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EFEITOS DE UM GRADIENTE TÉRMICO SOBRE COMUNIDADES DE MACROINVERTEBRADOS EM RIACHOS GEOTERMAIS TROPICAIS

São Carlos - SP

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Doutor em Ciências na área de concentração em Ecologia e Recursos Naturais

Orientador: Dr. Victor Satoru Saito

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- Ainda to bem vivo, mas se algo acontecer tu tens que estar preparado.
- Eu sei.
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RESUMO

O aquecimento promove impactos multifacetados sobre a biodiversidade aquática, especialmente em ecossistemas tropicais. Investigamos as respostas das comunidades de macroinvertebrados em riachos geotermais tropicais ao aumento natural da temperatura, enfocando componentes de composição, tróficos e evolutivos para compreender o efeito da variação térmica. No primeiro capítulo, analisamos a estabilidade dos espectros de tamanho e da distribuição da biomassa, assim como mudanças nos níveis tróficos de várias espécies. Apesar do aumento das demandas metabólicas, observou-se manutenção da biomassa e da estrutura de tamanho corporal, evidenciando plasticidade trófica por parte das espécies, que ajustam seus hábitos alimentares ao consumir em níveis tróficos inferiores, onde a biomassa é mais abundante. Essa flexibilidade trófica funcionou como mecanismo compensatório para suprir as maiores demandas energéticas do aquecimento e apontamos como fator-chave para a resistência e manutenção do funcionamento do ecossistema diante do aquecimento. No segundo capítulo, exploramos padrões de diversidade taxonômica e filogenética das assembleias de macroinvertebrados, avaliando os efeitos do gradiente térmico na estrutura filogenética das comunidades. Utilizando métricas de parentesco como o Net Relatedness Index (NRI) e o Nearest Taxon Index (NTI), identificamos padrões sensíveis de agrupamento filogenético relacionados à variação térmica, resultado do conservadorismo de nicho. Esse agrupamento em poucos riachos sugere filtragem ambiental para seleção de linhagens adaptadas a altas temperaturas, restringindo a diversidade taxonômica e filogenética em determinados locais. Entretanto, ao longo do gradiente térmico, não foram detectadas alterações sistemáticas na diversidade alfa e beta, sugerindo que múltiplos fatores ambientais, além da temperatura, influenciam a montagem das comunidades. Esses resultados ressaltam a complexidade dos processos ecológicos e evolutivos que moldam a biodiversidade em ambientes tropicais submetidos a mudanças climáticas, contribuindo para uma compreensão integrada da resistência e vulnerabilidade das comunidades aquáticas ao estresse ambiental. Portanto, este estudo reforça a complexidade dos efeitos do aquecimento sobre as comunidades de macroinvertebrados, evidenciando padrões não lineares e respostas multifacetadas. Embora o aumento da temperatura imponha demandas metabólicas elevadas, as respostas das comunidades não se traduzem em declínios lineares em biomassa ou diversidade, mas sim em ajustamentos comportamentais e estruturais, como a plasticidade trófica e alterações nos níveis tróficos para compensar as variações energéticas. Além disso, o impacto térmico atua como filtro ambiental seletivo, modelando a estrutura filogenética das assembleias e promovendo agrupamentos não uniformes que refletem a heterogeneidade ecológica local e a variabilidade espaço-temporal dos habitats. Esses achados sublinham que as comunidades aquáticas respondem de forma complexa e não linear ao aquecimento, resultando em respostas que desafiam previsões simplistas e apontam para a necessidade de abordagens integrativas para compreender e conservar a biodiversidade frente às mudanças climáticas.

Palavras-chave: Riachos Geotermais, Gradiente de temperatura, Plasticidade trófica, Padrões de diversidades complexos, Relações não lineares.

ABSTRACT

The warming causes multifaceted impacts on aquatic biodiversity, especially in tropical ecosystems. We investigated the responses of macroinvertebrate communities in tropical geothermal streams to natural temperature increases, focusing on compositional, trophic, and evolutionary components to understand the effect of thermal variation. In the first chapter, we analyzed the stability of size spectra and biomass distribution, as well as changes in the trophic levels of several species. Despite increased metabolic demands, biomass and body size structure were maintained, demonstrating trophic plasticity by species that adjust their feeding habits by consuming at lower trophic levels where biomass is more abundant. This trophic flexibility acted as a compensatory mechanism to meet the higher energy demands imposed by warming and was identified as a key factor for ecosystem resistance and functional maintenance under warming. In the second chapter, we explored taxonomic and phylogenetic diversity patterns of macroinvertebrate assemblages, assessing the effects of the thermal gradient on the phylogenetic structure of communities. Using relatedness metrics such as the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI), we identified sensitive patterns of phylogenetic clustering related to thermal variation, resulting from niche conservatism. This clustering in a few streams suggests environmental filtering selecting lineages adapted to high temperatures, which restricts taxonomic and phylogenetic diversity in certain locations. However, along the thermal gradient, no systematic changes in alpha and beta diversity were detected, indicating that multiple environmental factors beyond temperature influence community assembly. These results highlight the complexity of ecological and evolutionary processes shaping biodiversity in tropical environments exposed to climate change, contributing to an integrated understanding of aquatic community resistance and vulnerability to environmental stress. Therefore, this study reinforces the complexity of warming effects on macroinvertebrate communities, evidencing nonlinear patterns and multifaceted responses. Although temperature increases impose high metabolic demands, community responses do not translate into linear declines in biomass or diversity, but rather into behavioral and structural adjustments such as trophic plasticity and shifts in trophic levels to compensate for energetic variations. Moreover, the thermal impact acts as a selective environmental filter, shaping the phylogenetic structure of assemblages and promoting uneven clustering that reflects local ecological heterogeneity and the spatiotemporal variability of habitats. These findings emphasize that aquatic communities respond to warming in a complex and nonlinear manner, resulting in responses that challenge simplistic predictions and point to the need for integrative approaches to understand and conserve biodiversity under climate change.

Keywords: Geothermal Streams, Temperature Gradient, Trophic Plasticity, Complex Diversity Patterns, Nonlinear Relationships.

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LISTA DE ABREVIATURAS E SIGLAS

ANOVA – Análise de Variância

β_abund – Diferença de Abundância

β_repl – Substituição (*Replacement*)

β_total – Diversidade Beta Total

BMWP – Índice *Biological Monitoring Working Party*

CDR – Estratégias de Remoção de Carbono

CO2 – Dióxido de Carbono

Cond – Condutividade Elétrica (µS/cm)

DOS – Saturação de Oxigênio Dissolvido (mg/L)

DO% – Porcentagem de Oxigênio Dissolvido Relativa à Saturação

EPT – Ephemeroptera, Plecoptera e Trichoptera

Field_Temp – Temperatura de Campo (°C)

GDS – Maior Distância da Concha (mm)

GLMs – Modelos Lineares Generalizados

GtCO2 – Gigatoneladas de Dióxido de Carbono

ISD – Distribuição do Tamanho Individual

LM(s) – Modelos Lineares

Max_Temp – Temperatura Máxima (°C)

MLEbin – Método *Likelihood Bin*

MNND – Distância Média do Vizinho Mais Próximo

MPD – Distância Média entre Pares

MRM – Regressão Múltipla em Matrizes de Distância

NRI – Índice de Relacionamento Líquido

NTI – Índice do Táxon Mais Próximo

ORP_mV – Potencial de Oxidação-Redução (mV)

pH – Potencial Hidrogeniônico

PCA – Análise de Componentes Principais

PCoA – Análise de Coordenadas Principais

PD – Diversidade Filogenética de Faith

PERMDISP – Análise de Dispersão Multivariada

Salt – Salinidade (ppt)

Sn – Estanho

TBL – Comprimento Total do Corpo (mm)

TDS – Sólidos Totais Dissolvidos (mg/L)

TP – Posição Trófica

TME – Teoria Metabólica da Ecologia

VPDB – Vienna Pee Dee Belemnite

LISTA DE SÍMBOLOS

α – alfa

β – beta

$\delta^{13}C$ – Assinatura isotópica de Carbono 13

$\delta^{15}N$ – Assinatura isotópica de Nitrogênio 15

λ – inclinação do espectro de tamanho (*size spectra slope*)

SUMÁRIO

1 INTRODUÇÃO

As mudanças climáticas configuram uma das maiores ameaças à biodiversidade, cujos impactos têm sido extensivamente documentados na literatura ao longo dos anos (IPCC, 2021; 2023). É amplamente reconhecido que a temperatura média global aumentou 1,09 °C desde o final do século XIX, acompanhada de alterações nos padrões de precipitação e aumento na frequência de eventos climáticos extremos (Pearson e Dawson, 2003; Myhre et al., 2019; IPCC, 2021). Diversas iniciativas globais têm sido implementadas para mitigar os reais efeitos desse aumento de temperatura, embora muitas tenham apresentado altas taxas de insucesso. Como exemplo, destaca-se o Acordo de Paris, firmado em 2015 no âmbito da Convenção-Quadro das Nações Unidas, que consolidou um marco histórico de cooperação internacional visando limitar, a médio e longo prazo, o aumento da temperatura média global a níveis inferiores a 2 °C, com esforços para restringi-lo a 1,5 °C (UNFCCC, 2015). Para atingir essas metas, projeta-se que as emissões cumulativas totais de dióxido de carbono (CO2) entre 2011 e 2100 não ultrapassem aproximadamente 1350 gigatoneladas (GtCO2) para uma probabilidade de 50% de limitar o aquecimento a 2 °C, e 500 GtCO2 para a mesma probabilidade no limite de 1,5 °C. Contudo, o Sexto Relatório de Avaliação do Painel Intergovernamental sobre Mudanças Climáticas (IPCC AR6) evidencia que a simples redução das emissões não será suficiente para conservar essas faixas, tornando-se necessária a implementação em larga escala de tecnologias e estratégias de remoção de carbono (CDR) para assegurar os objetivos climáticos globais (IPCC, 2021).

O aumento contínuo das emissões de CO2, aliado ao descumprimento dos objetivos globais para preservação da saúde climática, tem impactado diretamente a biodiversidade. Estudos recentes indicam que cada tonelada de CO2 emitida está associada a um aumento mensurável no risco de extinção de espécies, estimado em cerca de $2{,}3 \times 10^{-7}$ espécies comprometidas para extinção por tonelada de CO2 equivalente emitida. Estas mudanças têm ocasionado extinções locais e globais, além da redução das distribuições geográficas das espécies (Mokany et al., 2023; Iordan et al., 2023; Davis, 2023). Em vista disso, grande parte da pesquisa científica sobre biodiversidade volta-se para uma questão central: como o funcionamento dos ecossistemas complexos responderá ao aquecimento a longo prazo? Esse desafio tem sido tradicionalmente abordado por meio de modelos matemáticos em escala de ecossistema, os quais integram relações gerais entre tamanho corporal, temperatura e taxas metabólicas em nível de espécie (Enquist et al., 2003; Schramski et al., 2015). Estes estudos se baseiam principalmente na Teoria Metabólica da Ecologia (TME) (Brown, 2004), que postula que a taxa metabólica dos organismos aumenta com a massa corporal elevada à potência de três quartos e varia com a temperatura segundo a equação de Boltzmann-Arrhenius, apresentando uma energia de ativação aproximada de 0,65 eV. A TME prevê com sucesso padrões amplos em taxas metabólicas, ciclagem de nutrientes e processos ecológicos em diferentes táxons e escalas, com muitos estudos encontrando expoentes médios próximos a 0,75 para a massa corporal e energias de ativação próximas a 0,65 eV, especialmente em sistemas controlados ou simples (Price et al., 2012; Gao et al., 2024). No entanto, a universalidade desses valores tem sido recentemente questionada, pois apresentam variação significativa tanto intra quanto interespecífica (Dell et al., 2011; Glazier et al., 2005; Munch et al., 2023). Ademais, as espécies podem modificar suas características metabólicas por meio de aclimatação, adaptação evolutiva ou ambos (Seebacher et al., 2025; Cloyed, et al., 2019; Kontopoulos et al., 2020). Esta flexibilidade nas respostas térmicas ao nível das espécies é denominada "plasticidade metabólica", entendida como a capacidade de grupos similares de organismos ajustarem suas taxas metabólicas coerentemente em resposta a alterações ambientais. A plasticidade metabólica pode impactar o funcionamento dos ecossistemas, influenciando o fluxo de energia nas teias alimentares (Barneche, 2021), embora ainda haja escassez de evidências empíricas dessas alterações entre espécies e níveis tróficos em sistemas naturais.

Para além da plasticidade metabólica, organismos submetidos a intensos episódios de aquecimento podem experimentar alterações na organização comunitária (i.e., composição, distribuição e processos ecológicos) em diferentes escalas espaciais. O aquecimento frequentemente exerce efeito direto sobre a diversidade local e regional, especialmente em ambientes aquáticos continentais como riachos. Dessa forma, o aquecimento pode levar a um aumento momentâneo ou localizado da diversidade taxonômica e filogenética alfa, uma vez que espécies termossensíveis adaptadas ao frio são substituídas ou complementadas por espécies generalistas e termotolerantes. Isso é especialmente pronunciado onde táxons intermediários e adaptados ao calor expandem seus alcances, trazendo novas características funcionais e linhagens para as comunidades locais (Manfrin et al., 2023; Milner et al., 2023; Theodoropoulos & Karaouzas, 2021). Contudo, apesar desses ganhos locais, o aquecimento geralmente provoca uma redução acentuada na diversidade beta, medida como a variação composicional entre comunidades em diferentes localidades (Whittaker, 1960). À medida que espécies termotolerantes se espalham regionalmente e os especialistas adaptados ao frio são perdidos, as comunidades tornam-se mais semelhantes entre si, caracterizando um processo de homogeneização ambiental (Brown et al., 2007; Miserendino et al., 2018). Este padrão é observado tanto do ponto de vista taxonômico quanto filogenético, com a substituição de linhagens evolutivas exclusivas por clados generalizados e tolerantes a condições térmicas extremas (Brown et al., 2007; Theodoropoulos & Karaouzas, 2021; Lencioni et al., 2022; Manfrin et al., 2023).

Os macroinvertebrados bentônicos desempenham papel fundamental na conservação da biodiversidade e na provisão de serviços ecossistêmicos em ambientes aquáticos continentais, atuando como componentes-chave nos ciclos biogeoquímicos, na decomposição da matéria orgânica e na regulação da qualidade da água (Nybakken, 1997; Callisto et al., 2001; Barros et al., 2012). Sua importância ecológica é reforçada pelo fato de constituírem base alimentar para uma ampla gama de consumidores superiores, como peixes e anfíbios, integrando as teias tróficas aquáticas (Rosenberg & Resh, 1993). Devido à alta sensibilidade a fatores ambientais, especialmente às variações da temperatura da água, estes organismos são reconhecidos como bioindicadores eficientes da qualidade ambiental e da saúde dos ecossistemas aquáticos (Vieira et al., 2012; Tampo et al., 2021). Em particular, estudos revelam que alterações térmicas, induzidas por mudanças climáticas ou perturbações locais, desencadeiam respostas rápidas e previsíveis nas comunidades de macroinvertebrados, refletindo tanto a perda de espécies termossensíveis quanto a inserção de espécies termotolerantes, modificando a composição e a estrutura comunitária (Balian et al., 2008; Donohue et al., 2009). Por exemplo, investigações em rios temperados mostram que aumentos moderados nas temperaturas reduzem a diversidade de grupos sensíveis de macroinvertebrados, como Plecoptera e Ephemeroptera, enquanto ordens menos sensíveis, como Diptera, tendem a proliferar (Braschler et al., 2012; Durance & Ormerod, 2009). Esses padrões de resposta fornecem subsídios valiosos para o monitoramento do aquecimento global e seus impactos, possibilitando avaliações acerca da resistência e resiliência das comunidades em diferentes cenários ambientais (Ledger et al., 2013; Silva et al., 2020). Além disso, a utilização de índices bióticos baseados em macroinvertebrados, como o Índice BMWP (Biological Monitoring Working Party), adaptado para diversos biomas, tem se mostrado eficaz para detectar alterações térmicas e outras pressões ambientais relacionadas à mudança climática (Armitage et al., 1983; Vieira et al., 2012). A capacidade desses índices de associar alterações na estrutura comunitária a fatores de estresse permite uma avaliação rápida e eficiente, subsidiando políticas públicas e estratégias de conservação (Gomes et al., 2019). Portanto, o monitoramento contínuo das comunidades bentônicas é imprescindível para compreender e mitigar os efeitos adversos do aquecimento em ecossistemas aquáticos, contribuindo para a manutenção da integridade funcional e dos serviços ecossistêmicos prestados por esses ambientes (Poff et al., 2010; Avelino et al., 2023).

Riachos geotermais naturais, caracterizados por gradientes térmicos precisos e estáveis, têm sido amplamente utilizados como laboratórios naturais in situ para estudar os efeitos do aquecimento na estrutura e funcionamento das comunidades aquáticas. Esses sistemas oferecem uma oportunidade singular para investigar como variações térmicas influenciam a composição, abundância e diversidade de macroinvertebrados, bem como a distribuição do tamanho corporal e os espectros de biomassa dentro dessas comunidades (Pander et al., 2022; Bonacina et al., 2022; O’Gorman et al., 2017). Estudos em riachos geotermais islandeses demonstram que mesmo aumentos moderados da temperatura podem causar mudanças significativas na organização comunitária bentônica, alterando o tamanho médio dos organismos e o fluxo energético nos ecossistemas aquáticos (Perkins et al., 2021a). Essas alterações refletem-se na inclinação dos espectros de tamanho, impactando processos bioenergéticos essenciais para o funcionamento do ecossistema. Além disso, evidências sugerem que a biomassa total das comunidades pode aumentar em resposta ao aquecimento, possivelmente devido ao aumento da disponibilidade de nutrientes que sustentam maiores demandas metabólicas em produtores e consumidores (Jackson et al., 2024). A seletividade térmica imposta pelo aquecimento favorece espécies tolerantes a temperaturas elevadas, enquanto reduz a presença de espécies termossensíveis, ocasionando reconfigurações na estrutura e dinâmica comunitária (Pander et al., 2022; Pedreros et al., 2020). Assim, estudos em riachos geotermais fornecem insights valiosos para entender e prever os impactos do aquecimento global sobre ecossistemas aquáticos.

Esses estudos em riachos geotermais, principalmente em regiões temperadas, têm avançado o entendimento sobre as respostas ecológicas e funcionais das comunidades de macroinvertebrados ao estresse provocado por um gradiente térmico natural. O’Gorman et al. (2014, 2017) demonstraram que o aquecimento nestes ambientes pode incrementar a biomassa e produtividade, alterando a estrutura trófica e os processos de decomposição, com reflexos diretos no fluxo energético. Em contrapartida, Bonacina et al. (2022, 2023) evidenciaram a complexidade dessas respostas, abrangendo desde ajustes metabólicos até mudanças na composição e diversidade, revelando a resiliência e a plasticidade das assembléias. Já estudos conduzidos por Perkins et al. (2021b) destacaram a importância dos espectros de tamanho corporal para compreender as mudanças na eficiência energética da comunidade. Estudos de Gjoni et al. (2024) e Junker et al. (2020) indicaram que a disponibilidade e o suprimento de recursos modulam a resposta dos macroinvertebrados ao aquecimento, estabelecendo relações não lineares entre temperatura, metabolismo e dinâmica trófica. Essas investigações reafirmam o papel dos riachos geotermais como modelos naturais para estudos ecológicos, proporcionando conhecimento essencial sobre os mecanismos que determinam a resistência e vulnerabilidade de comunidades aquáticas diante do aquecimento global. No entanto, apesar desses avanços em regiões temperadas, a compreensão dos efeitos do estresse térmico em riachos geotermais tropicais ainda permanece limitada, evidenciando uma lacuna importante no conhecimento que dificulta a previsão dos impactos das mudanças climáticas nesses ecossistemas altamente diversos e sensíveis.

Não obstante, estudos têm se debruçado sobre os padrões de diversidade taxonômica e filogenética, tanto alfa quanto beta, em comunidades de macroinvertebrados em riachos geotermais e suas respostas às variações térmicas. A diversidade alfa, que se refere à riqueza e diversidade locais, frequentemente apresenta variações modestas ao longo dos gradientes térmicos, indicando certa resiliência das comunidades mesmo sob estresse térmico (Li et al., 2024; Wu et al., 2022). Em contrapartida, a diversidade beta, que mede a variação composicional entre comunidades em diferentes locais, é significativamente influenciada por fatores ambientais locais, geomorfológicos e espaciais, sendo o turnover de espécies o principal componente dessa variação (Li et al., 2024). Padrões filogenéticos sugerem que a diversidade beta filogenética frequentemente acompanha a diversidade taxonômica, indicando conservadorismo do nicho filogenético, que restringe a distribuição das linhagens ao longo do gradiente térmico (Branco et al., 2020; Li et al., 2024). Considerando o conservadorismo do nicho, espécies tendem a manter suas preferências ambientais ao longo do tempo evolutivo, limitando a diversidade filogenética que pode responder efetivamente ao aquecimento. Consequentemente, a substituição de espécies termossensíveis por linhagens filogeneticamente próximas e termotolerantes promove a homogeneização local e regional das comunidades, fenômeno documentado em riachos geotermais e outros ecossistemas aquáticos submetidos a estresse térmico (Oliveira et al., 2023; da Silva, 2017; Basin et al., 2022; Callisto et al., 2017). Além disso, a diversidade funcional nas comunidades geotermais frequentemente permanece menor que as dimensões taxonômica e filogenética, refletindo redundância funcional entre espécies e reforçando a importância dos filtros ambientais e do conservadorismo de nicho na estruturação das assembléias (Biggs et al., 2020; Wu et al., 2022).

Esta tese está dividida em dois capítulos que exploram os efeitos do aquecimento ambiental sobre comunidades de macroinvertebrados em riachos geotermais tropicais, integrando fundamentos da TME e da Teoria do Conservadorismo de Nicho. Trata-se de um estudo inédito e pioneiro, pois é a primeira investigação a focar em macroinvertebrados de riachos geotermais tropicais da Amazônia, região detentora de uma imensa biodiversidade em em geral subamostrada sob essa perspectiva ecológica e evolutiva. A TME, que relaciona a taxa metabólica dos organismos à sua massa corporal e temperatura, fornece a base para compreender como o aumento térmico pode afetar o funcionamento e a estrutura das comunidades aquáticas. Por outro lado, a Teoria do Conservadorismo de Nicho, que postula que espécies relacionadas tendem a conservar preferências ecológicas e fenômenos adaptativos ao longo do tempo evolutivo, é essencial para interpretar as respostas filogenéticas às pressões térmicas. A proposta geral da tese é compreender como o aumento da temperatura impacta tanto o funcionamento ecológico — por meio das dinâmicas tróficas e distribuição de biomassa — quanto a estrutura evolutiva e diversidade das comunidades continentais aquáticas tropicais.

No primeiro capítulo, abordamos a influência do aumento natural da temperatura em riachos geotermais sobre a estrutura do tamanho corporal e as dinâmicas tróficas das comunidades de macroinvertebrados. Combinamos análise de espectros de tamanho e marcadores isotópicos estáveis para avaliar mudanças na biomassa, abundância e interações alimentares, investigando como a elevação térmica altera a organização da teia alimentar e a eficiência da transferência de energia. As perguntas centrais que norteiam este capítulo são: como o aquecimento modifica a distribuição da biomassa entre diferentes categorias de tamanho corporal? De que maneira essas alterações repercutem na complexidade e funcionamento das redes tróficas em ecossistemas aquáticos tropicais naturais? Este estudo fornece evidências cruciais sobre a resposta funcional das redes tróficas tropicais sob estresse térmico natural, um tema ainda pouco explorado.

