UNIVERSIDADE ESTADUAL PAULISTA - UNESP

Faculdade de ciências e letras - campus de Assis

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METACOMUNIDADES DE INSETOS AQUÁTICOS EM RIACHOS NEOTROPICAIS:

respostas à configuração espacial na rede dendrítica e ao desmatamento da vegetação ripária

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Dissertação apresentada à Universidade Estadual Paulista (UNESP), Faculdade de Ciências e Letras, Assis, para a obtenção do título de Mestra em Biociências (Área de Concentração: Caracterização e Aplicação da Diversidade Biológica).

Orientador(a): Profª Dra. Danielle Katharine Petsch

Co-Orientador(a): Dra. Barbbara da Silva Rocha

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IMPACTO POTENCIAL DESSA PESQUISA

Essa pesquisa amplia o conhecimento sobre como processos naturais e impactos antrópicos atuam na estrutura de metacomunidades aquáticas neotropicais, gerando subsídios para a conservação de riachos, proteção da vegetação ripária, além de traduzir o conhecimento científico para linguagem acessível, ampliando a comunicação científica.

POTENTIAL IMPACT OF THIS RESEARCH

This research expands knowledge on how natural processes and anthropogenic impacts act on the structure of Neotropical aquatic metacommunities, providing support for stream conservation, riparian vegetation protection, and translating scientific knowledge into accessible language, thereby expanding science communication.

UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Assis

ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DE LÍVIA SEREZANI MUNHOZ, DISCENTE DO PROGRAMA DE PÓS-GRADUAÇÃO EM BIOCIÊNCIAS, DA FACULDADE DE CIÊNCIAS E LETRAS - CÂMPUS DE ASSIS.

Aos 11 de junho de 2026, às 14h, no(a) Sala de Defesas da Pós-graduação e sala virtual: meet.google.com/she-awuv-ivq, realizou-se a defesa de DISSERTAÇÃO DE MESTRADO de LÍVIA SEREZANI MUNHOZ, intitulada "METACOMUNIDADES DE INSETOS AQUÁTICOS EM RIACHOS NEOTROPICAIS: respostas à configuração espacial na rede dendrítica e ao desmatamento da vegetação ripária". A Comissão Examinadora foi constituída pelos seguintes membros: Profa. Dra. DANIELLE KATHARINE PETSCH (Orientador(a) - Participação Presencial) do(a) UNESP / FCL - Assis, Prof. Dr. PITÁGORAS DA CONCEIÇÃO BISPO (Participação Presencial) do(a) UNESP / Câmpus de Assis - FCLAs, Profa. Dra. FRANCIELI DE FÁTIMA BOMFIM (Participação Virtual) do(a) Universidade Federal do Pará (UFPA), 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: APROVADA. Nada mais havendo, foi lavrada a presente ata, que após lida e aprovada, foi assinada pelo(a) Presidente(a) da Comissão Examinadora.

Profa. Dra. DANIELLE KATHARINE PETSCH

Dedico este trabalho aos meus pais,
Toni e Deborah, que sempre fizeram o possível e o impossível para me proporcionar a melhor educação que podiam. Esta pesquisa é a materialização de 24 anos de esforço, dedicação e amor investidos por eles em minha criação.

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"Para que todos vejam, e saibam, e considerem, e juntamente entendam que a mão do Senhor fez isto" - Isaías 41:20

RESUMO

Os ecossistemas lóticos fornecem uma gama de serviços ecossistêmicos essenciais. Entretanto, são um dos ambientes que mais sofrem com impactos antrópicos, como o desmatamento. Os insetos aquáticos são organismos cruciais na manutenção de dinâmicas ecológicas em ecossistemas lóticos. Compreender padrões naturais na estrutura de comunidades desses organismos, bem como respostas a impactos antrópicos como o desmatamento, pode fornecer importantes subsídios para planos de manutenção e conservação de ecossistemas aquáticos. No primeiro capítulo, demonstrei que a posição espacial dos riachos, dentro da rede dendrítica, é um fator importante para a estruturação funcional de comunidades de insetos aquáticos, com riachos de cabeceira apresentando comunidades mais únicas em termos de características funcionais e mais fortemente associadas à filtragem ambiental. Em contraste, riachos centrais apresentaram menor singularidade funcional e relações mais fracas entre a variabilidade ambiental e funcional, sugerindo diferenças na importância dos processos ecológicos ao longo da rede dendrítica. No segundo capítulo, demonstrei que o desmatamento da vegetação ripária nativa implica em uma perda ordenada de gêneros e características funcionais de insetos aquáticos, com locais mais degradados abrigando comunidades empobrecidas que formam subconjuntos aninhados daquelas em locais mais preservados. No terceiro capítulo, traduzi o conhecimento científico sobre insetos aquáticos e habilidades de dispersão, destacando formas de distribuição destes organismos na rede fluvial. Nossos resultados ajudam a ampliar a compreensão da estrutura de metacomunidades de insetos aquáticos, contribuindo para previsões ecológicas e na definição de locais com prioridade de conservação.

Palavras-chave: Rede dendrítica; Desmatamento; Diversidade funcional; Aninhamento.

ABSTRACT

Lotic ecosystems provide a range of essential ecosystem services. However, they are among the environments most affected by anthropogenic impacts, such as deforestation. Aquatic insects are crucial organisms in maintaining ecological dynamics in lotic ecosystems. Understanding natural patterns in the community structure of these organisms, as well as their responses to anthropogenic impacts such as deforestation, can provide important support for the maintenance and conservation of aquatic ecosystems. In the first chapter, I demonstrated that the spatial position of streams within the dendritic network is an important factor in the functional structuring of aquatic insect communities, with headwater streams presenting more unique communities in terms of functional traits and being more strongly associated with environmental filtering. In contrast, central streams showed lower functional uniqueness and weaker relationships between environmental and functional variability, suggesting differences in the importance of ecological processes along the dendritic network. In the second chapter, I demonstrated that deforestation of native riparian vegetation leads to an ordered loss of genera and functional traits of aquatic insects, with more degraded sites harboring impoverished communities that form nested subsets of those found in more preserved sites. In the third chapter, I translated scientific knowledge on aquatic insects and dispersal abilities, highlighting the distribution patterns of these organisms within the river network. Our results help broaden the understanding of the metacommunity structure of aquatic insects, contributing to ecological predictions and the identification of priority areas for conservation.

Keywords: Dendritic network; Deforestation; Functional diversity; Nestedness.

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dbRDA - *Distance-based Redundancy Analysis* (Análise de Redundância baseada em distância)

GLM - *Generalized Linear Model* (Modelo Linear Generalizado)

LCBD - *Local Contribution to Beta Diversity* (Contribuição Local para a diversidade beta)

LCBD-f - *Local Contribution to Beta Diversity- functional* (Contribuição Local para a diversidade beta funcional)

LCEH - *Local Contribution to Environmental Heterogeneity* (Contribuição Local para Heterogeneidade Ambiental)

NODF - *Nestedness metric based on Overlap and Decreasing Fill* (Métrica de aninhamento baseada em sobreposição e preenchimento decrescente)

PCA - *Principal Component Analysis* (Análise do Componente Principal)

PCoA - *Principal Coordinates Analysis* (Análise de Coodenadas Principais)

RDA - *Redundancy Analysis* (Análise de Redundância)

SUMÁRIO

INTRODUÇÃO GERAL

Os ecossistemas aquáticos continentais apresentam uma elevada biodiversidade e fornecem serviços ecossistêmicos fundamentais, como abastecimento de água e regulação do ciclo de chuvas (Petsch et al. 2022; Leal et al. 2023; Lynch et al. 2023). Entretanto, são um dos ambientes que mais sofrem com os impactos antrópicos, destacando-se o desmatamento da vegetação ripária para uso humano do solo (Sala et al. 2000; Dudgeon et al. 2006; Reid et al. 2018; Koehnken et al. 2020; Mello et al. 2020; Rovani et al. 2020; Petsch et al. 2021a; Tonello et al. 2021; Petsch et al. 2022; Wiebe & Wilcove 2025). Na Mata Atlântica, os ecossistemas lóticos são particularmente vulneráveis a esses impactos uma vez que o bioma apresenta histórico intenso de degradação ambiental (e.g. estima-se que 70% de sua cobertura florestal nativa tenha sido convertida para diferentes formas de uso do solo), comprometendo a qualidade de suas águas e o funcionamento desses ecossistemas (MMA 2010; Giri & Qiu 2016; SOS Mata Atlântica 2018; Rezende et al. 2018; Gebremicael et al. 2019; Santana et al. 2020).

Em condições naturais, as variações ambientais nos ecossistemas lóticos podem ocorrer ao longo da posição espacial na bacia hidrográfica (Vannote et al. 1980; Benda et al. 2004; Meyer et al. 2007; Clarke et al. 2008), a qual apresenta uma estrutura hierárquica, onde segmentos menores (e.g. riachos de cabeceiras) desaguam em segmentos maiores (e.g. trechos centrais), formando organizações complexas chamadas de redes dendríticas (Rice et al. 2001; Gomi et al. 2002; Fagan 2002; Campbell-Grant et al. 2007; Schmera et al. 2018). À medida que o tamanho dos cursos d'água aumentam, os cursos de maior ordem passam a ter naturalmente maior largura e profundidade, além de maior fluxo e temperatura (Vannote et al. 1980; Benda et al. 2004).

No entanto, a intensificação de desmatamento da vegetação ripária pode alterar drasticamente as características físico-químicas naturais dos ecossistemas aquáticos, como o aumento da temperatura e da deposição de sedimentos finos, e a redução do oxigênio dissolvido e da entrada de matéria orgânica nos riachos (Allan 2004; Leal et al. 2016; Castro et al. 2018; Petsch et al. 2021b). Além disso, essas mudanças reduzem a heterogeneidade ambiental, promovendo a homogeneização dos habitats e afetando a integridade e biodiversidade dos ecossistemas de água doce (Allan 2004; Rovani et al. 2020; Mello et al. 2020; Tonello et al. 2021).

Mudanças nas condições ambientais dos riachos, sejam naturais ou devido às ações antrópicas, podem atuar como um filtro ambiental, selecionando espécies de acordo com suas características funcionais, que determinam sua sobrevivência no ambiente (Statzner et al. 2004; Heino et al. 2015; Valente-Neto et al. 2015; Schmera et al. 2018; Wong et al. 2019; Faria et al. 2021; Li et al. 2021; Cantera et al. 2023). Por exemplo, táxons fragmentadores geralmente estão relacionados com maiores quantidades de matéria orgânica grosseira depositada nos riachos (Vannote et al. 1980). Essa característica tende a ser alterada naturalmente com o aumento da largura dos riachos, mas também está sujeita a ser alterada com a expansão do desmatamento da vegetação ripária. Neste caso, enquanto gradientes ambientais naturais ao longo da paisagem podem promover a substituição de espécies (Nicacio et. al. 2020), o desmatamento tende à reduzir a biodiversidade, comprometendo o funcionamento do ecossistema (Li et al. 2018; Mahmoud & Gan 2018; Fernandes et al. 2019; Bernhardt et al. 2022).

Neste contexto, abordagens que incluem a diversidade funcional (i.e., que consideram as características fisiológicas, morfológicas e ecológicas dos organismos) podem contribuir para uma melhor compreensão de como as comunidades respondem às mudanças do ambiente (Mokany et al. 2008; Cianciaruso et al. 2009), bem como de que forma essas respostas podem impactar os serviços ecossistêmicos essenciais. Em escala local, os filtros ambientais selecionam espécies com características semelhantes, levando a uma redundância funcional (Dee et al. 2016; Nash et al. 2016; Sanders et al. 2018). A redundância funcional, por sua vez, pode conferir certa estabilidade ao ecossistema por garantir vários táxons exercendo uma mesma função ecológica. Desta forma, a perda da diversidade funcional pode comprometer o funcionamento dos ecossistemas de forma mais intensa que a redução da diversidade taxonômica (Flynn et al. 2009). Além disso, métricas como singularidade funcional (i.e., locais com uma combinação única de atributos) e aninhamento funcional (i.e., quando comunidades funcionalmente mais pobres representam subconjuntos de comunidades mais ricas) permitem, respectivamente, identificar locais com composições funcionais únicas (Heino et al. 2022) e avaliar se ambientes degradados abrigam comunidades funcionais empobrecidas que formam subconjuntos de locais mais preservados (Melo et al. 2014). Dessa forma, essas abordagens funcionais podem contribuir para a definição de áreas prioritárias para conservação e manejo da biodiversidade.

Insetos aquáticos apresentam alta diversidade funcional, desempenhando diversos papeis fundamentais nas funções ecossistêmicas de ambientes aquáticos, principalmente em relação à ciclagem de nutrientes e composição da cadeia trófica (Esteves et al. 2011; Pilière et

al. 2016; Milesi et al. 2019). Esse grupo possui diversas estratégias alimentares, além de adaptações morfológicas para se movimentar e se fixar ao substrato (Brown & Swan 2010; Heino et al. 2015). Possuem também habilidades de dispersão distintas, incluindo dispersão ativa pelo voo dos adultos e passiva pela água e vento, caracterizando também seu potencial de distribuição diferenciada ao longo dos cursos d'água (Heino et al. 2013). Além disso, estudos anteriores identificaram sinais consistentes de resposta da estrutura de metacomunidades de insetos aquáticos às variações do ambiente, sejam estas naturais que selecionam espécies especializadas, ou provocadas pela ação humana que causam perda da biodiversidade (e.g. Lamouroux et al. 2004; Ippolito et al. 2012; Milesi et al. 2016; Ferreira et al. 2017; Gomes et al. 2018; Malacarne et al. 2023), tornando o grupo ideal para investigações ecológicas.

O principal objetivo da minha dissertação é entender como a estrutura das comunidades de insetos aquáticos em riachos da Mata Atlântica respondem à variação das características ambientais, sejam elas naturais (i.e. através da organização dendrítica) ou artificiais provocadas pelas atividades antrópicas (e.g. desmatamento da vegetação ripária). Para isso, dividi a minha dissertação em três capítulos. No capítulo 1, investiguei se a posição espacial do riacho determina locais com comunidades de insetos aquáticos mais únicas em termos de características funcionais e se a força da resposta aos fatores ambientais eram distintos em diferentes posições da rede. No capítulo 2, investiguei se as variações abióticas decorrentes da perda da vegetação ripária nativa por meio do desmatamento causam perdas ordenadas de táxons e características funcionais de insetos aquáticos, de modo a formar subconjuntos de comunidades empobrecidas, configurando em um padrão de aninhamento. Por fim, no capítulo 3, desenvolvi um artigo de divulgação científica descrevendo, em linguagem mais simples, os tipos de dispersão dos insetos aquáticos, onde descrevo a importância da organização espacial dendrítica e os organismos que se distribuem nela.

Referências

Allan, J. D. (2004). Landscapes and Riverscapes: the Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 257–284. https://doi.org/10.1146/annurev.ecolsys.35.120202.110122

Altermatt, F. (2013). Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology*, *47*(3), 365–377. https://doi.org/10.1007/s10452-013-9450-3

Barlow, J., França, F., Gardner, T. A., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J., & Graham, N. A. J. (2018). The future of hyperdiverse tropical ecosystems. *Nature*, *559*(7715), 517–526. https://doi.org/10.1038/s41586-018-0301-1

Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., & Pollock, M. (2004). The Network Dynamics Hypothesis: How Channel Networks Structure Riverine Habitats. *BioScience*, *54*(5), 413. https://doi.org/10.1641/0006-3568(2004)054[0413:tndhhc]2.0.co;2

Bernhardt, E. S., Savoy, P., Vlah, M. J., Appling, A. P., Koenig, L. E., Hall, R. O., Arroita, M., Blaszczak, J. R., Carter, A. M., Cohen, M., Harvey, J. W., Heffernan, J. B., Helton, A. M., Hosen, J. D., Kirk, L., McDowell, W. H., Stanley, E. H., Yackulic, C. B., & Grimm, N. B. (2022). Light and flow regimes regulate the metabolism of rivers. *Proceedings of the National Academy of Sciences*, *119*(8). https://doi.org/10.1073/pnas.2121976119

Brown, B. L., & Swan, C. M. (2010). Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology*, *79*(3), 571–580. https://doi.org/10.1111/j.1365-2656.2010.01668.x

Campbell Grant, E. H., Lowe, W. H., & Fagan, W. F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters*, *10*(2), 165–175. https://doi.org/10.1111/j.1461-0248.2006.01007.x

Cantera, I., Jézéquel, C., Dejean, T., Murienne, J., Vigouroux, R., Valentini, A., & Brosse, S. (2023). Deforestation strengthens environmental filtering and competitive exclusion in Neotropical streams and rivers. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2006). https://doi.org/10.1098/rspb.2023.1130

Castro, D., Dolédec, S., & Callisto, M. (2018). Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. *Ecological Indicators*, *84*, 573–582. https://doi.org/10.1016/j.ecolind.2017.09.030

Cianciaruso, M. V., Silva, I. A., & Batalha, M. A. (2009). Diversidades filogenética e funcional: novas abordagens para a Ecologia de comunidades. *Biota Neotropica*, *9*(3), 93–103. https://doi.org/10.1590/s1676-06032009000300008

Clarke, A., Mac Nally, R., Bond, N., & Lake, P. S. (2008). Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, *53*(9), 1707–1721. https://doi.org/10.1111/j.1365-2427.2008.02041.x

Dee, L. E., Miller, S. J., Peavey, L. E., Bradley, D., Gentry, R. R., Startz, R., Gaines, S. D., & Lester, S. E. (2016). Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1836), 20161435. https://doi.org/10.1098/rspb.2016.1435

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, *81*(02), 163–182.

Esteves , F. A., Leal , J. J. F., & Callisto, M. (2011). Comunidade Bentônica. In *Fundamentos de Limnologia* (pp. 581–603.). Editora Interciência.

Fagan, W. F. (2002). Connectivity, Fragmentation, and Extinction Risk in Dendritic Metapopulations. *Ecology*, *83*(12), 3243. https://doi.org/10.2307/3072074

Faria, A. P., Paiva, C. K., Calvão, L. B., Cruz, G. M., & Juen, L. (2021). Response of aquatic insects to an environmental gradient in Amazonian streams. *Environmental Monitoring and Assessment*, *193*(11). https://doi.org/10.1007/s10661-021-09553-6

Fernandes, A. C. P., Sanches Fernandes, L. F., Moura, J. P., Cortes, R. M. V., & Pacheco, F. A. L. (2019). A structural equation model to predict macroinvertebrate-based ecological status in catchments influenced by anthropogenic pressures. *Science of the Total Environment*, *681*, 242–257. https://doi.org/10.1016/j.scitotenv.2019.05.117

Ferreira, W. R., Hepp, L. U., Ligeiro, R., Macedo, D. R., Hughes, R. M., Kaufmann, P. R., & Callisto, M. (2017). Partitioning taxonomic diversity of aquatic insect assemblages and functional feeding groups in neotropical savanna headwater streams. *Ecological Indicators*, *72*, 365–373. https://doi.org/10.1016/j.ecolind.2016.08.042

Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., Simpson, N., Mayfield, M. M., & DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, *12*(1), 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Gebremicael, T. G., Mohamed, Y. A., & Van der Zaag, P. (2019). Attributing the hydrological impact of different land use types and their long-term dynamics through combining parsimonious hydrological modelling, alteration analysis and PLSR analysis. *Science of the Total Environment*, *660*, 1155–1167. https://doi.org/10.1016/j.scitotenv.2019.01.085

Giri, S., & Qiu, Z. (2016). Understanding the relationship of land uses and water quality in Twenty First Century: A review. *Journal of Environmental Management*, *173*, 41–48. https://doi.org/10.1016/j.jenvman.2016.02.029

Gomes, W. I. A., Jovem-Azevêdo, D. da S., Paiva, F. F., Milesi, S. V., & Molozzi, J. (2018). Functional attributes of Chironomidae for detecting anthropogenic impacts on reservoirs: A biomonitoring approach. *Ecological Indicators*, *93*, 404–410. https://doi.org/10.1016/j.ecolind.2018.05.006

Gomi, T., Sidle, R. C., & Richardson, J. S. (2002). Understanding Processes and Downstream Linkages of Headwater Systems. *BioScience*, *52*(10), 905. https://doi.org/10.1641/0006-3568(2002)052[0905:upadlo]2.0.co;2

Heino, J. (2013). Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? *Oecologia*, *171*(4), 971–980. https://doi.org/10.1007/s00442-012-2451-4

Heino, J., García Girón, J., Hämäläinen, H., Hellsten, S., Ilmonen, J., Karjalainen, J., Mäkinen, T., Nyholm, K., Ropponen, J., Takolander, A., & Tolonen, K. T. (2022). Assessing the conservation priority of freshwater lake sites based on taxonomic, functional and environmental uniqueness. *Diversity and Distributions*, *28*(9), 1966–1978. https://doi.org/10.1111/ddi.13598

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2014). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology*, *60*(5), 845–869. https://doi.org/10.1111/fwb.12533

Ippolito, A., Todeschini, R., & Vighi, M. (2011). Sensitivity assessment of freshwater macroinvertebrates to pesticides using biological traits. *Ecotoxicology*, *21*(2), 336–352. https://doi.org/10.1007/s10646-011-0795-x

Koehnken, L., Rintoul, M. S., Goichot, M., Tickner, D., Loftus, A., & Acreman, M. C. (2020). Impacts of riverine sand mining on freshwater ecosystems: A review of the scientific evidence and guidance for future research. *River Research and Applications*, *36*(3), 362–370. https://doi.org/10.1002/rra.3586

Lamouroux, N., Dolédec, S., & Gayraud, S. (2004). Biological traits of stream macroinvertebrate communities: effects of microhabitat, reach, and basin filters. *Journal of the North American Benthological Society*, *23*(3), 449–466. https://doi.org/10.1899/0887-3593(2004)023%3C0449:btosmc%3E2.0.co;2

Leal, C. G., Pompeu, P. S., Gardner, T. A., Leitão, R. P., Hughes, R. M., Kaufmann, P. R., Zuanon, J., de Paula, F. R., Ferraz, S. F. B., Thomson, J. R., Mac Nally, R., Ferreira, J., & Barlow, J. (2016). Multi-scale assessment of human-induced changes to Amazonian instream habitats. *Landscape Ecology*, *31*(8), 1725–1745. https://doi.org/10.1007/s10980-016-0358-x

Leal, J. S., González, A. L., Soares, B. E., Casa Nova, C., Marino, N. A. C., & Farjalla, V. F. (2023). Global and local drivers of the relative importance of allochthonous and autochthonous energy sources to freshwater food webs. *Ecography*, *2023*(4). https://doi.org/10.1111/ecog.06612

Li, K., Zhang, Z., Yang, H., Bian, H., Jiang, H., Sheng, L., & He, C. (2018). Effects of instream restoration measures on the physical habitats and benthic macroinvertebrates in an agricultural headwater stream. *Ecological Engineering*, *122*, 252–262. https://doi.org/10.1016/j.ecoleng.2018.08.007

Li, Z., Chen, X., Jiang, X., Tonkin, J. D., Xie, Z., & Heino, J. (2020). Distance decay of benthic macroinvertebrate communities in a mountain river network: Do dispersal routes and

dispersal ability matter? *The Science of the Total Environment*, *758*, 143630–143630. https://doi.org/10.1016/j.scitotenv.2020.143630

Lynch, A. J., Cooke, S. J., Arthington, A. H., Baigun, C., Bossenbroek, L., Dickens, C., Harrison, I., Kimirei, I., Langhans, S. D., Murchie, K. J., Olden, J. D., Ormerod, S. J., Owuor, M., Raghavan, R., Samways, M. J., Schinegger, R., Sharma, S., Tachamo‐Shah, R., Tickner, D., & Tweddle, D. (2023). People need freshwater biodiversity. *WIREs Water*, *10*(3). https://doi.org/10.1002/wat2.1633

Mahmoud, S. H., & Gan, T. Y. (2018). Impact of anthropogenic climate change and human activities on environment and ecosystem services in arid regions. *Science of the Total Environment*, *633*, 1329–1344. https://doi.org/10.1016/j.scitotenv.2018.03.290

Malacarne, T. J., Machado, N. R., & Moretto, Y. (2023). Influence of land use on the structure and functional diversity of aquatic insects in neotropical streams. *Hydrobiologia*, *851*(2), 265–280. https://doi.org/10.1007/s10750-023-05207-5

Mello, K. de, Taniwaki, R. H., Paula, F. R. de, Valente, R. A., Randhir, T. O., Macedo, D. R., Leal, C. G., Rodrigues, C. B., & Hughes, R. M. (2020). Multiscale land use impacts on water quality: Assessment, planning, and future perspectives in Brazil. *Journal of Environmental Management*, *270*, 110879. https://doi.org/10.1016/j.jenvman.2020.110879

Melo, A. S., Cianciaruso, M. V., & Almeida‐Neto, M. (2014). treeNODF: nestedness to phylogenetic, functional and other tree‐based diversity metrics. *Methods in Ecology and Evolution*, *5*(6), 563–572. https://doi.org/10.1111/2041-210x.12185

Meyer, J. L., Strayer, D. L., Wallace, J. B., Eggert, S. L., Helfman, G. S., & Leonard, N. E. (2007). The Contribution of Headwater Streams to Biodiversity in River Networks1. *JAWRA Journal of the American Water Resources Association*, *43*(1), 86–103. https://doi.org/10.1111/j.1752-1688.2007.00008.x

Milesi, S. V., Dolédec, S., & Melo, A. S. (2016). Substrate heterogeneity influences the trait composition of stream insect communities: an experimental in situ study. *Freshwater Science*, *35*(4), 1321–1329. https://doi.org/10.1086/688706

Milesi, S. V., Melo, A. S., & Dolédec, S. (2019). Assessing community functional attributes during substrate colonization: a field experiment using stream insects. *Hydrobiologia*, *838*(1), 183–192. https://doi.org/10.1007/s10750-019-03988-2

MMA- Ministério do Meio Ambiente. (2010). *Relatório parametrizado de Unidade de Conservação.* Ministério Do Meio Ambiente E Mudança Do Clima. http://www.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs/consultoria-gerar-relatorio-de-uc.

Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, *96*(5), 884–893. https://doi.org/10.1111/j.1365-2745.2008.01395.x

Nash, K. L., Graham, N. A. J., Jennings, S., Wilson, S. K., & Bellwood, D. R. (2015). Herbivore cross-scale redundancy supports response diversity and promotes coral reef

resilience. *Journal of Applied Ecology*, *53*(3), 646–655. https://doi.org/10.1111/1365-2664.12430

Nicacio, G., Cunha, E. J., Hamada, N., & Juen, L. (2020). How Habitat Filtering Can Affect Taxonomic and Functional Composition of Aquatic Insect Communities in Small Amazonian Streams. *Neotropical Entomology*, *49*(5), 652–661. https://doi.org/10.1007/s13744-020-00780-z

Petsch, D. K., Blowes, S. A., Melo, A. S., & Chase, J. M. (2021a). A synthesis of land use impacts on stream biodiversity across metrics and scales. *Ecology*, *102*(11). https://doi.org/10.1002/ecy.3498

Petsch, D. K., Cionek, V. de M., Thomaz, S. M., & dos Santos, N. C. L. (2022). Ecosystem services provided by river-floodplain ecosystems. *Hydrobiologia*, *850*, 1–22. https://doi.org/10.1007/s10750-022-04916-7

Petsch, D. K., Saito, V. S., Landeiro, V. L., Silva, T., Bini, L. M., Heino, J., Soininen, J., Tolonen, K., Jyrkänkallio‐Mikkola, J., Pajunen, V., Siqueira, T., & Melo, A. S. (2021). Beta diversity of stream insects differs between boreal and subtropical regions, but land use does not generally cause biotic homogenization. *Freshwater Science*, *40*(1), 53–64. https://doi.org/10.1086/712565

Pilière, A. F. H., Verberk, W. C. E. P., Gräwe, M., Breure, A. M., Dyer, S. D., Posthuma, L., de Zwart, D., Huijbregts, M. A. J., & Schipper, A. M. (2015). On the importance of trait interrelationships for understanding environmental responses of stream macroinvertebrates. *Freshwater Biology*, *61*(2), 181–194. https://doi.org/10.1111/fwb.12690

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2018). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*(3), 849–873. https://doi.org/10.1111/brv.12480

Rezende, C. L., Scarano, F. R., Assad, E. D., Joly, C. A., Metzger, J. P., Strassburg, B. B. N., Tabarelli, M., Fonseca, G. A., & Mittermeier, R. A. (2018). From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation*, *16*(4), 208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Rice, S. P., Greenwood, M. T., & Joyce, C. B. (2001). Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(4), 824–840. https://doi.org/10.1139/f01-022

Rovani, I. L., Decian, V. S., Zanin, E. M., Brandalise, M., Quadros, F. R., & Hepp, L. U. (2020). Socioeconomic Changes and Land Use and Land Cover of the Northern Region of Rio Grande do Sul, Brazil. *Floresta E Ambiente*, *27*(3). https://doi.org/10.1590/2179-8087.025818

Sala, O. E., Stuart Chapin, F., Armesto , J., Berlow, E., Bloomþeld, J., Dirzo , R., Huber-Sanwald, E., Huenneke, L., Jackson, R., Kinzig, A., Leemans, R., Lodge, D., Mooney, H., Oesterheld, M., Poff, M., Sykes, M., Walker , B., Walker , M., & Wall, D. (2000). Global

Biodiversity Scenarios for the Year 2100 . *Science*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sanders, D., Thébault, E., Kehoe, R., & Frank van Veen, F. J. (2018). Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences*, *115*(10), 2419–2424. https://doi.org/10.1073/pnas.1716825115

Santana, R. O., Delgado , R. C., & Schiavetti, A. (2020). The past, present and future of vegetation in the Central Atlantic Forest Corridor, Brazil. *Remote Sensing Applications: Society and Environment*, *20*, 100357. https://doi.org/10.1016/j.rsase.2020.100357

Schmera, D., Árva, D., Boda, P., Bódis, E., Bolgovics, Á., Borics, G., Csercsa, A., Deák, C., Krasznai, E. Á., Lukács, B. A., Mauchart, P., Móra, A., Sály, P., Specziár, A., Süveges, K., Szivák, I., Takács, P., Tóth, M., Várbíró, G., & Vojtkó, A. E. (2017). Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshwater Biology*, *63*(1), 74–85. https://doi.org/10.1111/fwb.12973

SOS Mata Atlântica. (2026). *Relatório anual* . Sosma.org.br. http://www.sosma.org.br/wpcontent/uploads/2019/07/RA_SOSMA_2018_DIGITAL.pdf.

Statzner, B., Dolédec, S., & Hugueny, B. (2004). Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography*, *27*(4), 470–488. https://doi.org/10.1111/j.0906-7590.2004.03836.x

Tonello, G., Decian, V. S., Restello, R. M., & Hepp, L. U. (2021). The conversion of natural riparian forests into agricultural land affects ecological processes in Atlantic forest streams. *Limnologica*, *91*, 125927. https://doi.org/10.1016/j.limno.2021.125927

Valente-Neto, F., Koroiva, R., Fonseca-Gessner, A. A., & Roque, F. de O. (2015). The effect of riparian deforestation on macroinvertebrates associated with submerged woody debris. *Aquatic Ecology*, *49*(1), 115–125. https://doi.org/10.1007/s10452-015-9510-y

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. https://doi.org/10.1139/f80-017

Wiebe, R. A., & Wilcove, D. S. (2025). Global biodiversity loss from outsourced deforestation. *Nature*, *639*. https://doi.org/10.1038/s41586-024-08569-5

Wong, M. K. L., Guénard, B., & Lewis, O. T. (2018). Trait‐based ecology of terrestrial arthropods. *Biological Reviews*, *94*(3), 999–1022. https://doi.org/10.1111/brv.12488

CAPÍTULO 1

ENVIRONMENTAL FILTERING DRIVES FUNCTIONAL UNIQUENESS OF AQUATIC INSECTS IN HEADWATERS BUT NOT IN CENTRAL STREAMS

O manuscrito foi elaborado de acordo com as normas da revista *Journal of Biogeography* (https://onlinelibrary.wiley.com/page/journal/13652699/homepage/forauthors.html)

Abstract

The structuring of metacommunities in dendritic networks results from the interaction between local environmental conditions and regional processes such as connectivity and dispersal. The environmental gradient along the dendritic network can modify the composition of aquatic insects through environmental filtering, which selects taxa based on their functional traits. The network position hypothesis (NPH) predicts that, in headwater streams, communities are primarily organized by environmental filtering, whereas in central reaches dispersal effects predominate. Accordingly, we tested whether headwater streams exhibit greater functional uniqueness than central streams, and whether the drivers of functional uniqueness differ between stream positions, reflecting shifts in the relative importance of environmental filtering. We sampled 11 stream pairs (headwater–central) in Atlantic Forest protected areas and collected abiotic variables and aquatic insects. We compiled the functional traits of identified genera. We calculated environmental uniqueness (LCEH) and functional uniqueness (LCBD-f) and tested differences in their values between headwater and central streams using paired models. We then fitted a General Linear Model (GLM) with Gamma distribution to evaluate the relationships between LCEH and LCBD-f across positions. We also explored the co-structure among environment, traits, and composition using RLQ. Environmental uniqueness did not differ between positions, but headwaters showed higher functional uniqueness. The relationship between LCEH and LCBD-f, as well as the RLQ results, was positive and significant only in headwaters, indicating a stronger influence of environmental variability on functional organization in these stream reaches. In contrast, central streams exhibited lower functional uniqueness and weaker associations between environmental and functional variability, suggesting that environmental filtering may be less dominant in these more central portions of the dendritic network. Our findings suggest that functional communities in headwater streams are structured by environmental filtering (i.e., species selection), whereas additional ecological processes may contribute to community organization in central reaches, partially supporting the NPH. Given that headwaters harbor functionally more unique communities, our results reinforce their importance for conserving functional diversity in dendritic stream networks.

KEYWORDS: Environmental singularity, Functional traits, Beta diversity, Dendritic network.

Introduction

The concept of metacommunity relates the interaction between species and environmental conditions while also considering the connectivity among sites through dispersal potential (Leibold et al. 2004; Leibold & Chase 2018). From this perspective, metacommunity approaches help reveal how local factors (e.g., abiotic characteristics) and regional processes (e.g., spatial structure) jointly shape community organization, providing an integrated framework for understanding ecosystems. (Leibold et al. 2004; Heino et al. 2015). In freshwater ecosystems, watersheds are generally organized in a hierarchical system of tributaries, where small streams (e.g., headwaters) flow into larger streams (e.g., central streams), forming a dendritic network (Gomi et al. 2002; Campbell-Grant et al. 2007). As a result, not only environmental conditions, but also the spatial arrangement and connectivity among sites may determine the structure of aquatic metacommunities within these networks (Carrara et al. 2012; Altermatt 2013; Eros et al. 2017; Tonkin et al. 2015).

In this context, the Network Position Hypothesis (NPH) provides important insights into how spatial position within a dendritic network determines the roles of the processes that structure metacommunities (Schmera et al. 2018). Specifically, the NPH predicts that environmental filtering processes (i.e., species sorting) are stronger in headwater regions, whereas they interact with other mechanisms, such as dispersal dynamics, in more central areas (i.e., mass effects) (Brown & Swan 2010; Gothe et al. 2013; Schmera et al. 2018). This is because headwater streams are generally small, unbranched, and geographically isolated, limiting access for colonization by new organisms (Brown & Swan 2010; Heino et al. 2015; Richardson 2019) and making them more making them more susceptible to physical disturbances associated with intense rainfall, floods, and windthrow (Gomi et al. 2002; Benda et al. 2004). In these environments, local effects (e.g., environmental filtering) tend to be more important in structuring communities, harboring more specialist taxa (Siqueira et al. 2012). In contrast, central watercourses exhibit greater connectivity (Brown & Swan 2010; Altermatt 2013) and, due to their geophysical characteristics, generally experience more stable environmental conditions tend to be more balanced (Finn et al. 2011), reducing selective pressure on communities. The greater connectivity also facilitates dispersal, contributing to the homogenization of communities in these regions (Siqueira et al. 2012; Swan & Brown 2014). Therefore, these aspects underscore an attenuation of environmentally driven dynamics at these downstream sites.

Although the Network Position Hypothesis has been tested primarily using taxonomic community composition (Brown et al. 2011), much less is known about how spatial position

within dendritic networks influences the functional organization of communities. According to the “Habitat Template Model”, environmental conditions can shape community structure through environmental filtering, favoring species with traits suited to local habitat conditions (Southwood 1977; Townsend & Hildrew 1994; Poff 1997; Heino 2005; Poff et al. 2006). Therefore, the use of functional (i..e, trait-based) approach may provide a promising framework for understanding the spatial structuring of metacommunities across environmental gradients (Brown et al. 2011). For this purpose, aquatic insects are an excellent group for investigating metacommunity structuring across dendritic stream networks because their functional traits and dispersal abilities respond strongly to both environmental filtering and spatial processes (Brown & Swan 2010). Additionally, they are one of the main components of freshwater macroinvertebrate communities, playing essential roles in nutrient cycling and trophic dynamics in streams (Esteves et al. 2011; Pilière et al. 2016).

Aquatic insects exhibit high diversity in functional traits related to resource use (e.g., feeding and respiration), morphology (e.g., body adapted for locomotion) and dispersal ability (Brown & Swan 2010; Heino et al. 2015; Van de Meutter et al. 2007; Heino 2013). These traits are closely linked to environmental conditions and resource availability. For example, shredding behavior is often associated with greater leaf litter input in streams (Vannote et al. 1980; Vimos-Lojano et al. 2020), whereas respiratory strategies are related to dissolved oxygen availability, which varies according to temperature and water flow (Mackay & Wiggins 1979; Verberk & Bilton 2013; Martins et al. 2017). Likewise, locomotion traits are linked to foraging strategies and adaptations for movement and attachment to the substrate (Salles & Ferreira-Júnior 2014), conditions that may vary according to the stream order. During the larval stage, dispersal occurs mainly passively (via water flow), potentially covering long distances and contributing to species distribution across the dendritic network (Bonada & Began 2024). Winged adults tend to move along stream corridors, but lateral dispersal can also occur, generally not exceeding 2 km (Clarke et al. 2008; Finn & Poff 2008; Ridley et al. 2011). Together, these ecological attributes make aquatic insects particularly suitable for investigating how environmental filtering and spatial processes interact to shape functional diversity across river networks. Beyond evaluating the functional structure of local communities, functional beta diversity metrics may provide a more holistic perspective of how aquatic insect metacommunities are structured along spatial gradients. This is because these metrics describe patterns of dissimilarity among communities and help identify both local and regional sources of variation relevant to conservation efforts (Whittaker 1960; Whittaker 1972; Legendre & De Cáceres 2013; Liu et al. 2024). In particular, identifying sites

that contribute disproportionately to overall functional beta diversity is an important step toward understanding how environmentally unique sites support rare combinations of functional traits, linking community assembly processes with ecosystem functioning and conservation value. One metric that quantifies this contribution is the Local Contribution to Functional Beta Diversity (LCBD-f), which measures the extent to which the functional composition of a site differs from that of regional metacommunity (Legendre & De Cáceres 2013; Nakamura et al. 2020; Heino et al. 2022).

In dendritic networks, where spatial position may generate different patterns of organization, functional uniqueness allows comparisons of how much communities from different positions in the network contribute to overall functional beta diversity. Moreover, the LCBD-f can help to reveal how environmental filtering contributes to variation in functional composition across the network (Nakamura et al. 2020; Heino et al. 2022). Because environmental filtering operates through the selection of species according to local environmental conditions (Kraft et al. 2015), environmentally unique sites are expected to impose distinct selective pressures on communities (Brandani et al.2023). In this context, environmental uniqueness (LCEH; Castro et al. 2019) reflects the degree to which the environmental conditions of a site differ from those across the regional network. Thus, examining the relationship between environmental and functional uniqueness, i.e., a beta-diversity perspective, may provide a useful framework for assessing the role of environmental filtering in structuring metacommunities, despite this approach remaining rarely explored in ecological studies. Therefore, within this framework, the Network Position Hypothesis (NPH) could be evaluated by testing whether the relationship between environmental and functional uniqueness varies among positions within dendritic networks, reflecting spatial differences in the strength of environmental filtering.

In this study, we investigated how spatial position within a dendritic network (headwaters and central reaches) influences the functional organization of aquatic insects. Specifically, we first assessed whether functional and environmental uniqueness differs between streams located at distinct positions in the network. We then evaluated whether the role of environmental filtering varies according to network position by evaluating the relationship between environmental uniqueness and functional uniqueness across different positions in the dendritic network. Additionally, we explored the relationships between environmental characteristics and functional traits using RLQ analysis, which simultaneously integrates environmental variables, functional traits, and genus composition to provide complementary insights and identify which environmental gradients are associated with trait

variation observed across network positions and, consequently, functional community structure. Thus, we hypothesized that headwater streams exhibit greater functional and environmental uniqueness than central streams due to stronger geographic isolation and local selective pressures (H1). Second, because the role of environmental filtering may vary along the network (as predicted by the NPH), with other processes (e.g., dispersal) tending to act more strongly in highly connected sites, we also hypothesized that the strength of the relationship between environmental uniqueness and functional uniqueness varies according to network position (H2). We expect that in headwater streams, greater environmental uniqueness will be positively associated with higher functional uniqueness, indicating stronger environmental filtering, while in central streams, this relationship will be weaker or absent.

Methods

Study area

The study was conducted in two large conservation areas of the Atlantic Forest biome: Intervales State Park and Carlos Botelho State Park, located in the southeastern region of Brazil, in the state of São Paulo, Brazil (Figure 1). The sampling occurred during the months of April and May 2024 which are indicated as the end of the rainy period and the beginning of the dry period (Blain et al. 2023). The sampled region is characterized by two well-defined seasons: rainy season (October to April) and dry season (May to September).

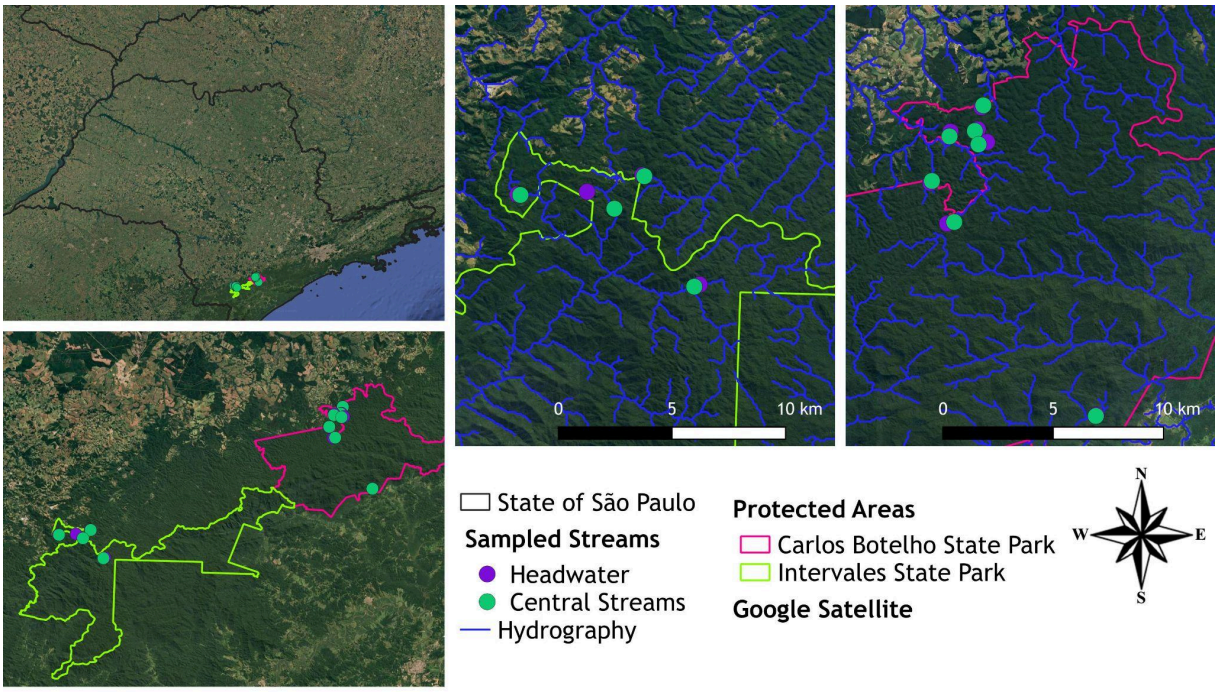

Figure 1. Map of the study area in the Atlantic Forest (São Paulo, Brazil). The sampled streams are divided into headwaters (purple) and central streams (green). The boundaries of Intervales State Park and Carlos Botelho State Park are shown in green and pink, respectively. The blue lines indicate the local hydrography, extracted using a Digital Elevation Model (DEM).

Sampling design

Samples were collected at two different positions in the dendritic network: 1st order (headwater streams) and 2nd and 3rd order (central streams), according to stream order *sensu* Strahler (1957) (Figure 2). We conduct the sampling in pairs, with one headwater reach and one downstream reach along the same stream, making the two reaches hydrologically dependent. In total, 11 pairs were sampled, totaling 22 streams, with longitudinal distance between paired positions ranging from 60 to ~1450 meters (see Supplementary Table S1). All stream pairs have similar high percentages (~100%) of native vegetation cover due to their location within conservation units.

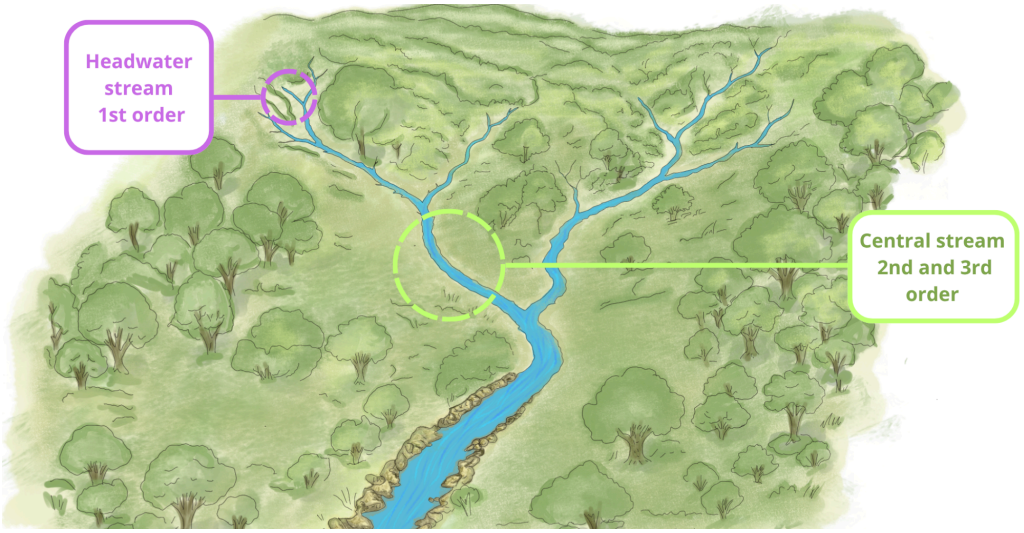

Figure 2. Diagram of the stream pair, showing one stream in the headwater region and one in the central region.

