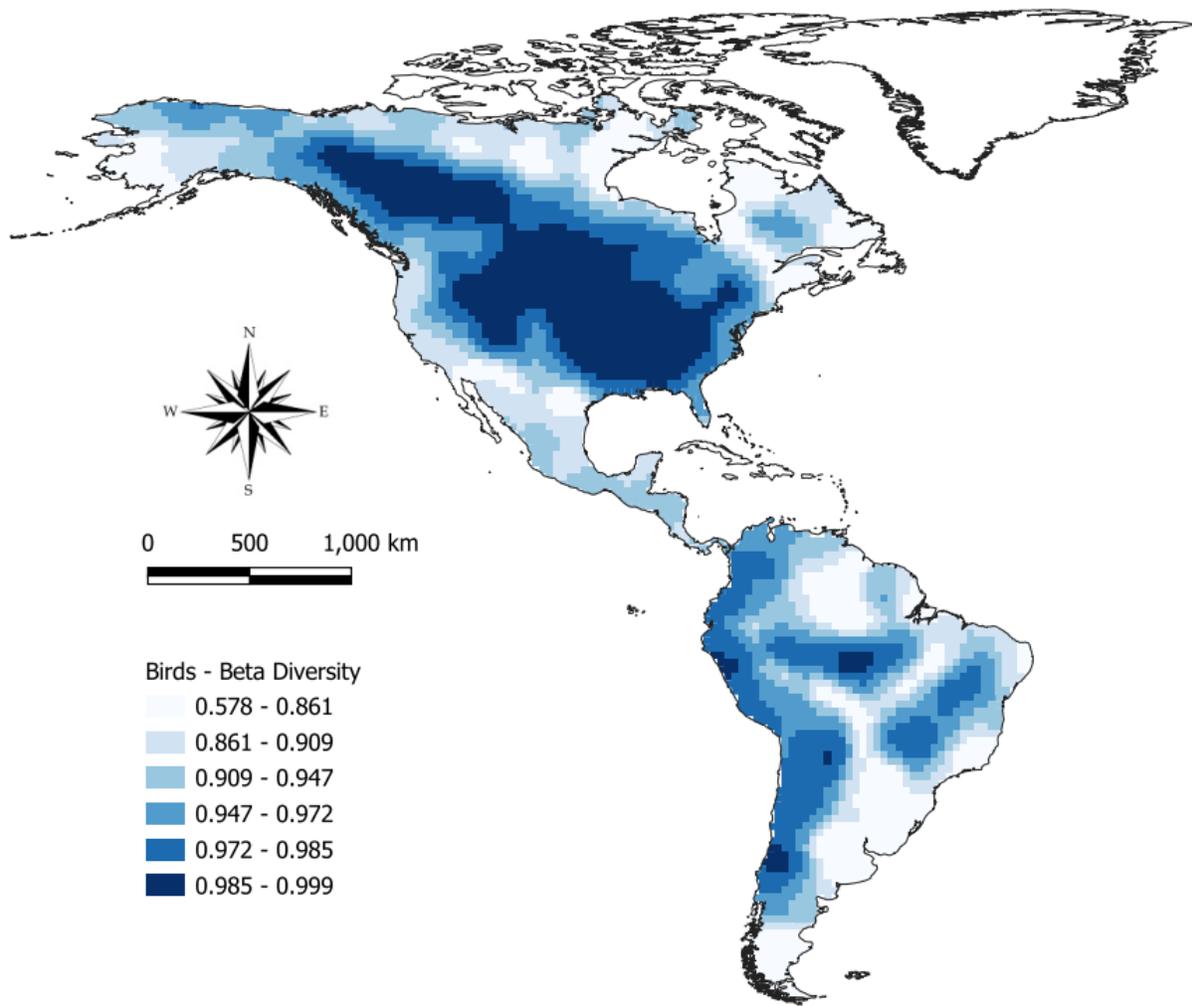


Figure 3. Grid map containing cells of  $1.0^{\circ} \times 1.0^{\circ}$  spatial resolution representing the obtained values of local r-squared of the relationship of bird beta diversity and differences in environmental variables in the American continent.

