UNIVERSIDADE ESTADUAL PAULISTA - UNESP
Faculdade de Ciências e Letras - Campus de Assis

CAROLINE DE MELLO CORREIA

Quais locais abrigam biodiversidade única? Investigando a singularidade biológica por meio de dados observacionais e revisão sistemática

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Orientadora: Profa. Dra. Danielle Katharine Petsch

Coorientador: Prof. Dr. Pitágoras da Conceição Bispo

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IMPACTO POTENCIAL DESTA PESQUISA

Esta pesquisa contribui para a ecologia teórica ao avançar o entendimento sobre raridade e singularidade ecológica em ecossistemas aquáticos tropicais. Seus resultados têm impacto aplicado, oferecendo subsídios para:

Priorização de áreas e estratégias de conservação baseadas em singularidade ecológica, e não apenas em riqueza de espécies;

Ampliação da representatividade geográfica e taxonômica em estudos de biodiversidade;

Planejamento e manejo integrado de redes de riachos e bacias hidrográficas;

Fortalecimento da comunicação científica e alfabetização ecológica junto ao público não-acadêmico, promovendo engajamento social e apoio a políticas ambientais.

POTENTIAL IMPACT OF THIS RESEARCH

This research advances theoretical ecology by improving understanding of rarity and ecological uniqueness in tropical freshwater ecosystems. Its applied impact includes:

Guiding conservation priorities based on ecological uniqueness rather than solely species richness;

Expanding geographic and taxonomic representation in biodiversity studies;

Supporting integrated planning and management of stream networks and watersheds;

Enhancing science communication and ecological literacy, fostering public engagement and support for environmental policies.

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DE CAROLINE DE MELLO CORREIA, DISCENTE DO PROGRAMA DE PÓS-GRADUAÇÃO EM BIOCIÊNCIAS, DA FACULDADE DE CIÊNCIAS E LETRAS - CÂMPUS DE ASSIS.

Aos 27 de fevereiro de 2026, às 14h, por meio de Videoconferência, realizou-se a defesa de DISSERTAÇÃO DE MESTRADO de CAROLINE DE MELLO CORREIA, intitulada "Quais locais abrigam biodiversidade única? Investigando singularidade biológica por meio de dados observacionais e revisão sistemática". A Comissão Examinadora foi constituída pelos seguintes membros: Profa. Dra. DANIELLE KATHARINE PETSCH (Orientador(a) - Participação Virtual) do(a) Departamento de Ciências Biológicas / UNESP / Câmpus de Assis - FCLAs, Prof. Dr. ADRIANO SANCHES MELO (Participação Virtual) do(a) Universidade Federal do Rio Grande do Sul (UFRGS), Profa. Dra. GISELE DAIANE PINHA (Participação Virtual) do(a) Universidade Federal do Sul da Bahia (UFSB), Após a exposição pela mestranda e arguição pelos membros da Comissão Examinadora que participaram do ato, de forma presencial e/ou virtual, a discente recebeu o conceito final: APROVADO. Nada mais havendo, foi lavrada a presente ata, que após lida e aprovada, foi assinada pelo(a) Presidente(a) da Comissão Examinadora.

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Profa. Dra. DANIELLE KATHARINE PETSCH

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Resumo Geral

Esta dissertação contribui significativamente para a ecologia teórica e aplicada, integrando revisão sistemática, pesquisa empírica e divulgação científica sobre raridade e singularidade ecológica. Nossos achados fornecem diretrizes para conservação, identificam lacunas críticas no conhecimento acerca da singularidade ecológica e promovem uma compreensão mais integrada da biodiversidade. O Capítulo 1 apresenta a primeira síntese meta-analítica global da métrica LCBD (Contribuição Local para a Diversidade Beta, que quantifica o quão único é um local em relação à composição de espécies em um conjunto de comunidades), consolidando uma década de pesquisas. Por meio de revisão sistemática, verificamos que locais ecologicamente únicos frequentemente apresentam menor riqueza de espécies. Foram identificados vieses geográficos (sub-representação de regiões tropicais e ecossistemas marinhos) e metodológicos (ênfase em dados taxonômicos), orientando futuras pesquisas e políticas de financiamento, especialmente em regiões megadiversas e ameaçadas. O Capítulo 2 consiste em um estudo empírico em 22 riachos preservados da Mata Atlântica, avaliando abundância, riqueza, raridade e contribuições locais para diversidade beta (LCBD) e heterogeneidade ambiental (LCEH). Os resultados mostraram que locais com alta singularidade ecológica e a raridade estão distribuídos ao longo da rede fluvial. Espécies comuns foram os principais responsáveis pela diversidade beta, ressaltando a importância de conservar habitats íntegros que sustentem toda a comunidade biológica. Por fim, o Capítulo 3 aborda a comunicação científica, traduzindo conceitos complexos de raridade e singularidade para uma linguagem acessível. Ao explicar por que "ser raro é comum na natureza" e as consequências ecológicas da perda de espécies raras, este capítulo fortalece a comunicação científica e o apoio público a políticas de conservação e educação ambiental. Em conjunto, os três capítulos oferecem uma compreensão integrada da raridade e singularidade ecológica, conectando padrões globais, evidências empíricas locais e engajamento social para informar a conservação da biodiversidade em ecossistemas aquáticos tropicais.

Palavras-chave: LCBD, diversidade beta, raridade, singularidade ecológica, Mata Atlântica, conservação.

General Abstract

This dissertation makes significant contributions to theoretical and applied ecology by integrating systematic review, empirical research, and science communication on rarity and ecological uniqueness. Its findings provide actionable guidelines for conservation, identify critical knowledge gaps, and promote a holistic understanding of biodiversity. Chapter 1 presents the first global meta-analytic synthesis of the LCBD metric (Local Contribution to Beta Diversity, a measure that quantifies how unique a given site is in relation to species composition across a set of communities), consolidating a decade of research. Through a systematic review, ecologically unique sites were found to often have lower species richness. Geographic biases (underrepresentation of tropical and marine ecosystems) and methodological biases (overreliance on taxonomic data) were identified, guiding future research and funding priorities, particularly in megadiverse and threatened regions. Chapter 2 reports a empirical study in 22 well-preserved Atlantic Forest streams, assessing abundance, richness, rarity, and local contributions to beta diversity (LCBD) and environmental heterogeneity (LCEH). Results showed that sites with high ecological uniqueness and rarity are distributed across the fluvial network. Common species were the main drivers of beta diversity, highlighting the importance of conserving intact habitats that support entire communities. Finally, Chapter 3 focuses on science communication, translating complex concepts of rarity and uniqueness into accessible language. By explaining why “being rare is common in nature” and the ecological consequences of rare species loss, it enhances ecological literacy and strengthens public support for conservation policies and environmental education. Together, the three chapters provide an integrated understanding of rarity and ecological uniqueness, linking global patterns, local empirical evidence, and societal engagement to inform biodiversity conservation in tropical freshwater ecosystems.

Key-words: LCBD, beta diversity, rarity, ecological uniqueness, Atlantic Forest, conservation.

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Introdução Geral

A singularidade ecológica, entendida como o grau em que comunidades, locais ou espécies se distinguem dos demais em sua composição biológica, tem se consolidado como um conceito central na ecologia (Ejrnæs et al., 2018). Compreender os mecanismos que determinam essa singularidade biológica é fundamental para o avanço das estratégias de conservação, especialmente em um cenário de intensas transformações ambientais decorrentes das atividades humanas (Snåre et al., 2024). Mudanças climáticas, perda de habitat, degradação do solo e poluição têm imposto pressões sem precedentes sobre os ecossistemas, afetando principalmente as espécies raras, que representam a maior parcela da diversidade biológica global (Ceballos et al., 2017; Li et al., 2022) e podem contribuir desproporcionalmente para a singularidade ecológica.

Entre os debates recentes na ecologia de comunidades, destaca-se a relação entre a riqueza de espécies e a contribuição dos locais para a singularidade biológica (Tolonen et al., 2018; Rocha et al. 2023). Áreas com elevada riqueza são tradicionalmente consideradas prioritárias para conservação. No entanto, locais com menor riqueza, mas compostos por espécies raras e ecologicamente únicas, podem ser igualmente insubstituíveis (Gaston, 1994; Landeiro et al., 2018). A métrica *Local Contribution to Beta Diversity* (LCBD) permite identificar essas áreas, ao quantificar o quanto cada local contribui para a variação na composição de espécies - ou seja, para a diversidade beta (Legendre & Cáceres, 2013; Whittaker, 1960). De forma complementar, a *Species Contribution to Beta Diversity* (SCBD) evidencia quais espécies são responsáveis por essa variação, revelando aquelas que definem a identidade ecológica de um local dentro de uma região (De et al., 2023; Legendre & Cáceres, 2013; Santos et al., 2021). A escolha por essas métricas alinha-se com a necessidade de operacionalizar os múltiplos conceitos de diversidade beta na prática ecológica (Anderson et al., 2011).

A dispersão das espécies e a filtragem ambiental também podem afetar os padrões de singularidade ecológica nos ecossistemas. Por exemplo, em ecossistemas aquáticos continentais, a estrutura dendrítica dos sistemas fluviais cria um mosaico de habitats e níveis de conectividade, que moldam a dispersão das espécies e a heterogeneidade ambiental (Carrara et al., 2012; Carvalho et al., 2023; Santiago & Beasley, 2023; Valente-Neto et al., 2020; Vannote et al., 1980), o que pode favorecer comunidades singulares.

Com o agravamento da crise da biodiversidade, torna-se urgente reconhecer o papel das espécies e locais singulares na manutenção da diversidade regional (Brito et al., 2020). A perda de locais ou espécies com alta contribuição para a diversidade beta implica em uma perda significativa da singularidade ecológica, reduzindo o potencial adaptativo e funcional dos ecossistemas (Bomfim et al., 2024; Mouillot et al., 2013). Minha dissertação busca compreender os padrões de raridade e singularidade ecológica em diferentes escalas e contextos ambientais, integrando abordagens teóricas, empíricas e de divulgação científica. Ao reunir diferentes perspectivas sobre a singularidade ecológica, esta dissertação busca ampliar a compreensão sobre como padrões de raridade e contribuição local moldam a diversidade biológica, oferecendo subsídios teóricos e práticos para estratégias de conservação mais eficazes e abrangentes (Duflot & Vähätalo, 2024; Liu et al., 2024; Rocha et al., 2023; Vellend, 2016).

No Capítulo 1, conduzi uma revisão sistemática dos estudos que aplicaram a métrica LCBD em distintos ecossistemas e grupos taxonômicos ao redor do mundo. Também realizei uma meta-análise para explorar a relação entre riqueza e LCBD. Esse capítulo tem como objetivo sintetizar o conhecimento disponível, identificar lacunas de pesquisa e apontar os principais fatores abióticos e bióticos que influenciam a singularidade ecológica (Dansereau et al., 2022; Wang et al., 2020). No Capítulo 2, coletei dados em campo para investigar como a posição do riacho na rede dendrítica (i.e., riachos de cabeceira ou mais centrais) influencia a

ocorrência de espécies aquáticas raras e suas contribuições para a diversidade beta, quantificadas por meio da métrica LCBD,que permite avaliar o grau de singularidade de cada local com base na composição de espécies. A raridade foi estimada a partir da abundância e frequência das espécies nos locais amostrados, permitindo identificar quais espécies contribuem de forma desproporcional para a singularidade ecológica. Por fim, o Capítulo 3 traduz um dos conceitos fundamentais da dissertação - a raridade de espécies - em uma linguagem acessível ao público não especializado. O capítulo aborda as razões pelas quais ser raro é uma condição comum na natureza, as implicações disso para a conservação e a importância de valorizar espécies pouco conhecidas.

Capítulo 1

The trade-off between ecological uniqueness and species richness: A global meta-analysis and systematic review of the Local Contribution to Beta Diversity (LCBD)

This manuscript was elaborated according to the style of *Ecological Indicators* journal (https://www.sciencedirect.com/journal/ecological-indicators/publish/guide-for-authors)

Abstract

The Local Contribution to Beta Diversity (LCBD) has emerged as a key metric for quantifying ecological uniqueness by measuring the distinctiveness of each site species composition within a regional context. Unlike traditional diversity measures, LCBD identifies sites that make exceptional contributions to overall beta diversity, serving as indicators of either unique habitats worthy of conservation or degraded sites requiring restoration. We conducted a systematic review of the global literature on LCBD to map the temporal and geographic trends of scientific production, cataloging the predominant methodological approaches, synthesizing the main findings and identifying from this integrative analysis the knowledge gaps. Furthermore, we performed a meta-analysis to quantitatively synthesize evidence on the relationship between LCBD and species richness, examining how this relationship varies across ecosystems, taxa, and methodological factors. Following the PRISMA protocol, we analyzed 471 studies published between 2013 and 2024, from which 160 met the inclusion criteria for the systematic review. For the meta-analysis, 117 studies were included, which contained the criteria for their inclusion. Our findings reveal exponential growth in publications, with a strong concentration in freshwater ecosystems and some countries (notably Brazil and China). We found a pronounced predominance of taxonomic approaches over functional or phylogenetic dimensions of LCBD. Most of the studies investigated fishes and invertebrates. We identified critical gaps in marine/estuarine systems, tropical regions, and temporal studies, providing a roadmap for expanding LCBD's role in biodiversity conservation. Our meta-analysis revealed a significant negative LCBD-richness relationship overall, though with high heterogeneity (strongest in freshwater systems and weaker in terrestrial ones). The negative LCBD-richness relationship poses a conservation challenge: species-rich sites are often less compositionally unique. These findings highlight that conserving regional biodiversity requires a dual strategy: protecting both high-richness areas and compositionally unique sites, while future research must address the

geographic and taxonomic biases to unlock LCBD's full potential as a tool for ecological assessment and prioritization.

Keywords

Local Contribution to Beta Diversity, , Ecological Uniqueness, Ecological Singularity, Beta diversity, Conservation

Introduction

Biodiversity is shaped by ecological processes that operate at different spatial and temporal scales, influencing community structure and beta diversity patterns. Beta diversity (i.e., the variation in species composition among sites within a region; Anderson et al., 2011) can reveal the mechanisms structuring biological communities and their spatial organization (Socolar et al., 2016). Among the metrics used to understand beta diversity patterns, Local Contribution to Beta Diversity (LCBD), proposed by Legendre & De Cáceres (2013), has emerged as a powerful tool for identifying ecologically unique areas. LCBD is derived from the total sum of squares in the community composition matrix, where each site's LCBD value represents its relative contribution to the overall beta diversity. This metric quantifies the uniqueness of biological communities by calculating the degree to which its species composition differs from the average composition across all sites in the study (Legendre & De Cáceres, 2013). Importantly, LCBD values are inherently context-dependent, as they are calculated relative to the specific set of sites included in each study.

From a conservation perspective, LCBD has been increasingly used to support the prioritization of areas, as it enables the identification of sites that disproportionately contribute to regional biodiversity patterns. However, the ecological interpretation of high LCBD values

remains context-dependent and requires careful consideration. High LCBD values can indicate two distinct ecological scenarios: (i) sites that may represent conservation priorities because they harbor rare, endemic, or functionally unique species (Silva & Hernández, 2014; but see Rocha et al., 2023) or (ii) sites that have been significantly impacted by anthropogenic disturbances, where compositional distinctiveness arises from the loss of sensitive species or colonization by disturbance-adapted taxa, potentially requiring ecological restoration interventions (Heino et al., 2021). Understanding how communities are structured and which factors determine their unique contribution to overall beta diversity is essential for explaining biodiversity patterns and improving conservation or restoration strategies (Chase et al., 2020; Heino et al., 2015; Leibold et al., 2004).

One of the most frequently used conceptually important variables for interpreting LCBD patterns is species richness (Legendre & De Cáceres, 2013; Cardoso et al., 2014; Heino et al., 2015; Siqueira et al., 2015; Qi et al., 2024). Because richness reflects the number of present at a site, its relationship with LCBD provides key insights into whether ecologically unique communities tend to be species-poor or species-rich. This relationship is central to conservation planning, as it directly influences whether priority areas should be selected based on uniqueness, richness, or a combination of both.

The LCBD values alone does not identify which specific species drive a site's high contribution to beta diversity. To address this limitation, researchers often complement LCBD analysis with Species Contribution to Beta Diversity (SCBD) metrics, which identify the individual species that contribute most to overall compositional differences (Heino & Gronroos, 2017; da Silva et al., 2018; Gavioli et al., 2022). In practice, studies applying LCBD routinely report additional community metrics, most commonly species richness, followed by SCBD and metrics of environmental heterogeneity, to contextualize and interpret patterns of ecological

uniqueness such as to test the relationship between uniqueness and local species richness (e.g., Heino & Grönroos, 2017) or to assess how habitat heterogeneity drives compositional uniqueness (e.g., Gallucci et al., 2020). Without examining species composition through SCBD or similar approaches, this critical distinction remains obscured. This interpretive ambiguity has direct conservation implications, as misclassification can lead to misguided management decisions. For example, sites dominated by invasive species might be incorrectly prioritized for protection, while truly unique habitats with high conservation value could be overlooked. Therefore, integrating LCBD with species-level analyses is helpful for accurate ecological assessment and effective conservation planning (Liu et al., 2024; Bórquez et al., 2024).

The application of LCBD has shed light on community dynamics in freshwater systems (e.g., Heino et al., 2021), terrestrial landscapes (e.g., Silva & Hernández, 2014), and marine environments (e.g., Louchart et al., 2024). In addition, the understanding of beta diversity and LCBD patterns has evolved from purely taxonomic approaches to incorporate functional (Hill et al., 2021; Chen et al., 2024) and phylogenetic (Heino et al., 2022; Liu et al., 2024) dimensions reflecting a search for metrics that better capture community assembly processes. However, accurately discerning the underlying cause of a high LCBD value remains a significant challenge in the field. A key insight from these studies is that high LCBD values are not random, but emerge from distinct mechanistic filters. Ecologically unique sites may result from environmental filtering in atypical or extreme habitats, which select for specialist and endemic species (Tameirão et al., 2021), or from dispersal limitation in isolated areas, fostering biogeographic singularity (Franklin et al., 2013; Guevara-Andino et al., 2021). The relationship between environmental heterogeneity and community uniqueness is frequently assessed by examining the correlation with the Local Contribution to Environmental Heterogeneity (LCEH; Castro et al. 2019) and LCBD.

Despite the growing use of LCBD since the seminal paper of Legendre & De Cáceres published in 2013, the literature on LCBD remains fragmented. Key knowledge gaps persist, such as geographical and taxonomic biases (i.e., it remains unclear whether research efforts are globally representative or concentrated in specific regions and biological groups). Furthermore, a comprehensive overview is needed to evaluate how consistently the theoretical promise of LCBD has been translated into concrete conservation and restoration applications. This knowledge can support public policies aimed at preserving vulnerable ecosystems worldwide. Within this LCBD framework, this study is structured as a systematic review with an integrated meta-analytical component. The systematic review provides a comprehensive synthesis of how LCBD has been applied across ecosystems, taxa, spatial and temporal scales, and how it has been related to multiple ecological predictors, including species richness, environmental heterogeneity, and disturbance. Among these predictors, species richness emerged as the most frequently examined variable in relation to LCBD. Given its central theoretical relevance and its recurrent use across studies, we treated species richness as a focal predictor and conducted a meta-analysis to quantitatively assess its relationship with LCBD.

A meta-analysis provides a formal statistical framework to quantitatively integrate results across independent studies, allowing the estimation of overall effect sizes and the assessment of heterogeneity among studies (Gurevitch & Hedges, 1999; Nakagawa et al., 2015). This approach is critically needed to resolve a pivotal and persistent debate in community ecology and conservation biogeography: the relationship between ecological uniqueness (LCBD) and species richness. This relationship tests a fundamental assumption about beta diversity, whether sites of compositional uniqueness are inherently species-poor due to strong environmental filters or historical isolation that limit richness but favor distinctiveness (Legendre & De Cáceres, 2013; Heino et al., 2017). Conversely, a positive or null relationship would suggest that uniqueness can emerge even in rich assemblages, potentially driven by high turnover among common species or

unique combinations of widespread taxa. The direction and strength of this relationship therefore determine whether LCBD and species richness are complementary or conflicting criteria for conservation or restoration planning (Legendre, 2014; Rocha et al. 2023). Despite its importance, empirical evidence remains contradictory, with studies reporting negative (Heino et al, 2017, da Silva et al., 2018; Vilmi et al., 2017), weak relationships of varying direction (both, positive and negative), (Landeiro et al., 2018; Tonkin et al., 2016), null (Brito et al., 2020; Pozzobom et al., 2020) or positive (Hill et al., 2021; Yao et al., 2021) relationships depending on ecosystem type, taxonomic group, and spatial scale. This lack of consensus limits the use of LCBD as a general indicator for conservation planning and ecological diagnosis (Rocha et al. 2023). A quantitative synthesis of this relationship is therefore necessary to determine whether a generalizable pattern exists across ecological contexts and to identify the main sources of variability among studies. Integrating a meta-analytical approach into this systematic review allows us to move beyond qualitative mapping and provides the first global quantitative assessment of the LCBD–species richness relationship.