Abiotic variables

In each stream, we measured limnological variables, including the physical characteristics of stream width and depth (cm; using a measuring tape), temperature (°C) with a multiparameter probe ("Horiba"), and substrate structure through visual inspection (e.g., percentage of gravel, pebbles, cobble, sand, or clay). We also measured the stream chemical characteristics: pH, dissolved oxygen (mg/L), total dissolved solids (g/L), and turbidity (NTU) using the multiparameter probe. Finally, we took canopy images in the field and analyzed for canopy cover percentage using specialized software (ImageJ; Rasband 2018). Three replicate

measurements were taken for each variable, except for substrate estimation, for which four replicates were conducted beside the aquatic insect sampling site.

Aquatic insects

We collected aquatic insects in a riffle section using a kick-net (0.25 mm mesh) at four points in each stream for 30 seconds each, for a total of 2 minutes per stream. Samples were preserved in alcohol 80% in the field and taken to the laboratory for sorting under a stereoscopic microscope. We identified all insects belonging to the orders Ephemeroptera, Plecoptera, Trichoptera, Odonata, and Megaloptera, as well as the family Chironomidae (Diptera) to genus level. In Brazil, species-level identification is infeasible because many species have not yet been described and/or are still being discovered (mainly in immature stages) (Cruz et al. 2013). Moreover, studies indicate that family-level assessments produce reliable results for addressing macroinvertebrate diversity in streams (Melo 2005). To identify organisms, we used the following keys: Pes et al. (2005), Domínguez et al. (2006), Heckman (2006), Domínguez & Fernández (2009), Trivinho-Strixino (2011), Ribeiro & Gorayeb (2013), Hamada et al. (2018) and Hamada et al. (2019). The identification process for individuals of the family Chironomidae included additional steps related to slide mounting and clarification of the cephalic capsule using Hoyer's medium according to Trivinho-Strixino (2011).

Functional traits

We selected seven groups of functional traits that best relate to environmental variation along the dendritic network: refuge building, body shape, type of locomotion, feeding guild, respiration strategies, body size and dispersal ability (Table 1). Traits were compiled from studies such as Calvert (1934); Santos (1969); De Marmels (1990); Gutiérrez (1995); Merritt & Cummins (1996); Novelo-Gutiérrez (1998); De Marmels (1999); Von Ellenrieder (2001); Moog (2002); Tolonen et al. (2003); Heino (2008); Merritt et al. (2008); Colzani et al. (2013), Heino (2013) and Santos et al. (2024). We initially compiled trait information at the genus level and, when records were unavailable (~3% of all sampled species), we extrapolated to the family level. Dispersal ability group (DAG) was assigned at the order level according to Heino (2013). The functional variables included both binary traits (presence/absence of attributes) and one ordinal trait (body size and dispersal ability), which was converted into an ordered numerical variable (1 = small, 2 = medium, 3 = large and 1= weak disperser, 2= intermediate disperser, 3= strong disperser, respectively).

Table 1. Functional characteristics of aquatic insects analyzed, adapted from Colzani et al. (2013) and Santos et al. (2024). DAG = Dispersal ability group.

Traits	Categories	*Definition*	*Importance*
Refuge building	No refuge	*Free living*	*The type of refuge is related to the type of available substrate and influences the distribution of aquatic insects through their adaptation for protection against predators and foraging (Rabeni et al. 2005).*
	Fixed nets and retreats	*Fixed silk nets used in the interception and capture of food sources.*	
	Portable shelters of silk	*Mobile shelters built from biologically produced silk fibers.*	
	Portable shelters of sand, debris and/or wood	*Mobile shelters built from sand, rubble, and/or wood*	
	Portable shelters of leaf parts	*Mobile shelters built from leaf parts*	
Body shape	Hydrodynamic	*Flat and/or fusiform*	*Body shape is related to the environment an organism inhabits. Organisms with more flattened bodies have greater hydrodynamic ability and are typically found in environments with stronger currents (Merritt & Cummins, 1996; Poff et al. 2006; Castro et al. 2018).*
	Not hydrodynamic	*Cylindrical and/or round*	
Locomotion groups	Burrowers	*Dig down and reside in the soft, fine sediment*	*Related to feeding strategies and adaptations for colonizing different environments. Locomotion adaptations enable organisms to move and attach to the substrate (Salles & Ferreira-Júnior 2014).*
	Climbers/crawlers	*Dwell on live aquatic plants or plant debris/have elongate bodies with thin legs, slowly move using legs*	
	Sprawlers	*Live on the bottom consisting of fine sediments*	
	Clingers	*Maintain a relatively fixed position on firm substrates in current*	
	Swimmers	*Adapted for moving through water*	

	Skaters	*Adapted to remain on the surface of water*	
Functional feeding guild	Collector-gatherers	*Eat fine detritus that has fallen out of suspension that is lying on the bottom or mixed with bottom sediments*	*Feeding habits indicate food availability in the environment and the mouthpart adaptations of organisms. Riparian vegetation directly influences food availability. For example, shredding insects depend on leaf litter inputs, and the presence or absence of groups with this trait can help assess environmental conditions (Cummins 1973; Cummins et al. 2005; Luiza-Andrade et al. 2020).*
	Collector-filterers	*Use special straining mechanisms to feed on fine detritus that is suspended in the water*	
	Herbivores	*Scraper and grazer organic plant material*	
	Predators	*Carnivores*	
	Shredders	*Break down plant material, intact or in large pieces*	
Respiration	Tegumental respiration	*By passive diffusion*	*Dissolved oxygen in water is influenced by temperature and current velocity; these characteristics directly affect the respiratory strategies of organisms and may favor or limit their occurrence (Mackay & Wiggins 1979; Verberk & Bilton 2013; Martins et al. 2017).*
	Gill respiration	*By branchial system*	
	Air	*By spiracles, tracheae, plastrons*	
Body size	1- Small-sized	*<9 mm*	*Variation in environmental habitat conditions can generate stress. This stress may lead to asynchronous emergence of males and females, compromising reproduction, as well as accelerating the post-embryonic development of immatures and consequently, affecting body size (Poff et al. 2006; Castro et al. 2018).*
	2- Medium-sized	*9-16 mm*	
	3- Large-sized	*>16 mm*	
Dispersal ability	1- DAG1	*Weak aerial dispersal with flyer adults*	*Dispersal ability contributes to the distribution of*

2- DAG2	*Intermediate aerial dispersal with flyer adults*	*individuals and their capacity to colonize more distant locations. Spatial isolation factors are more influential for weak dispersers (Heino, 2013).*
3- DAG3	*Strong aerial dispersal with flyer adults*	

Functional and Environmental uniqueness

The functional uniqueness was estimated using the Local Contribution to Functional Beta Diversity (LCBD-f; Local Contribution to Beta Diversity, Legendre & De Cáceres 2013, adapted by Nakamura et al. 2020), which measures how much each stream differs in functional composition relative to the regional mean. The calculation of LCBD-f was conducted in a series of steps (according to Heino et al. 2022; Mathers et al. 2024): (1) we used the aquatic insects functional traits matrix (genera in rows and traits in columns) and applied the function gawdis (package "*gawdis*"; de Bello et al. 2021) to build a dissimilarity matrix among genera; we selected gawdis because it balances the contribution of traits by standardizing them (de Bello et al. 2021); (2) we constructed a functional tree using hierarchical clustering via the function hclust (UPGMA method, "*stats*" package; base R); (3) we then used this functional tree together with the abundance matrix of genera across sites (sites in rows and genera in columns) to compute the functional community distance matrix based on the Chao-Jaccard index for each site using the function beta (package "*BAT*"; Cardoso et al. 2024; Cardoso et al. 2024); and (4) finally, we used the total functional beta diversity dissimilarity matrix to compute LCBD-f with the function beta.div (package "*adespatial*"; Dray et al. 2018; Dray et al. 2021).

To measure the values of environmental uniqueness of streams in each position, we calculated LCEH (Local Contribution to Environmental Heterogeneity) (Castro et al. 2019; Heino et al. 2022; Snare et al. 2024) from an environmental matrix composed of the following habitat structure and limnological variables: stream width, depth, substrate (categorized as fine sand, medium sand, coarse sand, granules, pebbles, boulders and leaf litter), pH, dissolved oxygen, water temperature, total dissolved solids, and turbidity. Environmental data were standardized (each variable standardized to zero mean and unit variance) using the function decostand (method "*standardize*", "*vegan*" package; Oksanen et al. 2023) to subsequently compute Euclidean distance with the function dist ("*stats*" package; base R; Legendre & Legendre 1998). We then calculated the LCEH value of each site using the

function LCBD.comp from the "adespatial" package (Dray et al. 2018; Dray et al. 2021). We also calculated the mean LCEH for headwater and central streams.

Statistical analyses

To test if headwater streams exhibit greater functional and environmental uniqueness than central streams due to stronger geographic isolation and local selective pressures (H1), we assessed differences between positions (headwater and central) within each pair. Differences in LCBD-f and LCEH were tested using paired t-tests to account for the paired study design (i.e., the dependence between the headwater and its central reach). To ensure that geographic distance between paired sites did not influence the observed differences, we additionally calculated the pairwise differences (ΔLCBD-f and ΔLCEH) and modeled them as a function of the geographic distance between sites within each pair, using a simple linear regression.

Moreover, to test if the strength of the relationship between environmental uniqueness and functional uniqueness varies according to network position (H2), we fitted a generalized linear model (GLM) with a Gamma distribution using the glmmTMB function from the package "*glmmTMB*" (Brooks et al. 2017). Because LCBD-f values were very close to zero, we used a Gamma distribution with a log link function (e.g., Astorg et al. 2025), which is more appropriate for models with many values near zero. In this model, the functional uniqueness (LCBD-f) of each stream was used as the response variable, while environmental uniqueness (LCEH) was used as the predictor variable. In addition, we included the stream position as an interaction with LCEH to evaluate whether the relationship between environmental and functional uniqueness varies along the dendritic network (Equation 1). If the interaction was significant, we estimated the slope for each level of the factor Position using the emtrends function in the "*emmeans*" package (Lenth et al. 2019). Model residual diagnostics were performed using the "*DHARMa"* package (Hartig 2004).

$$LCDB\text{-}F \sim LCEH + LCEH{:}Position \quad \text{(Equation 1)}$$

Finally, to better explore associations between environmental variables, species composition, and functional traits, we used RLQ analysis (Dolédec et al. 1996). For the RLQ analysis, each matrix was analyzed separately using the "*ade4*" package (Chessel et al. 2004): for matrix R (environmental variables), we performed a Principal Component Analysis (PCA)

using dudi.pca function; for matrix L (genus abundance), a Correspondence Analysis (CA) using the dudi.coa function, based on the abundance structure of species with identical functional traits removed; and for matrix Q (functional traits), a PCA (dudi.pca) weighted by species weights derived from matrix L. These were then combined in an RLQ analysis using the rlq function, which identifies relationships between environmental variables and traits mediated by community composition. The significance of the environment–trait relationship was tested separately for headwater and central streams, as well as for the full dataset, using Monte Carlo tests (999 permutations) with model 5 via the randtest function. We selected this model because it directly tests the effect of environmental filtering on functional traits, keeping matrix L fixed while permuting associations between matrices R and Q, thus returning the significance of the relationship. Additionally, we performed fourth-corner analyses to explore potential pairwise associations between environmental variables and functional traits.

The figures were produced using the "*ggplot2*" package (Wickham et al. 2016). All analyses were conducted in the R program (R Core Team 2024).

Results

We found 2,878 individuals distributed across 99 genera belonging to the orders Ephemeroptera, Plecoptera, Trichoptera, Odonata, Megaloptera, and the family Chironomidae (Diptera). In headwater streams, genus richness ranged from 13 to 46 (mean = 26 ± 8.42), whereas in central streams it ranged from 19 to 34 (mean = 28 ± 5.12). 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.

We also found that the mean values of environmental uniqueness (LCEH) were slightly higher in headwater streams (0.050 ± 0.029) than in central streams (0.040 ± 0.021), but no significant differences were found between paired sites ($t = 0.98$; $p = 0.347$; Figure 3a). In contrast, functional uniqueness (LCBD-f) was significantly higher in headwater streams (0.048 ± 0.004) than in central streams (0.042 ± 0.004) ($t = 2.45$; $p = 0.033$; Figure 3b). Geographical watercourse distance between pairs did not influence differences in functional uniqueness ($R^2 = 0.02$; $p = 0.30$).

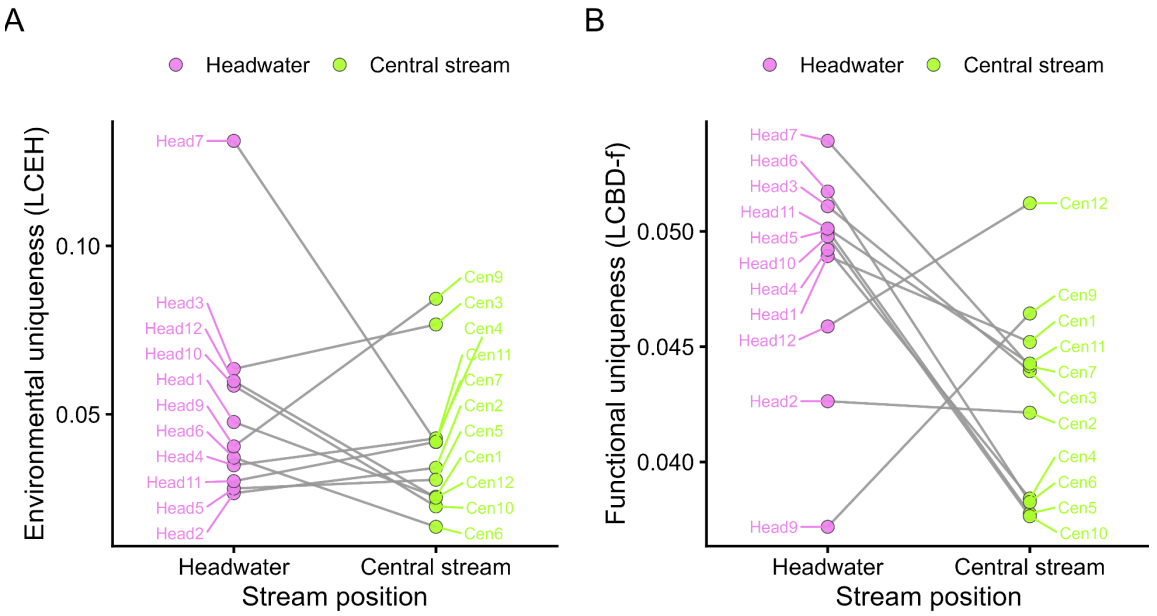

Figure 3. (A) LCEH values (Local Contribution to Environmental Heterogeneity) and (B) LCBD-f values (Local Contribution to Beta Diversity Functional) of aquatic insects for headwater streams (magenta) and central streams (green) from Atlantic Forest. Gray lines connect corresponding pairs, showing how functional and environmental uniqueness vary between the two positions in the dendritic network. Colored lines and labels indicate which stream each point represents. Head= Headwater streams; Cen= Central streams.

Additionally, we found that the relationship between environmental uniqueness (LCEH) and functional uniqueness (LCBD-f) varied with stream position within the dendritic network, as indicated by the significant interaction between LCEH and stream position (β = -1.26, p = 0.025). Specifically, stream position modulated the strength of the relationship between environmental and functional uniqueness, with the relationship becoming weaker in central streams. More specifically, in headwater streams, environmental uniqueness showed a positive and significant relationship with functional uniqueness ($\beta = 1.40 \pm 0.52$, p = 0.008), indicating that headwater streams with more unique environmental conditions also tended to harbor more functionally unique assemblages. In contrast, the relationship between LCEH and LCBD-f in central streams was weak and non-significant ($\beta = 0.16 \pm 0.67$, p = 0.815), suggesting that environmental uniqueness was less strongly associated with functional uniqueness in these more connected streams (Figure 4, Supplementary Table S2).

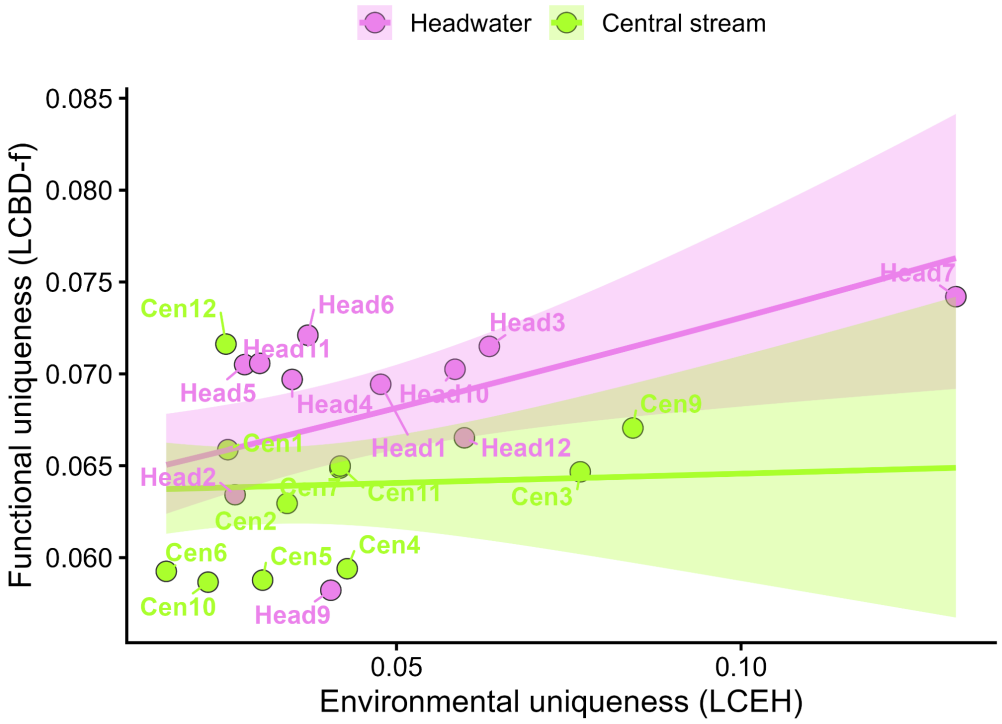

Figure 4. Generalized linear model (Gamma family with log link) indicating the relationships between LCEH values (Local Contribution to Environmental Heterogeneity) and LCBD-f values of aquatic insects (Local Contribution to Functional Beta Diversity) in headwater streams (magenta) and central streams (green) from the Atlantic Forest.

Finally, the RLQ analysis for the full dataset explained approximately 80% of the environment–trait–genus co-structure (Axis 1 = 60.3%, Axis 2 = 19.6%), revealing a significant association between abiotic characteristics and functional traits of aquatic insect communities across sites (model 5, p = 0.009). This relationship was significant in headwater streams (model 5, p = 0.046), but not in central streams (model 5, p = 0.11). We also observed that headwater streams with high LCBD-f values occupied more isolated positions in the ordination space, reinforcing their distinct environmental and functional characteristics (Figure 5). Associations between specific traits and environmental variables were observed, such as portable silk case-building being positively related to finer substrates and negatively related to pebble substrates; hydrodynamic body shape being positively associated with granular substrates and negatively with fine sand; stream width and depth showing a negative relationships with leaf case-builders; and pebble substrates being positively associated with fixed-net builders. However, after Holm's correction, these relationships were no longer significant.

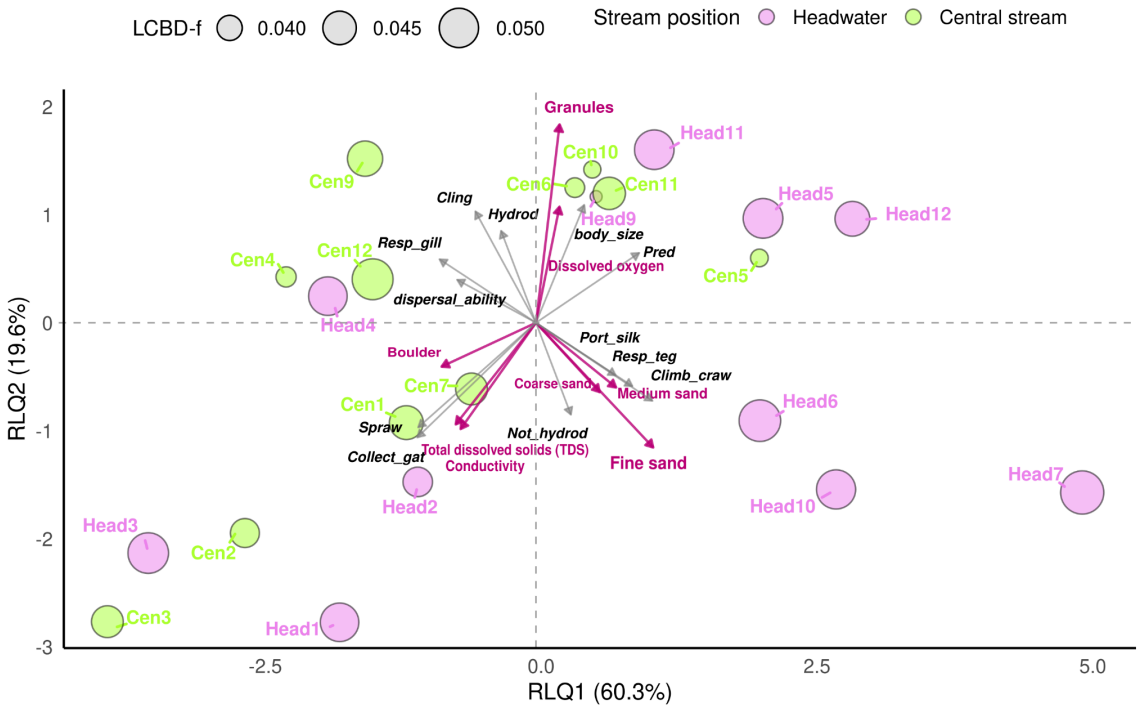

Figure 5. RLQ co-structure analysis for aquatic insects in headwater (Head) and central (Cen) streams from Atlantic Forest. Axes 1 and 2 explained 79.8% of the covariance among environmental conditions, biological composition, and functional traits of the taxa. The points represent the streams (headwaters in magenta and midstream sites in green), and the sizes of their circles vary with their LCBD-f value. Their position is determined by their strongest associations with each axis of the plot. In purple are the abiotic characteristics, and in gray the functional attributes ("Resp_gill" = gill respiration; "Resp_teg" = tegumentary respiration; "Silk_port" = portable silk case; "Pred" = predators; "Collect_gat" = collector-gatherers; "Spraw" = sprawlers; "Cling" = clingers; "Climb_craw" = Climbers_crawlers; "body_size" = body size; "Hydrod" = Hydrodynamic flat/fusiform; "Not_hydrod" = Not hydrodynamic cylindrical/round). The larger the arrow of each environmental or functional component, the more strongly it is associated with each RLQ axis.

Discussion

Our study investigated whether spatial position within a dendritic network (headwaters and central reaches) influences the functional organization of aquatic insects using a beta-diversity framework. We found that headwater streams harbored more functionally unique communities, where environmental uniqueness had a stronger and significant influence on the variation in functional uniqueness patterns, whereas central streams showed lower functional uniqueness and a non-significant relationship between environmental uniqueness and functional structure, suggesting that additional processes beyond local environmental filtering may contribute to community organization in these more connected regions. This pattern was further supported by the RLQ analysis, which revealed a significant environment–trait association across the study area and a significant relationship only in headwater streams. Notably, headwaters with the highest environmental uniqueness occupied more isolated positions in the RLQ ordination space and were associated with the most functionally unique

assemblages, highlighting a close correspondence between environmental and functional differentiation.

