UNIVERSIDADE FEDERAL DA BAHIA - UFBA

Programa de Pós-Graduação em Ecologia: Teoria, Aplicação e Valores

Doutorado em Ecologia: Teoria, Aplicação e Valores

EDSON SERAFIM DE ALMEIDA JÚNIOR

Através do tempo: Avaliando o padrão de decomposição foliar em um riacho de Mata Atlântica.

Salvador, agosto de 2025

EDSON SERAFIM DE ALMEIDA JÚNIOR

Através do tempo: Avaliando o padrão de decomposição foliar em um riacho de Mata Atlântica.

Tese apresentada ao Programa de Pós-Graduação em Ecologia: Teoria, Aplicação e Valores, como parte dos requisitos exigidos para obtenção do título de Doutor em Ecologia.

Orientador: Drª. Adriana Oliveira Medeiros
Co-orientador: Dr. Renan de Souza Rezende

Salvador, agosto de 2025

Dados Internacionais de Catalogação na Publicação (CIP)
Universidade Federal da Bahia (UFBA)
Sistema Universitário de Bibliotecas (SIBI)
Biblioteca Universitária Reitor Macedo Costa (BURMC)

A447a Almeida Júnior, Edson Serafim de.

Através do tempo: [recurso eletrônico] avaliando o padrão de decomposição foliar em um riacho de mata atlântica. / Edson Serafim de Almeida Júnior. – dados eletrônicos. 2025.

150 f.

Orientação: Profa. Dra. Adriana Oliveira Medeiros
Coorientação: Prof. Dr. Renan de Souza Rezende
Tese (Doutorado) – Programa de Pós-Graduação em Ecologia teoria aplicação e valores. Universidade Federal da Bahia. Instituto de Biologia, Salvador, 2025.
Disponível em formato digital, modo de acesso: https://repositório.ufba.br

1. Biodegradação. 2. Matéria orgânica. 3. Rios. I.Oliveira, Adriana Medeiros. II. Souza, Renan Rezende de, III. Universidade Federal da Bahia. IV. Título.

CDU: 631.962

Responsável pela Elaboração – Bibliotecária Juliana Braga (CRB-5/1396) (Os dados para catalogação foram enviados pelo usuário via correio eletrônico)

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA: TEORIA, APLICAÇÂO E VALORES
UNIVERSIDADE FEDERAL DA BAHIA – INSTITUTO DE BIOLOGIA
Rua Barão de Jeremoabo, s/n. Ondina – Salvador – Bahia – CEP. 40.170-000

ATA DA SESSÃO PÚBLICA DO COLEGIADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA: TEORIA, APLICAÇÃO E VALORES – INSTITUTO DE BIOLOGIA – UFBA

Título da Tese: “Através do tempo: Avaliando o padrão de decomposição foliar em um riacho de Mata Atlântica.”

Doutorando(a): **Edson Serafim de Almeida Junior**

Orientador(a): **Drª. Adriana Oliveira Medeiros**

De acordo com o regimento geral da UFBA e com o regimento interno deste programa de pós-graduação, foram iniciados os trabalhos da Comissão Examinadora, composta pela professora Dra. Adriana Oliveira Medeiros (Presidente), Dra. Paula Benevides de Morais, Prof. Dr. Marcelo da Silva Moretti, Prof. Dr. Manuel Augusto Simões Graça e Prof. Dr. Eduardo Mariano Neto, às 09:00h do dia 08 de agosto de 2025. O doutorando fez a apresentação oral da tese durante 42 minutos. Após o encerramento das arguições, às 12 horas, a Comissão Examinadora pronunciou-se pela sua aprovação, conforme parecer em anexo. Esta ata será assinada pelos membros da Comissão Examinadora e deste Colegiado de curso, para compor o processo de emissão do diploma.

Salvador, 08 de agosto de 2025.

COMISSÃO EXAMINADORA

Documento assinado digitalmente
gov.br
ADRIANA OLIVEIRA MEDEIROS
Data: 12/08/2025 09:04:20-0300
Verifique em https://validar.iti.gov.br

_____
Membro: Profa. Dra. Adriana Oliveira Medeiros
Universidade Federal da Bahia

Documento assinado digitalmente
gov.br
PAULA BENEVIDES DE MORAIS
Data: 14/08/2025 11:44:09-0300
Verifique em https://validar.iti.gov.br

_____
Membro: Profa. Dra Paula Benevides de Morais
Universidade Federal de Tocantins

Documento assinado digitalmente
gov.br
MARCELO DA SILVA MORETTI
Data: 13/08/2025 14:22:58-0300
Verifique em https://validar.iti.gov.br

_____
Membro: Prof. Dr. Marcelo da Silva Moretti
Universidade de Vila Velha

_____
Membro: Prof. Dr. Manuel Augusto Simoes Graça
Universidade de Coimbra

Documento assinado digitalmente
gov.br
EDUARDO MARIANO NETO
Data: 14/08/2025 08:58:19-0300
Verifique em https://validar.iti.gov.br

_____
Membro: Prof. Dr. Eduardo Mariano Neto
Universidade Federal da Bahia

Dedico esta tese a todas as pessoas que me fizeram acreditar que resistir também é construir.

Meu processo de doutorado foi a travessia de um corpo negro que resiste, que pensa e que se cura.

Conquistar este espaço não foi só sobre mim, foi sobre os que vieram antes e os que virão depois.

Agradecimentos

Ao Programa de Pós-graduação em Ecologia: Teoria, Aplicação e Valores, ao Instituto de Biologia e a Universidade Federal da Bahia, onde aprendi a ser biólogo e pesquisador.

À CAPES pelo fomento à pesquisa científica no Brasil e que é tão necessária para os alunos de graduação e pós-graduação. À FAPESB pelo financiamento de parte dessa pesquisa que foi realizada por longos cinco anos.

À Professora Adriana e Professor Renan pela orientação e apoio em todos as etapas da nossa pesquisa. Agradeço aos colaboradores do trabalho, em especial os Professores Adolfo, Daniela Mariano, Lenise, Alessandra e o Professor Júnior, muito obrigado.

Agradeço a todos os alunos do LMA; aos que me receberam e me ensinaram tudo o que foi preciso quando cheguei; e aos que eu pude receber e trocar um pouco de conhecimento. Em especial Danilo, Denis, Nati, Keisla, Pedro e Guilherme. Fui muito feliz compartilhando os momentos de aprendizado no laboratório com vocês.

Muito obrigado meu pai, minhas mães (Cristina e Cirlene) pelo apoio e por permitir através dos seus esforços que eu continuasse estudando e realizando os meus sonhos.

Muito obrigado aos meus amigos Vinicius, João, Indi, Marcy, Bruno que são meu porto seguro e a família que escolhi pra mim. À Laisa, Lucas, Vitor e Ivan que estão comigo desde a graduação e que eu amo muito.

Por fim, agradeço ao amor da minha vida, Marcos Oliveira, que me faz o homem mais feliz do mundo, todos os dias.

Muito obrigado!

Vida submersa: A importância da decomposição em riachos de cabeceira

Edson Serafim de Almeida Junior

Você já parou para pensar no que acontece com as folhas que caem nos riachos? Em riachos de cabeceira, que são pequenos cursos d'água cercados por mata densa, essas folhas não são apenas "lixo orgânico". Elas são a principal fonte de energia para a vida que habita ali.

Durante cinco anos, minha pesquisa acompanhou de perto esse processo invisível, mas essencial: a decomposição de folhas em um riacho da Mata Atlântica. Devido à sombra das árvores, há pouca luz solar nesses ambientes. Por isso, as folhas que caem das árvores e vão parar na água são os principais recursos para a teia alimentar desses ecossistemas.

A decomposição transforma essa matéria orgânica em nutrientes que alimentam fungos, invertebrados e, por fim, toda a vida aquática. Entre os protagonistas estão os fungos hifomicetos aquáticos e os invertebrados fragmentadores, pequenos organismos que desempenham um papel enorme: eles processam as folhas e tornam possível que outros seres vivos se alimentem e sobrevivam.

Mas o que acontece quando o clima muda, a temperatura sobe ou a água perde oxigênio? Nossa pesquisa buscou entender como variações ambientais, como temperatura, qualidade da água e as estações do ano influenciam esse processo de decomposição e a comunidade de organismos que depende dele.

Os resultados mostram que, mesmo em meio a variações climáticas, os riachos apresentam uma notável capacidade de manter sua função ecológica. Ainda assim,

identificar os limites dessa resiliência é essencial para proteger esses ecossistemas frágeis diante das mudanças climáticas.

Esse estudo nos ajuda a entender melhor como funcionam os pequenos riachos que correm escondidos sob as florestas e porque é tão importante cuidar deles. Afinal, proteger as águas que nascem nas cabeceiras é garantir vida para todo o caminho que elas percorrem e para todos nós.

Resumo

A decomposição de matéria orgânica é um processo ecológico fundamental para a ciclagem de carbono e nutrientes em riachos de cabeceira, especialmente em ecossistemas tropicais, onde o aporte de serapilheira alóctone é a principal fonte de energia para a teia alimentar aquática. No entanto, a compreensão da dinâmica desse processo em escalas temporais mais amplas, particularmente em regiões tropicais com alta heterogeneidade ambiental e biológica, ainda é limitada devido à escassez de dados de longo prazo. Este trabalho investigou a influência da variação temporal e de múltiplos fatores ambientais sobre a comunidade decompositora e o processo de decomposição da matéria orgânica, em um riacho de cabeceira da Mata Atlântica brasileira, ao longo de cinco anos. A pesquisa foi dividida em dois capítulos principais. O Capítulo 1 avaliou a estrutura da comunidade de fungos hifomicetos aquáticos cujo principal papel ecológico é o condicionamento foliar e mineralização, durante o processo de decomposição. Os resultados revelaram que a variação interanual teve uma influência mais significativa na estrutura da comunidade de hifomicetos aquáticos do que a variação intra-anual. Os principais fatores ambientais que moldaram essa comunidade foram a química da água e a qualidade da matéria orgânica foliar. Esse padrão contrastou com a hipótese inicial que previa uma maior influência da variação intra-anual, indicando uma notável estabilidade sazonal e a predominância de variações de longo prazo. O Capítulo 2 investigou as relações diretas e indiretas de fatores temporais e ambientais sobre a estrutura da comunidade decompositora e a decomposição da matéria orgânica, utilizando Modelos de Equações Estruturais. O modelo demonstrou que a escala temporal e a composição de nutrientes dissolvidos na água foram os principais impulsionadores da estrutura da comunidade decompositora. Curiosamente, a decomposição não foi diretamente explicada por nenhuma das variáveis incluídas no modelo, sugerindo a presença de

redundância funcional e resiliência ecológica no processo de decomposição. Por fim, esta tese avança o conhecimento sobre como a variabilidade temporal e as interações complexas entre fatores ambientais e biológicos moldam a decomposição em riachos tropicais. Os achados destacam a importância de abordagens de longo prazo para desvendar processos ecológicos em ecossistemas dinâmicos e fornecem contribuições valiosas para a conservação e o manejo da integridade de riachos de cabeceira sob as pressões das mudanças climáticas.

Palavras-chave: Mata Atlântica, Riachos de cabeceira, decomposição foliar, comunidade decompositora, padrão temporal.

Abstract

Organic matter decomposition is a fundamental ecological process for carbon and nutrient cycling in headwater streams, especially in tropical ecosystems where allochthonous leaf litter is the primary energy source sustaining the aquatic food web. However, understanding the dynamics of this process at broader temporal scales, particularly in tropical regions characterized by high environmental and biological heterogeneity, remains limited due to the scarcity of long-term data. This study investigated the influence of temporal variation and multiple environmental factors on the decomposer community and the process of organic matter decomposition in a headwater stream of the Brazilian Atlantic Forest over five years. The research was structured into two main chapters. Chapter 1 evaluated the structure of aquatic hyphomycete fungal communities, whose main ecological role is leaf conditioning and nutrient mineralization during decomposition. The results revealed that interannual variation had a stronger influence on hyphomycete community structure than intra-annual variation. The main environmental drivers shaping this community were water chemistry and leaf litter quality. This pattern contrasts with the initial hypothesis, which predicted a stronger influence of intra-annual variation, and instead indicates notable seasonal stability and the predominance of long-term environmental shifts. Chapter 2 investigated the direct and indirect relationships between temporal and environmental factors, the structure of the decomposer community, and organic matter decomposition using Structural Equation Modeling (SEM). The model showed that timescale and the composition of dissolved nutrients in the water were the main drivers of decomposer community structure. Interestingly, decomposition was not directly explained by any of the variables included in the model, suggesting the presence of functional redundancy and ecological resilience in the decomposition process. In conclusion, this thesis advances our understanding of how temporal variability and the

complex interactions among environmental and biological factors shape decomposition in tropical streams. The findings highlight the importance of long-term approaches for uncovering ecological processes in dynamic ecosystems and provide valuable insights for the conservation and management of headwater stream integrity under climate change pressures.

Keywords: Atlantic Forest, headwater streams, leaf litter decomposition, decomposer community, temporal pattern.

Sumário

Estrutura da tese

A presente tese está estruturada em dois capítulos como segue:

Capítulo I – Fatores temporais e ecológicos de Hifomicetos Aquáticos em um Riacho de Cabeceira Tropical.

Neste capítulo, investigamos a estrutura da comunidade de hifomicetos aquáticos ao longo de cinco anos, com ênfase nas variações intra e interanuais, bem como na influência de fatores abióticos e bióticos que moldaram essa comunidade. Os resultados evidenciam que a variação interanual exerceu uma influência mais significativa do que a variação intra-anual, e que a química da água e a qualidade da matéria orgânica foliar foram os principais fatores ambientais associados à composição da comunidade. Este capítulo contribui para o entendimento da estabilidade funcional e da variabilidade ecológica em ecossistemas tropicais e encontra-se atualmente em fase de revisão por pares na revista *Freshwater Biology*.

Capítulo II – Efeitos de escala temporal na decomposição revelam vias ambientais indiretas em um riacho da Mata Atlântica: insights de um estudo de cinco anos.

Neste capítulo, avaliamos a influência de fatores temporais e ambientais sobre a estrutura da comunidade decompositora e o processo de decomposição da matéria orgânica alóctone em um riacho tropical. Para isso, utilizamos Modelagem de Equações Estruturais (SEM) com o objetivo de identificar relações diretas e indiretas entre variáveis climáticas, características ambientais e a comunidade decompositora. Os resultados revelam que a escala temporal e a composição de nutrientes dissolvidos na água foram os principais

fatores que moldaram a estrutura da comunidade decompositora, enquanto a decomposição demonstrou resiliência a variações diretas desses fatores. Este capítulo aprofunda a compreensão dos mecanismos ecológicos subjacentes à decomposição em ecossistemas tropicais e fornece subsídios para o aprimoramento de modelos preditivos sobre os impactos das mudanças climáticas. O manuscrito está em fase de revisão pelos colaboradores e será submetido à revista *Ecology*.

Introdução geral

Riachos de cabeceira são ecossistemas cruciais para a manutenção da biodiversidade e a provisão de serviços ecossistêmicos globalmente, especialmente em regiões tropicais, onde a alta heterogeneidade ambiental e biológica os torna particularmente complexos (Gessner et al., 2010; Boyero et al., 2016, Rezende et al., 2016). Nesses ambientes, a variabilidade temporal, manifestada através de flutuações climáticas sazonais e interanuais, é um impulsionador ecológico chave, moldando a hidrologia, a disponibilidade de recursos e a atividade das comunidades biológicas (del Cid et al., 2019; Tonin et al., 2017). Apesar de sua relevância, a influência da escala temporal na integração desses fatores permanece subestimada, principalmente em sistemas tropicais onde conjuntos de dados de longo prazo são escassos (del Cid et al., 2019; Nguyen et al., 2023; Rabelo et al., 2024).

A decomposição de matéria orgânica é essencial para a ciclagem de carbono e nutrientes em riachos de cabeceira. Esse processo é responsável pela mineralização dos nutrientes disponibilizando-os para teias alimentares em ecossistemas terrestres e aquáticos (Boyero et al., 2016). Em riachos de cabeceira a disponibilidade de luz solar é limitada pela vegetação ripária de galeria, que pela copa das árvores bem desenvolvidas, bloqueiam a entrada de luz solar no riacho (Neres-Lima et al., 2017). Portanto a matéria orgânica alóctone se torna a principal fonte de energia para esses riachos, cujo metabolismo é predominantemente heterotrófico (Esteves and Gonçalves, 2011).

A entrada da matéria orgânica alóctone nos riachos pode ocorrer de duas formas: (1) o material senescente cai diretamente no corpo d'água (entrada direta ou vertical) ou (2) o

material é depositado no solo antes de ser carreado para água sob ação do vento, escoamento superficial ou pulso de inundação dos riachos (entrada indireta ou lateral) (Webster and Meyer, 1997). Dentre os materiais que compõe a matéria orgânica alóctone estão os galhos, flores, frutos, sementes e principalmente as folhas, que contribuem com mais de 70% de toda matéria orgânica encontrada nesses ecossistemas (del Cid et al., 2023, 2019; Rezende et al., 2017a). As características físicas das folhas (p.ex. dureza, tamanho, forma e presença de espinhos), os compostos estruturais das plantas (p.ex. lignina e celulose) e a qualidade nutricional delas (p.ex. teores de N, P, taninos e polifenóis) podem influenciar a decomposição da matéria orgânica nos riachos (Alvim et al., 2015; Gomes et al., 2016). Dessa forma, a comunidade de plantas que contribuem no aporte de matéria orgânica no ecossistema determina a composição funcional dos organismos associados à decomposição nos riachos de cabeceira (Rincón and Santelloco, 2009; Sanpera-Calbet et al., 2009; Tonello et al., 2014).

Além da comunidade de plantas que compõe a vegetação ripárias nos riachos, as características físicas e químicas da água (p.ex. pH, temperatura, vazão, oxigênio dissolvido e nutrientes) também influenciam a decomposição (Barreto et al., 2023; Gomes et al., 2018; Medeiros et al., 2009). As características dos riachos determinam a disponibilidade de nutrientes e alteram as taxas metabólicas dos organismos decompositores como os fungos hifomicetos aquáticos (Bärlocher, 1992; Barreto et al., 2023), e os invertebrados fragmentadores (Marks, 2019; Raposeiro et al., 2018; Wallace et al., 1982) e assim, afetam a estabilidade da comunidade decompositora nos riachos alterando a ocorrências das espécies, taxa de esporulação dos hifomicetos aquáticos, consumos dos fragmentadores e seus ciclos de vida (Marks, 2019).

Os fungos hifomicetos aquáticos, são considerados os principais atores na decomposição de matéria orgânica alóctone em riachos de cabeceira (Abelho, 2001).

Consequentemente, esses fungos são essenciais para a ciclagem de nutrientes nesses ecossistemas (Graça et al., 2016, 2015). Filogeneticamente, eles são classificados como fungos anamórficos, pertencentes ao filo Ascomycota, mas também são correlacionados com Basidiomycota (Shearer et al., 2007). A identificação desses fungos pode ser feita através da morfologia dos esporos assexuados encontrados em folhas em decomposição ou espuma presentes em riachos (Krauss et al., 2011), por conidiogênese (Seena et al., 2010) e por análise molecular do material genético (Bärlocher, 2007; Seena et al., 2010). Os hifomicetos aquáticos produzem e liberam enzimas hidrolíticas que degradam polímeros a matéria orgânica e as deixam mais palatáveis para a nutrição de outros organismos (Bärlocher, 1992).

Os invertebrados fragmentadores são um grupo importante para a estrutura e funcionamento dos ecossistemas aquáticos tropicais (Raposeiro et al., 2018). Os principais representantes desse grupo de fragmentadores são os insetos das ordens Díptera, Plecoptera e Trichoptera e macroconsumidores que desempenham um papel crucial na decomposição da matéria orgânica (Graça & Canhoto, 2006; Tonin et al., 2014; Jonsson & Sponseller, 2021). Sua presença pode ser influenciada pelas características físicas e químicas dos riachos, como o sedimento e morfologia das margens, bem como a qualidade de matéria orgânica, ou seja, das folhas disponíveis nos riachos pela vegetação ripária (Balibrea et al., 2020). Dessa forma, os fragmentadores são responsáveis pela transformação da matéria orgânica particulada grossa (MOPG), através do consumo da matéria orgânica foliar, em matéria orgânica particulada fina (MOPF), que é liberada durante a alimentação e através da excreção pelos organismos, promovendo a ciclagem de nutrientes através da mineralização (Halvorson et al., 2017; Marks, 2019; Wallace et al., 1982). Dentre os fatores que influenciam a colonização dos invertebrados fragmentadores no substrato é o condicionamento, ou seja, a colonização do detrito por

microrganismos decompositores, como os hifomicetos aquáticos (Marks, 2019). O condicionamento aumenta a palatabilidade do recurso e o valor nutricional para esses organismos. Portanto, a colonização inicial pelos microrganismos decompositores pode garantir a colonização e a utilização dos recursos foliares por invertebrados de forma mais eficiente no processo de decomposição (Marks, 2019).

O processo de decomposição, que consiste na transformação da MO em moléculas mais simples pela ação dos fatores químicos, físicos e biológicos do sistema (Tonin et al., 2021) é dividido em três fases, que se sobrepõem. São eles: (i) a lixiviação, onde ocorre a dissolução dos compostos solúveis do material foliar ao entrar em contato com a água; (ii) o condicionamento, que consiste na colonização do detrito foliar por microrganismos que atuam na intensificação e modificação química e física do recurso causando o aumento da palatabilidade das folhas e que permite a (iii) atuação dos invertebrados fragmentadores, que se alimentam do recurso, caracterizando a terceira fase do processo, nomeado de fragmentação (Gessner et al., 1999). O resultado final desse processo é a degradação da matéria orgânica e seus elementos, que serão disponibilizados no ambiente e reinseridos no sistema através da reabsorção dos nutrientes por outros organismos (Abelho, 2001; Datry et al., 2018).

Os hifomicetos aquáticos e invertebrados decompositores também tem sua atuação no processo de decomposição modificada sob influência de alguns fatores climáticos, dentre eles destacam-se a temperatura e a precipitação (Correa-Araneda et al., 2020). A temperatura pode influenciar a interação da atividade microbiana com o recurso, impedindo a disponibilidade de matéria orgânica de melhor qualidade para a microbiota aquática (Boyero et al., 2016) e a precipitação é apontada como o principal direcionador da entrada de matéria orgânica disponibilizando mais recurso para o riacho em biomas

mais úmidos (Tonin et al., 2017) e em ambos os casos esses fatores afetam a decomposição.

A sazonalidade (que determina as variações climáticas ao longo do tempo) também define variações na dinâmica de matéria orgânica e sua decomposição, na disponibilidade de nutrientes ao longo do tempo e na fenologia das plantas (Sanches et al., 2008; Tonin et al., 2021, 2017). Além disso, a variação temporal é crucial para a manutenção da comunidade decompositora, mediado pelas variação ambientais, como a precipitação e a matéria orgânica dissolvida na água (Li et al., 2022; Noacco et al., 2019). As variações interanuais podem ser mais interessantes para avaliar a estrutura da comunidade de invertebrados, como o grupo dos Chironomidae, que pode ser mais sensível a variações climáticas imprevisíveis, logo que as variações intra-anuais geralmente são influenciadas por eventos climáticos específicos (sazonalidade) (Hepp et al., 2021; Pio et al., 2022). Já os hifomicetos aquáticos podem exibir variações sazonais ao longo do ano, podendo apresentar picos de esporulação durante as estações de seca (del Cid et al., 2019) ou em períodos chuvosos, mediada pela variação climática que determina também a entrada da matéria orgânica nos riachos (del Cid et al., 2023; Graça et al., 2016; Sales et al., 2014).

Portanto, trabalhos que avaliam a dinâmica de decomposição em longa escala temporal são escassos, mas necessários para entender melhor o processo e seus padrões de forma mais robusta (Benson and Pearson, 2020; Gossiaux et al., 2019; Tonin et al., 2017). Este estudo tem como objetivo preencher essa lacuna, analisando a decomposição da matéria orgânica em um riacho de Mata Atlântica ao longo de cinco anos. Avaliamos como fatores abióticos, como parâmetros físicos e químicos da água e variáveis climáticas, juntamente com fatores bióticos, como a qualidade e diversidade das plantas, influenciam a decomposição e a estrutura da comunidade de decompositores. Esta

pesquisa contribui para um melhor entendimento dos processos ecológicos em riachos de cabeceira e fornece insights valiosos para a conservação e manejo desses ecossistemas.

Objetivo Geral

O objetivo da tese é avaliar a influência da variação temporal na comunidade decompositora e no processo de decomposição ao longo de 5 anos em um riacho de Mata Atlântica.

Objetivos específicos

Os objetivos específicos do trabalho serão avaliados em 2 capítulos:

(i) Avaliar a estrutura da comunidade de hifomicetos aquáticos intra e interanualmente ao longo de cinco anos, levando em consideração a influência, parâmetros ambientais, climáticos e de qualidade da matéria orgânica.

(ii) Investigar as relações diretas e indiretas das variações temporais e ambientais (climáticos, físico-químicos da água, e qualidade da matéria orgânica) sobre a estrutura da comunidade decompositora e as taxas de decomposição da matéria orgânica, explorando os mecanismos funcionais e as interações em cascata ao longo de cinco anos.

Metodologia Geral

Área de estudo

As atividades de campo foram iniciadas em janeiro de 2015 e encerradas em janeiro de 2020 no córrego Cai Camarão, um riacho de 2ª ordem situado no município de Varzedo - BA (S 12º 57.597' W 039º 26.932') dentro da Serra da Jibóia – BA, Brasil. A Serra está situada na porção sul do recôncavo baiano, que atravessa os municípios de Castro Alves, São Miguel das Matas, Varzedo, Elísio Medrado e Santa Terezinha. Ela possui sentido norte/sul e tem uma extensão de 8.611 hectares, sendo cerca de 5.616 hectares de remanescente florestal contínuo de Mata de Atlântica em diferentes estágios de conservação e regeneração, com paisagens transformadas pela agricultura e pecuária nas regiões mais baixas da Serra (Blengini et al., 2015). Possui um clima subúmido com temperatura média anual de 20ºC e precipitação média anual de 1.200mm. Sua vegetação está dentro do domínio Mata Atlântica e é caracterizada com floresta estacional semidecídua.

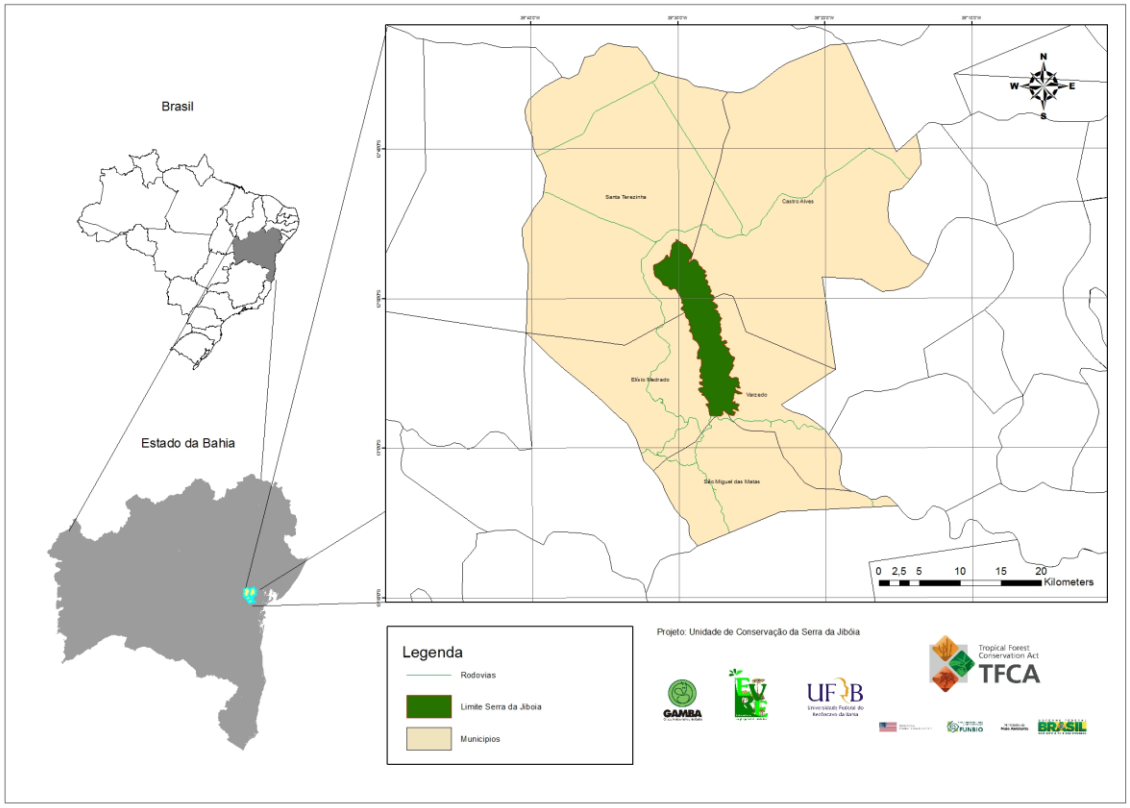


Figura 1. Mapa de Localização da Serra da Jibóia no recôncavo da Bahia-Brasil. (Blengini et al., 2015).

Desenho amostral

Para o presente trabalho o delineamento foi adaptado de Sales et al. (2015). Selecionamos três pontos no riacho Cai Camarão, equidistantes em 40 metros, totalizando 120 metros de riacho amostrado. Em cada ponto de coleta foram amarradas três fileiras de baldes (26 cm de diâmetro), com seis baldes em cada fileira, totalizando 18 baldes por ponto e 54 baldes totais no riacho. Estes baldes foram utilizados para determinar a quantidade de matéria orgânica proveniente das árvores por meio do aporte vertical (AV). O fundo do balde foi perfurado para permitir que a água da chuva escapasse.

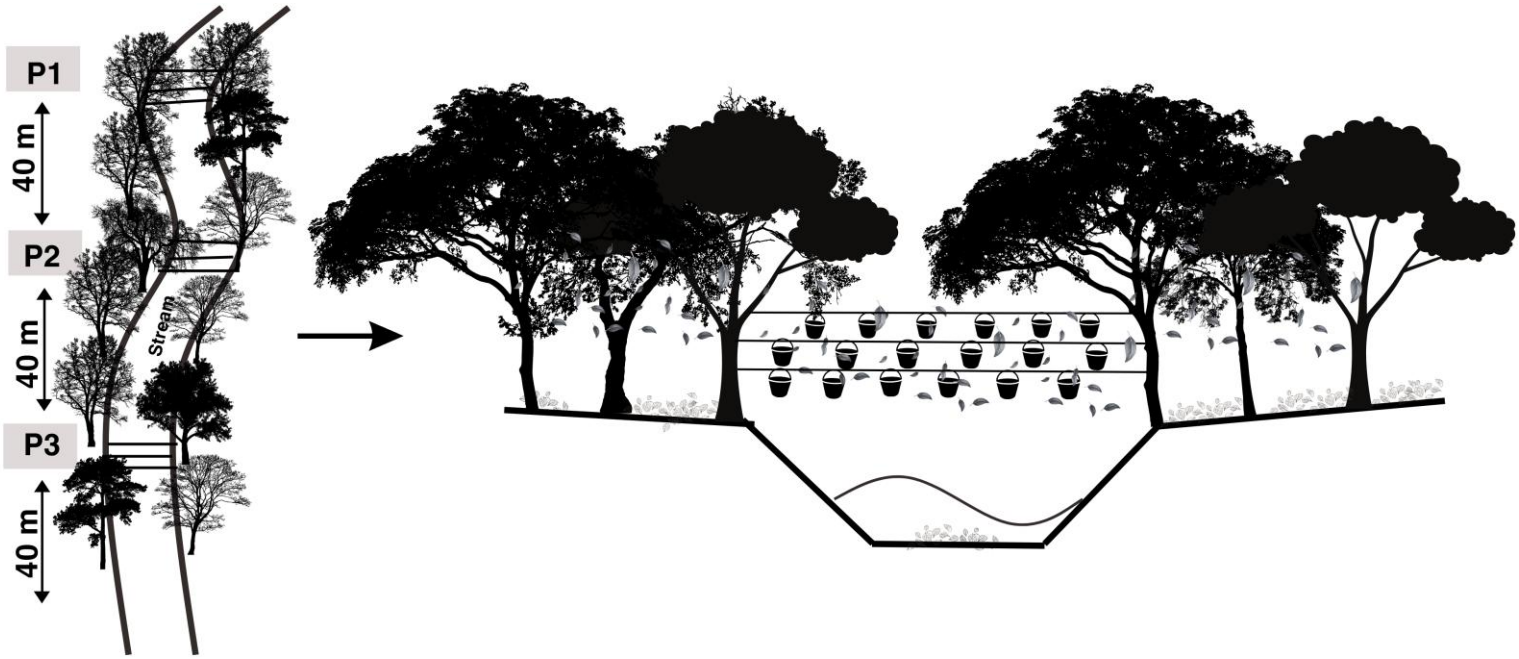


Figura 2. Esquema representando: (1) o riacho amostrado com as divisões de cada ponto de coleta e a distância entre os pontos e (2) a visão de um ponto dos pontos de coleta com as disposições dos baldes no riacho.

A matéria orgânica foi coletada numa periodicidade trimestral. No entanto, um mês antes das coletas, todos os amostradores foram limpos para que se coletasse apenas a MO acumulada nos últimos 30 dias. O material retido nos amostradores foram coletados no campo, armazenados separadamente e transportadas para o laboratório para secagem e realização dos protocolos de quantificação da entrada de matéria orgânica e concentração de fósforo, nitrogênio e carbono foliar. O material coletado no Aporte vertical, foi utilizado para a montagem do experimento da decomposição foliar descrita abaixo, pois representa a entrada direta e o maior aporte de folhas nos riachos (Bambi et al., 2016; de Souza Rezende et al., 2016).