Já o segundo capítulo dedica-se à análise integrada da diversidade taxonômica e filogenética das comunidades de macroinvertebrados em riachos geotermais, enfatizando a estrutura evolutiva das assembléias ao longo do gradiente térmico. Utilizamos métricas filogenéticas, como o Índice de Relacionamento Líquido (NRI) e o Índice do Táxon Mais Próximo (NTI), para investigar padrões de agrupamento e dispersão filogenética, interpretando processos de filtragem ambiental e competição. Com base na Teoria do Conservadorismo de Nicho, buscamos responder: como o aumento da temperatura afeta a diversidade taxonômica e filogenética? Até que ponto o conservadorismo filogenético restringe a composição e a diversidade das comunidades adaptadas a temperaturas elevadas? Este capítulo contribui para elucidar os processos ecológicos e evolutivos que regem a estrutura da biodiversidade em ambientes tropicais aquáticos sujeitos a mudanças ambientais.

1.1 OBJETIVO GERAL

Investigar os efeitos de um gradiente de temperatura em comunidades de macroinvertebrados de riachos geotermais tropicais amazônicos, integrando abordagens tróficas e evolutivas para compreender como o estresse térmico influencia a estrutura do tamanho corporal, as dinâmicas tróficas, e a diversidade taxonômica e filogenética dessas comunidades.

1.1.2 OBJETIVOS ESPECÍFICOS

Capítulo I:

- Avaliar como o aumento da temperatura em riachos geotermais tropicais influencia a estrutura do tamanho corporal das comunidades de macroinvertebrados.
- Investigar as mudanças nas dinâmicas tróficas dessas comunidades, considerando variações na biomassa, abundância e interações alimentares, por meio de análises de espectros de tamanho e marcadores isotópicos estáveis.
- Responder como o aquecimento impacta a distribuição da biomassa entre categorias de tamanho corporal e como essas alterações afetam a complexidade e o funcionamento das redes tróficas em ecossistemas aquáticos tropicais naturais.

Capítulo II:

- Analisar a diversidade taxonômica e filogenética das comunidades de macroinvertebrados ao longo do gradiente térmico em riachos geotermais tropicais.
- Investigar padrões de agrupamento e dispersão filogenética usando métricas como Índice de Relacionamento Líquido (NRI) e Índice do Táxon Mais Próximo (NTI) para entender os processos de filtragem ambiental e competição.
- Avaliar de que forma o aumento da temperatura afeta a diversidade taxonômica e filogenética, e em que medida o conservadorismo filogenético restringe a composição e diversidade das comunidades adaptadas a temperaturas elevadas.

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2 Capítulo I - TROPHIC REORGANIZATION MAINTAINS CONSTANT SIZE SPECTRA ACROSS A TEMPERATURE GRADIENT

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2.1 RESUMO

Aquecimento pode influenciar profundamente o metabolismo dos organismos de água doce, levando a mudanças na distribuição do tamanho corporal, nos nichos tróficos e na dinâmica geral da teia alimentar. Estudar riachos geotermais tropicais oferece uma oportunidade única para compreender como as comunidades de água doce respondem ao estresse térmico, proporcionando insights relevantes para projeções de mudanças climáticas e manejo de ecossistemas. Hipotetizamos que temperaturas elevadas alterariam tanto a estrutura de tamanho quanto a dinâmica trófica das comunidades de macroinvertebrados de riachos devido ao aumento das demandas metabólicas. Especificamente, esperávamos: 1) reduções na abundância e biomassa individual, 2) espectros de tamanho mais inclinados resultantes da diminuição da biomassa de organismos maiores, e 3) uma estrutura alimentar simplificada, impulsionada pela dominância de espécies termicamente tolerantes e redução da diversidade trófica. Para testar essas hipóteses, examinamos 15 riachos tropicais no Centro do Brasil. Avaliamos a estrutura da comunidade usando biomassa dos organismos e espectros de tamanho, tratando a temperatura como um gradiente contínuo (variação média: 23,8ºC a 39,9ºC). A dinâmica trófica foi avaliada utilizando assinaturas isotópicas estáveis de $\delta^{13}C$ e $\delta^{15}N$, comparando riachos geotermais e naturais como regimes térmicos discretos. A biomassa foi estimada por meio de equações alométricas, e os declives dos espectros de tamanho calculados usando abordagem de máxima verossimilhança. Métricas de diversidade, biomassa e tróficas foram analisadas em relação à temperatura por modelos lineares. Contrariamente às expectativas, não encontramos relação consistente entre temperatura e biomassa comunitária, declives dos espectros de tamanho ou diversidade local. Da mesma forma, a amplitude do nicho isotópico (dispersão de $\delta^{13}C$ e $\delta^{15}N$) não diferiu entre riachos geotermais e naturais. Contudo, foram detectadas mudanças populacionais nos valores de $\delta^{15}N$ em vários táxons, incluindo Dytiscidae, Hydrophilidae, Gomphidae, Belostomatidae e Chironomidae, que apresentaram posições tróficas mais baixas em ambientes geotermais. Esses resultados sugerem uma mudança comportamental para alimentar-se em níveis tróficos inferiores onde a biomassa é mais abundante, provavelmente como uma estratégia para suprir as maiores demandas energéticas sob condições de aquecimento. Essa plasticidade trófica pode amenizar alguns efeitos do aquecimento, mantendo as distribuições de biomassa e a estrutura de tamanho apesar das taxas metabólicas elevadas. Esses achados ressaltam a importância da flexibilidade comportamental e dietética para a manutenção do funcionamento dos ecossistemas diante das mudanças climáticas.

Palavras-chave: Riachos geotermais, Demandas metabólicas, Espectros de tamanho, Isótopos estáveis, Gradiente térmico, Mudanças no nicho trófico.

2.2 ABSTRACT

Warming can profoundly influence the metabolism of freshwater organisms, leading to shifts in body size distributions, trophic niches, and overall food web dynamics. Studying tropical geothermal streams offers a unique opportunity to understand how freshwater communities respond to thermal stress and provides novel insights relevant to climate change projections and ecosystem management. We hypothesized that elevated temperatures would alter both the size structure and trophic dynamics of stream macroinvertebrate communities due to increased metabolic demands. Specifically, we expected 1) reductions in individual abundance and biomass, 2) steeper size spectra resulting from decreased biomass of larger organisms, and 3) a simplified food web structure driven by a dominance of thermally tolerant species and reduced trophic diversity. To test these hypotheses, we examined 15 tropical streams in Central Brazil. We assessed community structure using organismal biomass and size spectra, treating temperature as a continuous gradient (average range: 23.8ºC to 39.9ºC). Trophic dynamics were evaluated using $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures, comparing geothermal and natural streams as discrete thermal regimes. Biomass was estimated via allometric equations, and size spectra slopes were calculated using a maximum likelihood approach. Diversity, biomass, and trophic metrics were analyzed in relation to temperature using linear models. Contrary to expectations, we found no consistent relationship between temperature and community biomass, size spectra slopes, or local diversity. Similarly, isotopic niche width (dispersion of $\delta^{13}C$ and $\delta^{15}N$) did not differ between geothermal and natural streams. However, population-level changes in $\delta^{15}N$ values were detected in several taxa, including Dytiscidae, Hydrophilidae, Gomphidae, Belostomatidae, and Chironomidae, which showed lower trophic positions in geothermal environments. These results suggest a behavioral shift toward feeding down in the food web where biomass is more abundant, likely as a strategy to meet increased energetic demands under warming conditions. Such trophic plasticity may buffer some effects of warming, maintaining biomass distributions and size structure despite elevated metabolic rates. These findings highlight the importance of behavioral and dietary flexibility in sustaining ecosystem functioning under climate change.

Key words: Geothermal streams, Metabolic demands, Size spectra, Stable isotopes, Thermal gradient, Trophic niche shifts.

2.3 INTRODUCTION

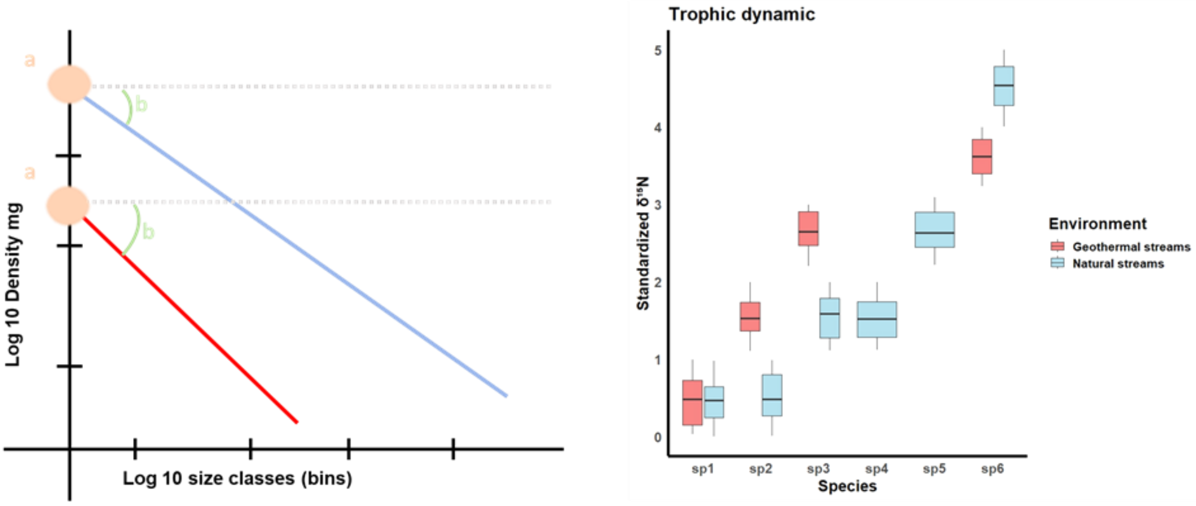
Rising temperatures have been recorded as one of the major drivers for severe changes in the physiology and energy demand of freshwater fauna, as they have impacts on adaptation and energy allocation by species at different trophic levels (Perkins et al., 2010; Woodward et al., 2010). Therefore, food web patterns, such as energy transferring efficiency, strength of top-down control, and relative arrangement of trophic interactions, are affected by climate change events and can undergo abrupt modifications (Winder & Schindler 2004; Ockendon et al. 2014; Danet et al., 2021). Despite extensive research, there is no established consensus on the impact of temperature changes on energy dynamics within food webs. Empirical evidence has shown mixed results: some studies have observed that rising temperatures increase energy flows by increasing interactions between consumers and their resources (Kratina et al., 2012; O'Gorman et al., 2017), while other studies reveal thermal mismatches between consumers and resources, which results in the energy flux imbalances across trophic levels (Barton, 2010; Álvarez-Codesal et al., 2023). Furthermore, some investigations have reported no effect of temperature on ecological interactions (Van De Velde et al., 2017; Gjoni et al., 2024). This variability underscores the complexity of ecological responses to temperature fluctuations, emphasizing the necessity for enhanced comprehension of how tropical ecosystems, which are inherently warm and often near the thermal optima of numerous ectothermic organism groups, respond and reorganize in the face of warming.

Size spectra provide a powerful lens through which to examine the structural organization of food webs, typically revealing a decline in organism abundance with increasing body size or biomass (Petchey & Belgrano, 2010; Glazier & Gjoni, 2024; Gjoni et al., 2025). This scaling pattern reflects fundamental ecological processes, where smaller-bodied organisms dominate numerically, while larger ones are less common—offering insight into energy flow and ecosystem functioning (Brose et al., 2019). The relationship is often formalized as $N \sim M^\lambda$, where N is abundance, M is body mass, and λ characterizes the slope of the size spectrum. Metabolic theory predicts that body size constraints metabolic rate, thereby linking community structure to ecosystem processes (Brown et al., 2004; Nee et al., 1991). As temperatures rise, metabolic rates are expected to increase, disproportionately affecting larger organisms due to higher maintenance costs and lower energetic efficiency, leading to steeper size spectra (Brown et al., 2004). However, empirical studies have shown mixed support for these predictions. For instance, recent studies observed that the impact of warming depends on the thermal adaptation of interacting species, with weaker effects in systems composed of taxa near their thermal optima (Pawar et al., 2016, Synodinos et al., 2021) This contrast between theory and evidences highlight the need to better understand how size structure responds to warming across ecological and thermal gradients.

Size-structured approaches provide key insights into energy distribution but assume predator-prey interactions are mainly driven by body size, overlooking complex trophic dynamics. Therefore, integrating stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) is crucial to reveal multitrophic interactions and their responses to thermal gradients (Boecklen et al., 2011; Van Der Lee et al., 2021). $\delta^{13}C$ helps distinguish sources of organic matter, while $\delta^{15}N$ indicates trophic positions and predator-prey mass relationships (Chappuis et al., 2017). While size spectra illustrate energy and mass distribution (Trebilco et al., 2013; Vasseur, 2020), stable isotopes detect shifts in trophic levels, such as food chain shortening under environmental change, clarifying energy allocation mechanisms (Layman et al., 2012; Effert-Fanta et al., 2022). The combination of these approaches may reveal how changes in feeding strategies may sustain similar patterns of biomass distribution. For example, under warming, predators may sustain similar biomass by changing from feeding on optimal prey to more dense but less rewarding prey at the bottom of the web (Gauzens et al. 2024). Together, these complementary methods can enhance our understanding of food web dynamics across temperature gradients.

Geothermal streams are naturally heated systems with strong temperature gradients at small scales, and offer valuable insights into how warming may impact natural ecosystems (Demars et al., 2011a, b; O'Gorman et al., 2014). These ecosystems offer a rare combination of high control and realism, optimizing space-per-time studies. Rasmussen et al. (2011), in their investigation of geothermal streams in the Icelandic region, demonstrated that increasing temperature enhances both primary production and decomposition rates. Overall, temperature acts as a key driver of both the structure and function of stream food webs, with its effects mediated by species' thermal preferences, body size, and the degree of functional redundancy within the community (O'Gorman et al., 2014; Nelson et al., 2019; Bonnaffé et al., 2021; Junker et al., 2024; Jackson et al., 2024a). However, there is a lack of studies on tropical geothermal streams, precluding our ability to predict how tropical streams may cope with potential climate changes (O'Gorman et al., 2019).

In this study, we investigated tropical streams in Central Brazil, exploring how macroinvertebrate communities behave to a natural temperature (i.e., geothermal) gradient. We hypothesized that the increase in temperature would alter size structure and trophic dynamics given an increased metabolic cost at higher temperatures. At local scale, we expected that both the number of individuals and the amount of biomass would be reduced (Saito et al., 2021). Moreover, we expected that this increased metabolism would decrease the energy moving up for higher trophic levels, steepening size spectra as a consequence of lower biomass of larger organisms. We also expected that the increase in temperature would change trophic dynamics, simplifying food webs, since only a few organisms that are well adapted to this costly environment would manage to persist in the food web. These changes in paths and energy demand in geothermal streams should cause: (i) Total and average community biomass decreases with increasing temperature; (ii) A steep decline in the size spectrum in warmed environments, revealing a proportionally higher decrease in biomass across potential trophic levels; (iii) A decrease in local diversity (i.e., Shannon and Chao1 indexes) and a simplification of the food web; (iv) A decrease in species trophic position between natural and geothermal environments (Fig. 1).



2.4 Methods

2.4.1 Field sampling

In October 2022, we sampled macroinvertebrates in geothermal and natural streams. Geothermal streams are characterized by rapid water flow with a short residence time, marked by significant inputs of thermal energy, and are generally restricted to small, spatially isolated areas with hydrological regimes distinct from the rest of the basin (Woodward 2010; O'Gorman et al., 2014). The thermal enhancement of stream water is primarily attributed to the steam released from boiling geothermal water reservoirs (Godoy & Godoy, 2016). This process involves the heating of the overlying cold groundwater, which contributes to the stream's flow, and the bedrock through which the streams traverse (Árnason et al. 1969; Godoy & Godoy, 2016). Our study was conducted in 15 streams (mostly first order), which were classified into geothermal and natural streams. The initial experimental design included sixteen streams, equally distributed between the two categories; however, one geothermal stream (stream number eight) was excluded from further analyses due to the absence of collected organisms. We sample in two hydrographic regions in the state of Mato Grosso (Brazil): Tocantins-Araguaia and Paraguay basins (Figure. 2).

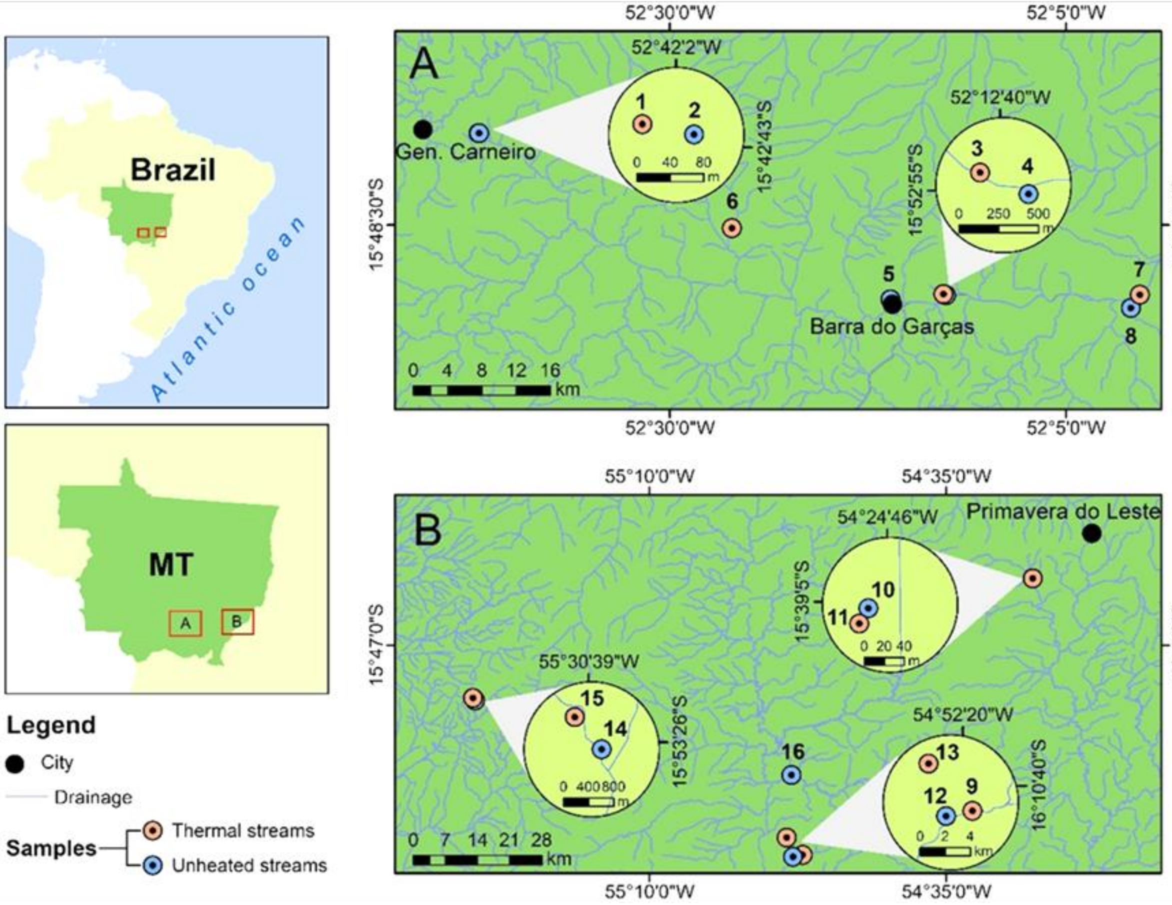


Figure 2. Geographic distribution of the 16 streams sampled in Mato Grosso, Brazil, spanning two major hydrographic regions: the Tocantins-Araguaia and Paraguay basins. Geothermal streams are represented by red circles, whereas natural streams (i.e., unheated streams) are marked by blue circles.

In each stream, within a 30 m stretch, six benthic macroinvertebrates samples were collected with a 30cm x 30cm Surber net (mesh size 250 µm) for a quantitative sample (for community composition and size spectra) and five kick net samples (20 seconds each) were collected for a qualitative sample for stable isotopes. From each Surber sample, we collected all the organic matter present to estimate the carbon signature to calculate resources baseline (i.e., basal resources). All samples were placed on ice in the field and frozen upon return to the laboratory. Quantitative and qualitative samples were readily sorted within one day after sampling. Quantitative samples were stored in absolute alcohol, and qualitative samples were stored dry and frozen.

We also measure chemical water quality parameters were measured in the field using a HORIBA multiparameter probe: water temperature (Field_Temp, °C), surface water temperature (Max_Temp, °C), oxidation-reduction potential (ORP_mV, mV), dissolved oxygen saturation (DOS, mg/L), dissolved oxygen percentage relative to saturation (%DO), total dissolved solids (TDS, mg/L), electrical conductivity (Cond, µS/cm), and salinity (Salt, ppt). Chemical variables were collected in triplicate at multiple sites along the streams to ensure the accuracy and reliability of the measurements. Physical parameters assessed included channel width (Width, cm) and depth (Depth, cm), each measured at ten evenly spaced points along the longitudinal gradient of the streams. Channel width was defined as the lateral distance across the water column, while depth corresponded to the vertical distance from the water surface to the streambed. For subsequent statistical analyses, only field temperature was considered as the thermal variable. To characterize the overall physical and chemical conditions of the streams, arithmetic means of all measured variables were calculated and used, providing standardized summary values for each site. (Figure S1).

2.4.2 Organisms' measurement and body mass estimation

Stream eight, a geothermal stream, yielded no individuals, and therefore, it was excluded from subsequent analyses. The individuals were identified at the lowest possible taxonomic level using specialized literature (Melo, 2003; Segura, 2011; Souza, 2012; Hamada et al. 2014). Most insects were identified at the genus level; when this was not possible, they were identified at the subfamily or family level. The individuals were placed on a Petri dish with 70% alcohol and with the aid of a LEICA EZ4 stereomicroscope and millimeter graph paper, the following measurements were taken: Total length, head length, and head width. Gastropoda were measured from the height of the shell along its longest axis; Huridinea and Oligochaeta were measured from the distance of one end to the other. Using measurements of body length and carapace width, and shell height, we estimated individual dry mass (mg) using published length-mass relationship equations (Table S1). When more than one equation was found for the same taxa, we selected the one with the highest R^2.

2.4.3 Size Spectra Analysis

In order to estimate the size spectrum for each stream, we employed the extended likelihood bin method (MLEbin) as described by Edwards et al (2020). This approach explicitly incorporates uncertainty in body sizes within each "bin", allowing for a range of sizes. Given that length-weight relationships are exponential, the discrepancy in dry weights derived from the lower and upper bin boundaries can be significant. Furthermore, because length-weight regressions are taxon-specific, these discrepancies may be more pronounced for certain groups. Consequently, size classes were initially defined on a log 2 scale (i.e., 0.5, 1, 2mm) intervals. Total counts per class were standardized to individuals per m^2. To mitigate bias from the under sampling of small body sizes, a minimum body size threshold of >0.1 mg was established. The Individual Size Distribution (ISD) was fitted to a bounded power law distribution using maximum likelihood methods (MLEbin), which account for the uncertainty of body sizes within classes. Total community biomass was calculated by multiplying the biomass of individuals by their density.

2.4.4 Stable Isotopes Analysis

Subsequently, 1 mg ± 0.2 mg of macroinvertebrate samples and 4~6 mg of decaying plant litter were weighed into tin (Sn) capsules (Elemental Microanalysis® 8 × 5 mm) prior to isotopic analysis. We conducted an analysis of macroinvertebrate samples and decaying plant litter to determine the stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). This analysis was performed at University of California, Davis, USA. The tissues of animals and small plant samples were assessed for their $\delta^{13}C$ and $\delta^{15}N$ isotopes using a PDZ Europa ANCA-GSL elemental analyzer coupled with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

The long-term standard deviation for $\delta^{13}C$ was found to be 0.2 ‰, while for $\delta^{15}N$ it was 0.3 ‰. The final delta values were expressed relative to international standards: VPDB (Vienna Pee Dee Belemnite) for carbon and atmospheric air for nitrogen.