The higher functional uniqueness observed in headwater streams likely results from the interaction between greater habitat heterogeneity and stronger spatial isolation. One possible explanation is the greater microhabitat heterogeneity typically found in headwater reaches, which often contain a diverse mosaic of habitat features including woody debris, leaf litter accumulations, pools, riffles, and patches of organic matter (Clarke et al. 2008; Richardson 2019). This habitat complexity can support a wider range of ecological strategies, including more specialized species, and contribute to distinct functional combinations among sites. In addition, Richardson (2019) highlights that the diversity of microhabitats in headwater streams also may provide refuges from predation and competition, creating enemy-free spaces that may promote the persistence of more vulnerable species to biotic pressures. Furthermore, the greater isolation of headwater streams within dendritic networks may limit species exchange, allowing local assemblages to maintain unique functional characteristics (Brown & Swan 2010; Finn et al. 2011; Altermatt 2013). In contrast, central streams occupy more connected positions within the network and have a greater potential to receive species through dispersal, particularly drift dispersal (Brown & Swan 2010; Heino et al. 2015; Altermatt & Fronhofer 2018). This increased connectivity may continuously introduce taxa from upstream reaches and regional species pool, reducing functional differentiation among communities through species replacement and promoting assemblages dominated by widespread and functionally common taxa (Siqueira et al. 2012; Swan and Brown 2014). These aspects may contribute to the lower functional uniqueness observed in central streams relative to their connected headwaters. Therefore, functional uniqueness appears to emerge from the balance between local environmental differentiation and network connectivity. This finding highlights the disproportionate contribution of headwater streams to regional functional diversity, as their unique habitat characteristics and relative isolation may promote the persistence of distinct functional strategies within river networks.

On the other hand, we observed similar patterns of environmental uniqueness throughout the dendritic network, with no clear distinction between streams at headwaters and those at central positions. Although environmental conditions between headwater and central streams are generally more distinct (Richardson, 2019; Altermatt & Fronhofer 2018), sampling streams up to the third order may not have been sufficient to capture major differences in environmental characteristics, since natural landscape changes are continuous and gradual (Benda et al. 2004). Thus, our results suggest that this gradual transition in

environmental conditions (i.e., habitat structure and limnological conditions) can also be detected in Neotropical stream networks. Given the lack of differences in environmental uniqueness associated with stream position, our results only partially support H1, i.e., that headwater streams exhibit greater functional and environmental uniqueness than central streams due to stronger geographic isolation and local selective pressures. While headwater streams consistently exhibited greater functional uniqueness, environmental uniqueness was not structured by network position, suggesting that functional differentiation may emerge even in the absence of clear differences in overall environmental uniqueness between headwater and central streams. Although environmental uniqueness did not vary systematically with network position, its effects on the functional organization of aquatic insect communities differed between headwater and central streams. This is because environmentally unique headwaters tended to support more functionally unique assemblages, whereas no such relationship was observed in central streams. This result indicates that environmental filtering exerts a stronger influence on functional organization in headwater reaches, where local environmental conditions are more closely linked to community trait composition. Accordingly, in these sites, abiotic characteristics were strongly associated with functional traits of the community in this position, suggesting a "Habitat Template" mechanism in which the environment acts as an ecological filter, shaping communities through species selection according to their functional traits (Southwood 1977; Townsend & Hildrew 1994; Poff 1997; Heino 2005; Poff et al. 2006). Thus, selective pressure tends to favor more specialized taxa, contributing to the formation of more unique functional communities, which, in turn, may be more sensitive to environmental variation (Buisson et al. 2008; Nyboer et al. 2019).

Contrary to the pattern found in headwaters, the environmental uniqueness of central reaches showed no clear relationship with the functional uniqueness values at this position, suggesting that the functional structure of communities in these sites does not result solely from environmental filtering, but also from other processes influencing functional variability, possibly related to unmeasured mechanisms such as dispersal (Amarasekare 2004), hydrological dynamics, or ecological stochasticity. Thus, we observed that the environment plays a stronger role in structuring functional communities in headwater streams, but its effect is attenuated in central streams.This finding partially supports the Network Position Hypothesis (NPH). Functional communities were more strongly associated with environmental factors in headwater streams, appearing to align with the species-sorting paradigm, which predicts the prevalence of local processes (e.g., environmental filtering) in

more isolated positions (Chase et al. 2005; Brown & Swan 2010; Schmera et al. 2018). On the other hand, in central streams the relationship between environmental factors and functional communities was less evident, while the weaker association between environmental uniqueness and functional structure in central streams suggests that local environmental filtering may be less dominant in these positions, potentially allowing a greater influence of regional dynamics, consistent with the possibility of mass-effect dynamics, which predict that in more centralized locations, communities are influenced by both local processes and spatial processes (e.g., dispersal-related processes) (Brown & Swan 2010; Schmera et al. 2018; Patrick et al. 2021). Our RLQ analysis revealed trait–environment associations that, although no longer significant after correction for multiple comparisons, provide complementary insights into how ecological filtering may shape local community structure. Traits such as leaf-case building were associated with shallower and narrower habitats, likely reflecting environments with greater leaf litter availability, whereas fixed retreat builders were associated with coarser substrates that provide stable anchoring surfaces in higher-flow conditions. These patterns are consistent with the idea that habitat characteristics impose selective pressures that favor specific functional trait combinations (Statzner et al. 2004; Poff et al. 2006). Visual inspection of the RLQ ordination further suggests that highly functionally unique sites, such as Headwater 7, may be associated with particular environmental conditions and distinct trait combinations, reinforcing the interpretation that environmental filtering contributes to functional differentiation in headwater communities.

Our findings identify headwater areas as refuges for unique functional communities that contribute to the overall functional structure of the hydrographic network and are strongly associated with the ecological filtering process, suggesting greater sensitivity of these communities to changes in environmental characteristics. Headwater streams represent most of the dendritic network and are naturally more unstable, being narrower and more isolated and therefore more susceptible to environmental changes (Lowe & Likens 2005; Brown & Swan 2010; Brown et al. 2011). Thus, minimal landscape changes in these positions may result in a disproportionate loss of biodiversity and associated ecosystem services (Jonsson & Malmqvist 2000; Cardinale et al. 2002; Meyer et al. 2007). At the same time, although central streams exhibited lower functional uniqueness, their ecological importance may lie in their role as highly connected sections of the dendritic network, facilitating dispersal and regional integration among communities. These features may therefore help maintain metacommunity dynamics and functional persistence at broader spatial scales (Milesi & Melo 2014; Altermatt & Fronhofer 2018; Milesi & Hepp 2025).

Finally, we acknowledge that the reduced sample size and the proximity between sampled positions may have constrained the environmental and spatial gradients represented in our dataset, potentially limiting not only our ability to partially detect patterns predicted by the Network Position Hypothesis, but also to perform a more integrative assessment of the relative contribution of different ecological processes structuring communities across the network. Nevertheless, the contrasting relationships observed between environmental uniqueness, spatial structure, and functional uniqueness across network positions provide evidence that ecological processes vary along the dendritic network in Neotropical streams.

Conclusion

In this study, we observed that the mechanisms responsible for metacommunity organization vary according to network position within the dendritic network. More isolated sites harbor distinct functional communities, which make a disproportionately strong contribution to the functional structure of the river network. However, we emphasize that both headwaters and central streams are ecologically important components of dendritic networks, contributing in complementary ways to the maintenance of regional biodiversity and metacommunity organization. Finally, to support future conservation planning, we suggest giving special attention to headwater streams due to their greater sensitivity to environmental changes and because they harbor irreplaceable functional assemblages that may be at risk of irreversible loss due to their isolation and strong dependence on local environmental conditions. Overall, our findings demonstrate the value of functional approaches for understanding metacommunity organization and provide a robust ecological framework to support biomonitoring programs and conservation strategies in dendritic river networks.

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References

Allan, J. D., & Castillo, M. M. (2007). *Stream Ecology : Structure and function of running waters*. Dordrecht: Springer Netherlands.

Altermatt, F. (2013). Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology*, *47*(3), 365–377. https://doi.org/10.1007/s10452-013-9450-3

Altermatt, F., & Fronhofer, E. A. (2018). Dispersal in dendritic networks: Ecological consequences on the spatial distribution of population densities. *Freshwater Biology*, *63*(1), 22–32. https://doi.org/10.1111/fwb.12951

Amarasekare, P. (2004). Spatial variation and density-dependent dispersal in competitive coexistence. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1547), 1497–1506. https://doi.org/10.1098/rspb.2004.2696

Astorg, L., Giguère‐Tremblay, R., Martineau, C., Cabana, G., Guillemette, F., Maire, V., … Fugère, V. (2025). eDNA Metabarcoding to Monitor Fish Communities in a Large River Floodplain. *Environmental DNA*, *7*(5). https://doi.org/10.1002/edn3.70182

Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., & Pollock, M. (2004). The Network Dynamics Hypothesis: How Channel Networks Structure Riverine Habitats. *BioScience*, *54*(5), 413. https://doi.org/10.1641/0006-3568(2004)054[0413:tndhhc]2.0.co;2

Blain, G. C., da Rocha Sobierajski, G., & Martins, L. L. (2023). Elevações na frequência de ocorrência de secas meteorológicas no Estado de São Paulo sob condições de mudanças climáticas. *Derbyana*, *44*. https://doi.org/10.14295/derb.v44.789

Bonada, N., & Bogan, M. T. (2024). Benthic Animals . In *Limnology* (pp. 621–655). Academic Press.

Brandani J, Peter H, Fodelianakis S, Kohler TJ,Bourquin M, Michoud G, Busi SB, Ezzat L, Lane S, Battin TJ. 2023. Homogeneous Environmental Selection Structures the Bacterial Communities of Benthic Biofilms in Proglacial Floodplain Streams. Appl Environ Microbiol 89:e02010-22. https://doi.org/10.1128/aem.02010-22

Brooks, Mollie,E., Kristensen, K., Benthem, Koen,J. ,van, Magnusson, A., Berg, Casper,W., Nielsen, A., … Bolker, Benjamin,M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378. https://doi.org/10.32614/rj-2017-066

Brown, B. L., & Swan, C. M. (2010). Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology*, *79*(3), 571–580. https://doi.org/10.1111/j.1365-2656.2010.01668.x

Brown, B. L., Swan, C. M., Auerbach, D. A., Campbell Grant, E. H., Hitt, N. P., Maloney, K. O., & Patrick, C. (2011). Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society*, *30*(1), 310–327. https://doi.org/10.1899/10-129.1

Buisson, L., Thuiller, W., Lek, S., Lim, P., & Grenouillet, G. (2008). Climate change hastens the turnover of stream fish assemblages. *Global Change Biology*, *14*(10), 2232–2248. https://doi.org/10.1111/j.1365-2486.2008.01657.x

Calvert, P. P. (1934). The Rates of Growth, Larval Development and Seasonal Distribution of Dragonflies of the Genus Anax (Odonata: Æshnidæ). *Proceedings of the American Philosophical Society*, *73*(1), 1–70. JSTOR. https://doi.org/10.2307/984740

Campbell Grant, E. H., Lowe, W. H., & Fagan, W. F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters*, *10*(2), 165–175. https://doi.org/10.1111/j.1461-0248.2006.01007.x

Cardinale, B. J., Palmer, M. A., & Collins, S. L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, *415*(6870), 426–429. https://doi.org/10.1038/415426a

Cardoso , P., Mammola , S., Rigal , F., & Carvalho , J. C. (2024). Biodiversity Assessment Tools [R package BAT version 2.11.1]. *R-Project.org*. https://cran.r-project.org/package=BAT

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., … Settele, J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, *242*(242), 108426. https://doi.org/10.1016/j.biocon.2020.108426

Carrara, F., Altermatt, F., Rodriguez-Iturbe, I., & Rinaldo, A. (2012). Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences*, *109*(15), 5761–5766. https://doi.org/10.1073/pnas.1119651109

Castro, D. M. P., Dolédec, S., & Callisto, M. (2018). Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. *Ecological Indicators*, *84*, 573–582. https://doi.org/10.1016/j.ecolind.2017.09.030

Castro, E., Siqueira, T., Melo, A. S., Bini, L. M., Landeiro, V. L., & Schneck, F. (2019). Compositional uniqueness of diatoms and insects in subtropical streams is weakly correlated with riffle position and environmental uniqueness. *Hydrobiologia*, *842*(1), 219–232. https://doi.org/10.1007/s10750-019-04037-8

Chase, J. M., Amarasekare, P., Cottenie, K., Gonzalez, A., Holt , R. D., Holyoak, M., … Tilman, D. (2005). Competing theories for competitive metacommunities. In *Metacommunities: Spatial Dynamics and Ecological Communities (eds M. Holyoak, M.A. Leibold & R.D. Holt)* (pp. 335–354). Chicago and London: University of Chicago Press.

Chessel , D., Dufour, A. B., & Thioulouse, J. (2004). The ade4 package-I-One-table methods. *R News*, *4*(1), 5–10.

Clarke, A., Mac Nally, R., Bond, N., & Lake, P. S. (2008). Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, *53*(9), 1707–1721. https://doi.org/10.1111/j.1365-2427.2008.02041.x

Colzani, E., Siqueira, T., Suriano, M. T., & Roque, F. O. (2013). Responses of Aquatic Insect Functional Diversity to Landscape Changes in Atlantic Forest. *Biotropica*, *45*(3), 343–350. https://doi.org/10.1111/btp.12022

Cruz, P. V., Salles, F. F., & Hamada, N. (2013). A new genus and species of Baetidae (Insecta: Ephemeroptera) from Brazil. *Annales de Limnologie - International Journal of Limnology*, *49*(1), 1–12. https://doi.org/10.1051/limn/2013033

Cummins, K. W. (1973). Trophic Relations of Aquatic Insects. *Annual Review of Entomology*, *18*(1), 183–206. https://doi.org/10.1146/annurev.en.18.010173.001151

Cummins, K. W., Merritt, R. W., & Andrade, P. C. (2005). The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. *Studies on Neotropical Fauna and Environment*, *40*(1), 69–89. https://doi.org/10.1080/01650520400025720

de Bello, F., Botta-Dukát, Z., Lepš, J., & Fibich, P. (2021). Towards a more balanced combination of multiple traits when computing functional differences between species. *Methods in Ecology and Evolution*, *12*(3), 443–448. https://doi.org/10.1111/2041-210x.13537

De Marmels, J. (1990). Nine new Anisoptera larvae from Venezuela (Gomphidae, Aeshnidae, Corduliidae, Libellulidae). *Odonatologica*, *19*(1), 1–15.

De Marmels, J. (1999). A new species of Dimeragrion Calvert 1913 from Pantepui, Venezuela (Odonata: Megapodagrionidae). *Boletín de Entomología Venezolana*, *14*(1), 27–36.

Dolédec, S., Chessel, D., ter Braak, C. J. F., & Champely, S. (1996). Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics*, *3*(2), 143–166. https://doi.org/10.1007/bf02427859

Domínguez , E., Molineri , C., Pescador , M. L., Hubbard, M. D., & Nieto , C. (2006). Ephemeroptera of South America . In *Aquatic biodiversity in Latin America*. Sofia, Bulgaria.: Pensoft.

DomínguezE., & FernándezH. R. (2009). *Macroinvertebrados bentónicos sudamericanos : sistemática y biología*. Tucumán, Argentina: Fundación Miguel Lillo.

Dray , S., Blanchet , G., Borcard , D., Guenard , G., Jombart , T., Legendre , P., & Wagner , H. (2021). *Package adespatial: Multivariate multiscale spatial analysis. Version 0.3–14.*

Dray, S., Blanchet , G., Borcard, D., Guenard , G., Jombart, T., Larocque, G., … Dray, M. S. (2018). *Package "adespatial". R package, 2018, 3-8.*

Erős, T., Takács, P., Specziár, A., Schmera, D., & Sály, P. (2017). Effect of landscape context on fish metacommunity structuring in stream networks. *Freshwater Biology*, *62*(2), 215–228. https://doi.org/10.1111/fwb.12857

Esteves, F. A., Leal, J. J. F., & Callisto, M. (2011). Comunidade Bentônica. In *Fundamentos de Limnologia* (pp. 581–603). Editora Interciência.

Finn, D. S., Bonada, N., Múrria, C., & Hughes, J. M. (2011). Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society*, *30*(4), 963–980. https://doi.org/10.1899/11-012.1

Finn, D. S., & Poff, N. L. (2008). Emergence and Flight Activity of Alpine Stream Insects in Two Years with Contrasting Winter Snowpack. *Arctic, Antarctic, and Alpine Research*, *40*(4), 638–646. https://doi.org/10.1657/1523-0430(07-072)[finn]2.0.co;2

Gomi, T., Sidle, R. C., & Richardson, J. S. (2002). Understanding Processes and Downstream Linkages of Headwater Systems. *BioScience*, *52*(10), 905. https://doi.org/10.1641/0006-3568(2002)052[0905:upadlo]2.0.co;2

Göthe, E., Angeler, D. G., & Sandin, L. (2013). Metacommunity structure in a small boreal stream network. *Journal of Animal Ecology*, *82*(2), 449–458. https://doi.org/10.1111/1365-2656.12004

Gutiérrez, R. N. (1995). Náyade de Brechmorhoga pertinax (Odonata: Libellulidae). *Anales Del Instituto de Biología. Serie Zoología*, *66*(2), 181–187.

Hamada, N., Nessimian, J. L., & Querino, R. B. (2019). *Insetos aquáticos na Amazônia brasileira : taxonomia, biologia e ecologia*. Manaus: Editora do INPA.

Hamada, N., Thorp, J. H., & Rogers, D. C. (2018). *Thorp and Covich's Freshwater Invertebrates*. Academic Press.

Hartig , F. (2024). *_DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models_.R package version 0.4.7*. https://cran.r-project.org/package=DHARMa.

Heckman, C. W. (2006). *Encyclopedia of South American Aquatic Insects: Odonata - Anisoptera : Illustrated Keys to Known Families, Genera, and Species in South America*. Dordrecht: Springer Netherlands.

Heino, J. (2005). Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. *Freshwater Biology*, *50*(9), 1578–1587. https://doi.org/10.1111/j.1365-2427.2005.01418.x

Heino, J. (2008). Patterns of functional biodiversity and function-environment relationships in lake littoral macroinvertebrates. *Limnology and Oceanography*, *53*(4), 1446–1455. https://doi.org/10.4319/lo.2008.53.4.1446

Heino, J. (2013). Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? *Oecologia*, *171*(4), 971–980. https://doi.org/10.1007/s00442-012-2451-4

Heino, J., García-Girón, J., Hämäläinen, H., Hellsten, S., Ilmonen, J., Karjalainen, J., … Tolonen, K. T. (2022). Assessing the conservation priority of freshwater lake sites based on

taxonomic, functional and environmental uniqueness. *Diversity and Distributions*, *28*(9), 1966–1978. https://doi.org/10.1111/ddi.13598

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2014). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology*, *60*(5), 845–869. https://doi.org/10.1111/fwb.12533

Jonsson, M., & Malmqvist, B. (2000). Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. *Oikos*, *89*(3), 519–523. https://doi.org/10.1034/j.1600-0706.2000.890311.x

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. and Levine, J.M. (2015), Community assembly, coexistence and the environmental filtering metaphor. Funct Ecol, 29: 592-599. https://doi.org/10.1111/1365-2435.12345

Legendre, L., & Legendre, P. (1988). Numerical Ecology. *2nd English Edition*, *Elsevier, Amsterdam.*

Legendre, P., & De Cáceres, M. (2013). Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters*, *16*(8), 951–963. https://doi.org/10.1111/ele.12141

Leibold, M. A., & Chase, J. M. (2018). *Metacommunity ecology*. Princeton, New Jersey, Princeton University Press.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., … Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lenth, R., Singmann, H., Love , J., Buerkner, P., & Herve, M. (2019). *Package "emmeans". R package version, 1(3.2).*

Liu, Y., Zhu, Y., Wu, S., Wang, Y., Xie, J., Zhang, K., & Xu, Y. (2024). Determinants of taxonomic, functional, and phylogenetic beta diversity in breeding birds within urban remnant woodlots: Implications for conservation. *Ecology and Evolution*, *14*(5). https://doi.org/10.1002/ece3.11426

Lowe, W. H., & Likens, G. E. (2005). Moving Headwater Streams to the Head of the Class. *BioScience*, *55*(3), 196. https://doi.org/10.1641/0006-3568(2005)055[0196:mhstth]2.0.co;2

Luiza-Andrade, A., Brasil, L. S., Torres, N. R., Brito, J., Silva, R. R., Maioli, L. U., … Juen, L. (2020). Effects of Local Environmental and Landscape Variables on the Taxonomic and Trophic Composition of Aquatic Insects in a Rare Forest Formation of the Brazilian Amazon. *Neotropical Entomology*, *49*(6), 821–831. https://doi.org/10.1007/s13744-020-00814-6

Mackay, R. J., & Wiggins, G. B. (1979). Ecological Diversity in Trichoptera. *Annual Review of Entomology*, *24*(1), 185–208. https://doi.org/10.1146/annurev.en.24.010179.001153

Martins, R. G., Melo, A. S., Gonçalves, J., Campos, C. M., & Hamada, N. (2017). Effects of climate change on leaf breakdown by microorganisms and the shredder Phylloicus elektoros (Trichoptera: Calamoceratidae). *Hydrobiologia*, *789*(1), 31–44. https://doi.org/10.1007/s10750-016-2689-7

Mathers, K. L., Robinson, C. T., Hill, M., Kowarik, C., Heino, J., Deacon, C., & Weber, C. (2024). How effective are ecological metrics in supporting conservation and management in degraded streams? *Biodiversity and Conservation*, *33*. https://doi.org/10.1007/s10531-024-02933-7

Melo, A. S. (2005). Effects of taxonomic and numeric resolution on the ability to detect ecological patterns at a local scale using stream macroinvertebrates. *Archiv Für Hydrobiologie*, *164*(3), 309–323. https://doi.org/10.1127/0003-9136/2005/0164-0309

Merritt , R. W., & Cummins, K. W. (1996). An Introduction to the Aquatic Insects of North America. *Journal of the North American Benthological Society*, *15*(3), 401–403. https://doi.org/10.2307/1467288

Merritt, R. W., Cummins , K. W., & Berg, M. B. (2008). An introduction to the aquatic insects of North America, (4th edition). *Revista Mexicana de Biodiversidad*, *81*(002). https://doi.org/10.22201/ib.20078706e.2010.002.247

Meyer, J. L., Strayer, D. L., Wallace, J. B., Eggert, S. L., Helfman, G. S., & Leonard, N. E. (2007). The Contribution of Headwater Streams to Biodiversity in River Networks1. *JAWRA Journal of the American Water Resources Association*, *43*(1), 86–103. https://doi.org/10.1111/j.1752-1688.2007.00008.x

Milesi, S. V., & Hepp, L. U. (2025). Stream position shapes functional composition of aquatic insect metacommunities. *Marine and Freshwater Research*, *76*(9). https://doi.org/10.1071/mf24260

Milesi, S. V., & Melo, A. S. (2014). Conditional effects of aquatic insects of small tributaries on mainstream assemblages: position within drainage network matters. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(1), 1–9. https://doi.org/10.1139/cjfas-2013-0092

Moog, O. (2002). *Fauna aquatica Austriaca : a comprehensive species inventory of Austrian aquatic organisms with ecological notes*. Bundesministerium für Land-und Forstwirtschaft, Wien: Wasserwirtschaftskataster .