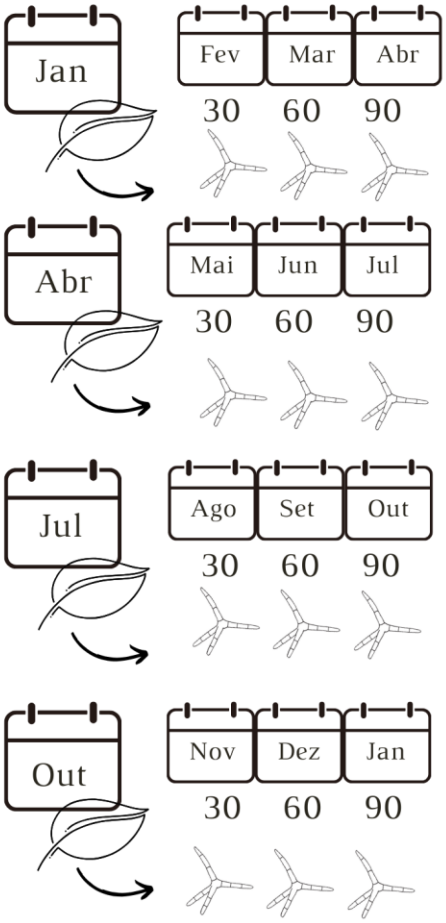


Figura 3. Representação das coletas trimestrais das folhas (janeiro, abril, julho e outubro) e tempos amostrais de retiradas dos experimentos de decomposição dentro de cada trimestre, explicada no tópico Taxa de Decomposição.

Parâmetros físicos e químicos da água

Os parâmetros foram medidos todos os meses durante os 5 anos, as medidas foram feitas três vezes em cada ponto de forma aleatória no espaço para posteriormente obtermos uma média de cada ponto analisado por mês.

Para medir a luminosidade do riacho, foi utilizado um luxímetro digital (minipa – Modelo MLM -100). O pH e a temperatura foram medidos com o auxílio de um pHmetro (digital Misura line – modelo ML1010). O oxigênio dissolvido foi analisado através da coleta da água em recipientes de vidro, adição de 1ml de sulfato manganoso e 1ml de azida para a fixação do OD e liberação de iodo elementar para posterior titulação em laboratório. O fluxo e a profundidade do riacho foram medidos com o auxílio de um fluxômetro (Global Water Flow, modelo FP111).

Macro e micronutrientes da água

Amostras de água foram coletadas com um tubo Falcon de 50 ml em cada ponto do riacho e transportadas para o laboratório em um cooler com gelo para preservar as amostras. As amostras de água foram filtradas em um filtro de acetato de celulose de 0,45 (Sartorius stedim) para remover partículas impuras e sólidos em suspensão e, em seguida, foram resfriadas para preservar as características da água. Utilizamos o cromatógrafo (Metrohm) para determinar a concentração dos ânions inorgânicos (cloreto, nitrito, brometo, nitrato, fosfato e sulfato) e cátions (âmônio, sódio, potássio, cálcio e magnésio), utilizando a técnica de cromatografia. A determinação dos cátions foi realizada na coluna MetroSep C4 250 / 4,0 mm usando um eluente de ácido nítrico 1,7 mM e ácido dipicolínico 0,7 nM com detecção de condutividade não suprimida. A amostra de ânion foi conduzida na coluna MetroSep A Supp 5 250/ 4,0 mm usando um eluente de 3,2 mmol/L de carbonato de sódio e 1 mmol/L de bicarbonato de sódio, com condutividade suprimida (Djam et al., 2019; Mohana Rangan et al., 2021).

Taxa de decomposição

Para a análise da decomposição foliar foram utilizados os materiais retidos no aporte vertical (AV). Os 18 baldes instalados em cada ponto de amostragem foram pesados e selecionados 6 com o maior peso em folhas. As amostras foram e transferidas para seus respectivos sacos de decomposição de malha grossa (10mm de abertura de malha). As bolsas foram submersas no riacho e 2 bolsas foram retiradas com 30, 60 e 90 dias para a avaliação da taxa de decomposição. O experimento foi refeito a cada trimestre durante os cinco anos de estudo. Após a retirada das bolsas de decomposição nos tempos amostrais indicado acima, as amostras foram transferidas em um cooler contendo gelo e transportadas para o laboratório.

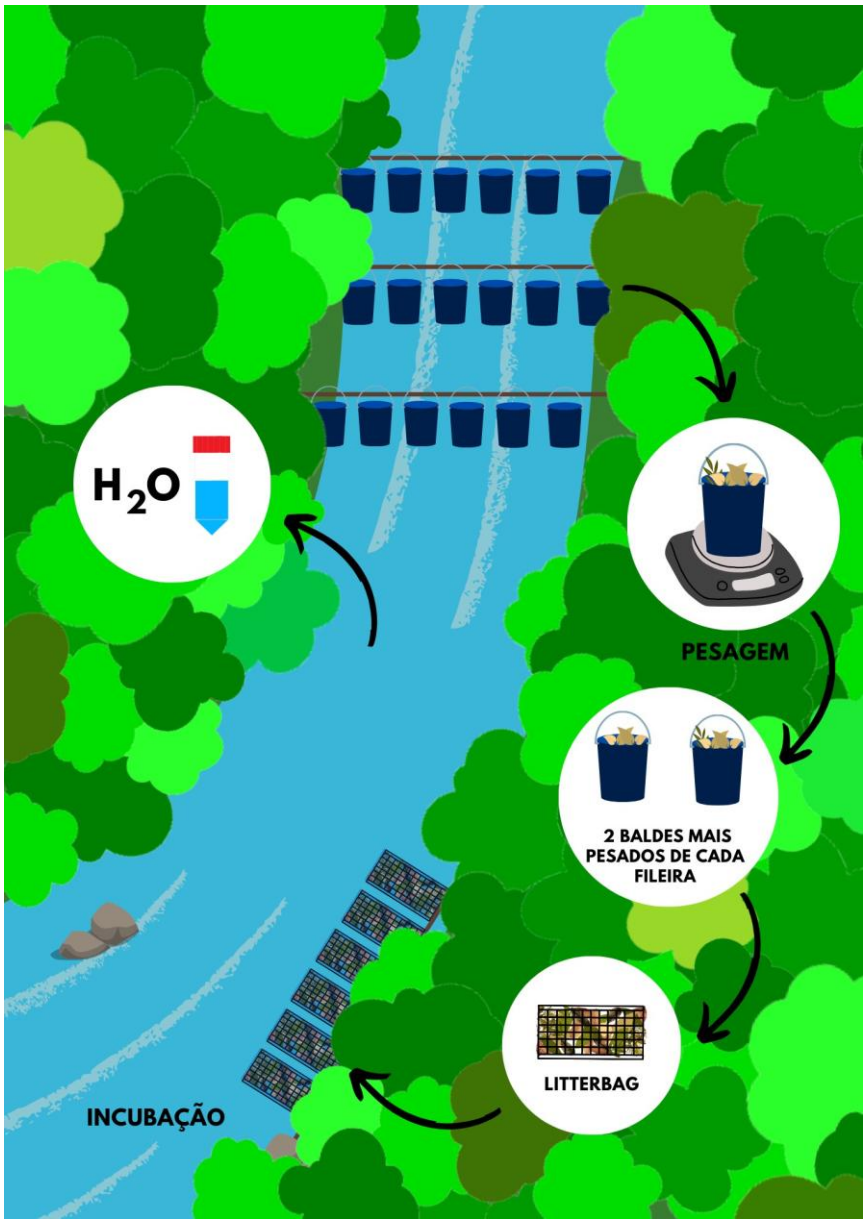


Figura 4. Figura demonstrando os baldes atravessados no riacho, pesagem, seleção e incubação das amostras (o esquema representa apenas um dos três pontos de coleta).

Em laboratório as amostras foram lavadas com água destilada para remover o excesso de sedimento e os invertebrados associados a decomposição. Todo o material foi retido em uma peneira de 12,5µm e posteriormente armazenado em tubo Falcon de 50ml contendo álcool 70% para triagem e identificação dos invertebrados fragmentadores associados as folhas. Após a lavagem das folhas, foram retirados 2 conjuntos de cinco

discos de 10mm de diâmetro (1) para esporulação e identificação dos hifomicetos aquáticos e (2) cálculo de perda de massa.

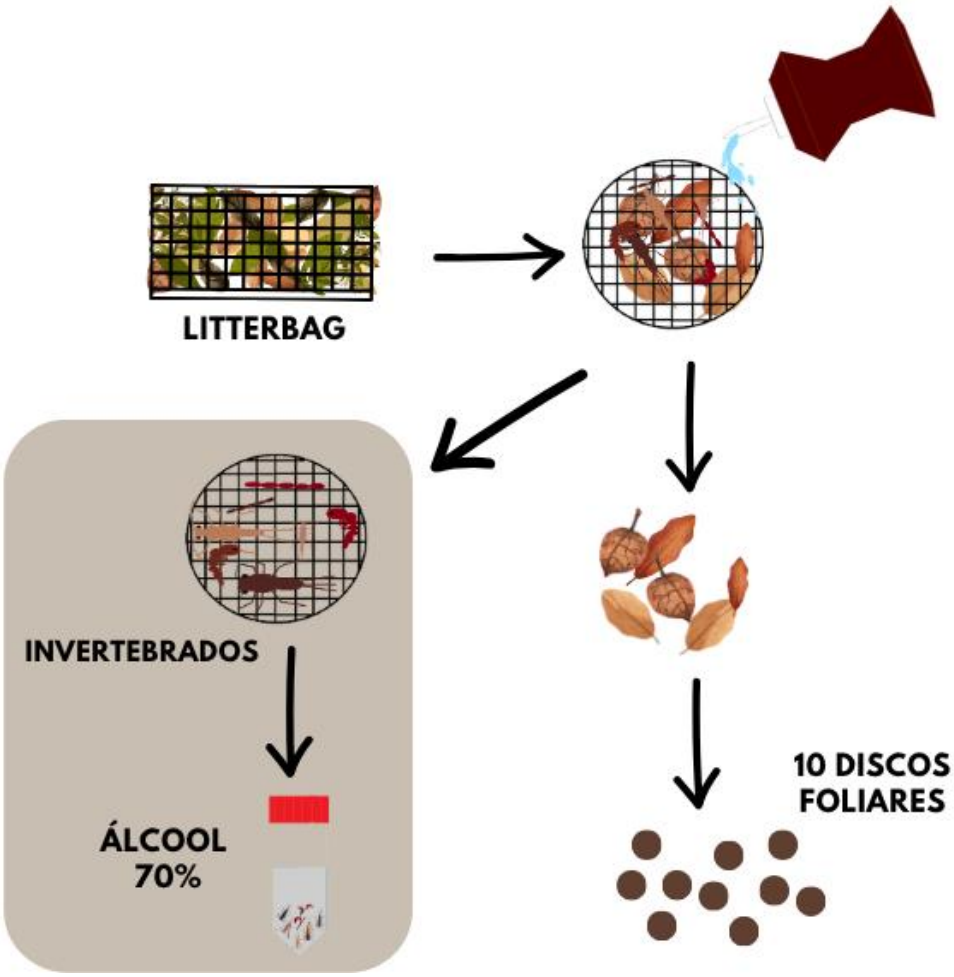


Figura 5. Ilustração do processo de lavagem das folhas, separação dos invertebrados e dos discos foliares para identificação dos invertebrados fragmentadores, hifomicetos aquáticos e perda de massa.

Identificação dos invertebrados

Para a identificação dos invertebrados, o material retido na lavagem das folhas e armazenados em tubos falcon de 50ml foram triados para separar todas as larvas do

sedimento e cada amostra foram identificadas até nível de família utilizando chave taxonômica específicas (Mungai et al., 2010).

Figura 6. Fotos demonstrando a identificação dos invertebrados até nível de família. A esquerda, ilustração do armazenamento dos invertebrados; no centro, identificação dos organismos com auxílio de lupa e chave taxonômica; a direita, um exemplar identificado.

Esporulação e identificação dos hifomicetos aquáticos

Para identificação dos hifomicetos aquáticos, um conjunto de cinco discos de 10mm de diâmetro foram cortados aleatoriamente das amostras. Os discos foram transferidos para um Erlenmeyer de 125ml contendo 30ml de água destilada e agitados a 90 rpm em temperatura de 18°C por 48 horas. Após esse período, a suspensão de conídios foi fixada com formalina (4%) e filtrada em membrana de nitrocelulose de 45µm (Milipore), corada com corante azul de algodão e observada em microscópio óptico (Olympus BX 43). Os esporos retidos nos filtros foram contados e sua morfologia utilizada na identificação das espécies de hifomicetos aquáticos presentes durante o

processo de decomposição utilizando chaves taxonômicas existentes. Os resultados para taxa de esporulação foram expressos em número de conídios/PSLC/dia e produção acumulativa de esporos (Bärlocher et al., 2020).

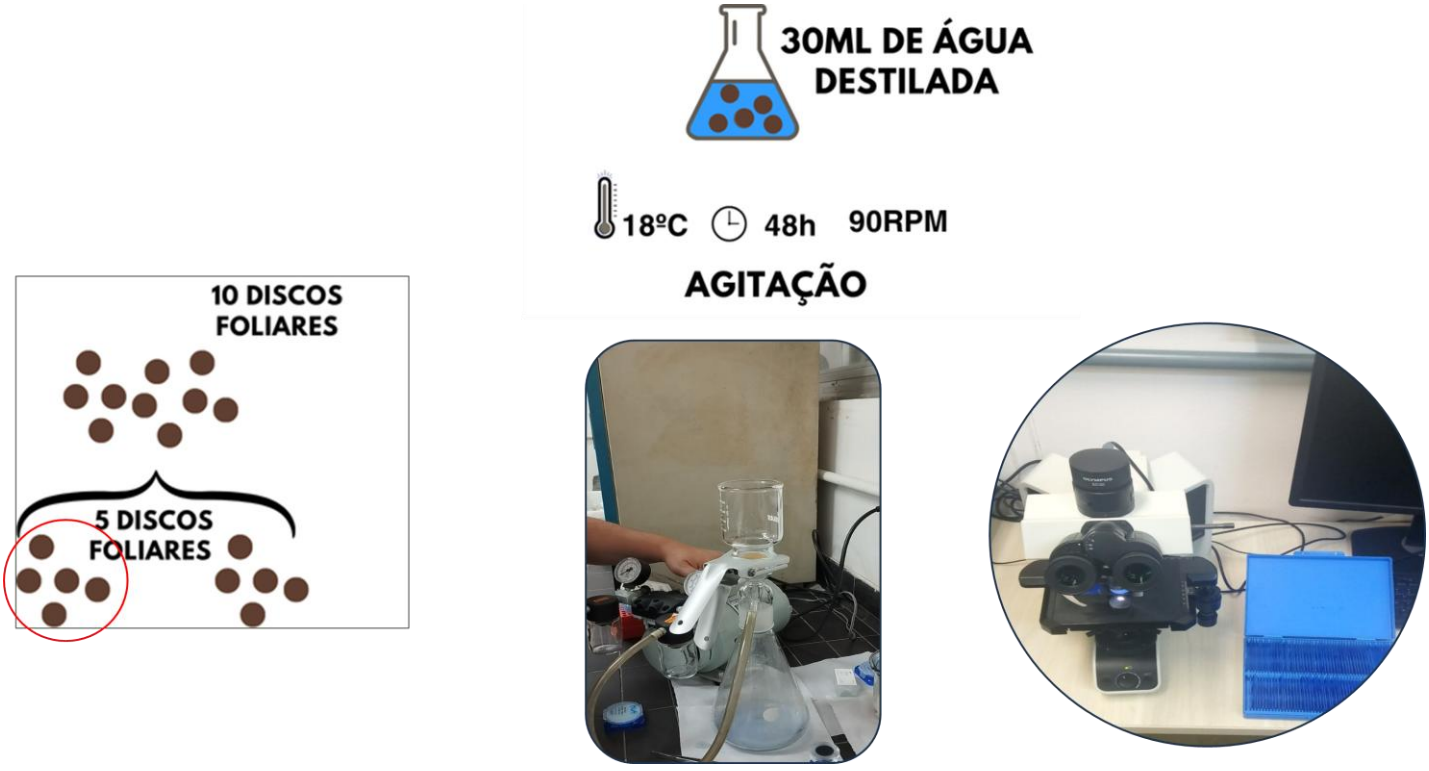


Figura 7. Esquema mostrando a divisão do conjunto de discos, o armazenamento em Erlenmeyer para agitação, a filtragem da alíquota e a identificação dos hifomicetos no microscópio.

Perda de massa

Para determinar a perda de massa, os coeficientes de decomposição foram calculados aplicando os dados de massa foliar ao modelo exponencial negativo Wt = Wo × e^(-kt), onde Wt representa a massa foliar restante no tempo t (em dias), Wo é a massa foliar inicial e k é o coeficiente de decomposição (Graça et al., 2020). Para este cálculo, é essencial comparar a massa seca inicial com a massa seca restante. Como as folhas

foram incubadas em seu estado natural (úmido/seco ao ar), a massa inicial (Wo) foi convertida em um equivalente seco em estufa. Isso foi obtido determinando uma proporção de umidade a partir de subamostras replicadas de detritos não incubados e secos ao ar. Essas subamostras foram pesadas, depois secas em estufa a 60 °C por 72 horas, pesadas novamente, e a massa seca em estufa foi dividida pela massa seca ao ar para gerar um fator de conversão. Este fator foi então aplicado à massa inicial de todas as folhas incubadas. Para obter a massa seca livre de cinzas (MSLC), cinco discos foliares das amostras recuperadas foram secos em estufa a 60 °C por 72 horas e pesados em balança de precisão para determinar seu peso seco. Os discos foram então incinerados em mufla a 550 °C por 4 horas, e as cinzas restantes foram pesadas. A MSLC foi calculada subtraindo o peso das cinzas do peso seco, e esse valor foi extrapolado para a amostra total. Esse valor de MSLC também foi aplicado à massa seca inicial (Wo) para comparações precisas da perda de matéria orgânica.

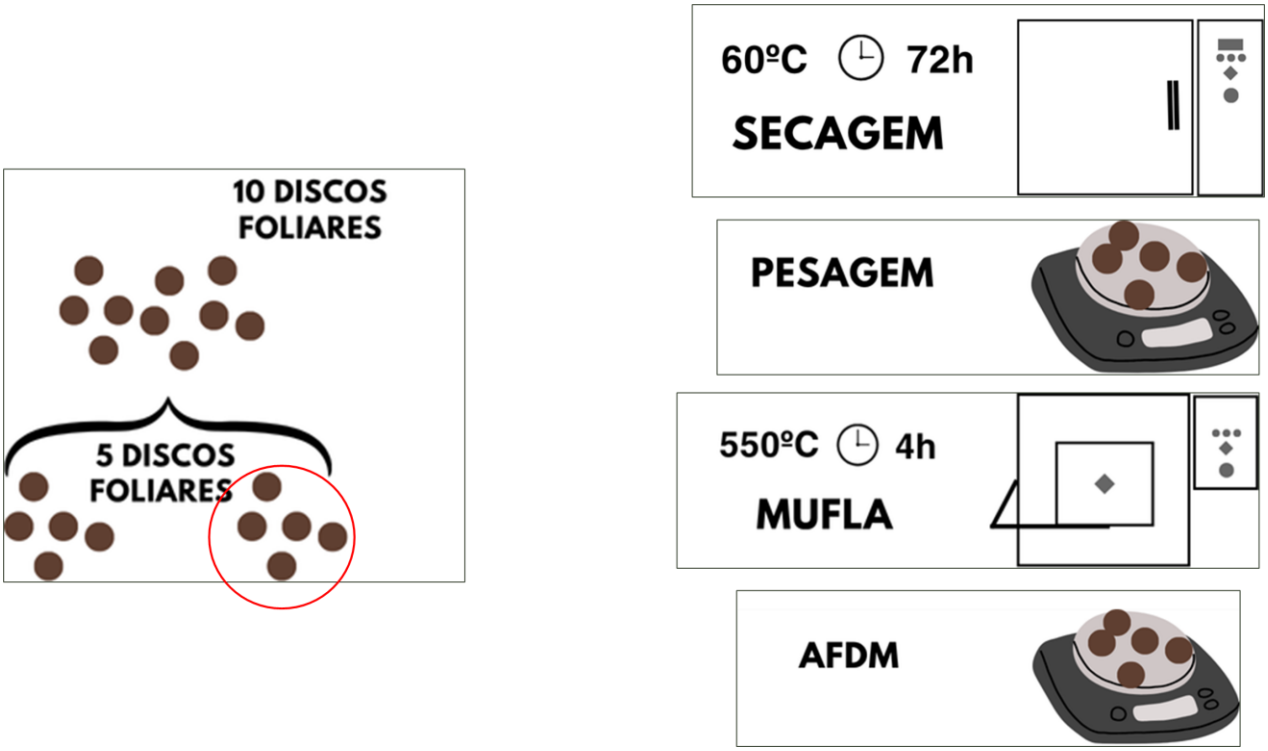


Figura 8. Representação da seleção do segundo conjunto de discos para secagem e pesagem dos discos, incineração e pesagem das cinzas para o cálculo de perda de massa.

Química foliar

Para a análise química foliar, utilizamos a metodologia proposta por Flindt et al., 2020. As amostras de folhas foram secas em estufa de circulação de ar a 60ºC por 72 horas, pesadas e moídas em um moinho de bolas até obter um pó para análise química da concentração de Carbono, Nitrogênio e Fósforo. As amostras moídas foram identificadas e armazenadas em eppendorfs de1.5ml.

Para avaliar o fósforo total, as amostras foram incineradas em mufla a 500ºC por 4 horas para determinar a massa seca e livre de cinzas. 5mg de cinzas foram pesados, e

transferidos para um Erlenmeyer com 25 ml de água deionizada e 1 ml de HCL concentrado. O Erlenmeyer foi aquecido em placa de aquecimento até que a água evaporasse e a solução ficasse amarela e translúcida. A solução foi filtrada com um filtro de fibra de vidro e analisada no espectrofotômetro. 10 ml da solução foi transferida para um tubo de ensaio, adicionados 1 ml do reagente de trabalho e a amostra foi agitada por 15 minutos. Após o tempo, a absorbância foi medida a 882 nm, usando água deionizada como referência e 10 ml de água deionizada tratada com as amostras. No final, a concentração de P foi calculada com base na curva-padrão (Flindt et al., 2020).

Para o Nitrogênio total, foi pesado 0,005g das amostras e transferidas para um tubo de ensaio com 0,2 ml de sulfato de cobre e 1 ml de ácido sulfúrico. O tubo de ensaio foi colocado em um bloco de digestão até a solução se tornar transparente e verde. Após a digestão, foram adicionados 10 ml de água destilada e 10 ml de NaOH, até a amostra flocular. A solução foi transferida para um balão volumétrico de 100 ml com água deionizada e filtrada em um filtro GF/C conectado a uma seringa. 10ml da amostra foi transferida para um frasco de NH4/NH3 para análise espectrofotométrica. Em seguida, os reagentes 0.5-Trione/0.4-Phenol/0.2-Citrate foram adicionados até que a amostra ficasse azul e assim foi medida a absorbância para calcular a concentração de nitrogênio nas amostras (Flindt et al., 2020).

Para analisar o carbono total nas folhas, foi utilizada a método de combustão. As amostras secas e moídas foram colocadas em cadinhos de porcelana e secas novamente em estufa de circulação de ar a 50ºC por 48 horas. Após 48 horas, as amostras foram resfriadas em temperatura ambiente com o auxílio de um dessecador para evitar a absorção de umidade pelas amostras e pesadas novamente para calcular a massa seca. Em seguida, as amostras foram incineradas em uma mufla a uma temperatura de 500°C por pelo menos 3 horas. As cinzas foram novamente resfriadas à temperatura ambiente com

o auxílio de um dessecador e pesadas para calcular a massa seca livre de cinzas das amostras (Flindt et al., 2020).

Dados climáticos

Os dados de Precipitação e Temperatura foram solicitados ao Instituto Nacional de Meteorologia (INMET) da estação de monitoramento do clima da Serra da Jiboia situado no município de Amargosa - BA, região mais próxima da área de estudo e de acordo com Alvares et al. (2013), a fitofisionomia da região estudada corresponde a mesma região da coleta dos dados climáticos coletados.

Referências Bibliográficas

Abelho, M., 2001. From Litterfall to Breakdown in Streams: A Review. Sci. World J. 1, 656–680. https://doi.org/10.1100/tsw.2001.103

Alvim, E.A.C.C., de Oliveira Medeiros, A., Rezende, R.S., Gonçalves, J.F., 2015. Small leaf breakdown in a Savannah headwater stream. Limnologica 51, 131–138. https://doi.org/10.1016/j.limno.2014.10.005

Balibrea, A., Ferreira, V., Balibrea, C., Gonçalves, V., Raposeiro, P.M., 2020. Contribution of macroinvertebrate shredders and aquatic hyphomycetes to litter decomposition in remote insular streams. Hydrobiologia 847, 2337–2355. https://doi.org/10.1007/s10750-020-04259-1

Bambi, P., Rezende, R.D.S., Joa, M., Figueiredo, G., Leite, M., Alvin, E., Gonc, F., 2016. Temporal and Spatial Patterns in Inputs and Stock of Organic Matter in Savannah Streams of Central. Ecosystems. https://doi.org/10.1007/s10021-016-0058-z

Bärlocher, F., 2007. Molecular approaches applied to aquatic hyphomycetes. Fungal Biol. Rev. 21, 19–24. https://doi.org/10.1016/j.fbr.2007.02.003

Bärlocher, F., 1992. Research on Aquatic Hyphomycetes: Historical Background and Overview 1–15. https://doi.org/10.1007/978-3-642-76855-2_1

Barreto, G.G., Hepp, L.U., Rezende, R. de S., Gonçalves Junior, J.F., Moretti, M. da S., Moretto, Y., Loureiro, R.C., Restello, R.M., Medeiros, A.O., 2023. The cooler the better: Increased aquatic hyphomycete diversity in subtropical streams along a neotropical latitudinal gradient. Fungal Ecol. 62. https://doi.org/10.1016/j.funeco.2022.101223

Benson, L.J., Pearson, R.G., 2020. Dynamics of organic material and invertebrates in a tropical headwater stream. Hydrobiologia 847, 121–136. https://doi.org/10.1007/s10750-019-04076-1

Blengini, I.A.D., Cintra, M.A.M. de U., Cunha, R.P.P. da, Caiafa, A.N., 2015. Proposta de unidade de conservação da serra da Jiboia 116.

Boyero, L., Pearson, R.G., Hui, C., Gessner, M.O., Pérez, J., Alexandrou, M.A., Graça, M.A.S., Cardinale, B.J., Albariño, R.J., Arunachalam, M., Barmuta, L.A., Boulton,

A.J., Bruder, A., Callisto, M., Chauvet, E., Death, R.G., Dudgeon, D., Encalada, A.C., Ferreira, V., Figueroa, R., Flecker, A.S., Gonçalves, J.F., Helson, J., Iwata, T., Jinggut, T., Mathooko, J., Mathuriau, C., M'Erimba, C., Moretti, M.S., Pringle, C.M., Ramírez, A., Ratnarajah, L., Rincon, J., Yule, C.M., 2016. Biotic and abiotic variables influencing plant litter breakdown in streams: A global study. Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.1098/rspb.2015.2664

Correa-Araneda, F., Tonin, A.M., Pérez, J., Álvarez, K., López-Rojo, N., Díaz, A., Esse, C., Encina-Montoya, F., Figueroa, R., Cornejo, A., Boyero, L., 2020. Extreme climate events can slow down litter breakdown in streams. Aquat. Sci. 82, 1–7. https://doi.org/10.1007/s00027-020-0701-9

Datry, T., Foulquier, A., Corti, R., Von Schiller, D., Tockner, K., Mendoza-Lera, C., Clément, J.C., Gessner, M.O., Moleón, M., Stubbington, R., Gücker, B., Albarinõ, R., Allen, D.C., Altermatt, F., Arce, M.I., Arnon, S., Banas, D., Banegas-Medina, A., Beller, E., Blanchette, M.L., Blanco-Libreros, J.F., Blessing, J.J., Boëchat, I.G., Boersma, K.S., Bogan, M.T., Bonada, N., Bond, N.R., Brintrup Barriá, K.C., Bruder, A., Burrows, R.M., Cancellario, T., Canhoto, C., Carlson, S.M., Cauvy-Fraunié, S., Cid, N., Danger, M., De Freitas Terra, B., De Girolamo, A.M., De La Barra, E., Del Campo, R., Diaz-Villanueva, V.D., Dyer, F., Elosegi, A., Faye, E., Febria, C., Four, B., Gafny, S., Ghate, S.D., Gómez, R., Gómez-Gener, L., Gracą, M.A.S., Guareschi, S., Hoppeler, F., Hwan, J.L., Jones, J.I., Kubheka, S., Laini, A., Langhans, S.D., Leigh, C., Little, C.J., Lorenz, S., Marshall, J.C., Martín, E., McIntosh, A.R., Meyer, E.I., Miliša, M., Mlambo, M.C., Morais, M., Moya, N., Negus, P.M., Niyogi, D.K., Papatheodoulou, A., Pardo, I., Pařil, P., Pauls, S.U., Pešić, V., Polášek, M., Robinson, C.T., Rodríguez-Lozano, P., Rolls, R.J., Sánchez-Montoya, M.M., Savić, A., Shumilova, O., Sridhar, K.R., Steward, A.L., Storey, R., Taleb, A., Uzan, A., Vander Vorste, R., Waltham, N.J., Woelfle-Erskine, C., Zak, D., Zarfl, C., Zoppini, A., 2018. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. Nat. Geosci. 11, 497–503. https://doi.org/10.1038/s41561-018-0134-4

de Souza Rezende, R., Graça, M.A.S., dos Santos, A.M., Medeiros, A.O., Santos, P.F., Nunes, Y.R., Gonçalves Júnior, J.F., 2016. Organic Matter Dynamics in a Tropical Gallery Forest in a Grassland Landscape. Biotropica 48, 301–310. https://doi.org/10.1111/btp.12308

del Cid, C.C., Caiafa, A.N., de Souza Rezende, R., Sousa, T.S., Guedes, L., Medeiros, A.O., 2023. Leaf litter dominance components respond to temporal variation in a tropical riparian zone. Wetl. Ecol. Manag. 31, 649–660. https://doi.org/10.1007/s11273-023-09939-y

del Cid, C.C., Rezende, R.S., Calor, A.R., Dahora, J.S., de Aragão, L.N., Guedes, M.L., Caiafa, A.N., Medeiros, A.O., 2019. Temporal dynamics of organic matter, hyphomycetes and invertebrate communities in a Brazilian savanna stream. Community Ecol. 20, 301–313. https://doi.org/10.1556/168.2019.20.3.10

Fiuza, P.O., Cantillo-Pérez, T., Gulis, V., Gusmão, L.F.P., 2017. Ingoldian fungi of Brazil: Some new records and a review including a checklist and a key. Phytotaxa 306, 171–200. https://doi.org/10.11646/phytotaxa.306.3.1

Fiuza, P.O., Costa, L.A., Medeiros, A.O., Gulis, V., Gusmão, L.F.P., 2019. Diversity of freshwater hyphomycetes associated with leaf litter of Calophyllum brasiliense in streams of the semiarid region of Brazil. Mycol. Prog. 18, 907–920. https://doi.org/10.1007/s11557-019-01501-6

Fiuza, P.O., de Paiva Ottoni-Boldrini, B.M., Monteiro, J.S., Catena, N.R., Hamada, N., Gusmão, L.F.P., 2015. First records of Ingoldian fungi from the Brazilian Amazon. Rev. Bras. Bot. 38, 615–621. https://doi.org/10.1007/s40415-015-0157-7

Flindt, M.R., Lillebø, A.I., Pérez, J., Ferreira, V., 2020. Total Phosphorus, Nitrogen and Carbon in Leaf Litter. Methods to Study Litter Decompos. 91–105. https://doi.org/10.1007/978-3-030-30515-4_11

Gessner, M.O., Chauvet, E., Dobson, M., 1999. Nordic Society Oikos A Perspective on Leaf Litter Breakdown in Streams. Source: Oikos 85, 377–384.

Gomes, P.P., Ferreira, V., Tonin, A.M., Medeiros, A.O., Júnior, J.F.G., 2018. Combined Effects of Dissolved Nutrients and Oxygen on Plant Litter Decomposition and Associated Fungal Communities. Microb. Ecol. 75, 854–862. https://doi.org/10.1007/s00248-017-1099-3

Gomes, P.P., Medeiros, A.O., Gonçalves Júnior, J.F., 2016. The replacement of native plants by exotic species may affect the colonization and reproduction of aquatic hyphomycetes. Limnologica 59, 124–130. https://doi.org/10.1016/j.limno.2016.05.005

Gossiaux, A., Jabiol, J., Poupin, P., Chauvet, E., Guérold, F., 2019. Seasonal variations overwhelm temperature effects on microbial processes in headwater streams : insights from a temperate thermal spring. Aquat. Sci. 81, 1–11. https://doi.org/10.1007/s00027-019-0627-2

Graça, M.A.S., Ferreira, V., Canhoto, C., Encalada, A.C., Guerrero-Bolaño, F., Wantzen, K.M., Boyero, L., 2015. A conceptual model of litter breakdown in low order streams. Int. Rev. Hydrobiol. https://doi.org/10.1002/iroh.201401757

Graça, M.A.S., Hyde, K., Chauvet, E., 2016. Aquatic hyphomycetes and litter decomposition in tropical - subtropical low order streams. Fungal Ecol. 19, 182–189. https://doi.org/10.1016/j.funeco.2015.08.001

Halvorson, H.M., Hall, D.J., Evans-White, M.A., 2017. Long-term stoichiometry and fates highlight animal egestion as nutrient repackaging.pdf. https://doi.org/doi: 10.1111/1365-2435.12875

Hepp, L.U., Milesi, S. V., Nava, D., Restello, R.M., 2021. Nestedness of stream insects in subtropical region: Importance of inter-annual temporal scale. Iheringia - Ser. Zool. 111, 1–7. https://doi.org/10.1590/1678-4766e2021005

Krauss, G.J., Solé, M., Krauss, G., Schlosser, D., Wesenberg, D., Bärlocher, F., 2011. Fungi in freshwaters: Ecology, physiology and biochemical potential. FEMS Microbiol. Rev. 35, 620–651. https://doi.org/10.1111/j.1574-6976.2011.00266.x

Li, S., Luo, J., Xu, Y.J., Zhang, L., Ye, C., 2022. Hydrological seasonality and nutrient stoichiometry control dissolved organic matter characterization in a headwater stream. Sci. Total Environ. 807, 150843. https://doi.org/10.1016/j.scitotenv.2021.150843

Marks, J.C., 2019. Revisiting the Fates of Dead Leaves That Fall into Streams. Annu. Rev. Ecol. Evol. Syst. 50, 547–568. https://doi.org/10.1146/annurev-ecolsys-110218-024755

Medeiros, A.O., Pascoal, C., Graça, M.A.S., 2009. Diversity and activity of aquatic fungi under low oxygen conditions. Freshw. Biol. 54, 142–149. https://doi.org/10.1111/j.1365-2427.2008.02101.x

Neres-Lima, V., Machado-Silva, F., Baptista, D.F., Oliveira, R.B.S., Andrade, P.M., Oliveira, A.F., Sasada-Sato, C.Y., Silva-Junior, E.F., Feijó-Lima, R., Angelini, R.,

Camargo, P.B., Moulton, T.P., 2017. Allochthonous and autochthonous carbon flows in food webs of tropical forest streams. Freshw. Biol. 62. https://doi.org/10.1111/fwb.12921

Nguyen, H.H., Welti, E.A.R., Haubrock, P.J., Haase, P., 2023. Long-term trends in stream benthic macroinvertebrate communities are driven by chemicals. Environ. Sci. Eur. 35. https://doi.org/10.1186/s12302-023-00820-6

Noacco, V., Duffy, C.J., Wagener, T., Worrall, F., Fasiolo, M., Howden, N.J., 2019. Drivers of interannual and intra-annual variability of dissolved organic carbon.