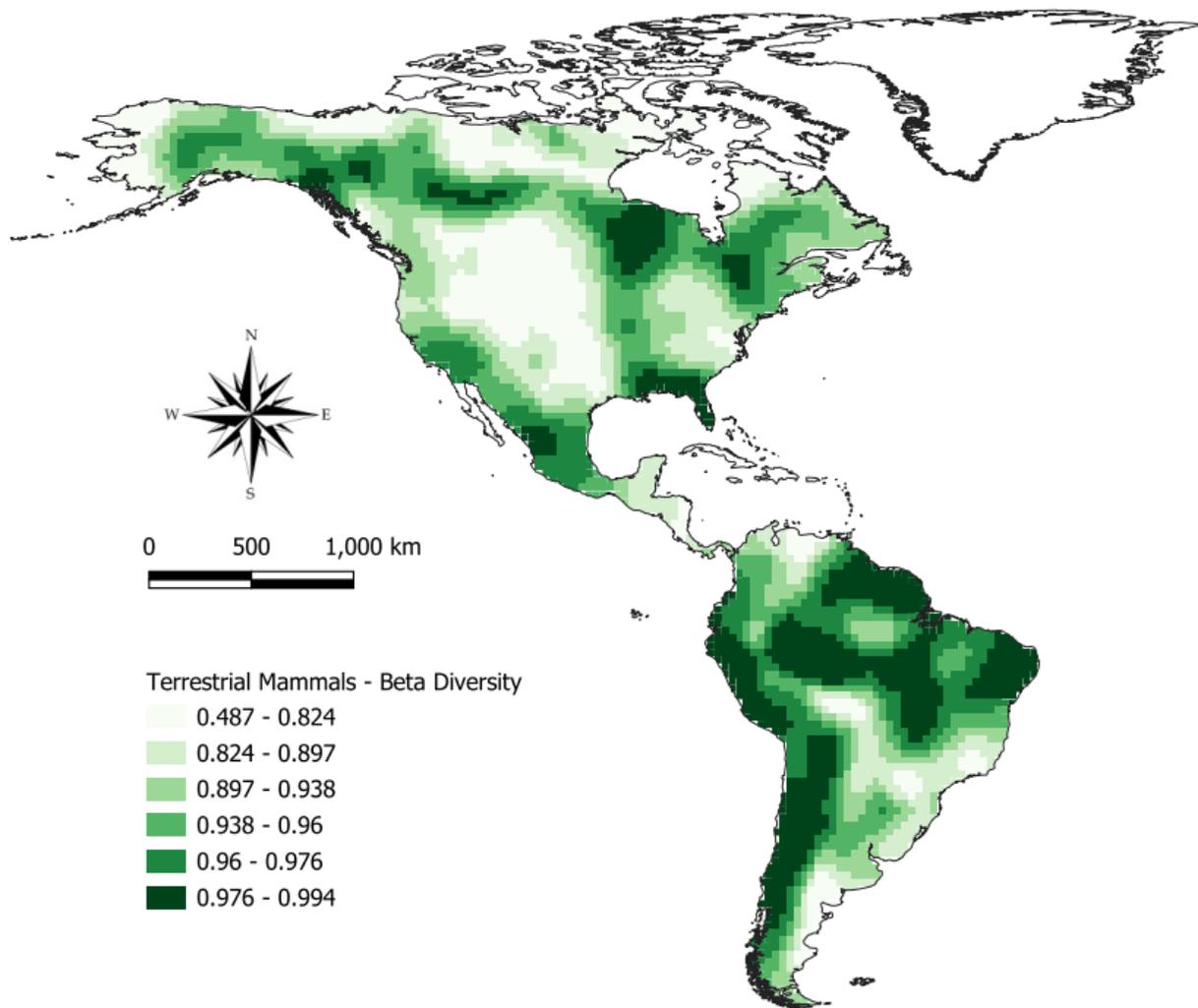


Figure 4. Grid map containing cells of  $1.0^{\circ} \times 1.0^{\circ}$  spatial resolution representing the obtained values of local  $r$ -squared of the relationship between terrestrial mammal beta diversity and differences in environmental variables in the American continent.

## Discussion

The beta diversity of birds and terrestrial mammals exhibited different patterns of spatial organization in the American continent. The environmental differences revealed to be fundamental predictors of the beta dissimilarities of birds and terrestrial mammals as the results of GWR analysis revealed explanations of 93% and 92%, respectively. My findings contribute as a novelty by investigating latitudinal effects on the relationships between beta diversity and environmental differences at continental scales controlling effects of non-stationarity. The results showed that the relationship between environmental differences and beta diversity depends on latitude for terrestrial mammals, but not for birds.

The Andean mountains are known as representative zones of high influence of altitudinal gradient over species richness and beta diversity (Melo *et al.* 2009, Tenorio *et al.* 2023), because the acute variation of the elevation affect many environmental variables such as temperature. The effects of elevation are indirect and, thus, elevation is a surrogate for many environmental variables such as temperature, precipitation and humidity that act directly on the species (Hawkins & Diniz-Filho 2004).