Nakamura, G., Vicentin, W., Súarez, Y. R., & Duarte, L. (2020). A multifaceted approach to analyzing taxonomic, functional, and phylogenetic β diversity. *Ecology*, *101*(10). https://doi.org/10.1002/ecy.3122

Novelo-Gutiérrez, R. (1998). Description of the larva of Remartinia secreta and notes on the larva of Remartinia luteipennis florida (Odonata: Aeshnidae). *The Canadian Entomologist*, *130*(6), 893–897. https://doi.org/10.4039/ent130893-6

Nyboer, E. A., Liang, C., & Chapman, L. J. (2019). Assessing the vulnerability of Africa's freshwater fishes to climate change: A continent-wide trait-based analysis. *Biological Conservation*, *236*, 505–520. https://doi.org/10.1016/j.biocon.2019.05.003

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., … Wagner, H. (2023). *vegan: Community Ecology Package*.

Patrick, C. J., Anderson, K. E., Brown, B. L., Hawkins, C. P., Metcalfe, A., Saffarinia, P., … Yuan, L. L. (2021). The application of metacommunity theory to the management of riverine ecosystems. *WIREs Water*, *8*(6). https://doi.org/10.1002/wat2.1557

Pes, A. M. O., Hamada, N., & Nessimian, J. L. (2005). Chaves de identificação de larvas para famílias e gêneros de Trichoptera (Insecta) da Amazônia Central, Brasil. *Revista Brasileira de Entomologia*, *49*(2), 181–204. https://doi.org/10.1590/s0085-56262005000200002

Pilière, A., Verberk, W. C. E. P., Gräwe, M., Breure, A. M., Dyer, S. D., Posthuma, L., … Schipper, A. M. (2015). On the importance of trait interrelationships for understanding environmental responses of stream macroinvertebrates. *Freshwater Biology*, *61*(2), 181–194. https://doi.org/10.1111/fwb.12690

Poff, N. L. (1997). Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. *Journal of the North American Benthological Society*, *16*(2), 391–409. https://doi.org/10.2307/1468026

Poff, N. L., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., & Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, *25*(4), 730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:ftnona]2.0.co;2

R Core Team. (2024). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, *Wien, Itävalta.*

Rabení, C. F., Doisy, K. E., & Zweig, L. D. (2005). Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences*, *67*(4), 395–402. https://doi.org/10.1007/s00027-005-0793-2

Rasband, W. S. (2024). ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA. Retrieved from imagej.net website: https://imagej.net/ij/

Ribeiro, J. M. F., & Gorayeb, I. D. S. (2016). Key to Plecoptera nymphs from the Brazilian Amazon (Insecta). *Zootaxa*, *4208*(5), 433. https://doi.org/10.11646/zootaxa.4208.5.2

Richardson, J. (2019). Biological Diversity in Headwater Streams. *Water*, *11*(2), 366. https://doi.org/10.3390/w11020366

Ridley, A. W., Hereward, J. P., Daglish, G. J., Raghu, S., Collins, P. J., & Walter, G. H. (2011). The spatiotemporal dynamics of Tribolium castaneum (Herbst): adult flight and gene flow. *Molecular Ecology*, *20*(8), 1635–1646. https://doi.org/10.1111/j.1365-294x.2011.05049.x

Salles , F., & Ferreira-Júnior, N. (2014). Hábitat e Hábitos. In *Insetos aquáticos na Amazônia brasileira: taxonomia, biologia e ecologia* (pp. 39–49). Manaus, AM: 1ª. Editora do INPA.

Santos, N. B. B., Cruz, G. M., Monteles, J. S., de Faria, A. P. J., Firmino, V. C., Shimano, Y., … Juen, L. (2024). Database of immature stage traits of Ephemeroptera, Plecoptera, and Trichoptera (EPT) genera for the Amazon. *Aquatic Sciences*, *86*(2). https://doi.org/10.1007/s00027-024-01051-4

Santos, N. D. (1969). Contribuição ao conhecimento da fauna do estado da Guanabara. 70--Descrição da ninfa de Perilestes fragilis Hagen in Selys, 1862 e notas sobre o imago (Odonata: Perilestidae). *Atas Da Sociedade de Biologia Do Rio de Janeiro* , *12*(5/6), 303–304.

Schmera, D., Árva, D., Boda, P., Bódis, E., Bolgovics, Á., Borics, G., … Vojtkó, A. E. (2018). Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshwater Biology*, *63*(1), 74–85. https://doi.org/10.1111/fwb.12973

Siqueira, T., Bini, L. M., Roque, F. O., Marques Couceiro, S. R., Trivinho-Strixino, S., & Cottenie, K. (2012). Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography*, *35*(2), 183–192. https://doi.org/10.1111/j.1600-0587.2011.06875.x

Snåre, H., García-Girón, J., Alahuhta, J., Bini, L. M., Boda, P., Bonada, N., … Heino, J. (2024). The relationships between biotic uniqueness and abiotic uniqueness are context dependent across drainage basins worldwide. *Landscape Ecology*, *39*(4). https://doi.org/10.1007/s10980-024-01883-3

Southwood, T. R. E. (1977). Habitat, the Templet for Ecological Strategies? *The Journal of Animal Ecology*, *46*(2), 336. https://doi.org/10.2307/3817

Statzner, B., Dolédec, S., & Hugueny, B. (2004). Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography*, *27*(4), 470–488. https://doi.org/10.1111/j.0906-7590.2004.03836.x

Strahler, A. N. (1957). Quantitative analysis of watershed geomorphology. *Transactions, American Geophysical Union*, *38*(6), 913. https://doi.org/10.1029/tr038i006p00913

Swan, C. M., & Brown, B. L. (2014). Using rarity to infer how dendritic network structure shapes biodiversity in riverine communities. *Ecography*, *37*(10), 993–1001. https://doi.org/10.1111/ecog.00496

Tolonen, K. T., Hämäläinen, H., Holopainen, I. J., Mikkonen, K., & Karjalainen, J. (2003). Body size and substrate association of littoral insects in relation to vegetation structure. *Hydrobiologia*, *499*(1/3), 179–190. https://doi.org/10.1023/a:1026325432000

Tonkin, J. D., Heino, J., Sundermann, A., Haase, P., & Jähnig, S. C. (2016). Context dependency in biodiversity patterns of central German stream metacommunities. *Freshwater Biology*, *61*(5), 607–620. https://doi.org/10.1111/fwb.12728

Townsend, C. R., & Hildrew, A. G. (1994). Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, *31*(3), 265–275. https://doi.org/10.1111/j.1365-2427.1994.tb01740.x

Trivinho-Strixino, S. (2011). *Larvas de Chironomidae. Guia de Identificação*. São Carlos, Depto Hidrobiologia/Lab. Entomologia Aquática/UFSCar.

Van de Meutter, F., Meester, L. D., & Stoks, R. (2007). Metacommunity structure of pond macroinvertebrates: effects of dispersal ability and generation time. *Ecology*, *88*(7), 1687–1695. https://doi.org/10.1890/06-0333.1

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. https://doi.org/10.1139/f80-017

Verberk, W. C. E. P., & Bilton, D. T. (2013). Respiratory control in aquatic insects dictates their vulnerability to global warming. *Biology Letters*, *9*(5), 20130473. https://doi.org/10.1098/rsbl.2013.0473

Vimos-Lojano, D., Hampel, H., Vázquez, R. F., & Martínez-Capel, F. (2020). Community structure and functional feeding groups of macroinvertebrates in pristine Andean streams under different vegetation cover. *Ecohydrology & Hydrobiology*, *20*(3), 357–368. https://doi.org/10.1016/j.ecohyd.2020.04.004

Von Ellenrieder, N. (2001). The larvae of Patagonian species of the genus Aeshna Fabricius (Anisoptera: Aeshnidae). *Odonatologica*, *30*(4), 423–434.

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Whittaker, R. H. (1972). Evolution and Measurement of Species Diversity. *Taxon*, *21*(2/3), 213. https://doi.org/10.2307/1218190

Wickham, H., Chang, W., & Wickham, M. H. (2016). Package “ggplot2”. Create elegant data visualisations using the grammar of graphics.. *Version*, *2*(1), 1–189.

SUPPLEMENTARY MATERIAL

Table S1: Geographic coordinates and hydrological distances between paired headwater and central stream sampling sites.

Pair	Coordinates		Hydrological distance
	Headwater	Central stream	(meters)
1	24.2730°S, 48.4547°W	24.2732°S, 48.4535°W	129.4
2	24.2646°S, 48.4004°W	24.2651°S, 48.3997°W	88.4
3	24.2718°S, 48.4245°W	24.2792°S, 48.4127°W	1453.6
4	24.3122°S, 48.3757°W	24.3131°S, 48.3780°W	251.6
5	24.0570°S, 47.9730°W	24.0562°S, 47.9722°W	121.6
6	24.0668°S, 47.9746°W	24.0676°S, 47.9760°W	160.8
7	24.1946°S, 47.9216°W	24.1950°S, 47.9219°W	60.8
9	24.1090°S, 47.9883°W	24.1083°S, 47.9852°W	325.8
10	24.0679°S, 47.9869°W	24.0700°S, 47.9873°W	238.3
11	24.0726°S, 47.9705°W	24.0736°S, 47.9743°W	403.6
12	24.0908°S, 47.9958°W	24.0900°S, 47.9952°W	114.6

n= 22

Table S2: Generalized linear model results for functional uniqueness (LCBD-f) as a function of environmental uniqueness (LCEH) and stream position, followed by simple slopes analysis.

Analysis Step / Parameter	Estimate	SE	95% CI (Lower)	95% CI (Upper)	z-value	p-value
Global GLM (glmmTMB)						
Intercept	-2.756	0.027	-2.80	-2.703	-99.77	**<2e-16**
LCEH (Headwater)	1.409	0.562	0.376	2.44	2.67	**0.007**
LCEH: Position (Central)	-1.218	0.531	-2.259	-0.177	-2.29	**0.021**
Simple Slopes (emtrends)						
LCEH:Headwater	1.41	0.527	0.376	2.44	2.674	**0.007**
LCEH:Central	0.19	0.675	-1.133	1.51	0.282	0.778

n= 22, df= 18

CAPÍTULO 2

DEFORESTATION AROUND SUBTROPICAL STREAMS DRIVES TAXONOMIC AND FUNCTIONAL NESTEDNESS OF AQUATIC INSECT COMMUNITIES

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Abstract
Deforestation in river catchments alters freshwater ecosystem conditions, leading to biodiversity loss. However, it remains unclear whether these losses occur sequentially, resulting in taxonomic and functional nested patterns among communities. We investigated whether deforestation surrounding streams leads to taxonomic and functional nestedness of aquatic insects, reflecting differences in species tolerance to anthropogenic disturbance. We sampled aquatic insects along an environmental gradient in 100 subtropical streams with different levels of riparian vegetation loss, ranging from highly impacted to well-preserved sites. Native vegetation cover explained a significant but small fraction of the environmental variation among streams. Deforestation revealed an ordered loss of genera, with some taxa significantly associated with more forested streams, such as *Macrogynoplax* (Plecoptera), *Hylister* (Ephemeroptera) and *Huleechius* (Coleoptera). The reduction of native vegetation was related to a significant taxonomic (NODF = 34.56) and functional nestedness (TraitNODF = 50.96), with communities in more deforested streams forming subsets of the species and traits present in more forested streams. Mantel tests and dbRDA indicated that differences in forest cover were associated with the taxonomic nestedness component of beta diversity, but not with taxonomic turnover or with functional beta diversity components. Thus, riparian vegetation loss was mainly related to the ordered loss of aquatic insect genera in subtropical streams. Our findings highlight the importance of preserving riparian vegetation for maintaining taxonomic and functional diversity in subtropical stream ecosystems.
Keywords: land use; lotic ecosystems; turnover; NODF; Atlantic Forest; treeNODF.

Introduction

Anthropogenic deforestation has been associated with major negative effects on the biodiversity and functioning of terrestrial and freshwater ecosystems (Sala et al. 2000; Petsch et al. 2021a; Wiebe and Wilcove 2025). In lotic ecosystems, deforestation can cause local extinctions and compromise ecosystem services such as flood control and water quality maintenance through natural filtration of sediments and pollutants (Dala-Corte et al. 2020; Petsch et al. 2021a; Lima et al. 2022; Malacarne et al. 2024). These impacts arise from changes in abiotic conditions, including higher temperatures, reduced dissolved oxygen, altered flow regimes, reduced input of coarse organic matter, and deteriorated water quality (Allan 2004; Leal et al. 2016; Castro et al. 2018; Petsch et al. 2021b). In addition, soil erosion and sedimentation can bury substrates used by aquatic organisms, further reducing habitat complexity and limiting species coexistence (Couceiro et al. 2010).

Abiotic alterations resulting from deforestation, together with the loss of habitat complexity, may lead to biodiversity loss in streams. This loss occurs particularly due to the disappearance of sensitive species, those naturally associated with environments characterized by specific conditions (Cantera et al. 2023). Specialized species, such as those dependent on woody matter consumption, also tend to decline whereas more generalist species capable of inhabiting multiple habitat types are often retained (Valente-Neto et al. 2015). Thus, deforestation can act as an environmental filter by reducing coarse woody debris or by changing other physiochemical conditions in the streams (i.e. sediment supply), selecting species according to the traits that enable them to persist in degraded sites (Faria et al. 2021). Consequently, communities in degraded streams may represent nested subsets of those found in more preserved environments. Nestedness describes a pattern in which communities with lower species richness contain subsets of taxa occurring in richer communities (Almeida-Neto et al. 2008). Therefore, stronger nestedness patterns may emerge along the degradation gradient.

To better understand whether biodiversity changes arise primarily from nested species loss or from species replacement along the degradation gradient, beta diversity assessments provide a useful framework for comparing variation in community composition across regions (Whittaker 1960; Whittaker 1972; Anderson et al. 2011; Chao et al. 2012; Liu et al. 2024). Beta diversity can be partitioned into two distinct components: nestedness and species turnover (Baselga 2010). In this context, species loss resulting from deforestation may not occur randomly, but sequentially, increasing the contribution of the nestedness component of beta diversity and leading to a pattern in which species composition at poorer (i.e., more

deforested) sites forms a subset of the diversity found in richer (i.e., more conserved) communities (Almeida-Neto et al. 2008; Schmera et al. 2020). Conversely, environmental changes generated by riparian vegetation degradation may contribute to species replacement, increasing turnover component of beta diversity by favoring specific taxa capable of colonizing newly created niches (Gutiérrez-Cánovas et al. 2013; Bishop et al. 2015; Zhao et al. 2021).

Although taxonomic diversity metrics are widely used, they may underestimate the ecological consequences of species loss because it does not account for differences in functional traits among taxa (Melo et al. 2014). Functional diversity is directly linked to the relationships between species and their environment (Brown et al. 2018), highlighting the ecological role of each species in ecosystem functioning (Poff et al. 2006; Ye et al. 2019). Loss of functional diversity may have more severe consequences for ecosystem functioning than reductions in taxonomic diversity alone (Flynn et al. 2009). In this sense, habitat loss resulting from native riparian vegetation deforestation may reduce the functional diversity of communities (Farneda et al. 2015; Lima et al. 2022), and previous studies indicate that this reduction may also produce a pattern of functional nestedness (e.g., Matthews et al. 2015; Almeida-Gomes et al. 2019). Functional nestedness would indicate the ordered loss of ecological strategies across sites, potentially reducing functional redundancy within communities and consequently increasing ecosystem vulnerability (Sanders et al. 2018).

Aquatic insects have been widely used to assess the impacts of deforestation on freshwater ecosystems, as their sensitivity to changes in habitat structure, water quality, and resource availability makes them excellent indicators of environmental degradation (Leal et al. 2020; Andrade 2022; Silva et al. 2025). Our study was conducted using a comprehensive subtropical database that has yielded several studies on aquatic insects (e.g., Siqueira et al. 2020; Petsch et al. 2021b; Schneck et al. 2022), including one showing that deforestation led to a loss of aquatic insect richness in Brazilian streams (Heino et al. 2018). However, it remains unclear whether deforestation restructures stream insect communities through ordered species loss (nestedness) or species replacement (turnover), and whether such patterns extend to functional structure.

We used data on aquatic insects collected from 100 subtropical streams in Brazil (Heino et al. 2018; Siqueira et al. 2020; Petsch et al. 2021b), spanning a broad gradient of native forest cover. We tested the hypothesis that deforestation surrounding streams would result in a nested loss of aquatic insect genera and functions along the vegetation gradient (Figure 1). First, we predicted that deforestation would be associated with the selective loss

of genera and functional traits linked to preserved vegetation, such as taxa dependent on coarse organic matter, shaded environments, or coarse substrates, thereby promoting a taxonomic (NODF - Nestedness Metric based on the Overlap and Decreasing Fill; Almeida-Neto et al. 2008) and functional (traitNODF; Melo et al. 2014) nestedness pattern across the deforestation gradient. Additionally, we predicted that decreasing forest cover would be associated with a higher nestedness component of taxonomic and functional beta diversity, rather than species turnover, indicating that communities in more deforested streams would represent subsets of those in more forested streams, reflecting stronger environmental filtering.

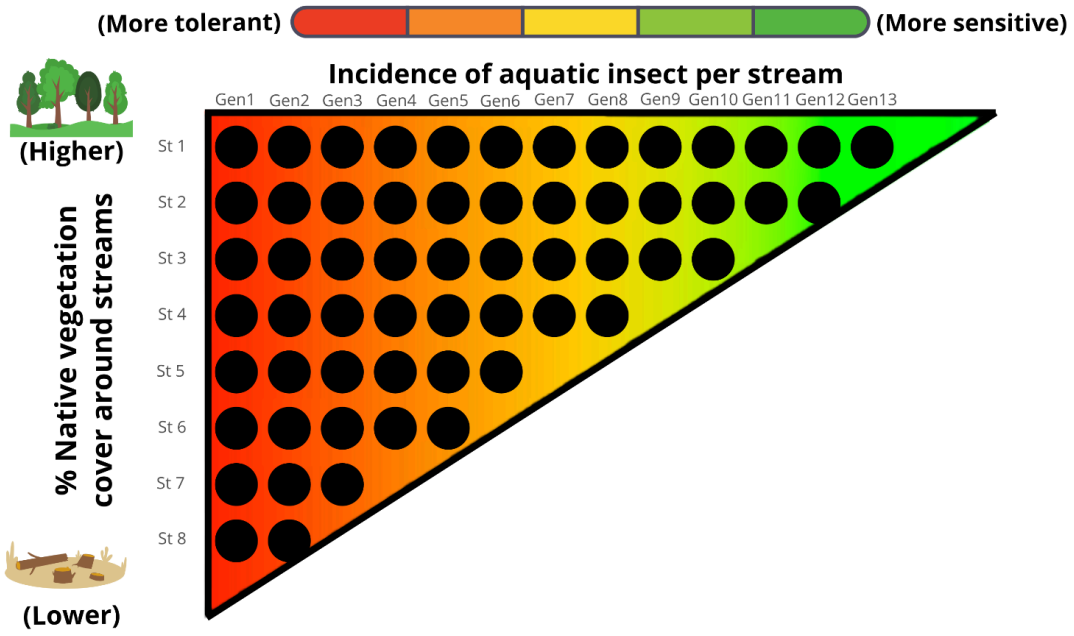

Figure 1. Conceptual representation of our hypothesis that deforestation around streams leads to a nested pattern of aquatic insects. Columns represent the incidence of aquatic insect genera ("Gen") per stream, with more tolerant genera on the left and more sensitive ones on the right. Rows represent streams ("St"), ordered from highest to lowest percentage of surrounding native vegetation cover.

Methods

Study area

We used a dataset comprising 100 streams sampled in the Southeast region of Brazil, between 23º49' - 24º20' S and 47º23' - 48º40' W, extending 70 km north-south and 120 km east-west (Figure 2). The sampled streams covered a wide variety of land uses, from regions almost completely deforested due to mechanized sugar cane plantation, pasture, or exotic forestry to pristine regions covered by native forest vegetation and located in protected areas of the state of São Paulo (Parque Estadual Intervales and Parque Estadual Carlos Botelho). The sampled

region has a long history of human land use, with most areas occupied predominantly by pasture and forestry between 1985 and 2000. From 2000 onwards, an expansion of agricultural and urban areas was observed (MapBiomas Project 2026) (Figure S1). Sampling occurred between September and November 2015 (beginning rainy season) and did not follow recent floods or extreme droughts. More details are available in Heino et al. (2018), Siqueira et al. (2020). Petsch et al. (2021b) and Schneck et al. (2022).

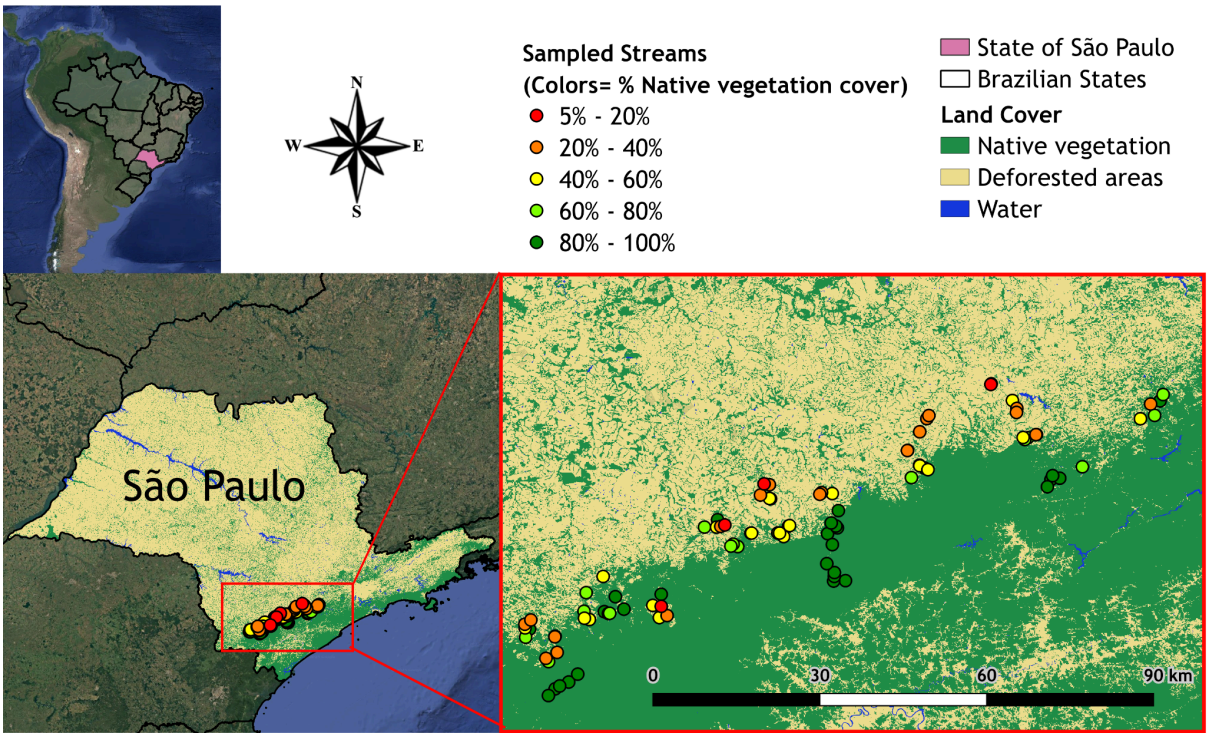

Figure 2. Map of the study area in the Atlantic Forest (São Paulo, Brazil). The sampled streams are shown along a continuous color gradient (red, orange, yellow, and green) representing the percentage of native vegetation cover. The colors range from 5% to 100% native vegetation cover, with red indicating the lowest cover and dark green the highest. Land cover is classified as native vegetation (green), deforested areas (beige), and water bodies (blue). Land-cover data were obtained from the MapBiomas platform and mapped in QGIS using images from 2015.