Pio, J.F.G., Hepp, L.U., Medeiros, A.O., da Silva, F.L., Copatti, C.E., 2022. Intra-annual colonization of Chironomidae on leaf litter in a Brazilian Cerrado stream. Zoologia 39. https://doi.org/10.1590/S1984-4689.V39.E22015

Rabelo, R.S., Sena, G., Gonçalves, J.F., 2024. Interrelationships among litter chemistry, plant species diversity, and litter decomposition in tropical stream environments: a review. Front. Geochemistry 2, 1–8. https://doi.org/10.3389/fgeoc.2024.1346457

Raposeiro, P.M., Ferreira, V., Gea, G., Gonçalves, V., 2018. Contribution of aquatic shredders to leaf litter decomposition in Atlantic island streams depends on shredder density and litter quality. Mar. Freshw. Res. 69, 1432–1439. https://doi.org/10.1071/MF18020

Rezende, R.S., Sales, M.A., Hurbath, F., Roque, N., Gonçalves, J.F., Medeiros, A.O., 2017a. Effect of plant richness on the dynamics of coarse particulate organic matter in a Brazilian Savannah stream. Limnologica 63, 57–64. https://doi.org/10.1016/j.limno.2017.02.002

Rincón, J., Santelloco, R., 2009. Aquatic fungi associated with decomposing ficus sp. leaf litter in a neotropical stream. J. North Am. Benthol. Soc. 28, 416–425. https://doi.org/10.1899/07-084.1

Sales, M.A., Dahora, J.S., Medeiros, A.O., 2014. Influence of Leaf Quality in Microbial Decomposition in a Headwater Stream in the Brazilian Cerrado : a 1-Year Study. https://doi.org/10.1007/s00248-014-0467-5

Sanches, L., Valentini, C.M.A., Pinto Júnior, O.B., Nogueira, J. de S., Vourlitis, G.L., Biudes, M.S., da Silva, C.J., Bambi, P., Lobo, F. de A., 2008. Seasonal and interannual litter dynamics of a tropical semideciduous forest of the southern

Amazon Basin, Brazil. J. Geophys. Res. Biogeosciences 113, 1–9. https://doi.org/10.1029/2007JG000593

Sanpera-Calbet, I., Lecerf, A., Chauvet, E., 2009. Leaf diversity influences in-stream litter decomposition through effects on shredders. Freshw. Biol. 54, 1671–1682. https://doi.org/10.1111/j.1365-2427.2009.02216.x

Seena, S., Pascoal, C., Marvanová, L., Cássio, F., 2010. DNA barcoding of fungi: A case study using ITS sequences for identifying aquatic hyphomycete species. Fungal Divers. 44, 77–87. https://doi.org/10.1007/s13225-010-0056-y

Sena, G., Francisco Gonçalves Júnior, J., Tavares Martins, R., Hamada, N., de Souza Rezende, R., 2020. Leaf litter quality drives the feeding by invertebrate shredders in tropical streams. Ecol. Evol. 10, 8563–8570. https://doi.org/10.1002/ece3.6169

Shearer, C.A., Descals, E., Kohlmeyer, B., Kohlmeyer, J., Marvanová, L., Padgett, D., Porter, D., Raja, H.A., Schmit, J.P., Thorton, H.A., Voglymayr, H., 2007. Fungal biodiversity in aquatic habitats. Biodivers. Conserv. 16, 49–67. https://doi.org/10.1007/s10531-006-9120-z

Stape, L., Sentelhas, P.C., Alvares, C.A., Gonc, L.D.M., 2014. Ko ¨ ppen ' s climate classification map for Brazil 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Tonello, G., Loureiro, R.C., Krause, P., Silva, C., Ongaratto, R.M., Sepp, S., Restello, R.M., Hepp, U., 2014. Colonização de Invertebrados Durante a Decomposição de Diferentes Detritos Vegetais em um Riacho Subtropical. Brazilian J. Biosci. 12, 98–105.

Tonin, A.M., Gonçalves, J.F., Bambi, P., Couceiro, S.R.M., Feitoza, L.A.M., Fontana, L.E., Hamada, N., Hepp, L.U., Lezan-Kowalczuk, V.G., Leite, G.F.M., Lemes-Silva, A.L., Lisboa, L.K., Loureiro, R.C., Martins, R.T., Medeiros, A.O., Morais, P.B., Moretto, Y., Oliveria, P.C.A., Pereira, E.B., Ferreira, L.P., Pérez, J., Petrucio, M.M., Reis, D.F., Rezende, R., Roque, N., Santos, L.E.P., Siegloch, A.E., Tonello, G., Boyero, L., 2017. Plant litter dynamics in the forest-stream interface: Precipitation is a major control across tropical biomes. Sci. Rep. 7, 1–14. https://doi.org/10.1038/s41598-017-10576-8

Tonin, A.M., Lima, L.S., Bambi, P., Figueiredo, M.L., Rezende, R.S., Gonçalves, J.F.,

2021. Litterfall Chemistry Is Modulated by Wet-Dry Seasonality and Leaf Phenology of Dominant Species in the Tropics. Front. For. Glob. Chang. 4, 1–11. https://doi.org/10.3389/ffgc.2021.666116

Wallace, J.B., Webster, J.R., Cuffney, T.F., 1982. Stream detritus dynamics: Regulation by invertebrate consumers. Oecologia 53, 197–200. https://doi.org/10.1007/BF00545663

Webster, J.R., Meyer, J.L., 1997. Stream Organic Matter Budgets: An Introduction. J. North Am. Benthol. Soc. https://doi.org/10.2307/1468223

Capítulo I

Artigo submetido à Freshwater Biology

Fatores temporais e ecológicos de Hifomicetos Aquáticos em um Riacho de Cabeceira Tropical

Temporal and ecological drivers of aquatic hyphomycetes in a tropical headwater stream

Edson Serafim de Almeida Júnior[1*], Renan de Souza Rezende[2], José Francisco Gonçalves-Júnior[3], Keisla Silva Batista de Oliveira[1], Daniela Mariano Lopes da Silva[4], Guilherme Pereira da Silva Sena[3], Jéssica Carneiro de Souza[4], Adriana Oliveira Medeiros [1].

[1] - Environmental Mycology Laboratory, Institute of Biology, Federal University of Bahia, 40170-115, Salvador, BA, Brazil.

[2] - Postgraduate Program in Environmental Sciences, Communitarian University of Chapecó Region – Unochapecó, 89809-000, Chapecó, SC, Brazil.

[3] - Aquaripária/Limnology Laboratory, Department of Ecology, University of Brasilia, 70910-900 Brasília, Brazil.

[4] - State University of Santa Cruz, Department of Biological Science, Rodovia Ilhéus Itabuna km 16, Salobrinho 45662900, Ilhéus, BA, Brazil.

*Corresponding author: edson.serafim@ufba.br

Open Research Statement: The data supporting the findings of this study have not yet been publicly archived. However, they will be permanently deposited in an open-access repository (e.g., Dryad or Zenodo) upon acceptance of the manuscript, in accordance with the journal's Open Research policy. The authors affirm that the data are available for editorial review and can be provided upon request during the peer-review process.

Abstract

Climate and environmental conditions are essential factors influencing aquatic hyphomycetes in headwater streams. This study assessed the temporal dynamics of aquatic hyphomycete communities in a tropical stream in the Atlantic Forest, Brazil. We evaluated how inter- and intra-annual environmental changes influence fungal richness, density, and community composition. The results revealed that water chemistry and leaf litter quality were stronger predictors of community structure than temporal variations. While seasonal environmental fluctuations occurred, the fungal communities showed remarkable temporal resilience and functional stability. Indicator species, such as *Anguillospora filiformis*, *Tricelophorus monosphorus*, and *Amniculicola longissima,* displayed distinct responses to interannual environmental gradients, reinforcing their value as bioindicators. Although some species responded to seasonal changes, no collective community shift was observed throughout the annual cycle. These findings suggest that abiotic factors are the primary drivers of aquatic fungal community dynamics in tropical streams, providing key insights into their ecological roles and the impact of environmental change.

Keywords: Aquatic hyphomycetes; Atlantic Forest; Fungal community structure; Headwater stream; Temporal variation; Tropical stream.

Introduction

Aquatic hyphomycetes play a crucial role in the decomposition of allochthonous organic matter in tropical streams, facilitating nutrient cycling and contributing to energy flow within these ecosystems (Abelho, 2001). In low-order streams, fungal breakdown is responsible for processing allochthonous organic matter and converting plant biomass into assimilable organic fractions, thereby promoting energy transfer in aquatic ecosystems (Graça et al., 2016). Furthermore, the biomass of aquatic hyphomycetes is a significant source of nutrients for aquatic food webs (Gessner and Chauvet, 1993; Seena et al., 2019). The dynamics of these fungal communities vary over time in response to environmental conditions and the quality of organic substrates, directly affecting the decomposition and nutrient availability in these ecosystems (Baldy et al., 2002; Ferreira et al., 2020).

The structure of aquatic hyphomycete communities in tropical streams is strongly influenced by abiotic and biotic factors, including riparian vegetation composition (Ferreira et al., 2016; Jabiol et al., 2013), quality of allochthonous organic matter (Boyero et al., 2016; Graça et al., 2016), and stream characteristics, such as water turbulence (Graça et al., 2015). The composition and diversity of riparian vegetation can regulate the quality and quantity of organic matter input (Tonin et al., 2021, 2017), thereby modulating the structure of the aquatic fungal communities. Additionally, the chemical composition of leaves is a determining factor in decomposition, as leaves with higher nitrogen and phosphorus content and lower concentrations of recalcitrant compounds, such as lignin, promote greater microbial activity and hyphomycete sporulation, influencing colonization and decomposition efficiency (Gonçalves et al., 2014; He et al., 2019; Zhang et al., 2019). Moreover, dissolved oxygen availability (Medeiros et al., 2009), pH (Barreto et al., 2023), and water temperature (Chauvet and Suberkropp, 1998) affect the stability of these communities and their ability to colonize submerged organic matter.

In tropical rainforest streams, the input of organic matter predominantly occurs during the rainy season, when increased water flow transports larger amounts of leaf litter and alters the availability of dissolved nutrients and physicochemical conditions of the water (Tonin et al., 2017). During the rainy period, the combination of increased substrate input and favorable environmental conditions stimulates aquatic hyphomycete sporulation and growth (del Cid et al., 2019; Sales et al., 2015). However, intra-annual variations in organic matter composition (del Cid et al., 2023; Tonin et al., 2021) and precipitation patterns can modify nutrient availability and differentially affect hyphomycete community structure over time (del Cid et al., 2019; Rezende et al., 2017c). Despite advances in our understanding of the dynamics of aquatic hyphomycetes, no study has analyzed the influence of intra- and interannual variations on these fungi over a satisfactory temporal scale. Therefore, understanding the temporal patterns and mechanisms that regulate the composition and functionality of fungal communities in tropical streams is essential for elucidating the decomposition dynamics in aquatic ecosystems.

Although community structure is expected to vary seasonally, it remains uncertain whether changes occur more intensely within each year or between consecutive years and what are the main environmental factors driving this variation. Considering the interaction between seasonality, organic matter quality, and dissolved nutrient availability, analyzing the structure of hyphomycete communities over time can provide valuable insights into their resilience and functionality in tropical streams. Therefore, in this study, we investigated changes in the structure of aquatic hyphomycete communities in a headwater stream of the Atlantic Forest over five years, considering the influence of intra- and interannual variations, dissolved nutrients in the water, and leaf chemistry. We hypothesized that the structure of hyphomycete communities would exhibit changes in response to intra-annual variations rather than inter-annual variations, as environmental conditions and organic substrate availability fluctuate more intensely within each annual cycle. We predicted that fluctuations in leaf chemical

quality, precipitation patterns, and dissolved nutrient levels would drive changes in the composition and functionality of fungal communities over time. By understanding these dynamics, we aimed to improve the ecological concept of the influence of temporal conditions on organic matter decomposition in tropical headwater streams.

Materials and Methods

Study area

The study was conducted in Serra da Jibóia, Bahia, Brazil, a mountainous region encompassing approximately 23,000 ha within the Atlantic Forest domain. Within this area, an expanse of 8,611 ha includes diverse forest fragments at various conservation stages, as reported by Blengini et al. (2015). Riparian vegetation is classified as secondary forest in the mid-successional stage. The local soils primarily consist of Haplic Cambisol and Litholic Neosol. The arboreal canopy ranges from open to closed formations and predominantly comprises small-diameter tree species. Although the average canopy height is approximately 9.4 meters, some individuals can reach up to 13 m (Blengini et al., 2015). This study was conducted over five years (2015–2020) in a second-order stream located in Serra da Jibóia (Varzedo, BA; S 12º 57.597’ W 039º 26.932’).

Experimental design and procedures

The experimental design was adapted from Sales et al. (2015) and consisted of three sampling sites along the stream spaced 40 m apart for a total sampling length of 120 m (Figure 1). At each site, 18 leaf

collection buckets were installed transversely across the streambed, in three rows of six buckets each. The buckets were perforated to prevent rainwater accumulation and were positioned to collect leaf litter entering the stream from the riparian zone. The collected leaf litter represented the organic input accumulated over the last 30 days. Leaf litter collection was performed quarterly (January, April, July, and October) for five consecutive years. At each collection event, two buckets with the highest leaf masses from each row were selected, resulting in six samples per sampling site. The collected leaf material was placed in coarse-mesh litter bags (10 mm mesh size) for in-stream incubation. At each sampling point, two bags were retrieved after 30, 60, and 90 d of incubation, totaling four incubation periods per year. After retrieval, litter bags were transported to the laboratory in sealed plastic bags inside a cooler with ice to ensure sample integrity. The samples were used to induce sporulation of aquatic hyphomycetes and identify fungal species in the stream. The remaining leaf litter collected from the buckets was stored in plastic bags for further chemical analysis of leaf composition.

The identification of aquatic hyphomycetes

In the laboratory, leaves were rinsed with distilled water to remove excess sediment. Five leaf discs were randomly selected for each sample. These discs were transferred into 125 ml Erlenmeyer flasks containing 30 ml of distilled water, placed on an orbital shaker at 90 rpm, and incubated for 48 h at 18°C. The resulting spore suspensions were fixed with 4% formalin, filtered through a 5 μm pore-size Millipore filter (Billerica, MA, USA), and stained with 0.05% cotton blue in 60% lactic acid (Figure 1.D). The filters were examined under a compound microscope (Olympus BX 43) at 400x magnification to estimate the number of retained conidia and identify the species present (Bärlocher et al., 2020). The

123 species composition of the aquatic hyphomycete community was determined based on spore
124 morphology using established taxonomic keys (e.g. Fiuza et al., 2015, 2017).

125

126 *Leaf litter chemistry*

127 For the leaf litter chemical analysis, we followed the methodology proposed by Flindt et al. (2020).
128 Leaves were collected from vertical inputs along the stream. The mixed leaf samples were dried in a
129 forced-air oven at 60°C for 72 h, weighed, and ground in a ball mill to obtain fine powder. This powder
130 was then used for the chemical analyses of carbon (C), nitrogen (N), and phosphorus (P) concentrations.
131 For phosphorus (P), the samples were incinerated in a muffle furnace for 4 h. Subsequently, 5 mg of ash
132 was dissolved in deionized water with HCl, filtered, and analyzed using a spectrophotometer at 882 nm.
133 P concentration was determined using a standard curve. For nitrogen (N), 0.005 g of the sample was
134 digested with copper sulfate and sulfuric acid and then neutralized with NaOH. The resulting solution
135 was filtered and analyzed spectrophotometrically after adding reagents that produced a blue coloration.
136 For carbon (C), the combustion method was employed: dried and ground samples were ignited in a
137 muffle furnace at 500°C, allowing the determination of the ash-free dry mass.

138

139 *Water physical-chemical*

140 Water samples were collected monthly at each headwater stream site using 50 ml Falcon tubes and
141 transported to the laboratory in a cooler containing ice to preserve sample integrity. The samples were
142 filtered through 0.45 μm cellulose acetate filters (Sartorius Stedim, Germany) to remove impurities and
143 suspended solids and then kept chilled to maintain their original properties. Inorganic anions (chloride,

144 nitrite, bromide, nitrate, phosphate, and sulfate) were determined using Metrohm ion chromatography.
145 Cations (ammonium, sodium, potassium, calcium, and magnesium) were also analyzed by
146 chromatography. Cation determination was performed on a MetroSep C4 250/4.0 mm column with an
147 eluent of 1.7 mM nitric acid and 0.7 mM dipicolinic acid and non-suppressed conductivity detection.
148 Anion determination employed a MetroSep A Supp 5 250/4.0 mm column and an eluent composed of
149 3.2 mmol/L sodium carbonate and 1 mmol/L sodium bicarbonate, with suppressed conductivity
150 detection (Djam et al., 2019; Mohana Rangan et al., 2021).

151

152 *Climatic Parameters*

153 Precipitation and temperature data were obtained from the National Institute of Meteorology (INMET)
154 at the Serra da Jibóia Weather Monitoring Station, located in the municipality of Amargosa (13°00'36.0"
155 S 39°37'12.0" W), Bahia, which is the nearest station to the study site. The phytophysiognomy of the
156 studied region corresponds to the same area where climatic data were collected (Stape et al., 2014).

157

158 *Data analysis*

159 Analysis of Similarity (ANOSIM) was used to evaluate differences in the composition of the aquatic
160 hyphomycete communities across different years. This approach is particularly effective for exploring
161 how species distribution patterns respond to environmental variables over time. Prior to performing
162 ANOSIM, the data were standardized using Hellinger transformation, which is well-suited for
163 abundance data. The ANOSIM function from the vegan package was used with Bray-Curtis
164 dissimilarity, and the test was run with 999 permutations to determine the significance of any observed

differences (Legendre and Legendre, 1998). These analyses were performed using the R platform version 4.3.1, which offers a detailed understanding of how environmental variables influence aquatic hyphomycete community composition over temporal scales.

To identify the most influential environmental variables affecting the density and species richness of aquatic hyphomycetes, we employed the boosted regression Trees (BRT) method. This technique integrates decision-tree algorithms with machine learning to generate robust predictive models. Analyses were conducted using the "gbm" function in R with the following parameters: 5,000 trees, interaction depth of 3, learning rate (shrinkage) of 0.01, and minimum of 10 observations per terminal node. Five-fold cross-validation was applied to prevent overfitting and to determine the optimal number of trees. The BRT output provided the relative importance of each predictor variable, enabling the identification of environmental factors that exerted the greatest influence on density and richness over time.

To examine the responses of individual species to environmental variables and identify potential thresholds across environmental gradients, we conducted Threshold Indicator Taxa Analysis (TITAN). This approach assesses how sporulation rates respond to environmental changes on two temporal scales: interannual (across consecutive years) and intra-annual (seasons or months within a single year). TITAN was implemented using the "titan" function in R, employing 1,000 bootstrap permutations to determine its significance. The analysis provided i) indicator species that respond positively or negatively to shifts in environmental gradients (increasers and degreasers); ii) environmental thresholds (e.g., pH, temperature, precipitation) at which abrupt changes in community structure occur; iii) species distribution plots along gradients, allowing the visualization of specific taxa responses; and iv) summary tables detailing the primary response indicators. This comprehensive output helps pinpoint the environmental variables that drive notable community transitions and highlights the species susceptible to these changes.

Generalized Additive Mixed Models (GAMMs) were employed to examine interannual and intra-annual variations in the richness and density of aquatic hyphomycetes. These models are well-suited for capturing nonlinear temporal patterns and their relationships with environmental variables. GAMMs were fitted using the "gamm" function in R, with richness and density as the response variables. Two explanatory variables were included: i) Adjusted Year (Adjusted_Year), modeled with a restricted cubic spline (cr) to represent interannual variation, and ii) month (month), modeled with a cyclic spline (cc) to capture seasonal (intra-annual) variation. The models were fitted using a Gaussian distribution with an identity link function, and smoothing parameters were automatically optimized. The statistical significance of the splines was assessed using p-values associated with the effective degrees of freedom (edf), indicating the complexity and strength of the temporal patterns modeled by the GAMMs.

Results

Stream Features Overview

The studied streams exhibited notable variations in environmental conditions over the observed years (Table 1). Precipitation fluctuated considerably, with the most significant accumulation recorded in 2015 (1,033 mm) and the lowest in 2018 (625 mm). The initial acidic pH value in 2015 (5.9) gradually increased to 7.4 2019, indicating a trend toward higher alkalinity. Dissolved oxygen (DO) concentrations declined steadily from 9.10 mg/L in 2015 to a minimum of 7.23 mg/L in 2018, followed by a slight recovery in 2019 (7.36 mg/L). Temperatures remained relatively stable, showing only minor variations between 2015 (23.3°C) and 2018 (22.7°C), and rising once again in 2019 (23.5°C).

The water chemistry of the stream has undergone notable changes in ion concentration over the years (Table 2). Sodium (Na) levels ranged from 3.93 mg/L in 2018 to 5.82 mg/L in 2015, with a slight increase to 5.06 mg/L by 2019. Ammonium (NH4) increased gradually, reaching 0.09 mg/L in 2019. Potassium (K) remained relatively stable, fluctuating between 0.98 mg/L (2017) and 1.15 mg/L (2016). Calcium (Ca) concentrations displayed a downward trend, declining from 0.67 mg/L in 2015 to just 0.02 mg/L by 2019. The magnesium (Mg) concentrations varied, peaking at 2.15 mg/L in 2016, and then dropping to 1.89 mg/L in 2019. Fluoride (F) remained relatively consistent, at 0.04 mg/L to 0.07 mg/L, while chloride (Cl) peaked in 2015 (2.36 mg/L) before declining significantly in the following years. Nitrite (NO_2) values ranged from 0.008 mg/L (2015) to 0.033 mg/L (2017), and bromide (Br) increased from 0.005 mg/L (2015) to 0.037 mg/L (2019). The nitrate (NO_3) also increased over time, peaking at 0.28 mg/L in 2019. The phosphate (PO_4) and sulfate (SO_4) concentrations tended to decrease throughout the study period. Data for copper (Cu), zinc (Zn), and iron (Fe) were available for 2016. Zinc levels increased steadily, reaching their highest value in 2019 (0.21 mg/L), whereas iron concentrations remained relatively stable across the years.

Regarding leaf litter chemistry (Table 3), carbon (C) concentrations exhibited notable fluctuations over the years and sampling quarters, ranging from 63.8% in October 2019 to 73.1% in April 2015. January values showed relative stability, fluctuating between 66.7% (2016) and 69.8% (2019). July 2017 had one of the highest values (71.6%), suggesting a potential peak in organic matter during this period. The nitrogen (N) concentrations varied considerably. The highest value occurred in October 2016 (0.34 mg/L), whereas the lowest was recorded in April 2015 (0.139 mg/L). Nitrogen levels increased notably in January 2017 (0.315 mg/L) and remained elevated throughout the year. However, in 2019, a decrease of 0.179 mg/L was observed in January. Phosphorus (P) concentrations demonstrated an upward trend over time. The lowest value was observed in January 2015 (0.00637 mg/L), whereas the highest was

recorded in January 2017 (0.0174 mg/L). In 2019, phosphorus levels continued to increase, reaching significant values in January (0.013 mg/L) and October (0.0136 mg/L), suggesting gradual phosphorus accumulation in the system over the years.

Aquatic Hyphomycetes Community Dynamics

Over the five-year study period, 23 species of aquatic hyphomycetes were identified (Figure 2). Only seven species were found every year: *Anguilospora filiformis*, *Anguillospora furtiva*, *Amniculicola longissima*, *Flagellospora curvula*, *Lunulospora curvula*, *Tricelophorus acuminatus,* and *Tricelophorus monosphorus.*

Significant differences were found in the aquatic hyphomycete community composition across years (ANOSIM, Figure 3). Although temporal variations existed, the community overlap between years was not extremely pronounced (R-value = 0.129). The significance value ($p = 0.001$) confirmed that these differences were not random. The dissimilarity ranks (Table 4) revealed that the variation within a single year was less pronounced than that observed in different years.

We identified the environmental variables influencing aquatic hyphomycete species richness and conidia density (boosted regression tree-BRT; Table 5; Figures 4 and 5). The most important variables for species richness were water chemistry parameters, such as bromide (Br, 7.71%), copper (Cu, 7.46%), dissolved oxygen (DO, 6.89%), sulfate (SO_4, 6.41%), potassium (K, 4.98%), and leaf litter chemistry: phosphorus (P, 5.74%). Regarding conidial density, the main predictors were water chemistry parameters, such as ammonium (NH_4, 10.37%), fluoride (F, 6.90%), and chloride (Cl, 5.71%), along

with climate variables, such as temperature (5.55%) and monthly precipitation (5.18%). Nitrogen (N, 5.41%) from the leaf litter also contributed significantly.

The Threshold Indicator Taxa Analysis (TITAN) revealed distinct interannual responses of aquatic hyphomycetes to environmental gradients, identifying key taxa (*A. filiformis, T. monosphorus,* and *A. longissima*) that indicate ecosystem changes (Table 6; Figure 6). Among the analyzed taxa, *A. filiformis* had the highest indicator value (IndVal = 88.63, p = 0.004), indicating a significant environmental change point (ienv.cp) in 2015. This species demonstrated high purity (0.992) and reliability (0.989), confirming its strong association with the environmental conditions during that year. Similarly, *T. monosphorus* displayed a notable threshold between 2017 and 2018 (IndVal = 66.58, p = 0.004), with high purity (0.991) and reliability (0.972), making it a reliable indicator of environmental shifts during that period. The TITAN analysis classified species into two groups: “increasers” (group 2), which responded positively to environmental gradients, and “decreasers” (group 1), which declined under similar conditions. *A. longissima* showed a pronounced increase (IndVal = 59.39, p = 0.004) between 2015 and 2018. The identified environmental change points (ienv.cp) and their associated confidence intervals provide valuable insights into the temporal dynamics of species responses. For instance, *A. filiformis* showed a sharp change point in 2015, with narrow confidence intervals, indicating a strong and consistent response to specific environmental conditions. Similarly, *A. longissima* and *T. monosphorus* displayed consistent responses across multiple years, supported by their high Z-scores (3.69 and 4.18, respectively) and strong reliability values.

TITAN analyses were also conducted to assess the intra-annual responses of the aquatic hyphomycete species to environmental gradients over the annual cycle (Table 7). Among the analyzed species, *A. filiformis* emerged as a robust indicator, with an environmental change point (ienv.cp) of 7.5, corresponding to the transition from the dry season to the rainy season (July-August). This species

exhibited high indicator value (IndVal = 83.55; p = 0.032), high purity (0.947), and moderate reliability (0.584). Similarly, *F. curvula* and *L. curvula* stood out as significant intra-annual indicators. Both species exhibited a change point (ienv.cp) at 7.5, with high indicator values (IndVal = 86.21 and 92.65, respectively) and significant z-scores (3.28 and 3.35, respectively). Purity and reliability values for *F. curvula* (0.950 and 0.737, respectively) and *L. curvula* (0.959 and 0.686, respectively). In contrast, *A. furtiva*, *C. curvata*, and *T. acuminatus* exhibited less consistent responses to environmental gradients. The change points (ienv.cp) were identified at 5.5 °and 6.5°, corresponding to the middle of the dry season (June – July). However, their indicator values were low (IndVal = 17.35, 33.22, and 45.24, respectively) and not statistically significant (p > 0.1). Furthermore, the low reliability scores of *A. furtiva* (0.121) and *C. curvata* (0.08) suggest that these species are unreliable indicators of intra-annual environmental variation.

Temporal variation on richness and density of Aquatic Hyphomycetes

The Generalized Additive Mixed Model (GAMM) was applied to assess temporal variation in the species richness of aquatic hyphomycetes across interannual and intra-annual scales (Figure 7). The intercept was significant (estimate = 4.6833; p < 0.001), representing baseline species richness. The smooth effect of the adjusted year indicated a linear response with an effective degree of freedom (edf) of 1.0; however, it was not statistically significant (F = 0.13; p = 0.720), suggesting no detectable interannual trends in richness. Similarly, the intra-annual variation modeled with a cyclic spline for months (months) revealed no significant seasonal patterns, with an edf close to zero (8.042e-09) and non-significant results (F = 0.00; p = 0.607). The model explained a negligible portion of the variance

(adjusted R^2 = -0.015), indicating that temporal factors did not significantly influence the observed fluctuations in species richness.

The Generalized Additive Mixed Model (GAMM) was also applied to examine the temporal variation in the density of aquatic hyphomycete conidia (Density.mL^{-1}) across the interannual and intra-annual scales (Figure 7). The parametric coefficient for the intercept was significant (estimate = 471.17; $p < 0.001$) and represented average initial conidial density. The smooth effect of adjusted_year showed a linear response with an effective degree of freedom (edf) of 1.0, but it was not statistically significant ($F = 3.066$; $p = 0.0852$), indicating weak interannual trends in conidial density. Similarly, intra-annual variation, modeled with a cyclic spline for months (*month*), showed no seasonal patterns, with an edf close to zero (6.761e-07) and non-significant results ($F = 0.000$; $p = 0.4235$). The model explained a limited proportion of the variance (adjusted $R^2 = 0.033$), suggesting that temporal variables alone were insufficient to account for the observed variability in conidial density.

Discussion

Temporal variation and environmental influence on Community structure

The findings of this study indicate that interannual variation has a more significant influence on the structure of aquatic hyphomycete communities than intra-annual variation. This outcome contrasts with the initial hypothesis, which anticipated a stronger effect of intra-annual dynamics on the community composition. Our results revealed no significant trends across months and failed to detect community-level inflection points associated with intra-annual transitions, indicating a high degree of seasonal stability within the community. In contrast, community structure responded significantly to interannual

environmental gradients, particularly variations in dissolved oxygen (DO), ammonium (NH_4^+), and bromide (Br^-). These variables were identified as the main drivers of changes in hyphomycete richness and density throughout the five-year study period.

DO has emerged as one of the most influential predictors of species richness and is known to influence the structure of aquatic hyphomycetes (Medeiros et al., 2009). Fluctuations in DO reflect broader environmental changes in tropical freshwater ecosystems driven by anthropogenic activities (Small et al. 2012, Umoren, et al. 2024). Rising temperatures associated with climate change may further deplete DO levels, thereby reducing the resilience of tropical streams to extreme events or pollutant discharges (Abdul-Aziz, 2023; Mendivil-García et al., 2022). This scenario is particularly critical in low-flow systems where the balance between deoxygenation and reoxygenation is increasingly disrupted by thermal stress (Graeber et al., 2013; Jane et al., 2021).

High NH_4^+ concentrations negatively affected the hyphomycete community, reducing the density of these microorganisms, likely due to a combination of direct toxic effects and competitive interactions with other microbial communities. Under elevated pH conditions, NH_4^+ is partially converted into un-ionized ammonia (NH_3), which exerts toxic effects on aquatic fungi by inducing oxidative stress and inhibiting sporulation (Leoni et al., 2018). Furthermore, ammonium-enriched environments favor the proliferation of heterotrophic bacteria, which compete with hyphomycetes for limited resources, such as carbon and nutrients, thereby negatively affecting fungal density (Rodríguez-Cardona et al., 2021).

Variations in bromide (Br) concentration were negatively correlated with hyphomycete richness, suggesting that bromide acts as an additional selective pressure, limiting the occurrence of sensitive species and favoring those more tolerant to this ion. This effect may result from atmospheric deposition or leaching of soil and sediment materials, especially during periods of high precipitation or in areas

prone to agricultural runoff (Röhl et al., 2017). Although directly understudied, bromide chemically resembles chloride, which negatively affects aquatic fungi via osmotic imbalance or enzymatic inhibition (Röhl et al., 2017). Therefore, Ammonium (NH_4^+) and bromide (Br) emerged as key determinants of hyphomycete density and richness over time, suggesting that these factors play crucial roles in shaping community structure.

Variations in phosphorus and nitrogen concentrations were associated with changes in species richness and conidial density over time. Our results indicated that phosphorus was one of the most influential variables in explaining species richness, while nitrogen had a strong effect on conidial density over time. These patterns suggest that phosphorus may contribute to greater fungal diversity by enabling niche differentiation and coexistence among species (Jabiol et al., 2018), while nitrogen availability stimulates sporulation and metabolic activity of dominant taxa, increasing conidial biomass productivity without necessarily altering species richness (Gulis et al., 2017; Jabiol et al., 2018). Taken together, these findings suggest that phosphorus primarily regulates functional diversity, whereas nitrogen influences community productivity.