2.4.5 Data analyses

We focused our analyses across the temperature gradient; there was no strong correlation between temperature and other variables (Figure S1). Due to isotopic data limitation, we analyzed our data in two ways. For size spectra analyses and associated regression models, temperature was treated as a continuous variable representing a thermal gradient, capturing fine-scale variation across streams by using the average temperature per stream. Conversely, for stable isotope analysis of trophic dynamics, temperature was treated as a categorical factor (geothermal vs. natural streams; Figure S2). This approach was necessitated by incomplete taxonomic representation across streams, where not all sites yielded sufficient individuals from all taxa for $\delta^{13}C$ and $\delta^{15}N$ quantification. Categorization enabled robust inter-regime comparisons by pooling available samples within thermal categories, thereby maintaining adequate statistical power despite reduced per-stream sample sizes.

To test the hypothesis that biomass decreases with increasing temperature (Hypothesis i), we employed Linear Models (LMs) using two response variables: average individual biomass per stream and total summed biomass per stream and temperature as a predictor. Similarly, to evaluate whether size spectra vary along the temperature gradient (Hypothesis ii), we fitted a Linear Model with the size spectra slope (λ) as the response and temperature as the predictor, allowing us to assess changes in size distribution patterns with warming.

To assess the impact of warming on local diversity (Hypothesis iii), we first modeled Shannon and Chao1 diversity indices against temperature using Linear Models, treating temperature as a continuous predictor. Subsequently, to determine whether the community trophic niche differed between natural and geothermal streams, we applied Permutational Analysis of Multivariate Dispersions (PERMDISP), which tests for differences in multivariate dispersion among groups using $\delta^{15}N$ and $\delta^{13}C$ data.

For investigating shifts in species trophic position between environments (Hypothesis iv), we used standardized $\delta^{15}N$ isotope values as proxies for trophic position (TP). Standardization was achieved by subtracting baseline $\delta^{15}N$ values—derived from primary sources such as leaf litter within each stream—from consumer $\delta^{15}N$ values, thereby normalizing for spatial isotopic variation and enabling direct comparison across taxa and sites. The distribution of standardized $\delta^{15}N$ values across taxa and thermal regimes was visualized using boxplots. For taxa present in both environments, differences in trophic position were tested using Student's t-tests when parametric assumptions were met, or Wilcoxon rank-sum tests otherwise.

For taxa exhibiting significant trophic position differences between natural and geothermal streams, we further modeled the relationship between population biomass and temperature using generalized linear models (GLMs) with a Gamma distribution and log link function. This approach accounted for the non-normal, positively skewed biomass data. To control for multiple testing, Bonferroni corrections were applied, setting a stringent significance threshold at an adjusted alpha level of 0.005, corresponding to the number of taxa analyzed.

2.5 Results

We found that geothermal streams typically had higher average temperatures, with maximum average values reaching up to 34.43°C and minimum average values around 30.61°C. In contrast, natural streams had a maximum average temperature of 29.29°C and a minimum average of 23.8°C. (Figure S2)

2.5.1 Macroinvertebrates

We obtained a total of 3,409 individuals distributed in four classes, 15 orders, 32 families, and 63 genera (Table S3). In geothermal streams, we recorded 30 taxa and 1842 individuals, while for natural streams we recorded 49 taxa and 1567 individuals.

2.5.2 Biomass

Geothermal individual biomass ranged from 0.0005 mg DM of a Chironominae to a Gastropoda of 395.02 mg DM, while natural streams individual biomass ranged from a Chironominae of 0.009 mg DM to a *Palaemon* with 1718.29 mg DM. We found that there was no relationship between total biomass and the temperature gradient (R2 = -0.045, F1,13 = 0.394, p = 0.540) (Figure 3b). The same was recorded for the average individual biomass model with the temperature gradient (R2 = 0.076, F1,13 = 2.157, p = 0.165) (Figure 3c), not supporting our first hypothesis (Table S2).

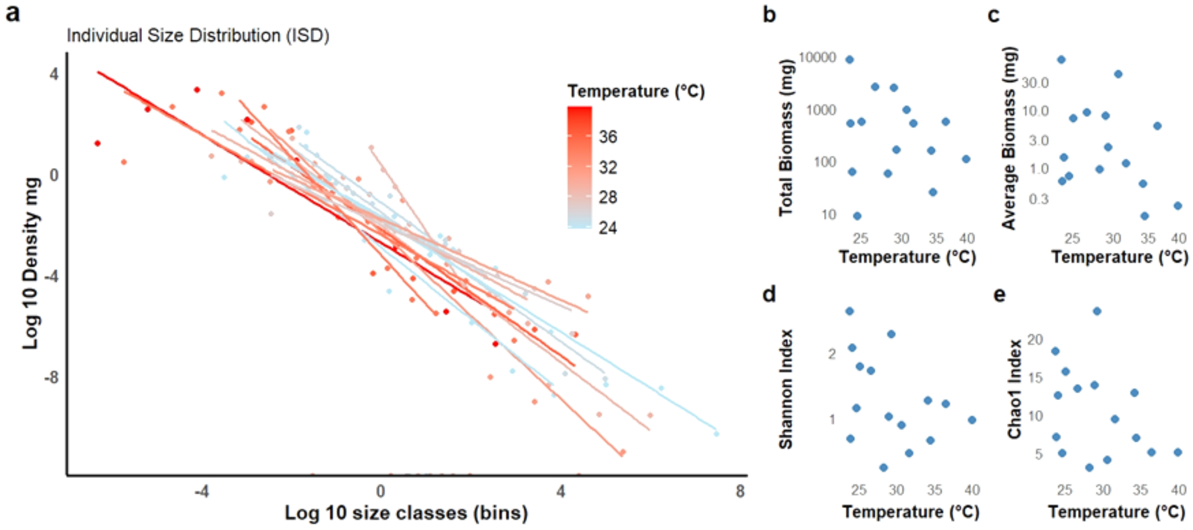


Figure 3. Association between community variables and the temperature gradient. The individual size spectra in 15 streams across the temperature gradient (a); The relationship between temperature and total biomass (b); mean biomass (c); Shannon diversity index (d) and Chao1 diversity index (e).

2.5.3 Individual Size Distribution

The size spectrum slope/exponent (λ) had a mean value of -1.2575 and a standard deviation of 0.5288, indicating that larger organisms were consistently less abundant than smaller organisms (Table S2). The size spectra slopes, however, were not related to the temperature gradient (R2 = -0.076, F1,13 = 0.0004, p = 0.983) (Figure 3a), not supporting our second hypothesis that size spectra would be steeper with increasing temperature.

2.5.4 Diversity

Our third hypothesis was also not corroborated, since we found no relationship between the Shannon diversity index and the temperature gradient (R2 = 0.089, F1,13 = 2.371, p = 0.147) (Figure 3d). The same lack of relationship was found between the Chao1 diversity index and the temperature gradient (R2 = 0.052, F1,13 = 1.783, p = 0.204) (Figure 3e).

2.5.5 Stable Isotopes

We conducted a Variance analyses (ANOVA) to compare the $\delta^{15}N$ values of baseline resources among streams, revealing significant differences (ANOVA, F = 73.5, P < 0.001). We observed that there was no difference in the dispersion of carbon and nitrogen signature values between stream groups (PERMIDISP, ANOVA, F=0.891, df=1, p=0.345) (Fig S4). This result indicates that the total community isotopic niche space used by macroinvertebrates in geothermal and natural streams was not different (Figure 4).

By comparing the standardized $\delta^{15}N$ of individual taxa among geothermal and natural streams, we detected population-level shifts in trophic position in temperature-sensitive taxa. Specifically, we observed lower standardized $\delta^{15}N$ in geothermal streams in comparison to natural ones in Dytiscidae (w=0, p<0.001), Gomphidae (w=16, p<0.001), Hydrophilidae (t= -5.17, df=11.4, p<0.001), Chironomidae (t= -4.61, df= 10.8, p<0.001), and Belostomatidae (t= -26.37, df=2.1, p=0.001), while we observed the opposite in Gastropoda (higher standardized $\delta^{15}N$ in natural streams, w=187, p<0.001) (Figure 5).

We also found some associations between temperature and the population biomass of multiple taxa. Gastropoda (estimate = 0.5563, p = 0.00162) and Gomphidae (estimate = 0.1070, p = 0.00051) exhibited positive biomass responses to increasing temperature, corresponding to approximate multiplicative increases of 74% and 11%, respectively, per one-unit increment in mean temperature (Figures S2). In contrast, Hydrophilidae (estimate = -1.1962, p = 0.00179) and Chironomidae (estimate = -0.0192, p = 0.00255) showed significant negative biomass responses, with declines of approximately 70% and 1.9%, respectively, per unit increase in temperature (Figure S2). No statistically significant effect of temperature on Dytiscidae biomass was detected (estimate = 0.0137, p = 0.426). These findings demonstrate taxon-specific differential biomass responses along the thermal gradient, reflecting variable sensitivities to temperature within the studied macroinvertebrate community. (Figure S4) (Table S4).

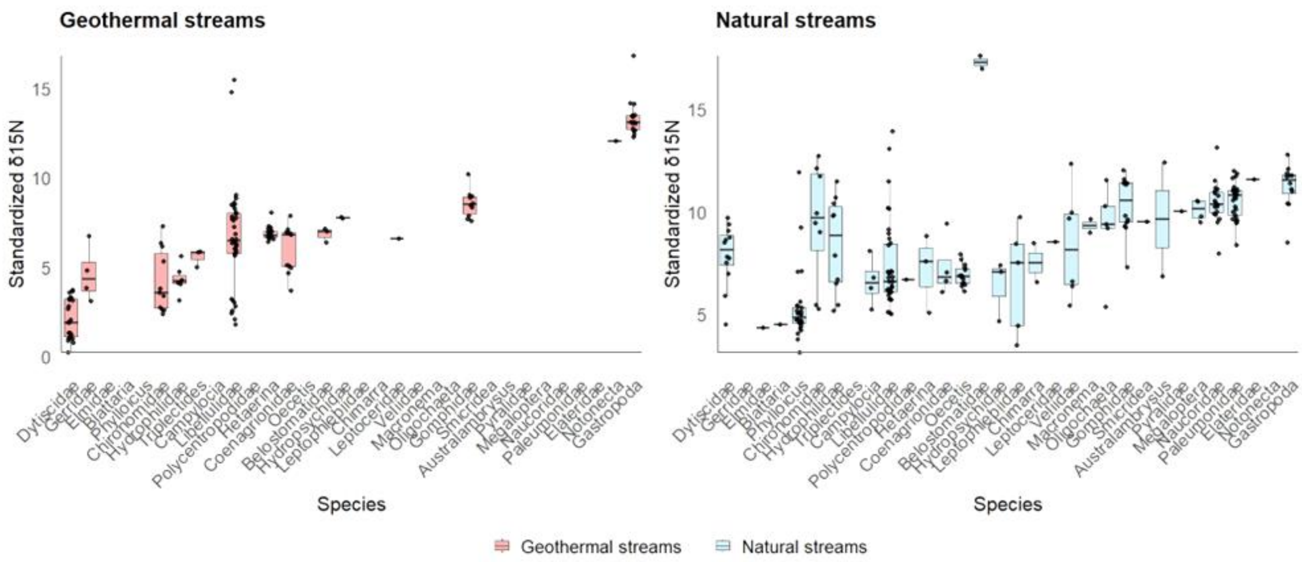


Figure 4. Standardized $\delta^{15}N$ of all taxa in geothermal streams (indicated in red) and natural streams (indicated in blue).

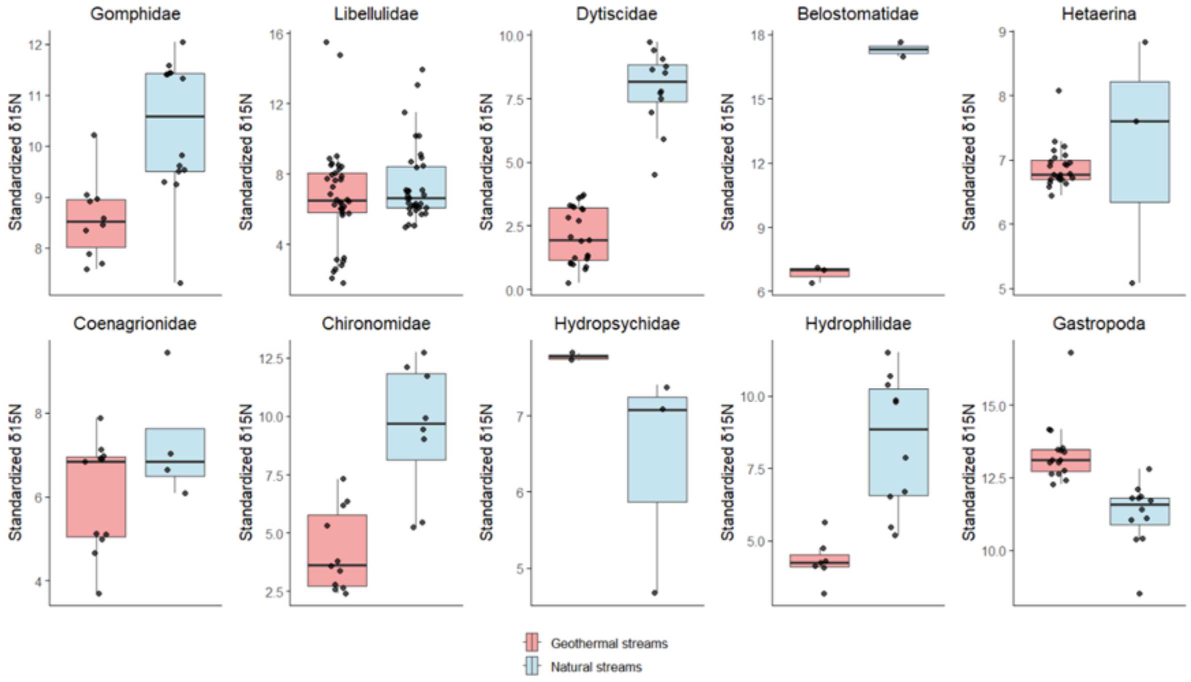


Figure 5. Standardized $\delta^{15}N$ of individuals within taxa between geothermal streams (indicated in red) and natural streams (indicated in blue).

2.6 Discussion

We conducted a novel investigation of how stream communities and food webs respond to warming in tropical geothermal streams. We surprisingly found that community size spectra did not change systematically with warming, nor did total biomass or diversity. However, individual biomasses of some taxa increased and decreased along the temperature gradient. Our findings revealed a trophic reorganization of some insects, such as predators (dragonflies and beetles) feeding closer to basal resources and grazers (Gastropoda) increasing in abundance. Altogether, our results reveal population-level dynamics that maintain consistent community-level size spectra and biomass patterns across temperature gradients. This result is in line with ideas of resource compensation mechanisms for communities that are in high-temperature environments (e.g., tropical regions) and experience warming, indicating that simplistic predictions of how size spectra patterns may change with warming must be viewed with caution.

Across geothermal streams, size spectra slopes should become steeper as temperatures increase, indicating a shift in the distribution of abundance and biomass within communities to the prevalence of small organisms (Brown et al. 2004). ISD exponents may represent the efficiency of energy transfer from small, abundant individuals to larger, less common predators (Trebilco et al., 2013). Less negative slopes indicate a balanced energy flow that supports larger consumers, while steeper slopes suggest inefficient transfer and fewer large individuals (Trebilco et al., 2013; Pomeranz et al., 2021). Across our 15 streams, the mean slope was −1.2, consistent with values that have been reported for freshwater communities across environmental gradients (Gjoni et al., 2024; Collyer et al., 2023; Pomeranz et al., 2020; Pomeranz et al., 2021). However, contrary to predictions from the Metabolic Theory of Ecology (MTE), a natural stream at 28 °C had a very steep slope (−3.007), while a hotter geothermal stream at 30.6 °C had a shallower slope and supported 17 times more biomass. Most streams, both geothermal and natural, had moderate slopes around −1.2, and, excluding extreme slopes, the variation in ISD exponents across a 10.6 °C gradient was low (~0.18), similar to Arctic streams (O'Gorman et al., 2017). These results corroborate previous findings that size spectrum slopes may vary little with temperature in natural settings, when other ecological mechanisms such as interspecific interactions and basal resources compensation may drive compensatory dynamics (O'Gorman et al., 2017).

Contrary to initial expectations of a uniform monotonic response of community biomass to temperature, our refined analyses reveal taxon-specific biomass responses along the temperature gradient. For example, while Gastropoda and Gomphidae exhibited significant positive biomass increases with rising temperature (approximately 74% and 11% per unit increase, respectively), Hydrophilidae and Chironomidae showed significant biomass declines (around 70% and 1.9% decreases per unit temperature increase, respectively). These contrasting patterns highlight a complex and heterogeneous interaction between temperature and biomass at the community level, suggesting that aggregate biomass responses may mask divergent strategies and sensitivities among taxa. Such differential responses challenge simplified assumptions in the literature that predict a consistent decline in biomass with warming (Brown et al., 2004; Saito et al., 2021) and underscore the importance of taxon-level analyses to understand ecosystem responses to climate change.

Our lack of warming effect on size spectra and total biomass can be explained by the potential trophic changes observed in Dytiscidae, Hydrophilidae and Gastropoda. We can highlight the findings of the family Dytiscidae, which are essentially one of the top predators in stream habitats. This family is considered generalist, feeding on zooplankton, aquatic macroinvertebrates, amphibian larvae, and fish (Culler et al., 2014; Frelik & Pakulnicka, 2015). However, some species show selectivity in feeding, and others end up engaging in cannibalism, intraguild predation and even necrophagy (Culler & Lamp, 2009; Culler et al., 2014; Silva-

Soares, 2019). This clearly demonstrates the dietary plasticity of this family of aquatic beetles. In our study, we observed a trophic downgrading of organisms in this family due to the potential increase in metabolic costs associated with warming, forcing them to feed down the web, where biomass is more available. Therefore, the lack of relationship between the biomass of this family and the temperature gradient, combined with the absence of significant differences in biomass between environments, may indicate that these organisms sustain their local biomass across a wide range of temperature degrees (Figure S3).

In an opposite situation, a group of grazers (Gastropoda) increased their individual biomass by 77% with increasing temperature. Warming in continental aquatic ecosystems frequently enhances primary productivity, thereby modulating food web dynamics and potentially favoring specific herbivorous and grazing rates, such as Gastropoda order. However, these effects are context-dependent, varying with local environmental conditions and community composition. Experimental warming studies in lotic systems have demonstrated up to a threefold increase in net primary productivity, which in turn drives significant biomass increases among herbivores and grazers (Hannesdóttir et al., 2013; Jackson et al., 2024a). This pattern arises because primary consumers capitalize on the increased availability of basal resources, such as algal biomass, often resulting in their numerical or biomass dominance in warmer stream environments (Jackson et al., 2024a). Consequently, the proliferation of resource-tolerant species that exploit enhanced basal productivity can offset declines in more temperature-sensitive rates, thereby contributing to ecosystem stability. Nonetheless, this compensatory mechanism may lead to reduced community diversity and increased homogenization (Junker et al., 2024; Jackson et al., 2024b).

2.7 Conclusion

Our study demonstrates that tropical geothermal environments possess a population-level energy compensation mechanism driven by shifts in the trophic positions of specific taxa within the food web. This dynamic adjustment stabilizes and maintains consistent size spectra, biomass distribution, and energy transfer relationships along rising temperature gradients. While temperature does not directly alter community biomass or size spectra in macroinvertebrate assemblages, it subtly modulates these compensatory processes, ensuring food web stability and optimizing biomass allocation across size classes. Notably, despite similarities in size structure between aquatic insect communities in geothermal and natural streams, ISD values consistently approximate -1.2. This consistency suggests that taxa operating near their thermal optima actively engage in compensatory mechanisms to preserve local energy structures. Moreover, temperature exerts both positive and negative effects on the biomass of certain taxa, reflecting complex population-level responses. These mechanisms likely involve streamlining energy pathways and adjusting foraging strategies to focus on basal resources, thereby enhancing ecosystem resilience amid thermal variability. Our findings highlight the critical role of trophic reorganization and energetic compensation in maintaining stable community structure and function under warming scenarios in tropical freshwater ecosystems.

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2.9 Supplementary Material

Table S 1 Length-mass relationship equations for both Power (DM = a * x ^ b) and Linear (ln(DM) = ln(a) + b * ln(x)) model. TBL = Total Body Length (mm) for insects and clitellata; and GDS = Greatest Distance from the Shell (mm). When the species/genus used for the equations did not belong to the observed genera, the one with the highest R^2 or the one most similar in shape was chosen.