We conducted a systematic review of the global literature on Local Contribution to Beta Diversity (LCBD) over the past decade, since the seminal paper published by Legendre & De Cáceres (2013). We specifically examined: (i) the temporal trajectory of LCBD research, (ii) the location of the studies, (iii) the predominant ecosystems and taxonomic groups studied, (iv) the beta diversity facets employed, and (v) the key ecological relationships and predictors (e.g., species richness and environmental uniqueness) associated with LCBD values. We also evaluated (vi) the number of spatial and temporal studies, (vii) the proportion of studies conducted in impacted versus conserved environments, and (viii) the extent to which studies explicitly included conservation or anthropogenic impact contexts. Finally, we complemented our synthesis with a meta-analysis of the relationship between LCBD and species richness. By integrating systematic review and meta-analysis, this work not only provides a comprehensive

overview of the first decade of LCBD research but also establishes a solid empirical basis for future application and methodological refinement in conservation and restoration ecology.

Methods

Data searching

Data collection followed a systematic approach based on the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) protocol (Page et al., 2021) to ensure transparency, reproducibility, and comprehensive coverage of the literature. The search was conducted in the Web of Science database on September 1, 2024, using a comprehensive set of keywords related to the LCBD metric and the concept of ecological uniqueness:

"LCBD" OR "Local Contribution to Beta Diversity" OR "Ecological Uniqueness" OR "Ecological Singularity" OR "Biotic Uniqueness" OR "Biotic Singularity" OR "LCEH" OR "Local Contribution to Environmental Heterogeneity" OR "Taxonomic Uniqueness" OR "Functional Uniqueness" OR "Phylogenetic Uniqueness" OR "Taxonomic Singularity" OR "Functional Singularity" OR "Phylogenetic Singularity".

Data sampling

The initial search in the Web of Science database yielded 471 records. Following the PRISMA protocol, a two-phase screening process was conducted (Figure 1). In the first phase, 300 records were excluded based on title and abstract analysis. The remaining 171 studies underwent full-text assessment for eligibility, resulting in the exclusion of 11 articles. In the end, we included 160 primary research studies that explicitly used the LCBD metric. The search was restricted to articles published between 2013 (the year of the seminal paper by Legendre & De

Cáceres, 2013) and 2024. Records were included if they were primary research articles explicitly calculating or discussing LCBD using empirical data. Exclusion criteria were applied during the screening phase, primarily for studies where the full text was inaccessible (n = 9) or whose content was out of scope: i) they did not calculate or report LCBD values (e.g., focused only on other beta diversity metrics); or ii) they presented only theoretical or methodological discussions without empirical data (i.e., were not primary research articles), upon full-text assessment (n = 302).

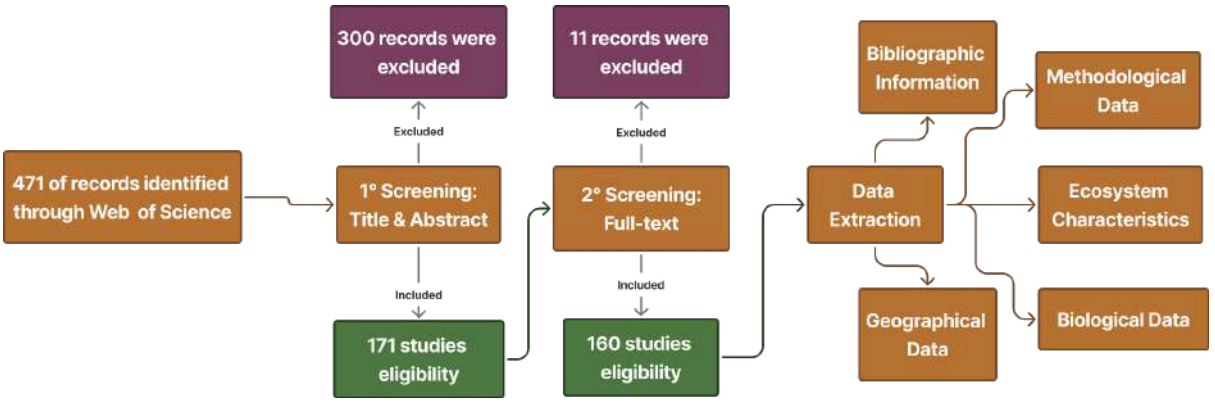

Fig. 1. The PRISMA protocol employed in our systematic review. Bibliographic information = journal and year of publication; Geographical Data = geographical distribution of studies; Ecosystem Characteristics = realm and type of ecosystem; Biological Data = taxa; Methodological Data = biodiversity facet (i.e., taxonomic, functional or phylogenetic) and predictors (i.e., richness, LCEH, and SCBD).

For each included study, we searched for the following information: 1) year of publication; 2) geographical distribution of studies; 3) realm (marine, freshwater, and terrestrial); 4) taxonomic groups; 5) biodiversity facets (taxonomic, functional, and phylogenetic); 6) metrics

explored (richness, environmental singularity and species contribution to beta diversity - SCBD); 7) scale (spatial and temporal); and 8) impact (preserved, impacted or both).

To evaluate temporal trends in the scientific production on LCBD, we quantified the annual number of published studies and tested its relationship with publication year using a linear regression model. Publication year was treated as a continuous predictor, and the number of studies per year was used as the response variable. Model significance and goodness of fit were assessed based on the regression coefficient, p-value, and coefficient of determination (R^2).

Meta-analysis

In addition to the systematic mapping of the literature on LCBD, we conducted a meta-analysis to quantitatively synthesize the relationship between LCBD and species richness across studies. Studies were included in the meta-analysis if they reported regression coefficients (Pearson's r or Spearman's p) between LCBD and species richness along with sample sizes. From 160 studies in our systematic review, 117 studies met these inclusion criteria. Effect sizes were extracted as correlation coefficients (r) describing the association between LCBD values and local species richness. To stabilize variances and ensure normality, correlation coefficients were transformed to Fisher's z values prior to analysis. Sampling variance was calculated as a function of sample size ($n - 3$), allowing appropriate weighting of studies based on their precision.

We fitted random-effects meta-analytical models using restricted maximum likelihood (REML) estimation to account for both within-study sampling error and between-study heterogeneity. Given the ecological and methodological diversity among studies, a random-effects framework was considered appropriate. Overall pooled effect sizes were back-transformed to Pearson's r for interpretation. Subgroup analyses were conducted according to taxonomic group, ecological realm, and LCBD facet (taxonomic, functional, or phylogenetic).

We also performed a meta-regression to evaluate temporal trends in effect sizes across publication years.

Finally, we assessed the potential publication bias using funnel plot asymmetry (Light & Pillemer, 1984) and Egger's regression test (Egger et al., 1997). The robustness of the results was evaluated using trim-and-fill procedures (Duval & Tweedie, 2000) and Orwin's fail-safe N (Orwin, 1983).

We conducted all analyses in the R program (R Core Team, 2023) using the tidyverse (Wickham et al., 2019) and ggplot2 (Wickham, 2016) packages for data manipulation and visualization. All meta-analytical procedures were conducted using the metafor (Viechtbauer, 2010) package.

Results

We observed exponential growth in LCBD research since its formal introduction in 2013 (Figure 2). Linear regression analysis revealed a positive relationship between publication year and the annual number of studies ($\beta = 3.47$, $df = 8$, $p < 0.001$, $R^2 = 0.90$), indicating a consistent growth in publication activity. The period between 2015 and 2018 was characterized as modest publication activity, with fewer than five studies per year. A pronounced increase began in 2019, culminating in a peak of over 40 studies in 2024, underscoring the rapid adoption and consolidation of LCBD as a key metric in community ecology.

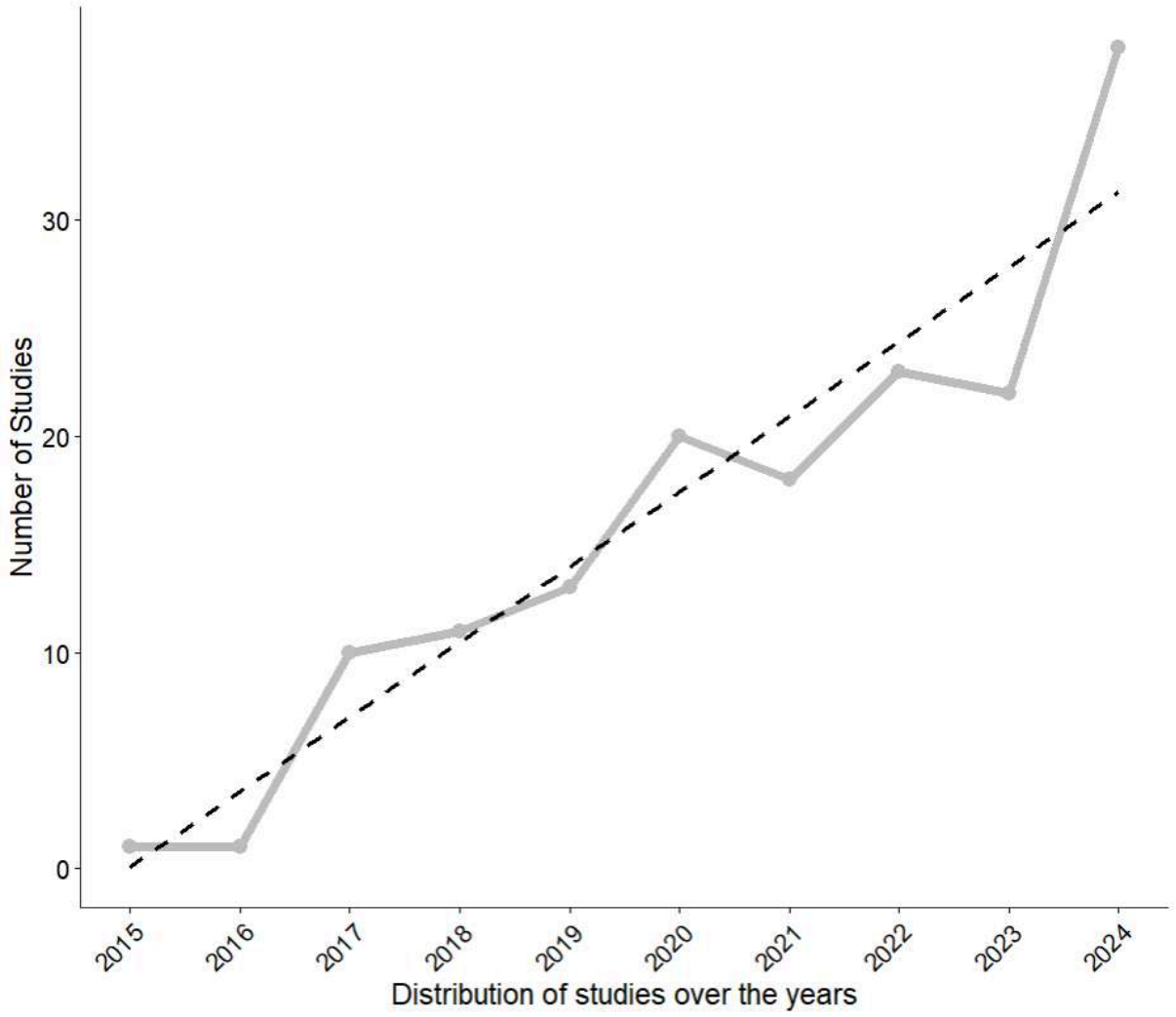

Fig. 2. Temporal trend in the number of scientific publications on the Local Contribution to Beta Diversity (LCBD) metric from 2015 to 2024 included in our systematic review. The gray line represents the observed (raw) number of studies per year, while the dashed line indicates the fitted linear trend. No eligible studies were found for the period 2013–2014.

The included studies showcased a wide yet asymmetric global distribution (Figure 3). Research efforts were heavily concentrated in a few specific regions, with South America, particularly Brazil, emerging as the dominant contributor, followed by Europe and Asia (mainly China). In contrast, vast tropical regions, particularly Central Africa and Southeast Asia, constituted pronounced knowledge gaps, with few or no studies applying the LCBD metric. Boreal biomes also showed uneven coverage, although Canada stood out with a considerable

number of studies, other major boreal zones such as Russia and Scandinavia remained severely understudied.

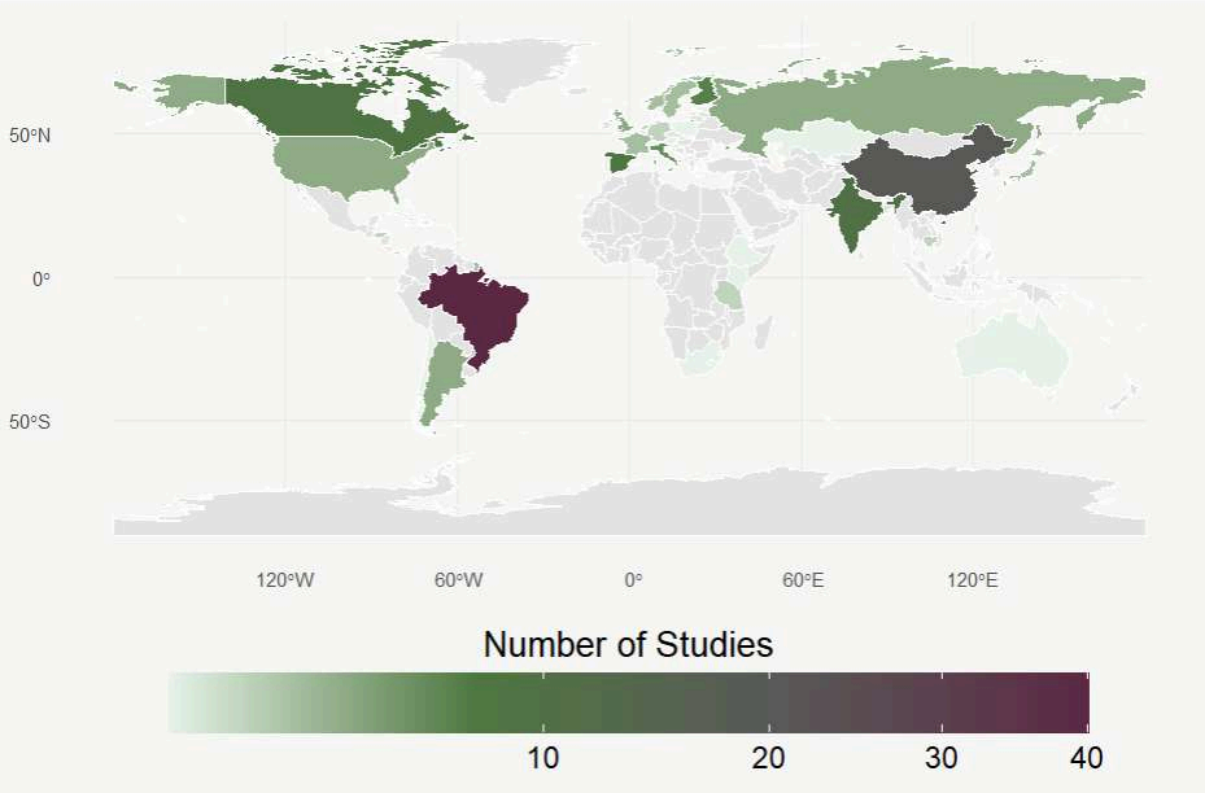

Fig. 3. Number of studies recorded for each country in our synthesis on LCBD metric.

The scientific application of the LCBD framework was disseminated across a wide range of journals, however, a subset of periodicals emerged as the primary outlets for this research (Figure 4). The journals *Ecological Indicators* and *Diversity and Distributions* were the most prominent, collectively publishing a significant portion of the studies. Other key journals included *Aquatic Sciences*, *Hydrobiologia*, and *Science of the Total Environment*, reflecting the interdisciplinary nature of LCBD applications spanning general ecology, biogeography, and aquatic sciences.

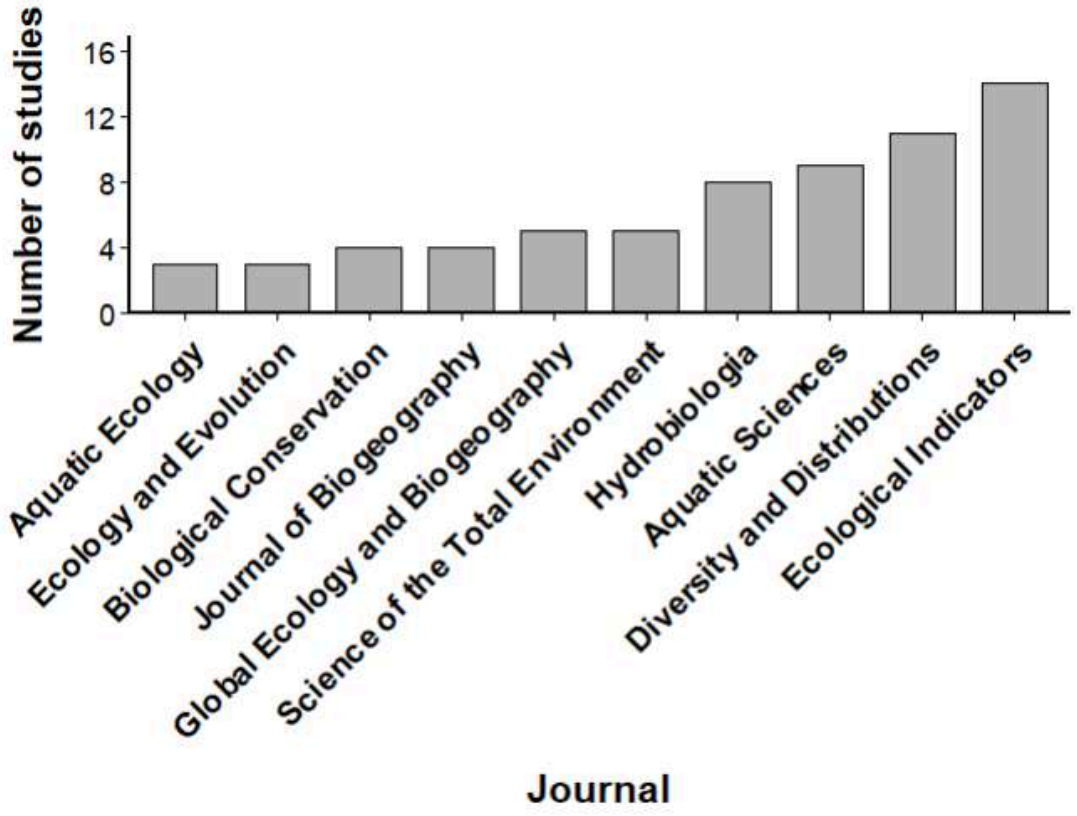

Fig. 4. The top 10 journals, ranked by the number of studies published on LCBD metric.

Freshwater ecosystems were the predominant realm in the analyzed literature, constituting 61.3% of all studies (Figure 5A). Within this category, small-order streams and rivers were the most frequently investigated systems (Supplementary Table 1). Terrestrial ecosystems comprised the second largest group (33.1%), with a focus on forests and grasslands (Supplementary Table 2). Marine and estuarine environments were significantly underrepresented, collectively accounting for only nine studies (5.5%).

Regarding the biodiversity dimensions used for LCBD calculation, the taxonomic approach was overwhelmingly dominant, employed in 87.7% of the studies (Figure 5B). The functional dimension was incorporated in 14.1% of publications, while the phylogenetic approach was the least common, present in only 3.14% of included studies.

Taxonomic analysis revealed a broad diversity of studied organisms (Figure 5F). Fishes, invertebrates and plants were the main taxa investigated. In freshwater ecosystems, fishes and aquatic invertebrates (particularly aquatic insects) were the most studied groups. Among terrestrial organisms, plants and terrestrial invertebrates (e.g., ants and bees) were the most frequent focus (Supplementary Table 2). Substantial representation was also found for microorganisms and algae. We also found studies covering mammals, amphibians, and only one article addressed birds.

Analysis of the specific metrics used alongside LCBD revealed species richness as the most frequently employed metric (71.7% of included studies), followed by SCBD (37.1%), while LCEH (5.7%) was utilized in a smaller subset of studies (Figure 5C).