This result may also be attributed to the heterogeneity of detritus incubated during the different sampling periods. Since the material was collected from litter traps, differences in chemical composition or the degree of prior fungal colonization might have influenced subsequent fungal dynamics, limiting broader correlations. It is known that seasonal shifts in leaf phenology and precipitation patterns are known to affect litter chemistry and alter leaf litter input and nutrient concentrations in tropical streams (Tonin et al., 2017; Tonin et al., 2021). In addition, fluctuations in litter dominance and quality over time can modulate the structure of decomposer communities and the trajectory of fungal colonization (del Cid et al., 2023). These factors are particularly relevant in systems where detritus input is variable and the initial quality of leaf material significantly influences fungal colonization and decomposition dynamics

(Sales et al., 2015). Nevertheless, these findings highlight the potential regulatory role of leaf nutrients in fungal activity and emphasize the importance of controlling detritus variability in future research.

Indicator species and ecological thresholds

Species such as *Anguillospora filiformis*, *Tricelophorus monosphorus*, and *Amniculicola longissima* have emerged as robust bioindicators of interannual environmental changes because of their sensitivity to factors such as NH_4^+ and DO (Breda et al., 2021a; Fiuza et al., 2019; Medeiros et al., 2009). Among the diverse taxa found in tropical and subtropical streams, these species are frequently reported as dominant and ecologically relevant components (Breda et al., 2021; Barreto et al., 2023), which not only contribute significantly to organic matter breakdown, but also act as sensitive bioindicators, responding to environmental fluctuations in parameters such as dissolved oxygen, pH, and nutrient concentrations (Medeiros et al., 2009; Fiuza et al., 2019). These taxa respond rapidly to environmental changes, reinforcing their value as effective bioindicators of tropical aquatic ecosystem health and stability (Breda et al., 2021; Medeiros et al., 2009). Their dynamic responses highlight the importance of continuous monitoring, as these organisms play critical roles in organic matter decomposition and nutrient cycling (Chauvet et al., 2016; Suberkropp, 1984).

Species, such as *Flagellospora curvula* and *Lunulospora curvula,* responded to specific intra-annual gradients; however, no collective inflection point was identified for the hyphomycete community over the annual cycle. The absence of strong seasonal turnover suggests that although some species are sensitive to short-term environmental fluctuations, the overall community composition and functionality remain stable across seasons (Graça et al., 2016). In tropical ecosystems, relatively mild variations in temperature and precipitation throughout the year promote environmental stability, which likely

383 contributes to the seasonal resilience of aquatic hyphomycete communities (Graça et al., 2016; Pérez et
384 al., 2018). In Neotropical streams, changes in the hyphomycete community structure are often associated
385 with local habitat alterations rather than environmental seasonality (Rincón and Santelloco, 2009). These
386 findings highlight that *F. curvula* and *L. curvula* may serve as sensitive indicators of subtle intra-annual
387 changes, even though the broader fungal community maintains functional stability under tropical
388 conditions. Although the overall hyphomycete community exhibited temporal stability, the presence of
389 these species suggests that fine-scale environmental shifts can influence community dynamics.

390 *Climatic variables and the aquatic hyphomycete community*

391 Despite the initial expectation that precipitation would directly influence the structure of the aquatic
392 hyphomycete community, particularly by modulating the input of allochthonous organic matter and
393 nutrient availability (Tonin et al., 2017; del Cid et al., 2019), our findings did not support this
394 hypothesis. The results did not indicate any direct or consistent effect of precipitation on community
395 structure, although its role in organic matter input and nutrient transport are well-documented in tropical
396 streams (Tonin et al., 2021; Mendivil-García et al., 2022).

397 In contrast, temperature and its stability over time play crucial roles in sustaining hyphomycete
398 communities, likely because of the adaptation of these species to thermally constant conditions in
399 tropical zones (Graça et al., 2016; Pérez et al., 2018). In temperate streams, seasonal temperature
400 fluctuations lead to periodic successional changes in fungal communities (Dang et al., 2009), whereas in
401 tropical systems, thermal stability reduces the temporal variability, promoting the persistence of species
402 adapted to steady-state regimes. This constancy supports essential ecological functions such as organic
403 matter decomposition and contributes to the functional stability of decomposer communities (Abelho et
404 al., 2005; Graça et al., 2016).

Conclusion

Our findings demonstrate that the structure of aquatic hyphomycete communities in tropical headwater streams is primarily shaped by interannual gradients from environmental variables rather than predictable seasonal patterns. This pattern may be linked to the relatively stable climatic regime typical of tropical systems, functional redundancy among fungal species, and the adaptation of tropical hyphomycetes to environmental variability. To the best of our knowledge, this is the first study to show that annual litterfall variation could be responsible for stabilizing and adapting the fungal community to tropical streams. Most studies have been conducted with simple leaf species or a few mixes over time in temperate zones (with low plant species diversity). In contrast, in our case, our mixtures differed from month to month, considering monthly variation and high plant species diversity. Understanding these dynamics is crucial for monitoring and conserving key ecological processes, particularly in the face of increasing pressures on aquatic ecosystems. Moreover, more long-term experiments are needed to identify the effects of interannual variations in leaf chemistry and microbiological colonization, as well as to understand the relationship between environmental gradients and climate change. Moreover, when well documented, the relationship between riparian zones and aquatic processes is essential for restoration programs and conservation policies.

Acknowledgments

Edson Serafim de Almeida Junior received a scholarship from CAPES (process number: 88887.814735/202300). The financial support by the Foundation for Research Support of the State of Bahia (FAPESB- Termo de Outorga – RED 0022/2013) and Institutional Program for Scientific Initiation Scholarships – PIBIC UFBA (process numbers: CNPq - 104207/2023 and CNPq - 126625/2023-9, The authors are grateful with the help of Federal University of Bahia with the field

support to all undergraduate students who participated in this fields work over the five years. Finally, we thank Mr. Getúlio and his family for allowing us to conduct the experiments on their farms.

Authors contribution: Conceptualization: JF, AM, RR and EJ; Developing methods: JF, AM and RR; Conducting the research: EJ with contribution from all other authors; Water chemistry analysis: GS; Leaf litter chemistry analysis: DS and JS; Data analysis: EJ; Data interpretation: EJ with contribution from AM and RR. Preparation of figures and tables: EJ and KO; Writing: EJ with support from all authors. **Conflict of Interest Statement:** The authors declare no conflicts of interest related to the content of this manuscript.

References

Abdul-Aziz, O.I.. G.A.K., 2023. Emergent Scaling of Dissolved Oxygen (DO) in Freshwater Streams Across Contiguous USA.

Abelho, Manuela; Cressa, Claudia; Graça, M.A.S., 2005. L . (Euphorbiaceae) Leaves in a Tropical Stream 1. Biotropica 37, 397–402.

Abelho, M., 2001. From Litterfall to Breakdown in Streams: A Review. Sci. World J. 1, 656–680. https://doi.org/10.1100/tsw.2001.103

Alvim, E.A.C.C., de Oliveira Medeiros, A., Rezende, R.S., Gonçalves, J.F., 2015. Small leaf breakdown in a Savannah headwater stream. Limnologica 51, 131–138. https://doi.org/10.1016/j.limno.2014.10.005

Andriotti, J., Petrucio, M.M., Lemes da Silva, A.L., 2022. Exploring the impacts of non-native leaf litter

449 on invertebrate community and leaf decomposition in a Atlantic Forest stream. Acta Limnol. Bras.
450 34. https://doi.org/10.1590/S2179-975X7121

451 Baldy, V., Chauvet, E., Charcosset, J.Y., Gessner, M.O., 2002. Microbial dynamics associated with
452 leaves decomposing in the mainstem and floodplain pond of a large river. Aquat. Microb. Ecol. 28,
453 25–36. https://doi.org/10.3354/ame028025

454 Balibrea, A., Ferreira, V., Balibrea, C., Gonçalves, V., Raposeiro, P.M., 2020. Contribution of
455 macroinvertebrate shredders and aquatic hyphomycetes to litter decomposition in remote insular
456 streams. Hydrobiologia 847, 2337–2355. https://doi.org/10.1007/s10750-020-04259-1

457 Bambi, P., Rezende, R.D.S., Joa, M., Figueiredo, G., Leite, M., Alvin, E., Gonc, F., 2016. Temporal and
458 Spatial Patterns in Inputs and Stock of Organic Matter in Savannah Streams of Central.
459 Ecosystems. https://doi.org/10.1007/s10021-016-0058-z

460 Bärlocher, F., 2007. Molecular approaches applied to aquatic hyphomycetes. Fungal Biol. Rev. 21, 19–
461 24. https://doi.org/10.1016/j.fbr.2007.02.003

462 Bärlocher, F., 1992. Research on Aquatic Hyphomycetes: Historical Background and Overview 1–15.
463 https://doi.org/10.1007/978-3-642-76855-2_1

464 Bärlocher, F., Gessner, M.O., Editors, M.A.S.G., 2020. Methods to Study Litter Decomposition,
465 Methods to Study Litter Decomposition. https://doi.org/10.1007/978-3-030-30515-4

466 Barreto, G.G., Hepp, L.U., Rezende, R. de S., Gonçalves Junior, J.F., Moretti, M. da S., Moretto, Y.,
467 Loureiro, R.C., Restello, R.M., Medeiros, A.O., 2023. The cooler the better: Increased aquatic
468 hyphomycete diversity in subtropical streams along a neotropical latitudinal gradient. Fungal Ecol.
469 62. https://doi.org/10.1016/j.funeco.2022.101223

Barros, J., Seena, S., 2022. Fungi in Freshwaters: Prioritising Aquatic Hyphomycetes in Conservation Goals. Water (Switzerland) 14. https://doi.org/10.3390/w14040605

Benson, L.J., Pearson, R.G., 2020. Dynamics of organic material and invertebrates in a tropical headwater stream. Hydrobiologia 847, 121–136. https://doi.org/10.1007/s10750-019-04076-1

Beveridge, O.S., Petchey, O.L., Humphries, S., 2010. Direct and indirect effects of temperature on the population dynamics and ecosystem functioning of aquatic microbial ecosystems. J. Anim. Ecol. 79, 1324–1331. https://doi.org/10.1111/j.1365-2656.2010.01741.x

Biggs, C.R., Yeager, L.A., Bolser, D.G., Bonsell, C., Dichiera, A.M., Hou, Z., Keyser, S.R., Khursigara, A.J., Lu, K., Muth, A.F., Negrete, B., Erisman, B.E., 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11. https://doi.org/10.1002/ecs2.3184

Blengini, I.A.D., Cintra, M.A.M. de U., Cunha, R.P.P. da, Caiafa, A.N., 2015. Proposta de unidade de conservação da serra da Jiboia 116.

Boyero, L., Pearson, R.G., Hui, C., Gessner, M.O., Pérez, J., Alexandrou, M.A., Graça, M.A.S., Cardinale, B.J., Albariño, R.J., Arunachalam, M., Barmuta, L.A., Boulton, A.J., Bruder, A., Callisto, M., Chauvet, E., Death, R.G., Dudgeon, D., Encalada, A.C., Ferreira, V., Figueroa, R., Flecker, A.S., Gonçalves, J.F., Helson, J., Iwata, T., Jinggut, T., Mathooko, J., Mathuriau, C., M'Erimba, C., Moretti, M.S., Pringle, C.M., Ramírez, A., Ratnarajah, L., Rincon, J., Yule, C.M., 2016. Biotic and abiotic variables influencing plant litter breakdown in streams: A global study. Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.1098/rspb.2015.2664

Breda, M., Binotto, A.C., Biasi, C., Hepp, L.U., 2021a. Influence of environmental predictors on hyphomycete assemblages in subtropical streams. Acta Oecologica 113, 103778.

https://doi.org/10.1016/j.actao.2021.103778

Breda, M., Binotto, A.C., Biasi, C., Hepp, L.U., 2021b. Influence of environmental predictors on hyphomycete assemblages in subtropical streams. Acta Oecologica 113, 103778. https://doi.org/10.1016/j.actao.2021.103778

Bruder, A., Schindler, M.H., Moretti, M.S., Gessner, M.O., 2014. Litter decomposition in a temperate and a tropical stream: The effects of species mixing, litter quality and shredders. Freshw. Biol. 59, 438–449. https://doi.org/10.1111/fwb.12276

Carey, N., Chester, E.T., Robson, B.J., 2021. Flow regime change alters shredder identity but not leaf litter decomposition in headwater streams affected by severe, permanent drying. Freshw. Biol. 66, 1813–1830. https://doi.org/10.1111/fwb.13794

Chauvet, E., Cornut, J., Sridhar, K.R., Selosse, M.A., Bärlocher, F., 2016. Beyond the water column: Aquatic hyphomycetes outside their preferred habitat. Fungal Ecol. 19, 112–127. https://doi.org/10.1016/j.funeco.2015.05.014

Chauvet, E., Suberkropp, K., 1998. Temperature and sporulation of aquatic hyphomycetes. Appl. Environ. Microbiol. 64, 1522–1525. https://doi.org/10.1128/aem.64.4.1522-1525.1998

Correa-Araneda, F., Tonin, A.M., Pérez, J., Álvarez, K., López-Rojo, N., Díaz, A., Esse, C., Encina-Montoya, F., Figueroa, R., Cornejo, A., Boyero, L., 2020. Extreme climate events can slow down litter breakdown in streams. Aquat. Sci. 82, 1–7. https://doi.org/10.1007/s00027-020-0701-9

da Costa, E.N.D., de Souza, J.C., Pereira, M.A., de Souza, M.F.L., de Souza, W.F.L., da Silva, D.M.L., 2017. Influence of hydrological pathways on dissolved organic carbon fluxes in tropical streams. Ecol. Evol. 7, 228–239. https://doi.org/10.1002/ece3.2543

da Silva, H.F., Assunção, A.R., Aciole, D. de S.B., Barbosa, F.R., Fiuza, P.O., 2023. Aquatic hyphomycetes associated with plant debris in freshwater ecosystems of the Atlantic Forest of Rio Grande do Norte, Brazil. New Zeal. J. Bot. 1–18. https://doi.org/10.1080/0028825X.2023.2201456

Dang, C.K., Schindler, M., Chauvet, E., Gessner, M.O., 2009. Temperature oscillation coupled with fungal community shifts pi can modulate warming effects on litter decomposition. Ecology 90, 122–131. https://doi.org/10.1890/07-1974.1

Datry, T., Foulquier, A., Corti, R., Von Schiller, D., Tockner, K., Mendoza-Lera, C., Clément, J.C., Gessner, M.O., Moleón, M., Stubbington, R., Gücker, B., Albarinõ, R., Allen, D.C., Altermatt, F., Arce, M.I., Arnon, S., Banas, D., Banegas-Medina, A., Beller, E., Blanchette, M.L., Blanco-Libreros, J.F., Blessing, J.J., Boëchat, I.G., Boersma, K.S., Bogan, M.T., Bonada, N., Bond, N.R., Brintrup Barriá, K.C., Bruder, A., Burrows, R.M., Cancellario, T., Canhoto, C., Carlson, S.M., Cauvy-Fraunié, S., Cid, N., Danger, M., De Freitas Terra, B., De Girolamo, A.M., De La Barra, E., Del Campo, R., Diaz-Villanueva, V.D., Dyer, F., Elosegi, A., Faye, E., Febria, C., Four, B., Gafny, S., Ghate, S.D., Gómez, R., Gómez-Gener, L., Gracą, M.A.S., Guareschi, S., Hoppeler, F., Hwan, J.L., Jones, J.I., Kubheka, S., Laini, A., Langhans, S.D., Leigh, C., Little, C.J., Lorenz, S., Marshall, J.C., Martín, E., McIntosh, A.R., Meyer, E.I., Miliša, M., Mlambo, M.C., Morais, M., Moya, N., Negus, P.M., Niyogi, D.K., Papatheodoulou, A., Pardo, I., Pařil, P., Pauls, S.U., Pešić, V., Polášek, M., Robinson, C.T., Rodríguez-Lozano, P., Rolls, R.J., Sánchez-Montoya, M.M., Savić, A., Shumilova, O., Sridhar, K.R., Steward, A.L., Storey, R., Taleb, A., Uzan, A., Vander Vorste, R., Waltham, N.J., Woelfle-Erskine, C., Zak, D., Zarfl, C., Zoppini, A., 2018. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. Nat. Geosci. 11, 497–503. https://doi.org/10.1038/s41561-018-0134-4

de Souza Rezende, R., Graça, M.A.S., dos Santos, A.M., Medeiros, A.O., Santos, P.F., Nunes, Y.R.,

Gonçalves Júnior, J.F., 2016. Organic Matter Dynamics in a Tropical Gallery Forest in a Grassland Landscape. Biotropica 48, 301–310. https://doi.org/10.1111/btp.12308

del Cid, C.C., Caiafa, A.N., de Souza Rezende, R., Sousa, T.S., Guedes, L., Medeiros, A.O., 2023. Leaf litter dominance components respond to temporal variation in a tropical riparian zone. Wetl. Ecol. Manag. 31, 649–660. https://doi.org/10.1007/s11273-023-09939-y

del Cid, C.C., Rezende, R.S., Calor, A.R., Dahora, J.S., de Aragão, L.N., Guedes, M.L., Caiafa, A.N., Medeiros, A.O., 2019. Temporal dynamics of organic matter, hyphomycetes and invertebrate communities in a Brazilian savanna stream. Community Ecol. 20, 301–313. https://doi.org/10.1556/168.2019.20.3.10

Djam, S., Najafi, M., Ahmadi, S.H., Shoeibi, S., 2019. Determination of bromate in bottled water marketed in Iran by ion chromatography. J. Chem. Metrol. 13, 47–52. https://doi.org/10.25135/jcm.28.19.10.1432

Duarte, S., Cássio, F., Pascoal, C., 2017. Environmental drivers are more important for structuring fungal decomposer communities than the geographic distance between streams. Limnetica 36, 491–506. https://doi.org/10.23818/limn.36.17

Esteves, F. de A., Gonçalves, J.F.J., 2011. Etapas do Metabolismo Aquático. researchgate 119–124.

Fenoy, E., Pradhan, A., Pascoal, C., Rubio-Ríos, J., Batista, D., Moyano-López, F.J., Cássio, F., Casas, J.J., 2022. Elevated temperature may reduce functional but not taxonomic diversity of fungal assemblages on decomposing leaf litter in streams. Glob. Chang. Biol. 28, 115–127. https://doi.org/10.1111/gcb.15931

Ferreira-Santos, K., Garbin, M.L., Carrijo, T.T., Torres-Leite, F., Cavatte, P.C., Dias, A.T.C., 2024.

Post-drought community turnover and functional redundancy in a tropical forest understorey. J. Veg. Sci. 35, 1–14. https://doi.org/10.1111/jvs.13256

Ferreira, V., Castela, J., Rosa, P., Tonin, A.M., Boyero, L., Graça, M.A.S., 2016. Aquatic hyphomycetes, benthic macroinvertebrates and leaf litter decomposition in streams naturally differing in riparian vegetation. Aquat. Ecol. 50. https://doi.org/10.1007/s10452-016-9588-x

Ferreira, V., Elosegi, A., Tiegs, S.D., von Schiller, D., Young, R., 2020. Organic matter decomposition and ecosystem metabolism as tools to assess the functional integrity of streams and rivers–a systematic review. Water (Switzerland) 12. https://doi.org/10.3390/w12123523

Fiuza, P.O., Cantillo-Pérez, T., Gulis, V., Gusmão, L.F.P., 2017. Ingoldian fungi of Brazil: Some new records and a review including a checklist and a key. Phytotaxa 306, 171–200. https://doi.org/10.11646/phytotaxa.306.3.1

Fiuza, P.O., Costa, L.A., Medeiros, A.O., Gulis, V., Gusmão, L.F.P., 2019. Diversity of freshwater hyphomycetes associated with leaf litter of Calophyllum brasiliense in streams of the semiarid region of Brazil. Mycol. Prog. 18, 907–920. https://doi.org/10.1007/s11557-019-01501-6

Fiuza, P.O., de Paiva Ottoni-Boldrini, B.M., Monteiro, J.S., Catena, N.R., Hamada, N., Gusmão, L.F.P., 2015. First records of Ingoldian fungi from the Brazilian Amazon. Rev. Bras. Bot. 38, 615–621. https://doi.org/10.1007/s40415-015-0157-7

Flindt, M.R., Lillebø, A.I., Pérez, J., Ferreira, V., 2020. Total Phosphorus, Nitrogen and Carbon in Leaf Litter. Methods to Study Litter Decompos. 91–105. https://doi.org/10.1007/978-3-030-30515-4_11

Gessner, M.O., Chauvet, E., 1993. Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. Appl. Environ. Microbiol. 59, 502–507. https://doi.org/10.1128/aem.59.2.502-507.1993

578 Gessner, M.O., Chauvet, E., Dobson, M., 1999. Nordic Society Oikos A Perspective on Leaf Litter
579 Breakdown in Streams. Source: Oikos 85, 377–384.

580 Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler, S.,
581 2010. Diversity meets decomposition. Trends Ecol. Evol. 25, 372–380.
582 https://doi.org/10.1016/j.tree.2010.01.010

583 Gomes, P.P., Ferreira, V., Tonin, A.M., Medeiros, A.O., Júnior, J.F.G., 2018. Combined Effects of
584 Dissolved Nutrients and Oxygen on Plant Litter Decomposition and Associated Fungal
585 Communities. Microb. Ecol. 75, 854–862. https://doi.org/10.1007/s00248-017-1099-3

586 Gomes, P.P., Medeiros, A.O., Gonçalves Júnior, J.F., 2016. The replacement of native plants by exotic
587 species may affect the colonization and reproduction of aquatic hyphomycetes. Limnologica 59,
588 124–130. https://doi.org/10.1016/j.limno.2016.05.005

589 Gonçalves, J.F., de Souza Rezende, R., Gregório, R.S., Valentin, G.C., 2014. Relationship between
590 dynamics of litterfall and riparian plant species in a tropical stream. Limnologica 44, 40–48.
591 https://doi.org/10.1016/j.limno.2013.05.010

592 Gonçalves, J.F., Rezende, R.S., Martins, N.M., Gregório, R.S., 2012. Leaf breakdown in an Atlantic
593 Rain Forest stream. Austral Ecol. 37, 807–815. https://doi.org/10.1111/j.1442-9993.2011.02341.x

594 Gossiaux, A., Jabiol, J., Poupin, P., Chauvet, E., Guérold, F., 2019. Seasonal variations overwhelm
595 temperature effects on microbial processes in headwater streams : insights from a temperate
596 thermal spring. Aquat. Sci. 81, 1–11. https://doi.org/10.1007/s00027-019-0627-2

597 Graça, M.A.S., Ferreira, V., Canhoto, C., Encalada, A.C., Guerrero-Bolaño, F., Wantzen, K.M., Boyero,
598 L., 2015. A conceptual model of litter breakdown in low order streams. Int. Rev. Hydrobiol.

https://doi.org/10.1002/iroh.201401757

Graça, M.A.S., Hyde, K., Chauvet, E., 2016. Aquatic hyphomycetes and litter decomposition in tropical - subtropical low order streams. Fungal Ecol. 19, 182–189. https://doi.org/10.1016/j.funeco.2015.08.001

Graeber, D., Pusch, M.T., Lorenz, S., Brauns, M., 2013. Cascading effects of flow reduction on the benthic invertebrate community in a lowland river. Hydrobiologia 717, 147–159. https://doi.org/10.1007/s10750-013-1570-1

Gulis, V., Kuehn, K.A., Schoettle, L.N., Leach, D., Benstead, J.P., Rosemond, A.D., 2017. Changes in nutrient stoichiometry, elemental homeostasis and growth rate of aquatic litter-associated fungi in response to inorganic nutrient supply. ISME J. 11, 2729–2739. https://doi.org/10.1038/ismej.2017.123

Halvorson, H.M., Hall, D.J., Evans-White, M.A., 2017. Long-term stoichiometry and fates highlight animal egestion as nutrient repackaging.pdf. https://doi.org/doi: 10.1111/1365-2435.12875

He, M., Zhao, R., Tian, Q., Huang, L., Wang, X., Liu, F., 2019. Predominant effects of litter chemistry on lignin degradation in the early stage of leaf litter decomposition. Plant Soil 442, 453–469. https://doi.org/10.1007/s11104-019-04207-6

Hepp, L.U., Milesi, S. V., Nava, D., Restello, R.M., 2021. Nestedness of stream insects in subtropical region: Importance of inter-annual temporal scale. Iheringia - Ser. Zool. 111, 1–7. https://doi.org/10.1590/1678-4766e2021005

Isaak, D.J., Wollrab, S., Horan, D., Chandler, G., 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. Clim.

620 Change 113, 499–524. https://doi.org/10.1007/s10584-011-0326-z

621 Jabiol, J., Bruder, A., Gessner, M.O., Makkonen, M., McKie, B.G., Peeters, E.T.H.M., Vos, V.C.A.,
622 Chauvet, E., 2013. Diversity patterns of leaf-associated aquatic hyphomycetes along a broad
623 latitudinal gradient. Fungal Ecol. 6, 439–448. https://doi.org/10.1016/j.funeco.2013.04.002

624 Jabiol, J., Cornut, J., Tlili, A., Gessner, M.O., 2018. Interactive effects of dissolved nitrogen, phosphorus
625 and litter chemistry on stream fungal decomposers. FEMS Microbiol. Ecol. 94, 1–11.
626 https://doi.org/10.1093/femsec/fiy151

627 Jane, S.F., Hansen, G.J.A., Kraemer, B.M., Leavitt, P.R., Mincer, J.L., North, R.L., Pilla, R.M., Stetler,
628 J.T., Williamson, C.E., Woolway, R.I., Arvola, L., Chandra, S., DeGasperi, C.L., Diemer, L.,
629 Dunalska, J., Erina, O., Flaim, G., Grossart, H.P., Hambright, K.D., Hein, C., Hejzlar, J., Janus,
630 L.L., Jenny, J.P., Jones, J.R., Knoll, L.B., Leoni, B., Mackay, E., Matsuzaki, S.I.S., McBride, C.,
631 Müller-Navarra, D.C., Paterson, A.M., Pierson, D., Rogora, M., Rusak, J.A., Sadro, S., Saulnier-
632 Talbot, E., Schmid, M., Sommaruga, R., Thiery, W., Verburg, P., Weathers, K.C., Weyhenmeyer,
633 G.A., Yokota, K., Rose, K.C., 2021. Widespread deoxygenation of temperate lakes. Nature 594,
634 66–70. https://doi.org/10.1038/s41586-021-03550-y

635 Kleba Lisboa, L., Lemes Da Silva, A.L., Siegloch, A.E., Gonçalves Júnior, J.F., Mello Petrucio, M.,
636 2015. Temporal dynamics of allochthonous coarse particulate organic matter in a subtropical
637 Atlantic rainforest Brazilian stream. Mar. Freshw. Res. 66. https://doi.org/10.1071/MF14068

638 Krauss, G.J., Solé, M., Krauss, G., Schlosser, D., Wesenberg, D., Bärlocher, F., 2011. Fungi in
639 freshwaters: Ecology, physiology and biochemical potential. FEMS Microbiol. Rev. 35, 620–651.
640 https://doi.org/10.1111/j.1574-6976.2011.00266.x

641 Lemes da Silva, A.L., Kleba Lisboa, L., Siegloch, A.E., Petrucio, M.M., Gonçalves Júnior, J.F., 2017.

642 Connecting the litterfall temporal dynamics and processing of coarse particulate organic matter in a
643 tropical stream. Mar. Freshw. Res. 68, 1260–1271. https://doi.org/10.1071/MF16032

644 Leoni, B., Patelli, M., Soler, V., Nava, V., 2018. Ammonium transformation in 14 lakes along a trophic
645 gradient. Water (Switzerland) 10. https://doi.org/10.3390/w10030265

646 Li, S., Luo, J., Xu, Y.J., Zhang, L., Ye, C., 2022. Hydrological seasonality and nutrient stoichiometry
647 control dissolved organic matter characterization in a headwater stream. Sci. Total Environ. 807,
648 150843. https://doi.org/10.1016/j.scitotenv.2021.150843

649 Marks, J.C., 2019. Revisiting the Fates of Dead Leaves That Fall into Streams. Annu. Rev. Ecol. Evol.
650 Syst. 50, 547–568. https://doi.org/10.1146/annurev-ecolsys-110218-024755

651 Martins, R.T., Rezende, R.D.S., Gonçalves, J.F., Lopes, A., Piedade, M.T.F., Cavalcante, H.D.L.,
652 Hamada, N., 2017. Effects of increasing temperature and, CO2 on quality of litter, shredders, and
653 microorganisms in Amazonian aquatic systems. PLoS One 12.
654 https://doi.org/10.1371/journal.pone.0188791

655 Medeiros, A.O., Pascoal, C., Graça, M.A.S., 2009. Diversity and activity of aquatic fungi under low
656 oxygen conditions. Freshw. Biol. 54, 142–149. https://doi.org/10.1111/j.1365-2427.2008.02101.x

657 Mendivil-García, K., Amabilis-Sosa, L.E., Salinas-Juárez, M.G., Pat-Espadas, A., Rodríguez-Mata,
658 A.E., Figueroa-Pérez, M.G., Roé-Sosa, A., 2022. Climate change impact assessment on a tropical
659 river resilience using the Streeter-Phelps dissolved oxygen model. Front. Environ. Sci. 10, 1–15.
660 https://doi.org/10.3389/fenvs.2022.903046

661 Mohana Rangan, S., Krajmalnik-Brown, R., Delgado, A.G., 2021. An Ion Chromatography Method for
662 Simultaneous Quantification of Chromate, Arsenate, Selenate, Perchlorate, and Other Inorganic

663 Anions in Environmental Media. Environ. Eng. Sci. 38, 626–634.
664 https://doi.org/10.1089/ees.2020.0347

665 Neres-Lima, V., Machado-Silva, F., Baptista, D.F., Oliveira, R.B.S., Andrade, P.M., Oliveira, A.F.,
666 Sasada-Sato, C.Y., Silva-Junior, E.F., Feijó-Lima, R., Angelini, R., Camargo, P.B., Moulton, T.P.,
667 2017. Allochthonous and autochthonous carbon flows in food webs of tropical forest streams.
668 Freshw. Biol. 62. https://doi.org/10.1111/fwb.12921

669 Nguyen, H.H., Welti, E.A.R., Haubrock, P.J., Haase, P., 2023. Long-term trends in stream benthic
670 macroinvertebrate communities are driven by chemicals. Environ. Sci. Eur. 35.
671 https://doi.org/10.1186/s12302-023-00820-6

672 Noacco, V., Duffy, C.J., Wagener, T., Worrall, F., Fasiolo, M., Howden, N.J., 2019. Drivers of
673 interannual and intra-annual variability of dissolved organic carbon.

674 Pérez, J., Martínez, A., Descals, E., Pozo, J., 2018. Responses of Aquatic Hyphomycetes to Temperature
675 and Nutrient Availability: a Cross-transplantation Experiment. Microb. Ecol. 76, 328–339.
676 https://doi.org/10.1007/s00248-018-1148-6

677 Pio, J.F.G., Hepp, L.U., Medeiros, A.O., da Silva, F.L., Copatti, C.E., 2022. Intra-annual colonization of
678 Chironomidae on leaf litter in a Brazilian Cerrado stream. Zoologia 39.
679 https://doi.org/10.1590/S1984-4689.V39.E22015

680 Prieto, I., Almagro, M., Bastida, F., Querejeta, J.I., 2019. Altered leaf litter quality exacerbates the
681 negative impact of climate change on decomposition. J. Ecol. 107, 2364–2382.
682 https://doi.org/10.1111/1365-2745.13168

683 Rabelo, R.S., Sena, G., Gonçalves, J.F., 2024. Interrelationships among litter chemistry, plant species

684 diversity, and litter decomposition in tropical stream environments: a review. Front. Geochemistry
685 2, 1–8. https://doi.org/10.3389/fgeoc.2024.1346457

686 Raposeiro, P.M., Ferreira, V., Gea, G., Gonçalves, V., 2018. Contribution of aquatic shredders to leaf
687 litter decomposition in Atlantic island streams depends on shredder density and litter quality. Mar.
688 Freshw. Res. 69, 1432–1439. https://doi.org/10.1071/MF18020

689 Rezende, R.S., Sales, M.A., Hurbath, F., Roque, N., Gonçalves, J.F., Medeiros, A.O., 2017a. Effect of
690 plant richness on the dynamics of coarse particulate organic matter in a Brazilian Savannah stream.
691 Limnologica 63, 57–64. https://doi.org/10.1016/j.limno.2017.02.002

692 Rezende, R.S., Sales, M.A., Hurbath, F., Roque, N., Gonçalves, J.F., Medeiros, A.O., 2017b. Effect of
693 plant richness on the dynamics of coarse particulate organic matter in a Brazilian Savannah stream.
694 Limnologica 63, 57–64. https://doi.org/10.1016/j.limno.2017.02.002

695 Rezende, R.S., Santos, A.M., Medeiros, A.O., Gonçalves, J.F., 2017c. Temporal leaf litter breakdown in
696 a tropical riparian forest with an open canopy. Limnetica 36, 445–459.
697 https://doi.org/10.23818/limn.36.14

698 Rincón, J., Santelloco, R., 2009. Aquatic fungi associated with decomposing ficus sp. leaf litter in a
699 neotropical stream. J. North Am. Benthol. Soc. 28, 416–425. https://doi.org/10.1899/07-084.1

700 Rodríguez-Cardona, B.M., Wymore, A.S., McDowell, W.H., 2021. Nitrate uptake enhanced by
701 availability of dissolved organic matter in tropical montane streams. Freshw. Sci. 40, 65–76.
702 https://doi.org/10.1086/713070

703 Röhl, O., Peršoh, D., Mittelbach, M., Elbrecht, V., Brachmann, A., Nuy, J., Boenigk, J., Leese, F.,
704 Begerow, D., 2017. Distinct sensitivity of fungal freshwater guilds to water quality. Mycol. Prog.