Taxa	*Measure*	*a*	*b*	*Source*	*Model type*	*Comments*
INSECTA						
Coleoptera						
Berosus sp.	*TBL*	*-4.0399*	*2.58*	*Mroczyński & Daliga (2016)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydrophilidae*
Dytiscidae	*TBL*	*-4.0399*	*2.58*	*Mroczyński & Daliga (2016)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydrophilidae*
Hydroporus sp.	*TBL*	*-4.0399*	*2.58*	*Mroczyński & Daliga (2016)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydrophilidae*
Laccophilus sp.	*TBL*	*-4.0399*	*2.58*	*Mroczyński & Daliga (2016)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydrophilidae*
Laccornellus sp.	*TBL*	*-4.0399*	*2.58*	*Mroczyński & Daliga (2016)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydrophilidae*
Luchoelmis sp.	*TBL*	*0.0074*	*2.879*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Elmidae*

Microcylloepus sp.	*TBL*	*0.0074*	*2.879*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Elmidae*
Neobidessus sp.	*TBL*	*-4.0399*	*2.58*	*Mroczyński & Daliga (2016)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydrophilidae*
Ptilodactylidae	*TBL*	*0.0011*	*3.1*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original por Anchytarsus bicolor*
Stegoelmis sp.	*TBL*	*0.0074*	*2.879*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Elmidae*
Tropisternus sp.	*TBL*	*0.0275*	*2.39*	*Mroczyński & Daliga (2016)*	*DM = a * x ^ b*	*Original for Hydrophilidae*
Diptera						
Chironominae	*TBL*	*-6.815*	*2.739*	*Dekanov√° et al. (2021)*	*ln(DM) = ln(a) + b * ln(x)*	
Empididae	*TBL*	*0.004*	*2.655*	*Benke et al. (1999)*	*DM = a * x ^ b*	
Hexatoma sp.	*TBL*	*0.0029*	*2.681*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Tipulidae*

Orthocladius sp.	*TBL*	*-6.311*	*2.435*	*Dekanov√° et al. (2021)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Orthocladiinae*
Palpomuia sp.	*TBL*	*0.0025*	*2.469*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Ceratopogonidae*
Tanypodinae	*TBL*	*-5.368*	*1.886*	*Dekanov√° et al. (2021)*	*ln(DM) = ln(a) + b * ln(x)*	
Ephemeroptera						
Campylocia sp.	*TBL*	*-5.29*	*2.682*	*Giustini et al. (2008)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Ephemeroptera*
Hemiptera						
Australambrysus sp.	*TBL*	*0.0108*	*2.734*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Cryphocricos*
Aquarius sp.	*TBL*	*0.015*	*2.596*	*Smock (1980)*	*DM = a * x ^ b*	*Original for Gerris remigis*
Brachymetra sp.	*TBL*	*0.015*	*2.596*	*Smock (1980)*	*DM = a * x ^ b*	*Original for Gerris remigis*

Limnocoris sp.	*TBL*	*0.0108*	*2.734*	*Benke et al. (1999)*	$DM = a * x ^\wedge b$	*Original for Cryphocricos*
Neogerris sp.	*TBL*	*0.015*	*2.596*	*Smock (1980)*	$DM = a * x ^\wedge b$	*Original for Gerris remigis*
Ranatra sp.	*TBL*	*-7.893*	*1.692*	*Bailey (1986)*	$\ln(DM) = \ln(a) + b * \ln(x)$	*Original for Ranatra dispar*
Tenagobia sp.	*TBL*	*0.0108*	*2.734*	*Benke et al. (1999)*	$DM = a * x ^\wedge b$	*Original for Siagra sp.*
Lepidoptera						
Petrophila sp.	*TBL*	*2.879*	*0.0074*	*Benke et al. (1999)*	$DM = a * x ^\wedge b$	
Megaloptera						
Corydalus flavicornis	*TBL*	*0.0037*	*2.873*	*Benke et al. (1999)*	$DM = a * x ^\wedge b$	*Original for Corydalidae*
Chloronia sp.	*TBL*	*0.0037*	*2.873*	*Benke et al. (1999)*	$DM = a * x ^\wedge b$	*Original for Corydalidae*

Odonata

Aeschnosoma sp.	*TBL*	*0.0096*	*2.787*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Corduliidae*
Anatya sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	*DM = a * x ^ b*	*Original for Libellulidae*
Aphylla sp.	*TBL*	*0.0025*	*3.474*	*Dekanov√° et al. (2021)*	*DM = a * x ^ b*	*Original for Gomphidae*
Argia sp.	*TBL*	*0.0086*	*2.666*	*Smock (1980)*	*DM = a * x ^ b*	*Original for Coenagrionoidea*
Brachymesia sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	*DM = a * x ^ b*	*Original for Libellulidae*
Brechmorhoga sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	*DM = a * x ^ b*	*Original for Libellulidae*
Cannaphila sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	*DM = a * x ^ b*	*Original for Libellulidae*
Dasythemis sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	*DM = a * x ^ b*	*Original for Libellulidae*

Epigomphus sp.	*TBL*	*0.0025*	*3.474*	*Dekanov√° et al. (2021)*	_DM = a * x ^ b_	*Original for Gomphidae*
Libellula sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	_DM = a * x ^ b_	*Original for Libellulidae*
Libellulidae	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	_DM = a * x ^ b_	
Macrothemis sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	_DM = a * x ^ b_	*Original for Libellulidae*
Paracordulia sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	_DM = a * x ^ b_	*Original for Libellulidae*
Perithemis sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	_DM = a * x ^ b_	*Original for Libellulidae*
Phyllocycla sp.	*TBL*	*0.0088*	*2.787*	*Benke et al. (1999)*	_DM = a * x ^ b_	
Phyllogomphoides sp.	*TBL*	*0.0025*	*3.474*	*Dekanov√° et al. (2021)*	_DM = a * x ^ b_	*Original for Gomphidae*
Progomphus sp.	*TBL*	*0.0025*	*3.474*	*Dekanov√° et al. (2021)*	_DM = a * x ^ b_	*Original for Gomphidae*

Progomphus clendoni	*TBL*	*0.0025*	*3.474*	*Dekanov√° et al. (2021)*	*DM = a * x ^ b*	*Original for Gomphidae*
Striped sp.	*TBL*	*0.0096*	*2.787*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Corduliidae*
Tholymis sp.	*TBL*	*0.0081*	*2.94*	*Dekanov√° et al. (2021)*	*DM = a * x ^ b*	*Original for Libellulidae*
Rhynchobdellida						
Glossiphoniidae	*TBL*	*-2.12*	*2*	*Edwards et al. (2009)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hirudinea*
Trichoptera						
Calosopsyche sp.	*TBL*	*-1.843*	*2.102*	*Paciencia (2012)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydropsychidae*
Diplectrona sp.	*TBL*	*-1.843*	*2.102*	*Paciencia (2012)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydropsychidae*
Grumicha grumicha	*TBL*	*0.0074*	*2.741*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Agarodes libalis*

Helicopsyche sp.	*TBL*	*0.012*	*3.096*	*Benke et al. (1999)*	*DM = a * x ^ b*	
Macronema sp.	*TBL*	*-1.843*	*2.102*	*Paciencia (2012)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Hydropsychidae*
Nerophilus sp.	*TBL*	*0.0064*	*3.241*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Psilotreta sp*
Oecetis sp.	*TBL*	*0.0034*	*3.212*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Leptoceroidea*
Phylloicus sp.	*TBL*	*-1.844*	*2.075*	*Paciencia (2012)*	*ln(DM) = ln(a) + b * ln(x)*	
Wormaldia sp.	*TBL*	*0.005*	*2.511*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Philopotamidae*
BIVALVE						
Bivalve	*GDS*	*0.0204*	*2.45*	*Benke et al. (1999)*	*DM = a * x ^ b*	*Original for Corbicula fluminea*
CLITELLATA						

Hirudinea	*TBL*	*-2.12*	*2*	*Edwards et al. (2009)*	*ln(DM) = ln(a) + b * ln(x)*	
Oligochaeta	*TBL*	*0.008*	*1.888*	*Miyasaka et al. (2008)*	*DM = a * x ^ b*	
GASTROPODA	*GDS*	*-2.369*	*2.348*	*Ajani et al. (2020)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Bithyniidae*
MALACOSTRACA						
Decapoda						
Macrobrachium sp.	*TBL*	*-5.08*	*3.76*	*Miserendino (2001)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Aegla neuquensis*
Palaemon sp.	*TBL*	*-5.08*	*3.76*	*Miserendino (2001)*	*ln(DM) = ln(a) + b * ln(x)*	*Original for Aegla neuquensis*

Table S 2. Environmental variables associated with all streams.

Stream	**Temperature (°C)**	**λ**	**Average Biomass (mg)**	**sd**	**Total biomass (mg)**	**sd**
Stream1	39.91	-1.11708	0.218936	1.000.921	1.070598	0.999897
Stream2	29.29	-0.96395	2.186619	4.635.155	161.8098	4.60373
Stream3	24.12	-1.03334	1.466092	2.213538	61.57585	2.187028
Stream4	25.68	-1.12816	0.526188	1.773297	154.1731	1.770268
Stream5	23.8	-1.06423	70.52728	236.8713	8.463.273	235.8823
Stream6	34.42	-1.43196	0.142509	0.309801	25.08155	0.308919
Stream7	26.64	-0.96536	8.8524	11.95849	2602.606	11.93813
Stream9	30.61	-0.5538	39.51566	2.694149	948.3759	26.37424
Stream10	24.66	-1.38119	0.709293	1.123864	8.511519	1.076018
Stream11	28.97	-1.19053	7.718442	4.530137	2446.746	45.22986
Stream12	25.12	-1.13965	6.962258	19.77432	543.0561	19.64715
Stream13	36.47	-1.33293	5.169922	15.26678	542.8418	15.19391
Stream14	28.24	-3.00372	0.929498	0.732975	55.7699	0.726841
Stream15	31.64	-1.32529	1.156891	10.27299	506.7181	10.26126
Stream16	23.9	-1.23152	0.579757	2.79688	514.2442	2.795303

Table S 3. Species distribution in all streams.

Taxa	Streams

	1	**2**	**3**	**4**	**5**	**6**	**7**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Aeschnosoma sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Australambrysus sp.	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0
Anatya sp.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Aphylla sp.	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Aquarius sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Argia sp.	0	7	1	18	1	0	0	0	0	0	0	0	0	2	0
Berosus sp.	222	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalve	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Brachymesia sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Brachymetra sp.	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
Brechmorhoga sp.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Calosopsyche sp.	0	0	0	0	6	0	1	0	0	0	0	0	0	0	0

Campylocia sp.	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0
Cannaphila sp.	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chironominae	230	10	5	176	10	0	47	0	0	4	4	48	0	395	723
Chloronia sp.	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Corydalus flavicornis	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Dasythemis sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Diplectrona sp.	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
Dytiscidae	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Empididae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Epigomphus sp.	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0
Gastropoda	0	0	0	0	0	0	16	0	0	60	11	0	0	1	0
Glossiphoniidae	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Grumicha grumicha	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0

Helicopsyche sp.	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0
Hexatoma sp.	0	0	0	0	7	0	1	0	0	0	0	0	0	0	0
Hirudinea	0	0	0	0	0	1	0	0	0	21	13	0	0	0	0
Hydroporus sp.	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laccophilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0
Laccornellus sp.	0	0	0	0	0	0	0	0	0	0	0	0	57	0	0
Leptonema sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Libellula sp.	0	3	0	0	0	0	0	0	0	0	0	8	0	0	0
Libellulidae	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Limnocoris sp.	0	0	0	0	4	0	1	0	0	0	0	0	0	0	67
Luchoelmis sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Macrobrachium sp.	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0
Macronema sp.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0

Macrothemis sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Microcylloepus sp.	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0
Neobidessus sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neogerris sp.	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Nerophilus sp.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Oecetis sp.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Oligochaeta	0	1	0	0	0	26	0	0	5	4	2	0	2	5	0
Orthocladius sp.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Palaemon sp.	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
Palpomyia sp.	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0
Paracordulia sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Perithemis sp.	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0
Petrophila sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllocycla sp.	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0

Phyllogomphoides sp.	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Phylloicus sp.	0	1	0	0	0	0	113	0	0	0	0	0	0	1	8
Progomphus sp.	0	12	0	0	14	0	0	17	0	1	1	12	0	0	4
Progomphus clendoni	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
Ptilodactylidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranatra sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Stegoelmis sp.	0	18	0	0	2	3	0	0	0	2	0	0	0	1	0
Corduliinae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanypodinae	0	10	15	55	17	142	3	4	1	218	27	36	0	22	81
Tenagobia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Tholymis sp.	0	0	3	8	1	0	45	0	1	0	1	0	0	0	2
Tropisternus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Wormaldia sp.	0	0	0	0	7	0	51	0	0	0	0	0	0	0	0

Table S 4. Results of generalized linear models assessing the relationship between individual biomass of taxa exhibiting variations in nitrogen isotopic signatures in response to temperature.

Family/Order	Intercept (Estimate ± SE)	Temp_mean Coef. (Estimate ± SE)	t-value (Temperature)	p-value (Temperature)	Dispersion Parameter	Residual Deviance (df)	AIC	Temperature Effect Interpretation
Gomphidae	0.0711 ± 0.8370	0.1070 ± 0.0296	3.610	0.00051 ***	1.56	153.95 (88)	729.69	Significant positive effect; biomass increases ~11%
Dytiscidae	-0.6421 ± 0.5200	0.0137 ± 0.0171	0.800	0.426 (ns)	0.45	40.22 (83)	110.97	Non-significant effect; biomass does not vary with temp
Gastropoda	-12.5310 ± 4.8095	0.5563 ± 0.1709	3.255	0.00162 **	5.55	274.86 (86)	666.21	Significant positive effect; biomass increases ~74%
Chironomidae	-1.0508 ± 0.1920	-0.0192 ± 0.0064	-3.021	0.00255 **	2.71	3322.6 (2277)	-2853.8	Significant negative effect; biomass decreases ~1.9%
Hydrophilidae	45.7714 ± 15.0995	-1.1962 ± 0.3784	-3.161	0.00179 **	1.69	306.63 (221)	-421.77	Significant negative effect; biomass decreases ~70%

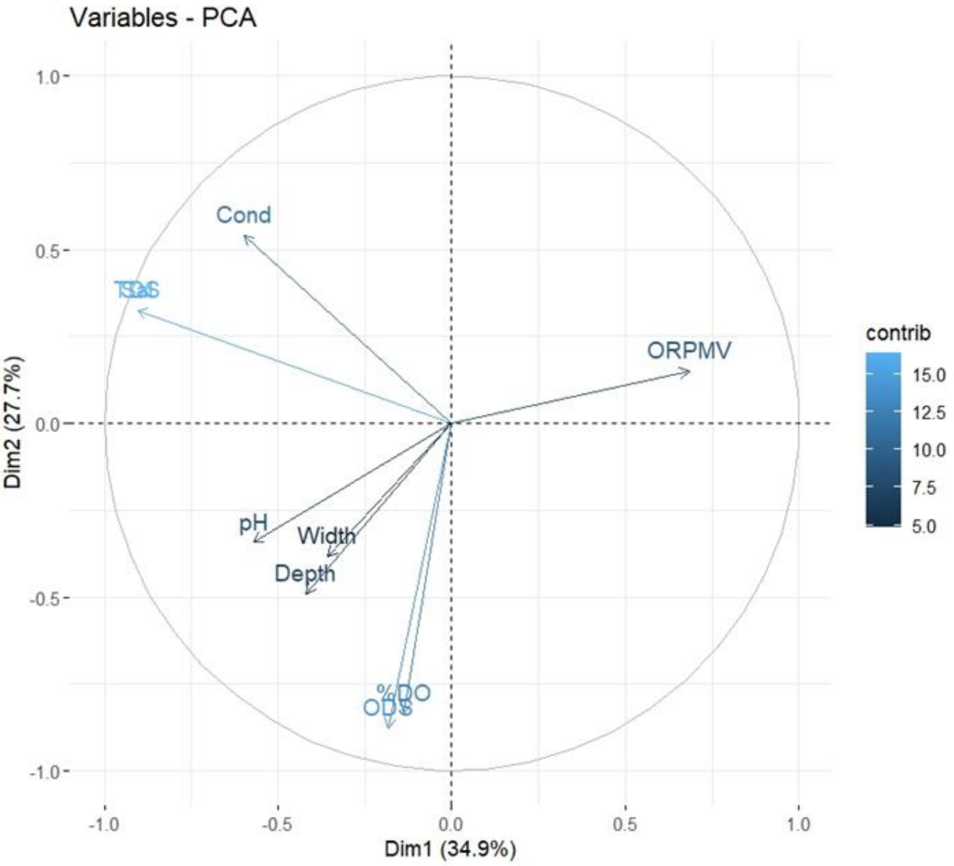

Figure S 1. Environmental Principal Components analyses (PCA).

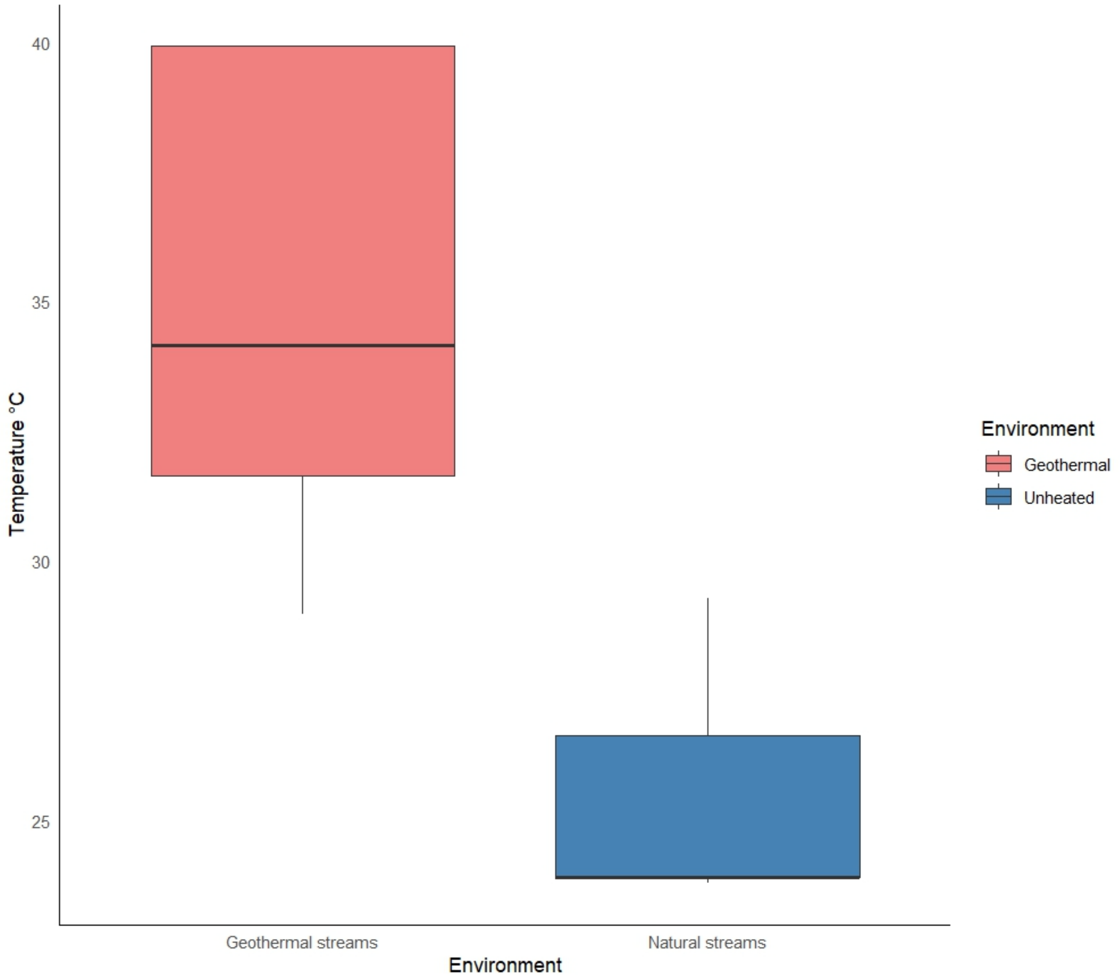

Figure S 2. Temperature difference between geothermal and natural (i.e., unheated) streams.

Figure S 3. Dispersion of signature values of stable isotopes of carbon δ¹³C and nitrogen δ¹⁵N.

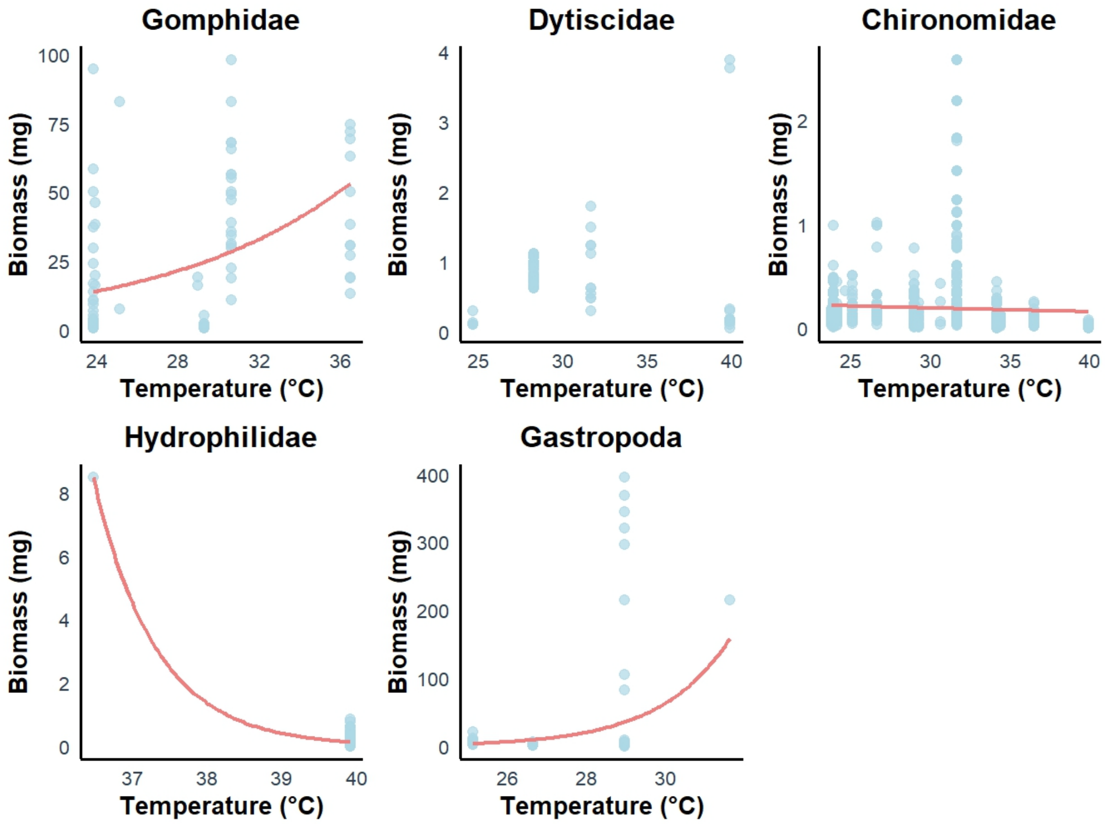

Figure S 4. Individual biomass macroinvertebrate families and order plots along the temperature gradient. Blue dots represent individual macroinvertebrate biomass and red lines represent tendency relationships.

3 Capítulo II - STRUCTURING ALPHA AND BETA PHYLOGENETIC DIVERSITY IN TROPICAL GEOTHERMAL STREAM COMMUNITIES: ABSENCE OF CLEAR CLUSTERING AND OVERDISPERSION PATTERNS ACROSS A THERMAL GRADIENT

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3.1 RESUMO

Compreender a influência do aquecimento sobre a diversidade taxonômica e filogenética das comunidades de água doce é fundamental para prever as respostas dos ecossistemas às mudanças climáticas. Riachos geotermais tropicais oferecem um sistema único para examinar os padrões de biodiversidade ao longo de fortes gradientes térmicos. Neste estudo, investigamos assembleias de macroinvertebrados em 15 riachos tropicais com um gradiente de temperatura de 23,8ºC a 39,9ºC. Hipotetizamos que temperaturas elevadas levariam a declínios e mudanças na diversidade alfa e beta taxonômica e filogenética, respectivamente, por meio de filtragem ambiental, resultando também em agrupamentos filogenéticos detectáveis dentro das comunidades. A variabilidade ambiental foi sintetizada por meio de análise de componentes principais (PCA). A diversidade alfa taxonômica foi quantificada usando o estimador de riqueza Chao1, enquanto a diversidade alfa filogenética foi medida pela Diversidade Filogenética de Faith (PD). A diversidade beta foi particionada em componentes de turnover de espécies e diferença de abundância usando o índice de Ruzicka. A estrutura filogenética comunitária foi caracterizada usando a Distância Média do Táxon Mais Próximo (MNND) e a Distância Média entre Pares (MPD), com métricas de tamanho do efeito padronizado — Índice do Táxon Mais Próximo (NTI) e Índice de Relacionamento Líquido (NRI) — empregadas para detectar padrões de agrupamento ou sobredispersão filogenética. Contrariando as expectativas a priori, nem a diversidade alfa taxonômica nem a filogenética apresentaram declínios significativos ao longo do gradiente térmico ou com a variação ambiental. A diversidade beta foi predominantemente impulsionada pelo turnover de espécies, sem associação significativa com a temperatura. Análises filogenéticas revelaram agrupamentos localizados em certos riachos — particularmente em sítios geotermais —, mas esses sinais foram inconsistentes e não convergiram com a temperatura. A diversidade beta filogenética exibiu um padrão heterogêneo, compreendendo agrupamento, sobredispersão e aleatoriedade, indicando processos complexos de montagem comunitária que vão além de uma simples filtragem ambiental térmica. Assim, nossos resultados revelam que o aquecimento térmico isoladamente não domina os padrões de diversidade taxonômica e filogenética nas assembléias de macroinvertebrados de riachos geotermais tropicais. As análises filogenéticas mostraram agrupamentos localizados em alguns riachos, mas nenhum padrão consistente em toda a comunidade ao longo dos gradientes térmicos. Esses achados ressaltam a natureza complexa e heterogênea da montagem comunitária nesses ecossistemas e sugerem que fatores além da temperatura, incluindo degradação do habitat e condições ambientais locais, têm influência mais forte nos padrões de diversidade.