Most of the environmental differences able to explain the beta diversity of terrestrial mammals, in total number of variables, are related to precipitation (Precipitation of Wettest Month, Precipitation Seasonality, and Precipitation of Coldest Quarter), in contrast to temperature variables. Importantly, previous research has shown that precipitation is a significant factor influencing the beta diversity of vascular plants and mammals along the latitudinal gradient (Qian *et al.* 2007, Qian *et al.* 2009), which is consistent with my results. Therefore, similar spatial beta diversity between plants and mammals may reveal the influence of vegetation habitat on mammal communities, especially for herbivores mammals (Bogoni *et al.* 2021, Eronen *et al.* 2010).

My results are consistent with the result of other studies that pointed out that latitudinal gradients are associated to beta diversity (Qian *et al.* 2009, Tang *et al.* 2013, Zhang *et al.* 2020, Montaña-Centellas *et al.* 2021). The regions found with high explanation of environmental difference over the beta diversity (*i.e.*, local r-squared values) may be result of historical processes and species isolation. Qian *et al.* (2009) advocate that patterns of beta diversity found in the north of Canada and Alaska are related to processes of historical glaciation that resulted in refugia patches. In contrast, environmental filtering may exert strong control in other regions (Qian & Ricklefs 2007).

The local r-squared values found for terrestrial mammals were correlated with the latitudinal gradient effect; however, my results did not indicate the same effect for birds. Although latitudinal gradient effects have been reported to be fundamental to the beta diversity of birds (Williams *et al.* 1999, Koleff & Gaston 2001), the same expectation does not apply when analyzing latitudinal effects for the relationship between beta diversity and environmental differences. One plausible explanation for that may be the difference of dispersal ability (Tello & Stevens 2010, Qian & Wang 2015), or historical diversification of the taxonomical groups (Weir & Schluter 2007, Salisbury *et al.* 2012, Meltesen *et al.* 2023). The historical diversification of birds differs from the diversification of mammals, which includes a combination of unique effects of dispersal barriers, competition, and niche conservatism (Kennedy *et al.* 2014). Moreover, it is possible that terrestrial mammal beta diversity is more sensitive to high-range variation of the environmental differences.

Although my data indicate the possibility that latitude is a modulator of the relationships between environmental differences and beta diversity of terrestrial mammals, it is still necessary to understand what mechanisms are responsible for creating such patterns. Furthermore, from my

results, it is not possible to draw a causal inference of the latitudinal gradient on the strength of the relationship between beta diversity and environmental differences. It is also important to highlight that the same pattern was not observed for birds. Therefore, it is necessary to investigate specific attributes of taxonomic groups that should be important to create the observed divergence. Other possible factors include differences associated with historical processes such as diversification and distinct dispersal processes of the taxonomic groups. Finally, my results converge with the results of previous studies and raise the question of the existence of a moderating effect of latitude on the relationships between environmental differences and beta diversity.

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## Supplementary Material

Table S1. Summary of Pearson correlations between mean differences of environmental variables between adjacent neighbor cells.

	Elev.	Bio-1	Bio-2	Bio-3	Bio-4	Bio-5	Bio-6	Bio-7	Bio-8	Bio-9	Bio-10	Bio-11	Bio-12	Bio-13	Bio-14	Bio-15	Bio-16	Bio-17	Bio-18
Bio-1	<b>0.92</b>																		
Bio-2	0.47	0.47																	
Bio-3	0.49	0.43	0.43																
Bio-4	0.22	0.18	0.39	0.13															
Bio-5	<b>0.87</b>	<b>0.90</b>	0.51	0.46	0.35														
Bio-6	<b>0.82</b>	<b>0.87</b>	0.60	0.38	0.38	<b>0.74</b>													
Bio-7	0.31	0.29	0.65	0.16	<b>0.88</b>	0.44	0.52												
Bio-8	0.62	0.68	0.43	0.28	0.29	0.67	0.62	0.37											
Bio-9	0.58	0.64	0.38	0.20	0.32	0.59	0.63	0.36	0.63										
Bio-10	<b>0.93</b>	<b>0.96</b>	0.48	0.49	0.27	<b>0.97</b>	<b>0.80</b>	0.35	0.69	0.61									
Bio-11	0.85	<b>0.92</b>	0.52	0.36	0.37	<b>0.80</b>	<b>0.97</b>	0.46	0.64	0.65	<b>0.84</b>								
Bio-12	0.43	0.44	0.35	0.35	0.04	0.39	0.47	0.20	0.29	0.24	0.41	0.44							
Bio-13	0.47	0.48	0.40	0.41	0.05	0.42	0.50	0.22	0.29	0.24	0.45	0.47	<b>0.92</b>						
Bio-14	0.25	0.25	0.16	0.21	-0.06	0.22	0.28	0.07	0.19	0.14	0.23	0.26	<b>0.81</b>	0.63					
Bio-15	0.61	0.55	0.40	0.46	0.18	0.57	0.50	0.25	0.40	0.30	0.59	0.50	0.30	0.33	0.23				
Bio-16	0.48	0.48	0.40	0.41	0.05	0.43	0.51	0.22	0.30	0.25	0.46	0.47	<b>0.94</b>	<b>0.99</b>	0.65	0.33			
Bio-17	0.27	0.27	0.19	0.21	-0.05	0.24	0.30	0.08	0.20	0.15	0.25	0.28	<b>0.84</b>	0.66	<b>0.99</b>	0.25	0.68		
Bio-18	0.46	0.44	0.28	0.37	-0.10	0.37	0.44	0.05	0.24	0.18	0.42	0.41	<b>0.82</b>	<b>0.79</b>	<b>0.72</b>	0.30	<b>0.80</b>	<b>0.74</b>	
Bio-19	0.21	0.23	0.18	0.27	-0.04	0.22	0.25	0.11	0.16	0.11	0.22	0.22	<b>0.74</b>	0.69	0.63	0.22	<b>0.70</b>	0.65	0.53