16, 155–169. https://doi.org/10.1007/s11557-016-1261-1

Rubenstein, M.A., Crowther, T.W., Maynard, D.S., Schilling, J.S., Bradford, M.A., 2017. Decoupling direct and indirect effects of temperature on decomposition. Soil Biol. Biochem. 112, 110–116. https://doi.org/10.1016/j.soilbio.2017.05.005

Sales, M.A., Dahora, J.S., Medeiros, A.O., 2014. Influence of Leaf Quality in Microbial Decomposition in a Headwater Stream in the Brazilian Cerrado : a 1-Year Study. https://doi.org/10.1007/s00248-014-0467-5

Sales, M.A., Gonçalves, J.F., Dahora, J.S., Medeiros, A.O., 2015. Influence of Leaf Quality in Microbial Decomposition in a Headwater Stream in the Brazilian Cerrado: a 1-Year Study. Microb. Ecol. 69, 84–94. https://doi.org/10.1007/s00248-014-0467-5

Sanches, L., Valentini, C.M.A., Pinto Júnior, O.B., Nogueira, J. de S., Vourlitis, G.L., Biudes, M.S., da Silva, C.J., Bambi, P., Lobo, F. de A., 2008. Seasonal and interannual litter dynamics of a tropical semideciduous forest of the southern Amazon Basin, Brazil. J. Geophys. Res. Biogeosciences 113, 1–9. https://doi.org/10.1029/2007JG000593

Sanpera-Calbet, I., Lecerf, A., Chauvet, E., 2009. Leaf diversity influences in-stream litter decomposition through effects on shredders. Freshw. Biol. 54, 1671–1682. https://doi.org/10.1111/j.1365-2427.2009.02216.x

Seena, S., Bärlocher, F., Sobral, O., Gessner, M.O., Dudgeon, D., McKie, B.G., Chauvet, E., Boyero, L., Ferreira, V., Frainer, A., Bruder, A., Matthaei, C.D., Fenoglio, S., Sridhar, K.R., Albariño, R.J., Douglas, M.M., Encalada, A.C., Garcia, E., Ghate, S.D., Giling, D.P., Gonçalves, V., Iwata, T., Landeira-Dabarca, A., McMaster, D., Medeiros, A.O., Naggea, J., Pozo, J., Raposeiro, P.M., Swan, C.M., Tenkiano, N.S.D., Yule, C.M., Graça, M.A.S., 2019. Biodiversity of leaf litter fungi in

streams along a latitudinal gradient. Sci. Total Environ. 661, 306–315. https://doi.org/10.1016/j.scitotenv.2019.01.122

Seena, S., Pascoal, C., Marvanová, L., Cássio, F., 2010. DNA barcoding of fungi: A case study using ITS sequences for identifying aquatic hyphomycete species. Fungal Divers. 44, 77–87. https://doi.org/10.1007/s13225-010-0056-y

Sena, G., Francisco Gonçalves Júnior, J., Tavares Martins, R., Hamada, N., de Souza Rezende, R., 2020. Leaf litter quality drives the feeding by invertebrate shredders in tropical streams. Ecol. Evol. 10, 8563–8570. https://doi.org/10.1002/ece3.6169

Shearer, C.A., Descals, E., Kohlmeyer, B., Kohlmeyer, J., Marvanová, L., Padgett, D., Porter, D., Raja, H.A., Schmit, J.P., Thorton, H.A., Voglymayr, H., 2007. Fungal biodiversity in aquatic habitats. Biodivers. Conserv. 16, 49–67. https://doi.org/10.1007/s10531-006-9120-z

Silva-Junior, E.F., Moulton, T.P., Boëchat, I.G., Gücker, B., 2014. Leaf decomposition and ecosystem metabolism as functional indicators of land use impacts on tropical streams. Ecol. Indic. 36, 195–204. https://doi.org/10.1016/j.ecolind.2013.07.027

Small, G.E., Ardón, M., Jackman, A.P., Duff, J.H., Triska, F.J., Ramírez, A., Snyder, M., Pringle, C.M., 2012. Rainfall-Driven Amplification of Seasonal Acidification in Poorly Buffered Tropical Streams. Ecosystems 15, 974–985. https://doi.org/10.1007/s10021-012-9559-6

Stape, L., Sentelhas, P.C., Alvares, C.A., Gonc, L.D.M., 2014. Ko ¨ ppen ' s climate classification map for Brazil 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Suberkropp, K., 1984. Effect of temperature on seasonal occurrence of aquatic hyphomycetes. Trans. - Br. Mycol. Soc. 82, 53–62. https://doi.org/10.1016/S0007-1536(84)80211-9

748 Swan, C.M., Boyero, L., Canhoto, C., 2021. The Ecology of Plant Litter Decomposition in Stream
749 Ecosystems: An Overview, The Ecology of Plant Litter Decomposition in Stream Ecosystems.
750 https://doi.org/10.1007/978-3-030-72854-0_1

751 Taniwaki, R.H., Matthaei, C.D., Cardoso, T.K.M., Ferraz, S.F.B., Martinelli, L.A., Piggott, J.J., 2019.
752 The effect of agriculture on the seasonal dynamics and functional diversity of benthic biofilm in
753 tropical headwater streams. Biotropica 51, 18–27. https://doi.org/10.1111/btp.12617

754 Tonello, G., Loureiro, R.C., Krause, P., Silva, C., Ongaratto, R.M., Sepp, S., Restello, R.M., Hepp, U.,
755 2014. Colonização de Invertebrados Durante a Decomposição de Diferentes Detritos Vegetais em
756 um Riacho Subtropical. Brazilian J. Biosci. 12, 98–105.

757 Tonin, A.M., Gonçalves, J.F., Bambi, P., Couceiro, S.R.M., Feitoza, L.A.M., Fontana, L.E., Hamada,
758 N., Hepp, L.U., Lezan-Kowalczuk, V.G., Leite, G.F.M., Lemes-Silva, A.L., Lisboa, L.K., Loureiro,
759 R.C., Martins, R.T., Medeiros, A.O., Morais, P.B., Moretto, Y., Oliveria, P.C.A., Pereira, E.B.,
760 Ferreira, L.P., Pérez, J., Petrucio, M.M., Reis, D.F., Rezende, R., Roque, N., Santos, L.E.P.,
761 Siegloch, A.E., Tonello, G., Boyero, L., 2017. Plant litter dynamics in the forest-stream interface:
762 Precipitation is a major control across tropical biomes. Sci. Rep. 7, 1–14.
763 https://doi.org/10.1038/s41598-017-10576-8

764 Tonin, A.M., Lima, L.S., Bambi, P., Figueiredo, M.L., Rezende, R.S., Gonçalves, J.F., 2021. Litterfall
765 Chemistry Is Modulated by Wet-Dry Seasonality and Leaf Phenology of Dominant Species in the
766 Tropics. Front. For. Glob. Chang. 4, 1–11. https://doi.org/10.3389/ffgc.2021.666116

767 Umoren, O.D.1*, Akinbola, S.A.,2 Sowemimo, R.O.,2 Edem, F.P.1,3 and Babalola, E.B.., 2024. Impact
768 of Human Activities on the Physiochemical Quality of Streams Around Ijeun- Titun and Kuto
769 Community in Abeokuta, Ogun State, Nigeria. Biol. Environ. Sci. J. Trop. 21, 22–32.

Wallace, J.B., Webster, J.R., Cuffney, T.F., 1982. Stream detritus dynamics: Regulation by invertebrate consumers. Oecologia 53, 197–200. https://doi.org/10.1007/BF00545663

Webster, J.R., Meyer, J.L., 1997. Stream Organic Matter Budgets: An Introduction. J. North Am. Benthol. Soc. https://doi.org/10.2307/1468223

Yue, K., De Frenne, P., Van Meerbeek, K., Ferreira, V., Fornara, D.A., Wu, Q., Ni, X., Peng, Y., Wang, D., Heděnec, P., Yang, Y., Wu, F., Peñuelas, J., 2022. Litter quality and stream physicochemical properties drive global invertebrate effects on instream litter decomposition. Biol. Rev. 97, 2023–2038. https://doi.org/10.1111/brv.12880

Zhang, M., Cheng, X., Geng, Q., Shi, Z., Luo, Y., Xu, X., 2019. Leaf litter traits predominantly control litter decomposition in streams worldwide. Glob. Ecol. Biogeogr. 28, 1469–1486. https://doi.org/10.1111/geb.12966

Table 1. Annual values of precipitation accumulation (mm) and the average values of pH, dissolved oxygen (DO), and temperature (Temp) in the Cai Camarão stream over five years.

Year	Precipitation	pH	DO	Temperature
2015	1033.0	5.93	9.10	23.35
2016	701.6	6.37	8.65	23.33
2017	719.0	6.17	7.43	22.8
2018	625.0	7.07	7.23	22.7
2019	968.4	7.45	7.36	23.49

Note:

These values provide an overview of environmental variations and water quality in the stream.

Table 2. Average concentrations of dissolved chemical parameters in the water of Cai Camarão stream.

Year	Na	NH4	K	Ca	Mg	F	Cl	NO2	Br	NO3	PO4	SO4	Cu	Zn	Fer
2015	5.82	0.08	1.14	0.67	0.75	0.04	2.36	0.008	0.005	0.08	0.001	0.99	NA	NA	NA
2016	4.49	0.06	1.15	0.09	2.15	0.04	0.03	0.027	0.025	0.25	0.042	0.03	0.07	0.16	1.40
2017	4.51	0.06	0.98	0.04	2.25	0.07	0.01	0.033	0.027	0.27	0.055	0.02	0.07	0.15	1.31
2018	3.93	0.07	1.14	0.03	1.87	0.07	0.03	0.022	0.030	0.27	0.032	0.02	0.06	0.12	1.41
2019	5.06	0.09	1.046	0.02	1.89	0.05	0.01	0.023	0.037	0.28	0.021	0.01	0.06	0.21	1.39

Notes:

The analyzed variables included sodium (Na), ammonium (NH4), potassium (K), calcium (Ca), magnesium (Mg), fluoride (F), chloride (Cl), nitrite (NO2), bromide (Br), nitrate (NO3), phosphate (PO4), sulfate (SO4), copper (Cu), zinc (Zn), and iron (Fe). Some concentrations are missing for the year 2015, indicated as "NA" (data not available). The concentrations are expressed in milligrams per liter (mg/L).

Table 3. Average concentrations of Carbon (C), Nitrogen (N), and Phosphorus (P) (%) in four quarterly periods (January, April, July, and October) from 2015 to 2019 in the Cai Camarão stream.

Year	Quarter	Carbon (C)	Nitrogen (N)	Phosphorus (P)
2015	Jan	69.252	0.205	0.006
	Apr	73.118	0.139	0.007
	Jul	65.419	0.232	0.006
	Oct	70.909	0.181	0.007
2016	Jan	66.730	0.199	0.010
	Apr	67.012	0.195	0.006
	Jul	69.913	0.263	0.009
	Oct	66.970	0.340	0.009
2017	Jan	68.745	0.315	0.017
	Apr	70.729	0.267	0.009
	Jul	71.566	0.245	0.012
	Oct	65.168	0.300	0.010
2018	Jan	68.665	0.273	0.008
	Apr	65.357	0.267	0.008
	Jul	68.726	NA	0.009
	Oct	67.781	0.203	0.016
2019	Jan	69.818	0.179	0.013
	Apr	69.168	0.252	0.012
	Jul	68.757	0.253	0.014
	Oct	63.807	0.242	0.014

Table 4. Dissimilarity ranks of aquatic hyphomycete community between different years and within each specific year.

Dissimilarity Ranks Between and Within Classes						
Group	**0%**	**25%**	**50%**	**75%**	**100%**	**N**
Between	1	455.5	889.5	1301.5	1691	1392
2015	80	566	1122	1557.75	1691	66
2016	6	297.5	591	927	1455	55
2017	11	342.25	898	1416.25	1691	66
2018	4	338.75	570.5	928.5	1570	66
2019	2	243.75	577	982	1596	66

850 **Table 5.** Boosted regression tree (BRT) model. Relative influence of environmental variables on the
851 richness and density of aquatic hyphomycetes.

852

Relative Influence (%)			
Richness		**Density**	
Br	7.71	NH4	10.37
Cu	7.46	F	6.90
DO	6.89	Cl	5.71
SO4	6.41	Temp.	5.55
P	5.74	N	5.41
K	4.98	Precip.	5.18
PO4	4.73	Cu	5.11
Na	4.73	Fe	4.78
Zn	4.54	Br	4.70
CL	4.37	PO4	4.54
Mg	4.34	Na	4.49
F	4.29	SO4	4.05
NO3	3.95	K	3.90
NH4	3.90	Zn	3.84
pH	3.66	DO	3.82
Precip.	3.63	P	3.73
NO2	3.56	pH	3.56
Ca	3.45	Mg	3.24
C	3.22	Ca	3.17
Fe	3.12	C	3.09
Temp.	2.91	NO3	2.76
N	2.31	NO2	1.99

853

854

855

856

857

Table 6. Threshold Indicator Taxa Analysis (TITAN) for aquatic hyphomycete species, identifying interannual changes in sporulation rates.

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	obsiv.prob	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Ac	2018	2018	5	2	20.07	0.028	3.22	2016	2016	2018	2018	2019	0.884	0.515	2.778636	0
Af	**2015**	**2015**	**17**	**1**	**88.63**	**0.004**	**6.75**	**2015**	**2015**	**2015**	**2016**	**2016**	**0.992**	**0.989**	**6.699698**	**1**
Afu	2015	2018	19	1	28.87	0.128	1.23	2015	2015	2016	2018	2018	0.692	0.43	1.837709	0
Al	**2015**	**2018**	**43**	**2**	**59.39**	**0.004**	**3.69**	**2015**	**2015**	**2017**	**2018**	**2019**	**0.995**	**0.973**	**4.54944**	**2**
Bt	2018	2018	3	1	6.67	0.576	0.17	2016	2016	2017	2018	2018	0.464	0.071	1.242906	0
Cc	2015	2015	5	1	34.74	0.044	3.61	2015	2015	2015	2017	2017	0.965	0.721	4.129279	0
Fc	2015	2015	54	2	70.93	0.12	1.32	2015	2015	2017	2019	2019	0.719	0.623	2.090325	0
Lct	2015	2015	6	1	24.52	0.008	3.9	2015	2015	2016	2017	2017	0.99	0.826	4.131182	0
Lc	2016	2016	42	2	51.93	0.108	1.44	2015	2015	2016	2018	2018	0.779	0.524	2.016755	0
Ma	2016	2016	3	1	7.62	0.456	0.6	2015	2016	2016	2019	2019	0.53	0.271	2.035395	0
Ta	2019	2019	28	2	52.66	0.088	1.35	2015	2016	2018	2019	2019	0.632	0.514	1.923741	0
Tm	**2018**	**2018**	**41**	**1**	**66.58**	**0.004**	**4.18**	**2017**	**2017**	**2017**	**2018**	**2018**	**0.991**	**0.972**	**4.332338**	**1**

Note:

The species are represented by the following codes: *Ac = Anguillospora crassa*, *Af = Anguillospora filiformis*, *Afu = Anguillospora furtiva*, *Al = Amniculicola longissima*, *Bt = Brachiosphera tropicalis*, *Cc = Colispora curvata*, *Fc = Flagellospora curvula*, *Lct = Lemonniera centrosphaera*, *Lc = Lunulospora curvula*, *Ma = Mimelanolocus aquatilis*, *Ta = Tricelophorus acuminatus*, and *Tm = Tricelophorus monosphorus*. The columns include the environmental thresholds for decline (*ienv.cp*) and increase (*zenv.cp*), species frequency (*freq*), group with the highest indicator value (*maxgrp*), indicator value (*IndVal*), observed probability of significance (*obsiv.prob*), Z-score (*z-score*), confidence intervals of the thresholds (5, 10, 50, 90, and 95%), purity (*purity*), reliability (*reliability*), median Z-score (*z.median*),

and filter (*filter*, indicating significance: 0 = not significant, 1 = significant for decline, and 2 = significant for increase).

888 **Table 7.** Intra-annual Threshold Indicator Taxa Analysis (TITAN) for aquatic hyphomycete species
889 identified changes in the sporulation rates of these taxa across monthly intervals.

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	obsiv.prob	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Af	7.5	7.5	8	1	83.55	0.032	2.51	4	4.5	7	8.5	9.5	0.947	0.584	2.238881	0
Afu	5.5	5.5	3	1	17.35	0.904	-1.01	3.5	4	7	9	9.5	0.563	0.121	0.783458	0
Al	5.5	5.5	5	1	46.24	0.316	0.68	4	4.5	6.5	8.5	9.5	0.637	0.122	-0.49074	0
Cc	5.5	5.5	3	1	33.22	0.356	0.39	3.5	4	6	9	9.5	0.644	0.08	0.912279	0
Fc	7.5	6.5	8	2	86.21	0.012	3.28	4	5	7	8	9	0.95	0.737	2.931065	0
Lct	5.5	5.5	3	2	42.86	0.18	1.36	4.5	5	6	9	9.5	0.752	0.104	1.202155	0
Lc	7.5	7.5	7	2	92.65	0.012	3.35	4	5	7	8.5	9	0.959	0.686	2.770265	0
Ta	6.5	6.5	5	2	45.24	0.184	0.36	3.5	4.5	6.5	8.5	9.5	0.811	0.124	0.613118	0
Tm	7.5	7.5	10	1	63.75	0.316	0.51	4	4.5	6.5	9	9.5	0.582	0.225	0.792964	0

890

891 **Note:**

892 The analysis included species with significant associations with environmental thresholds. Af =
893 *Anguillospora filiformis*, Afu = *Anguillospora furtiva*, Al = *Amniculicola longissima*, Cc = *Colispora*
894 *curvata*, Fc = *Flagellospora curvula*, Lct = *Lemonniera centrosphaera*, Lc = *Lunulospora curvula*, Ta =
895 *Tricelophorus acuminatus*, and Tm = *Tricelophorus monosphorus*. The columns include the
896 environmental thresholds for decline (*ienv.cp*) and increase (*zenv.cp*), species frequency (*freq*), group
897 with the highest indicator value (*maxgrp*), indicator value (*IndVal*), observed probability of significance
898 (*obsiv.prob*), Z-score (*zscore*), confidence intervals of the thresholds (5%, 10%, 50%, 90%, 95%), purity
899 (*purity*), reliability (*reliability*), median Z-score (*z.median*), and filter (*filter*, indicating significance: 0 =
900 not significant).

Figure 1. Sampling design, where (A) represents the headwater stream and sampling points. (B) Sampling points for visualizing buckets and collecting leaves. (C) Representative weighing, bucket selection, and incubation of litter bags. (D) Methodology for the sporulation of aquatic hyphomycetes in the laboratory.

Figure 2. Graph representing the diversity of aquatic hyphomycetes over five years at sampling times of 30, 60, and 90 days of leaf retention in the studied stream. The graph illustrates the sporulation rates of the species across different sampling periods, highlighting their behavior over time.

Figure 3. ANOSIM plot showing R-statistic values ranging from -1 to 1, where values close to 1 indicate a clear separation between aquatic hyphomycete communities across different years, and values close to 0 suggest minimal differences between the groups. The plot also displays the p-value for significance.

Figure 4. Effects of the six most influential environmental variables on the richness of aquatic hyphomycetes. Each panel represents the fitted response curve for one environmental variable derived from the Boosted Regression Trees (BRT) model and the respective relative influences (R.I). The y-axis indicates the predicted richness of hyphomycetes, and the x-axis shows the range of each environmental variable. The response curves illustrate how variations in each factor, such as bromide (Br), copper (Cu), dissolved oxygen (DO), sulfate (SO4), phosphorus (P), and potassium (K)affect hyphomycete density, highlighting the sensitivity of hyphomycete communities to these environmental drivers.

Figure 5. Effects of the six most influential environmental variables on the density of aquatic hyphomycetes. Each panel represents the fitted response curve for one environmental variable derived from the Boosted Regression Trees (BRT) model and the respective relative influences (R.I). The y-axis indicates the predicted density of hyphomycetes, whereas the x-axis represents the range of each

environmental variable. The response curves illustrate variations in ammonium (NH4), fluoride (F), chloride (Cl), and temperature (Temp.), Nitrogen (N), and precipitation (Precip.) affects hyphomycete density, highlighting the sensitivity of hyphomycete communities to these environmental drivers.

Figure 6. The figure displays the taxa ridge plot from the Threshold Indicator Taxa Analysis (TITAN), illustrating the response of indicator taxa along the environmental gradient. The analysis identified three indicator taxa out of the 90 possible: two taxa showing significant declines ("Decreasers") and one taxon showing significant increases ("Increasers") across the evaluated environmental thresholds. Ridges represent the distribution of change points (thresholds) for each indicator taxon, highlighting their sensitivity to environmental gradients. Af = *Anguillospora filiformes*, Tm = *Tricelophorus monosphorus*, Al = *Amniculicula longissima*.

Figure 7. Generalized Additive Mixed Model (GAMM) results for species richness (top row) and density of aquatic hyphomycetes (bottom row), highlighting interannual (left column) and intra-annual (right column) variations. The interannual graphs (left column) display the richness and conidial density as functions of the year (Adjusted_Year). The x-axis represents years, and the y-axis shows the predicted values for species richness (top left) and conidial density (bottom left). Smooth curves highlight interannual trends, with shaded regions representing 95% confidence intervals. The intra-annual graphs (right column) illustrate the seasonal (monthly) variation in richness and conidial density modeled using cyclic splines. The x-axis represents months, and the y-axis shows the predicted values for species richness (top right) and conidial density (bottom right). Smooth curves represent intra-annual patterns, with shaded areas indicating 95% confidence intervals.

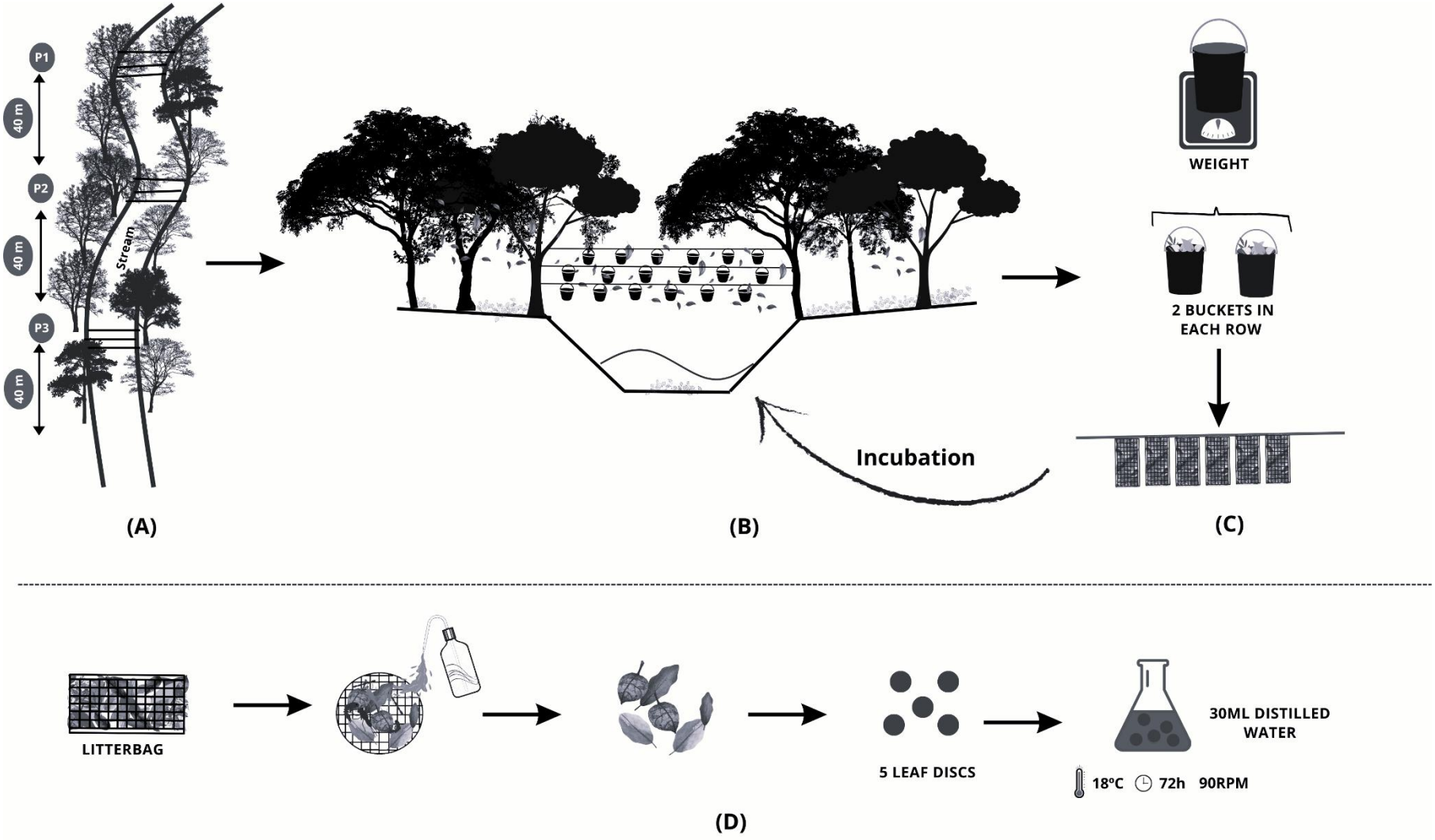

P1
40 m
P2
40 m
P3
40 m
Stream
(A)
Incubation
(B)
WEIGHT
2 BUCKETS IN EACH ROW
(C)
LITTERBAG
5 LEAF DISCS
30ML DISTILLED WATER
18°C
72h
90RPM
(D)

Figure 1.

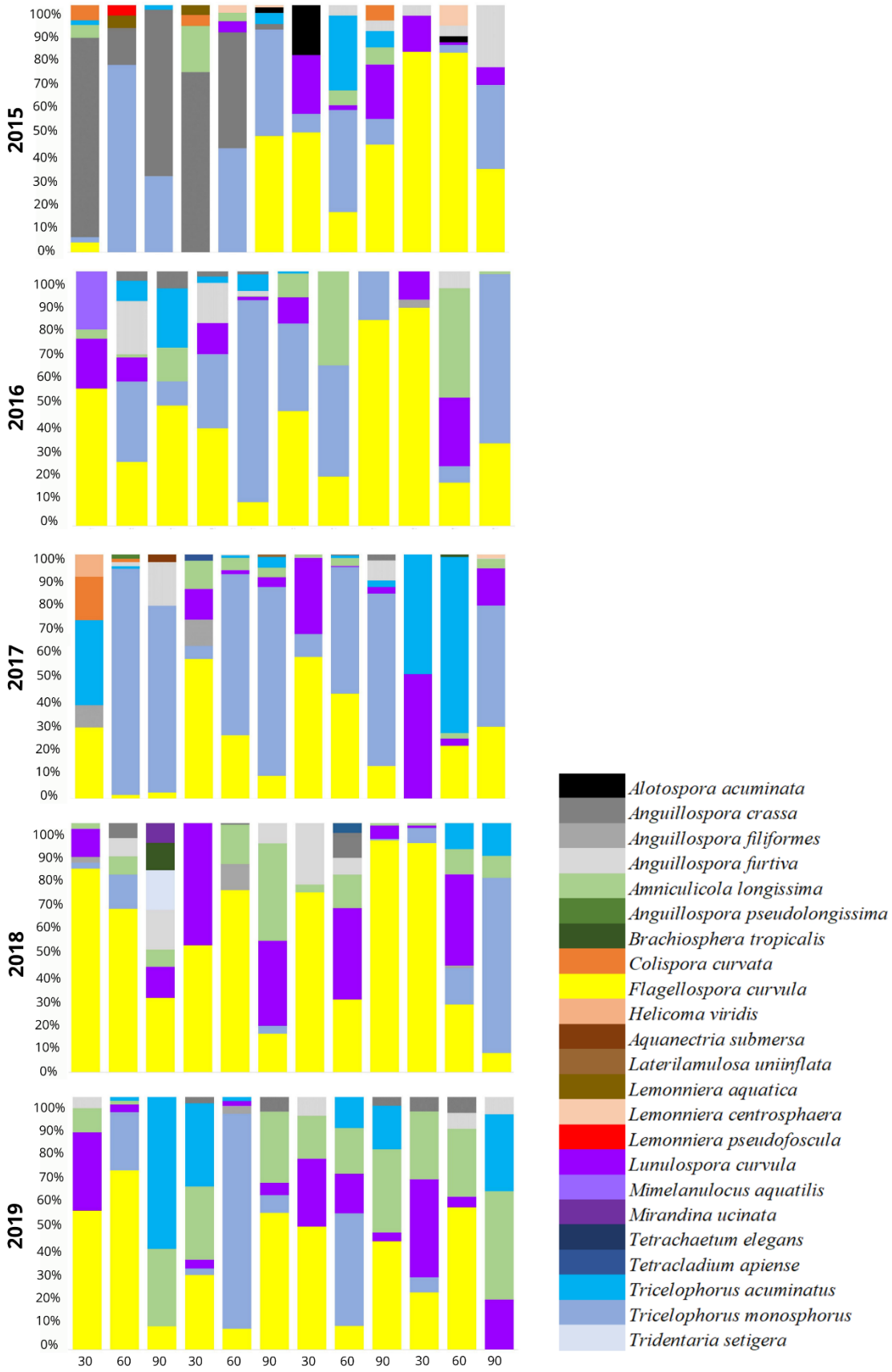
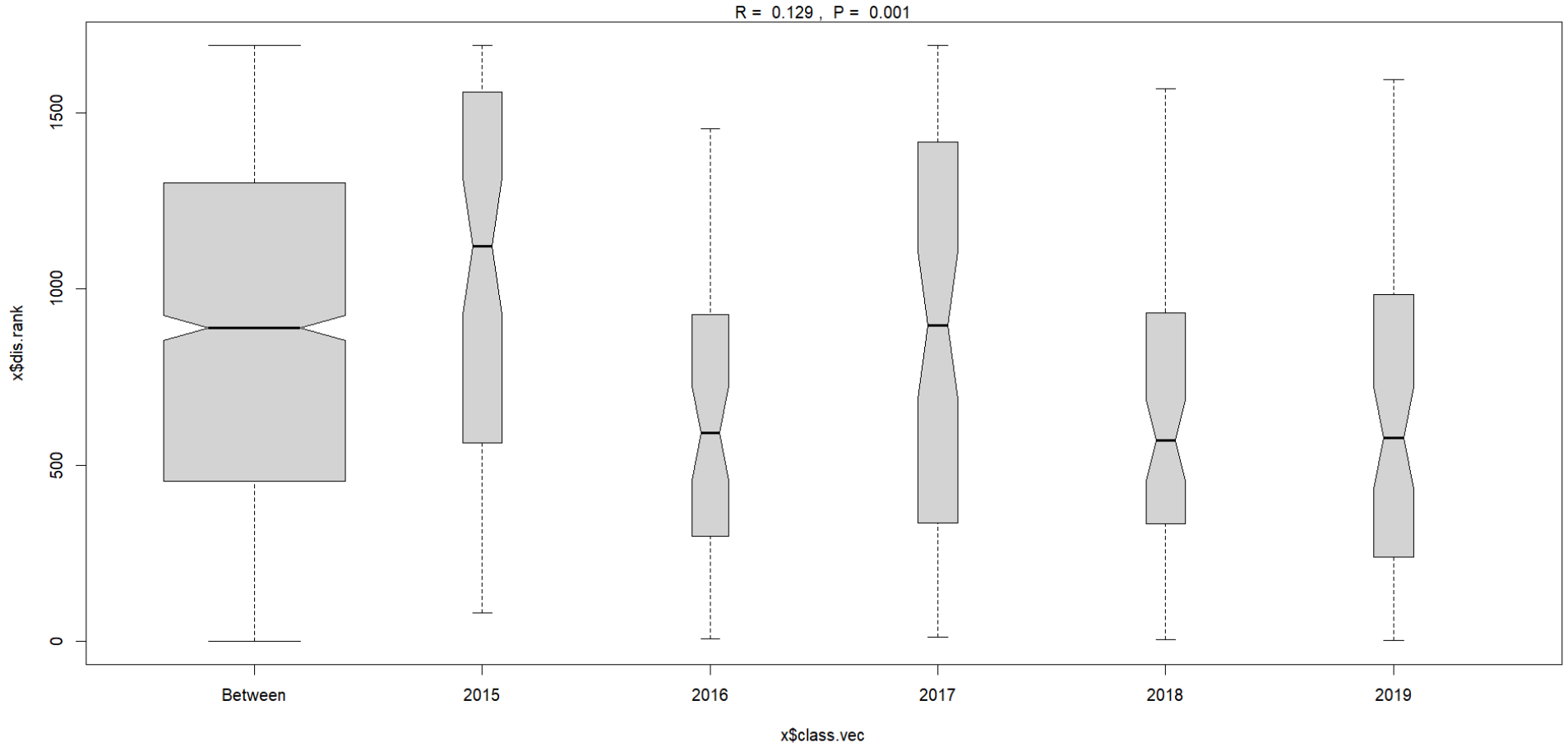

2015
2016
2017
2018
2019
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
30
60
90
Alotospora acuminata
Anguillospora crassa
Anguillospora filiformes
Anguillospora furtiva
Amniculicola longissima
Anguillospora pseudolongissima
Brachiosphera tropicalis
Colispora curvata
Flagellospora curvula
Helicoma viridis
Aquanectria submersa
Laterilamulosa uniinflata
Lemonniera aquatica
Lemonniera centrosphaera
Lemonniera pseudofoscula
Lunulospora curvula
Mimelanulocus aquatilis
Mirandina ucinata
Tetrachaetum elegans
Tetracladium apiense
Tricelophorus acuminatus
Tricelophorus monosphorus
Tridentaria setigera

Figure 2.