Palavras-chave: Diversidade filogenética alfa e beta, Riachos geotermais, Montagem comunitária, Agrupamento filogenético.

3.2 ABSTRACT

Understanding the influence of warming on taxonomic and phylogenetic diversity of freshwater communities is critical for forecasting ecosystem responses to climate change. Tropical geothermal streams provide a unique system to examine biodiversity patterns along strong thermal gradients. In this study, we investigated macroinvertebrate assemblages across 15 tropical streams exhibiting a temperature gradient from 23.8ºC to 39.9ºC. We hypothesized that elevated temperatures would drive declines and changes in taxonomic and phylogenetic alpha and beta diversity, respectively, through environmental filtering, resulting also in detectable phylogenetic clustering within communities. Environmental variability was synthesized via principal component analysis (PCA). Taxonomic alpha diversity was quantified using the Chao1 richness estimator, while phylogenetic alpha diversity was measured by Faith's Phylogenetic Diversity (PD). Beta diversity was partitioned into species turnover and abundance difference components using the Ruzicka index. Phylogenetic community structure was characterized using Mean Nearest Taxon Distance (MNND) and Mean Pairwise Distance (MPD), with standardized effect size metrics—Nearest Taxon Index (NTI) and Net Relatedness Index (NRI)—employed to detect patterns of phylogenetic clustering or overdispersion. Contrary to a priori expectations, neither taxonomic or phylogenetic alpha diversity showed significant declines across the temperature gradient or with environmental variation. Beta diversity was predominantly driven by species turnover, with no significant association with temperature. Phylogenetic analyses revealed localized clustering in certain streams—particularly geothermal sites—but these signals were inconsistent and did not converge with temperature. Phylogenetic beta diversity exhibited a heterogeneous pattern comprising clustering, overdispersion, and randomness, indicating complex community assembly processes that extend beyond simple thermal environmental filtering. Thus, our results reveal that thermal warming alone does not dominate patterns of taxonomic and phylogenetic diversity in tropical geothermal stream macroinvertebrate assemblages. Phylogenetic analyses revealed localized clustering in some streams but no consistent community-wide pattern along thermal gradients. These findings underscore the complex and heterogeneous nature of community assembly in these ecosystems and suggest that factors other than temperature, including habitat degradation and local environmental conditions, have stronger influences on diversity patterns.

Keywords: Alpha and beta phylogenetic diversity, Geothermal streams, Community assembly, Phylogenetic clustering.

3.3 Introduction

A comprehensive understanding of biodiversity requires integrating multiple facets—e.g. taxonomic and phylogenetic diversity—rather than relying solely on species richness (Devictor et al., 2010; Schmera et al., 2017). Although taxonomic diversity is frequently employed as the primary metric in biodiversity studies, phylogenetic diversity often yields complementary or more robust insights into ecosystem functioning and community structure. (Pavoine et al., 2011; Gravel et al., 2012; Bagousse-Pinguet et al., 2019). Given that taxonomic and phylogenetic diversity may exhibit divergent and occasionally antagonistic influences on ecosystems, their joint assessment is essential (Reiss et al., 2009; Plas, 2019; Zhang, 2023). Incorporation of evolutionary history via phylogenetic metrics refines interpretations of community structure, where patterns such as phylogenetic clustering and overdispersion infer processes like environmental filtering and competitive exclusion, respectively (Petchey & Gaston, 2006; Cadotte et al., 2011; Hardy et al., 2012; Saito et al., 2016a,b; Veron et al., 2019; Gaüzère et al., 2022). These biotic and abiotic drivers shape community composition, diversity, and evolutionary trajectories aiding us at understanding adaptive traits and persistence strategies, especially under stressors like global warming.

Phylogenetic diversity approaches provide profound insights into historical biogeographic processes influenced by geological events and paleoclimatic fluctuations over extensive evolutionary timescales (Rangel et al., 2018; Mascarenhas & Carnaval, 2025). This ability to integrate evolutionary history and adaptive dynamics provides phylogenetic diversity a powerful framework for understanding large-scale ecological changes through time, such as the impacts of global temperature variations on the structure and organization of aquatic communities. This approach is grounded in the theory of niche conservatism, which posits that closely related species tend to retain similar ecological traits and environmental preferences across evolutionary timescales (Wiens & Graham, 2005). For instance, Saito et al. (2015)

demonstrated that ecological traits related to microhabitat preferences in aquatic insects exhibit significant phylogenetic signals, indicating that closely related species tend to occupy similar ecological niches. Therefore, clusters of closely related species in local communities could be an indicator of environmental filtering. This pattern of niche conservatism is further exemplified by recent findings in aquatic insects showing that metabolic traits are strongly shaped by phylogenetic heritage (Leahy et al., 2025). These examples highlight the role of phylogenetic niche conservatism in constraining ecological similarity among related taxa, offering a robust framework to understand community responses to environmental changes. Consequently, investigating how local and global biodiversity respond to environmental filters—such as temperature increases linked to climate change—requires integrating phylogenetic and taxonomic perspectives. Such an integrated approach is essential to unravel the mechanisms driving shifts in species composition, abundance, and distribution (García-Robledo et al., 2016; Wagner, 2020).

Temperature increases driven by climate change have complex and spatially variable effects on biodiversity, often leading to declines—especially in tropical ecosystems (Nunez et al., 2019; Habibullah et al., 2021; Bastazini et al., 2021). Geothermal streams represent distinctive thermal habitats that support specialized biological communities, notably macroinvertebrates, which exhibit significant adaptations to high temperatures. These geothermal streams serve as prominent natural laboratories for investigating the effects of environmental warming on aquatic ecosystems. According to the Metabolic Theory of Ecology (MTE), temperature controls metabolic rates, which directly affect physiological performance, growth, and ecological interactions (Brown et al., 2004). So, in these streams, rising temperatures could accelerate metabolism, increase energy demands, and consequently influence species survival and community dynamics. Studies in temperate regions have already demonstrated the effects of warming on species richness, evenness, abundances, and the dominance of thermotolerant taxa (O'Gorman et al., 2014; O'Gorman et al., 2017; Junker et al., 2024; Duggan et al., 2007; Živić et al., 2013). These studies also show that rising temperatures alter community structure and complexity by simplifying food webs and affecting diversity and ecological functions (O’Gorman et al., 2014, 2017; Junker et al., 2024). Tropical regions, on the other hand, present a lower amount of studies, which jeopardizes a full understanding of biodiversity responses to temperature changes.

The phylogenetic structure of macroinvertebrate assemblages in tropical geothermal streams provides critical insights into the ecological and evolutionary processes underlying community assembly. Phylogenetic clustering, detected by metrics such as Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNND), may reflect environmental filtering associated with thermal constraints, favoring closely related taxa adapted to geothermal conditions (Mazel et al., 2016; Herzog et al., 2022; Quenta-Herrera et al., 2021). Conversely, phylogenetic overdispersion could indicate competitive interactions promoting the coexistence of distantly related lineages, or distantly related species with convergent adaptive strategies (Mazel et al., 2016; Galván-Cisneros et al., 2023). Decomposing alpha and beta phylogenetic diversity allows disentangling within-community evolutionary relationships and lineage turnover across sites, elucidating how spatial and thermal gradients shape biodiversity patterns in these unique aquatic habitats (Ricotta et al., 2020; Galván-Cisneros et al., 2023).

Based on metabolic theory and the principle of niche conservatism, we hypothesize that aquatic macroinvertebrate species inhabiting tropical streams along a thermal gradient—from cooler natural streams to warmer geothermal streams—exhibit distinct metabolic adaptations that confer enhanced thermal tolerance, shaped by long-term selective pressures (Bowles et al., 2022; Poff, 1997; Cortes et al., 2011). We predict that phylogenetic diversity within these communities will be negatively correlated with temperature, reflecting evolutionary niche conservatism and the filtering effect of thermal stress that selects for clades with specific adaptations to elevated temperatures (Blanchet et al., 2020; Quenta-Herrera et al., 2021). In geothermal stream communities, consistently higher temperatures are expected to restrict the phylogenetic breadth to a subset of closely related lineages adapted to thermal regimes, resulting in phylogenetic clustering compared to natural tropical streams (Mazel et al., 2016; Herzog et al., 2022). This conserved phylogenetic structure is anticipated to limit the dispersal and establishment of species lacking adaptations to elevated temperatures, resulting in phylogenetic clustering of communities under thermal stress. Accordingly, we predict that (i) taxonomic diversity, as well as phylogenetic alpha and beta diversity, will change progressively along the temperature gradient; and (ii) phylogenetic clustering will be evident in both alpha and beta diversity metrics, as quantified by the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI), reflecting environmental filtering by temperature acting as a strong selective force over evolutionary timescales that favors lineages possessing traits and strategies enhancing thermal tolerance (Zhang et al., 2020; Bowles et al., 2022).

3.4 Methods

3.4.1 Field Sampling and Community identification

We conducted our samples in October 2022 into 15 streams, following an increasing natural water temperature gradient ranging from: 23.8ºC to 39.9ºC on average. The initial experimental design was composed of sixteen streams, evenly divided between geothermal and natural categories. However, Stream number eight, a geothermal stream with an average temperature of 37.6°C, was excluded from subsequent analyses due to the absence of any collected organisms. Geothermal streams exhibit rapid water flow and short residence times driven by substantial thermal energy inputs. These systems are generally confined to small, spatially isolated areas and display hydrological regimes that differ markedly from those of the surrounding catchment. (Woodward et al., 2010; Demars et al., 2011a,b; O'Gorman et al., 2014). The temperature increase of stream water primarily results from steam discharge originating from boiling geothermal reservoirs. This mechanism involves the heating of the overlying cold groundwater, which contributes to streamflow, as well as the thermal influence of the bedrock through which these streams flow (Arnason et al., 1969). The present study encompassed sites located at the state of Mato Grosso, Brazil, into two major hydrographic regions: the Tocantins-Araguaia and Paraguay basins. (Figure S2).

In each stream, within a 30 m stretch, six benthic macroinvertebrate samples were collected with a 30cmx30cm Surber net (mesh size 250 μm) for community composition. All samples were stored in absolute alcohol and transported to the laboratory. The individuals were identified at the lowest possible taxonomic level using specialized literature (Melo, 2003; Segura, 2011; Souza, 2012; Hamada et al. 2014). Most insects were identified at the genus level; when this was not possible, they were identified at the subfamily or family level.

3.4.2 Local environmental variables

We collected a set of chemical water quality parameters, including potential hydrogen (pH), oxidation-reduction potential measured in millivolts (ORP_mV), field temperature (Field_Temp, °C), maximum temperature (Max_Temp, °C), dissolved oxygen saturation (DOS, mg/L), dissolved oxygen percentage relative to saturation (%DO), total dissolved solids (TDS, mg/L), electrical conductivity (Cond, μS/cm), and salinity (Salt, ppt), using a HORIBA multiparameter probe. Chemical variables were measured in triplicate along the streams to ensure data reliability. Physical parameters included channel width (Width, cm) and depth (Depth, cm), each quantified at ten points evenly distributed along the streams. Channel width represents the lateral distance through the water column, while depth refers to the vertical distance from the water surface to the streambed. For subsequent statistical analyses, only field temperature was used as a thermal variable. Furthermore, only the arithmetic means of these variables were used to characterize the physical and chemical conditions of the streams.

To summarize environmental variability, we performed a Principal Component Analysis (PCA) on measured environmental parameters. The first PCA axis, which explained most of the variation (34.9%), was used as a synthetic environmental predictor in all subsequent data analyses. Hereafter, the term "environmental variables" refers to this PCA axis, alongside the mean temperature values directly measured for each stream.

3.4.3 Alpha diversity

Alpha taxonomic diversity was calculated using the Chao1 richness estimator and alpha phylogenetic diversity using Faith's Phylogenetic Diversity (αPD). The phylogenetic diversity was estimated based on Linnaean taxonomy, using taxonomic levels from class to genus. The phylogenetic tree was constructed using these taxonomic classifications. Hierarchical clustering was performed using both UPGMA and Ward's methods applied to a Gower distance matrix suitable for mixed data types. The resulting dendrograms were then converted to Newick format for further analysis (following Saito et al., 2015, 2016).

Phylogenetic community structure at the alpha level was further evaluated using the Nearest Taxon Index (αNTI) and the Net Relatedness Index (αNRI). These indices were derived from the Mean Nearest Neighbor Distance (MNND) and Mean Pairwise Distance (MPD) measurements, following Webb (2000). The MNND captures fine-scale phylogenetic structure by measuring average distance to the closest relative within a community, while MPD reflects overall phylogenetic relatedness among all individuals or species. αNTI and αNRI were calculated as standardized effect sizes against null models generated by the taxa shuffle procedure (Kembel, 2009; Swenson, 2014), which randomizes taxa positions within the phylogenetic distance matrix while preserving sample abundances to infer phylogenetic clustering or dispersion.

3.4.4 Beta diversity

Taxonomic beta diversity was quantified using the Ruzicka index, which accounts for species composition and abundances. We partitioned total beta diversity (β_total) into replacement (β_repl) and abundance difference (β_abund) components following Podani et al. (2013) and Carvalho et al. (2012). To visualize community dissimilarity across streams and investigate patterns along the temperature gradient, we conducted a Principal Coordinate Analysis (PCoA) based on the Ruzicka dissimilarity matrix.

Phylogenetic beta diversity (βPD) structure was evaluated via beta versions of βNTI and βNRI, also following the standardized effect sizes against null models generated by the taxa shuffle procedure, in analogy to how we calculated alpha diversity metrics (Kembel, 2009; Swenson, 2014). Phylogenetic beta diversity matrices were generated by calculating cophenetic distances from a pruned phylogenetic tree, with cophenetic distances representing the sum of branch lengths connecting each pair of species in the tree, thus providing a measure of phylogenetic distance.

3.4.5 Analytical framework

Our first hypothesis stated that alpha taxonomic and phylogenetic diversity would decline progressively along the temperature gradient due to increasing thermal stress. This should be accompanied by changes in both taxonomic and phylogenetic beta diversity across the temperature gradient. To test this, we first applied Multiple Linear Regression models (LMs) relating alpha diversity metrics (Chao1 and Faith's Phylogenetic Diversity) to temperature and environmental variation. Subsequently, two Multiple Regression on distance Matrices (MRM) models were fitted to relate beta diversity components to environmental predictors. The first model used a taxonomic beta diversity matrix, represented by Ruzicka distances, as the response variable, with predictor matrices derived from mean temperature values and the first principal component axis from the PCA representing environmental variation. The second model used a phylogenetic beta diversity matrix, represented by cophenetic distances, as the response variable, with the same predictor matrices of temperature and environmental variation. Both environmental predictors were transformed into Euclidean distance matrices for the MRM analyses. For our second hypothesis, which predicts phylogenetic clustering will be evident in both alpha and beta diversity metrics, as quantified by the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI), we compared the observed and predicted values by chance from the NTI and NRI models for both alpha and beta diversity. Alpha and beta NTI and NRI values <-1.96 and >1.96 will be interpreted as evident overdispersion or clustering, respectively.

3.5 Results

The first axis of the environmental PCA, explained 34.9% of the environmental variation and represented gradient characterized mainly by salinity, dissolved solids, pH, and conductivity, which directly affect water quality in the studied streams. The variables that contributed most positively to the first axis were salinity (Sal) and total dissolved solids (TDS) and negatively the Oxidation-Reduction Potential (ORPV). The second axis, which explained 27.7% of total variation, on the other hand, represented variation mainly linked to water oxygenation parameters and physical aspects such as depth and width, which influence the aquatic environment differently. The largest shares of variation in the second axis were explained by ODS and %DO (Figure S3).

Taxonomic alpha diversity values varied between 3 and 24, with a standard deviation of 6.04 (Figure 6). Multiple regression analysis revealed no significant association between alpha diversity and either the temperature gradient or the environmental PCA first axis (F(2,12) = 1.406, $R^2 = 0.054$, $p = 0.282$).

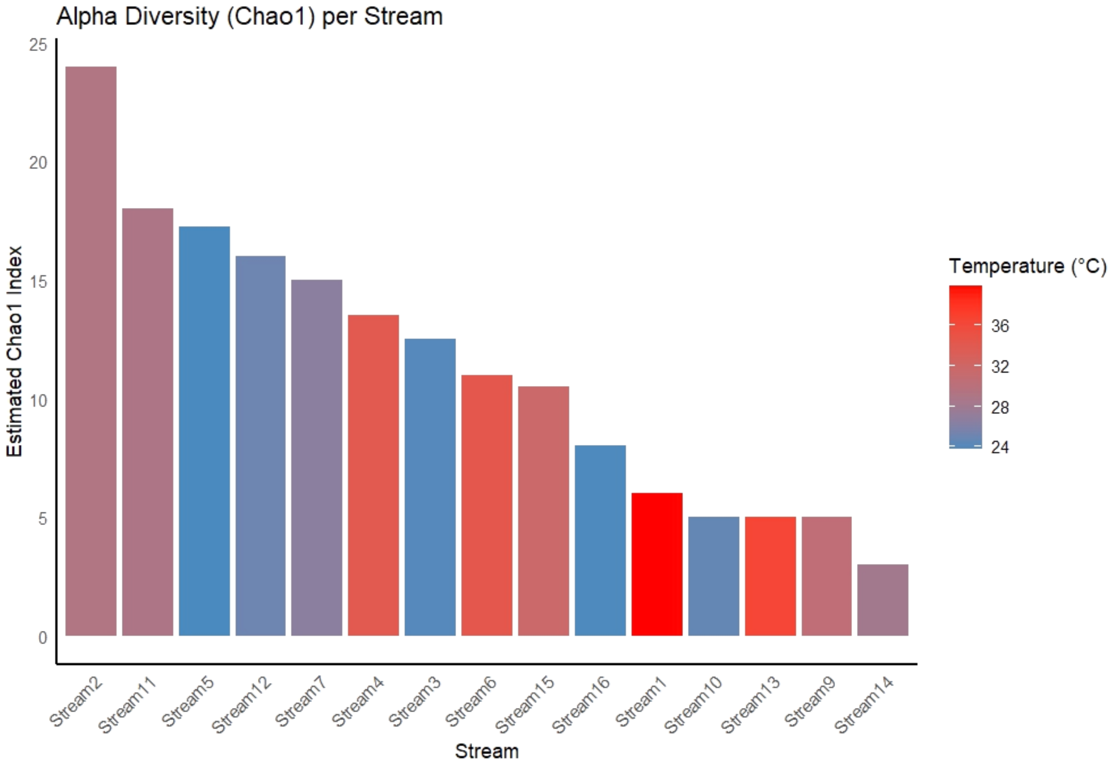

Figure 6. Chao1 richness estimator representing alpha diversity in each stream following the temperature gradient. The bar color represents temperature across the gradient.

Meanwhile, beta diversity partitioning analysis indicated that species replacement (β_repl = 0.933) was the dominant driver of compositional dissimilarity among streams. Conversely, the contribution of differences in species abundance (β_abund = 0.040), representing species loss or gain without direct replacement, was marginal. Therefore, the observed total beta diversity (β_total = 0.973) is primarily a consequence of species turnover. Also, after PCoA we did not find any relationship between taxonomic composition and temperature variation (Figure 7). This was supported by MRM analysis showing the lack of association between taxonomic beta diversity with the Euclidean distance using temperature (coefficient =0.0018, $p = 0.452$) and with the Euclidean distance using environmental variables (coefficient= -0.0011, p=0.847) (Table 1).

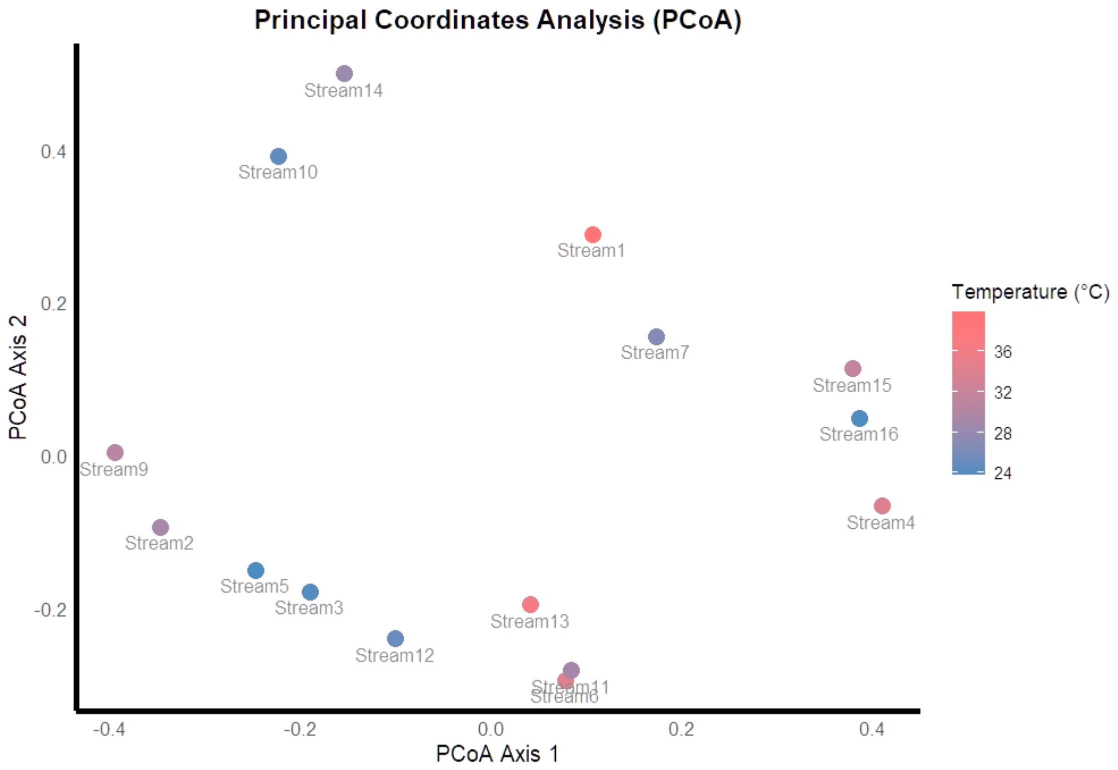

Figure 7. Principal Coordinates Analysis (PCoA) depicting the dissimilarity (beta diversity) among stream sites based on Bray-Curtis distances. Points are colored according to a temperature gradient, with red tones representing higher temperatures and blue tones lower temperatures. Stream site labels are colored to indicate stream types: red labels correspond to geothermal streams (Stream 1, 4, 15, 13, 11, 6, 9), and blue labels correspond to natural streams (Stream 16, 7, 14, 10, 12, 3, 5, 2).

Table 1. Multiple Regression on Distance Matrices (MRM) analysis using taxonomic beta diversity (β) as the response variable. Predictors included Euclidean distance using Temperature (°C) and Euclidean distance using environmental variables. The table reports estimated regression coefficients for the intercept and predictors, p-values, coefficient of determination (R²), F-test statistics, and associated p-values (p).

Model		**Coefficient**	**p**	**R²**	**F test**	**p (F test)**
Taxonomic diversity(βPD)	Intercept	0.9244	0.8629	0.0106	0.5488	0.7868
	Temperature(°C)	0.0018	0.4525			
	Environment	-0.0011	0.8478			

Phylogenetic diversity (αPD) varied considerably, reflecting differences in the total amount of evolutionary history represented in each stream. (Table 2) and (Figures S7 to S21). We found no relationship between the temperature gradient, the environmental PCA first axis and the alpha phylogenetic diversity values for the communities ($F_{2,12}$=1.77, R^2=0.099, p=0.21) (Figure S22). However, macroinvertebrate communities from Stream 2 and Stream 5, both natural streams, presented high αPD values, indicating greater evolutionary diversity. In contrast, Stream 9, a geothermal stream, presented low αPD values, suggesting lower phylogenetic diversity. (Table 2).