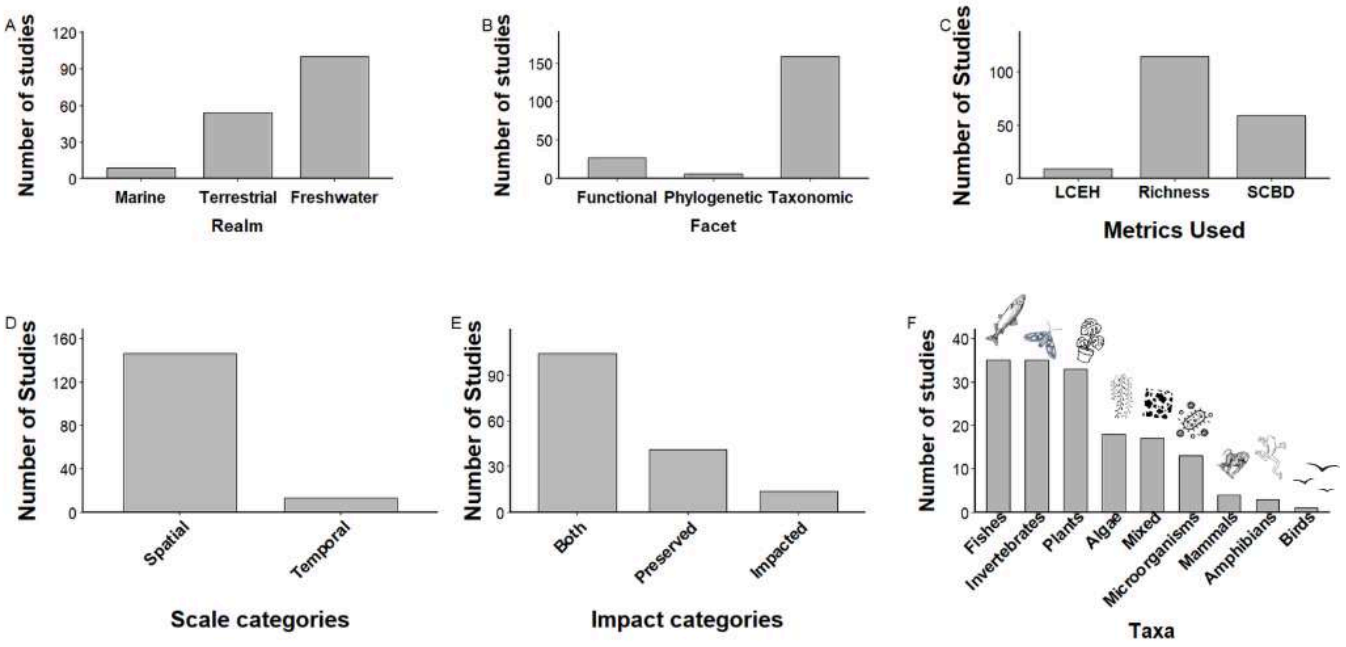

Fig. 5. Number of studies included in our systematic review on LCBD metric according to (A) realm, (B) LCBD facet (taxonomic, functional and phylogenetic), (C) metrics explored, (D) scale (E), impact categories and (F) taxa.

The meta-analysis conducted including only the studies investigating species richness (n = 117 studies) revealed a significant negative overall relationship between LCBD and species richness (pooled r = −0.207, 95% CI: −0.324 to −0.084), indicating that sites with higher species richness tend to contribute less to regional beta diversity (Fig 6). Heterogeneity among studies was high ($I^2 \approx 98.9\%$), reflecting substantial variability in effect sizes across ecological contexts.

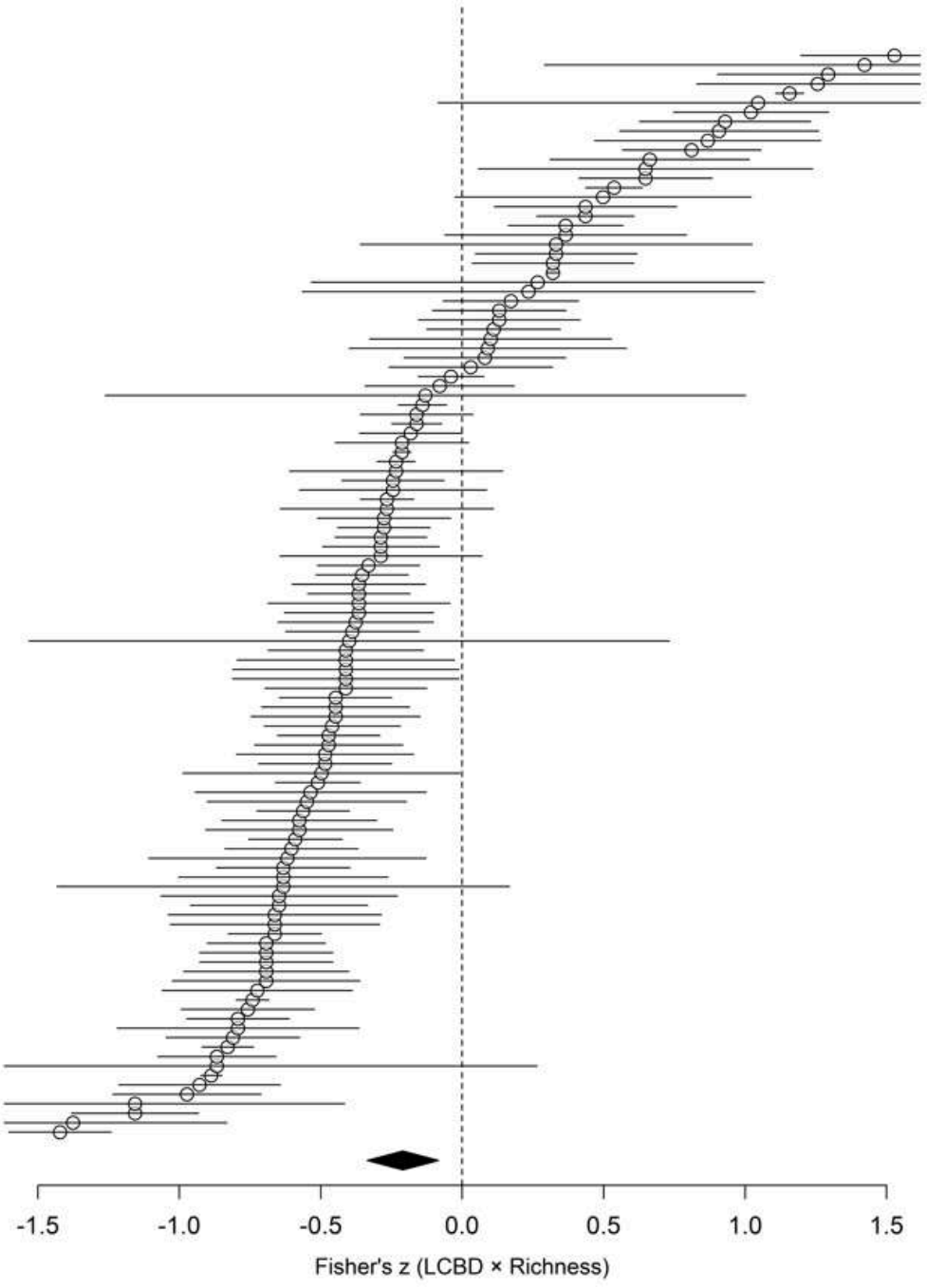

Fig. 6. Forest plot showing individual effect sizes (Fisher's z transformed correlations) describing the relationship between Local Contribution to Beta Diversity (LCBD) and species richness across studies included in the meta-analysis (n = 117 studies). Each point represents an individual effect size, with horizontal lines indicating 95% confidence intervals. Effect sizes are ordered from the most negative to the most positive. The black diamond at the bottom represents the overall mean effect size estimated using a random-effects model, with its width corresponding to the 95% confidence interval.

Subgroup analyses showed that negative LCBD–richness relationships were particularly strong for fishes and aquatic invertebrates (Fig. 7A) and for freshwater ecosystems, whereas terrestrial systems exhibited weak and non-significant patterns (Fig. 7B). Marine ecosystems were represented by few studies and showed highly uncertain estimates. Analyses by LCBD facet suggested stronger negative associations for functional and phylogenetic LCBD compared to taxonomic LCBD (Fig. 7C), although these results should be interpreted cautiously due to low sample sizes. Meta-regression indicated no significant temporal trend in effect sizes, suggesting that, despite the exponential increase in LCBD studies, the magnitude and direction of the LCBD–richness relationship have remained stable over time (Figure 7D).

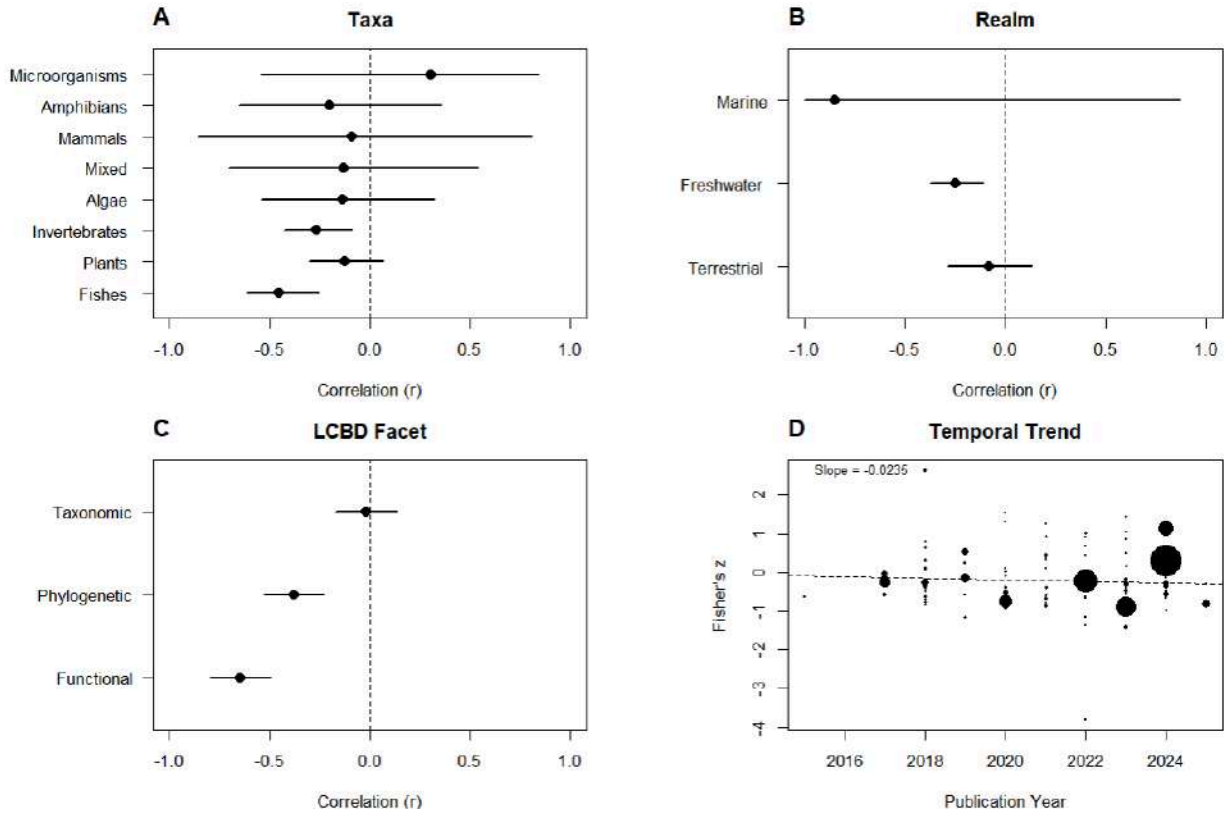

Fig. 7. Subgroup analyses and temporal trends of the relationship between Local Contribution to Beta Diversity (LCBD) and species richness. (A) Effect sizes grouped by taxonomic group, including Plants (37 effect sizes from 18 studies), Invertebrates (27/19), Fishes (21/13), Mixed taxa (14/7), Algae (9/6), Mammals (3/3), Microorganisms (3/2), Amphibians (2/1), and Birds (1/1). (B) Effect sizes grouped by ecological realm, showing a predominance of freshwater studies (73 effect sizes from 46 studies), followed by terrestrial (41/22) and marine systems (3/2). (C) Effect sizes grouped by LCBD facet, with most estimates based on taxonomic LCBD (21 effect sizes from 11 studies), compared to phylogenetic (3/1) and functional LCBD (2/2). (D) Temporal trend of effect sizes, with Fisher's z-transformed correlation coefficients plotted against year of publication. The above numbers in parentheses indicate the number of effect sizes and the number of independent studies, respectively. All subgroup estimates were obtained using random-effects meta-analytic models.

Discussion

The exponential growth in LCBD publications, particularly since 2019, confirms that this framework fills an important conceptual gap in ecology (Heino et al., 2021). Unlike traditional diversity measures that focus solely on species counts, LCBD quantifies each site's compositional uniqueness within a regional context, highlighting locations that contribute disproportionately to beta diversity (Legendre & De Cáceres, 2013). However, the empirical application of LCBD is geographically biased and represented mainly by freshwater ecosystems, with most studies concentrated in South America and marked underrepresentation in megadiverse regions such as Central Africa and Southeast Asia, which harbor exceptional biodiversity under intense anthropogenic pressures (Myers et al., 2000; Barlow et al., 2018; Jung et al., 2021). Consequently, current syntheses are based on a geographically skewed evidence base, limiting our ability to generalize patterns of ecological uniqueness globally.

The spatial bias of LCBD studies may reflect multiple factors: the strong tradition of freshwater ecology and beta diversity research in Brazilian institutions (Heino et al., 2015), the extensive and threatened freshwater networks of South America (Latrubesse et al., 2017; Albert et al., 2020), and the diffusion of methodological innovations within established research networks, particularly after the introduction of the LCBD framework (Legendre & De Cáceres, 2013). Additionally, this pattern may also reflect broader dynamics of scientific production, as countries such as Brazil and China share rapidly expanding research systems, strong investment in biodiversity science, and high publication output, which can accelerate the adoption and dissemination of emerging analytical frameworks. In this context, the proliferation of LCBD studies may partially reflect a “research trend effect”, in which recently proposed and methodologically accessible approaches gain rapid popularity within active research networks. In addition, LCBD studies show a pronounced taxonomic bias, with a disproportionate focus on fishes and freshwater invertebrates, while birds, mammals, amphibians, and many terrestrial

invertebrates remain underrepresented. Such concentration affects the interpretation of meta-analytic findings, as relationships observed in freshwater taxa may not extend to more mobile or broadly distributed organisms, which may exhibit LCBD patterns driven more by stochastic processes or broad-scale environmental gradients (Shurin et al., 2009; De Bie et al., 2012).

Most LCBD applications use taxonomic data probably due to data accessibility, but the incorporation of functional (14.1%) and phylogenetic (3.14%) dimensions represents a promising expansion. Functional LCBD identifies sites sustaining unique ecological traits critical for ecosystem functioning (Mouillot et al., 2021), while phylogenetic LCBD highlights areas harboring evolutionarily distinct lineages (Li et al., 2022). Although phylogenetic approaches remain less represented, this pattern likely reflects their relatively recent incorporation into the LCBD framework, suggesting that their application is still emerging.

Although LCBD–richness relationships are commonly reported, recent studies increasingly consider additional predictors. Environmental conditions (such as Local Contribution to Environmental Heterogeneity; Castro et al. 2019), anthropogenic stressors, and spatial factors often exceed the explanatory power of richness alone (Liu et al., 2024; Cordova et al., 2025). Yet, the relative importance of these drivers is rarely synthesized quantitatively, representing a key opportunity for future LCBD research.

The applied relevance of LCBD is evident in its use along anthropogenic gradients. More than half of the reviewed studies examined LCBD in relation to disturbance or conservation status, often to identify conservation priorities rather than diagnose impacted systems. Human disturbances such as deforestation, agricultural intensification, and urbanization can generate compositionally distinct communities, resulting in high LCBD values relative to regional baselines (de Paiva et al., 2021; Ortega et al., 2021; Schneck et al., 2022). This dual capacity, to

identify both conservation priorities and restoration targets, highlights its value for ecosystem management when interpreted within ecological contexts (Heino et al., 2021; Rocha et al., 2023).

Our meta-analysis provides robust quantitative evidence for a significant negative overall relationship between LCBD and species richness, supporting the prevailing idea that ecological uniqueness often emerges in species-poor communities. High-richness sites tend to be compositionally similar, whereas species-poor sites frequently represent environmentally extreme, isolated, or disturbed conditions, resulting in atypical assemblages that disproportionately contribute to beta diversity (Chase et al., 2020; Heino et al., 2017). This general pattern, which positions LCBD as an identifier of irreplaceable and often overlooked contributors to regional beta diversity (Hill et al., 2021; Heino et al., 2022), is exemplified by studies identifying headwater streams and intermittent rivers during dry phases as high-LCBD sites (Jyrkänkallio-Mikkola et al., 2018; Soria et al., 2024).

Our subgroup analyses and the broader literature underscore that the LCBD–species richness relationship, although predominantly negative, is highly context-dependent. The high heterogeneity observed among studies, and the variation across realms and taxa, reflect the influence of distinct ecological processes. For instance, the negative relationship was strongest in freshwater systems and for taxa like fishes and aquatic invertebrates, whereas it was weak or non-significant in terrestrial realms. This variation highlights that LCBD and species richness capture complementary but distinct dimensions of biodiversity, and their relationship with conservation priorities can vary. A clear illustration is provided by Rocha et al. (2023), who found that for freshwater mussels, high-LCBD sites were species-poor and did not overlap with areas harboring threatened species. This negative relationship presents a central conservation challenge: sites prioritized for species richness may not coincide with those contributing most to regional compositional uniqueness, creating potential trade-offs in conservation and restoration planning. This high heterogeneity underscores that there is no universal LCBD-richness

relationship and reinforces the critical need for system- and taxon-aware interpretations when applying LCBD in conservation or restoration contexts.

By integrating a global systematic review with a meta-analytical approach, this study provides the first quantitative synthesis of LCBD–richness relationships. Our study does not propose LCBD as a novel indicator, but provides the comprehensive, evidence-based framework needed to apply it effectively. We confirm its role in identifying singularity, quantify the prevalent negative relationship with richness, which supports its application in identifying sites with high ecological singularity, and chart the research priorities necessary to transform it from a specialized metric into a general tool for biodiversity assessment. However, the application of LCBD should be conducted with caution, as its interpretation is strongly shaped by its dual relationship with species richness, which is predominantly negative across studies. Accounting for this interaction is essential to avoid conflating ecological uniqueness with patterns driven primarily by richness gradients. Expanding LCBD applications to underrepresented ecosystems, taxa, and biodiversity dimensions, particularly through the incorporation of temporal analyses, will be essential for advancing ecological theory and informing conservation practice.

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Supplementary Material

Figure 1. Funnel plot showing effect sizes of the relationship between Local Contribution to Beta Diversity (LCBD) and species richness across the studies included in the meta-analysis. Points represent individual studies, and the dashed line indicates the overall pooled effect.

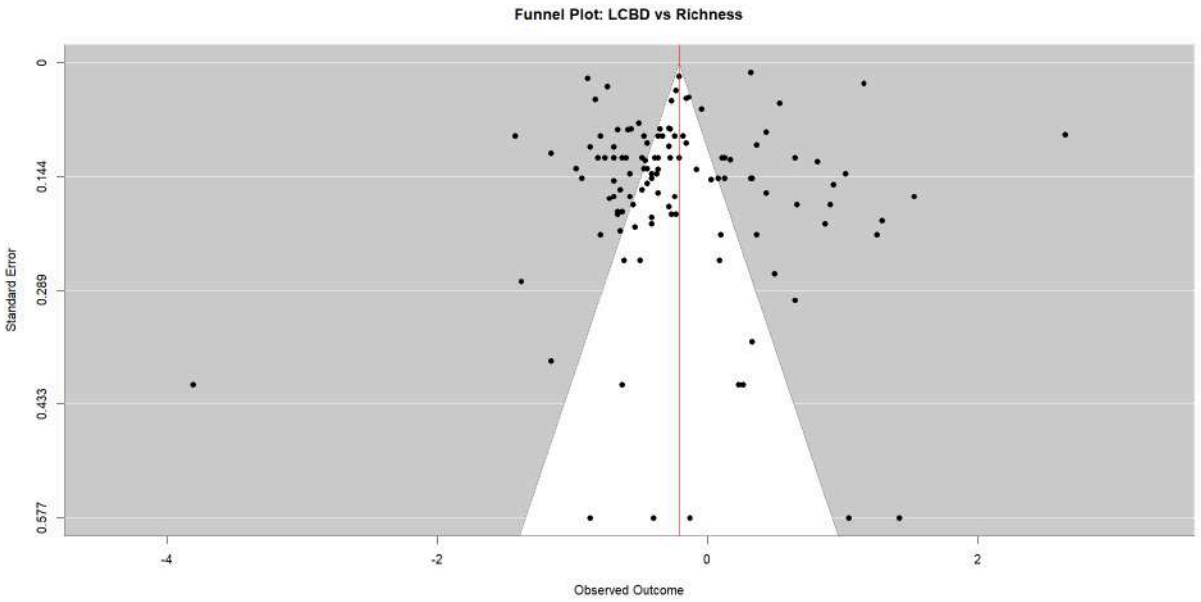
Funnel Plot: LCBD vs Richness
Standard Error
0
0.144
0.289
0.433
0.577
-4
-2
0
2
Observed Outcome

Table 1. Ecosystem classification by domain with number of articles from the systematic literature review.

Main Domain	Subdomain	Consolidated Ecosystem Type	Number of Articles
Freshwater	Low-Order Streams	Streams, creeks, headwaters, springs and small watercourses (includes intermittent, subtropical, tropical, high-altitude)	38
	Rivers	Rivers (perennial, intermittent, temporary, tropical, watersheds and river systems)	24
	Lakes/Ponds	Lakes (include natural, artificial, urban, quarry, floodplain)	22
	Floodplains	Floodplains and flooded areas	9
	Wetlands	Wetlands and swamps	5
	Reservoirs	Reservoirs and dam lakes	6
	Thermal Waters	Thermal waters	1
	Groundwater	Groundwater	1
Marine	Coastal	Coastal environments (reefs, mangroves, bays)	8
	Open Ocean	Marine ecosystems	3
	Estuaries	Estuaries	3
Terrestrial	Forest	Forests (tropical, temperate, subtropical)	24

	Agricultural	Agricultural areas and pastures	11
	Grassland	Prairies, natural pastures, savannas	8
	Riparian	Riparian forests and ecosystems	5
	Mountain	High-altitude/mountain ecosystems	6
	Urban	Urban parks and fragmented landscapes	4
	Various	Multiple terrestrial ecosystems	6
	Coastal	Coastal dunes - terrestrial part without water influence	2
	Soils	Soils	2
	Peatlands	Boreal peatlands	2
	Vegetation Formations	Diverse vegetation formations	2
Total			**160**

Table 2: Classification system for biological groups used in the systematic literature review on ecological uniqueness.