947

948 **Figure 3.**

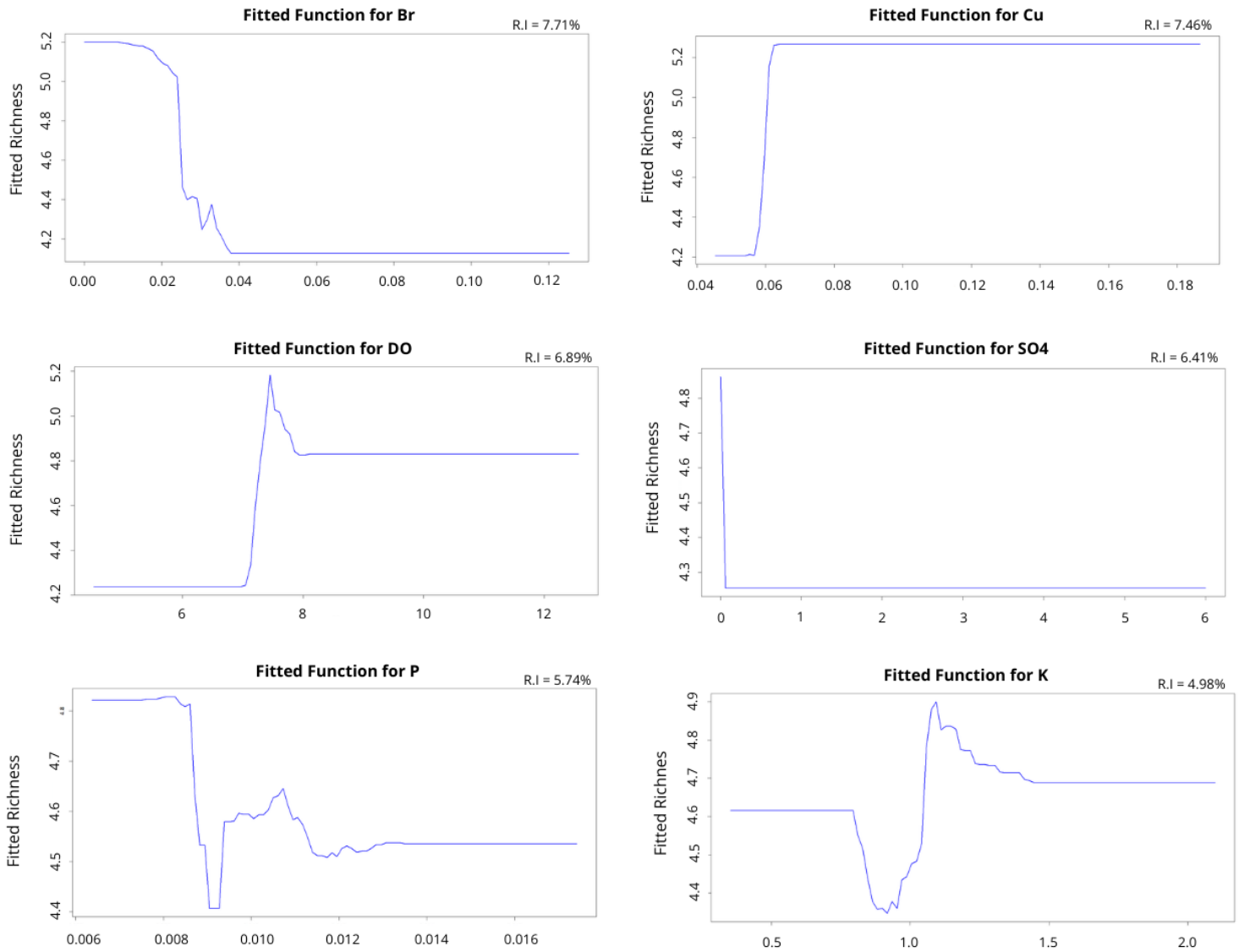

Fitted Function for Br
R.I = 7.71%
Fitted Richness
Fitted Function for Cu
R.I = 7.46%
Fitted Richness
Fitted Function for DO
R.I = 6.89%
Fitted Richness
Fitted Function for SO4
R.I = 6.41%
Fitted Richness
Fitted Function for P
R.I = 5.74%
Fitted Richness
Fitted Function for K
R.I = 4.98%
Fitted Richnes

Figure 4.

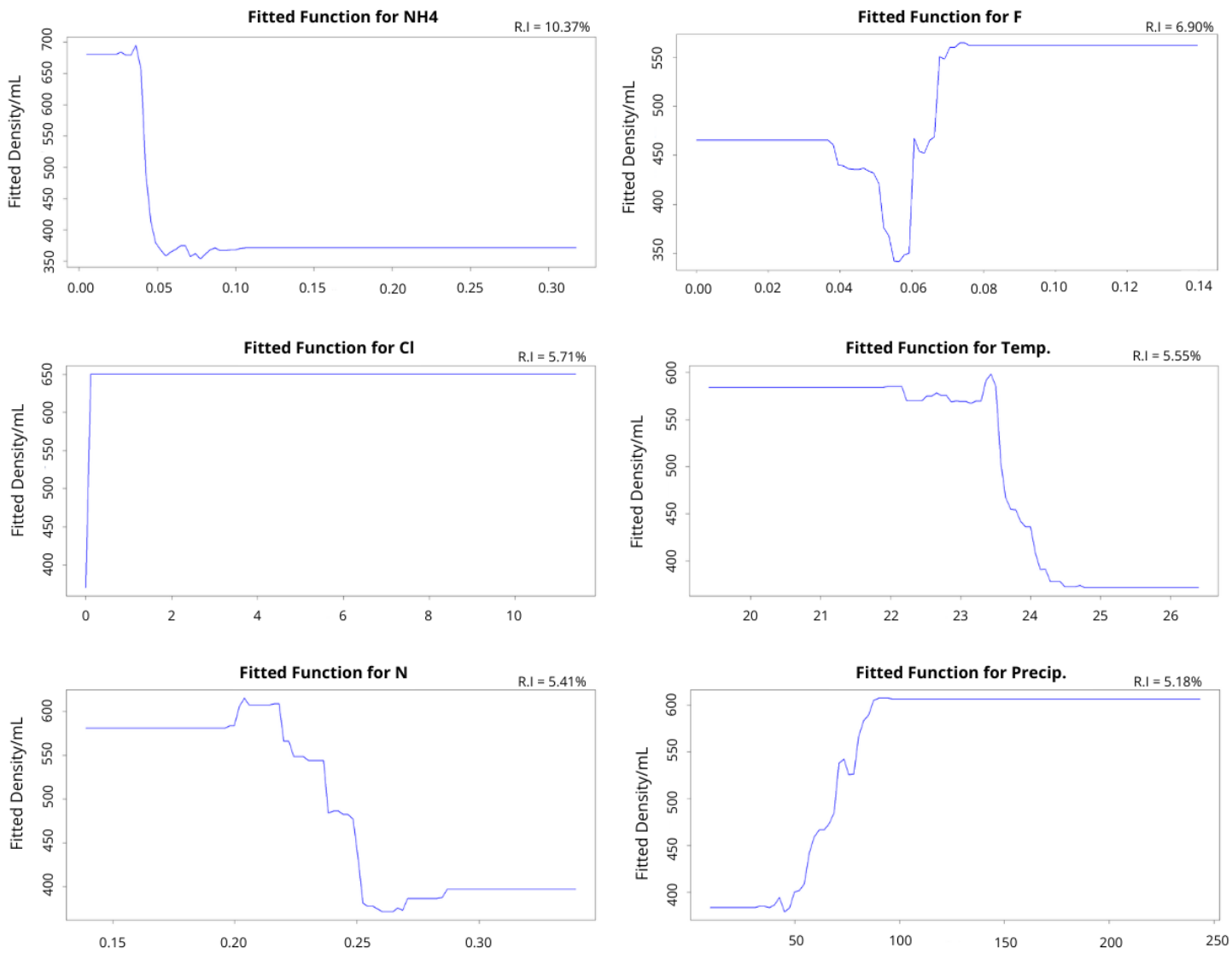
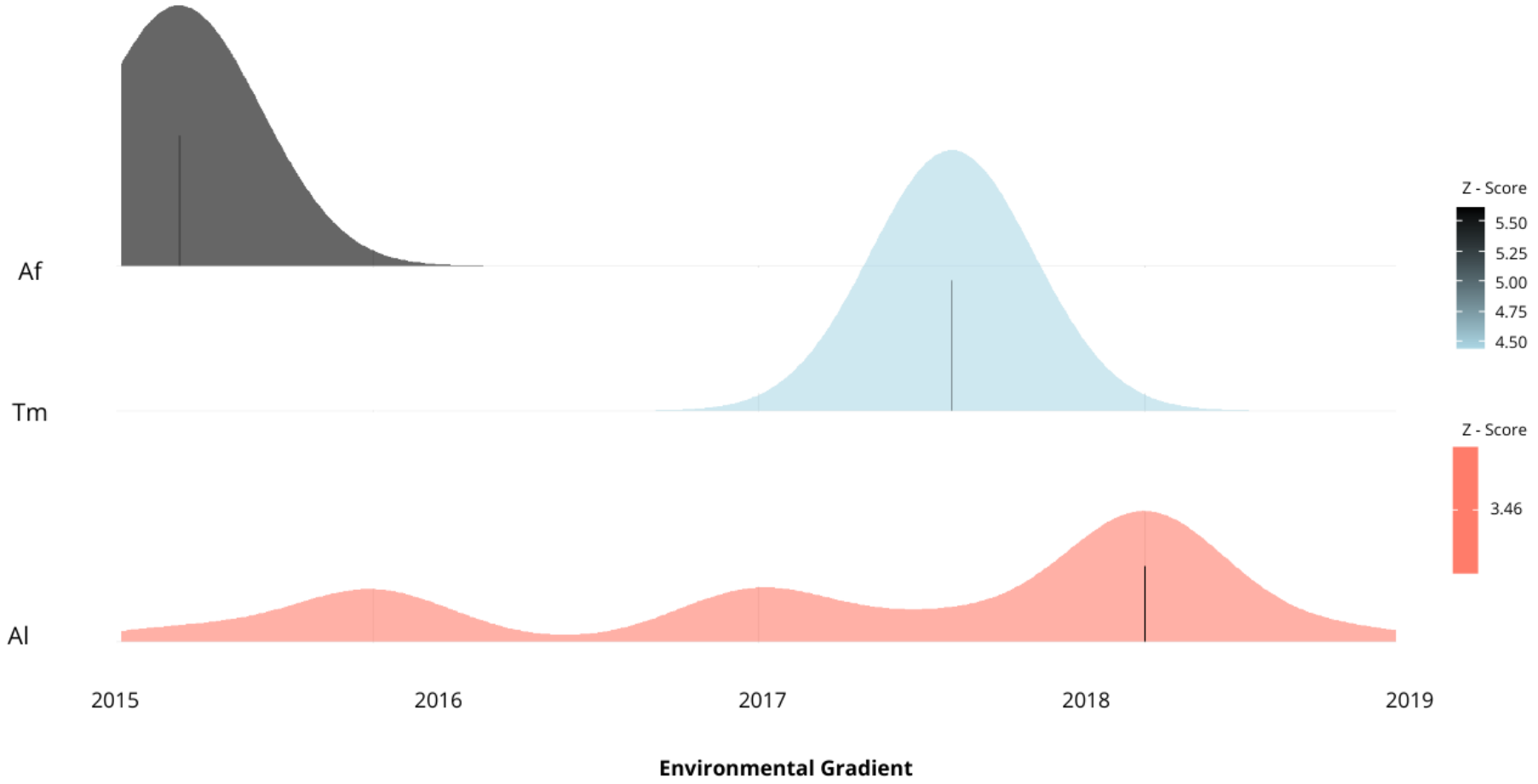

Fitted Function for NH4
R.I = 10.37%
Fitted Density/mL
Fitted Function for F
R.I = 6.90%
Fitted Density/mL
Fitted Function for Cl
R.I = 5.71%
Fitted Density/mL
Fitted Function for Temp.
R.I = 5.55%
Fitted Density/mL
Fitted Function for N
R.I = 5.41%
Fitted Density/mL
Fitted Function for Precip.
R.I = 5.18%
Fitted Density/mL

Figure 5.

975



976

977 **Figure 6.**

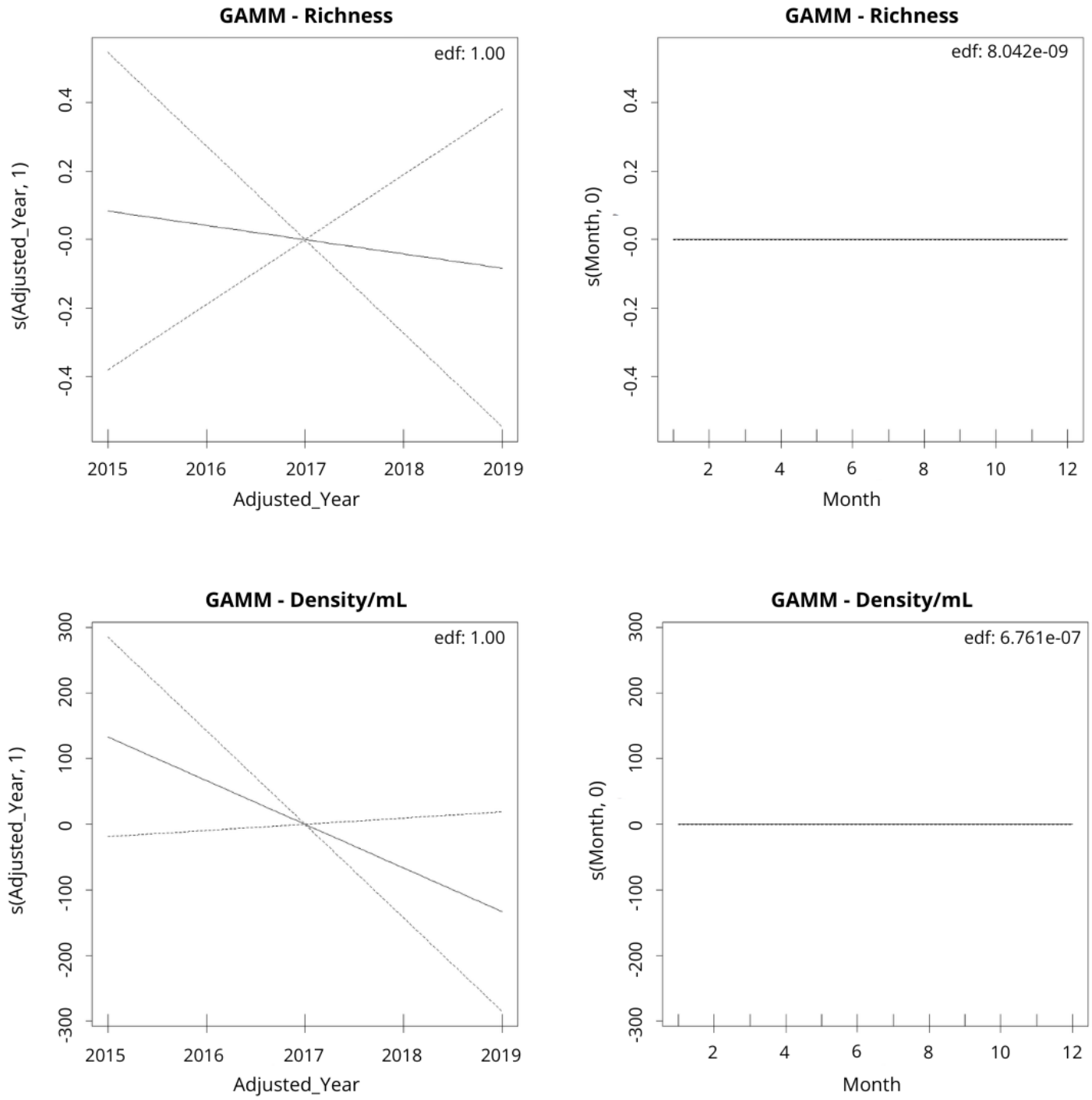

GAMM - Richness
edf: 1.00
s(Adjusted_Year, 1)
0.4
0.2
-0.0
-0.2
-0.4
2015
2016
2017
2018
2019
Adjusted_Year
GAMM - Richness
edf: 8.042e-09
s(Month, 0)
0.4
0.2
-0.0
-0.2
-0.4
2
4
6
8
10
12
Month
GAMM - Density/mL
edf: 1.00
s(Adjusted_Year, 1)
300
200
100
0
-100
-200
-300
2015
2016
2017
2018
2019
Adjusted_Year
GAMM - Density/mL
edf: 6.761e-07
s(Month, 0)
300
200
100
0
-100
-200
-300
2
4
6
8
10
12
Month

Figure 7.

Capítulo II

Artigo a ser submetido ao periódico *Ecology*

Efeitos de escala temporal na decomposição revelam vias ambientais indiretas em um riacho da Mata Atlântica: insights de um estudo de cinco anos

Timescale effects on decomposition reveal indirect environmental pathways in an Atlantic Forest stream: insights from a five-year study

Edson Serafim de Almeida Junior[1*], Renan de Souza Rezende[2], José Francisco Gonçalves-Júnior[3], Adolfo Ricardo Calor[4], Maria Lenise Silva Guedes[5], Alessandra Nasser Caiafa[6], Daniela Mariano Lopes da Silva[7], Guilherme Pereira da Silva Sena[3], Jéssica Carneiro de Souza[7], Adriana Oliveira Medeiros[1].

[1] - Environmental Mycology Laboratory, Institute of Biology, Federal University of Bahia, 40170-115, Salvador, BA, Brazil.

[2] - Postgraduate Program in Environmental Sciences, Communitarian University of Chapecó Region – Unochapecó, 89809-000, Chapecó, SC, Brazil.

[3] - Aquaripária/Limnology Laboratory, Department of Ecology, University of Brasilia, 70910-900 Brasília, Brazil.

[4] - Aquatic Entomology Laboratory, Institute of Biology, Federal University of Bahia, 40170-115, Salvador, BA, Brazil.

[5] - Herbarium Alexandre Leal Costa, Institute of Biology, Federal University of Bahia, 40170-115, Salvador, BA, Brazil.

[6] - Plant Ecology Laboratory and Ecological Restoration, Center of agrarian, environmental and biological sciences, Federal University of Recôncavo da Bahia, 44380-000, Cruz das Almas, BA, Brazil.

[7] - State University of Santa Cruz, Departament of Biological Science, Rodovia Ilhéus Itabuna km 16- Salobrinho, 45662900 - Ilhéus, BA, Brazil.

*Corresponding author: edsonjunior.bio@outlook.com

Abstract

The decomposition of allochthonous organic matter is a fundamental process for carbon and nutrient cycling in headwater streams. This study investigated the temporal scale and environmental drivers of organic matter decomposition in an Atlantic Forest stream over a five-year period. Using Principal Component Analyses and Structural Equation Models, we assessed the direct and indirect effects of climatic, environmental, and biotic variables on the decomposer community structure and leaf litter decomposition. Leaf litter decomposition rates have not been directly predicted by environmental, climatic, or biological variables, thus challenging the prevailing paradigm of a tightly coupled relationship between short-term drivers and decomposition processes. Instead, this finding suggests that indirect, time-lagged mechanisms are the primary forces shaping ecosystem functioning. However, the temporal scale and dissolved nutrient gradients were the main drivers of the decomposer community structure, showing significant direct effects. Indirectly, the temporal scale had a negative influence on air temperature, which in turn positively affected water chemistry, thereby affecting the decomposer community. Such dynamics reveal the buffering capacity of tropical headwater streams and highlight the critical value of long-term ecological observations in detecting subtle yet consequential patterns in ecosystem processes.

Introduction

Temporal variability, manifested through seasonal and interannual climatic fluctuations, is a key ecological driver in tropical headwater streams, where it shapes the hydrology, resource availability, and activity of biological communities (Tonin et al. 2017, del Cid et al. 2019, Taniwaki et al. 2019). In these ecosystems, precipitation and temperature influence the magnitude and timing of organic matter inputs, metabolic capacity of decomposers, and rate of ecosystem processes, such as organic matter decomposition (Martins et al. 2017, Tonin et al. 2017, Correa-Araneda et al. 2020). Moreover, extreme events, such as droughts and floods, can alter stream functioning by disrupting decomposer communities and decoupling biotic-environmental interactions (Prieto et al. 2019, Carey et al. 2021).

In tropical forest streams, allochthonous leaf litter is the primary source of energy and nutrients for the aquatic food web, accounting for up to 90% of total organic matter input (Tonin et al. 2017, Sena et al. 2020). Once retained in the stream, the leaves undergo microbial conditioning and fragmentation, initiating the decomposition process (Gessner et al. 2010, Gonçalves et al. 2012). This process is primarily mediated by aquatic hyphomycete fungi, which release enzymes capable of breaking down complex polymers, and by shredding invertebrates, which convert coarse litter into finer particulate matter (Sena et al. 2020, Barros and Seena 2022). The efficiency of this trophic interaction depends on both the quality of the leaves and physicochemical conditions of the stream, including dissolved oxygen, pH, and nutrient concentrations (Raposeiro et al. 2018, Yue et al. 2022).

While the influence of individual environmental drivers on decomposition is well documented, less is known about how these drivers interact in combination over longer temporal scales (Isaak et al. 2012, Rubenstein et al. 2017, Nguyen et al. 2023). In

particular, the temporal scale acts both directly by modulating environmental conditions and indirectly by reshaping decomposer community structure and function. For example, seasonal temperature peaks may accelerate microbial activity but lower DO levels, whereas interannual variations in rainfall may affect nutrient input, species turnover, or substrate accumulation (Fenoy et al. 2022, Rabelo et al. 2024). Despite its ecological relevance, the influence of timescale on the integration of these factors remains understudied, especially in tropical systems, where long-term datasets are scarce (del Cid et al., 2019; Rabelo et al., 2024).

To address this knowledge gap, we conducted a five-year study in an Atlantic Forest headwater stream to investigate how temporal variation (both seasonal and interannual) affects leaf litter decomposition and the associated decomposer community. We developed a conceptual model (Figure 1) that integrates environmental (e.g., precipitation, temperature, pH, and dissolved nutrients), chemical (leaf quality), and biological (fungal and invertebrate communities) variables to evaluate the direct and indirect effects on decomposition. Specifically, we hypothesized that (1) decomposition rates and decomposer community structure would vary over time in response to seasonal and interannual climate variability and water quality; and (2) decomposition would be enhanced under conditions of higher precipitation and nutrient availability but could be constrained by extreme hydrological events or low oxygen levels. By identifying the environmental and biological drivers of decomposition over time, this study contributes to our understanding of tropical stream functioning and provides insights into ecosystem resilience under changing climatic conditions.

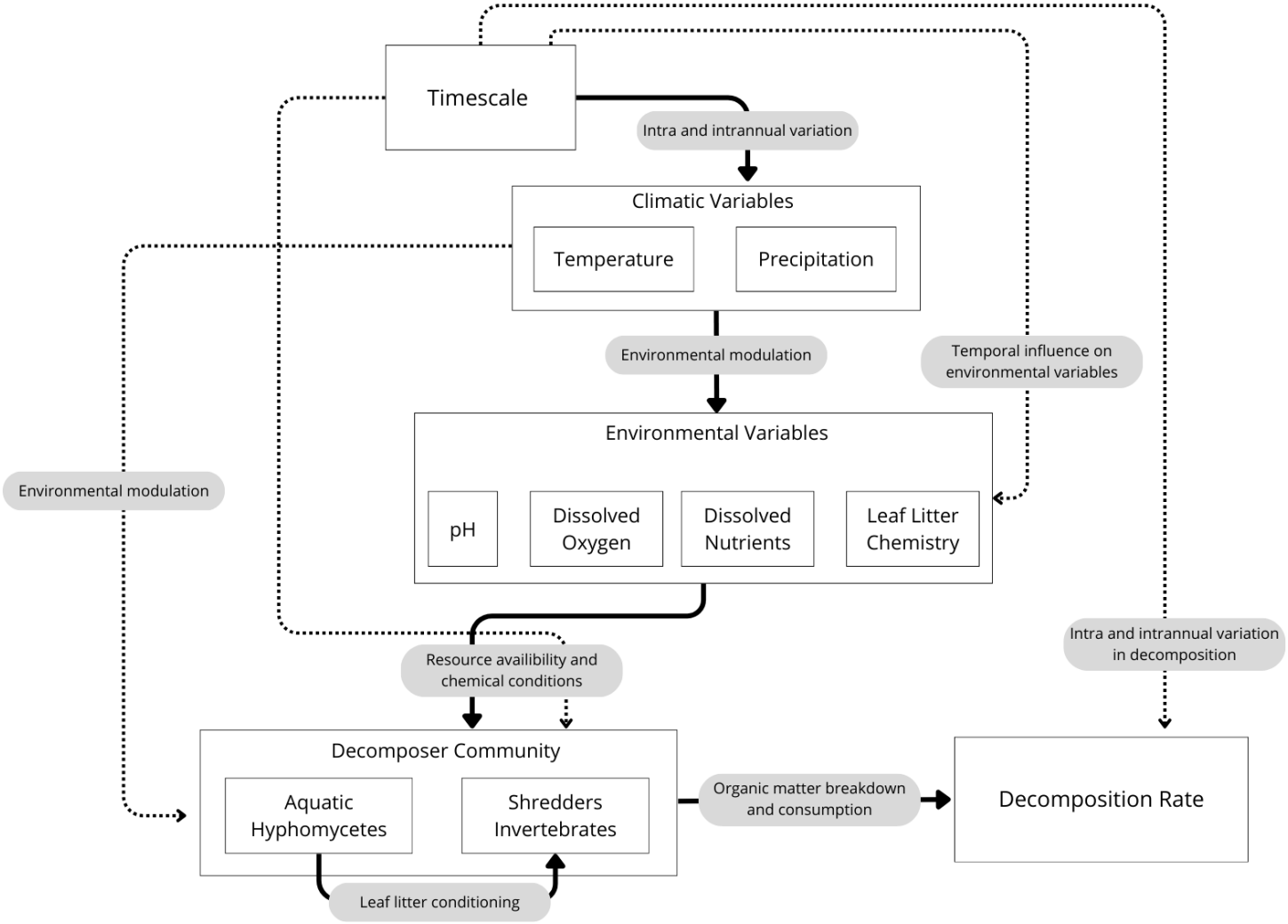


Figure 1. The diagram illustrates a conceptual model designed to assess both the direct and indirect effects of temporal scales, as well as environmental and climatic variables, on the decomposition of allochthonous organic matter in tropical headwater streams. Solid arrows represent direct interactions between system components, whereas dashed arrows indicate indirect pathways. The model integrates intra- and interannual variability, emphasizing the role of the temporal dimension in shaping ecological processes.

Materials and Methods

Study area

The study was conducted in Serra da Jibóia, Bahia, Brazil, a mountainous region within the Atlantic Rainforest, covering approximately 23,000 ha. Serra da Jibóia spans five counties: Varzedo, Castro Alves, Santa Teresinha, São Miguel das Matas, and Elísio Medrado. The area encompasses 8,611 ha and features forest fragments at various stages of conservation (Blengini et al. 2015). Riparian vegetation is classified as secondary forest at an intermediate stage of regeneration. The soil in the region is a combination of Haplic Cambisol and Litholic Neosol soils. The arboreal canopy ranges from open to closed and is dominated by small-diameter tree species, with an average height of 9.4 meters, although some trees reach up to 13 m (Blengini et al., 2015). The study was carried out over five years, from 2015 to 2020, in the riparian zone of a second-order stream located in Serra da Jibóia, within Varzedo County, BA (S 12º 57.597', W 039º 26.932'), situated in the southern portion of the mountain range.

Experimental design and procedures

Our experimental design, adapted from del Cid et al. (2019), aimed to assess the input and decomposition of allochthonous organic matter. The study was conducted across three distinct reaches of the Cai Camarão stream, each spaced 40 m apart, encompassing a total sampling length of 120 m. In each reach, 18 perforated buckets were deployed in three of six rows to collect leaf litter. These buckets were emptied monthly 30 days before each sampling event to ensure that only leaf litter accumulated over a precise 30-day period was collected. This collection procedure was repeated quarterly (in January, April, July, and October) over five consecutive years, ensuring a comprehensive temporal coverage of litterfall dynamics.

The leaf litter collected from these buckets served two purposes: (1) to analyze leaf litter chemistry (C, N, and P concentrations) and (2) to set up in-stream decomposition experiments (below). From all the collected buckets, the two with the highest leaf weights from each row (totaling six buckets per sampling point) were selected. The accumulated leaves from these selected buckets were then carefully placed into coarse-mesh litter bags (10 mm mesh size) and submerged in the stream for incubation. Litter bags were retrieved at 30, 60, and 90-day post-incubation, resulting in four distinct incubation periods per year.

Upon retrieval, the samples were transported to the laboratory in ice coolers to preserve their integrity. In the laboratory, leaves were gently rinsed with distilled water over a 0.45 µm sieve to separate associated invertebrates and excess sediment. The retained invertebrates and sediment were transferred to 50 ml Falcon tubes containing 70% ethanol for preservation and later sorted under a stereomicroscope. From the rinsed leaf material, two sets of five leaf discs were prepared per sample; one set was used to measure the sporulation rate of aquatic hyphomycete fungi, and the other set was designated for ash-free dry mass (AFDM) determination, which is essential for mass loss calculations. The remaining leaf litter was stored for chemical analysis of the leaf composition.

Decomposition rate

To determine mass loss, decomposition coefficients were calculated by applying the leaf mass data to the negative exponential model Wt = Wo × e^(-kt), where Wt represents the remaining leaf mass at time t (in days), Wo is the initial leaf mass, and k is the decomposition coefficient (Graça et al., 2020). For this calculation, it was essential to compare the initial dry mass with the remaining dry mass. Because the leaves were incubated in their natural state (either wet or air-dried), the initial mass (Wo) was

converted to an oven-dry equivalent. This was achieved by determining the proportion of moisture in replicate subsamples of non-incubated air-dried detritus. The subsamples were weighed, oven-dried at 60°C for 72 h, and weighed again. The oven-dry mass was divided by the air-dry mass to generate the conversion factor. This factor was then applied to the initial mass of all the incubated leaves.

To obtain the ash-free dry mass (AFDM), five leaf discs from the retrieved samples were dried in an oven at 60°C for 72 h and weighed on a precision balance to determine their dry weight. The discs were then incinerated in a muffle furnace at 550°C for 4 h and the remaining ash was weighed. AFDM was calculated by subtracting the ash weight from the dry weight, and this value was extrapolated to the total sample. This AFDM value was also applied to the initial dry mass (Wo) for accurate comparison of organic matter loss.

Sporulation rates and the aquatic hyphomycetes community

Five random leaf discs were taken from each sample for fungal analysis. These discs were transferred to 125 mL Erlenmeyer flasks containing 30 mL of distilled water and placed on an orbital shaker at 90 rpm for 48 h at 18°C. The resulting spore suspensions were fixed in 4% formalin, filtered through 5-µm pore size Millipore filters (Billerica, MA, USA), and stained with 0.05% cotton blue in 60% lactic acid. The filters were examined under a compound microscope (Olympus BX 43) at 400x magnification to estimate the number of retained conidia and to identify the species present (Bärlocher et al. 2020). Spore morphology was used to determine the composition of the aquatic hyphomycete community following existing taxonomic keys (Fiuza et al. 2015, 2017). The results were expressed as hyphomycete richness and conidial density.

Identification of invertebrates

179 The initial washing step described for aquatic hyphomycetes also enabled the collection
180 of invertebrates associated with leaf material. After washing the leaves to remove excess
181 sediment and dislodged invertebrates, the residue was retained on a 45µm sieve. The
182 retained material was then sorted, and the invertebrates were identified to the family level
183 using specific taxonomic keys (Mungai et al., 2010). The number of individuals in each
184 sample was counted. The results were expressed in terms of invertebrate richness and
185 density.

186 *Leaf litter chemistry*

187 For the leaf litter chemical analysis, we followed the methodology outlined by Flindt et
188 al. 2020. Leaves were collected from the vertical inputs along the stream. The mixed leaf
189 samples were dried in a forced-air oven at 60°C for 72 h, weighed, and ground into a fine
190 powder using a ball mill. This powdered material was then used for the chemical analyses
191 of carbon (C), nitrogen (N), and phosphorus (P) concentrations. For phosphorus (P)
192 analysis, the samples were incinerated in a muffle furnace for 4 h. After incineration, 5
193 mg of ash was dissolved in deionized water with HCl, filtered, and spectrophotometrically
194 analyzed at 882 nm. P concentrations were determined using a standard curve. For
195 nitrogen (N) analysis, 0.005 g of the sample was digested with copper sulphate and
196 sulfuric acid, followed by neutralization with NaOH. The resulting solution was filtered,
197 and reagents producing a blue colour were added. The nitrogen concentration was
198 measured spectrophotometrically. Carbon (C) is used as the combustion method. The
199 dried and ground samples were ignited in a muffle furnace at 500°C to determine the ash-
200 free dry mass, which was used to calculate the carbon concentrations.

201 *Water physical-chemical*

Water samples were collected monthly from each headwater stream site using 50 ml Falcon tubes and transported to the laboratory in a cooler with ice to preserve sample integrity. The samples were filtered through 0.45 µm cellulose acetate filters (Sartorius Stedim, Germany) to remove impurities and suspended solids and were kept chilled to maintain their original properties. Inorganic anions, including chloride, nitrite, bromide, nitrate, phosphate, and sulphate, were analyzed by Metrohm ion chromatography. Cations such as ammonium, sodium, potassium, calcium, and magnesium were also analyzed using chromatography techniques. Cation determination was conducted on a MetroSep C4 250/4.0 mm column with an eluent of 1.7 mM nitric acid and 0.7 mM dipicolinic acid, using non-suppressed conductivity detection. Anion determination utilized a MetroSep A Supp 5 250/4.0 mm column with an eluent composed of 3.2 mmol/L sodium carbonate and 1 mmol/L sodium bicarbonate, employing suppressed conductivity detection (Djam et al. 2019, Mohana Rangan et al. 2021).

Climatic Parameters

Precipitation and temperature data were obtained from the National Institute of Meteorology (INMET) at the Serra da Jiboia Weather Monitoring Station, located in Amargosa, Bahia, the station closest to the study site. The phytophysiognomy of the studied region aligns with the area where climatic data were collected (Stape et al. 2014).

Data analysis

All statistical analyses were performed in R software (version 4.3.2; R Core Team, 2023), utilizing the zoo, mice, dplyr, FactoMineR, factoextra, missMDA, vegan, ggplot2, lme4, car, piecewiseSEM, lavaan, and semPlot packages.

Initially, data were inspected for missing values. To address punctual gaps in the continuous time series, linear interpolation by approximation (na.approx, zoo package) was applied. For variables that presented more than one missing point or did not follow a simple temporal distribution, multiple imputations by predictive mean matching (mice, 'pmm' method) were used.

To reduce dimensionality and explore the main environmental and biotic gradients over time, Principal Component Analyses (PCA) were performed using the PCA() function from the FactoMineR package, with visualizations generated by fviz_pca_var() (factoextra package). PCAs was conducted separately for four groups of variables: (i) climate (precipitation and temperature), (ii) dissolved nutrients (15 inorganic and ionic parameters), (iii) leaf quality (C, N, and P in leaves), and (iv) decomposer community (hyphomycete and invertebrate richness and density).