Table 2. Alpha phylogenetic diversity (PD) and its components (NTI and NRI).

Communities	**αNTI**	***p***	**αNRI**	***p***	**αPD**
Stream1	1.157011012	0.152	0.355965	0.294	4.118232437
Stream2	-0.041408117	0.533	-0.8042	0.781	9.75416693
Stream3	1.350774061	0.077	1.203769	0.141	6.463471466
Stream4	1.199527613	0.092	1.556282	0.079	6.851931655
Stream5	1.772427435	0.042	-0.58294	0.685	9.407485455
Stream6	1.58996418	0.036	0.99757	0.157	4.377020208
Stream7	-1.201966131	0.875	0.069889	0.399	7.441535468
Stream9	2.482494654	0.001	1.618763	0.075	2.702204788
Stream10	-1.32358189	0.906	-0.53054	0.604	4.178773069
Stream11	0.986038505	0.151	0.329915	0.309	7.763282655
Stream12	0.333010591	0.371	0.307359	0.341	7.389858184
Stream13	1.638913104	0.064	1.310489	0.122	4.06142839
Stream14	-0.144826903	0.48	0.027376	0.45	2.944043105
Stream15	1.86719987	0.016	3.302718	0.003	6.561116653
Stream16	1.455639033	0.045	1.731638	0.059	5.363603866

No relationships were also detected between αNTI index and environmental predictors (i.e., temperature gradient and environmental variation) (F2,12 = 1.189, R^2 = 0.026, p = 0.337) (Figure S23), neither between αNRI index and the environmental predictors (F2,12 = 0.614, R^2 = -0.058, p = 0.557) (Figure S24). However, Stream 15 presented a phylogenetic clustering pattern into the αNRI index. Similarly, several streams, such as six and nine, showed positive and significant αNTI values, indicating a strong phylogenetic clustering at the tip of the phylogenetic tree (Figure 8). This suggests that the most abundant species in these communities are phylogenetically closer than randomly expected. Only two natural streams, 5 and 16, presented phylogenetic clustering. In contrast, geothermal streams 6, 9 and 15 presented the same type of clustering. On the other hand, some communities presented values close to zero or not significant, indicating the absence of a clear phylogenetic pattern in the structure of the dominant species. No significant patterns of phylogenetic overdispersion were detected.

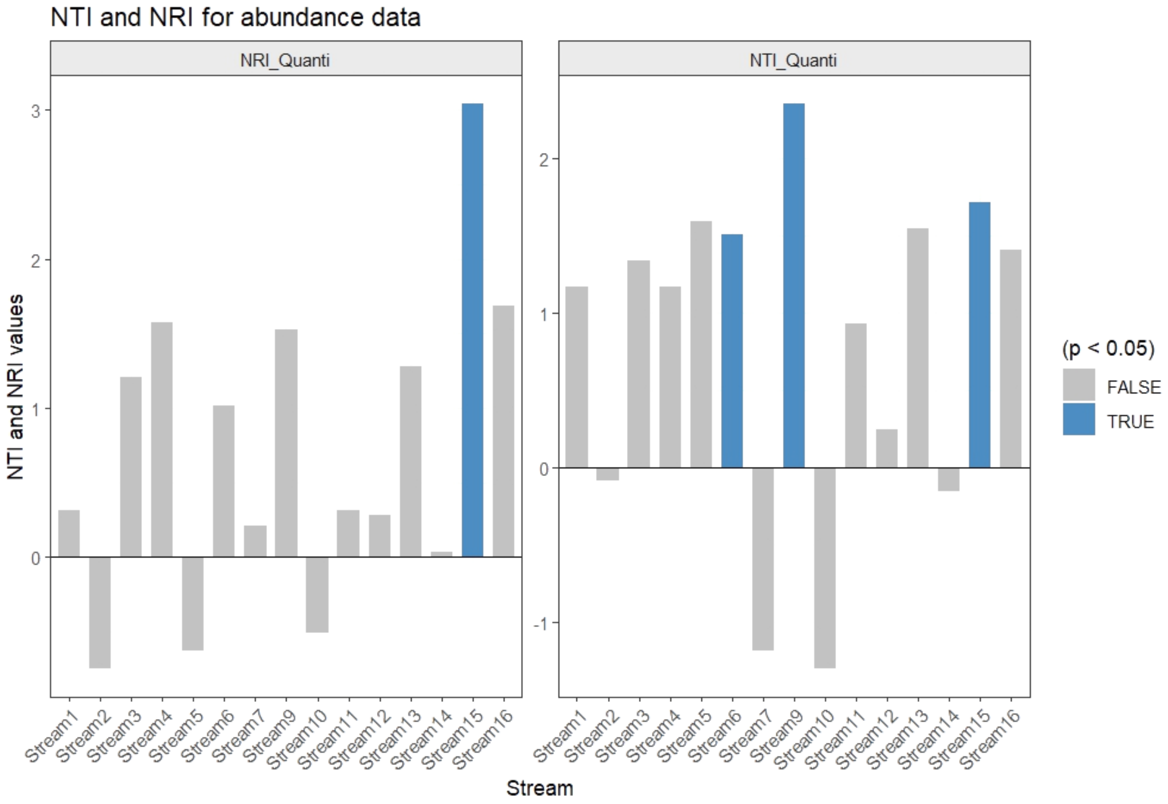

Figure 8. Graphical depiction of observed values exceeding those expected under a null model, indicating significant phylogenetic clustering. Blue bars denote instances of phylogenetic clustering.

Upon analyzing the Beta Phylogenetic Diversity (βPD) across communities, no discernible structuring patterns were observed. The Beta Net Relatedness Index (βNRI) and Beta Nearest Taxon Index (βNTI), revealed a complex and heterogeneous pattern. Multiple Regression on distance Matrices (MRM) analysis indicated no significant associations between phylogenetic dissimilarity among streams and either the temperature gradient (coefficient =-0.001, p = 0.491) or environmental variables (coefficient = 0.005, p = 0.392) (see Table 3).

Table 3. Multiple Regression on Distance Matrices (MRM) analysis of phylogenetic beta diversity and its components: Net Relatedness Index (NRI) and Nearest Taxon Index (NTI). Each model used one of these metrics as the response variable, with Temperature (°C) and Euclidean distance using environmental variables. Estimated regression coefficients for the intercept and predictors, along with corresponding p-values, coefficients of determination (R^2), F-test values, and associated significance levels (p-value of F-test).

Models		**Coefficient**	***p***	**R^2**	**F test**	***p* (F test)**
βPD	Intercept	17.786	0.5191	0.0270	14.178	0.5015
	Temperature(°C)	-0.00175	0.4916			
	Environment	0.00569	0.3928			
βNRI	Intercept	0.01923	0.9418	0.0307	16.143	0.4367
	Temperature(°C)	0.02808	0.4395			
	Environment	-0.0870	0.3601			
βNTI	Intercept	-0.6981	0.6218	0.0209	10.873	0.5982
	Temperature(°C)	-0.03435	0.5187			
	Environment	0.09060	0.4792			

βNRI presented no relationship with temperature gradient (coef = 0.028, p = 0.439) and no relationship with environmental features (coef= -0.087, p=0.360). Despite this, some streams presented beta phylogenetic clustering and beta overdispersion. Notably, pairs of communities from streams 6 and 1, 15 and 1, 15 and 6, and 13 and 16 displayed positive and significant βNRI values, indicating a shared presence of phylogenetically closely related species in terms of abundance within these pairs. Conversely, phylogenetic overdispersion was evident in pairs involving stream 14 with streams 3 and 4. Nonetheless, a pattern of phylogenetic randomness prevailed across the majority of the analyzed streams. For the Beta Nearest Taxon Index (βNTI), a similar absence of a significant relationship was found with both temperature (coefficient = -0.034, p = 0.518) and environmental variables (coefficient = 0.090, p = 0.479). This index revealed beta phylogenetic clustering at the tip of the phylogenetic tree in specific stream pairs, such as 12 and 11, and 16 and 4. Prominent overdispersion, characterized by very low negative βNTI values, was clearly observed between stream 14 and streams 1, 3, and 5. These findings collectively demonstrate that processes of both phylogenetic clustering and beta overdispersion contribute to the structuring of beta diversity within these communities, but were not systematically structured along the temperature gradient.

Thus, there is no clear and predominant pattern in the phylogenetic structure of macroinvertebrate communities in these tropical geothermal streams. We observed beta phylogenetic clustering in some pairs of streams, overdispersion in others, and random patterns in many cases.

3.6 Discussion

Our study aimed to test that (i) elevated temperatures would drive declines and changes in taxonomic and phylogenetic alpha and beta diversity, respectively, along the thermal gradient due to thermal stress, and (ii) phylogenetic clustering would emerge as evidence of environmental filtering driven by temperature, which acts as a strong selective force shaping phylogenetic structure over evolutionary timescales. To investigate these, we analyzed macroinvertebrate communities in tropical geothermal streams, relating their taxonomic and phylogenetic diversity patterns to a temperature gradient simulating climate change scenario. Contrary to our expectations, we found no significant direct relationships between temperature or environmental features and diversity metrics, with no clear pattern of species occupancy or diversity variation along the gradient. Although some streams exhibited phylogenetic clustering and others overdispersion, these patterns were isolated and inconsistent, indicating that temperature alone does not dominate community assembly.

We found no significant association between taxonomic alpha diversity and predictors related to temperature or environmental variation, thereby rejecting the hypothesis of a progressive decline in diversity with increasing temperature. Similarly, alpha phylogenetic diversity, assessed by Faith's Phylogenetic Diversity (Faith's PD), showed no significant relationship with these variables. These results align with Bonacina et al. (2022), who emphasize the complexity and multifaceted nature of temperature effects on macroinvertebrates, impacting processes from genetic to community levels but not necessarily leading to consistent direct correlations with community composition, richness, or abundance. In a similar vein, we previously also found no direct relationship between temperature and community biomass or macroinvertebrate composition in the same tropical geothermal streams, further highlighting the complexity of this system (Siqueira et al., submitted). These findings partially contrast with some of O'Gorman et al. (2017) and Gjoni et al. (2025) in temperate geothermal systems, who reported clearer patterns of temperature responses. Our previous study, (Siqueira et al., submitted), complements the findings of O'Gorman et al. (2017) by revealing an alternative compensatory mechanism in tropical geothermal stream ecosystems. While O'Gorman et al. (2017) demonstrated that increased nutrient supply at basal trophic levels can offset rising metabolic demands, thereby sustaining larger consumers in temperate geothermal systems, we did not detect a direct effect of temperature on body size or biomass in our tropical study sites. Instead, through analyses of stable nitrogen isotopes, we identified a trophic repositioning of larger consumers toward the basal levels of the food web, indicating an adaptive shift in trophic strategy to mitigate potential metabolic constraints induced by warming. These complementary mechanisms underscore the complexity of ecological responses to temperature gradients across different biogeographic contexts. In this way, several studies could highlight that local environmental variables—such as habitat complexity, groundwater influence, riparian shading, and water chemistry— were more consistent predictors of stream biodiversity and resilience than temperature alone (Silva et al., 2024;

Sánchez Herrera et al., 2024; Brito et al., 2024; Rivera-Pérez et al., 2024; Heino et al., 2015; Bao et al., 2024; da Silva et al., 2025).

Regarding our second hypothesis—that phylogenetic clustering, quantified by Net Relatedness Index (NRI) and Nearest Taxon Index (NTI), would reflect environmental filtering by temperature—it was only partially supported. A few streams showed clustering, but no general pattern emerged. Previous studies similarly found that climatic variables, including temperature, rarely exert direct influence on macroinvertebrate phylogenetic beta diversity, often playing a secondary or indirect role compared to spatial and local environmental controls (Li et al., 2020; Jiang et al., 2021; Li et al., 2024). Empirical evidence consistently demonstrates that spatial variables such as dispersal limitation and geographic distance can be principal drivers of phylogenetic beta diversity in stream macroinvertebrate assemblages, frequently exceeding the influence of temperature and other climatic factors (Li et al., 2020; Jiang et al., 2021; Lin et al., 2024). This emphasizes that local environmental filters, combined with broader spatial processes, jointly influence community assembly, and that temperature alone may not emerge as the primary structuring factor in these systems. This interpretation is consistent with studies demonstrating the significance of spatial scale in regulating ecological patterns and evolutionary relationships (Cavender-Bares et al., 2009; Wisnoski et al., 2023; Quenta-Herrera et al., 2021).

Our study was conducted in Mato Grosso state, Central-West Brazil—a core area within the Amazon's deforestation arc that lies within the Cerrado biome, where intense habitat fragmentation, agricultural expansion, and biodiversity loss are driving rapid ecological change. (Kuschnig et al., 2021). Vegetation removal reduces regional rainfall and alters microclimates, disrupting vital ecosystem services including water regulation and ecological cycles (Leite-Filho et al., 2021). These pressures disproportionately affect sensitive ecosystems such as small streams, whose heterogeneity demands rigorous monitoring and adaptive management (Somlyai et al., 2019; Hughes et al., 2023). In this way, sensitive macroinvertebrate groups—especially Ephemeroptera, Plecoptera, and Trichoptera (EPT)—are well-established indicators of pristine aquatic habitats (Reynoldson et al., 1997). Our field observations revealed significant environmental impacts across the region, including limited riparian forest cover, intensive agricultural activity adjacent to streams, and substantial sedimentation of streambeds, all contributing to habitat degradation. This is reflected in our phylogenetic analyses, where degraded streams exhibited clustering dominated by tolerant taxa such as Chironomidae and Gomphidae families (Figures 8, S14), suggesting habitat simplification driven by riparian vegetation loss and agricultural pressures (Tampo et al., 2021; Brysiewicz et al., 2022). In contrast, geothermal streams harbored taxa more resilient to thermal stress, including Diptera (e.g. *Chironomus*), Mollusca, and certain Odonata (e.g. Gomphidae), which possess specialized adaptations to low oxygen and elevated temperatures (Figures 8, S12, S14, S20; Haldar et al., 2016; Edegbene et al., 2020; Tampo et al., 2021). Pollution-tolerant groups increased in disturbed environments, further evidencing ecological impacts. Overall, these phylogenetic clustering patterns reveal evolutionary adaptations to localized environmental stressors, with niche conservatism shaping community assembly. The decline of sensitive taxa serves as a robust bioindicator of ongoing habitat degradation, which undermines biodiversity and ecological processes, underscoring the urgent need for enhanced environmental management and restoration efforts to sustain stream ecosystem integrity (Cao et al., 2018; Li et al., 2024; Camana et al., 2024). Notably, habitat degradation appeared to exert a stronger influence on phylogenetic community structure than temperature gradients, highlighting the dominant role of anthropogenic disturbance in structuring these aquatic communities.

3.7 Conclusion

In our study, contrary to our initial hypotheses, thermal warming alone does not exert a dominant or consistent influence on the taxonomic and phylogenetic diversity patterns of macroinvertebrate assemblages in tropical geothermal streams. The absence of significant declines in alpha and beta diversities, as well as the lack of consistent phylogenetic clustering attributable to temperature, probably indicates that regional-scale processes, dispersal limitations, and local environmental factors play more substantial roles in shaping community structure. Furthermore, we observe that variability in taxon sensitivity reflects the compounding effects of anthropogenic disturbances and climate stressors, which appear to obscure clear signals of environmental filtering and community assembly mechanisms. This scenario is especially concerning for tropical geothermal streams, known for their inherent fragility, whose vulnerability is exacerbated by the lack of formal protection. These ecosystems serve as natural laboratories for understanding biodiversity responses to warming, making their preservation crucial for advancing ecological and evolutionary knowledge under global change. These findings highlight the complex multifactorial factors governing biodiversity patterns in these ecosystems and underscore the need for integrated conservation frameworks and adaptive management approaches to safeguard the evolutionary and functional integrity of tropical geothermal stream communities amid escalating climate change and anthropogenic pressures.

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3.9 Supplementary Material

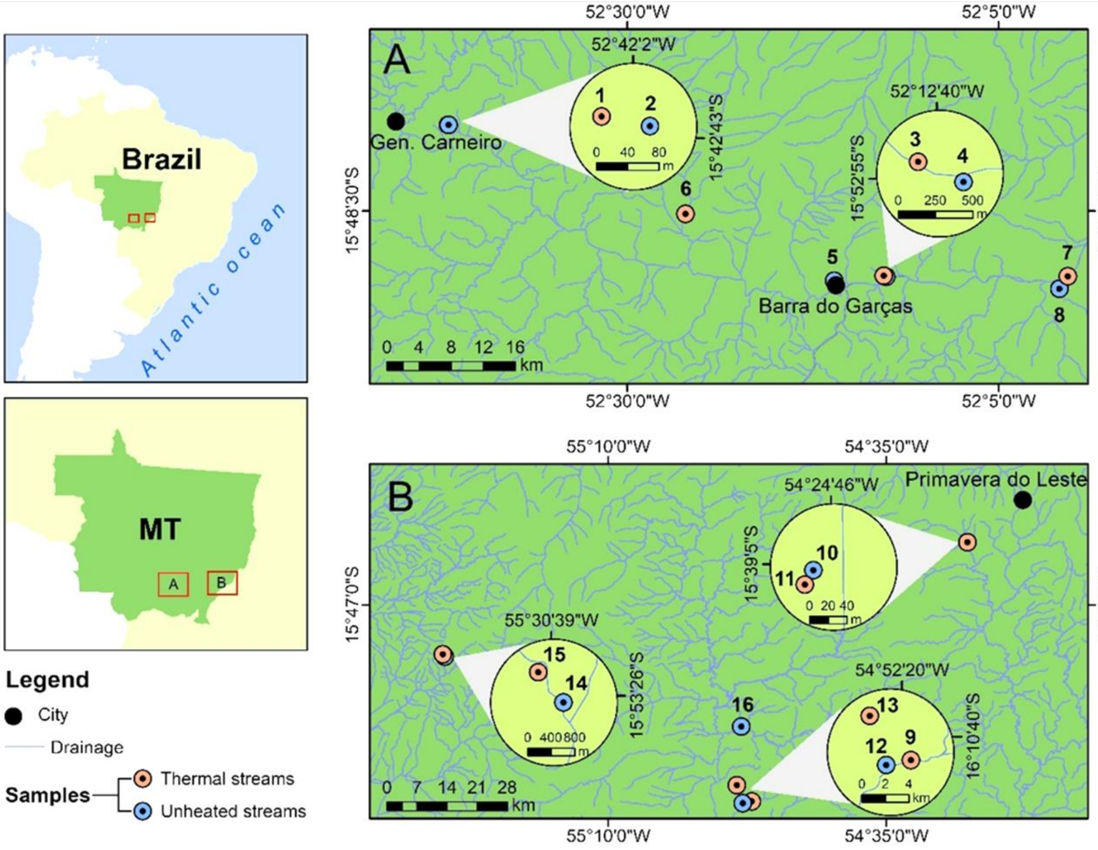


Figure S 5. Map of the state of Mato Grosso, Brazil, depicting sampling locations within two river basins: the Tocantins-Araguaia and Paraguay basins. Red points indicate geothermal (thermal) streams, whereas blue points correspond to natural (unheated) streams.

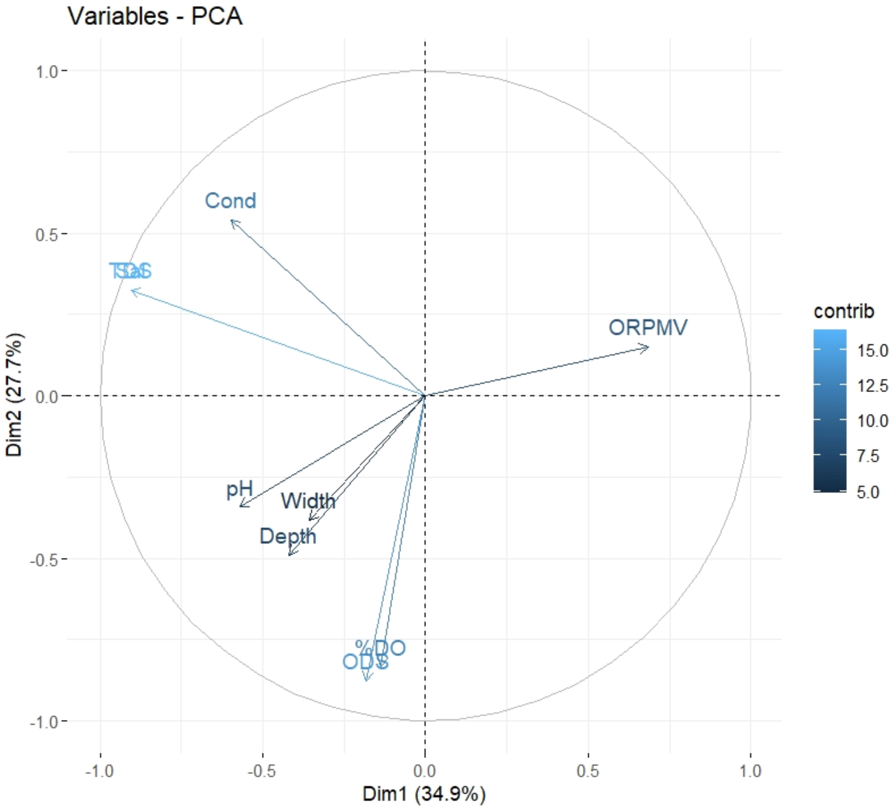
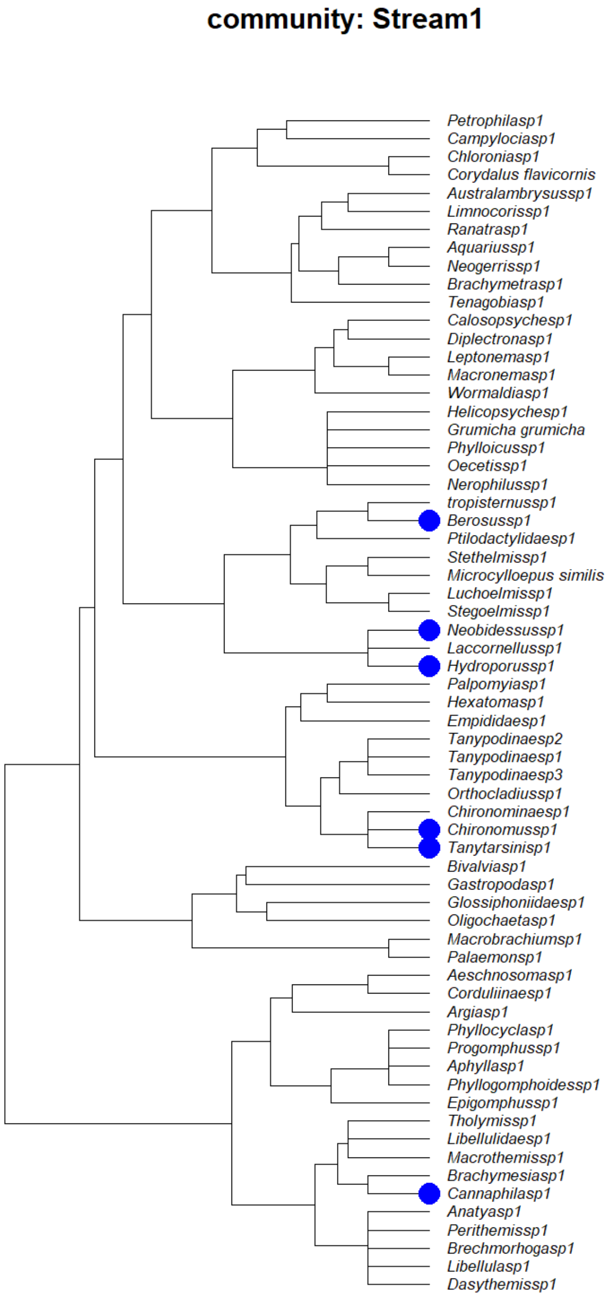