## Considerações Finais

No primeiro capítulo não encontrei evidências de que a amplitude das diferenças ambientais (extensão ambiental) tenha alguma influência nos tamanhos de efeito representados pela relação entre diversidade beta e variáveis ambientais em ambientes aquáticos continentais. É importante destacar que inúmeras variáveis foram consideradas como variáveis ambientais (total de 76 variáveis) o que dificulta a obtenção acurada de uma medida comparativa de extensão ambiental em uma análise de revisão. Além disso, estudos ecológicos possuem problemas de replicabilidade como também de vieses associados ao tempo de publicação de alguns resultados. Os vieses de tempo de publicação são uma tendência em que artigos com baixo número amostral com tamanhos de efeito alto são publicados, enquanto os artigos com baixo tamanho de efeito acabam não sendo publicados ou são publicados após um longo período após a publicação de trabalhos com tamanhos de efeito alto. Outra possível explicação para os resultados obtidos está associada a algumas características intrínsecas das ferramentas estatísticas, como por exemplo a baixa eficiência em capturar relações não-lineares.

No segundo capítulo, custos de dispersão demonstraram ser relevantes na determinação da dissimilaridade taxonômica e funcional de peixes. A distância entre localidades por curso d'água são responsáveis por criar dissimilaridade composicional de espécies de peixes em três das quatro principais bacias hidrográficas do estado da Carolina do Norte. Porém, quando analisado os efeitos das distâncias entre localidades, em conjunto com os efeitos atribuídos a barragens e a declividade do canal, somente a diversidade beta da bacia do *Cape Fear* apresentou resultados que indicaram efeito destes custos de dispersão. Além disso, grupos funcionais de peixes periódicos são mais afetados pelos custos de dispersão do que os demais grupos funcionais de peixes (oportunistas e de equilíbrio). É plausível que espécies periódicas sejam mais dependentes dos processos de

dispersão na ocupação de locais, pois dependem da dispersão tanto para reprodução como também na ocupação de habitats com condições ambientais favoráveis.

No terceiro capítulo, meus resultados seguiram a tendência de estudos anteriores que demonstraram que variáveis bioclimáticas e a elevação são importantes para determinar a dissimilaridade de aves e mamíferos terrestres. Também encontrei que a latitude modera a relação entre as diferenças ambientais e a dissimilaridade de mamíferos terrestres, mas não para aves. Porém, ainda é um desafio compreender quais os mecanismos que estão por trás destes padrões, sendo que alguns possíveis fatores estão associados a diferenças de capacidade de dispersão e processos históricos de diversificação dos grupos taxonômicos.

Por fim, os três capítulos demonstraram que é possível investigar a diversidade beta em diferentes contextos. Além disso, medidas de diversidade beta são bastante flexíveis podendo ser aplicadas, por exemplo, em estudos de diversidade filogenética e diversidade funcional. Características morfológicas associadas a estratégia de vida são importantes para o entendimento de padrões ecológico-evolutivos e auxiliam na compreensão e detecção de mecanismos. Outros fatores importantes que merecem maior atenção são os efeitos antrópicos (no caso, efeitos de barramento de ambientes lóticos), que demonstraram ser relevantes na determinação da composição de espécies. Portanto, instituições tomadoras de decisão em assuntos relacionados a conservação de espécies devem considerar os efeitos de barramento de ambientes lóticos como fator responsável pela redução e perda da biodiversidade.