Vegetation cover

The percentage of native vegetation cover was assessed within a 200 m buffer (100 m on each side) along a 500 m stream segment, using hydrological and topographic data associated with high-resolution images from the Google Earth™ platform. The percentage of native vegetation cover was mapped by manually digitizing land use and land cover at 5 m spatial resolution from orthorectified RapidEye (Berlin, Germany) multispectral imagery (Planet 2016). We considered two types of native vegetation cover: primary (old growth) and secondary (forest that suffered human interference but presented significant natural regeneration). We decided to consider both types of native vegetation since secondary

vegetation provides considerable protection for the soil from erosion and the input of sediments to streams (Feldpausch et al. 2004; Chazdon et al. 2009). However, we repeated our analysis considering only primary vegetation as native vegetation to explore our deforestation hypothesis.

Abiotic variables

We measured the physical characteristics of current velocity (m/s), depth (cm), mean width (cm), and shading (%), as well as the chemical variables pH and conductivity (µS/cm), using a YSI 556 MPS probe (YSI Inc., Ohio, USA) in the field. We also collected water samples to determine total nitrogen (µg/L) and total phosphorus (µg/L) following the protocols of Golterman et al. (1978) and Mackereth et al. (1978). Substrate composition was visually estimated (%) within 0.25 m² quadrats at random locations along the sampled site, using a modified Wentworth scale for particle size classes: sand (0.25–2 mm), gravel (2–16 mm), pebble (16–64 mm), cobble (64–256 mm), and boulder (256–1024 mm).

Aquatic insects

We sampled aquatic insects using a kick-net (with 0.5 mm mesh) during four 30-second periods in riffles in each stream. The samples were preserved in alcohol (80%) in the field and sorted in the laboratory. The identification of larvae and nymphs at the species level is not feasible for most aquatic insects in the Neotropics since many species have not been described yet (Cruz et al. 2013). Therefore, we identified the aquatic insects of the orders Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera and Megaloptera at genus level with the help of specialized literature. Data on the abundance of the genera of aquatic insects found and land use around the streams are publicly available (Siqueira et al. 2019).

Traits

The functional traits were selected considering characteristics potentially affected by anthropogenic land use (adapted from Colzani et al. 2013). Deforestation around streams may reduce the amount of leaf litter and, consequently, the abundance of shredding organisms; in turn, the input of fine sediments, intensified by siltation, favors burrowing organisms; small-bodied organisms are also associated with deforested environments (Castro et al. 2018). The traits were organized into six categories (Table 1): case construction; body shape; locomotion groups; functional feeding guilds; respiration and body size. The information was obtained from the literature and through consultation with specialists.

Table 1. Functional characteristics of aquatic insects analyzed, adapted from Colzani et al. (2013) and Santos et al. (2024).

Traits	Categories	*Definition*	*Importance*
Refuge building	No refuge	*Free living*	*The type of refuge is related to the type of available substrate and influences the distribution of aquatic insects through their adaptation for protection against predators and foraging (Rabeni et al. 2005).*
	Fixed nets and retreats	*Fixed silk nets used in the interception and capture of food sources.*	
	Portable shelters of silk	*Mobile shelters built from biologically produced silk fibers.*	
	Portable shelters of sand, debris and/or wood	*Mobile shelters built from sand, rubble, and/or wood*	
	Portable shelters of leaf parts	*Mobile shelters built from leaf parts*	
Body shape	Hydrodynamic	*Flat and/or fusiform*	*Body shape is related to the environment an organism inhabits. Organisms with more flattened bodies have greater hydrodynamic ability and are typically found in environments with stronger currents (Merritt & Cummins, 1996; Poff et al. 2006; Castro et al. 2018).*
	Not hydrodynamic	*Cylindrical and/or round*	
Locomotion groups	Burrowers	*Dig down and reside in the soft, fine sediment*	*Related to feeding strategies and adaptations for colonizing different environments. Locomotion adaptations enable organisms to move and attach to the substrate (Salles & Ferreira-Júnior 2014).*
	Climbers/ crawlers	*Dwell on live aquatic plants or plant debris/have elongate bodies with thin legs, slowly move using legs*	
	Sprawlers	*Live on the bottom consisting of fine sediments*	
	Clingers	*Maintain a relatively fixed position on firm substrates in current*	
	Swimmers	*Adapted for moving through water*	

	Skaters	*Adapted to remain on the surface of water*	
Functional feeding guild	Collector-gatherers	*Eat fine detritus that has fallen out of suspension that is lying on the bottom or mixed with bottom sediments*	*Feeding habits indicate food availability in the environment and the mouthpart adaptations of organisms. Riparian vegetation directly influences food availability. For example, shredding insects depend on leaf litter inputs, and the presence or absence of groups with this trait can help assess environmental conditions (Cummins 1973; Cummins et al. 2005; Luiza-Andrade et al. 2020).*
	Collector-filterers	*Use special straining mechanisms to feed on fine detritus that is suspended in the water*	
	Herbivores	*Scraper and grazer organic plant material*	
	Predators	*Carnivores*	
	Shredders	*Break down plant material, intact or in large pieces*	
Respiration	Tegumental respiration	*By passive diffusion*	*Dissolved oxygen in water is influenced by temperature and current velocity; these characteristics directly affect the respiratory strategies of organisms and may favor or limit their occurrence (Mackay & Wiggins 1979; Verberk & Bilton 2013; Martins et al. 2017).*
	Gill respiration	*By branchial system*	
	Air	*By spiracles, tracheae, plastroms*	
Body size	1- Small-sized	*<9 mm*	*Variation in environmental habitat conditions can generate stress. This stress may lead to asynchronous emergence of males and females, compromising reproduction, as well as accelerating the post-embryonic development of immatures and consequently, affecting body size (Poff et al. 2006; Castro et al. 2018).*
	2- Medium-sized	*9-16 mm*	
	3- Large-sized	*>16 mm*	

Data analyses

To investigate whether the loss of genera due to deforestation caused a nested pattern, we first analyzed whether native vegetation cover was related to the genera richness of aquatic insects (this relationship has already been described by Heino et al. 2018, but not visually explored). For this, we fitted a generalized linear model (GLM) between aquatic insect genera richness (response variable) and the percentage of native vegetation cover around streams (predictor variable), considering the Poisson distribution. Because of the large variability in total abundance across studied streams (Heino et al. 2018), we also calculated rarefied species richness (minimum n = 20) for streams with more than 20 individuals (n = 90 streams). Then, we fitted a linear model between rarefied genus richness (response variable) and the percentage of native vegetation cover around streams (predictor variable). We repeated it using total native vegetation cover or only primary native vegetation cover as predictor variables. The assumptions of homoscedasticity and linearity of residuals were visually inspected and met. We used the 'lme4' package (Bates et al. 2014) from the R program (R Core Team 2023).

We also performed a PCA (Principal Component Analysis) to explore the relationship between the percentage of native vegetation cover and the abiotic characteristics of the streams. For this, we included native vegetation cover together with stream width, depth, current velocity, shading, pH, conductivity, phosphorus, nitrogen and substrate characteristics (gravel, pebble, stone, boulders, and fine sediment). We standardized the environmental variables using the *decostand* function from the 'vegan' package (Oksanen et al. 2023) and conducted the PCA with the *PCA* function from the 'FactoMineR' package (Husson et al. 2016). The contribution and orientation of variables in the ordination space were interpreted based on PCA loadings. In addition, we tested the relationship between native vegetation cover and each environmental variable separately using Spearman rank correlations. To control for multiple comparisons, p-values were adjusted using the Benjamini–Hochberg correction.

To calculate the nestedness of aquatic insects along the deforestation gradient, we ordered the streams in descending order according to the percentage of native forest cover (rows). We used the NODF metric (Nestedness Metric based on the Overlap and Decreasing Fill; Almeida-Neto et al. 2008), which quantifies nestedness by performing pairwise comparisons among sites. Our hypothesis is that more deforested sites harbor impoverished communities that form subsets of preserved sites, i.e., with lower species richness. If this condition is not met and the more deforested site has higher richness, the metric assigns a nesting value of zero to the pair. If the condition is met, the metric calculates the proportion of

genera present in the species-poor site that are also present in the species-rich site. Thus, nestedness is detected when communities with fewer species represent subsets of more species-rich communities. To perform the calculation, we constructed a presence–absence matrix of genera (rows = streams; columns = genera) and ordered the streams in descending order according to the percentage of native vegetation cover, reflecting our hypothesis of directional loss of genera as deforestation progresses. NODF values range from 0 (no nestedness) to 100 (perfect nestedness), with higher values indicating stronger patterns of directional loss forming subsets.The calculation of NODF requires consistent overlap of genera between species-poor and species-rich communities; differences in richness alone do not automatically produce high values of the index. In other words, nestedness will be detected when more deforested sites exhibit lower richness than more preserved ones and only when the genera present in those sites are subsets of those found in areas with greater vegetation cover. The occurrence of distinct genera among sites along the gradient characterizes species replacement, reducing the NODF value.

For functional nestedness, we created a site matrix with the streams (rows) ordered in descending order of native forest cover and genus richness (columns). We also calculated a functional dissimilarity matrix among genera (obtained from a matrix with genera in rows and functional traits in columns) using the *gowdis* function from the 'FD' package (Laliberté et al. 2014). Then, we generated a dendrogram with the *hclust* function from the 'ape' package (Paradis et al. 2019) and applied the *treeNODF* function from the 'CommEcol' package (Melo et al. 2014), which extends the traditional NODF by incorporating functional distances among genera into the nestedness calculation through a functional similarity dendrogram; when treeNODF is computed this way, it is referred to as traitNODF.

The NODF and traitNODF metrics are obtained by averaging pairwise comparisons. However, our data included 17 streams with 100% native vegetation cover, precluding pairwise comparisons as they lack differences in vegetation cover. To overcome this issue, we excluded comparisons between pairs of sites with identical vegetation values before obtaining averages. We performed 4,999 randomizations of the environmental variable (row order) to generate a null distribution of nestedness values (taxonomic and functional). This procedure allowed us to test the statistical significance of observed patterns. We estimated the p-value as the proportion of permutations in which the randomized NODF or traitNODF was equal to or higher than the observed value.

Taxonomic and functional nestedness are characterized by the ordered loss of genera and functions, forming increasingly impoverished subsets of richer communities. To explore

which taxa and traits are lost along the forest gradient, we filtered genera occurring in at least five sites and fitted generalized linear models (occurrence ~ % vegetation), where the coefficient associated with forest cover represented the direction of the response: $\beta > 0$ = higher probability of occurrence in forested environments and $\beta < 0$ = higher probability of occurrence in deforested environments. For the functional analysis, we organized a genera × traits matrix and, using a presence–absence matrix, calculated Community Weighted Means (CWM) for each trait and site using the *functcomp* function from the 'FD' package. We compared the extreme environmental quartiles, as in the taxonomic analysis, and fitted simple linear models (CWM ~ % vegetation) to examine continuous functional changes along the vegetation gradient.

In addition to the NODF and traitNODF analyses, we partitioned taxonomic and functional beta diversity to investigate turnover and nestedness patterns (following Baselga 2010 approach). We decomposed taxonomic beta diversity, as total Sørensen dissimilarity (*β_sor*), into turnover (*β_sim*) and nestedness (*β_sne*) components using the *beta.pair* function implemented in the 'betapart' package (Baselga et al. 2018). For functional beta diversity, we first reduced the multidimensional trait space through Principal Coordinates Analysis (PCoA) based on Gower distances among genera. The first three PCoA axes were retained to represent the functional space. We then used these coordinates to calculate pairwise total functional dissimilarities and partitioned them into functional turnover (*β_sim*) and functional nestedness (*β_sne*) using the *functional.betapart.core* and *functional.beta.pair* functions in the 'betapart' R package. Streams with fewer than four genera (n = 7 streams) were excluded from the functional analyses to avoid instability in the estimation of multidimensional volume.

Finally, to assess whether beta diversity components were associated with differences in forest cover, we performed Mantel tests between pairwise dissimilarity matrices (taxonomic and functional components) and Euclidean distances in forest cover percentage among streams. Significance was evaluated using 999 permutations. Additionally, we also used partial distance-based redundancy analysis (dbRDA) to test the effect of forest cover on the components of taxonomic and functional beta diversity. The dbRDA models were fitted using the *capscale* function in the 'vegan' package, with total beta diversity dissimilarity and its turnover and nestedness dissimilarity components as response variables and forest cover as the predictor variable. We controlled for spatial autocorrelation among sampling sites by including spatial eigenvectors derived from geographic coordinates (dbMEM; distance-based Moran's eigenvector maps) in the models. We performed tests with 999 permutations to assess

the significance of each model. To estimate the fraction of variation explained exclusively by the vegetation gradient and by spatial structure, we performed a variation partitioning analysis using the *varpart* function from the 'vegan' package.

Results

The Principal Component Analysis (PCA) revealed substantial environmental variation among streams, with the first two accounting for 32.7% of the total variation (PCA1 = 18.6%; PCA2 = 14.1%). The first axis (PCA1) was mainly associated with substrate composition and channel structure, particularly cobbles, boulders, pebbles, velocity, channel width, and native vegetation cover. Streams with higher native vegetation cover were also deeper and larger, with greater boulder availability and higher water velocity. The second axis was primarily related to water chemistry variables, especially pH and conductivity, with conductivity and fine sediment positioned opposite to native vegetation cover in the ordination space (Figure 3). Spearman correlation analyses between native vegetation cover and individual abiotic variables indicated a significant positive association only with channel width (rho = 0.32, adjusted p = 0.017).

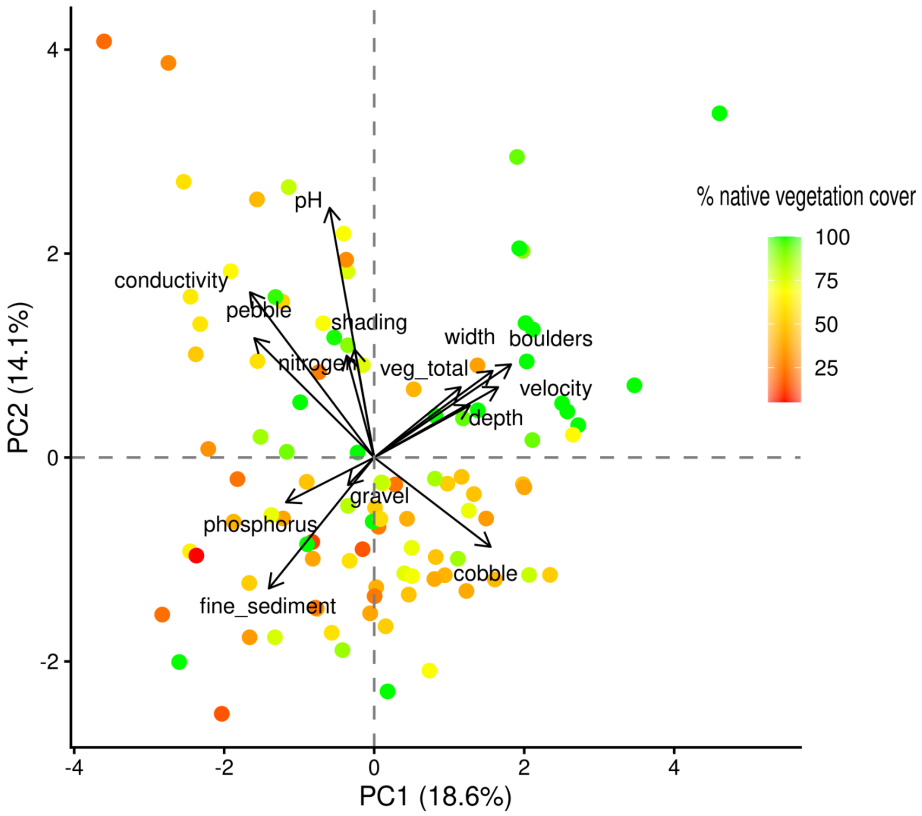

Figure 3. Principal Component Analysis (PCA) of stream abiotic variables along a gradient of native vegetation cover. Streams are colored along a gradient from red (indicating the lowest percentage of native riparian vegetation) to green (indicating the highest).Veg_total = Native vegetation cover (%);

Streams had 1 to 39 genera of aquatic insects, with a total of 83 genera. We found a positive relationship between the genera richness of aquatic insects and total percentage of native forest (primary and secondary vegetation) surrounding the streams (observed richness: pseudo $R^2_{(1,98)}$= 0.543; z = 8.779; p < 0.001; rarefied richness: $F_{(1,88)}$= 9.61; R^2= 0.098; p = 0.003; Figure 4A). We repeated this analysis considering only primary vegetation as a predictor variable and found the same pattern, albeit with a stronger relationship between vegetation cover and genera richness of aquatic insects (observed richness: pseudo $R^2_{(1,98)}$= 0.644; z = 10.06 ; p < 0.001; rarefied richness: $F_{(1,88)}$= 19.42; R^2= 0.189; p < 0.001; Figure 4B).

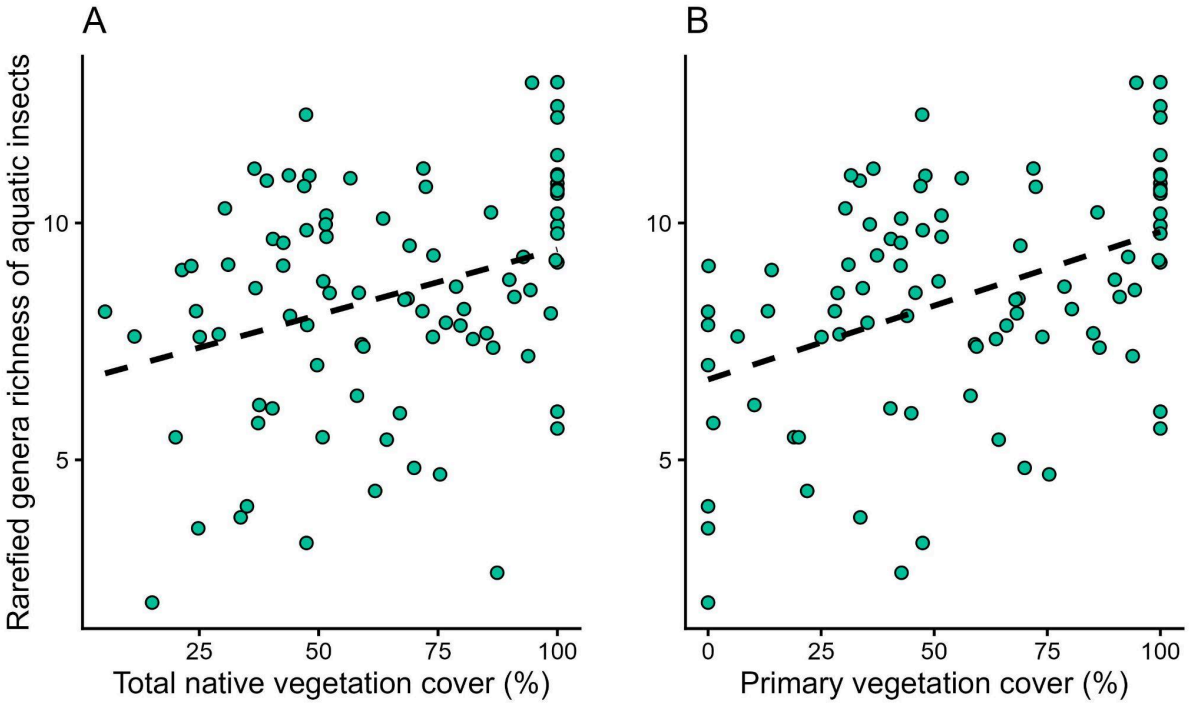

Figure 4. Rarefied genera richness of aquatic insects according to the percentage of primary and secondary (total) (A) and only primary (B) vegetation cover (%) around streams in the Atlantic Forest (Brazil).

The genera most strongly associated with high percentages of native vegetation were *Macrogynoplax* (Plecoptera) (β = 5.76; p = 0.003), *Hylister* (Ephemeroptera) (β = 4.21; p < 0.001), *Huleechius* (Coleoptera) (β = 3.41; p = 0.025), *Baetodes* (Ephemeroptera) (β = 3.08; p = 0.002) and *Anacroneuria* (Plecoptera) (β = 2.87; p < 0.001). In contrast, only *Ulmeritoides* (Ephemeroptera) was significantly associated with more deforested sites (β = -6.37; p = 0.023) (Table S1). In turn, the functional traits most strongly associated with more forested environments were substrate-clinging organisms (β = 0.121; p = 0.039), non-swimming

organisms (β = 0.077; p = 0.015), aerial respiration (β = 0.073; p < 0.001), and absence of gills (β = 0.071; p = 0.003).

When analyzing the loss of aquatic insect richness along the gradient of decreasing total vegetation cover, we detected a taxonomic nested pattern (NODF = 34.56; p < 0.001; NODF values found in permutations ranged from 18.55 to 33.40). We observed slightly higher NODF values when considering only primary vegetation (NODF = 35.89; p < 0.001). We also found a significant functional nestedness pattern along the deforestation gradient (traitNODF = 50.96; p < 0.001; traitNODF values found in permutations ranged from 28.24 to 49.62), corroborating our expectations.

Finally, when we partitioned taxonomic beta diversity into species turnover and nestedness components, we found strong differentiation across the entire study area (average pairwise comparison; *β_sor*= 0.649), driven more by turnover (*β_sim* = 0.464) than nestedness (*β_sne* = 0.185). Despite the predominance of taxonomic turnover in total beta diversity, Mantel tests revealed that the nestedness component was significantly associated with differences in forest cover (r = 0.093, p = 0.003), while taxonomic turnover showed no significant relationship (r = −0.02, p = 0.745). We corroborated these findings using partial distance-based redundancy analysis (dbRDA), controlling for spatial structure: forest cover significantly explained variation in the nestedness component ($F_{(1,94)}$ = 2.34, p = 0.015), but not in turnover ($F_{(1,94)}$ = 1.08, p = 0.359). Variation partitioning showed that vegetation cover independently explained about 6% of the variation in nestedness, whereas spatial variables accounted only for 1.4%, with an additional 5.9% shared between vegetation and spatial structure. In contrast, turnover was not related to vegetation cover and was mainly associated with spatial structure (7.4% of the variation explained).

In turn, pairwise functional dissimilarity showed a mean total functional beta diversity (*β_sor* = 0.53) predominantly explained by the nestedness component (*β_sne* = 0.32), whereas functional turnover (*β_sim* = 0.22) contributed less to total functional dissimilarity. However, Mantel tests revealed no significant association between differences in total vegetation cover and the components of functional beta diversity (functional turnover: r = 0.046, p = 0.10; functional nestedness: r = 0.016, p = 0.319). We found similar findings using dbRDA analyses controlling for spatial autocorrelation: vegetation cover did not significantly explain functional turnover ($F_{(1,87)}$ = 0.66, p = 0.749) or functional nestedness ($F_{(1,87)}$ = 0.71, p = 0.582). The variation partitioning analysis indicated that only spatial variables explained part of the variation in the nestedness component of functional beta diversity (approximately 14%).