Figure S 6. Principal Component Analysis (PAC) of environmental variables. Variables measured at streams include: Cond - Conductivity; Salt - Salinity; TDS - Total Dissolved Solids; pH - Potential of Hydrogen; Width and Depth of the stream channels; %DO - Percentage of Dissolved Oxygen; ODS - Dissolved Oxygen Concentration; and ORPMV - Oxidation-Reduction Potential.



community: Stream1

Figure S 7. Stream 1 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

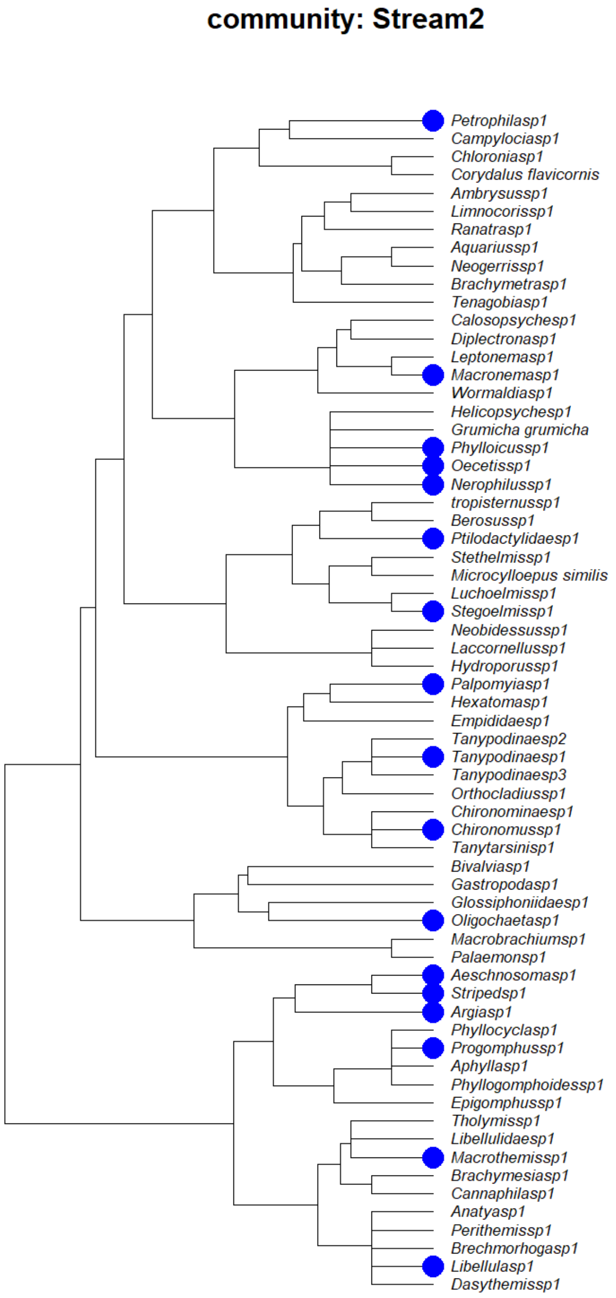


Figure S 8. Stream 2 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

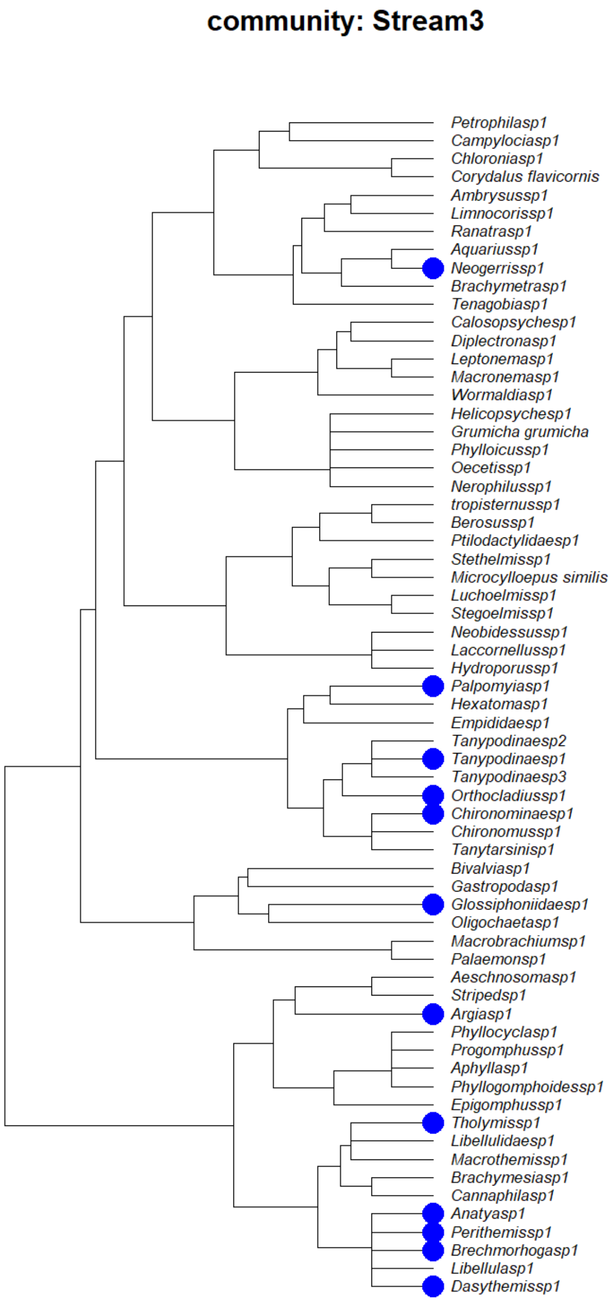


Figure S 9. Stream 3 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

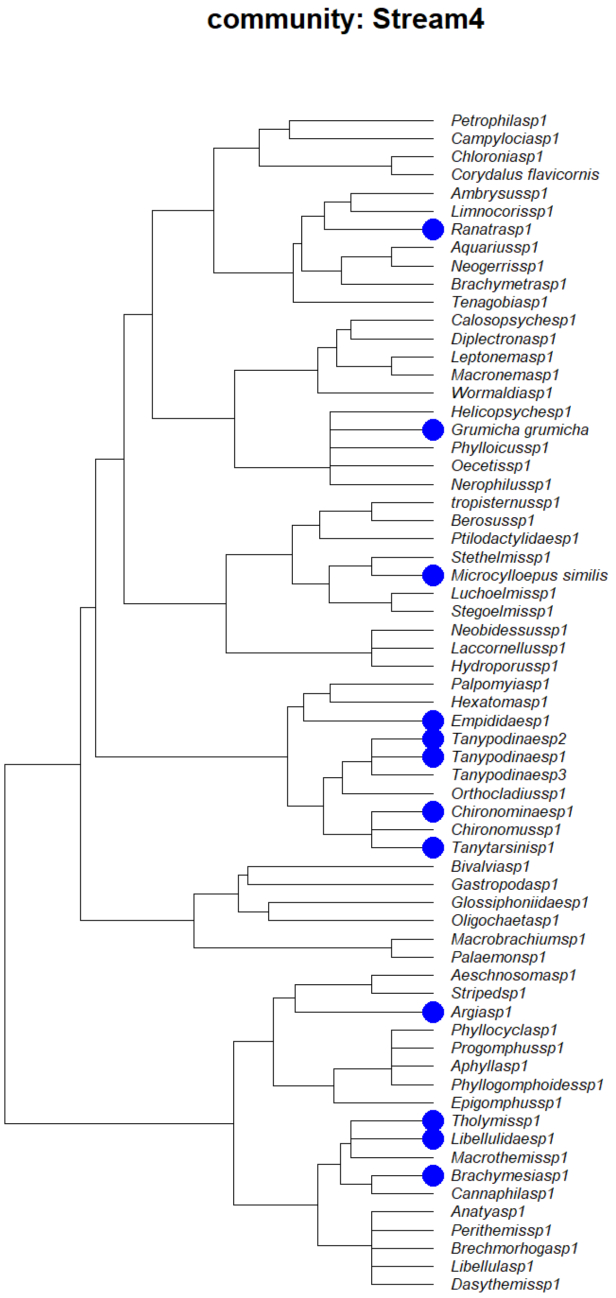


Figure S 10. Stream 4 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

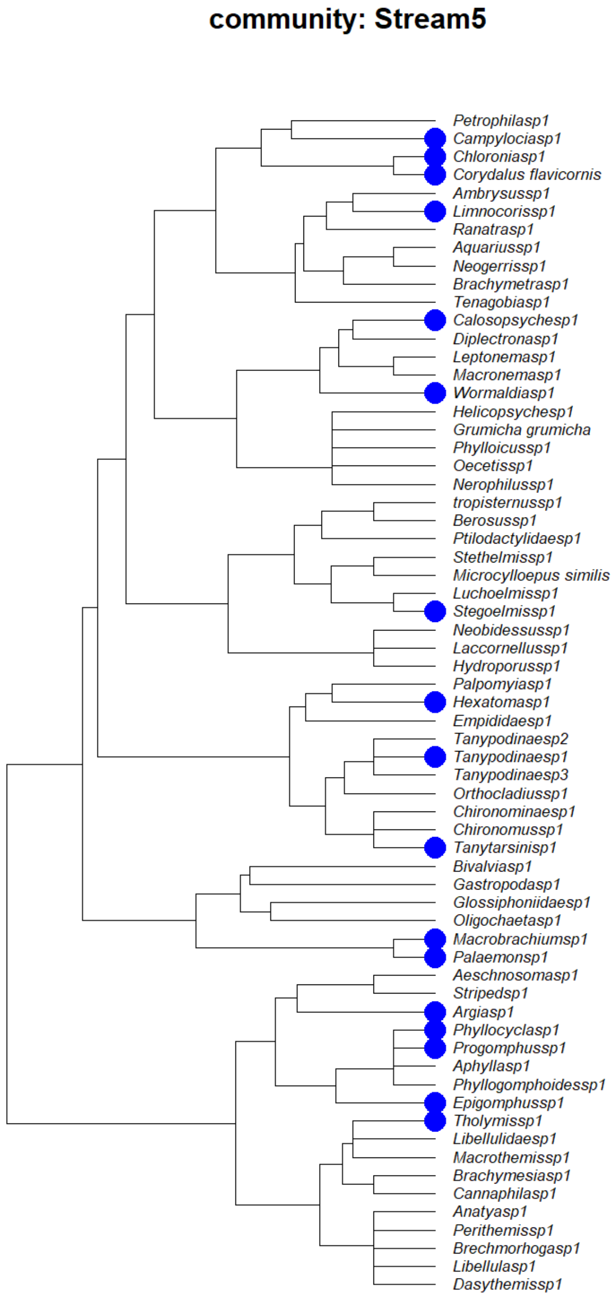


Figure S 11. Stream 5 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

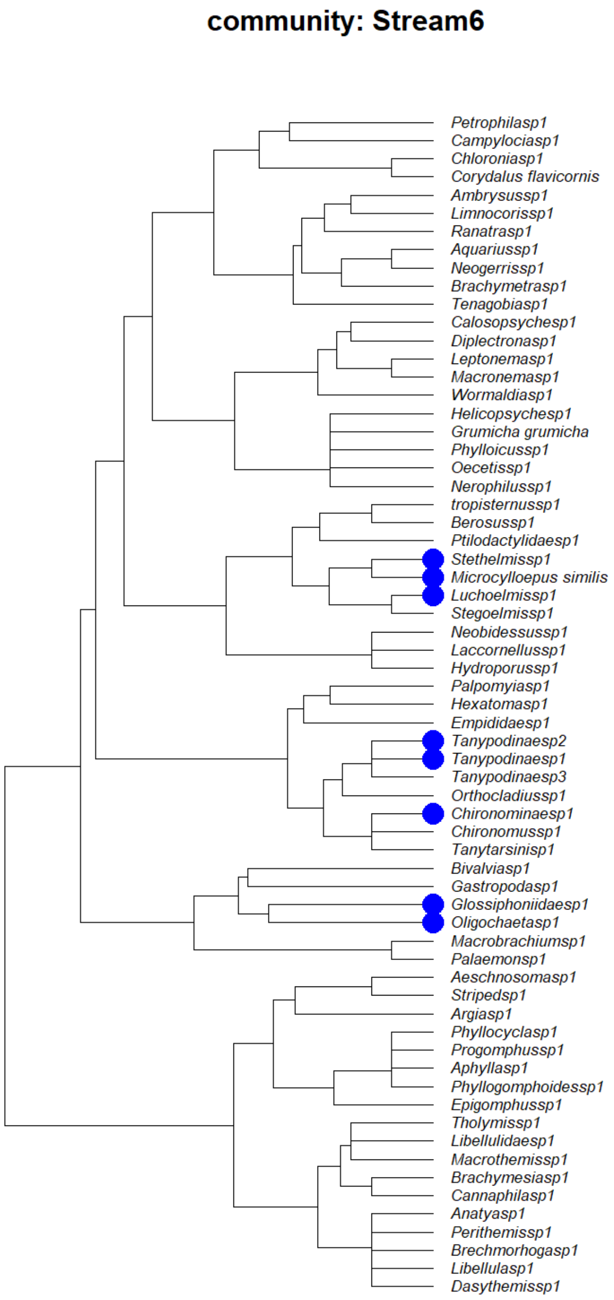


Figure S 12. Stream 6 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

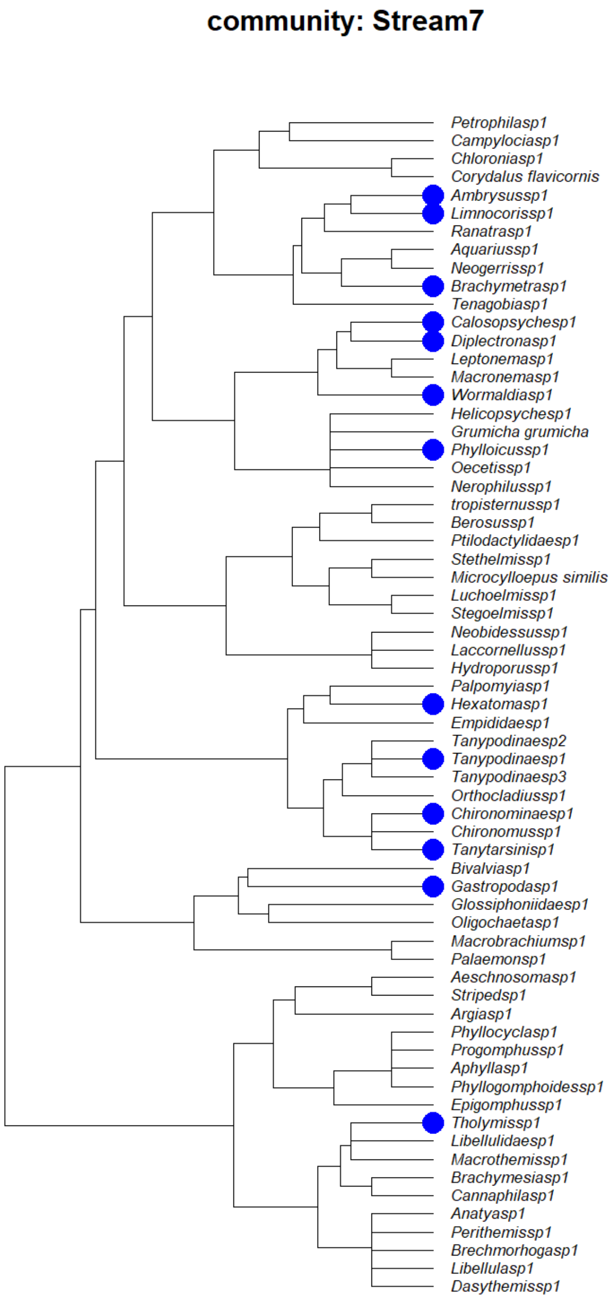


Figure S 13. Stream 7 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

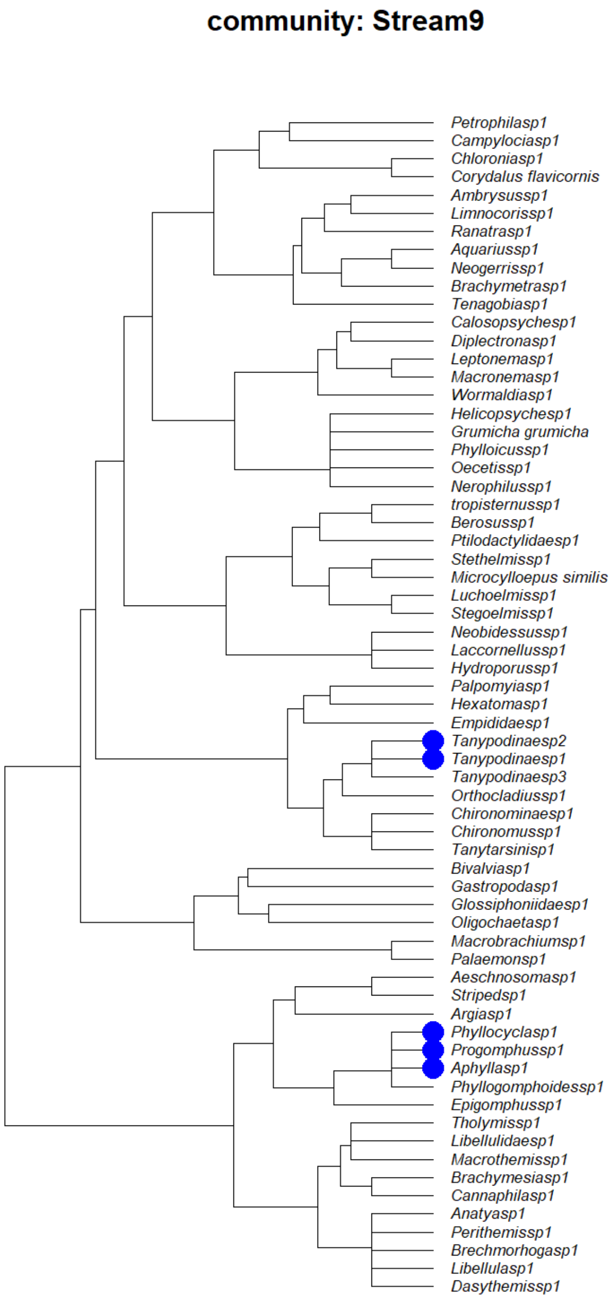


Figure S 14. Stream 9 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

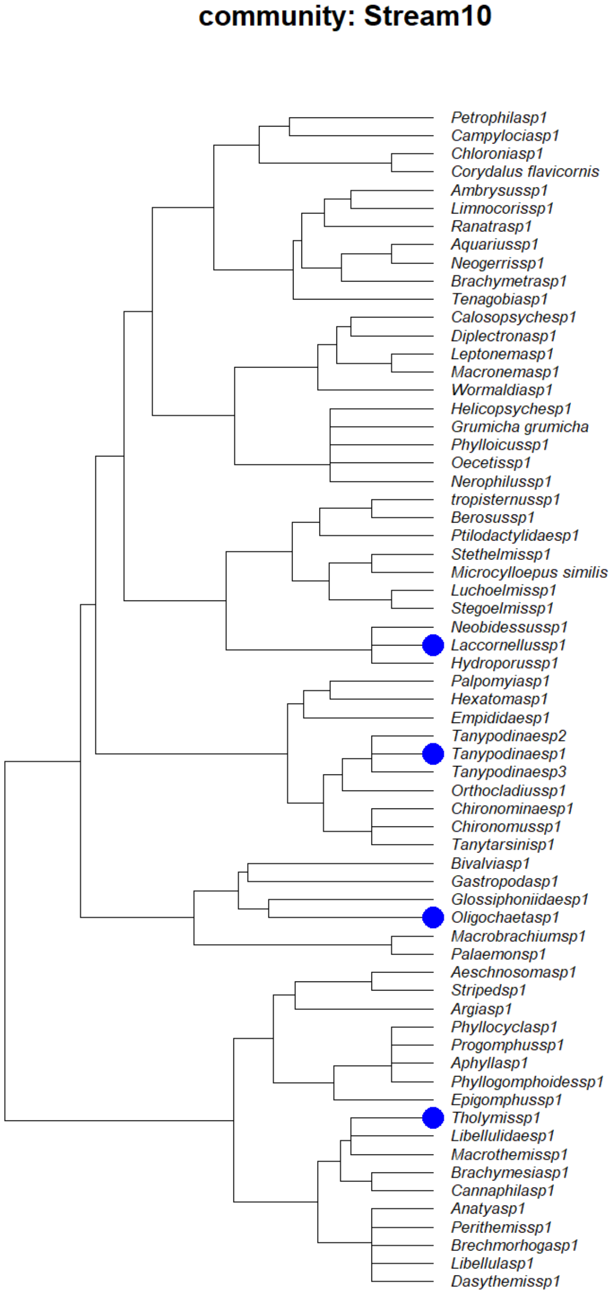


Figure S 15. Stream 10 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

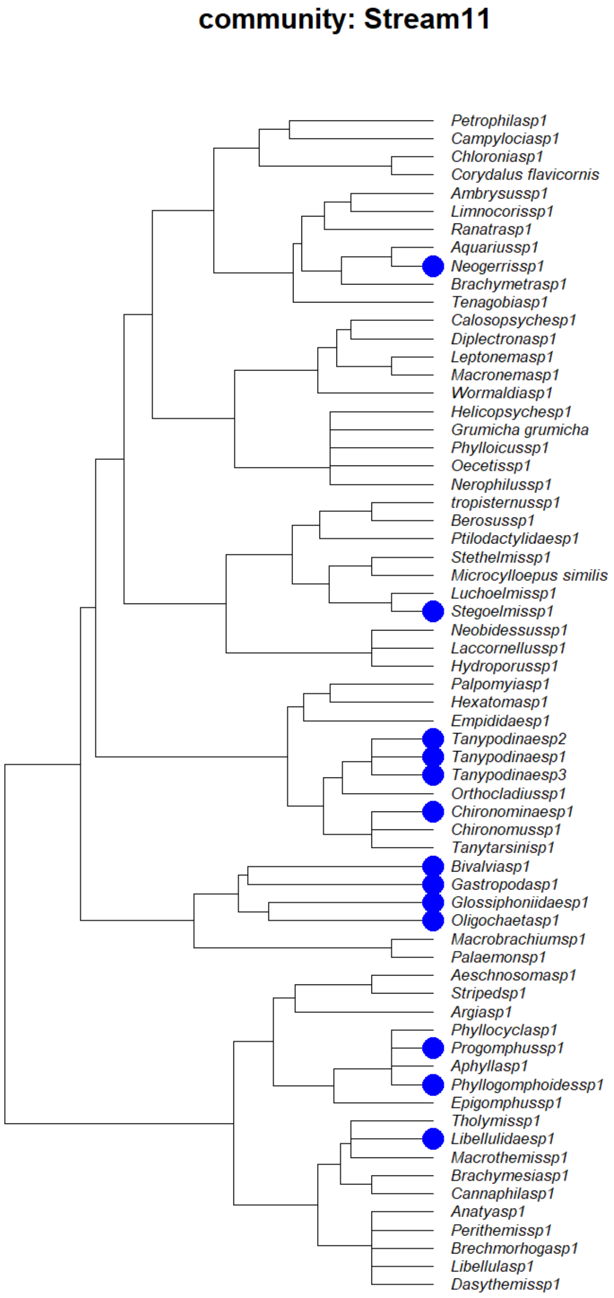


Figure S 16. Stream 11 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

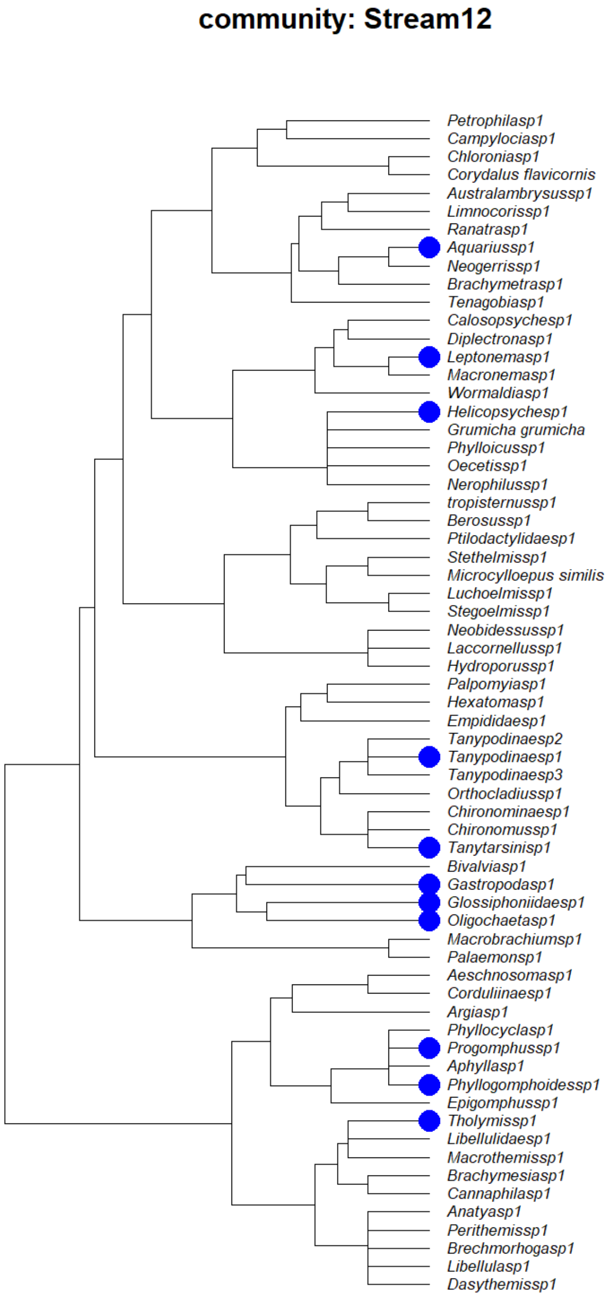


Figure S 17. Stream 12 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

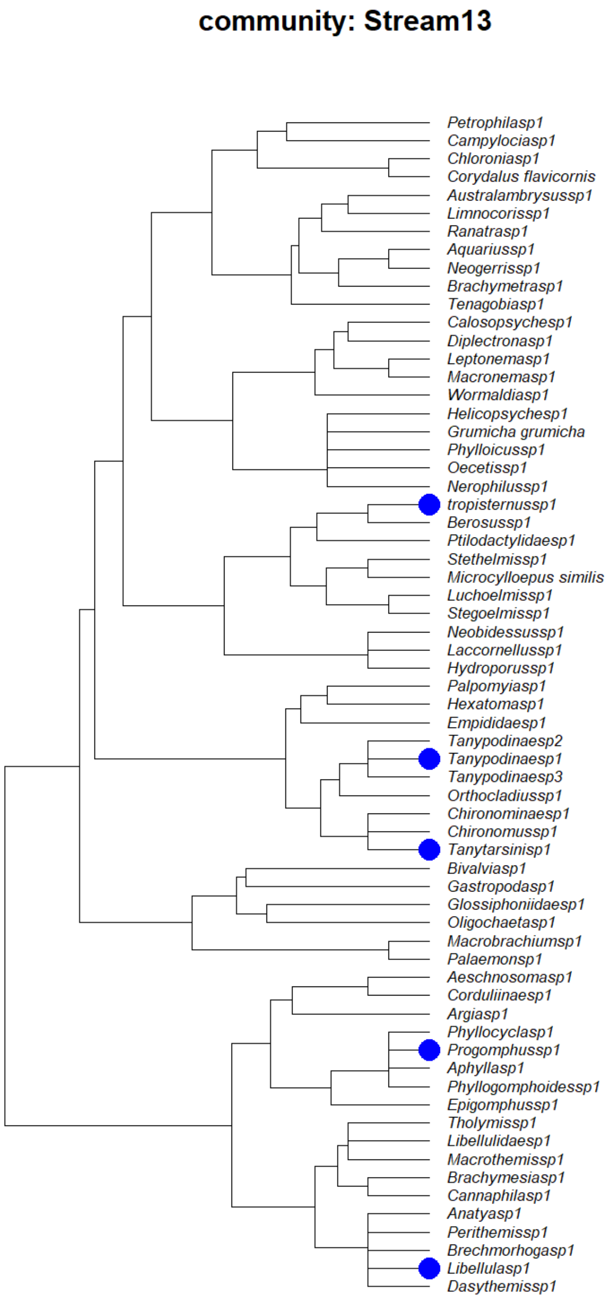


Figure S 18. Stream 13 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

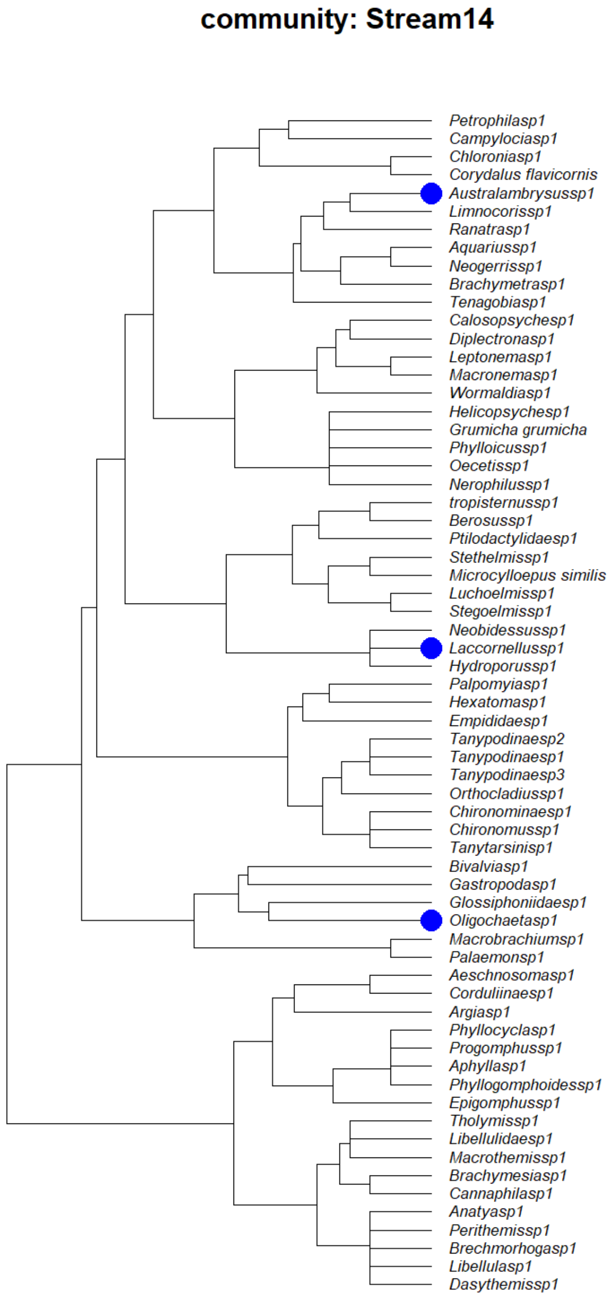


Figure S 19. Stream 14 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

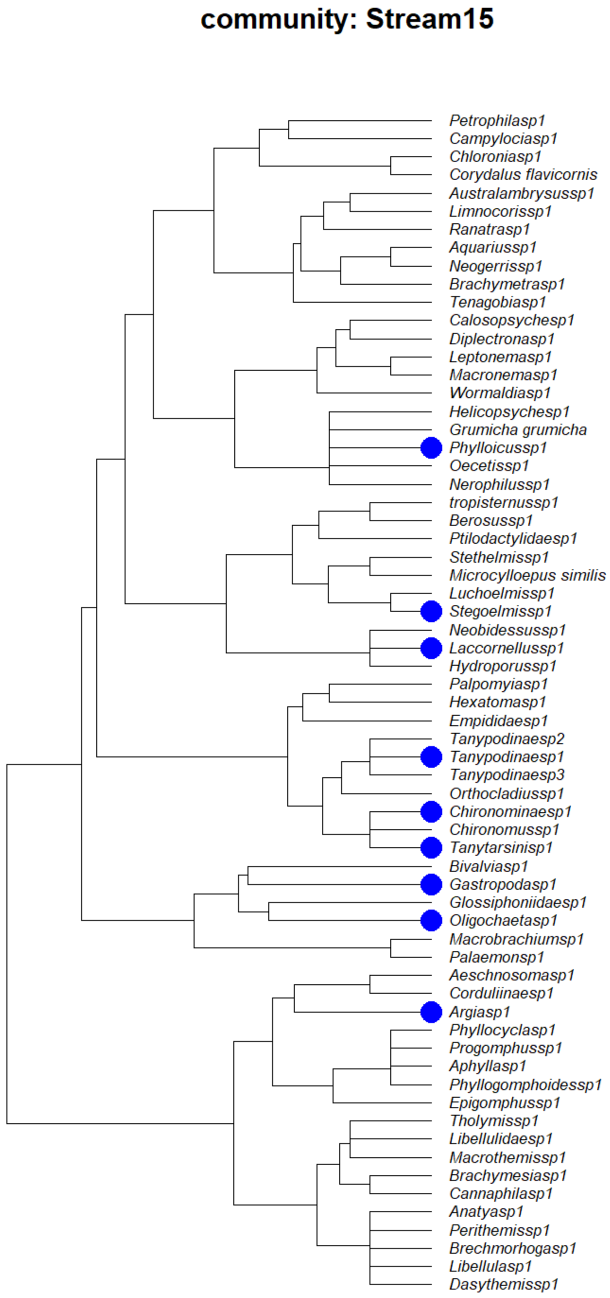


Figure S 20. Stream 15 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

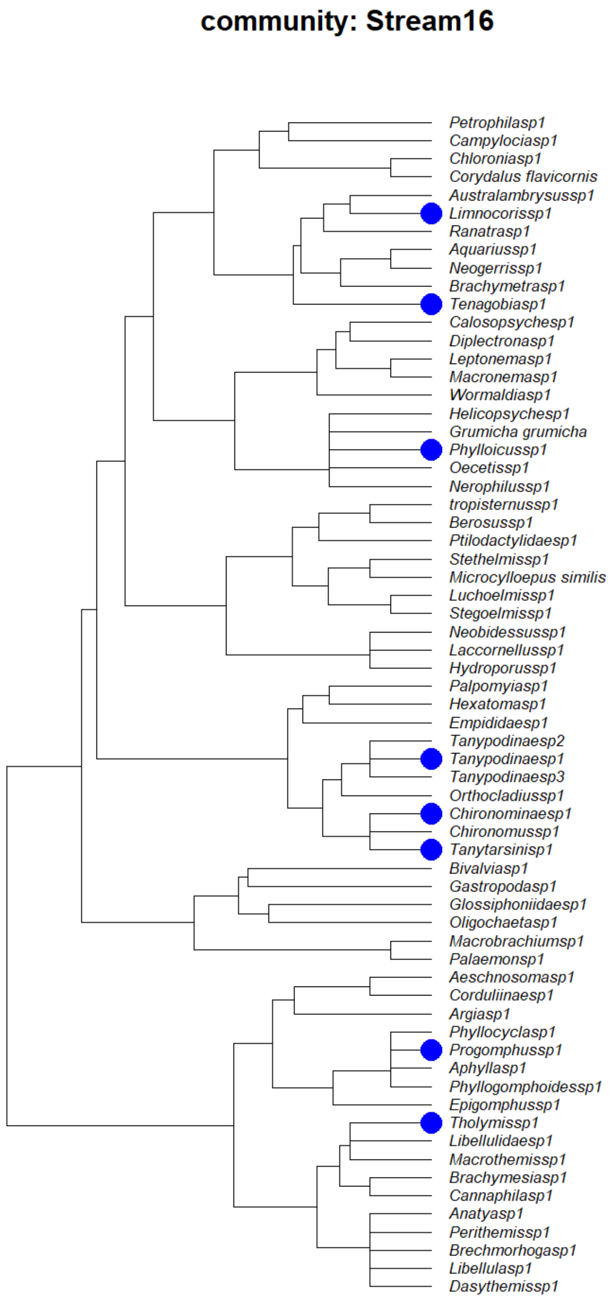


Figure S 21. Stream 16 community phylogenetic composition. The filogram illustrates the taxonomic composition and phylogenetic relationships among taxa. Taxon names are indicated along the branches, with blue circles adjacent to the names representing occurrences into the stream.

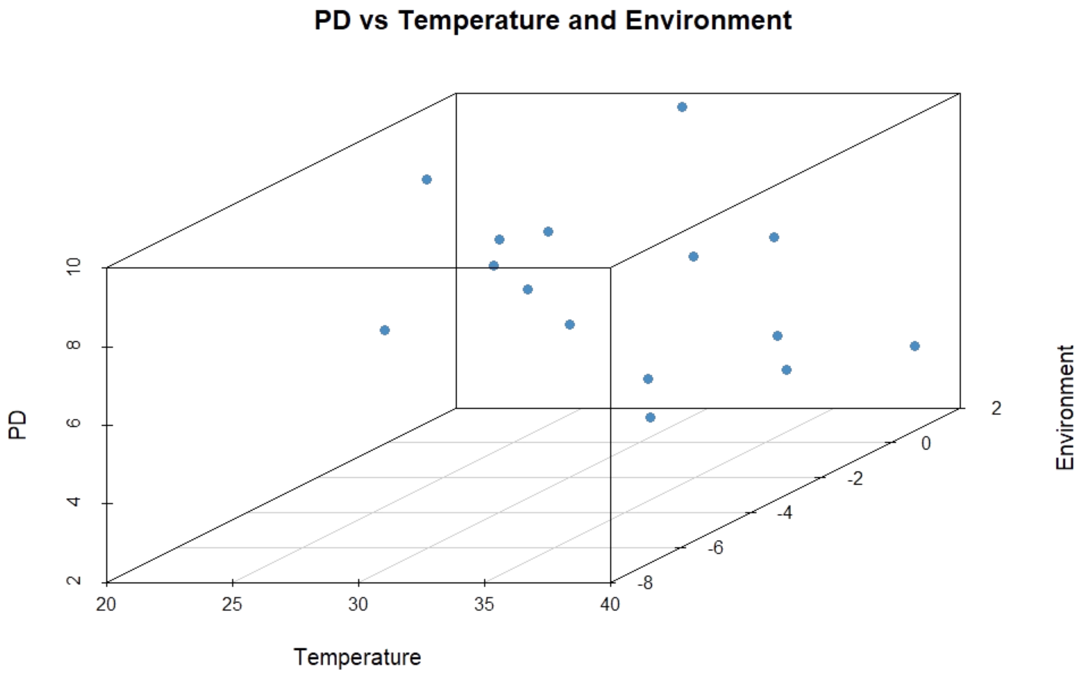


Figure S 22. Three-dimensional depiction illustrating the lack of relationship between phylogenetic diversity (PD) and the predictors temperature (°C) and environmental variation (first principal component axis obtained from PCA) in stream communities. This representation indicates that PD values were not explained by temperature gradients or environmental variation.

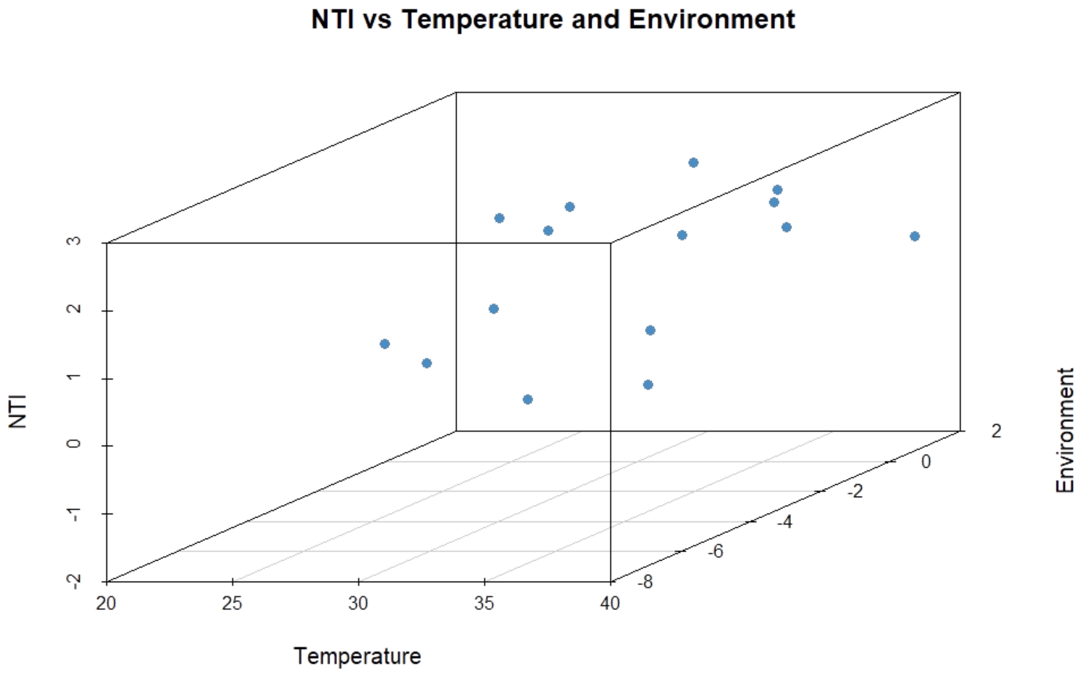


Figure S 23. Three-dimensional depiction illustrating the lack of relationship between Nearest Taxon Index (NTI) and the predictors temperature (°C) and environmental variation (first principal component axis obtained from

PCA) in stream communities. This representation indicates that NTI values were not explained by temperature gradients or environmental variation.

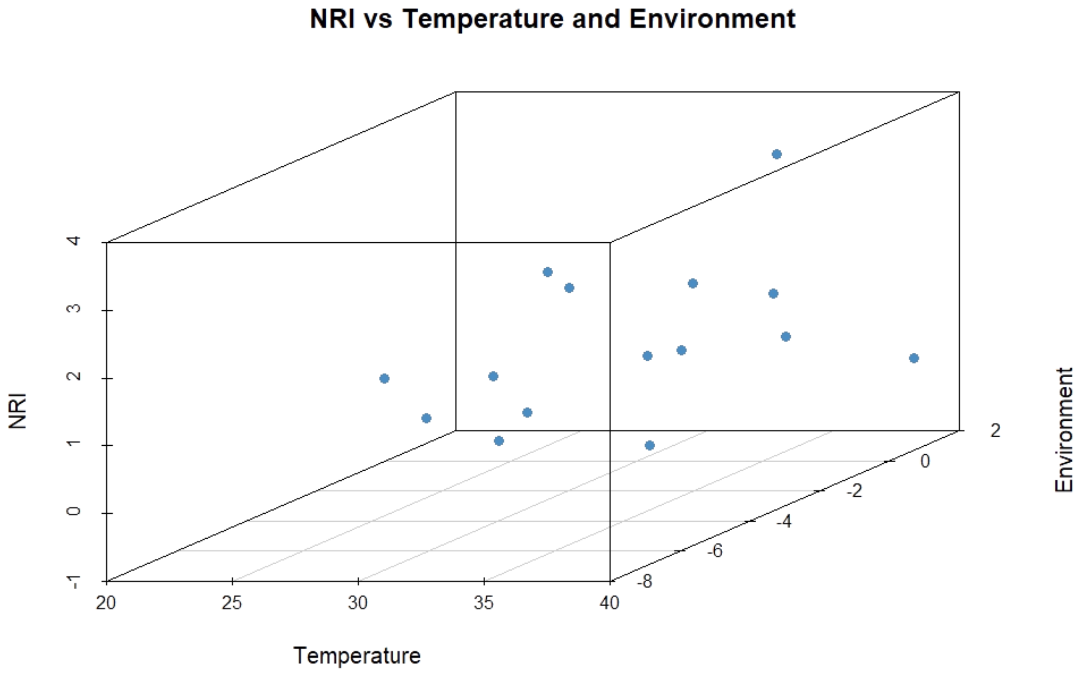