Main Category	**Subcategory**	**Included Terms**

Fishes	Fishes	Fishes (native, non-native, benthic, benthopelagic), fish communities
Plants	Terrestrial Plants	Plants, forest vegetation, plant communities, woody flora, arable plants, trees (angiosperms), vascular plants
	Aquatic Plants	Aquatic macrophytes, aquatic plants
	Bryophytes	Bryophytes
Invertebrates	Macroinvertebrates	Aquatic macroinvertebrates, benthic macroinvertebrates, stream invertebrates, aquatic communities with macroinvertebrates
	Aquatic Insects	Aquatic Insects, Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera, Chironomidae, Megaloptera.
	Crustaceans	Crustaceans
	Terrestrial Insects	Insects (terrestrial), wild bees, ants, hoverflies (Syrphidae), lepidopterans (butterflies/moths).
	Arachnids	Spiders
	Parasites	Parasites (helminths, nematodes, fleas, ectoparasites, endoparasites), plant parasites
	Zooplankton	Zooplankton, rotifers, cladocerans
Algae		

	Phytoplankton	
	Diatoms	Phytoplankton, Diatoms, benthic algae, periphytic algae, planktonic diatoms
	Other Algae	Microphytobenthos, periphyton (as algal community)
Microorganisms (bacteria and fungi)	Soil microorganisms, soil fungi	Bacteria, archaea, microeukaryotes, prokaryotic communities, aquatic microorganisms
	Terrestrial Microorganisms	Soil microorganisms, soil fungi
Amphibians	Amphibians	Amphibians, anurans, frogs
Mammals	Mammals	Mammals, terrestrial mammals, bats, rodents
Birds	Birds	Birds
Mixed	Mixed	Aquatic communities (general, when unspecified), mixed communities with diverse organisms, "various biological species"

Capítulo 2

Dendritic network position does not drive rarity or ecological uniqueness of aquatic insects in subtropical streams

This manuscript was elaborated according to the style of *Hydrobiologia* (https://link.springer.com/journal/10750/submission-guidelines#Instructions%20for%20Authors)

Abstract

The dendritic network structure of lotic ecosystems supports high species diversity along fluvial gradients. Headwater streams, characterized by higher geographical isolation, are often considered hotspots of ecological uniqueness. We investigated how stream position influences aquatic insect rarity and beta diversity in Atlantic Forest conservation units, testing the following hypotheses: (i) central streams had more abundance and species richness than headwaters; (ii) headwaters contain higher proportion of rare species; (iii) headwaters exhibit higher beta diversity; (iv) headwaters show greater ecological uniqueness (LCBD); and (v) rare species contribute more to beta diversity (SCBD) than common species. We sampled aquatic insects from 11 pairs of streams, each pair consisting of one headwater and one central stream. We identified Ephemeroptera, Plecoptera, Trichoptera, Odonata and Chironomidae to genus level. First, we calculated paired t-test for species abundance or occupancy (i.e., proportion of sampled sites in which each species was recorded) between headwater and central streams. We also calculated Permutation Analysis of Multivariate Dispersions (PERMDISP) and Permutational Multivariate Analysis of Variance (PERMANOVA) for all genera together and separately for each taxonomic group. We then investigated patterns of ecological uniqueness and species contributions to beta diversity. We found similar abundance and richness of aquatic insects between headwater and central streams. We also did not find a difference in rarity or LCBD between stream positions. Genera with intermediate abundance and occupancy contribute the most to beta diversity. In conclusion, within these well-preserved Atlantic Forest streams, our findings point to minimal ecological distinction between headwaters and central streams. Rarity is not concentrated in headwaters, intermediate species are the primary drivers of beta diversity, and ecological uniqueness is dispersed across the river network. These results challenge conservation paradigms that prioritize specific river sections and instead advocate for holistic, watershed-scale protection strategies.

Keywords

Aquatic Insects, Beta Diversity, Ecological Singularity, Dendritic Network, Streams

Introduction

Freshwater communities are naturally structured by a combination of spatial processes, dispersal limitations, and environmental filtering, even in landscapes with high native forest cover and minimal direct human disturbance (Brown and Swan, 2010; Heino et al., 2015). Accordingly, species abundance distributions are typically highly uneven, with most taxa occurring at low abundances and only a few being locally common (Preston, 1948; Siqueira et al., 2012; Petsch et al., 2015; Enquist et al., 2019). Rarity is an intrinsic feature of species-rich communities and represents a critical stage in population dynamics, frequently preceding local extinction (Hessen & Walseng, 2008), including in aquatic metacommunities. Although anthropogenic activities can intensify rarity and accelerate biodiversity loss in freshwater ecosystems (Dobson et al., 2006; Dudgeon et al., 2006; Petsch et al., 2021), pronounced patterns of community composition and rarity may also emerge in conserved systems as a consequence of natural spatial organization, particularly related to position within dendritic stream networks (Carrara et al., 2012; Heino et al., 2015). Dendritic networks are hierarchical ecosystems, corresponding to a geometric pattern of tree-like branching, where there is a main trunk and branches that decrease in size (Campbell-Grant et al., 2007).

In preserved ecosystems with high native vegetation cover and low levels of direct human disturbance, rare species are more likely to persist, as reduced anthropogenic pressure is associated with greater environmental stability, favoring the survival and reproduction of more vulnerable species (i.e., more susceptible to unpredictable events) (Souza, 2023). There are several ways to define rare and common species, such as in relation to abundance or distribution (Rabinowitz, 1981; Gaston, 1994, Siqueira et al., 2021). More widely distributed species tend to occur in high abundances (i.e., common species), while species with more restricted distributions

often exhibit low abundances (i.e., rare species) (Gaston, 1994). It is important to note the rarity in empirical datasets is often inferred from low counts of individuals (e.g.,"singletons" and "doubletons,"), which do not necessarily represent true ecological rarity but may instead result from sampling limitations. In preserved stream networks, variation in species rarity, expressed as differences in local abundance and spatial occupancy across sites, is expected to be associated with longitudinal position along the dendritic network. Headwater streams are typically smaller, more isolated, and less connected than central reaches, which may limit dispersal and increase local extinction probability. These features can promote higher frequencies of locally rare or spatially restricted taxa in upstream sections, whereas central reaches, due to greater connectivity and higher habitat heterogeneity, may support more widespread and abundant taxa (Carrara et al., 2012; Altermatt, 2013).

In lotic ecosystems such as streams, benthic invertebrates are diverse and crucial for ecosystem functioning (Covich et al., 1999). They have a wide distribution, are strongly influenced by environmental conditions, and have relatively low mobility (Moretti & Callisto, 2005; Würdig et al., 2007; Petsch et al., 2013). These characteristics make the benthic invertebrate community one of the most used in the biomonitoring of aquatic ecosystems, particularly Ephemeroptera, Plecoptera, and Trichoptera (EPT) assemblages that are sensitive to environmental stress (Rosenberg & Resh, 1993). On the other hand, we have the often-neglected Chironomidae (Diptera) assemblage, one of the main components of benthic communities in continental waters, due to their high density and diversity (Ferrington, 2008). They have a wide distribution and live in the most diverse environmental conditions, with species inhabiting from pristine to impacted environments (Pinder, 1986; Ferrington, 2008; Petsch et al., 2015; Martins et al., 2021).

Different taxonomic groups of aquatic insects have distinct dispersal capacities that significantly influence their distribution patterns along stream gradients (Heino et al., 2015).

Among the EPT groups (Ephemeroptera, Plecoptera and Trichoptera), a considerable variation in dispersal strategies is observed. Ephemeroptera generally presents more limited dispersal, with short-lived adults (only 1-2 days) and restricted flight, where energy is primarily directed toward reproduction rather than exploration of new habitats (Saito et al., 2021). Plecoptera also demonstrates moderate dispersal capabilities, whereas Trichoptera exhibits substantial interspecific variation in dispersal ability. Although some species can disperse over long distances within and even across catchments, many others show limited dispersal, challenging the assumption that caddisflies are uniformly strong dispersers (Kärnä et al., 2015; Lancaster et al., 2023). In contrast, Odonata exhibits excellent aerial mobility as adults and many species can actively disperse for several kilometers along water bodies (Li et al., 2019). Chironomidae, in turn, exhibit active dispersal as flying adults, although their dispersal can be strongly influenced by wind currents and passive transport processes such as drift in the water column (May, 2019). These eco-physiological differences highlight the importance of considering taxonomic groups separately when analyzing community patterns in dendritic networks, as they may respond distinctly to connectivity and isolations processes.

The position of streams within a dendritic network affects the structure and dynamics of aquatic metacommunities, including those of aquatic insects (Carrara et al., 2012; Santiago & Beasley, 2023). For example, in experimental laboratory stream networks, headwater sections showed lower species richness due to reduced connectivity and more dissimilar to each other, resulting in higher beta diversity compared to more homogenous communities among central sections (Carrara et al., 2012). As a consequence, headwaters are expected to exhibit higher Local Contribution to Beta Diversity (LCBD), reflecting their increased ecological uniqueness when compared to more centrally connected stream sections, where dispersal tends to homogenize species composition (Legendre & De Cáceres, 2013; Carrara et al., 2012; Altermatt,

2013). However, comprehensive empirical tests of these theoretical expectations in real-world stream networks remain scarce (but see Milesi and Melo, 2014; Milesi & Hepp, 2025).

Environmental heterogeneity is a key driver of metacommunity structure, shaping species distributions by promoting environmental filtering and niche differentiation among sites (Li et al., 2021). These spatial and environmental processes do not affect all species equally. Because rare species are typically more sensitive to dispersal limitation and environmental filtering (Gaston, 1994; Hessen & Walseng, 2008; Heino et al., 2015), they are expected to play a disproportionate role in driving community differentiation along dendritic networks. Ecological uniqueness in stream networks may therefore arise not only from taxonomic composition but also from environmental differentiation among sites, which can be quantified using metrics such as the Local Contribution to Environmental Heterogeneity (LCEH; Castro et al. 2019). Headwater streams often exhibit high environmental singularity due to local variation in channel morphology, substrate composition, riparian vegetation, and hydrological conditions, which can reinforce patterns of ecological uniqueness when combined with dispersal limitation.

The rarity of aquatic insects can also be influenced by the position of the water body within a dendritic network. Headwater streams are expected to harbor a higher proportion of rare aquatic insects due to their hydrological isolation from the rest of the network (Carrara et al., 2012; Altermatt, 2013), as dispersal among headwater streams is generally limited (Carrara et al., 2012; Altermatt & Fronhofer, 2018). In contrast, more centrally located streams tend to experience higher dispersal rates, which can promote regional homogenization of biota. At the same time, high connectivity may increase the occurrence of rare species through mass effects, as continuous immigration allows the persistence of species that would otherwise be excluded under local environmental conditions (Leibold et al., 2004; Cadotte & Fukami, 2005). Consequently, at the site level, headwater streams are expected to exhibit higher compositional dissimilarity and therefore greater contributions to beta diversity.

At the species level, rare aquatic insects occurring within a dendritic network may exhibit a greater Species Contribution to Beta Diversity (SCBD; Legendre & De Cáceres, 2013). This metric quantifies the relative importance of each taxon in structuring beta diversity and is associated with species abundance, occupancy, niche breadth, and biological traits. Thus, species that are spatially restricted or occur at low abundances may disproportionately drive compositional differentiation among sites. This information is crucial for applied ecology due to the greater vulnerability of rare species to extinction and the role of headwaters in important ecosystem services (Alexander et al., 2016; Freeman et al., 2007).

We investigated the relationships between stream position in the dendritic network and the patterns of richness, rarity and ecological uniqueness of aquatic insects in a subtropical region of the Atlantic Forest. Beyond overall diversity patterns, we also evaluated the extent to which individual sites contribute uniquely to regional beta diversity using the Local Contribution to Beta Diversity (LCBD), a metric that identifies sites with distinct species composition relative to the metacommunity. Because hydrological isolation is a determining factor in structuring communities in fluvial systems, we test the central hypothesis that headwater streams, due to their peripheral position and reduced connectivity, function as hotspots of ecological uniqueness. However, we recognize that spatial proximity among streams may also influence community patterns, as nearby sites tend to be more similar due to dispersal processes, potentially confounding the effects of network position. Specifically, we expect in headwaters: (i) lower total abundance and richness; (ii) higher proportion of rare species, both in terms of abundance (fewer individuals) and occupancy (occurrence in fewer locations); (iii) higher beta diversity when compared to central position streams; (iv) distinct community composition from central streams; (v) greater local contribution to beta diversity (LCBD) in headwater sections compared to central streams; (vi) that rare species contribute more significantly to beta diversity (SCBD) than common species; and (vii) sites with higher local environmental heterogeneity (LCEH) may

exhibit higher LCBD. Based on differences in dispersal ability of aquatic insects, we expect results may differ among taxonomic groups. More specifically, aquatic insects with lower dispersal capacity (e.g., Ephemeroptera and Plecoptera) will show stronger patterns of rarity and ecological uniqueness in headwater streams, whereas groups with higher dispersal ability (e.g., Odonata and some Trichoptera species with greater flight capacity and longer-lived adults) are expected to present more homogeneous patterns between headwater and central stream sections. Chironomidae, due to their strong passive dispersal by wind and current water, may exhibit intermediate or context-dependent responses, as their distribution can be influenced by both local environmental conditions and spatial factors such as hydrological connectivity and flow dynamics (Heino et al., 2015; Kärnä et al., 2015; Li et al., 2019). To explore how environmental gradients influence community composition across streams and taxonomic groups, we additionally applied distance-based redundancy analysis (dbRDA), which allows partitioning variation in community structure attributable to measured environmental variables while accounting for multivariate patterns among sites. This approach provides a complementary perspective to LCBD and SCBD analyses, linking environmental heterogeneity with observed patterns of ecological uniqueness and rarity.

Methods

Study area

Our research was conducted in two adjacent, well-preserved protected areas within the Atlantic Forest continuum of São Paulo state, Brazil: the Carlos Botelho State Park and the Intervales State Park. These contiguous Conservation Units form one of the largest and most ecologically significant remnants of the Brazilian Atlantic Forest, collectively recognized as a UNESCO World Heritage Site (Ribeiro et al., 2009; UNESCO, 2019). The parks' adjacency minimizes external disturbance, while their extensive and intact hydrographic networks provided

sufficient replicate stream pairs for sampling. Moreover, the continuous forest cover across both parks, documented in their respective management plans (Fundação Florestal, 2005; 2018), ensured consistent riparian vegetation among sites. This setting offered an ideal opportunity to examine natural ecological patterns in stream networks under minimal anthropogenic influence.

Sampling design

The sampling of aquatic insects was conducted in 11 pairs of streams located in the Carlos Botelho and Intervales State Parks (São Paulo, Brazil). We sampled during the months of April and May 2024, corresponding to the end of the rainy period and the beginning of the dry period in the study area (INMET, 2023; Alvares et al., 2013).

In each stream, we defined two sampling sites: one headwater reach (first or second order sensu Strahler 1957) and one central position reach (third or fourth order sensu Strahler 1957), totaling 22 streams (Figure 1). The pairs of streams were chosen for similarity in drainage density (i.e., the ratio of the total length of water courses to the total area of the microbasin are similar between the microbasins) and land use (i.e., all with a similar percentage of native vegetation cover ranging from 100%, guaranteed by insertion within conservation units).

We also estimated the geographic distance along the river network between headwater and central stream sections using Google Earth. Distances ranged between headwater and central sections between 100 and 1.500 m. This range ensured comparability among sites while maintaining feasible access for field sampling, as only stream sections reachable during the sampling period were considered. This approach allowed us to incorporate spatial distance while minimizing biases related to unequal sampling effort.

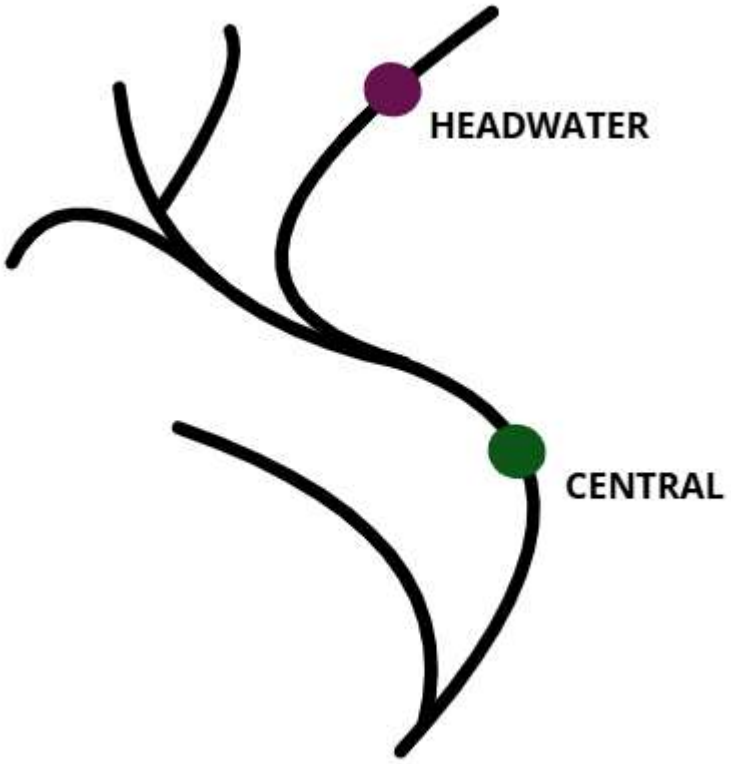

Figure 1. Sampled paired headwater and central stream sections within a dendritic network. Each pair represents a headwater stream spatially associated with a downstream central stream along the same flow path. The purple circle represents the headwater stream, while the green circle represents the central stream. Water flows from the top to the bottom of the figure.

Data sampling

We sampled the aquatic insects using a kick-net (0.250 mm mesh) in a rifle section for two minutes (consisting of four sub-samplings of 30 seconds). The material was fixed in the field using alcohol 80%, placed in properly identified plastic bags and taken to the laboratory (LEIA - Laboratory of Aquatic Invertebrate Ecology - Unesp-Assis), where they were sorted with the aid of a stereomicroscope. Subsequently, the identification of the following groups of aquatic insects was done at the genus level: Ephemeroptera, Plecoptera, Trichoptera, Odonata, and

Chironomidae (Diptera). We used Pes et al. (2005), Domínguez et al. (2006), Heckman (2006a,b), Domínguez & Fernández (2009), Trivinho-Strixino (2011), Ribeiro (2013) and Hamada et al. (2014) to help in aquatic insects identification.

Although species-level resolution would ideally provide a more precise characterization of rarity patterns, genus-level identification remains a widely adopted and ecologically meaningful approach in studies of aquatic insects, particularly in highly diverse tropical and subtropical regions. Many aquatic insect groups exhibit high species richness, taxonomic impediments, and frequent occurrence of undescribed or cryptic species, which constrains reliable species-level identification across large datasets. Genus-level analyses have been shown to retain strong ecological signals related to environmental gradients, dispersal processes, and beta diversity patterns, while reducing taxonomic uncertainty and identification bias (Heino & Soininen, 2007; Siqueira et al., 2012; Petsch et al., 2015). Nevertheless, we acknowledge that the use of genus-level resolution may underestimate fine-scale patterns of species rarity and ecological specialization, and our interpretations should therefore be viewed as conservative estimates of rarity and ecological uniqueness within stream networks.

We measured limnological variables (pH, dissolved oxygen, total dissolved solids, turbidity and temperature) using the Horiba U-50 multiparameter probe. The substrate structure variables (e.g., sand, gravel, pebble and boulders) were estimated visually using a 50 x 50 cm sampler area (e.g., Heino et al., 2018). We also measured the stream width and depth. Finally, we obtained the canopy cover percentage from canopy images taken in the field and analyzed using specialized software (ImageJ; Rasband, 2018).

Data analysis

We determined genus abundance and diversity for each stream, considering all aquatic insect genera pooled as well as each taxonomic group separately (i.e., Ephemeroptera,

Plecoptera, Trichoptera, Odonata and Chironomidae). For each response variable, we compared headwater and central streams using paired designs (11 stream pairs), in which each headwater stream was directly paired with its corresponding central reach.

To account for differences in sampling effort and total abundance among streams, we estimated rarefied species richness using an individual-based rarefaction approach applied at the pair level. For each pair of streams, richness was rarefied only for the site with higher abundance, using the minimum number of individuals within the pair as the standardization level. This procedure allowed standardized and ecologically meaningful comparisons of species richness between headwater and central streams. Rarefied richness was calculated for all aquatic insects pooled and separately for each taxonomic group.