Discussion

We found significant taxonomic (NODF) and functional (traitNODF) nestedness of aquatic insects across the deforestation gradient, supporting our hypothesis that deforestation is related to an ordered loss of genera and traits, resulting in impoverished subsets of communities in otherwise more preserved streams. Also, when relating the taxonomic beta diversity components to the vegetation gradient, only taxonomic nestedness was significantly associated, suggesting that deforestation contributes to the ordered loss of genera. In contrast, turnover was not related to the vegetation gradient and appears to be partially structured by spatial processes, indicating that differences among streams may also reflect dispersal-related dynamics and the spatial organization of communities. However, neither turnover nor nestedness components of functional beta diversity were associated with deforestation.

The apparent mismatch between significant NODF/traitNODF values and the weaker or non-significant nestedness components from beta diversity partitioning likely reflects methodological differences between these approaches. While NODF explicitly tests whether communities ordered along the vegetation gradient form subsets of richer communities (Almeida-Neto et al. 2008), beta diversity partitioning decomposes pairwise dissimilarities into turnover and nestedness components across the whole metacommunity (Baselga 2010). Therefore, significant NODF indicates an ordered loss pattern along the deforestation gradient, while beta diversity partitioning shows that, overall, compositional differences among streams are still largely influenced by turnover.

We detected a nested pattern in both taxonomic (NODF) and functional (traitNODF) diversity facets along the deforestation gradient. These findings suggest that streams with lower native vegetation cover are subsets associated not only with lower taxonomic richness but also with lower functional diversity, compared to streams with higher percentages of native vegetation (Melo et al. 2014; Almeida-Gomes et al. 2019). However, no component of functional beta diversity was significantly related to the vegetation gradient; at a local scale, environmental filters select species with similar traits that determine their survival in the environment, leading to functional redundancy (Dee et al. 2016; Nash et al. 2016; Sanders et al. 2018; Cantera et al. 2023). Functional redundancy may buffer the effects of environmental degradation on functional structure. However, the loss of sensitive and specialized species in deforested streams tends to impoverish functional diversity (Tonkin et al. 2017), potentially decreasing community functional redundancy and compromising ecosystem stability

(Sanders et al. 2018). High species loss, beyond the buffer provided by functional redundancy, can affect the functional structure and, in more extreme cases, is likely to result in severe effects on ecosystem functions (Flynn et al. 2009).

Our study indicated the impact of deforestation on organisms that cling to the substrate, such as *Macrogynoplax* (Plecoptera), *Hylister* (Ephemeroptera), and *Leptonema* (Trichoptera), possibly due to fine sediment deposition resulting from soil erosion processes. In turn, swimming habit and the presence of gills were positively related to more deforested environments; gill structures make it possible for organisms to adapt to less oxygenated environments through the mechanism of reoxygenation by gas exchange and water flow, leading to short-term tolerance (Wang et al. 2025), while swimming abilities may favor organisms during soil erosion processes. In parallel, Lima et al. (2022) observed that riparian deforestation negatively affected insects of the orders Ephemeroptera, Plecoptera, and Trichoptera with shredding and collector feeding habits, likely due to alluvial deposition and the loss of environmental complexity caused by the removal of riparian vegetation.

Although streams with low levels of deforestation generally exhibited higher genus richness, some sites with substantial vegetation, including areas with primary and secondary vegetation cover, showed low richness. This pattern may reflect the history of land use and land cover changes and land use intensification, where negative effects persist even after vegetation regeneration (Roque et al. 2018; Santos et al. 2020; Tabi et al. 2025). This interpretation is reinforced by the stronger positive relationship between genus richness and vegetation cover, as well as the slightly higher NODF value, when only primary vegetation is considered, since the lower richness observed in streams with higher percentages of vegetation reduces NODF values (Almeida-Neto et al. 2008). Furthermore, even after forest regeneration, aquatic insect communities may differ from those found in primary forests, an effect that favors turnover and reduces the observed nestedness (Fuchs et al. 2003). Thus, the calculation considering only primary vegetation may more adequately reflect our hypotheses.

The Principal Component Analysis (PCA) indicated environmental variation among streams, although the first two axes explained a relatively small proportion of the total variation, suggesting that other unmeasured variables also contribute to these environmental differences. Native vegetation cover was positioned in the ordination alongside wider channels and coarser substrates, and opposite to conductivity and fine sediment, suggesting some overlap between vegetation cover and habitat characteristics. However, only channel width showed a significant association with native vegetation cover. Sweeney et al. (2004) also observed that more forested streams were associated with wider channels. In deforested

environments, channel narrowing may occur due to the invasion of riparian margins by grasses, whose growth tends to be naturally limited by forest cover (Sweeney 1993; Allan & Castillo 2007). This narrowing may reduce benthic habitat availability (Sweeney et al. 2004), which may help explain the functional patterns observed in our study, particularly the association of more forested streams with substrate-clinging and non-swimming organisms. Water velocity may also contribute to structuring aquatic insect communities by influencing habitat conditions, such as oxygen availability and the persistence of organisms with different respiratory and locomotion traits (Mackay & Wiggins 1979; Verberk & Bilton 2013; Martins et al. 2017). However, as this relationship was not strongly supported by our data, this interpretation should be viewed with caution. Different land-use types contribute to specific changes in habitat characteristics and different compositional responses (Saberi-Pirooz et al. 2024; Bae & Kim 2025). In our study, we focused on analyzing the effects of riparian native vegetation loss, but we acknowledge that these effects may be more or less severe depending on the type of land use that replaces the original forest. However, our considerable sample size supports a consistent pattern of nested loss of aquatic insect genera along the deforestation gradient.

Our study revealed important information about community responses to riparian vegetation deforestation. First, the loss of primary riparian forest is accompanied by the ordered loss of aquatic insect genera, where functional traits favor or limit the persistence of these organisms along the vegetation gradient. Functional diversity also undergoes an ordered loss according to the deforestation gradient, although more subtle in the short term compared to taxonomic diversity. We suggest that indirect physical consequences of deforestation on habitat structure may result in the loss of aquatic insect functions, which may in the long term destabilize important ecosystem processes. Our findings highlight the importance of native riparian vegetation for the conservation and maintenance of streams and biotic communities, underscoring the relevance of conserving at least a buffer strip of vegetation that may mitigate the severity of land-use effects. Importantly, we identified a consistent pattern of taxonomic and functional nestedness, highlighting preserved areas as conservation priorities, as they support not only a larger portion of the regional species pool but also a more diverse set of functional traits, emphasizing their central role in maintaining regional biodiversity.

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References

Allan, J. D. (2004). Landscapes and Riverscapes: the Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 257–284. https://doi.org/10.1146/annurev.ecolsys.35.120202.110122

Almeida-Gomes, M., Vieira, M. V., Frederico, C., & Melo, A. S. (2019). Habitat amount drives the functional diversity and nestedness of anuran communities in an Atlantic Forest fragmented landscape. *Biotropica*, *51*(6), 874–884. https://doi.org/10.1111/btp.12687

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, *117*(8), 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., … Swenson, N. G. (2010). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, *14*(1), 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Andrade, A. L., Silva, R. R., Shimano, Y., Faria, J., Cardoso, M. N., Brasil, L. S., … Juen, L. (2022). Niche breadth and habitat preference of Ephemeroptera, Plecoptera, and Trichoptera (Insecta) in streams in the Brazilian Amazon. *Hydrobiologia*, *849*(19), 4287–4306. https://doi.org/10.1007/s10750-022-04987-6

Bae, M.-J., & Kim, E.-J. (2025). Taxonomic and functional responses of stream macroinvertebrates across different land use types. *Npj Biodiversity*, *4*(1). https://doi.org/10.1038/s44185-025-00110-9

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Bates , D., Maechler , M., Bolker, B., & Walker , S. (2014). lme4: Linear Mixed-Effects Models Using Eigen and S4. *R Package Version 1.1-7*.

Bishop, T. R., Robertson, M. P., Rensburg, van, & Parr, C. L. (2015). Contrasting species and functional beta diversity in montane ant assemblages. *Journal of Biogeography*, *42*(9), 1776–1786. https://doi.org/10.1111/jbi.12537

Brown, L. E., Khamis, K., Wilkes, M., Blaen, P., Brittain, J. E., Carrivick, J. L., … Milner, A. M. (2018). Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution*, *2*(2), 325–333. https://doi.org/10.1038/s41559-017-0426-x

Cantera, I., Jézéquel, C., Dejean, T., Murienne, J., Vigouroux, R., Valentini, A., & Brosse, S. (2023). Deforestation strengthens environmental filtering and competitive exclusion in Neotropical streams and rivers. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2006). https://doi.org/10.1098/rspb.2023.1130

Castro, D. M. P., Dolédec, S., & Callisto, M. (2018). Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. *Ecological Indicators*, *84*, 573–582. https://doi.org/10.1016/j.ecolind.2017.09.030

Chao, A., Chiu, C.-H., & Hsieh, T. C. (2012). Proposing a resolution to debates on diversity partitioning. *Ecology*, *93*(9), 2037–2051. https://doi.org/10.1890/11-1817.1

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., … Miller, S. E. (2009). The Potential for Species Conservation in Tropical Secondary Forests. *Conservation Biology*, *23*(6), 1406–1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x

Colzani, E., Siqueira, T., Suriano, M. T., & Roque, F. O. (2013). Responses of Aquatic Insect Functional Diversity to Landscape Changes in Atlantic Forest. *Biotropica*, *45*(3), 343–350. https://doi.org/10.1111/btp.12022

Couceiro, S. R. M., Hamada, N., Forsberg, B. R., & Padovesi-Fonseca, C. (2009). Effects of anthropogenic silt on aquatic macroinvertebrates and abiotic variables in streams in the Brazilian Amazon. *Journal of Soils and Sediments*, *10*(1), 89–103. https://doi.org/10.1007/s11368-009-0148-z

Cruz, P. V., Salles, F. F., & Hamada, N. (2013). A new genus and species of Baetidae (Insecta: Ephemeroptera) from Brazil. *Annales de Limnologie - International Journal of Limnology*, *49*(1), 1–12. https://doi.org/10.1051/limn/2013033

Cummins, K. W. (1973). Trophic Relations of Aquatic Insects. *Annual Review of Entomology*, *18*(1), 183–206. https://doi.org/10.1146/annurev.en.18.010173.001151

Cummins, K. W., Merritt, R. W., & Andrade, P. C. (2005). The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. *Studies on Neotropical Fauna and Environment*, *40*(1), 69–89. https://doi.org/10.1080/01650520400025720

Dala‐Corte, R. B., Melo, A. S., Siqueira, T., Bini, L. M., Martins, R. T., Cunico, A. M., … Souza, F. N. (2020). Thresholds of freshwater biodiversity in response to riparian vegetation loss in the Neotropical region. *Journal of Applied Ecology*, *57*(7), 1391–1402. https://doi.org/10.1111/1365-2664.13657

Dee, L. E., Miller, S. J., Peavey, L. E., Bradley, D., Gentry, R. R., Startz, R., … Lester, S. E. (2016). Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1836), 20161435. https://doi.org/10.1098/rspb.2016.1435

Farneda, F. Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J. M., … Meyer, C. F. J. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, *52*(5), 1381–1391. https://doi.org/10.1111/1365-2664.12490

Feldpausch, T. R., Rondón, M. A., Fernandes, E. C. M., Riha, S. J., & Wandelli, E. V. (2004). Carbon and nutrient accumulation in secondary forests regenerating on pastures in Central Amazonia. *Ecological Applications*, *14*(sp4), 164–176. https://doi.org/10.1890/01-6015

Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., … DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, *12*(1), 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Fuchs, S. A., Hinch, S. G., & Mellina, E. (2003). Effects of streamside logging on stream macroinvertebrate communities and habitat in the sub-boreal forests of British Columbia, Canada. *Canadian Journal of Forest Research*, *33*(8), 1408–1415. https://doi.org/10.1139/x03-070

Golterman, H. L. (1978). Methods for physical and chemical analysis of fresh waters . *Blackwell Scientific Publications, Oxford*, *2nd edn.*

Gutiérrez-Cánovas, C., Millán, A., Velasco, J., Vaughan, I. P., & Ormerod, S. J. (2013). Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Global Ecology and Biogeography*, *22*(7), 796–805. https://doi.org/10.1111/geb.12060

Heino, J., Melo, A. S., Jyrkänkallio‐Mikkola, J., Petsch, D. K., Saito, V. S., Tolonen, K., … Siqueira, T. (2018). Subtropical streams harbour higher genus richness and lower abundance of insects compared to boreal streams, but scale matters. *Journal of Biogeography*, *45*(9), 1983–1993. https://doi.org/10.1111/jbi.13400

Husson , F., Josse , J., Le , S., & Mazet , J. (2019). FactoMineR: Multivariate Exploratory Data Analysis and Data Mining. *R Package Version 1.41*.

J David Allan, & CastilloM. M. (2007). *Stream Ecology : Structure and function of running waters*. Dordrecht: Springer Netherlands.

Laliberté , E., Legendre , P., & Shipley, B. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. *R Package Version 1.0-12*.

Leal, C. G., Lennox, G. D., Ferraz, S. F. B., Ferreira, J., Gardner, T. A., Thomson, J. R., … Moura, N. G. (2020). Integrated terrestrial-freshwater planning doubles conservation of tropical aquatic species. *Science*, *370*(6512), 117–121. https://doi.org/10.1126/science.aba7580

Leal, C. G., Pompeu, P. S., Gardner, T. A., Leitão, R. P., Hughes, R. M., Kaufmann, P. R., … Barlow, J. (2016). Multi-scale assessment of human-induced changes to Amazonian instream habitats. *Landscape Ecology*, *31*(8), 1725–1745. https://doi.org/10.1007/s10980-016-0358-x

Lima, M., Firmino, V. C., de Paiva, C. K. S., Juen, L., & Brasil, L. S. (2022). Land use changes disrupt streams and affect the functional feeding groups of aquatic insects in the Amazon. *Journal of Insect Conservation*. https://doi.org/10.1007/s10841-022-00375-6

Liu, Y., Zhu, Y., Wu, S., Wang, Y., Xie, J., Zhang, K., & Xu, Y. (2024). Determinants of taxonomic, functional, and phylogenetic beta diversity in breeding birds within urban remnant woodlots: Implications for conservation. *Ecology and Evolution*, *14*(5). https://doi.org/10.1002/ece3.11426

Luiza-Andrade, A., Brasil, L. S., Torres, N. R., Brito, J., Silva, R. R., Maioli, L. U., … Juen, L. (2020). Effects of Local Environmental and Landscape Variables on the Taxonomic and Trophic Composition of Aquatic Insects in a Rare Forest Formation of the Brazilian Amazon. *Neotropical Entomology*, *49*(6), 821–831. https://doi.org/10.1007/s13744-020-00814-6

Mackay, R. J., & Wiggins, G. B. (1979). Ecological Diversity in Trichoptera. *Annual Review of Entomology*, *24*(1), 185–208. https://doi.org/10.1146/annurev.en.24.010179.001153

Mackereth , F. J. H. (1978). Water analysis: some revised methods for limnologists. *Freshw Biol Assoc Sci*, *Publ 36*.

Malacarne, T. J., Machado, N. R., & Moretto, Y. (2024). Influence of land use on the structure and functional diversity of aquatic insects in neotropical streams. *Hydrobiologia*, *851*(2), 265–280. https://doi.org/10.1007/s10750-023-05207-5

MapBiomas Project. (2026). Collection 10.1 of the Annual Land Use and Land Cover Maps of Brazil. Retrieved from http://mapbiomas.org.

Martins, R. G., Melo, A. S., Gonçalves, J., Campos, C. M., & Hamada, N. (2017). Effects of climate change on leaf breakdown by microorganisms and the shredder Phylloicus elektoros (Trichoptera: Calamoceratidae). *Hydrobiologia*, *789*(1), 31–44. https://doi.org/10.1007/s10750-016-2689-7

Matthews, T. J., Sheard, C., Cottee-Jones, H. E. W., Bregman, T. P., Tobias, J. A., & Whittaker, R. J. (2015). Ecological traits reveal functional nestedness of bird communities in habitat islands: a global survey. *Oikos*, *124*(7), 817–826. https://doi.org/10.1111/oik.02370

Melo, A. S., Cianciaruso, M. V., & Mário Almeida‐Neto. (2014). treeNODF: nestedness to phylogenetic, functional and other tree‐based diversity metrics. *Methods in Ecology and Evolution*, *5*(6), 563–572. https://doi.org/10.1111/2041-210x.12185

Merrit, R. W., & Cummins, K. W. (1996). An Introduction to the Aquatic Insects of North America. *Journal of the North American Benthological Society*, *15*(3), 401–403. https://doi.org/10.2307/1467288

Nash, K. L., Graham, N. A. J., Jennings, S., Wilson, S. K., & Bellwood, D. R. (2016). Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. *Journal of Applied Ecology*, *53*(3), 646–655. https://doi.org/10.1111/1365-2664.12430

Oksanen , J., Blanchet , F. G., Friendly , M., Kindt , R., Legendre , P., McGlinn , D., … Wagner , H. (2023). vegan: Community Ecology Package. *R Package Version 2.6-4*.

Paradis , E., Blomberg , S., Bolker , B., Brown , J., Claude, J., Cuong, H. S., … Louveaux , J. (2019). ape: Analyses of Phylogenetics and Evolution. *R Package Version 5.4-1*.

Paula, A., Kaory, C., Calvão, L. B., Cruz, G. M., & Juen, L. (2021). Response of aquatic insects to an environmental gradient in Amazonian streams. *Environmental Monitoring and Assessment*, *193*(11). https://doi.org/10.1007/s10661-021-09553-6

Petsch, D. K., Blowes, S. A., Melo, A. S., & Chase, J. M. (2021a). A synthesis of land use impacts on stream biodiversity across metrics and scales. *Ecology*, *102*(11). https://doi.org/10.1002/ecy.3498

Petsch, D. K., Saito, V. S., Landeiro, V. L., Silva, T. S., Bini, L. M., Heino, J., … Melo, A. S. (2021b). Beta diversity of stream insects differs between boreal and subtropical regions, but land use does not generally cause biotic homogenization. *Freshwater Science*, *40*(1), 53–64. https://doi.org/10.1086/712565

Planet . (2016). RapidEye™ imagery product specifications. Version 6.1. Retrieved from Planet website: https://www.planet.com/products/satellite-imagery/files/160625-RapidEye%20Image-Product-Specifications.pdf

Poff, N. L., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., & Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, *25*(4), 730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:ftnona]2.0.co;2

R Core Team . (2023). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*.

Rabení, C. F., Doisy, K. E., & Zweig, L. D. (2005). Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences*, *67*(4), 395–402. https://doi.org/10.1007/s00027-005-0793-2

Roque, F. O., Menezes, J. F. S., Northfield, T., Ochoa-Quintero, J. M., Campbell, M. J., & Laurance, W. F. (2018). Warning signals of biodiversity collapse across gradients of tropical forest loss. *Scientific Reports*, *8*(1), 1622. https://doi.org/10.1038/s41598-018-19985-9

Saberi-Pirooz, R., Ahmadzadeh, F., & Javidkar, M. (2024). Nightmare of forests: Secondary forestation silently alters soil macroinvertebrate communities. *Applied Soil Ecology*, *196*, 105279. https://doi.org/10.1016/j.apsoil.2024.105279

Sala, O. E. (2000). Global Biodiversity Scenarios for the Year 2100 . *Science*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Salles , F., & Ferreira-Júnior, N. (2016). Hábitat e Hábitos . In *Insetos aquáticos na Amazônia brasileira: taxonomia, biologia e ecologia* (pp. 39–49). Manaus, AM: 1a. Editora do INPA.

Sanders, D., Thébault, E., Kehoe, R., & van Veen, F. F. (2018). Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences*, *115*(10), 2419–2424. https://doi.org/10.1073/pnas.1716825115

Santos, E. P., Wagner, H. H., Ferraz, S. F. B., & Siqueira, T. (2020). Interactive persistent effects of past land‐cover and its trajectory on tropical freshwater biodiversity. *Journal of Applied Ecology*, *57*(11), 2149–2158. https://doi.org/10.1111/1365-2664.13717

Santos, N. B. B., Cruz, G. M., Monteles, J. S., de Faria, A. P. J., Firmino, V. C., Shimano, Y., … Juen, L. (2024). Database of immature stage traits of Ephemeroptera, Plecoptera, and Trichoptera (EPT) genera for the Amazon. *Aquatic Sciences*, *86*(2). https://doi.org/10.1007/s00027-024-01051-4

Schmera, D., Podani, J., & Legendre, P. (2020). What do beta diversity components reveal from presence-absence community data? Let us connect every indicator to an indicandum! *Ecological Indicators*, *117*, 106540. https://doi.org/10.1016/j.ecolind.2020.106540

Schneck, F., Bini, L. M., Melo, A. S., Petsch, D. K., Saito, V. S., Wengrat, S., & Siqueira, T. (2022). Catchment scale deforestation increases the uniqueness of subtropical stream communities. *Oecologia*, *199*(3), 671–683. https://doi.org/10.1007/s00442-022-05215-7

Silva, E. C., Souza, F., Geraldo, F., Juen, L., Rocha, T. S., & Oliveira-Junior, J. M. B. (2025). Impacts of oil palm monocultures on freshwater ecosystems in the Amazon: a case study of dragonflies and damselflies (Insecta: Odonata). *Aquatic Sciences*, *87*(1). https://doi.org/10.1007/s00027-024-01126-2

Siqueira , T., Bini , L. M., Jyrkänkallio-Mikkola , J., Landeiro, V. L., Melo, A. S., Pajunen , V., … Heino, J. (2019). Data and script: relationship between community size and beta diversity in tropical and boreal streams . Retrieved from (1.3). Zenodo.

Siqueira, T., Saito, V. S., Bini, L. M., Melo, A. S., Petsch, D. K., Landeiro, V. L., … Heino, J. (2020). Community size can affect the signals of ecological drift and niche selection on biodiversity. *Ecology*, *101*(6). https://doi.org/10.1002/ecy.3014

Sweeney, B. W. (1993). Effects of Streamside Vegetation on Macroinvertebrate Communities of White Clay Creek in Eastern North America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *144*, 291–340. JSTOR. https://doi.org/10.2307/4065013

Sweeney, B. W., Bott, T. L., Jackson, J. K., Kaplan, L. A., Newbold, J. D., Standley, L. J., … Horwitz, R. J. (2004). Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proceedings of the National Academy of Sciences*, *101*(39), 14132–14137. https://doi.org/10.1073/pnas.0405895101

Tabi, A., Santos, E. P., Brejão, G. L., & Siqueira, T. (2025). The ecological memory of landscape complexity shapes diversity of freshwater communities. *Oikos*. https://doi.org/10.1002/oik.11253

Tonkin, J. D., Bogan, M. T., Bonada, N., Rios‐Touma, B., & Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology*, *98*(5), 1201–1216. https://doi.org/10.1002/ecy.1761

Valente-Neto, F., Koroiva, R., Fonseca-Gessner, A. A., & Roque, F. de O. (2015). The effect of riparian deforestation on macroinvertebrates associated with submerged woody debris. *Aquatic Ecology*, *49*(1), 115–125. https://doi.org/10.1007/s10452-015-9510-y

Verberk, W. C. E. P., & Bilton, D. T. (2013). Respiratory control in aquatic insects dictates their vulnerability to global warming. *Biology Letters*, *9*(5), 20130473. https://doi.org/10.1098/rsbl.2013.0473

Wang, N., Zhang, J., Zhao, C., Gao, Y., Dong, J., Gao, X., … Li, X. (2025). Effects of different land use types on macroinvertebrate community structure and diversity in the middle reaches of the Yellow River basin. *Ecological Indicators*, *179*, 114259. https://doi.org/10.1016/j.ecolind.2025.114259

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Whittaker, R. H. (1972). Evolution and Measurement of Species Diversity. *Taxon*, *21*(2/3), 213. https://doi.org/10.2307/1218190

Wiebe, R. A., & Wilcove, D. S. (2025). Global biodiversity loss from outsourced deforestation. *Nature*, *639*. https://doi.org/10.1038/s41586-024-08569-5

Ye, L., Chang, C., Matsuzaki, S. S., Takamura, N., Widdicombe, C. E., & Hsieh, C. (2019). Functional diversity promotes phytoplankton resource use efficiency. *Journal of Ecology*, *107*(5), 2353–2363. https://doi.org/10.1111/1365-2745.13192

Zhao, Y., Sanders, N. J., Liu, J., Jin, T., Zhou, H., Lu, R., … Si, X. (2021). β diversity among ant communities on fragmented habitat islands: the roles of species trait, phylogeny and abundance. *Ecography*, *44*(10), 1568–1578. https://doi.org/10.1111/ecog.05723

SUPPLEMENTARY MATERIAL

Land use in the sampled region

To evaluate the history of deforestation and land-use changes in the sampled region, we used the MapBiomas platform to obtain land-use and land-cover maps for the 30 years preceding sampling (1985–2015). The data indicate that deforestation in the region occurred relatively early, with pasturelands and forest plantations dominating the landscape during the 1980s and 1990s. From the 2000s onward, an expansion of agricultural and urban areas can be observed. In the year of sampling (2015), the landscape appeared to be mainly composed of pastures, agricultural areas, and forest plantations, with relatively few urbanized areas. Furthermore, the most preserved areas are largely located within the boundaries of protected areas, namely Intervales State Park and Carlos Botelho State Park. However, over time, the buffer zones surrounding these protected areas have become increasingly occupied by human land-use activities.