Causal relationships between environmental and biotic variables and organic matter decomposition were evaluated using Structural Equation Models (SEM) with the psem() function from the piecewiseSEM package. Two models were constructed: (1) a complete model, with all ecologically relevant variables based on the created theoretical model, and (2) an optimized model, built by progressive elimination of non-significant paths ($p > 0.05$), based on parsimony criteria and model fit (AIC, Fisher's C). The optimized model retained only the paths with statistical support found in the full model.

The quality of the model fit was assessed based on the d-separation test (Fisher's C), the model's chi-square value, and the coefficients of determination (R^2) for each equation. Direct and indirect effects were interpreted based on standardized coefficients (standardized = TRUE). Multicollinearity was checked using the vif() function (car package), and all variables with a VIF greater than five were reviewed and adjusted to

avoid redundancies. Graphical representations of the SEM models were produced using the semPlot package and PCA graphs with ggplot2 and factorextra.

Results

Environmental, Climatic, and Stream Features Overview

The streams studied showed significant variations in environmental conditions over five years. Precipitation fluctuated notably, peaking at 1.033 mm in 2015 and hitting a low of 625 mm in 2018. Temperatures, however, stayed relatively stable, with minor variations between 23.3°C in 2015 and 22.7°C in 2018, before rising slightly again in 2019 to 23.5∘C.

The water's physical and chemical parameters also changed. The pH increased from an initial acidic value of 5.9 in 2015 to 7.4 in 2019, suggesting a trend toward higher alkalinity. Dissolved oxygen (DO) concentrations declined steadily from 9.10 mg/L in 2015 to a minimum of 7.23 mg/L in 2018, with a small recovery to 7.36 mg/L in 2019.

Water chemistry showed significant changes in ion concentrations. Ammonium (NH4) and nitrate (NO3) increased gradually over the years, while calcium (Ca), phosphate (PO4), and sulfate (SO4) concentrations generally decreased. Other ions like sodium (Na) and potassium (K) remained relatively stable. Regarding leaf litter chemistry, carbon (C) and nitrogen (N) concentrations fluctuated, but phosphorus (P) concentrations showed a clear upward trend, suggesting a gradual accumulation of phosphorus in the system over time.

Leaf litter decomposition pattern

Based on the calculated mass loss and decomposition coefficients for each quarter over the five-year study period (Figure 2), leaf litter decomposition behaved as follows: The year 2015 began with the study's highest decomposition rate in the first quarter (k=0.0237). The process then decelerated in the second quarter (k=0.0128), recovering in the third and fourth quarter (k=0.0211; k=0.0189). n 2016, decomposition rates were lower, with decomposition coefficients varying between k=0.0145 and k=0.0195. The year 2017 was notable for the study's highest overall decomposition rate, observed in the third quarter (k=0.0279), which contrasted with the year's lowest rate in the first quarter (k=0.0107). The second and fourth quarters had rates of k=0.0269 and k=0.0254, respectively. Although 2018 started with a low rate in the first quarter (k=0.0107), the decomposition process accelerated consistently, peaking in the second quarter (k=0.0233), followed by in the third and the fourth (k=0.0209; k=0.0197, respectively). Finally, 2019 presented the most uniform decomposition pattern, with very similar rates across the quarters, ranging from k=0.0195 to k=0.0205.

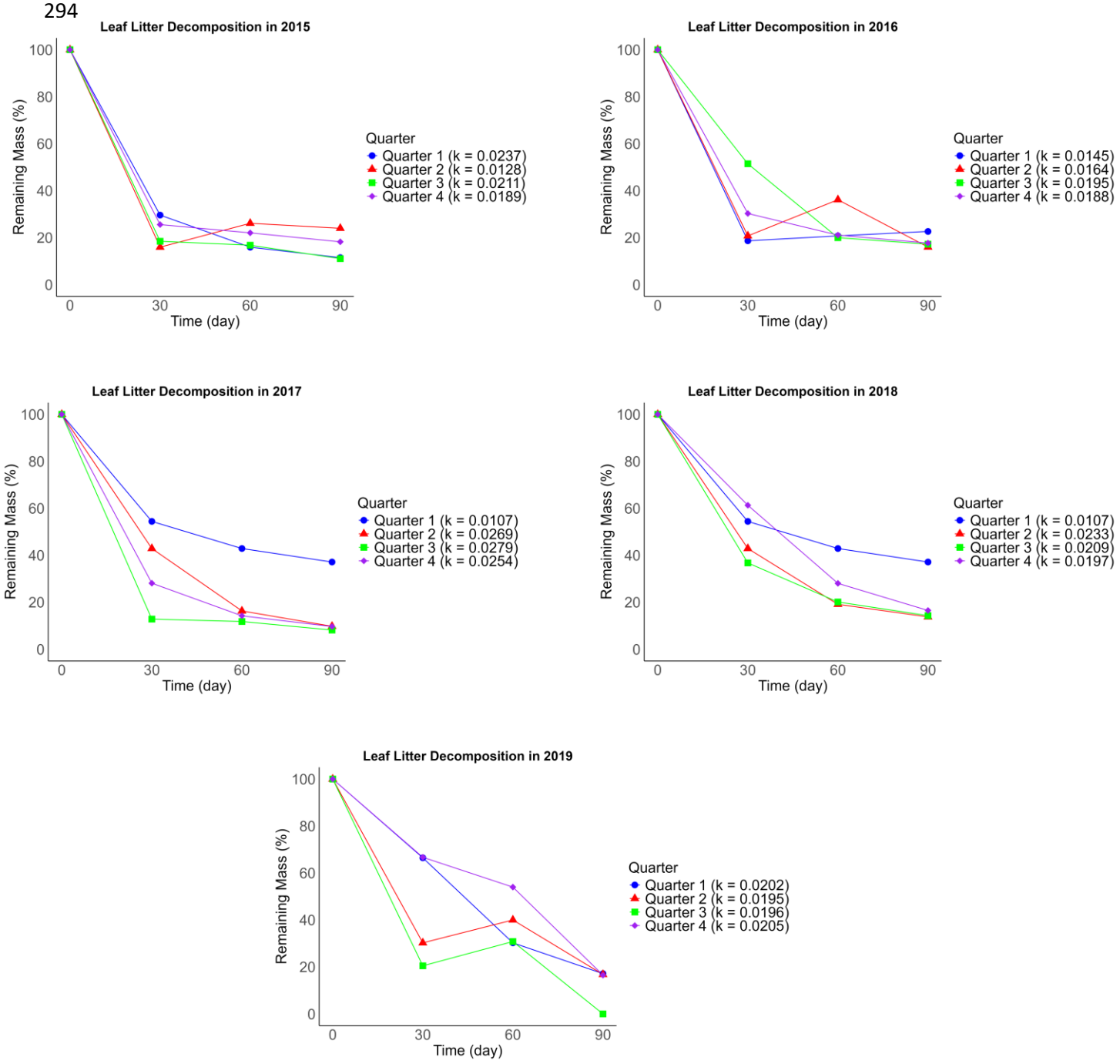


Figure 2. Variation in leaf litter decomposition over 90 days across different quarters and years (2015–2019) in a tropical headwater stream. Each panel represents a specific year, showing the percentage of remaining mass (%) at three incubation times (30, 60, and 90 days). Colors indicate the four quarters (Quarter 1 = February–April; Quarter 2 = May–July; Quarter 3 = August–October; Quarter 4 = November–January). Values of *k* (decomposition coefficient) are shown in the legend of each graph.

318

319 *Decomposer Community*

320

321 The decomposer community was characterized by two main groups: (I) aquatic
322 hyphomycetes and (II) aquatic invertebrates.

323

324 *(I) Aquatic Hyphomycetes*

325 Over the five-year study period, a total of 23 species of aquatic hyphomycetes were
326 identified (Table 1). A core group of seven species was found consistently in every year:
327 *Anguillospora filiformis*, *Anguillospora furtiva*, *Amniculicola longissima*, *Flagellospora*
328 *curvula*, *Lunulospora curvula*, *Tricelophorus acuminatus*, and *Tricelophorus*
329 *monosphorus*.

330 In contrast to these consistent species, the remaining taxa exhibited more sporadic or
331 intermittent occurrences. The highest richness of these rare species was observed in 2017,
332 with five taxa: *Anguillospora pseudolongissima*, *Helicoma viridis*, *Heliscus submersus*,
333 *Laterilamulosa uniinflata*, *and Tetracladium apiense,* documented exclusively in that
334 year. Other species with limited temporal presence included *Alatospora acuminata* and
335 *Lemonniera aquatica*, which were recorded only in 2015; *Mimelanolocus aquatilis*,
336 unique to 2016; and *Mirandina ucinata* and *Tetrachaetus elegans*, found solely in 2018.
337 This pattern of interannual variation suggests that a significant portion of the total richness
338 is composed of taxa sensitive to specific environmental conditions or of transient
339 colonizers of the leaf litter.

340

341

342 **Table 1.** Temporal occurrence of aquatic hyphomycete species recorded in a tropical
343 headwater stream over five years (2015–2019). The symbol "X" indicates the presence of the
344 species in each study year.

Species	2015	2016	2017	2018	2019
Alatospora acuminata	X				
Anguillospora crassa		X	X	X	X
Anguillospora filiformis	X	X	X	X	X
Anguillospora furtiva	X	X	X	X	X
Amniculicula longissima	X	X	X	X	X
Anguillospora pseudolongissima			X		
Brachiosphera tropicalis			X	X	
Colispora curvata	X		X		
Flagellospora curvula	X	X	X	X	X
Helicoma viridis			X		
Heliscus submersus			X		
Laterilamulosa uniinflata			X		
Lemonniera aquatica	X				
Lemonniera centrosphaera	X			X	
Lemonniera pseudofoscula	X				
Lunulospora curvula	X	X	X	X	X
Mimelanolocus aquatilis		X			
Mirandina ucinata				X	
Tetrachaetus elegans				X	
Tetracladium apiense			X		
Tridentária setigera				X	
Tricelophorus acuminatus	X	X	X	X	X
Tricelophorus monosphorus	X	X	X	X	X

345

346

347 *(II) Aquatic Invertebrates*

348 A total of 9 orders and 47 families of aquatic invertebrates associated with leaf litter
349 decomposition were identified (Table 2, Figure 3). The total taxonomic diversity was
350 dominated by the orders Trichoptera and Diptera, each exhibiting the highest family
351 richness with nine families. These were followed by the orders Hemiptera and Odonata,
352 which contributed seven and six families, respectively. The orders Coleoptera and

353 Ephemeroptera accounted for six and four families, while Plecoptera, Heteroptera, and
354 Crustacea were represented by two, two, and one family, respectively.

355 The family richness of the invertebrate community varied from year to year. The highest
356 diversity was recorded in 2017, with 31 families identified across 9 orders, followed by
357 2019, with 26 families. The years 2016 and 2018 showed similar richness (24 families
358 each), while the lowest diversity was observed in 2015, with only 21 families in 8 orders.

359

360 **Table 2.** Diversity of aquatic macroinvertebrates associated with leaf litter decomposition in a
361 tropical headwater stream. The table presents the recorded orders, the number of families
362 identified within each order, and the corresponding family list.

	Order	No. of Families	Families Identified
1	Coleoptera	6	Dytiscidae, Elmidae, Lampyridae, Lutrochidae, Psephenidae, Scirtidae.
2	Crustacea	1	Copepoda
3	Diptera	9	Ceratopogonidae, Chaboridae, Chaoboridae, Chironomidae, Culicidae, Empididae, Simulidae, Tabanidae, Tipulidae.
4	Ephemeroptera	4	Baetidae, Caenidae, Leptohyphidae, Leptophlebiidae.
5	Hemiptera	7	Hebridae, Helotrephidae, Hydrometridae, Mesoveliidae, Naucoridae, Pleidae, Saldidae.
6	Heteroptera	2	Gelastocoridae, Potamocoridae.
7	Odonata	6	Calopterigidae, Coenagrionidae, Dicteriadidae, Libellulidae, Megapodagrionidae, Perilestidae.
8	Plecoptera	2	Gripopterygidae, Perlidae.
9	Trichoptera	9	Calamoceratidae, Glossomatidae, Helicopsychidae, Hydropsychidae, Leptoceridae, Limnephilidae, Odontoceridae, Philopotamidae, Polycentropodidae, Hydroptilidae.

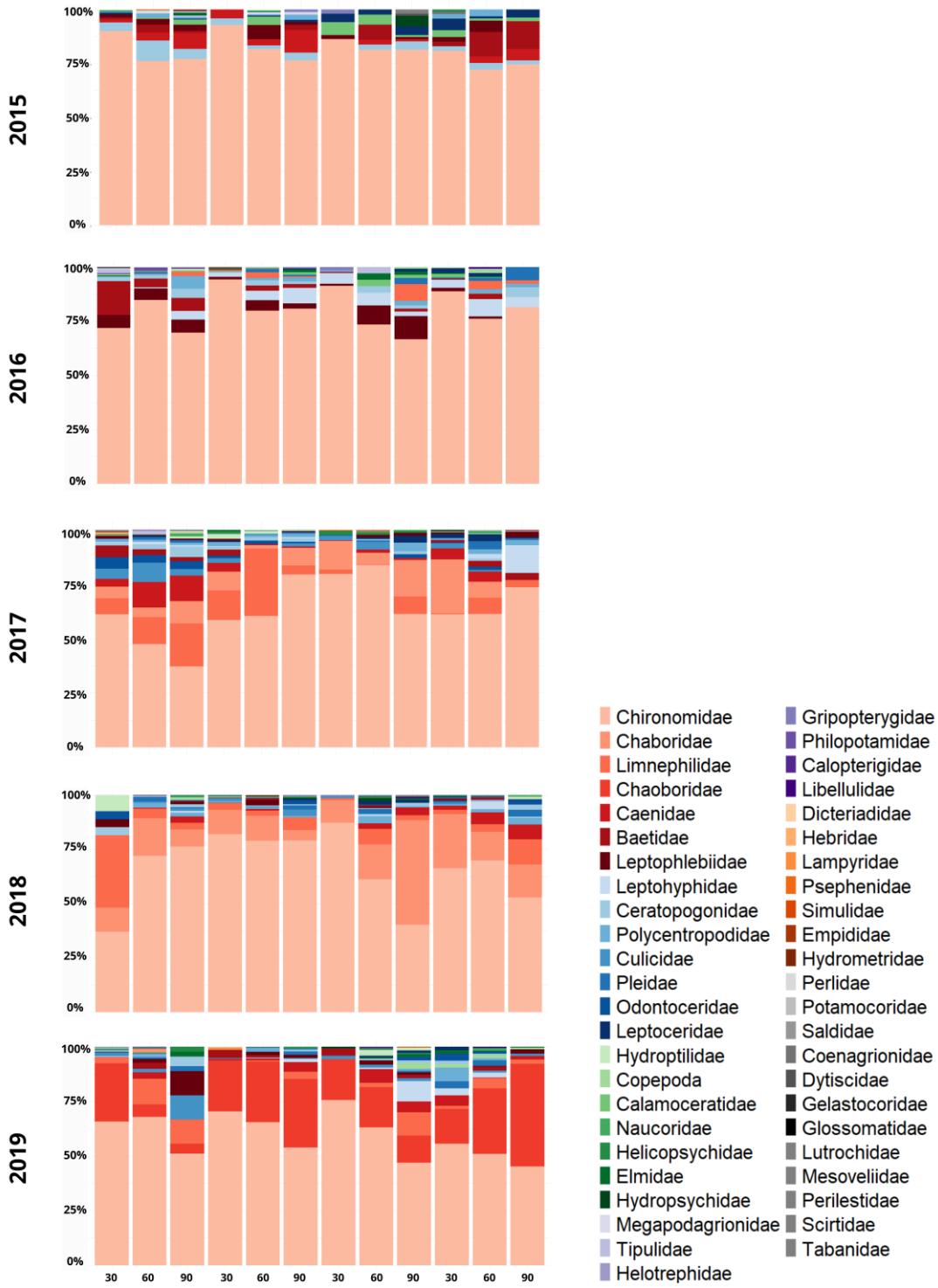


Figure 3. Relative composition of aquatic invertebrate communities during leaf litter decomposition in a tropical headwater stream from 2015 to 2019. Each panel represents a specific year, showing the relative abundance (%) of invertebrate families associated with submerged leaf litter at different incubation times (30, 60, and 90 days) across seasons. Colors indicate the different families identified.

The structural equation model

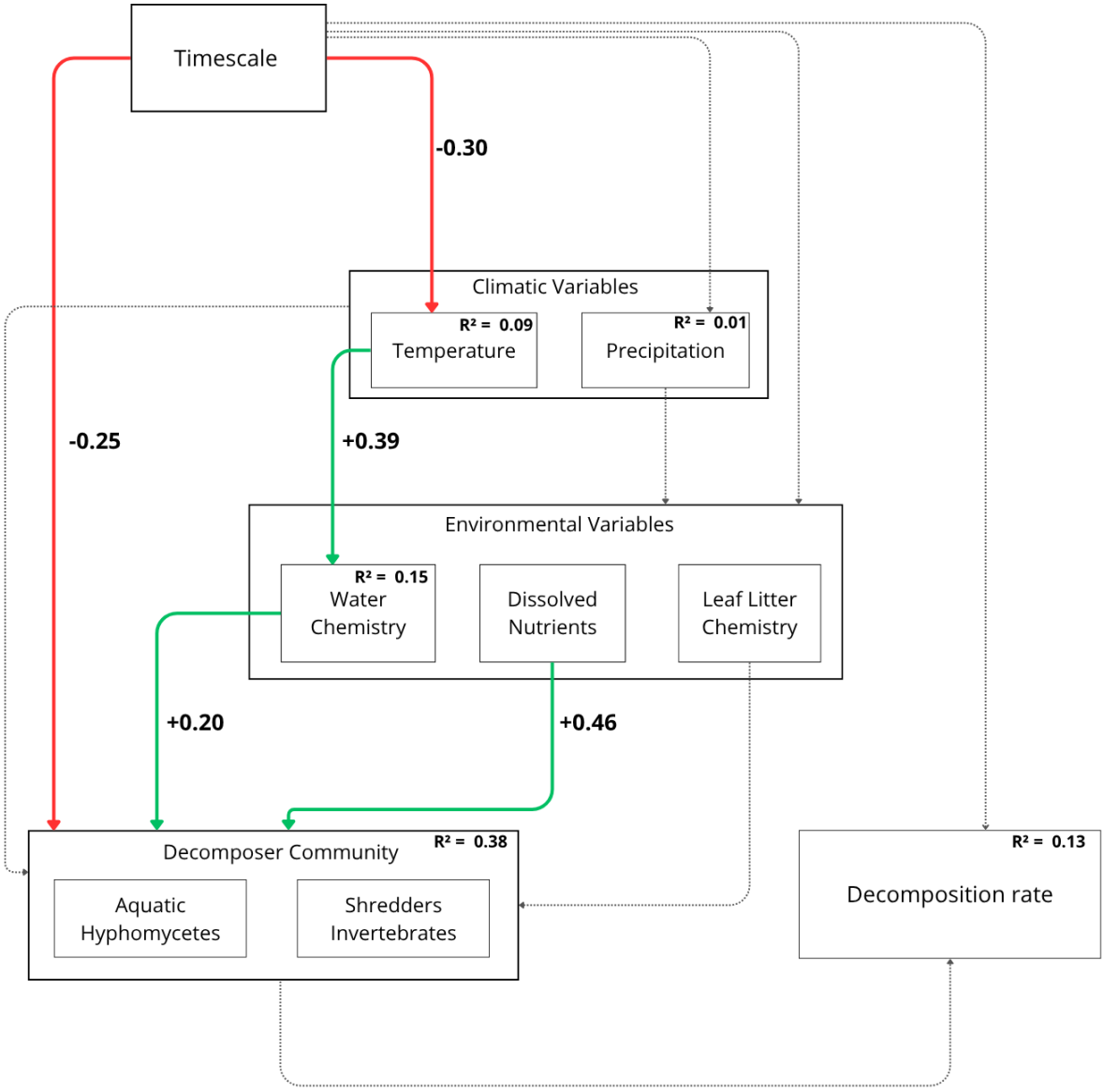


Figure 4. The structural equation model (SEM) illustrates the direct and indirect effects of climatic, environmental, and temporal variables on the decomposer community and leaf litter decomposition in a tropical headwater stream. Colored arrows represent significant ($p < 0.05$) standardized path coefficients: green = positive effect and red = negative effect. Grey dashed arrows indicate non-significant relationships ($p \geq 0.10$). Each box labelled with R^2 indicates the proportion of variance explained by the model for that component. "Decomposer Community" includes aquatic hyphomycetes (density) and shredding invertebrates (richness and density). "Water Chemistry" is derived from pH and dissolved oxygen; "Dissolved Nutrients" from multiple ions (e.g., NO_3^-, Br^-, Ca^{2+}); and "Leaf Litter Chemistry" from leaf C: N:P ratios. "Timescale" integrates sampling year and quarter.

382 The structural equation model (Figure 4; Tables 2 and 3) showed a satisfactory fit to the
383 data (Fisher's C = 25.248; p = 0.285), indicating compatibility between the proposed
384 relationships and observed data. The Timescale variable, which synthesizes the temporal
385 dimension of the experiment (year and quarter), negatively influenced the air temperature
386 (β = –0.305; p = 0.018). Temperature, in turn, was positively associated with water
387 chemistry (β = 0.391; p = 0.002), as represented by the combined values of pH and
388 dissolved oxygen. The structure of the decomposer community was explained by a set of
389 environmental and temporal variables: dissolved nutrients (β = 0.462; p < 0.001), water
390 chemistry (β = 0.200; p = 0.084), leaf chemistry (β = 0.212; p = 0.144), and again by
391 timescale (β = –0.253; p = 0.034).

392 However, the decomposition process was not significantly explained by any of the
393 variables included in the model, including the decomposer community (β = –0.012; p =
394 0.941), dissolved nutrients (β = 0.214; p = 0.225), leaf chemistry (β = 0.222; p = 0.210),
395 water chemistry (β = 0.196; p = 0.165), timescale (β = –0.061; p = 0.677), and
396 precipitation (β = 0.063; p = 0.641).The model explained 38% of the variance in the
397 decomposer community and 13% of the variance in leaf decomposition, indicating a
398 moderate influence of environmental and biotic factors on the leaf biomass accumulation
399 at the end of the experiment.

400

401

402

403

404

405

Table 2. Coefficients of the Structural Equation Model (SEM) describing the relationships among temporal, climatic, environmental, and biotic variables and the decomposition process in an Atlantic Forest stream (2015-2020). This table presents the direct effects (paths) of the model, including Unstandardized Estimates, Standard Error, Degrees of Freedom (DF), Critical Values, P-values, and Standardized Estimates (β). Asterisks indicate the significance levels: $p <$ 0.05, *$p < 0.01$, and **$p < 0.001$. This model was constructed to evaluate the complex interconnections that influence the decomposition dynamics in the studied ecosystem.

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate
Temp	**Time_scale**	**-5,031**	**2,066**	**58**	**-24,357**	**180**	**-3,046***
Precip	Time_scale	-47,926	6.3740	58	-7,519	4,551	-983
Water_chemistry	**Temp**	**2,435**	**752**	**58**	**3.2385**	**20**	**3,913****
Decomposer_community	**Nutrientes_PC1**	**3,314**	**944**	**54**	**3.5106**	**9**	**4,623*****
Decomposer_community	Foliar_PC1	2,235	1,506	54	1.4839	1,436	2,123
Decomposer_community	**Time_scale**	**-3,276**	**1,505**	**54**	**-21,768**	**339**	**-2,532***
Decomposer_community	Precip	23	29	54	7,784	4,397	865
Decomposer_community	Water_chemistry	2,517	1,430	54	1.7596	841	2,000
Leaf_remnant	Decomposer_community	-1,725	2.3005	53	-750	9,405	-122
Leaf_remnant	Nutrientes_PC1	1.1900	1.7688	53	1.2290	2,245	2,143
Leaf_remnant	Foliar_PC1	3.3004	2.5977	53	1.2705	2,095	2,215
Leaf_remnant	Time_scale	-11,105	2.6533	53	-4,185	6,773	-607
Leaf_remnant	Precip	235	501	53	4,687	6,412	626
Leaf_remnant	Water_chemistry	3.4996	2.4865	53	1.4074	1,651	1,964

Table 3. Individual R-squared Coefficients for Response Variables in the Structural Equation Model (SEM) of decomposition dynamics in an Atlantic Forest stream (2015-2020). This table details the proportion of variance (R^2) for each response variable (Temp, Precip, Water_chemistry, Decomposer_community, and Leaf_remnant) explained by its respective predictor variables within the SEM. R^2 values indicate the explanatory power of each sub-model, reflecting the ability of the predictor variables to account for the observed variability in the response variables.

Response	Method	R.squared
Temp	none	0.09
Precip	none	0.01
Water_chemistry	none	0.15
Decomposer_community	none	0.38
Leaf_remnant	none	0.13

Discussion

Overview

This study offers new insights into the long-term drivers of organic matter decomposition in tropical headwater streams by integrating five years of environmental, biological, and temporal data. The structure of decomposer communities, comprising aquatic hyphomycetes and shredding invertebrates, is primarily shaped by dissolved nutrient gradients and, to a lesser extent, by temporal dynamics. Surprisingly, none of the measured environmental, climatic, or biological variables directly explained the variation in leaf litter decomposition rates, suggesting a high functional redundancy and ecosystem-level resilience (Biggs et al. 2020). These findings challenge the prevailing assumption that decomposition in tropical streams is tightly coupled to short-term climatic variability or litter quality (Cararo and Rezende, 214). Instead, our results suggest that indirect and cascading drivers, such as the role of the temporal scale in modulating temperature, influence water chemistry and community composition. Despite considerable ecological variability, the observed stability of the decomposition rates underscores the functional buffering capacity of tropical streams. This highlights the critical role of long-term monitoring in revealing the latent ecosystem processes.

Climatic drivers and temporal signals in tropical stream ecosystems

Temporal variation emerged as a significant determinant in our model, exerting a negative influence on the air temperature. This finding corroborates the importance of long-term studies in capturing environmental trends and fluctuations that may not be evident at shorter temporal scales (Gossiaux et al. 2019, Benson and Pearson 2020). Fluctuations in temperature were positively correlated with water quality, consistent with known cascading effects in stream ecosystems. Increasing temperatures can affect oxygen solubility and metabolic activity, thereby altering the chemical and biological equilibrium in freshwater environments (Graeber et al. 2013, Jane et al. 2021). Although the temporal

451 scale variation is a complex driver, our results indicate that the aquatic environment of the Atlantic
452 Forest responds to annual trends, which may have implications for ecological processes.

453 Interestingly, precipitation, despite being a climatic factor widely recognized for influencing organic
454 matter input and nutrient dynamics in tropical streams (Tonin et al. 2017; del Cid et al. 2019), did not
455 show a significant direct influence on the decomposer community or the remaining leaf biomass in our
456 model. This absence suggests that within the specific context of this Atlantic Forest stream,
457 precipitation may act through more complex, indirect pathways that are not fully captured by the
458 measured variables (da Costa et al. 2017). In systems with dense riparian cover and continuous detritus
459 input, rainfall may function more as a redistributive pulse, mobilizing existing organic matter rather
460 than directly limiting the decomposition rates (Kleba Lisboa et al. 2015). This may differ from biomes
461 with less riparian cover or more extreme flood regimes, in which precipitation may play a more
462 pronounced role (Rezende et al. 2017, Tonin et al. 2017). Furthermore, the relative thermal and
463 hydrological stability of tropical streams may buffer the ecosystem from the direct influence of isolated
464 climatic variables (Graça et al. 2016, Pérez et al. 2018).

465

466 *Decomposer community structure as a nutrient- and time-responsive component*

467 The structure of the decomposer community emerged as a highly responsive component in our model,
468 being significantly driven by dissolved nutrient composition and, to a lesser extent, by temporal
469 factors. The strong influence of dissolved nutrients highlights the critical importance of water
470 stoichiometry and nutrient availability on the metabolism and composition of aquatic hyphomycetes
471 and shredding invertebrate communities (Ferreira et al. 2016, Graça et al. 2016, Jabiol et al. 2018). In
472 stream environments, where aquatic primary productivity is limited, the decomposer community
473 directly depends on available nutrients in the water column for its growth and enzymatic activity,
474 making these chemical variations an important environmental filter (Breda et al. 2021, da Silva et al.

2023). In systems where shredders are scarce or functionally absent, aquatic fungi may play a dominant role in litter decomposition, and their performance is shaped by nutrient availability and litter quality (Balibrea et al. 2020).

The significant influence of timescale on the decomposer community reinforces the idea that interannual and seasonal variations exert continuous control over the dynamics of these communities in tropical streams (Sales et al. 2015). Although tropical streams exhibit relative thermal stability (Graça et al., 2016), annual fluctuations in rainfall regimes and the characteristics of allochthonous organic matter can still impose selective pressures or opportunities for different taxa, shaping the community composition over time (Tonin et al. 2017, del Cid et al. 2019, 2023).

This temporal variability may also reflect changes in the realized niche of decomposer organisms, as shifting environmental conditions create a dynamic availability of ecological space throughout the year (del Cid et al. 2019, Bao et al. 2024). Such variation requires adaptation among decomposer taxa, making a diverse pool of species with functionally redundant traits essential for sustaining ecosystem processes (Wang et al. 2023). In this context, functional favors compensatory dynamics that help maintain decomposition or promote recovery even as individual taxa fluctuate or decline in response to environmental stressors (Ferreira-Santos et al. 2024). This perspective is particularly relevant in tropical streams, where many studies in different systems tend to focus on specific periods, such as autumn or dry seasons, potentially overlooking the ecological relevance of taxa adapted to warm or rainy periods in sustaining ecosystem stability year-round (del Cid et al. 2019, Taniwaki et al. 2019, Ferreira-Santos et al. 2024).

In our model, neither water chemistry nor leaf litter quality had a direct effect on the decomposer community. These results suggest that the composition of the decomposer community responds to multiple environmental factors, with particular emphasis on the direct effects of nutrients and time. The absence of a robust direct effect of water chemistry may be surprising given that these parameters are frequently cited as essential factors for hyphomycete and invertebrate communities (Medeiros et

al. 2009, Lemes da Silva et al. 2017). However, it is possible that a strong response to dissolved nutrients may mediate the influence of these factors. Similarly, the non-significance of leaf chemistry as a direct predictor of the decomposer community, despite its recognized importance for palatability and colonization, may indicate functional redundancy in the Atlantic Forest, where the diversity of leaf species and decomposers can mitigate the effects of punctual variations in leaf chemistry (Sanpera-Calbet et al. 2009, Andriotti et al. 2022, Rabelo et al. 2024).

In addition, the lack of a significant effect of leaf chemistry on decomposition rate may be related to the use of mixed litter throughout the experiment. The high diversity of leaf inputs in the system may have acted as a composite detrital pool, dampening or diluting the chemical influence of individual species (Santonja et al., 2019). This mixing may have reduced the model's sensitivity in detecting specific litter quality effects, a pattern also observed in other decomposition studies (Frainer et al. 2015, Santonja et al. 2020). Another important aspect to consider is the temporal dynamics of the decomposer communities themselves, as seasonal structural variation in fungi and invertebrates may interfere with expected functional responses, particularly when coupled with non-linear interactions involving environmental factors (Mora-Gómez et al. 2016, Lemes da Silva et al. 2017). The structure of these communities over the five-year period was influenced by multiple components, reinforcing the need to integrate biotic dynamics into discussions of environmental drivers and ecosystem functioning.

Indirect effects and ecological buffering in leaf decomposition

The absence of significant direct effects on the decomposition rate can be attributed to various ecological mechanisms, which reflect the complexity and resilience of the decomposition process in tropical streams (Silva-Junior et al. 2014, Fenoy et al. 2022). First, it is plausible that substantial functional redundancy exists in ecosystems (Fenoy et al., 2022). Different groups of decomposers

(fungi and invertebrates), as well as interactions among multiple environmental factors, may compensate for one another over time or under various conditions, maintaining a relatively stable basal decomposition rate, even in the face of fluctuations in individual drivers (Lemes da Silva et al., 2017; Silva-Junior et al., 2014). In diverse systems such as the Atlantic Forest, this redundancy can ensure the continuity of nutrient cycling, thereby masking the effects of isolated factors at broader temporal and spatial scales (Graça et al. 2016). This pattern aligns with the notion that litter decomposition is regulated by a balance between biotic and abiotic factors, which operate at multiple spatial and temporal scales and may exert influence through direct or interactive pathways (Tonin et al. 2021).

Although no significant direct effects were observed, the model demonstrated the presence of relevant indirect pathways. For example, by negatively modulating the temperature, the temporal scale significantly influenced water chemistry, which in turn showed a tendency to contribute to the structure of the decomposer community. This cascade of indirect effects, although not culminating in a statistically robust direct pathway to the remaining decomposition rate, illustrates a complex network of interactions that may operate subtly (Beveridge et al. 2010, Taniwaki et al. 2019). It is crucial to recognize that climatic and hydrological factors can exert both direct effects on decomposition and indirect effects, by influencing, for example, detritus quality or the composition of decomposer communities. (Tonin et al., 2021). It is possible that the cumulative effect or nonlinear interactions of these multiple factors are significant but are not fully captured as linear direct effects in our model (Dang et al. 2009, Rubenstein et al. 2017).

In addition, the quality of allochthonous organic matter is often considered to be a key predictor of decomposition (Boyero et al. 2016, Graça et al. 2016). However, this did not show a significant direct effect. This may reflect the inherent nature of collecting "mixed" detritus from vertical input buckets, which could have introduced variability in substrate quality that diluted the detection of an apparent direct effect (Bruder et al. 2014). Alternatively, in streams with high leaf input diversity, the decomposer community may be adaptable and generalized enough to process different leaf litter

549 qualities without a single leaf chemical characteristic, which is a primary limiting factor at the
550 evaluated scale (Sanpera-Calbet et al. 2009, Sena et al. 2020, Swan et al. 2021).