To test our predictions regarding rarity, we calculated the proportion of rare aquatic insect taxa (i.e., number of rare species divided by the total number of species). Taxa were classified as rare in terms of abundance when represented by only one or two individuals per stream (i.e., singletons and doubletons, respectively). Taxa were considered rare in terms of occupancy when occurring in only one headwater stream or one central stream section. This proportional approach was used to minimize the potential influence of variation in total species richness among streams, as absolute numbers of rare species tend to increase with higher overall richness, potentially confounding comparisons between stream positions. Differences in proportional rarity between headwater and central streams were evaluated using beta regression models, which are appropriate for response variables bounded between 0 and 1(Ferrari & Cribari-Neto, 2004), using a paired design that accounted for the dependence between stream pairs.

We evaluated differences in community variability among headwater and central streams using a Permutational Analysis of Multivariate Dispersions (PERMDISP; Anderson, 2006). PERMDISP was performed based on dissimilarity matrices derived from presence–absence data (Sørensen dissimilarity) and log-transformed abundance data (Bray-Curtis dissimilarity),

considering headwater and central streams as groups, with permutation tests restricted within stream pairs. To test whether headwater and central streams differed significantly in their overall community composition, we conducted a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) using the same dissimilarity matrices and the paired model structure, ensuring that permutations respected the headwater-central stream pairing. PERMANOVA evaluates differences in the centroid of multivariate community composition between groups while accounting for the structure of ecological community data. Together, PERMDISP and PERMANOVA allowed us to distinguish whether differences between stream positions were driven by changes in community variability or by shifts in overall species composition.

We further investigated relationships between community composition and environmental variables using distance-based redundancy analysis (dbRDA) based on Bray-Curtis dissimilarity matrices derived from log-transformed abundance data. Analyses were conducted considering all taxonomic groups together and separately for each group. Environmental variables were standardized prior to analyses to ensure comparability among predictors. The dbRDA models also followed the paired design, incorporating the pairing of headwater and central streams into the permutation scheme to account for dependency between paired sites.

Local Contribution to Beta Diversity (LCBD) was calculated following Legendre and De Cáceres (2013). Abundance data were Hellinger-transformed prior to analysis, and total beta diversity was estimated for the full set of streams. LCBD values were then used to identify sites contributing disproportionately to overall beta diversity.

Local contribution to environmental heterogeneity (LCEH) was calculated based on a site-by-environmental variables matrix. Prior to analysis, environmental variables were standardized to ensure comparability among different measurement scales. Euclidean distance

was then used to compute a pairwise environmental dissimilarity matrix among sites. Following the logic of LCBD (Legendre & De Cáceres, 2013), LCEH was calculated as the relative contribution of each site to total environmental dissimilarity. Specifically, for each site i, we computed the sum of its pairwise environmental distances to all other sites (S_i) and divided it by the total sum of all pairwise environmental distances (S_total). Thus:

$$LCEH_i = S_i / S\_total$$

where S_total equals half of the sum of all elements in the symmetric environmental distance matrix. This approach quantifies how environmentally unique each site is relative to the entire study system. Statistical significance of LCEH values was assessed using permutation tests (999 permutations), obtained by randomly permuting rows and columns of the environmental distance matrix. For each permutation, LCEH values were recalculated, generating a null distribution for each site. Observed LCEH values were then compared to their respective null distributions to obtain p-values. Differences in LCEH between headwater and central streams were evaluated using beta regression models. Finally, the relationship between LCBD and LCEH was assessed using beta regression models, including stream position as a categorical predictor.

Finally, we investigated the relationship between Species Contribution to Beta Diversity (SCBD) and species rarity metrics (total abundance and occupancy) using beta generalized linear models. Models were fitted with a logit link function and included second-order polynomial terms to test for potential non-linear relationships between SCBD and rarity metrics.

All analyses were performed in R (R Core Team, 2023) using the packages vegan (Oksanen et al., 2020), adespatial (Dray et al., 2019), betapart (Baselga et al., 2019), iNEXT (Hsieh et al., 2016), BiodiversityR (Kindt & Coe, 2015), mgcv (Wood, 2020), betareg (Ferrari & Cribari-Neto, 2004) and ggplot2 (Wickham, 2016).

Results

We recorded a total of 2,920 organisms distributed across 104 taxa belonging to Ephemeroptera, Plecoptera, Trichoptera, Odonata, Megaloptera and Chironomidae (Diptera). The abundance ranged from 33 to 276 individuals (mean = 122 ± 87.9) in headwater streams and from 67 to 242 individuals (mean = 140 ± 48.9) in central streams. Regarding genus richness, headwaters varied from 13 to 46 (mean = 26 ± 8.42), whereas in central streams it ranged from 19 to 34 genera (mean = 28 ± 5.12). However, contrary to our expectations, we found similar mean abundance ($t_{(1,10)}$ = 0.81, p = 0.436; Figure 2A) and observed species richness ($t_{(1,10)}$ = 0.75, p = 0.465 Figure 2B) between stream positions. Rarefied species richness also did not differ significantly between headwater and central streams ($t_{(1,10)}$ = 1.64, p = 0.131; Figure 2C), confirming that differences in sampling effort did not affect the observed patterns. We also did not find differences in abundance and observed species richness between stream position for most of the taxonomic groups (Figure 4A-J; Table S1). However, when analyzing taxonomic groups separately, Ephemeroptera emerged as the only group showing significant differences between stream positions, with both abundance ($t_{(1,10)}$= -2.41, p = 0.026) and species richness ($t_{(1,10)}$= 2.23, p = 0.037) being significantly lower in headwater streams (Figure 3A-B; Table S1). In contrast, Plecoptera($t_{(1,10)}$= 0.149, p= 0.883), Trichoptera ($t_{(1,10)}$<0.001, p= 0.99), Odonata($t_{(1,10)}$= 0.792, p= 0.438) and Chironomidae ($t_{(1,10)}$= -0.259, p= 0.798 showed no significant differences in abundance or richness between stream positions (Figure S2.C-J; Table S1).

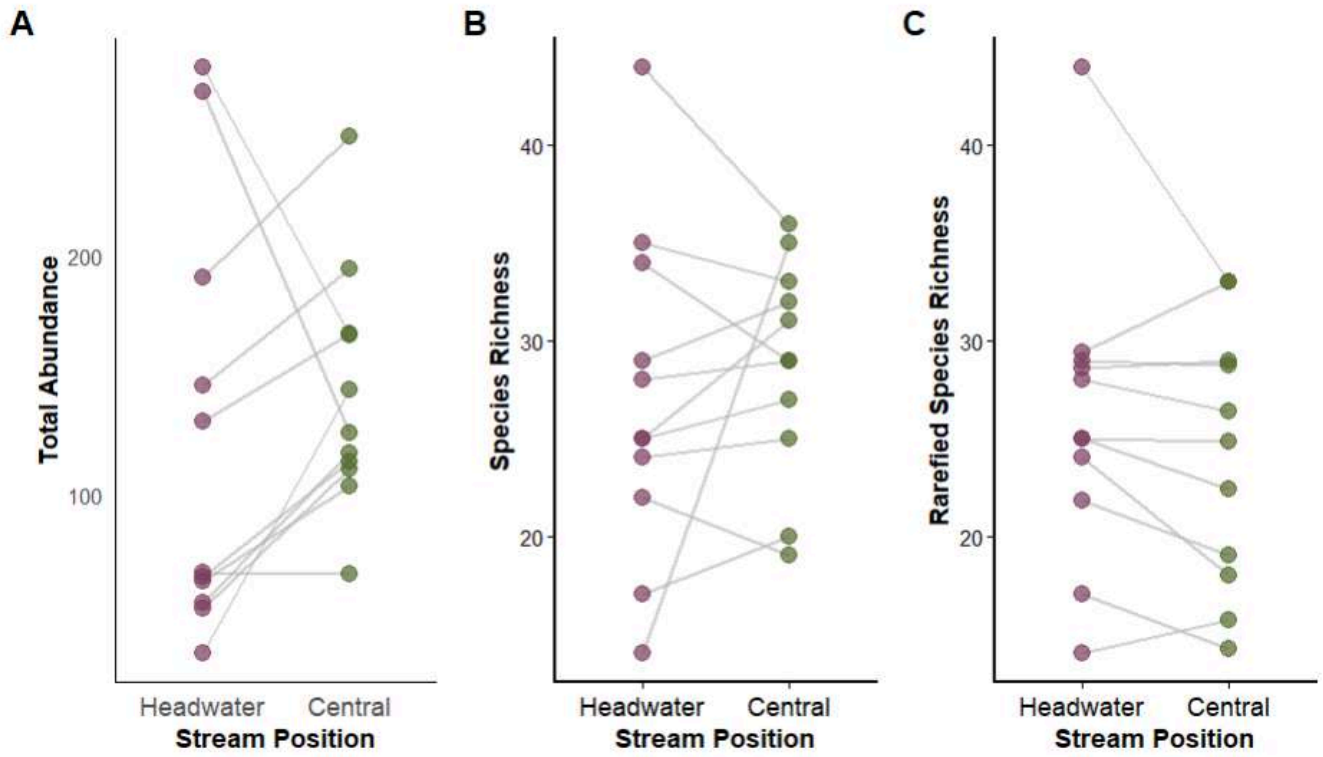

Figure 2: Abundance (A), observed species richness (B) and rarefied species richness (C) of aquatic insects in headwater and central streams of Atlantic Forest. Each line connects a pair of streams (headwater and its central reach).

The rarefied species richness curve indicated that the sampling effort was sufficient to capture the expected taxa richness in the studied environments. Most of the curves for both stream types, central and headwater, increased with sampling effort and showed a slight tendency to stabilize, although a clear asymptote was not reached. The curve for central streams reached its asymptote with approximately 80 sampled individuals, while the curve for headwater streams stabilized with a similar sampling effort. This demonstrates that, despite potential differences in total abundance, the inventory of the aquatic insect community was representative in both stream types within the studied Atlantic Forest.

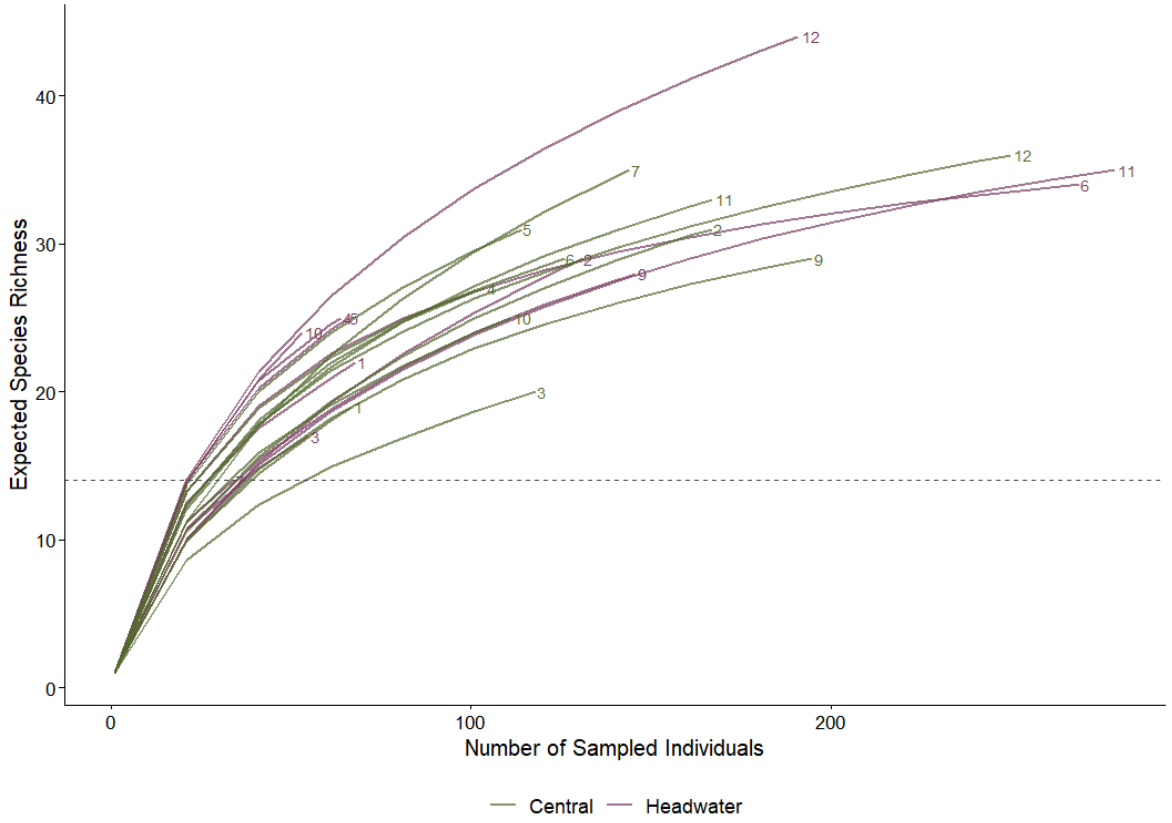

Figure 3. Rarefied curves of aquatic insect communities in central and headwater streams of the Atlantic Forest. The curves show the expected species richness as a function of the number of sampled individuals. Each curve corresponds to one stream, and numbers indicate the paired sampling units (1–11), with each number representing a headwater–central stream pair. The dashed horizontal line indicates a common reference level of expected species richness used for comparison among streams.

We observed the dominance by a few taxa of aquatic insects, with the 10 most abundant - *Smicridea* (331 individuals), *Anacroneuria* (259), *Leptonema* (129), *Lopescladius* (122), *Traverhyphes* (120), *Tricorythode*s (110), Prox. *Paratendipes* (105), *Simothraulopsis* (104), *Tanytarsus* (103), and *Campylocia* (99) - collectively representing 51.2% of the total abundance. In contrast, a high proportion of rare taxa was detected, with 21 singletons (taxa represented by only one individual, 20.2% of the total) and 7 doubletons (taxa with two individuals, 6.7%), including genera such as *Beardius*, *Cardiocladius*, *Cricotopus*, and *Ablabesmyia* among the 10 rarest. Based on occupancy (taxa present in only one stream), we found 61 rare taxa. No significant effect of position was detected for the proportion of individuals belonging to rare

species ($\beta = 0.18 \pm 0.26$ SE, $z = 0.71$, $p = 0.48$; Figure 5A). Similarly, proportional occupancy did not differ between positions ($\beta = 0.14 \pm 0.24$ SE, $z = 0.61$, $p = 0.54$; Figure 5B).

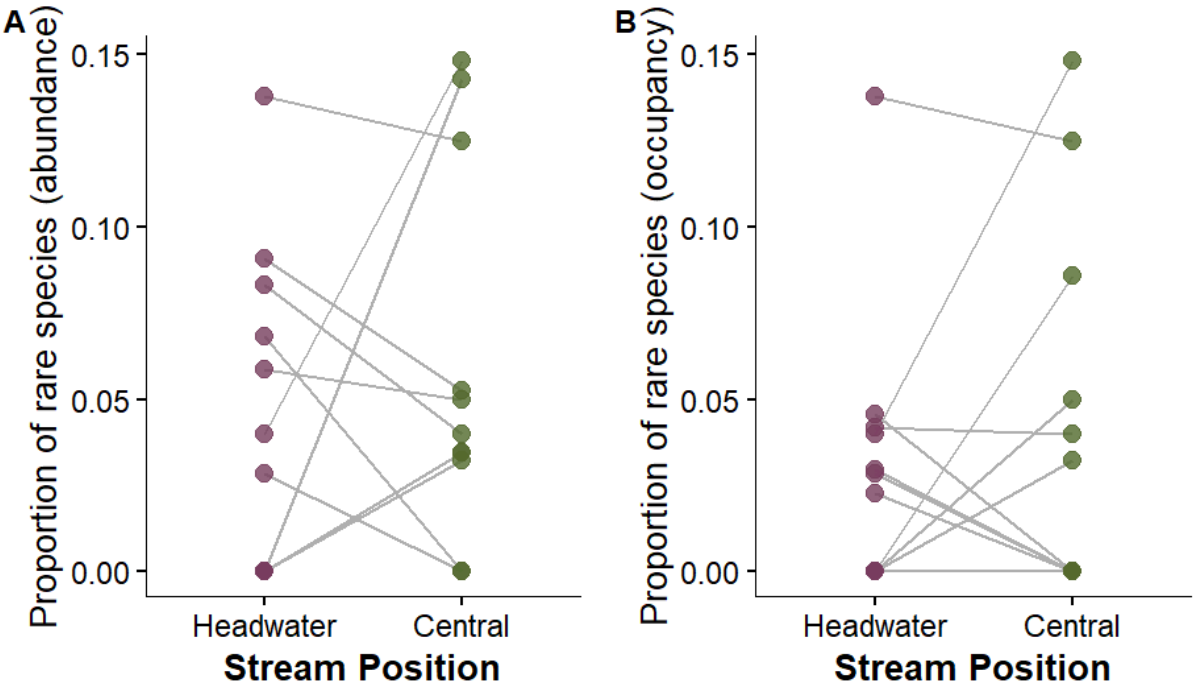

Figure 4. Proportion of rare genera of aquatic insects in headwater and central streams. (A) Rarity by abundance in streams (i.e., genera represented by few individuals in the samples, such as singletons and doubletons). (B) Rarity by occupancy (species present in only one stream). Each line connects a pair of streams (headwater and its central reach).

We also did not find significant differences in community composition between headwater and central streams. For Sørensen dissimilarity, PERMDISP showed no significant difference in multivariate dispersion (average distance to median: Headwater = 0.380, Central = 0.348; $F_{1,20} = 0.759$, $p = 0.383$), and PERMANOVA indicated no significant effect of stream position ($F_{1,20} = 1.07$, $R^2 = 0.051$, $p = 0.360$). PCoA based on Sørensen dissimilarity showed some spatial separation but centroids were relatively close. For Bray–Curtis dissimilarity, PERMDISP also indicated no significant difference in dispersion (average distance to median: Headwater = 0.435, Central = 0.399; $F_{1,20} = 1.33$, $p = 0.258$), and PERMANOVA revealed no significant differences in abundance-based composition ($F_{1,20} = 1.24$, $R^2 = 0.058$, $p = 0.199$).

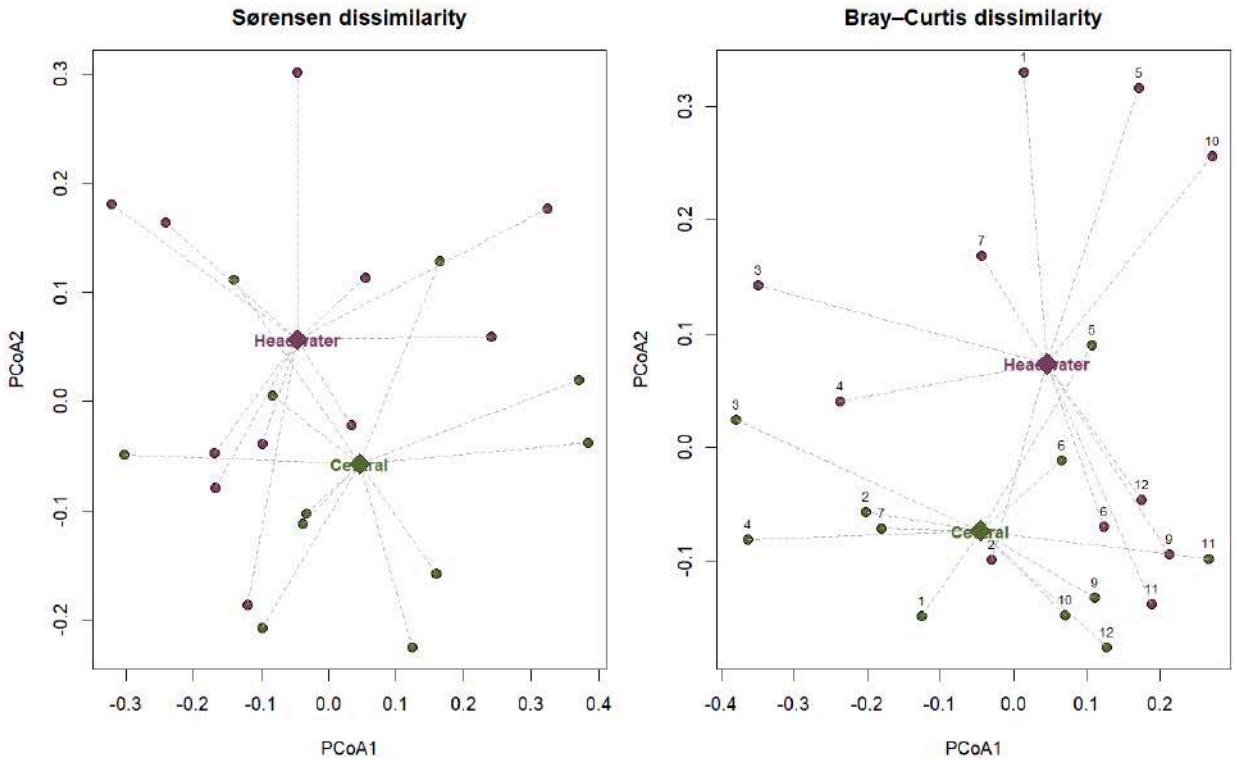

Figure 5. Principal Coordinates Analysis (PCoA) based on Sørensen (presence–absence; left) and Bray–Curtis (log-transformed abundance; right) dissimilarities for aquatic insect communities in headwater and central streams. Points represent individual sampling sites, with colors indicating stream position (Headwater and Central). Numbers correspond to paired sites. Dashed lines connect each site to the centroid of its respective group, illustrating within-group dispersion. Group centroids are indicated by larger symbols.