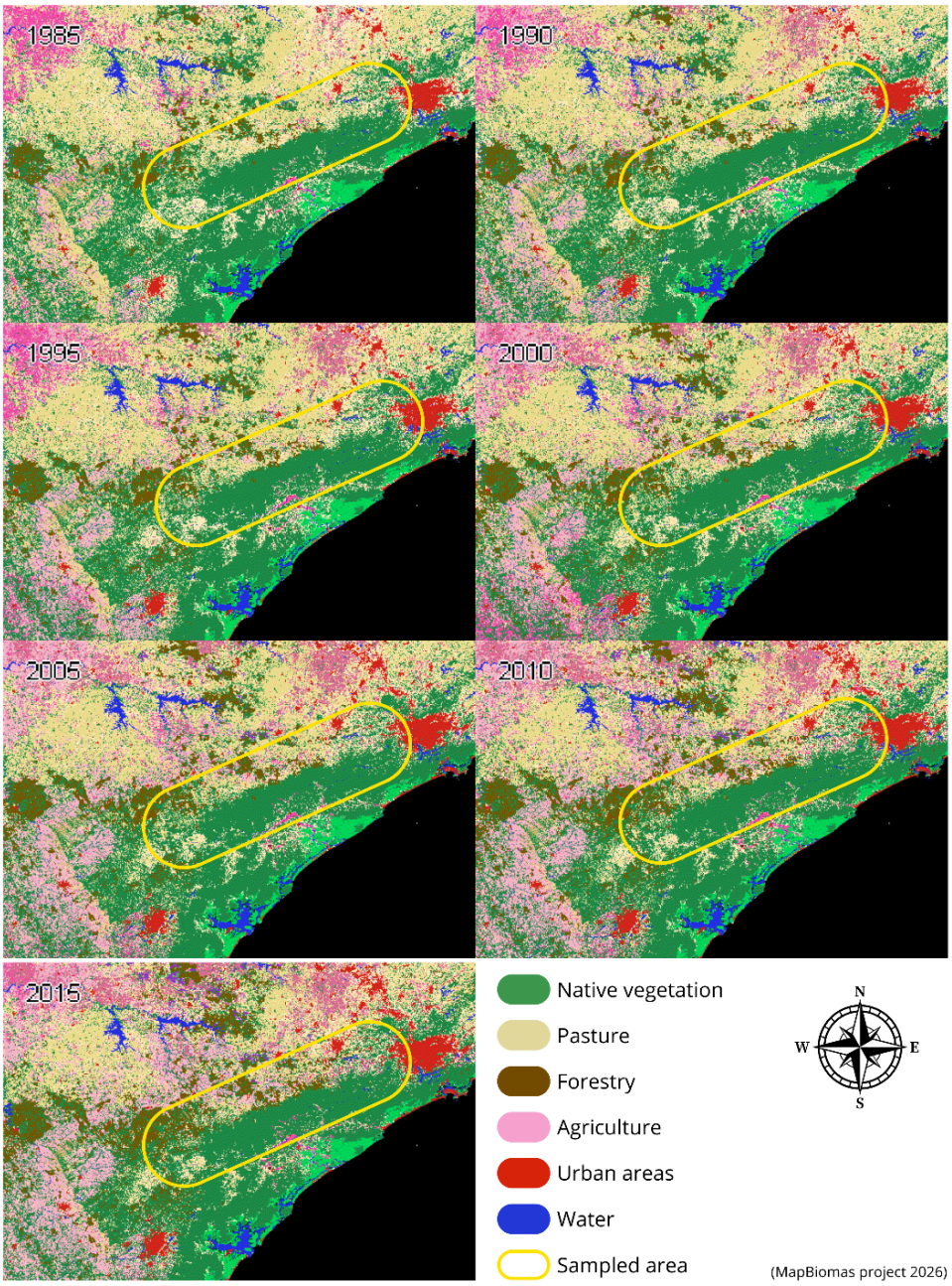

Figure S1. Land-use and land-cover history of the sampled area (1985–2015), obtained from the MapBiomas Project (http://mapbiomas.org). The images show land cover in the southeastern region of São Paulo state, including native forest (green), pasture (beige), forest plantations (brown), agriculture (purple), urban areas (red), and water bodies (blue). The yellow outline indicates the area where the sampling points are located.

Table S1. Results of the generalized linear models testing the effect of native vegetation cover on genus occurrence. β corresponds to the estimated coefficient of the predictor (% native vegetation), and p to the significance value of the test. Only genera occurring in at least five streams were included in the analyses.

Order	Genera	β	p value
Ephemeroptera	*Americabaetis*	1.098	0.273
	Baetodes	3.076	0.001*
	Caenis	0.008	0.994
	Callibaetis	-0.452	0.661
	Campylocia	1.638	0.074
	Cloeodes	-0.768	0.303
	Farrodes	0.969	0.229
	Hagenulopsis	1.627	0.209
	Hylister	4.207	0.000*
	Massartella	-0.306	0.695
	Thraulodes	2.229	0.085
	Traverhyphes	1.549	0.046*
	Tricorythodes	2.008	0.275
	Tricorythopsis	1.830	0.048*
	Ulmeritoides	-6.365	0.023*
	Zelusia	0.464	0.672
Plecoptera	*Anacroneuria*	2.873	0.000*
	Gripopteryx	1.573	0.071
	Kempnyia	2.296	0.025*
	Macrogynoplax	5.759	0.003*
Trichoptera	*Atopsyche*	1.217	0.111
	Austrotinodes	1.606	0.037*
	Blepharopus	-0.566	0.500
	Cernotina	0.505	0.681
	Chimarra	1.252	0.137
	Cyrnellus	0.144	0.902
	Helicopsyche	2.488	0.015*
	Leptonema	1.881	0.015*
	Marilia	1.312	0.351*
	Mortoniella	0.942	0.521
	Nectopsyche	1.849	0.037*
	Neotrichia	-0.457	0.606
	Oecetis	1.892	0.171

	Phylloicus	1.482	0.057
	Polyplectropus	0.291	0.830
	Protoptila	-0.274	0.870
	Smicridea	0.681	0.445
	Triplectides	1.349	0.183
Odonata	*Argia*	-1.047	0.178
	Cacoides	2.899	0.070
	Dythemis	0.748	0.315
	Heliocharis	1.137	0.443
	Hetaerina	2.215	0.043*
	Heteragrion	0.011	0.988
	Progomphus	1.917	0.039*
Megaloptera	*Corydalus*	1.777	0.140
Coleoptera	*Austrolimnius*	2.368	0.011*
	Cylloepus	1.188	0.141
	Heterelmis	2.047	0.046*
	Hexacylloepus	1.100	0.145
	Huleechius	3.408	0.025*
	Macrelmis	2.482	0.004*
	Microcylloepus	2.057	0.022*
	Neoelmis	1.794	0.020*
	Phanocerus	2.707	0.004*
	Psephenus	1.122	0.190
	Xenelmis	1.568	0.050

CAPÍTULO 3

A DISPERSÃO DE INSETOS AQUÁTICOS AO LONGO DA REDE DENDRÍTICA

O artigo de divulgação científica foi elaborado de acordo com as normas da revista *Aprendendo Ciência* (https://seer.assis.unesp.br/index.php/aprendendociencia) e foi publicado em junho de 2025 na edição v. 13 n. 1 (2024): Aprendendo Ciência. Disponível em: <https://seer.assis.unesp.br/index.php/aprendendociencia/article/view/2801>

Você sabia que existem insetos que vivem na água? Além dos tradicionais insetos terrestres que conhecemos, como as borboletas, besouros e formigas, também existem insetos que são aquáticos. São considerados insetos aquáticos aqueles que vivem pelo menos uma fase de sua vida dentro da água, geralmente em **ecossistemas de água doce** (Figura 1). Existem vários grupos de insetos aquáticos. A libélula (ordem Odonata) e o borrachudo (ordem Diptera) são alguns dos exemplos mais conhecidos.

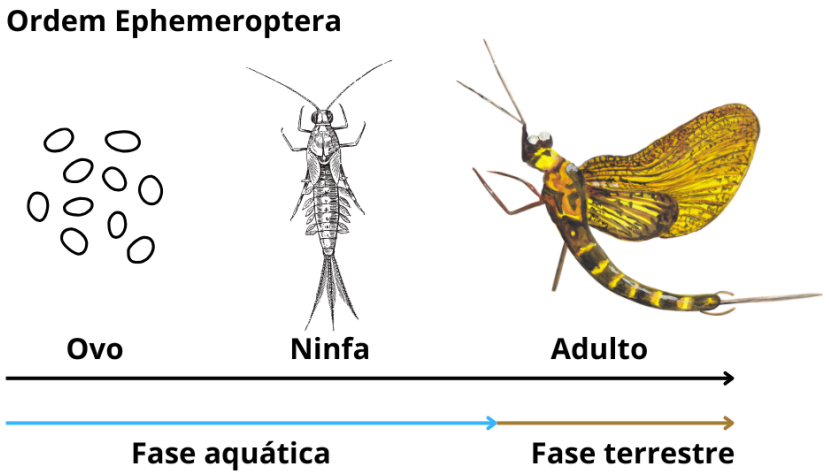

Figura 1. Representação da fase aquática da ordem Ephemeroptera, um grupo de insetos aquáticos. Fonte: © 2024 Lívia Serezani Munhoz.

Os insetos aquáticos são capazes de dispersar entre os ambientes de água doce. Mas o que é dispersão? A biologia entende por dispersão um ser vivo que sai do local onde vivem seus "pais" e se estabelece em outro lugar. Existem vários tipos de dispersão: a dispersão de sementes que ocorre pelo vento ou através de animais; a dispersão de **esporos** que podem ocorrer também pelo vento ou água; e a dispersão de animais que pode ocorrer da forma ativa (como quando o animal nada, voa ou caminha) ou de uma forma passiva (quando o animal se dispersa ao ser carregado pelo vento ou correnteza). Os insetos aquáticos se dispersam de diferentes formas entre os locais em que podem viver, como em uma rede dendrítica. Para entender como os insetos aquáticos se dispersam em uma rede dendrítica, vamos primeiro entender o que ela é.

Quando vemos um rio por uma imagem de drone ou satélite, percebemos que este possui ramificações que em certo ponto se ligam. A água surge através das nascentes que

formam os pequenos córregos ou **riachos** (cabeceira), que se juntam formando grandes riachos (centrais), que por sua vez, se unem formando corpos de água ainda maiores que conhecemos como rio. Essa configuração forma um tipo de rede, e chamamos esta de **rede dendrítica** (a origem desse nome meio esquisito remete à semelhança aos ramos de uma árvore; Figura 2).

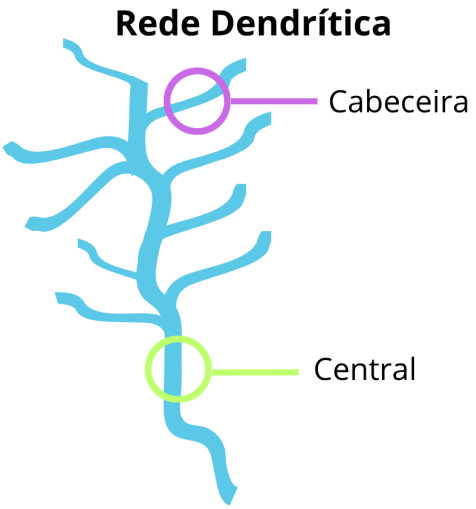

Figura 2. Representação de uma rede dendrítica. Fonte: © 2024 Lívia Serezani Munhoz.

A dispersão dentro de uma rede dendrítica geralmente é direcionada no sentido da correnteza da água, pois os insetos em sua fase aquática são muito frágeis e dificilmente conseguem subir o rio (Figura 3). Por isso, a sua posição inicial na rede dendrítica interfere em sua dispersão. Riachos de cabeceira recebem poucos insetos em fase aquática de outros locais, por isso consideramos como isolados. Já os riachos em uma posição mais central na rede dendrítica podem receber as fases juvenis de insetos aquáticos vindos de vários riachos menores.

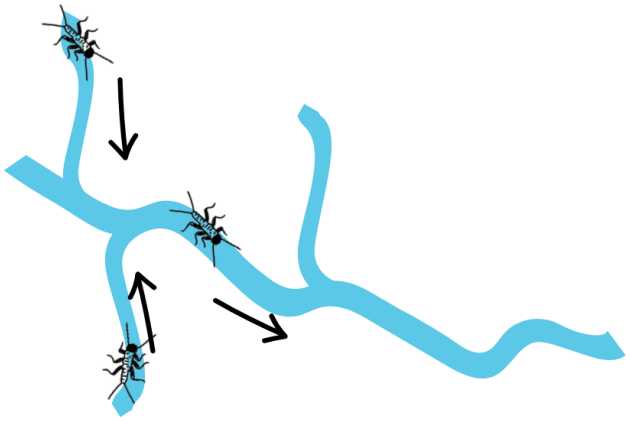

Figura 3. Representação da dispersão passiva em uma rede dendrítica. Fonte: © 2024 Lívia Serezani Munhoz.

Nem todos os insetos aquáticos possuem as mesmas habilidades de dispersão. Agora vamos falar um pouquinho sobre elas. Um cientista finlandês que estuda os insetos aquáticos chamado Jani Heino classificou os insetos em sua fase terrestre quanto à capacidade de dispersão em voadores fracos, intermediários e fortes (Figura 4). Por exemplo, um grupo de organismos semelhante ao pernilongo (Chironomidae), que possui um corpo bem pequeno, é um dispersor fraco. Já a libélula (Odonata) possui um tamanho do corpo maior, e é uma dispersora forte - por isso pode alcançar habitats mais distantes. Já na fase aquática a principal maneira de se locomover é por meio da **dispersão passiva** (pela correnteza da água seguindo o fluxo do riacho) enquanto a **dispersão ativa** (através do nado) é mais fraca.

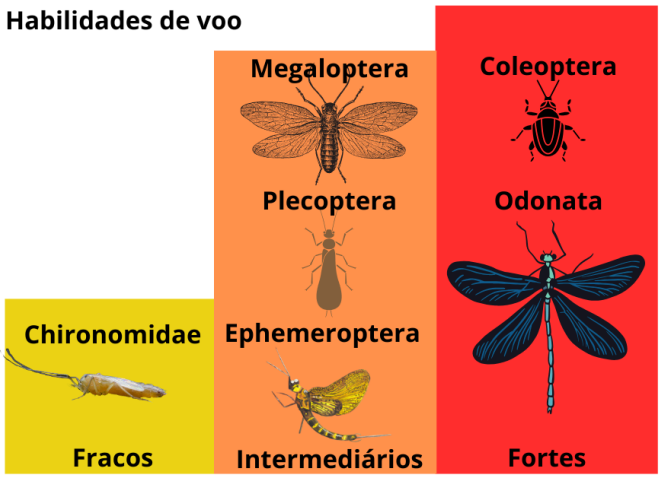

Figura 4. Representantes de insetos aquáticos adultos com habilidade de voo fraca, intermediária e forte. Fonte: © 2024 Lívia Serezani Munhoz.

Entender os tipos de dispersão dos insetos aquáticos ao longo da rede dendrítica é muito importante para também compreender a troca de espécies entre **habitats**. Este é um tema muito importante para a ecologia de **comunidades**, e ajuda os pesquisadores a compreender os padrões de biodiversidade nos ecossistemas de água doce e assim, poder conservá-los melhor.

Glossário

Comunidades: Conjunto de várias populações.

Dispersão passiva: Deslocamento de espécies com a ajuda de vetores, como por meio de elementos naturais não vivos (como vento e correnteza da água) e vivos (como uma semente pre.

Dispersão ativa: Deslocamento de espécies com o próprio esforço, como voo, nado ou caminhada.

Ecossistemas de água doce: São ambientes aquáticos continentais, que comportam comunidades de seres vivos que vivem em contato com a água doce, como os ecossistemas lênticos (água mais parada, como lagos, represas e poças) e lóticos (como rios e riachos).

Esporos: Estruturas que fazem parte da reprodução de alguns seres vivos, como bactérias, algas, fungos e plantas. Cada esporo pode formar um novo indivíduo.

Habitat: Local onde uma espécie vive.

Rede dendrítica: Disposição de riachos e rios formando ramificações que se unem em certo ponto.

Riachos: Pequenos rios.

Referências

Campbell Grant, E. H., Lowe, W. H., & Fagan, W. F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters*, *10*(2), 165–175. https://doi.org/10.1111/j.1461-0248.2006.01007.x

Gomi, T., Sidle, R. C., & Richardson, J. S. (2002). Understanding Processes and Downstream Linkages of Headwater Systems. *BioScience*, *52*(10), 905. https://doi.org/10.1641/0006-3568(2002)052[0905:upadlo]2.0.co;2

Heino, J. (2013). Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? *Oecologia*, *171*(4), 971–980. https://doi.org/10.1007/s00442-012-2451-4

Torres Lema, E. M. (2027). Evaluación de la contribución de los ríos de cabecera a la diversidad de macroinvertebrados acuáticos en cuatro cuencas hidrográficas de los Andes de Ecuador. *PUCE - Quito*.

CONSIDERAÇÕES FINAIS

Esta dissertação teve como objetivo principal compreender como a comunidade de insetos aquáticos da Mata Atlântica respondem a variações ambientais naturais e antrópicas, considerando a organização espacial da rede dendrítica, bem como os efeitos da perda de vegetação ripária. Ao integrar diversas abordagens ecológicas, incluindo a singularidade ambiental e funcional, aninhamento e decomposição da diversidade beta, os resultados evidenciam que a estrutura de comunidades de água doce são moldadas por diferentes padrões, que variam de acordo com a escala espacial e sob diferentes contextos ecológicos.

Os resultados do primeiro capítulo demonstraram que a organização dendrítica da rede hidrográfica vai além da característica geomorfológica da paisagem, demonstrando ser um importante componente ecológico na estruturação de comunidades de insetos aquáticos. A posição dos riachos dentro da rede influencia a conectividade entre ambientes, o potencial de dispersão e a intensidade com que filtros ambientais atuam sobre as comunidades. Esses resultados reforçam a importância de considerar a organização espacial natural dos ecossistemas lóticos para melhor compreender padrões de estrutura de metacomunidades e distribuição de espécies.

No segundo capítulo, observou-se um padrão de resposta das comunidades de insetos aquáticos frente às alterações antrópicas associadas à perda da vegetação ripária, com a perda ordenada de espécies ao longo do gradiente de desmatamento. Diferentemente das investigações do primeiro capítulo, onde o gradiente natural favoreceu mudanças na composição das comunidades através de processos ecológicos associados à heterogeneidade ambiental e à conectividade espacial, o desmatamento esteve associado à simplificação das comunidades, demonstrada pela perda ordenada de gêneros e características funcionais ao longo do gradiente de perda de cobertura vegetal nativa, gerando um padrão de aninhamento. Esses resultados reforçam a importância da vegetação ripária na manutenção da biodiversidade de ecossistemas de água doce e sugerem atenção especial para ambientes ainda preservados em planos de conservação, por funcionarem como importantes reservatórios da diversidade regional.

De forma integrada, nossos resultados evidenciam que mudanças naturais na paisagem ambiental e as geradas pela degradação ambiental antrópica, não demonstram respostas equivalentes sobre a biodiversidade aquática. Enquanto processos naturais

distribuem e reorganizam as comunidades ao longo da rede dendrítica, a degradação ambiental tende a reduzir a riqueza biológica e limitar a persistência de táxons mais sensíveis às alterações no ambiente. A visão unificada dos padrões encontrados sugere que possivelmente o efeito do desmatamento possa gerar consequência mais severas sobre comunidades inseridas em posições iniciais na rede, destacando a urgência de atenção para riachos nessas posições em planos de proteção e conservação.

Com o objetivo de ampliar a comunicação científica e democratizar o conhecimento científico, esta dissertação também conta com um capítulo de divulgação da ciência voltado ao público não familiarizado com processos ecológicos e insetos aquáticos. O capítulo abordou a organização dendrítica da rede hidrológica e a distribuição de insetos aquáticos por meio de diferentes estratégias e habilidades de dispersão, destacando a importância dos fatores de dispersão para compreender como as comunidades são estruturadas e auxiliar no biomonitoramento e planos de conservação. Aproximar a sociedade do conhecimento científico pode ser uma importante estratégia para sensibilização ambiental, a fim de aumentar a pressão popular para o fortalecimento de ações de conservação.

Embora o estudo tenha contribuído para ampliar a compreensão sobre ecologia de comunidades aquáticas em riachos subtropicais, algumas limitações nos estudos dirigidos devem ser consideradas. A identificação taxonômica a nível de gênero, embora muito utilizada por grande parte de estudos com insetos aquáticos, assim como o déficit de informação de características funcionais das espécies, pode não capturar respostas mais refinadas em nível específico. Além disso, respostas funcionais às características do ambiente representam informações importantes para compreender a estrutura de comunidades, mas não substituem medições diretas de processos ecossistêmicos. O pequeno esforço amostral no primeiro capítulo também pode ter reduzido o poder de generalização dos resultados obtidos. Destacamos também a importância de considerar que outros fatores paralelos como dinâmica de dispersão, histórico do uso do solo, tipos de perturbação natural ou antrópica na paisagem e fatores temporais, também podem influenciar a estrutura das comunidades além das variáveis consideradas neste estudo.

Concluindo, essa dissertação reforça a importância ecológica dos riachos da Mata Atlântica como sistemas complexos e altamente dinâmicos, que sofrem influência tanto de processos naturais quanto da degradação antrópica. A conservação desses ambientes depende não somente da proteção da vegetação ripária ou de diferentes posições espaciais na rede dendrítica, mas também do avanço de estudos que integrem diferentes abordagens de análise da biodiversidade e ampliem o diálogo entre a ciência e a sociedade.