Figure S 24. Three-dimensional depiction illustrating the lack of relationship between Net Relatedness Index (NRI) and the predictors temperature (°C) and environmental variation (first principal component axis obtained from PCA) in stream communities. This representation indicates that NRI values were not explained by temperature gradients or environmental variation.

4 CONSIDERAÇÕES FINAIS

Por fim, esta tese contribui para o entendimento da organização ecológica e evolutiva de comunidades de macroinvertebrados em riachos geotermais tropicais, destacando os mecanismos que sustentam a estabilidade energética e os padrões de diversidade frente a um gradiente de estresse térmico natural. Os resultados do primeiro capítulo revelam que, apesar das variações térmicas ao longo do gradiente, as comunidades mantêm um mecanismo compensatório a nível populacional, o que pode reestruturar as posições tróficas de determinados táxons, assegurando a estabilidade dos espectros de tamanho, a distribuição da biomassa e o fluxo energético. Essa reorganização trófica permite a manutenção da estabilidade da teia alimentar e otimiza a alocação de biomassa, revelando uma resiliência funcional notável das assembleias aquáticas tropicais diante do aquecimento natural.

Por outro lado, os achados do segundo capítulo indicam que o aquecimento térmico por si só não determina de forma dominante os padrões de diversidade taxonômica e filogenética dessas comunidades. A ausência de declínios significativos na diversidade alfa e beta, bem como a falta de um agrupamento filogenético consistente associado à temperatura, sugere que outros fatores em escalas regionais e locais, como processos de dispersão, variação ambiental e pressões antrópicas, exercem influências mais complexas e multifatoriais sobre a composição comunitária. Alguns estudos recentes evidenciam que a inadequada classificação e mapeamento da vegetação nativa, aliada a alterações legislativas que reduzem os requisitos de reservas legais em importantes biomas brasileiros, intensificam o desmatamento e a degradação dos habitats. Essa complexa interação de distúrbios antropogênicos — incluindo extração de água, poluição, mudanças no uso da terra e estressores climáticos — contribui para obscurecer os padrões filogenéticos esperados, dificultando a detecção dos processos ecológicos de montagem comunitária e filtragem ambiental térmica isolada. Essa complexidade reforça a fragilidade intrínseca desses ecossistemas tropicais, cuja proteção formal é ainda insuficiente, e ressalta sua importância como laboratórios naturais para estudos sobre respostas da biodiversidade ao aquecimento global.

Em conjunto, a presente tese apresenta a organização das comunidades de macroinvertebrados em riachos geotermais tropicais e como essa está sendo sustentada por um equilíbrio dinâmico entre mecanismos funcionais compensatórios e múltiplos fatores ecológicos e evolutivos que moldaram a diversidade e estrutura comunitária. A resiliência energética demonstrada pela reestruturação trófica coexistindo com uma diversidade comunitária moldada por processos além do estresse térmico chama a atenção para a necessidade de abordagens integradas de conservação e manejo adaptativo que considerem tanto o funcionamento ecológico quanto os padrões evolutivos para garantir a manutenção da integridade dessas assembleias frente às mudanças climáticas e pressões antrópicas crescentes.