The distance-based redundancy analysis (dbRDA) results indicated that environmental variables explained 40.35% of the variation in aquatic insect community composition, with the first two axes explaining 16.43% (dbRDA1) and 7.04% (dbRDA2) of the total variance. Among the measured environmental variables, stream type and temperature emerged as significant predictors, while other factors did not show detectable effects. When examining taxonomic groups individually, responses to environmental gradients differed markedly: Chironomidae (42 genera, 41.7% explained variance, $p = 0.025$) and Trichoptera (15 genera, 44.5%, $p = 0.034$) exhibited clear environmental structuring, whereas Ephemeroptera (24 genera, 38.2%, $p = 0.169$) and Odonata (14 genera, 36.5%, $p = 0.295$) displayed intermediate patterns without statistical significance. Plecoptera (5 genera, 51.9%, $p= 0.649$) showed the highest proportion of variance

explained, although significance was not achieved, likely due to the small number of sampled genera.

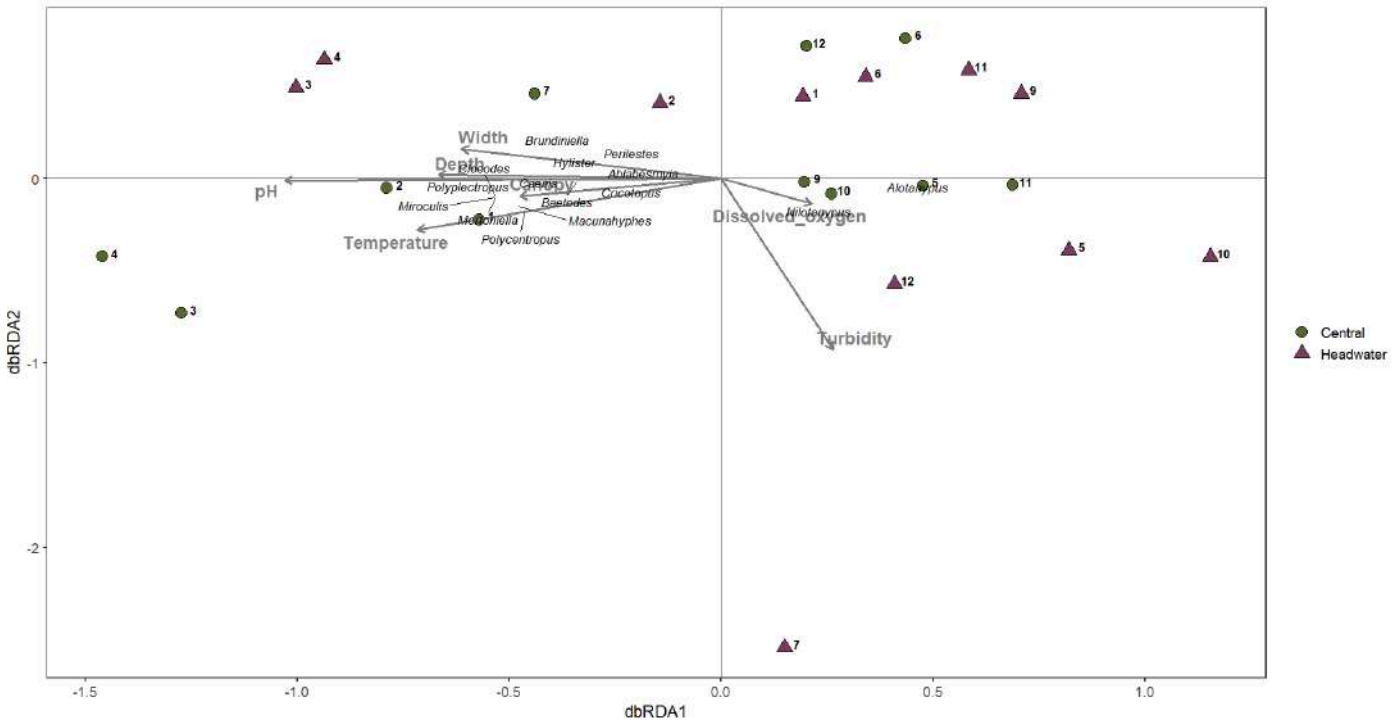

Figure 6. Distance-based redundancy analysis (dbRDA) of aquatic insect communities in headwater (triangles) and central (circles) streams of the Atlantic Forest. Numbers represent stream identification. Environmental vectors show the direction and strength of correlation for: Depth, Width, pH, Dissolved oxygen, Temperature, Turbidity, and Canopy cover. The 15 most influential insect genera are shown in italics.

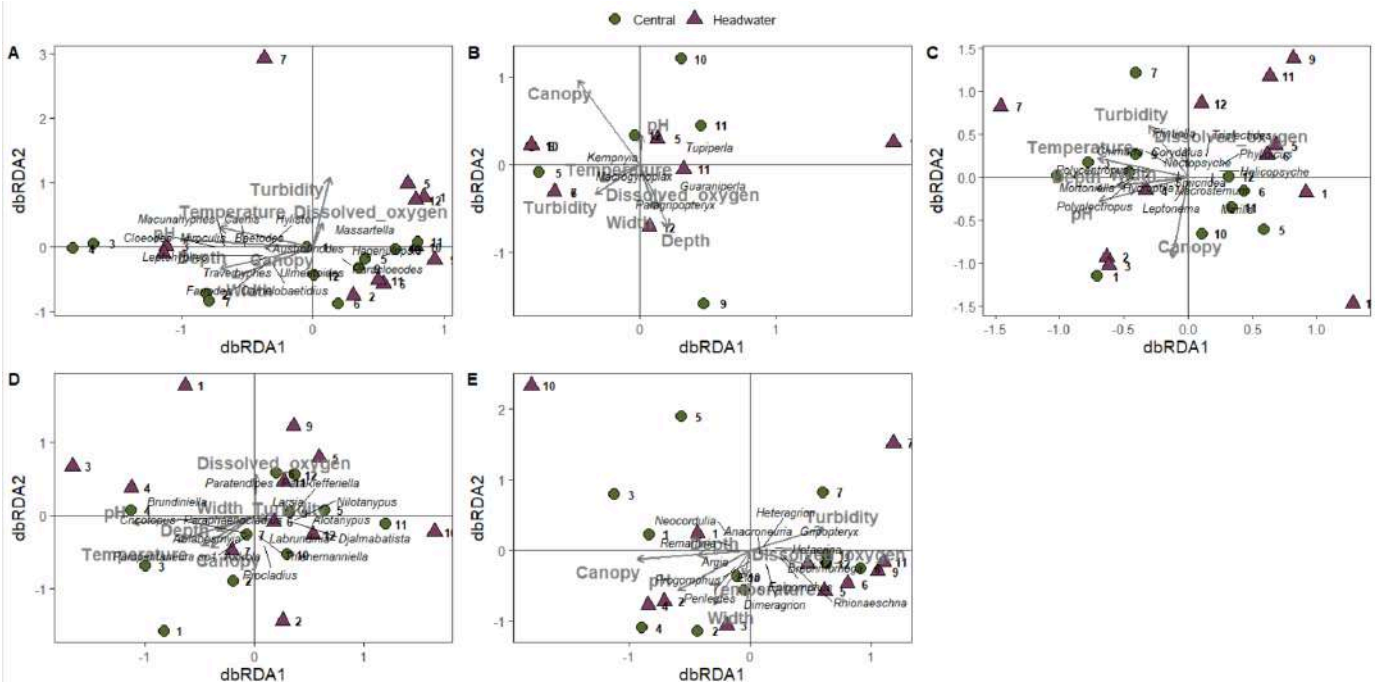

Figure 7. Distance-based redundancy analysis (dbRDA) of major aquatic insect orders in Atlantic Forest streams: (A) Ephemeroptera, (B) Plecoptera, (C) Trichoptera, (D) Odonata, and (E) Chironomidae (Diptera). Each ordination shows the relationship between environmental variables and the respective insect group. Symbol shapes represent stream types: circles = central streams, triangles = headwater streams. Only significant environmental vectors ($p < 0.05$) are shown for each group.

Of the 22 sampled streams, only 3 showed significant contributions to total beta diversity (LCBD). The distribution consisted of 2 significant headwater streams and 1 significant central stream (Supplementary Material Figure 1). LCEH values varied among streams, ranging from 0.06 to 0.16. Mean LCEH was slightly higher in central streams (mean ± SD = 0.09 ± 0.04) than in headwater streams (0.09 ± 0.02); however, this difference was not statistically significant (t-test: t = 0.40, df: 16.43, p = 0.6928; Figure 8C). No stream exhibited significant contributions to environmental heterogeneity based on permutation tests ($p<0.005$). Beta regression analysis revealed no significant relationship between environmental heterogeneity (LCEH) and local contribution to beta diversity (LCBD) ($\beta = 0.33 \pm 1.26$ SE, $p = 0.796$). Stream position also had no significant effect on LCBD ($p = 0.442$), and the model explained a low proportion of variance

(pseudo-R^2 = 0.027), indicating that variation in community uniqueness was largely independent of measured environmental heterogeneity and stream position.

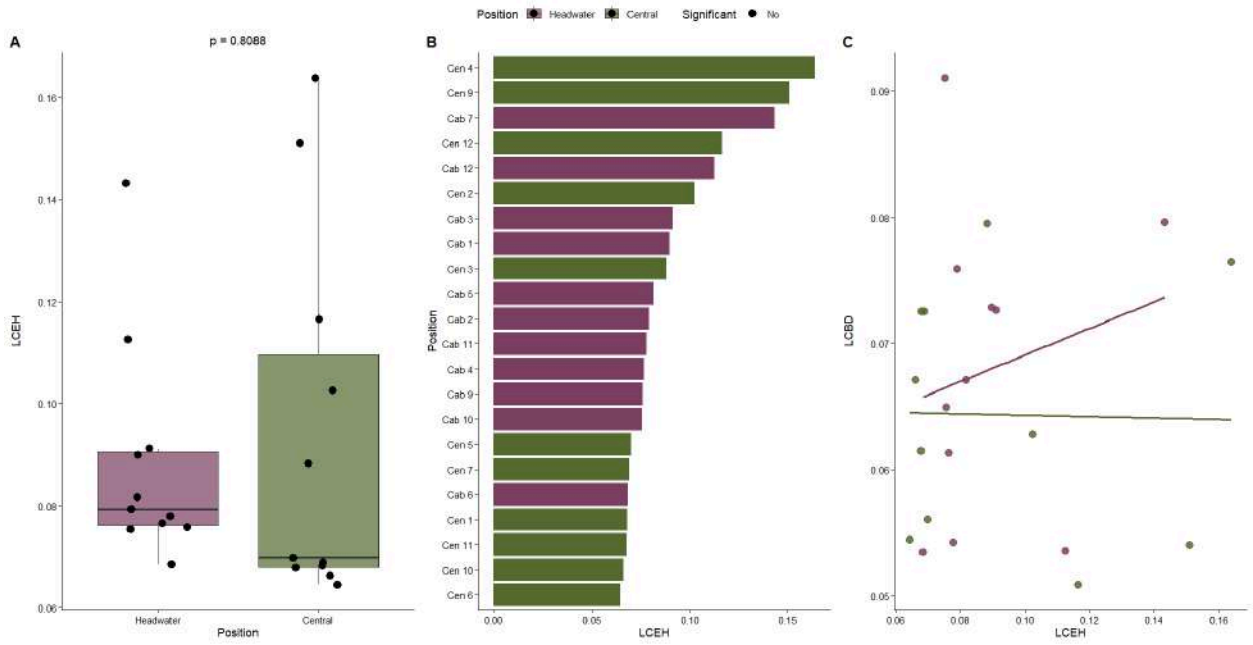

Figure 8. Comparison of diversity metrics among river positions. (A) Boxplot of local contribution to environmental heterogeneity (LCEH) between Headwater and Central positions. Dots represent individual sites.(B) Bar plot showing LCEH values for each site, grouped by position (Headwater = purple, Central = green). (C) Relationship between LCEH and local contribution to beta diversity (LCBD) for each site, with separate trend lines for Headwater and Central positions.

The Species Contribution to Beta Diversity (SCBD) analysis identified the 15 genera that most contributed to total beta diversity (Figure 10). The species with highest SCBD were *Traverhyphes* (SCBD = 0.0322), *Tricorythodes* (0.0295), *Thraulodes* (0.0291), *Simothraulopsis* (0.0289) and *Macunahyphes* (0.0265). These genera, predominantly from the order Ephemeroptera, represent the main contributors to variation in species composition among the sampled streams. All top contributors were not classified as rare genera, with substantial abundances (ranging from 80 to 120 individuals) and wide distributions across sampling sites.

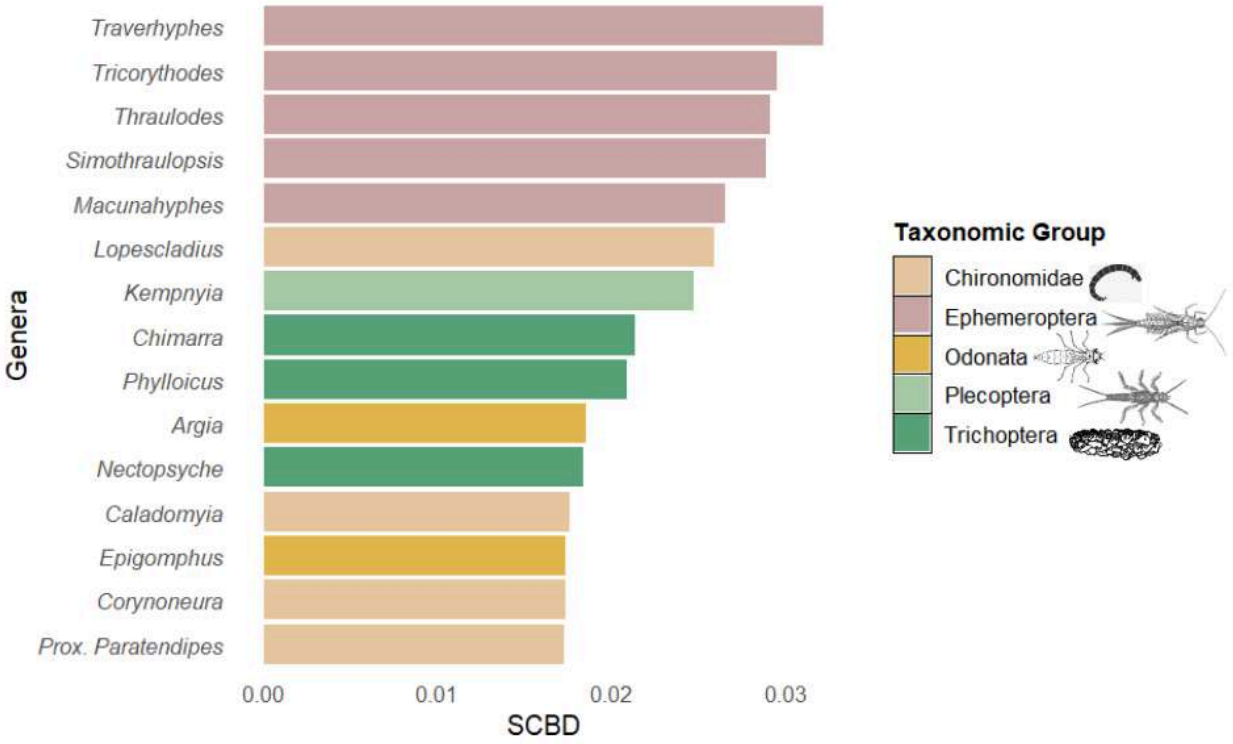

Figure 9. Top 15 genera of aquatic insects with higher SCBD values in headwater and central streams of Atlantic Forest.

The Species Contribution to Beta Diversity (SCBD) analysis revealed strong and highly significant relationships with species rarity metrics based on beta regression models. Using beta generalized linear models with a logit link and second-order polynomial terms, we found a significant non-linear relationship between SCBD and total abundance, with the quadratic term being highly significant ($\beta_2 < 0.001^5$, $z = -7.96$, $p < 0.0001$; Figure 10A). This pattern indicates that species with intermediate abundance values contribute disproportionately more to overall beta diversity. Similarly, SCBD exhibited a strong non-linear relationship with species occupancy, as evidenced by significant quadratic effect in the beta regression model ($\beta_2 = -3.99$, $z = -11.12$, $p < 0.0001$; Figure 10B). Species with intermediate occupancy across streams showed the highest contributions to beta diversity, whereas very rare and very widespread species tended to have lower SCBD values. Overall, these results demonstrate that species rarity

metrics, particularly abundance and occupancy, strongly and non-linearly structured species contributions to beta diversity in Atlantic Forest streams.

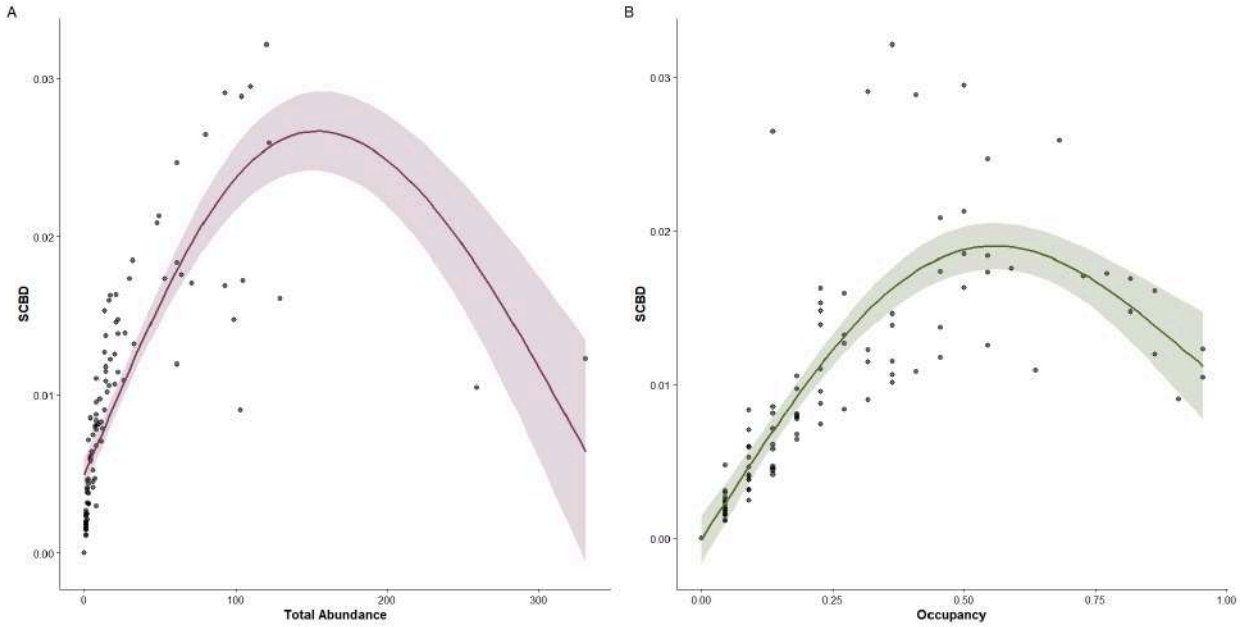

Figure 10. Relationship between Species Contribution to Beta Diversity (SCBD) (A) total abundance (B) occupancy of aquatic insect genera from Atlantic Forest streams, showing a significant non-linear pattern fitted by a beta regression model.

Discussion

Contrary to our initial predictions, stream position within the dendritic network did not emerge as a dominant driver of species richness, proportion of rare species, or ecological uniqueness of aquatic insect communities in these well-preserved Atlantic Forest streams. Most community-level metrics, including total abundance, species richness, proportion of rare species, multivariate dispersion, community composition, and local contributions to beta diversity, were remarkably similar between headwater and central streams studied. These results suggest that, at the spatial scale considered, longitudinal position alone is insufficient to generate strong differentiation in aquatic insect assemblages, particularly in highly connected and conserved landscapes.

The similar proportions of rare taxa between headwater and central streams indicate that rarity in this system is not primarily structured by hydrological isolation or network position. In

this study, rare taxa were defined based on their total abundance across all sampled streams (e.g., singletons and doubletons), suggesting that rarity reflects intrinsic properties of highly diverse tropical metacommunities, where many taxa naturally occur at low abundances and with restricted occupancies (Preston, 1948; Gaston, 1994; Magurran & Henderson, 2003). The high frequency of singletons and doubletons observed in our dataset is consistent with abundance distributions commonly reported for tropical freshwater communities (Siqueira et al., 2012; Petsch et al., 2015, 2021) and supports the idea that rarity is an inherent feature of these systems rather than a spatially clustered phenomenon. Such patterns may arise from stochastic colonization dynamics, fine-scale habitat specialization, historical contingencies that operate independently of stream position (Hubbell, 2001; Heino et al., 2021), or limited sampling intensity.

When taxonomic groups were analyzed separately, however, Ephemeroptera stood out as an exception, showing significantly lower abundance and species richness in headwater streams. This pattern likely reflects their comparatively limited dispersal ability and short adult lifespan, which may restrict recolonization and population maintenance in more isolated upstream reaches (Saito et al., 2021; Arce et al., 2021). In contrast, Plecoptera, Trichoptera, Odonata, and Chironomidae showed little differentiation between stream positions, suggesting that either dispersal-mediated processes promote homogenization across the network or that environmental conditions do not differ sufficiently between headwaters and central reaches to impose strong taxon-specific filters (Heino et al., 2015; Sarremejane et al., 2017; Kärnä et al., 2015). These contrasting responses reinforce the importance of taxonomic resolution in stream ecology, as community-level patterns can mask biologically meaningful group-specific dynamics. Future analyses at finer taxonomic scales, such as species level, may reveal additional patterns that are not detectable at coarser resolutions.

Our findings evidence varying degrees of environmental sensitivity among aquatic insect groups, with Chironomidae and Trichoptera demonstrating more defined responses to measured environmental variables, while Ephemeroptera, Odonata and Plecoptera appear to be influenced by other unmeasured factors or exhibit broader environmental tolerances. Stream type and temperature emerged as key predictors at the community level, explaining 46.6% of total variation, with dbRDA1 and dbRDA2 accounting for 19.8% and 8.2%, respectively.

The similarity in multivariate dispersion and overall community composition between headwater and central streams further challenges the expectation that headwaters function as inherently more variable or unique components of dendritic networks. Classical theory predicts higher beta diversity in headwaters due to isolation and reduced connectivity (Carrara et al., 2012; Altermatt, 2013; Tonkin et al., 2016). However, empirical studies increasingly suggest that such effects are scale-dependent and context-specific (Grönroos et al., 2013; Vilmi et al., 2017; Heino et al., 2015). In this study, the relatively short distances between paired sites and the high degree of landscape preservation may facilitate sufficient dispersal to counteract isolation effects, resulting in comparable levels of community variability across the network.

Consistent with this interpretation, only a small subset of streams exhibited significant LCBD values, and these were not disproportionately associated with headwaters. This indicates that ecological uniqueness, as expressed through taxonomic composition, is distributed across the network rather than concentrated in upstream sections. Similar patterns have been reported in preserved fluvial systems, where local uniqueness arises from idiosyncratic site conditions rather than systematic longitudinal gradients (Legendre & De Cáceres, 2013; Siqueira et al., 2018). Similarly, environmental uniqueness quantified through LCEH did not differ between headwater and central streams and was not related to LCBD values. This indicates that sites contributing disproportionately to overall environmental heterogeneity were not necessarily those contributing most to beta diversity. Such a pattern suggests a partial decoupling between abiotic

heterogeneity and community uniqueness in the system. The lack of association between LCEH and LCBD may indicate that the measured environmental variables did not fully capture the ecological gradients structuring community composition, or that biotic interactions, dispersal dynamics, and historical contingencies play a stronger role than local abiotic conditions in determining species assemblages. Similar mismatches between environmental heterogeneity and community uniqueness have been reported in stream metacommunities, where dispersal limitation, stochasticity, and mass effects may override purely environmental control (e.g., Heino et al., 2021). Moreover, the absence of differences in LCEH between stream positions suggests that headwaters and central reaches may not differ substantially in the magnitude of measured environmental heterogeneity, even if they differ in other ecological dimensions. This finding reinforces the idea that environmental variation alone does not necessarily translate into compositional singularity, particularly in dendritic systems where connectivity and spatial processes are strong drivers of community assembly.

Perhaps the most striking result was the pattern revealed by the SCBD analysis. Contrary to our expectation that rare taxa would disproportionately drive beta diversity (Legendre & De Cáceres, 2013; Socolar et al., 2016), species with intermediate to high abundance and broad occupancy contributed most strongly to regional compositional variation. The strong non-linear relationships between SCBD and both abundance and occupancy indicate that beta diversity in these streams is primarily structured by spatial variation in common species rather than by the sporadic occurrence of rare taxa. This finding aligns with growing evidence that common species can exert a dominant influence on ecological patterns, particularly in species-rich systems (Gaston, 2011; Auerbach & Poff, 2011; Mori et al., 2018).

This pattern of higher SCBD values associated with intermediate and widespread species is consistent with a mass-effect–like mechanism (Shmida & Wilson, 1985; Leibold et al., 2004), whereby widespread taxa with flexible ecological requirements respond more strongly to subtle

environmental gradients, thereby generating compositional differences among sites. In contrast, very rare species, despite their conservation relevance, may be too infrequent to meaningfully influence multivariate community structure at the metacommunity scale. These results highlight the need to reconsider the assumption that rarity necessarily equates to ecological importance in shaping beta diversity, particularly in highly diverse tropical systems (Gaston & Fuller, 2008; Winfree et al., 2015).

Several non-mutually exclusive mechanisms may explain the overall similarity between headwater and central streams observed in this study. First, the relatively small spatial extent of the network may not capture the full gradient of isolation and connectivity typically associated with dendritic systems (Levin, 1992; Heino et al., 2015). Second, the high integrity of the surrounding forest matrix likely enhances dispersal and reduces environmental contrast among streams (Fausch et al., 2002; Fullerton et al., 2010). Third, the use of genus-level resolution, while ecologically meaningful, may smooth fine-scale species-level patterns of specialization and rarity, leading to conservative estimates of differentiation (Heino & Soininen, 2007; Siqueira et al., 2012).

In conclusion, our findings indicate that, in well-preserved Atlantic Forest streams and at relatively small spatial scales, ecological differentiation between headwaters and central reaches is weak. Rarity is broadly distributed across the network, ecological uniqueness is not restricted to upstream sections, and beta diversity is primarily driven by common taxa with intermediate abundance and occupancy. These results challenge the widespread assumption that headwaters universally function as hotspots of rarity and uniqueness (Carrara et al., 2012; Altermatt, 2013) and suggest that conservation strategies should prioritize the protection of entire interconnected stream networks rather than focusing exclusively on specific positions within the dendritic system. Future studies extending across larger spatial scales, incorporating functional traits and dispersal metrics, and encompassing gradients of anthropogenic disturbance will be essential to

refine our understanding of how rarity and ecological uniqueness are structured in tropical freshwater ecosystems.

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Supplementary Material

Supplementary Table 1. Compositional summary and statistical comparisons of aquatic insect groups between headwater and central streams in the Atlantic Forest. Columns include sample size (Samples), number of taxa (Taxa), total abundance (Total abundance), and results of univariate t-tests for abundance and richness differences between stream types. Multivariate dispersion (PERMDISP) is shown using Sørensen (presence–absence) and Bray–Curtis (abundance) distances. Asterisks denote statistical significance (* $p < 0.05$; † $p < 0.10$). Significant differences in abundance and richness were found only for Ephemeroptera.

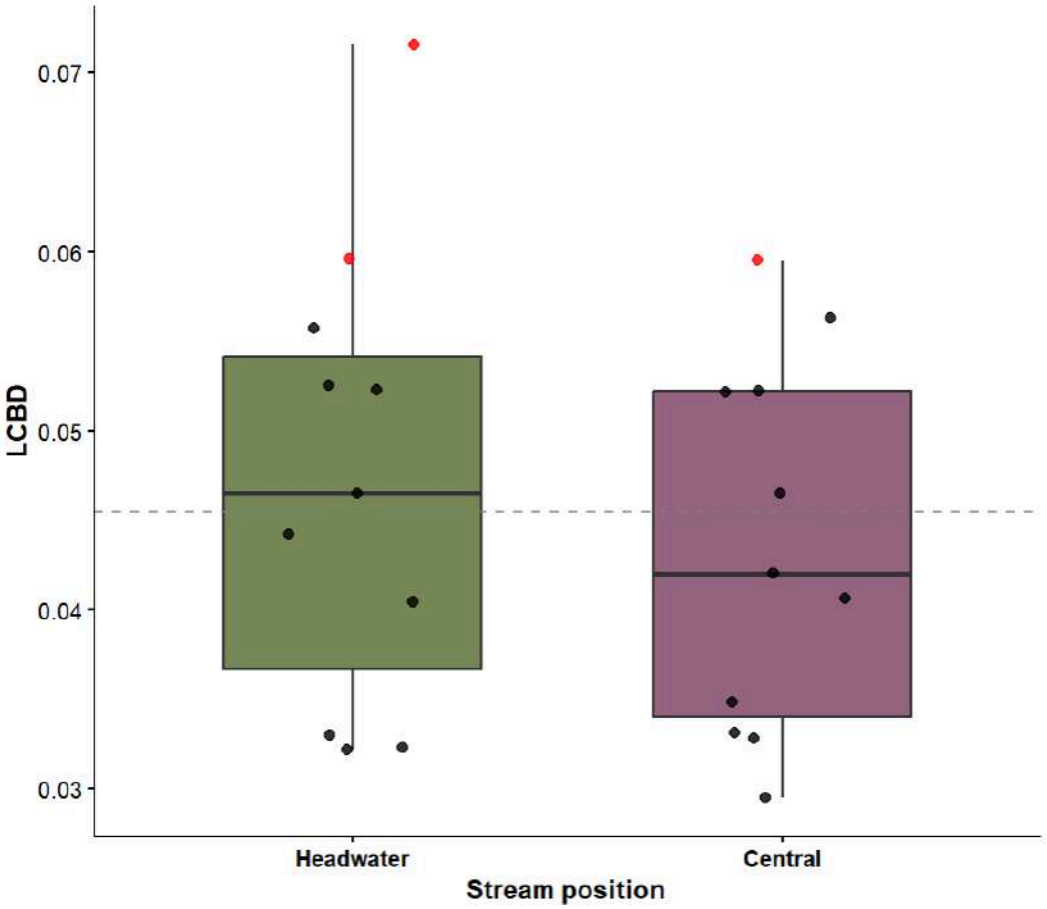
Insect group	Samples	Taxa	Total abundance	Abundance (t, p)	Richness (t, p)	PERMDISP Sørensen (F, p)	PERMDISP Bray–Curtis (F, p)
Ephemeroptera	22	24	793	-2.412, 0.026*	-2.236, 0.037*	0.759, 0.379	1.327, 0.246
Plecoptera	22	7	366	-0.361, 0.722	0.149, 0.882	1.348, 0.260	1.643, 0.210
Trichoptera	22	17	661	0.177, 0.862	0.149, 0.883	0.759, 0.379	1.327, 0.246
Odonata	22	14	199	0.686, 0.501	0.792, 0.438	0.759, 0.379	1.327, 0.246
Chironomidae	22	42	901	0.046, 0.964	792, 0.438	0.759, 0.379	1.327, 0.246

Note: * $p < 0.05$; † $p < 0.10$. Abundance and richness tested using t-tests. Multivariate dispersion assessed using PERMDISP with Sørensen and Bray–Curtis distances.

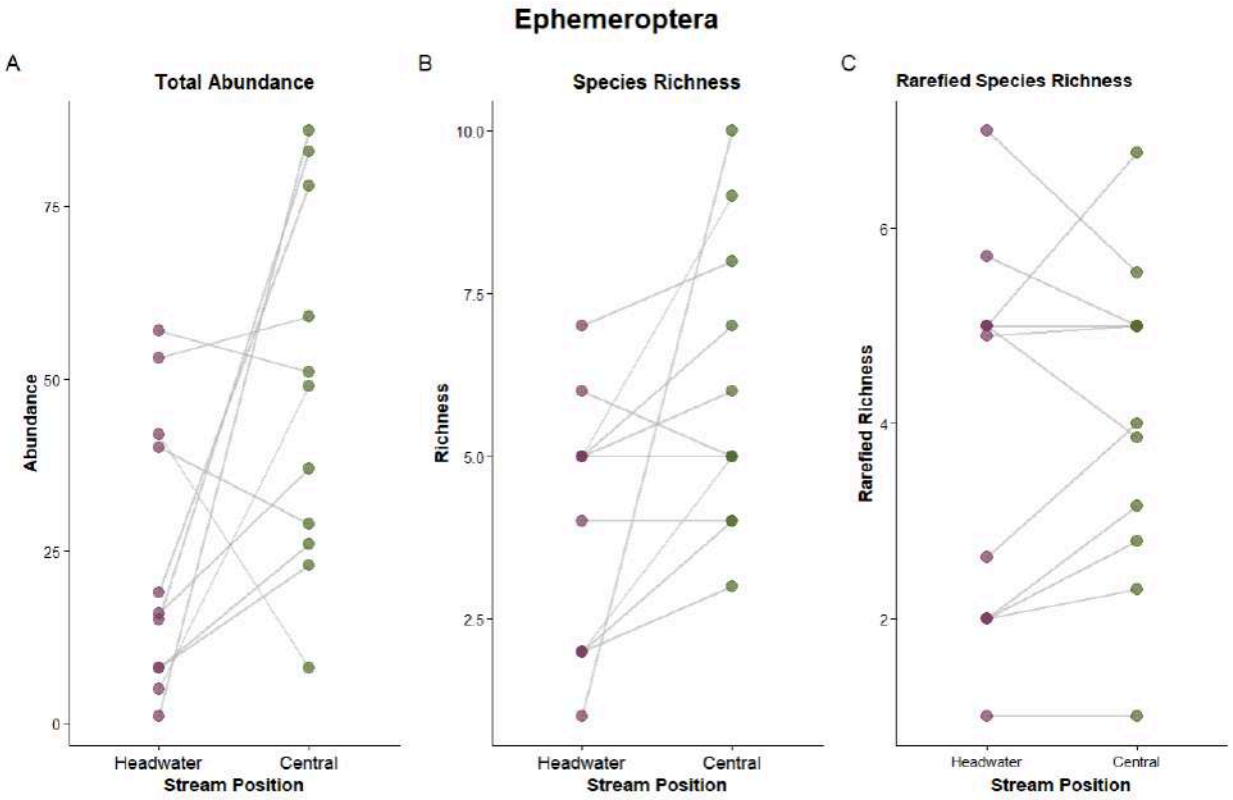
Supplementary Table 2. Detailed results of the distance-based redundancy analysis (dbRDA) for aquatic insect taxonomic groups in Atlantic Forest streams. Absolute values represent the percentage of total variance explained by each axis, while values in parentheses represent the percentage of constrained variance explained by each axis relative to the total variance explained by the model. Significance was determined at $\alpha = 0.05$. Chironomidae and Trichoptera were the only groups showing significant responses to the measured environmental variables.

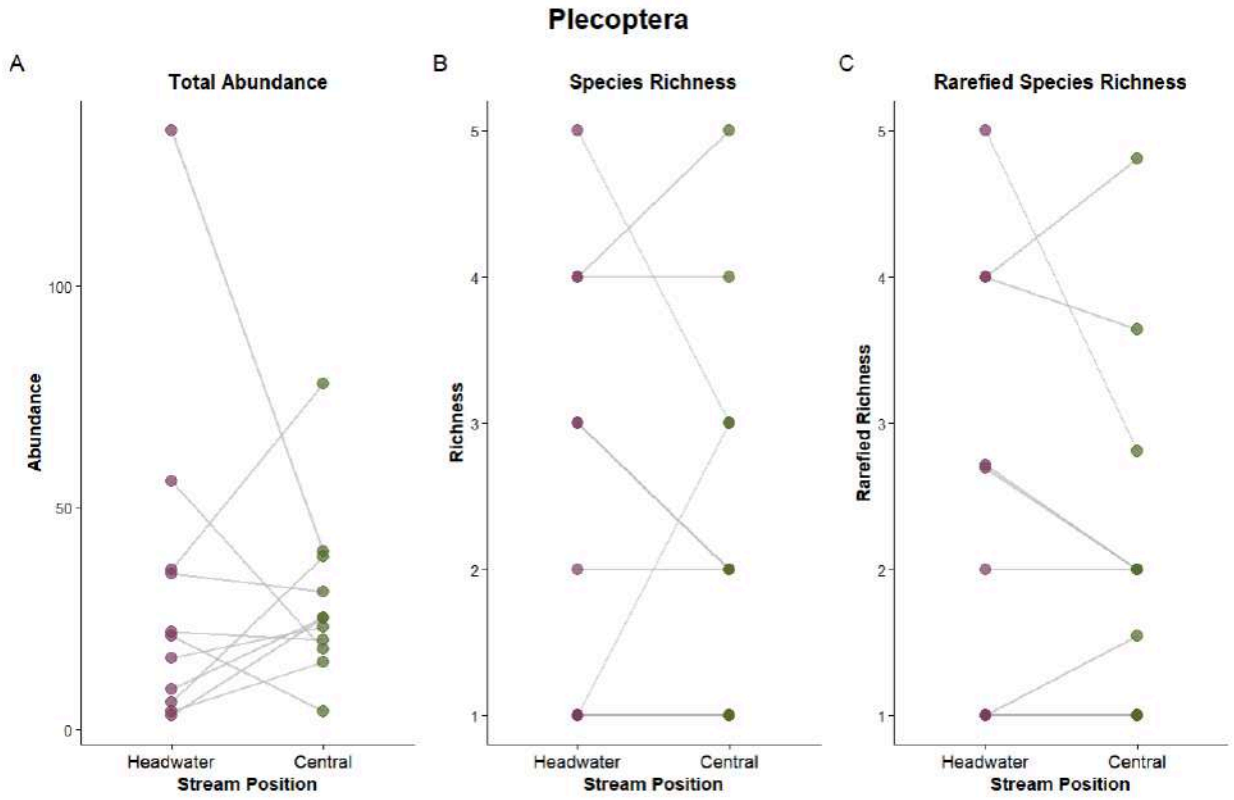
Insect Group	Number of Genera	Total Variance Explained	Model p-value	Significance Level	dbRDA1 (Absolute)	dbRDA2 (Absolute)	dbRDA1 (Total Variance)	dbRDA2 (Total Variance)
Chironomidae	**42**	**41.7%**	**0.025**	**Significant**	**5.8%**	**4%**	**13.9%**	**9.6%**
Ephemeroptera	24	38.2%	0.169	**Not significant**	7.4%	4%	19.4%	10.5%
Trichoptera	**15**	**44.5%**	**0.034**	**Significant**	**9.1%**	**5.9%**	**20.4%**	**13.3%**
Odonata	14	36.5%	0.295	**Not significant**	6%	3.6%	16.4%	9.9%
Plecoptera	5	51.9%	0.649	**Not significant**	21.3%	5.3%	41%	10.2%

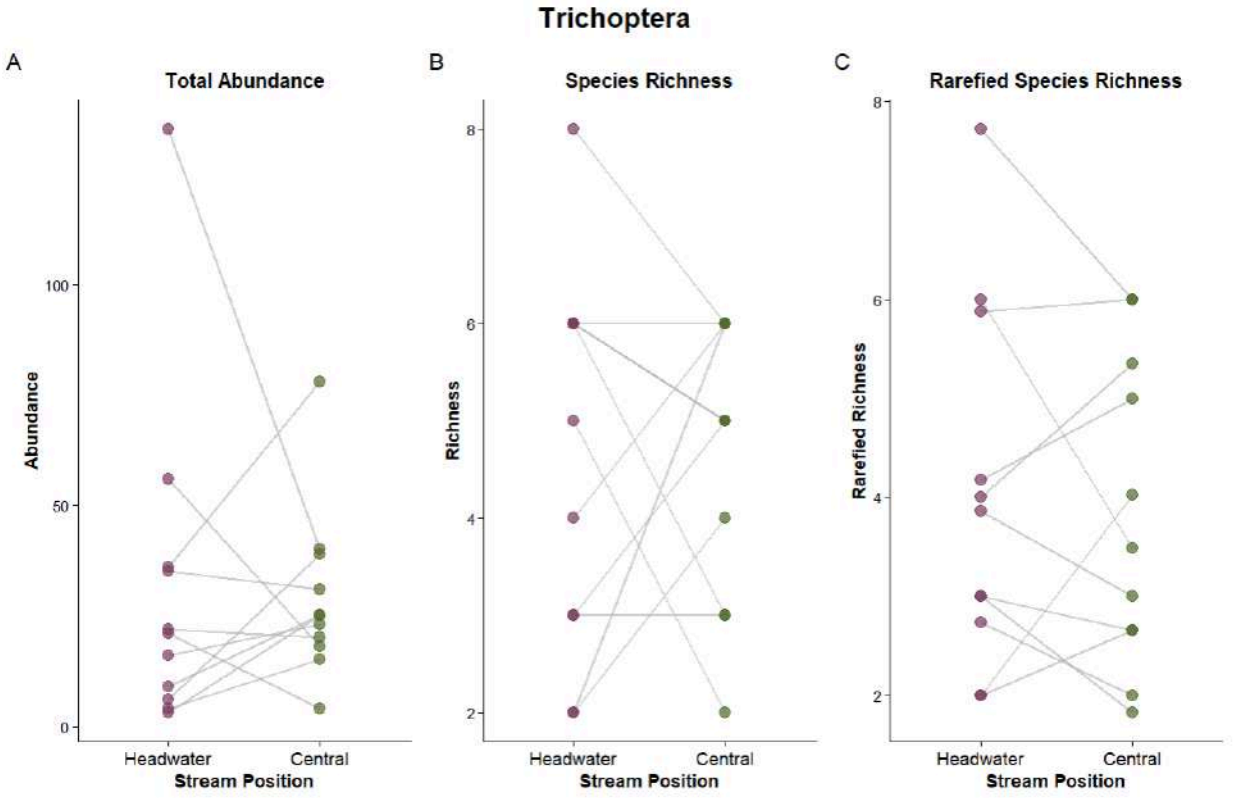
Note: Absolute values represent percentage of total variance explained by each axis. Values in parentheses represent percentage of constrained variance explained by each axis.

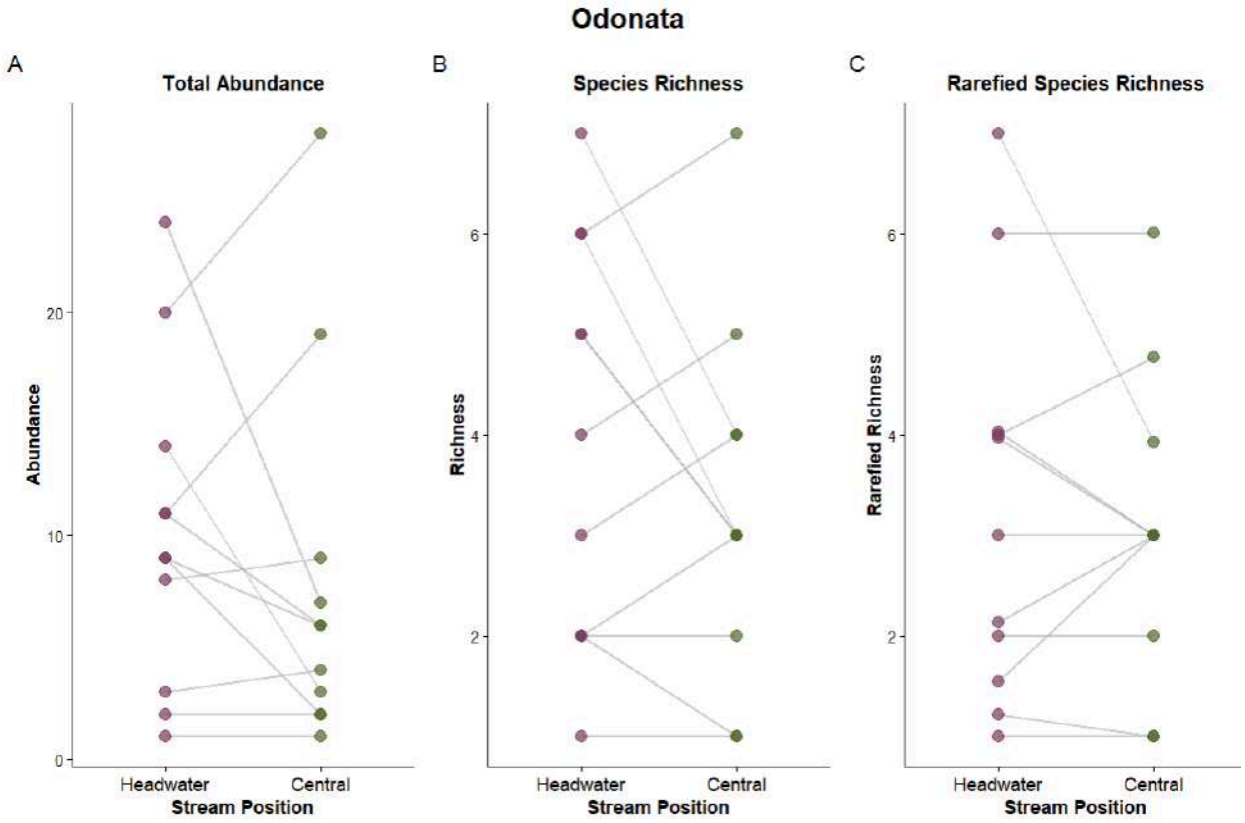


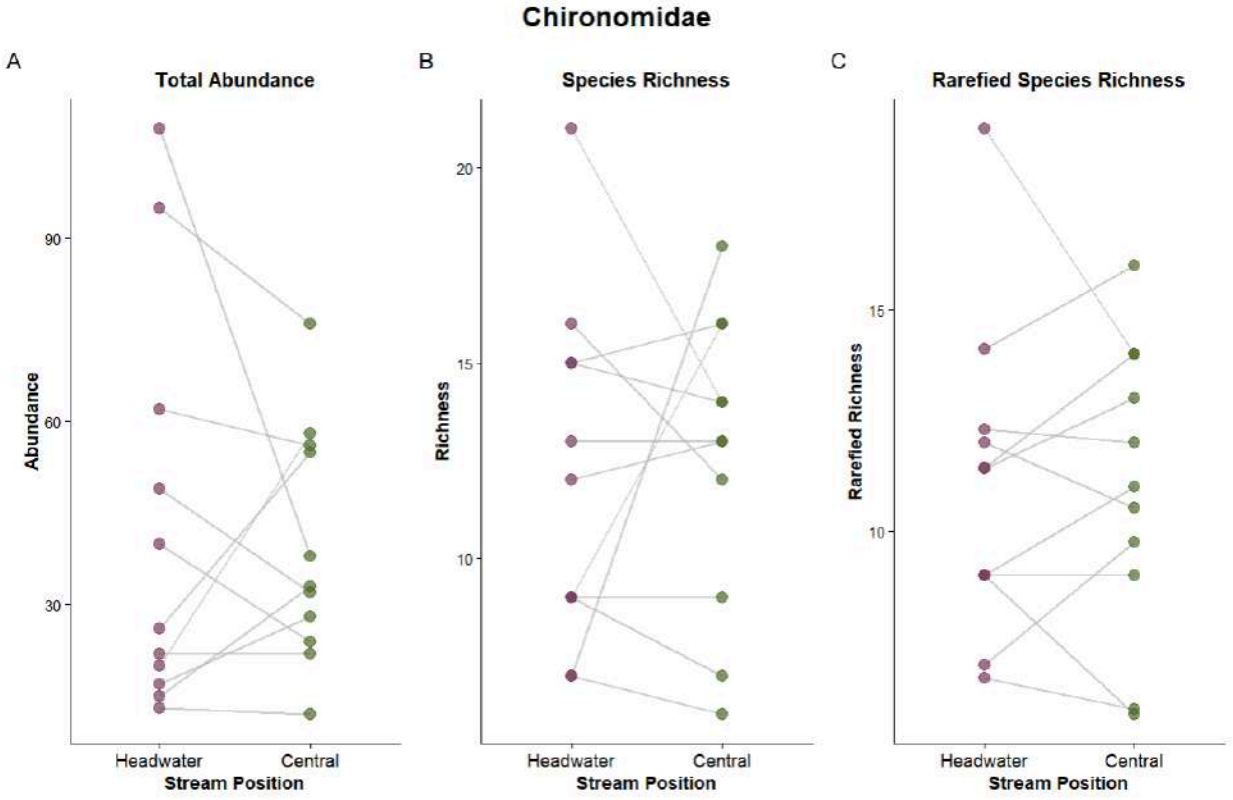
Supplementary Figure 1. Cumulative contributions of headwater and central streams to total beta diversity (Local Contribution to Beta Diversity – LCBD) along a gradient of sampling coverage. Values represent the proportion of total beta diversity explained cumulatively by streams of each type when ordered from highest to lowest LCBD value. The dashed vertical line indicates the threshold for statistical significance, above which only three streams (2 headwater and 1 central) showed significant LCBD values.


Ephemeroptera
A
Total Abundance
Abundance
75
50
25
0
Headwater
Central
Stream Position
B
Species Richness
Richness
10.0
7.5
5.0
2.5
Headwater
Central
Stream Position
C
Rarefied Species Richness
Rarefied Richness
6
4
2
Headwater
Central
Stream Position


Plecoptera
A
Total Abundance
Abundance
100
50
0
Headwater
Central
Stream Position
B
Species Richness
Richness
5
4
3
2
1
Headwater
Central
Stream Position
C
Rarefied Species Richness
Rarefied Richness
5
4
3
2
1
Headwater
Central
Stream Position


Trichoptera
A
Total Abundance
Abundance
100
50
0
Headwater
Central
Stream Position
B
Species Richness
Richness
8
6
4
2
Headwater
Central
Stream Position
C
Rarefied Species Richness
Rarefied Richness
8
6
4
2
Headwater
Central
Stream Position


Odonata
A
Total Abundance
Abundance
0
10
20
Headwater
Central
Stream Position
B
Species Richness
Richness
2
4
6
Headwater
Central
Stream Position
C
Rarefied Species Richness
Rarefied Richness
2
4
6
Headwater
Central
Stream Position


Chironomidae
A
Total Abundance
Abundance
30
60
90
Headwater
Central
Stream Position
B
Species Richness
Richness
10
15
20
Headwater
Central
Stream Position
C
Rarefied Species Richness
Rarefied Richness
10
15
Headwater
Central
Stream Position

Supplementary Figure 2. Abundance, richness and rarefied richness of Ephemeroptera, Plecoptera, Trichoptera, Odonata and Chironomidae in headwater and central streams of Atlantic Forest. Each line connects a pair of streams (headwater and its central reach).

Capítulo 3

É comum ser raro na natureza

This manuscript was prepared according to the journal *Aprendendo Ciência,* which was accepted for publication. (https://seer.assis.unesp.br/index.php/aprendendociencia/about/submissions)

Você sabia que a **raridade** desperta o nosso interesse em diferentes aspectos da vida? Pense, por exemplo, em uma coleção de figurinhas do álbum da Copa do Mundo. Algumas figurinhas aparecem várias vezes e são fáceis de encontrar nos pacotinhos. Essas figuras são comuns. No entanto, nós também temos as figurinhas que são muito difíceis de encontrar, pois há poucas unidades disponíveis, sendo consideradas raras.

Com os seres vivos, ocorre um processo parecido. Do mesmo jeito que existem figurinhas mais fáceis de serem encontradas em um pacotinho, existem espécies que apresentam vários indivíduos em uma área — o que chamamos de alta **abundância** — e são amplamente distribuídas em diversos locais (como a pomba-doméstica; *Columba livia;* Figura 1).

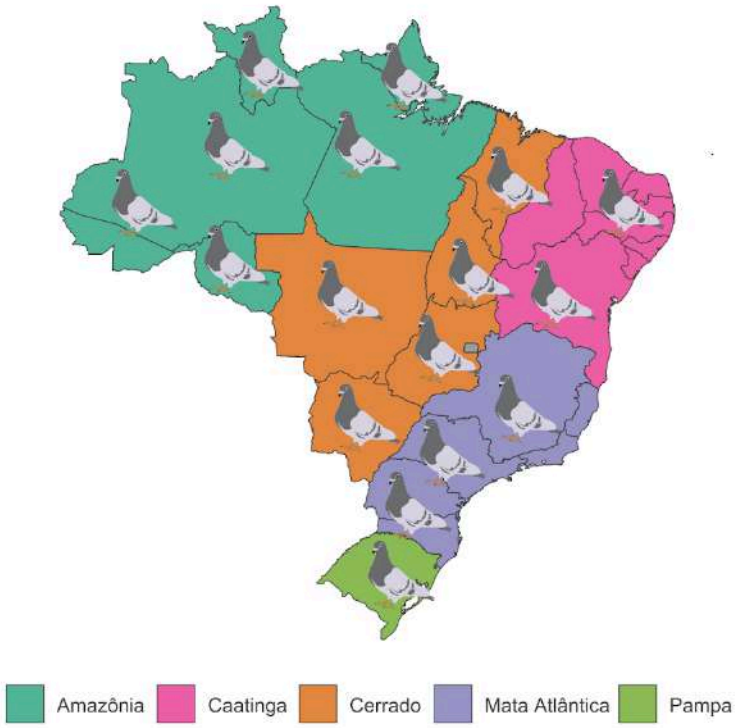


Figura 1: Mapa do Brasil destacando os biomas, com indicação da pomba-doméstica - exemplo de espécie comum com distribuição ampla

Essas são as espécies que denominamos comuns. Já as espécies raras são mais restritas e com poucos indivíduos, como a arara-azul-de-lear (*Anodorhynchus leari*), em que apenas 1500 indivíduos são encontrados no nordeste do Brasil, especificamente no estado da Bahia, em regiões de caatinga (Arara-azul-de-lear e Mico-leão-dourado Figura 2). E por mais contraintuitivo que isso possa parecer, a maior parte das espécies é rara, enquanto poucas são comuns. Por isso, é comum ser raro na natureza!

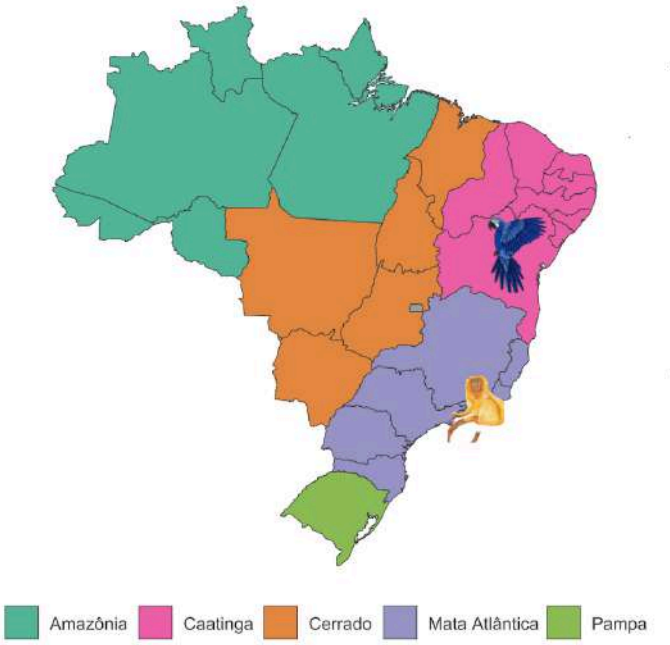


Figura 2:Mapa do Brasil destacando os biomas, com indicação da área de ocorrência de espécies raras. Arara-azul-de-lear (Bahia/Caatinga) e Mico-leão-dourado (Mata Atlântica) - exemplos de espécies raras com distribuição restrita.

Há várias formas de definir a raridade das espécies, sendo a maneira mais habitual através da sua abundância, ou seja, se há muitos ou poucos indivíduos presentes em uma área. Além da abundância, podemos avaliar a raridade através da ocupância, que se refere ao número de locais em que uma espécie ocorre. Uma espécie com baixa ocupância é aquela que aparece em poucas áreas, mesmo que possa ser abundante em alguns desses locais específicos.

Uma espécie também pode ser rara em relação à sua **distribuição geográfica**, ou seja, à extensão da área onde é encontrada. Uma espécie com distribuição geográfica restrita ocupa uma área pequena, independentemente de sua abundância em cada local. Assim, mesmo que a espécie tenha alta ocupância dentro de uma área específica, sua distribuição geográfica pode ser limitada a um único habitat ou região. É o caso do mico-leão-dourado (*Leontopithecus rosalia*), encontrado apenas em uma pequena porção da Mata Atlântica (Figura 2). Por isso, o mico-leão-dourado é **endêmico** dessa região.

Vários cientistas buscam compreender o motivo de tantas espécies serem raras. As causas para esse fenômeno da raridade são naturais, como especialização de **nichos** ou ciclos de vida sazonais e curtos. A dispersão (isto é, a capacidade de conseguir se estabelecer em ambientes que antes aquela espécie não ocupava), em conjunto com o grau de **isolamento**, também são fatores que podem contribuir para que a raridade de espécies ocorra.

Apesar das causas naturais de raridade de espécies, as atividades antrópicas como destruição de habitats, mudanças climáticas e sobre-exploração têm levado ao declínio da abundância e à limitação da ocupação, tornando as espécies ainda mais raras. As espécies raras, por sua vez, são mais vulneráveis à extinção do que as espécies comuns. Isso ocorre quando a baixa abundância e ocupação as tornam mais vulneráveis a **eventos estocásticos** e podem acabar desaparecendo.

A perda de espécies raras pode desencadear efeitos em cadeia nos ecossistemas, assim como a falta de uma figurinha rara pode impedir alguém de completar um álbum. Pense na arara-azul-de-lear ou no mico-leão-dourado que mencionamos anteriormente: se desaparecerem, todo o ecossistema onde vivem

será impactado. Por exemplo, a extinção de uma planta rara, polinizada apenas por uma abelha específica, poderia levar ao declínio desse **polinizador**, afetando consequentemente outras plantas que dependem dele. Da mesma forma, o desaparecimento de um predador raro, como a onça-pintada na Mata Atlântica, pode causar a explosão populacional de suas presas, desequilibrando toda a comunidade biológica. Cada espécie rara, mesmo com poucos indivíduos como a arara-azul-de-lear, pode desempenhar um papel único e insubstituível na manutenção dos **processos ecológicos** - são como peças essenciais no quebra-cabeça da natureza.

A **conservação** das espécies raras é um desafio. Compreender todas as formas de raridade e as suas implicações ajuda a criar maneiras eficazes para sua conservação. Pois, embora as espécies raras possam passar despercebidas, elas desempenham papéis essenciais nos ecossistemas. A perda de uma única espécie rara pode ter consequências na manutenção do equilíbrio ecológico. Assim, a conservação tanto das espécies raras quanto das comuns é fundamental para manter a biodiversidade e o funcionamento dos ecossistemas.

Glossário

Abundância - Refere-se à quantidade de indivíduos de uma determinada espécie presente em uma área específica.

Conservação - O conjunto de ações e estratégias voltadas para proteger e preservar a biodiversidade e os ecossistemas.

Distribuição geográfica - A forma como uma espécie está espalhada por diferentes locais ou regiões.

Endêmico - Refere-se a espécies ou organismos que ocorrem naturalmente em uma região ou local específico e não são encontrados em outras partes do mundo.

Eventos estocásticos - São eventos aleatórios e imprevisíveis que podem influenciar populações e ecossistemas. Exemplo: uma seca extrema, um incêndio florestal ou uma tempestade intensa podem reduzir drasticamente o número de indivíduos de uma espécie, aumentando o risco de extinção.

Isolamento - A separação de populações de uma espécie, que pode reduzir a possibilidade de interação entre indivíduos e aumentar a raridade.

Nichos - Conjunto de condições ambientais, recursos utilizados e interações que permitem que uma espécie sobreviva e se reproduza em determinado ambiente. Inclui, por exemplo, o tipo de alimento que consome, o local onde vive e seu papel na cadeia alimentar. Exemplo: o *Leontopithecus rosalia* (mico-leão-dourado) ocupa o nicho de frugívoro-insetívoro na Mata Atlântica, alimentando-se de frutos e insetos e ajudando na dispersão de sementes.

Polinizador - Animal que transporta pólen entre flores, possibilitando a reprodução das plantas.

Processos ecológicos - Conjunto de atividades naturais que mantêm o funcionamento dos ecossistemas, como decomposição, ciclagem de nutrientes e relação alimentar.

Raridade - O estado de ser raro, que pode se referir à abundância, frequência (número de locais ou de períodos de tempo em que uma espécie é observada), distribuição geográfica ou temporal de uma espécie. Exemplo: a *Anodorhynchus leari* (arara-azul-de-lear) é considerada rara por apresentar poucos indivíduos e distribuição restrita ao estado da Bahia.

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CONCLUSÃO GERAL

Minha dissertação realizou uma investigação multidimensional sobre os padrões de raridade e singularidade ecológica, abrangendo desde uma síntese global até aplicações locais e sua tradução para a sociedade. A integração dos três capítulos revela como a biodiversidade é organizada e como podemos protegê-la de forma mais eficaz em um mundo em mudança.

O Capítulo 1 mostrou, por meio de um mapeamento sistemático de dez anos de pesquisas sobre LCBD, que a ecologia da singularidade alcançou maturidade científica, mas ainda carece de maturidade geográfica. A concentração de estudos em ecossistemas de água doce em poucos países (China, Brasil e Canadá) gera uma visão distorcida da singularidade ecológica global. Além disso, a ênfase em abordagens taxonômicas, em detrimento das dimensões funcional e filogenética, limita a compreensão dos aspectos ecológicos e evolutivos da singularidade, especialmente em regiões megadiversas e pouco estudadas, como a África Central e o Sudeste Asiático.

O Capítulo 2 trouxe uma contribuição empírica importante ao testar hipóteses fundamentais da ecologia de metacomunidades em riachos tropicais da Mata Atlântica. Contrariando expectativas teóricas, as proporções de espécies raras, a variabilidade das comunidades, a contribuição para a diversidade beta e a heterogeneidade ambiental foram semelhantes entre nascentes e trechos intermediários. Esses resultados sugerem que, em sistemas bem preservados e conectados, a distinção entre esses trechos pode ser menos relevante do que se supunha. A constatação de que as espécies comuns, e não as raras, são as principais

responsáveis pela diversidade beta desafia paradigmas tradicionais de conservação e reforça a importância de estratégias que considerem toda a comunidade biológica.

O Capítulo 3 traduziu um conceito importante da dissertação para uma linguagem acessível: a raridade de espécies. A ideia de que “ser raro é comum na natureza” vai além de uma curiosidade ecológica: é um princípio essencial para a conservação. Ao divulgar os diferentes tipos de raridade (em abundância, ocorrência e distribuição geográfica) e suas vulnerabilidades, o capítulo contribui para formar uma sociedade mais informada e engajada na proteção da biodiversidade.