551 The low variance explained by the decomposition rate in the model suggests that other factors not
552 included in our Structural Equation Models may play a predominant role in regulating the remaining
553 leaf biomass. These may consist of physical abrasion, material transport by uncaptured nonlinear high-
554 flow events, or the activity of other unquantified groups of organisms (e.g., non-hyphomycete
555 microorganisms) (de Souza Rezende et al. 2016, Marks 2019, Yue et al. 2022). Additionally, stochastic
556 processes and compensatory interactions among decomposers may buffer decomposition rates against
557 environmental stressors (Fenoy et al. 2022, Ferreira-Santos et al. 2024). Thus, although our model did
558 not detect a significant direct effect of precipitation on decomposition, we acknowledge that short-
559 term hydrological pulses, such as flash floods or dry spells, may cause physical abrasion, leaf export,
560 or desiccation of decomposer communities (Marks 2019, Correa-Araneda et al. 2020). This reinforces
561 the idea that long-term and multi-scale approaches are essential for understanding decomposition
562 dynamics in tropical streams (Tonin et al. 2021). However, the finding that decomposition, as a final
563 mass loss process, appears to be resilient to the direct fluctuation of the investigated drivers is an
564 essential contribution to understanding the functionality of tropical ecosystems (Sales et al. 2015).

565

566 **Conclusion**

567 Our findings demonstrated that the temporal scale and dissolved nutrient gradient in the water are the
568 main drivers of decomposer community structure, with cascading effects on environmental variables
569 such as temperature and water chemistry. The apparent resilience of the remaining leaf biomass to
570 direct fluctuations in the investigated factors suggest robustness in nutrient cycling in tropical
571 environments, possibly due to mechanisms of functional redundancy. These discoveries are crucial for
572 monitoring and conserving tropical aquatic ecosystems, underscoring the need for long-term

573 approaches focused on maintaining water quality. Future investigations should explore the complexity
574 of biotic interactions and nonlinear effects to refine predictive models in a scenario of environmental
575 change.

576

577 **Acknowledgments**

578 Edson Serafim de Almeida Junior received a scholarship from CAPES (process number:
579 88887.814735/202300). Financial support was provided by the Foundation for Research Support of
580 the State of Bahia (FAPESB; Term of Grant, RED 0022/2013). The authors are grateful to the
581 Federal University of Bahia for providing field support to all undergraduate students who
582 participated in this fieldwork over five years. Finally, we would like to thank Mr. Getúlio and his
583 family for allowing us to conduct the experiments on their farms.

584

585 **Author contributions:** Conceptualization: JF, AM, RR and EJ; Developing methods: JF, AM, RR,
586 LG, AN and AC; Conducting the research: EJ with contributions from all other authors; water
587 chemistry analysis: GS; Leaf litter chemistry analysis: DS and JS; Data analysis: EJ with
588 contribution from RR; Data interpretation: EJ with contribution from AM and RR. Preparation of
589 figures and tables: EJ; Writing: EJ with support from all authors. Decomposer community
590 identification: EJ with contributions from AC and AM.
591 **Conflict of Interest Statement:** The authors declare no conflict of interest related to the content of
592 this manuscript.

593

594

595

596

References

Andriotti, J., M. M. Petrucio, and A. L. Lemes da Silva. 2022. Exploring the impacts of non-native leaf litter on invertebrate community and leaf decomposition in a Atlantic Forest stream. Acta Limnologica Brasiliensia 34.

Balibrea, A., V. Ferreira, C. Balibrea, V. Gonçalves, and P. M. Raposeiro. 2020. Contribution of macroinvertebrate shredders and aquatic hyphomycetes to litter decomposition in remote insular streams. Hydrobiologia 847:2337–2355.

Bao, Y., J. Dolfing, X. Li, R. Chen, X. Cui, Z. Li, X. Lin, and Y. Feng. 2024. Functional redundancy across space and time in litter-degrading fungal communities. Journal of Sustainable Agriculture and Environment 3.

Bärlocher, F., M. O. Gessner, and M. A. S. G. Editors. 2020. Methods to Study Litter Decomposition. Page Methods to Study Litter Decomposition.

Barros, J., and S. Seena. 2022. Fungi in Freshwaters: Prioritising Aquatic Hyphomycetes in Conservation Goals. Water (Switzerland) 14.

Benson, L. J., and R. G. Pearson. 2020. Dynamics of organic material and invertebrates in a tropical headwater stream. Hydrobiologia 847:121–136.

Beveridge, O. S., O. L. Petchey, and S. Humphries. 2010. Direct and indirect effects of temperature on the population dynamics and ecosystem functioning of aquatic microbial ecosystems. Journal of Animal Ecology 79:1324–1331.

Biggs, C. R., L. A. Yeager, D. G. Bolser, C. Bonsell, A. M. Dichiera, Z. Hou, S. R. Keyser, A. J. Khursigara, K. Lu, A. F. Muth, B. Negrete, and B. E. Erisman. 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11.

Blengini, I. A. D., M. A. M. de U. Cintra, R. P. P. da Cunha, and A. N. Caiafa. 2015. Proposta de unidade de conservação da serra da Jiboia:116.

622 Boyero, L., R. G. Pearson, C. Hui, M. O. Gessner, J. Pérez, M. A. Alexandrou, M. A. S. Graça, B. J.
623 Cardinale, R. J. Albariño, M. Arunachalam, L. A. Barmuta, A. J. Boulton, A. Bruder, M.
624 Callisto, E. Chauvet, R. G. Death, D. Dudgeon, A. C. Encalada, V. Ferreira, R. Figueroa, A. S.
625 Flecker, J. F. Gonçalves, J. Helson, T. Iwata, T. Jinggut, J. Mathooko, C. Mathuriau, C.
626 M'Erimba, M. S. Moretti, C. M. Pringle, A. Ramírez, L. Ratnarajah, J. Rincon, and C. M. Yule.
627 2016. Biotic and abiotic variables influencing plant litter breakdown in streams: A global study.
628 Proceedings of the Royal Society B: Biological Sciences 283.
629 Breda, M., A. C. Binotto, C. Biasi, and L. U. Hepp. 2021. Influence of environmental predictors on
630 hyphomycete assemblages in subtropical streams. Acta Oecologica 113:103778.
631 Bruder, A., M. H. Schindler, M. S. Moretti, and M. O. Gessner. 2014. Litter decomposition in a
632 temperate and a tropical stream: The effects of species mixing, litter quality and shredders.
633 Freshwater Biology 59:438–449.
634 Carey, N., E. T. Chester, and B. J. Robson. 2021. Flow regime change alters shredder identity but not
635 leaf litter decomposition in headwater streams affected by severe, permanent drying. Freshwater
636 Biology 66:1813–1830.
637 del Cid, C. C., A. N. Caiafa, R. de Souza Rezende, T. S. Sousa, L. Guedes, and A. O. Medeiros.
638 2023. Leaf litter dominance components respond to temporal variation in a tropical riparian
639 zone. Wetlands Ecology and Management 31:649–660.
640 del Cid, C. C., R. S. Rezende, A. R. Calor, J. S. Dahora, L. N. de Aragão, M. L. Guedes, A. N.
641 Caiafa, and A. O. Medeiros. 2019. Temporal dynamics of organic matter, hyphomycetes and
642 invertebrate communities in a Brazilian savanna stream. Community Ecology 20:301–313.
643 Correa-Araneda, F., A. M. Tonin, J. Pérez, K. Álvarez, N. López-Rojo, A. Díaz, C. Esse, F. Encina-
644 Montoya, R. Figueroa, A. Cornejo, and L. Boyero. 2020. Extreme climate events can slow
645 down litter breakdown in streams. Aquatic Sciences 82:1–7.
646 da Costa, E. N. D., J. C. de Souza, M. A. Pereira, M. F. L. de Souza, W. F. L. de Souza, and D. M. L.

da Silva. 2017. Influence of hydrological pathways on dissolved organic carbon fluxes in tropical streams. Ecology and Evolution 7:228–239.

Dang, C. K., M. Schindler, E. Chauvet, and M. O. Gessner. 2009. Temperature oscillation coupled with fungal community shifts pi can modulate warming effects on litter decomposition. Ecology 90:122–131.

Djam, S., M. Najafi, S. H. Ahmadi, and S. Shoeibi. 2019. Determination of bromate in bottled water marketed in Iran by ion chromatography. Journal of Chemical Metrology 13:47–52.

Fenoy, E., A. Pradhan, C. Pascoal, J. Rubio-Ríos, D. Batista, F. J. Moyano-López, F. Cássio, and J. J. Casas. 2022. Elevated temperature may reduce functional but not taxonomic diversity of fungal assemblages on decomposing leaf litter in streams. Global Change Biology 28:115–127.

Ferreira-Santos, K., M. L. Garbin, T. T. Carrijo, F. Torres-Leite, P. C. Cavatte, and A. T. C. Dias. 2024. Post-drought community turnover and functional redundancy in a tropical forest understorey. Journal of Vegetation Science 35:1–14.

Ferreira, V., J. Castela, P. Rosa, A. M. Tonin, L. Boyero, and M. A. S. Graça. 2016. Aquatic hyphomycetes, benthic macroinvertebrates and leaf litter decomposition in streams naturally differing in riparian vegetation. Aquatic Ecology 50.

Fiuza, P. O., T. Cantillo-Pérez, V. Gulis, and L. F. P. Gusmão. 2017. Ingoldian fungi of Brazil: Some new records and a review including a checklist and a key. Phytotaxa 306:171–200.

Fiuza, P. O., B. M. de Paiva Ottoni-Boldrini, J. S. Monteiro, N. R. Catena, N. Hamada, and L. F. P. Gusmão. 2015. First records of Ingoldian fungi from the Brazilian Amazon. Revista Brasileira de Botanica 38:615–621.

Flindt, M. R., A. I. Lillebø, J. Pérez, and V. Ferreira. 2020. Total Phosphorus, Nitrogen and Carbon in Leaf Litter. Methods to Study Litter Decomposition:91–105.

Frainer, A., M. S. Moretti, W. Xu, and M. O. Gessner. 2015. No evidence for leaf-trait dissimilarity effects on litter decomposition, fungal decomposers, and nutrient dynamics. Ecology 96:550–

561.

Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hättenschwiler. 2010. Diversity meets decomposition. Trends in Ecology and Evolution 25:372–380.

Gonçalves, J. F., R. S. Rezende, N. M. Martins, and R. S. Gregório. 2012. Leaf breakdown in an Atlantic Rain Forest stream. Austral Ecology 37:807–815.

Gossiaux, A., J. Jabiol, P. Poupin, E. Chauvet, and F. Guérold. 2019. Seasonal variations overwhelm temperature effects on microbial processes in headwater streams : insights from a temperate thermal spring. Aquatic Sciences 81:1–11.

Graça, M. A. S., K. Hyde, and E. Chauvet. 2016. Aquatic hyphomycetes and litter decomposition in tropical - subtropical low order streams. Fungal Ecology 19:182–189.

Graeber, D., M. T. Pusch, S. Lorenz, and M. Brauns. 2013. Cascading effects of flow reduction on the benthic invertebrate community in a lowland river. Hydrobiologia 717:147–159.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. Climatic Change 113:499–524.

Jabiol, J., J. Cornut, A. Tlili, and M. O. Gessner. 2018. Interactive effects of dissolved nitrogen, phosphorus and litter chemistry on stream fungal decomposers. FEMS Microbiology Ecology 94:1–11.

Jane, S. F., G. J. A. Hansen, B. M. Kraemer, P. R. Leavitt, J. L. Mincer, R. L. North, R. M. Pilla, J. T. Stetler, C. E. Williamson, R. I. Woolway, L. Arvola, S. Chandra, C. L. DeGasperi, L. Diemer, J. Dunalska, O. Erina, G. Flaim, H. P. Grossart, K. D. Hambright, C. Hein, J. Hejzlar, L. L. Janus, J. P. Jenny, J. R. Jones, L. B. Knoll, B. Leoni, E. Mackay, S. I. S. Matsuzaki, C. McBride, D. C. Müller-Navarra, A. M. Paterson, D. Pierson, M. Rogora, J. A. Rusak, S. Sadro, E. Saulnier-Talbot, M. Schmid, R. Sommaruga, W. Thiery, P. Verburg, K. C. Weathers, G. A.

Weyhenmeyer, K. Yokota, and K. C. Rose. 2021. Widespread deoxygenation of temperate lakes. Nature 594:66–70.

Kleba Lisboa, L., A. L. Lemes Da Silva, A. E. Siegloch, J. F. Gonçalves Júnior, and M. Mello Petrucio. 2015. Temporal dynamics of allochthonous coarse particulate organic matter in a subtropical Atlantic rainforest Brazilian stream. Marine and Freshwater Research 66.

Lemes da Silva, A. L., L. Kleba Lisboa, A. E. Siegloch, M. M. Petrucio, and J. F. Gonçalves Júnior. 2017. Connecting the litterfall temporal dynamics and processing of coarse particulate organic matter in a tropical stream. Marine and Freshwater Research 68:1260–1271.

Marks, J. C. 2019. Revisiting the Fates of Dead Leaves That Fall into Streams. Annual Review of Ecology, Evolution, and Systematics 50:547–568.

Martins, R. T., R. D. S. Rezende, J. F. Gonçalves, A. Lopes, M. T. F. Piedade, H. D. L. Cavalcante, and N. Hamada. 2017. Effects of increasing temperature and, CO2 on quality of litter, shredders, and microorganisms in Amazonian aquatic systems. PLoS ONE 12.

Medeiros, A. O., C. Pascoal, and M. A. S. Graça. 2009. Diversity and activity of aquatic fungi under low oxygen conditions. Freshwater Biology 54:142–149.

Mohana Rangan, S., R. Krajmalnik-Brown, and A. G. Delgado. 2021. An Ion Chromatography Method for Simultaneous Quantification of Chromate, Arsenate, Selenate, Perchlorate, and Other Inorganic Anions in Environmental Media. Environmental Engineering Science 38:626–634.

Mora-Gómez, J., A. Elosegi, S. Duarte, F. Cássio, C. Pascoal, and A. M. Romaní. 2016. Differences in the sensitivity of fungi and bacteria to season and invertebrates affect leaf litter decomposition in a Mediterranean stream. FEMS Microbiology Ecology 92:1–13.

Nguyen, H. H., E. A. R. Welti, P. J. Haubrock, and P. Haase. 2023. Long-term trends in stream benthic macroinvertebrate communities are driven by chemicals. Environmental Sciences Europe 35.

722 Pérez, J., A. Martínez, E. Descals, and J. Pozo. 2018. Responses of Aquatic Hyphomycetes to
723 Temperature and Nutrient Availability: a Cross-transplantation Experiment. Microbial Ecology
724 76:328–339.
725 Prieto, I., M. Almagro, F. Bastida, and J. I. Querejeta. 2019. Altered leaf litter quality exacerbates the
726 negative impact of climate change on decomposition. Journal of Ecology 107:2364–2382.
727 Rabelo, R. S., G. Sena, and J. F. Gonçalves. 2024. Interrelationships among litter chemistry, plant
728 species diversity, and litter decomposition in tropical stream environments: a review. Frontiers
729 in Geochemistry 2:1–8.
730 Raposeiro, P. M., V. Ferreira, G. Gea, and V. Gonçalves. 2018. Contribution of aquatic shredders to
731 leaf litter decomposition in Atlantic island streams depends on shredder density and litter
732 quality. Marine and Freshwater Research 69:1432–1439.
733 Rezende, R. S., M. A. Sales, F. Hurbath, N. Roque, J. F. Gonçalves, and A. O. Medeiros. 2017.
734 Effect of plant richness on the dynamics of coarse particulate organic matter in a Brazilian
735 Savannah stream. Limnologica 63:57–64.
736 Rubenstein, M. A., T. W. Crowther, D. S. Maynard, J. S. Schilling, and M. A. Bradford. 2017.
737 Decoupling direct and indirect effects of temperature on decomposition. Soil Biology and
738 Biochemistry 112:110–116.
739 Sales, M. A., J. F. Gonçalves, J. S. Dahora, and A. O. Medeiros. 2015. Influence of Leaf Quality in
740 Microbial Decomposition in a Headwater Stream in the Brazilian Cerrado: a 1-Year Study.
741 Microbial Ecology 69:84–94.
742 Sanpera-Calbet, I., A. Lecerf, and E. Chauvet. 2009. Leaf diversity influences in-stream litter
743 decomposition through effects on shredders. Freshwater Biology 54:1671–1682.
744 Santonja, M., H. Rodríguez-Pérez, N. Le Bris, and C. Piscart. 2020. Leaf Nutrients and
745 Macroinvertebrates Control Litter Mixing Effects on Decomposition in Temperate Streams.
746 Ecosystems 23:400–416.

747 Sena, G., J. Francisco Gonçalves Júnior, R. Tavares Martins, N. Hamada, and R. de Souza Rezende.
748 2020. Leaf litter quality drives the feeding by invertebrate shredders in tropical streams.
749 Ecology and Evolution 10:8563–8570.
750 Silva-Junior, E. F., T. P. Moulton, I. G. Boëchat, and B. Gücker. 2014. Leaf decomposition and
751 ecosystem metabolism as functional indicators of land use impacts on tropical streams.
752 Ecological Indicators 36:195–204.
753 da Silva, H. F., A. R. Assunção, D. de S. B. Aciole, F. R. Barbosa, and P. O. Fiuza. 2023. Aquatic
754 hyphomycetes associated with plant debris in freshwater ecosystems of the Atlantic Forest of
755 Rio Grande do Norte, Brazil. New Zealand Journal of Botany:1–18.
756 de Souza Rezende, R., M. A. S. Graça, A. M. dos Santos, A. O. Medeiros, P. F. Santos, Y. R. Nunes,
757 and J. F. Gonçalves Júnior. 2016. Organic Matter Dynamics in a Tropical Gallery Forest in a
758 Grassland Landscape. Biotropica 48:301–310.
759 Stape, L., P. C. Sentelhas, C. A. Alvares, and L. D. M. Gonc. 2014. Ko ¨ ppen ' s climate
760 classification map for Brazil 22:711–728.
761 Swan, C. M., L. Boyero, and C. Canhoto. 2021. The Ecology of Plant Litter Decomposition in
762 Stream Ecosystems: An Overview. Page The Ecology of Plant Litter Decomposition in Stream
763 Ecosystems.
764 Taniwaki, R. H., C. D. Matthaei, T. K. M. Cardoso, S. F. B. Ferraz, L. A. Martinelli, and J. J.
765 Piggott. 2019. The effect of agriculture on the seasonal dynamics and functional diversity of
766 benthic biofilm in tropical headwater streams. Biotropica 51:18–27.
767 Tonin, A. M., J. F. Gonçalves, P. Bambi, S. R. M. Couceiro, L. A. M. Feitoza, L. E. Fontana, N.
768 Hamada, L. U. Hepp, V. G. Lezan-Kowalczuk, G. F. M. Leite, A. L. Lemes-Silva, L. K. Lisboa,
769 R. C. Loureiro, R. T. Martins, A. O. Medeiros, P. B. Morais, Y. Moretto, P. C. A. Oliveria, E.
770 B. Pereira, L. P. Ferreira, J. Pérez, M. M. Petrucio, D. F. Reis, R. Rezende, N. Roque, L. E. P.
771 Santos, A. E. Siegloch, G. Tonello, and L. Boyero. 2017. Plant litter dynamics in the forest-

772 stream interface: Precipitation is a major control across tropical biomes. Scientific Reports 7:1–
773 14.
774 Tonin, Alan M. ; Gonçalves Júnior, José F. ; Pearson, Richard G. ; Graça, Manuel A. S. ; Pérez,
775 Javier ; Boyero, Luz . Multi-Scale Biophysical Factors Driving Litter Dynamics in Streams. The
776 Ecology of Plant Litter Decomposition in Stream Ecosystems. 36ed.: Springer International
777 Publishing, 2021, v. , p. 7-21.
778 Wang, L., J. Li, L. Tan, and B. P. Han. 2023. Seasonal patterns of functional alpha and beta
779 redundancies of macroinvertebrates in a disturbed (sub)tropical river. Ecological Indicators
780 146:109777.
781 Yue, K., P. De Frenne, K. Van Meerbeek, V. Ferreira, D. A. Fornara, Q. Wu, X. Ni, Y. Peng, D.
782 Wang, P. Heděnec, Y. Yang, F. Wu, and J. Peñuelas. 2022. Litter quality and stream
783 physicochemical properties drive global invertebrate effects on instream litter decomposition.
784 Biological Reviews 97:2023–2038.
785
786
787
788
789
790
791

792 **Supplementary Materials**

Supplementary Material 1. Monthly abundance table of aquatic macroinvertebrate families associated with leaf decomposition in a tropical headwater stream over an annual cycle (**2015**). The table presents the occurrence and number of individuals recorded per family from February to January, distributed among different orders.

Order	Family	February	March	April	May	June	July	August	September	October	November	December	January
Diptera	Chironomidae	198	207	165	91	147	65	44	35	83	76	70	41
Diptera	Ceratopogonidae	9	26	10	3	3	3	-	1	4	2	3	1
Ephemeroptera	Caenidae	3	10	16	4	5	9	-	1	1	-	3	3
Ephemeroptera	Baetidae	2	10	2	-	-	2	-	3	-	2	11	7
Ephemeroptera	Leptophlebiidae	3	7	6	-	12	1	1	-	1	2	5	-
Trichoptera	Calamoceratidae	-	2	5	-	7	-	3	2	1	3	1	1
Trichoptera	Leptoceridae	2	-	1	-	1	1	2	1	4	5	1	2
Trichoptera	Polycentropodidae	1	5	2	-	1	2	-	-	-	2	3	-
Odonata	Megapodagrionidae	-	3	1	-	2	1	-	-	-	-	-	-
Trichoptera	Hydropsychidae	-	-	1	-	0	-	-	-	5	-	-	-
Coleoptera	Elmidae	1	-	2	-	1	-	-	-	-	-	-	-
Trichoptera	Hydroptilidae	1	1	1	-	1	-	-	-	-	-	-	-
Plecoptera	Gripopterygidae	-	-	-	-	-	1	1	-	-	-	-	-
Odonata	Calopterigidae	-	-	1	-	-	-	-	-	-	-	-	-
Odonata	Coenagrionidae	-	-	-	-	-	-	-	-	-	1	-	-
Coleoptera	Dytiscidae	-	-	-	-	-	-	-	-	1	-	-	-
Diptera	Empididae	-	-	1	-	-	-	-	-	-	-	-	-

Trichoptera	Helicopsychidae	-	-	-	-	-	-	-	-	-	1	-	-
Coleoptera	Scirtidae	-	-	-	-	-	-	-	-	1	-	-	-
Diptera	Simulidae	-	1	-	-	-	-	-	-	-	-	-	-
Diptera	Tabanidae	-	-	-	-	-	-	-	-	1	-	-	-

808 **Supplementary Material 2.** Monthly abundance table of aquatic macroinvertebrate families associated with leaf decomposition in a tropical headwater
809 stream over an annual cycle (**2016**). The table presents the occurrence and number of individuals recorded per family from February to January, distributed
810 among different orders.

Order	Family	February	March	April	May	June	July	August	September	October	November	December
Diptera	Chironomidae	133	508	379	295	567	135	202	25	94	167	217
Ephemeroptera	Leptophlebiidae	11	32	32	4	31	4	2	3	15	3	3
Ephemeroptera	Leptohyphidae	-	3	22	6	31	12	11	2	3	7	23
Ephemeroptera	Baetidae	29	24	33	-	15	3	1	-	2	1	7
Diptera	Ceratopogonidae	4	10	23	1	19	2	-	1	2	-	1
Trichoptera	Polycentropodidae	-	3	32	1	8	3	2	-	3	-	5
Trichoptera	Limnephilidae	-	1	11	2	18	1	-	-	11	-	11
Hemiptera	Pleidae	-	5	-	-	13	1	-	-	4	1	4
Trichoptera	Calamoceratidae	-	2	2	-	2	2	-	1	2	3	1
Coleoptera	Elmidae	1	-	-	2	1	2	-	1	2	1	1
Trichoptera	Leptoceridae	-	-	-	-	-	1	-	-	2	4	4
Crustacea	Copepoda	1	-	1	-	1	-	-	-	1	-	5
Trichoptera	Philopotamidae	1	7	-	1	-	-	-	-	-	-	-
Trichoptera	Hydroptilidae	-	-	4	-	-	-	-	-	-	1	-
Diptera	Tipulidae	3	-	-	-	-	-	-	1	-	-	1
Odonata	Calopterigidae	-	3	1	-	-	-	-	-	-	-	-
Plecoptera	Gripopterygidae	-	-	-	-	-	1	3	-	-	-	-
Odonata	Libellulidae	-	-	1	-	-	-	-	-	-	-	2

Odonata	Megapodagrionidae	1	1	1	-	-	-	-	-	-	-	-
Odonata	Dicteriadidae	-	-	-	-	1	-	-	-	-	-	-
Diptera	Empididae	-	-	-	1	-	-	-	-	-	-	-
Heteroptera	Gelastocoridae	1	-	-	-	-	-	-	-	-	-	-
Hemiptera	Helotrephidae	-	-	-	-	1	-	-	-	-	-	-
Odonata	Perilestidae	-	-	1	-	-	-	-	-	-	-	-

814 **Supplementary Material 3.** Monthly abundance table of aquatic macroinvertebrate families associated with leaf decomposition in a tropical headwater
815 stream over an annual cycle (**2017**). The table presents the occurrence and number of individuals recorded per family from February to January, distributed
816 among different orders.

Order	Family	February	March	April	May	June	July	August	September	October	November	December	January
Diptera	Chironomidae	310	230	243	189	224	596	267	345	138	172	288	285
Trichoptera	Limnephilidae	37	60	129	44	115	31	7	1	18	1	35	13
Diptera	Chaboridae	27	21	67	28	6	61	44	22	38	70	34	-
Ephemeroptera	Caenidae	18	57	77	13	2	5	1	6	2	14	22	-
Diptera	Culicidae	24	43	20	7	-	11	7	15	-	7	4	-
Trichoptera	Odontoceridae	27	17	23	4	6	5	1	2	4	1	7	-
Ephemeroptera	Baetidae	27	13	12	9	-	-	-	-	-	3	12	12
Diptera	Ceratopogonidae	6	11	32	4	6	12	-	2	3	-	5	1
Ephemeroptera	Leptohyphidae	2	6	5	1	-	4	-	-	-	-	10	49
Trichoptera	Polycentropodidae	7	4	7	6	4	12	-	-	9	2	10	9
Hemiptera	Pleidae	-	6	7	-	1	5	-	2	-	1	18	3
Trichoptera	Leptoceridae	1	4	1	2	-	1	-	2	7	5	15	2
Ephemeroptera	Leptophlebiidae	7	1	4	3	-	3	-	5	3	2	-	10
Trichoptera	Hydroptilidae	1	-	7	7	5	3	-	-	-	1	1	1
Trichoptera	Helicopsychidae	2	-	1	3	1	1	7	4	2	1	-	-
Hemiptera	Naucoridae	-	1	7	1	-	-	-	2	1	-	6	-
Diptera	Tipulidae	-	8	-	-	-	-	-	-	-	-	-	-
Crustacea	Copepoda	-	-	4	-	-	-	-	-	-	-	-	-
Odonata	Dicteriadidae	1	-	3	-	-	-	-	-	-	-	-	-
Hemiptera	Hebridae	4	-	-	-	-	-	-	-	-	-	-	-

Odonata	Megapodagrionidae	-	1	1	-	1	-	-	-	-	-	-	-
Coleoptera	Psephenidae	-	-	-	-	-	-	1	2	-	-	-	-
Hemiptera	Helotrephidae	-	-	2	-	-	-	-	-	-	-	-	-
Hemiptera	Hydrometridae	2	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	Hydropsychidae	-	-	1	1	-	-	-	-	-	-	-	-
Heteriotera	Potamocoridae	-	-	-	-	-	-	-	-	-	-	2	-
Hemiptera	Saldidae	2	-	-	-	-	-	-	-	-	-	-	-
Odonata	Calopterigidae	-	-	-	-	-	-	-	-	-	-	-	1
Coleoptera	Elmidae	-	-	-	1	-	-	-	-	-	-	-	-
Trichoptera	Glossomatidae	-	-	-	-	-	-	-	-	-	1	-	-
Plecoptera	Gripopterygidae	-	-	-	-	-	-	-	1	-	-	-	-
Odonata	Libellulidae	-	1	-	-	-	-	-	-	-	-	-	-
Hemiptera	Mesoveliidae	1	-	-	-	-	-	-	-	-	-	-	-
Diptera	Simulidae	-	-	-	-	-	-	-	-	-	-	-	1

Supplementary Material 4. Monthly abundance table of aquatic macroinvertebrate families associated with leaf decomposition in a tropical headwater stream over an annual cycle (**2018**). The table presents the occurrence and number of individuals recorded per family from February to January, distributed among different orders.

Order	Family	February	March	April	May	June	July	August	September	October	November	December	January
Diptera	Chironomidae	10	361	492	352	487	132	185	145	56	381	503	132
Diptera	Chaboridae	3	87	51	48	71	8	22	38	67	144	95	38
Trichoptera	Limnephilidae	9	22	20	13	15	10	2	17	3	11	25	29
Ephemeroptera	Caenidae	-	2	19	1	5	-	-	6	5	11	40	17
Trichoptera	Polycentropodidae	-	11	11	3	5	1	-	8	1	4	10	8
Ephemeroptera	Leptohyphidae	-	-	5	-	-	-	-	2	-	-	27	1
Diptera	Culicidae	-	3	9	6	2	5	2	1	-	4	2	-
Hemiptera	Pleidae	-	11	2	-	-	3	-	5	-	5	-	8
Diptera	Ceratopogonidae	1	2	9	-	3	1	-	1	2	-	2	6
Ephemeroptera	Leptophlebiidae	1	-	7	1	15	-	-	1	-	2	-	-
Ephemeroptera	Baetidae	-	-	2	-	5	-	-	2	-	4	8	-
Trichoptera	Odontoceridae	1	-	3	-	2	3	-	1	-	2	1	5
Crustacea	Copepoda	-	-	9	3	2	-	-	-	-	1	1	-
Trichoptera	Leptoceridae	-	-	1	1	-	1	-	3	2	3	3	1
Trichoptera	Hydropsychidae	-	-	-	-	4	1	-	4	-	-	-	-
Trichoptera	hydroptilidae	2	1	-	-	-	-	-	-	-	-	1	3
Hemiptera	Naucoridae	-	-	2	-	-	1	-	1	-	1	-	2
Trichoptera	Helicopsychidae	-	-	3	1	-	-	-	-	-	2	-	-

Coleoptera	Elmidae	-	-	-	-	-	-	-	1	1	-	1	-
Odonata	Gripopterygidae	-	-	-	-	-	1	1	1	-	-	-	-
Odonata	Libellulidae	-	1	-	-	-	-	-	-	1	-	-	-
Diptera	Chaoboridae	-	-	-	-	1	-	-	-	-	-	-	-
Coleoptera	Lutrochidae	-	-	-	-	-	-	-	-	1	-	-	-
Plecoptera	Perlidae	-	-	-	-	-	-	-	-	-	-	1	-

828

829

830

831

832

833

834

835

836

837

838

839

840

841 **Supplementary Material 5.** Monthly abundance table of aquatic macroinvertebrate families associated with leaf decomposition in a tropical headwater
842 stream over an annual cycle (**2019**). The table presents the occurrence and number of individuals recorded per family from February to January, distributed
843 among different orders.

Order	Family	February	March	April	May	June	July	August	September	October	November	December	January
Diptera	Chironomidae	596	365	23	205	271	146	93	92	144	35	163	116
Diptera	Chaoboridae	242	31	2	68	115	85	23	27	38	10	96	121
Trichoptera	Limnephilidae	24	63	5	-	2	9	-	3	33	1	15	5
Ephemeroptera	Caenidae	1	16	-	2	4	12	-	9	15	3	1	4
Ephemeroptera	Leptohyphidae	3	-	-	-	1	4	-	1	29	2	7	-
Diptera	Culicidae	15	9	5	1	1	1	2	2	4	-	3	3
Ephemeroptera	Baetidae	-	15	-	11	4	-	4	-	5	-	6	-
Ephemeroptera	Leptophlebiidae	1	9	5	-	6	4	-	3	3	-	1	5
Hemiptera	Pleidae	4	4	1	-	1	4	-	-	2	2	8	-
Trichoptera	Polycentropodidae	1	6	-	-	7	1	-	-	3	4	3	-
Crustacea	Copepoda	3	-	-	-	-	-	-	-	8	1	5	2
Diptera	Ceratopogonidae	2	2	2	-	-	2	-	1	4	1	2	-
Trichoptera	Odontoceridae	-	2	-	-	-	1	-	-	5	2	3	-
Coleoptera	Elmidae	2	-	1	-	1	-	-	1	4	1	1	1
Hemiptera	Naucoridae	2	2	-	-	-	1	-	-	1	-	4	-
Diptera	Chaboridae	-	9	-	-	-	-	-	-	-	-	-	-
Trichoptera	Leptoceridae	-	2	-	-	-	-	-	1	4	1	1	-
Hemiptera	Helotrephidae	7	-	-	-	1	-	-	-	-	-	-	-
Trichoptera	Hydroptilidae	-	-	-	-	-	-	-	4	4	-	-	-
Trichoptera	Calamoceratidae	3	2	-	-	-	-	-	-	-	-	-	-

Trichoptera	Helicopsychidae	-	-	1	-	-	1	-	1	-	-	-	-
Coleoptera	Lampyridae	-	-	-	3	-	-	-	-	-	-	-	-
Odonata	Calopterigidae	-	1	-	-	-	-	-	1	-	-	-	-
Trichoptera	Hydropsychidae	-	-	-	-	-	-	1	-	-	-	-	-
Odonata	Libellulidae	-	-	-	-	-	-	-	-	-	-	1	-
Plecoptera	Perlidae	-	-	-	1	-	-	-	-	-	-	-	-
Diptera	Simulidae	-	-	-	-	-	-	-	-	1	-	-	-

844

Considerações Finais

Esta tese analisou como a escala temporal influencia a decomposição de matéria orgânica e a estrutura das comunidades decompositoras em um riacho tropical, com base em uma série temporal de cinco anos. Os resultados mostraram que a decomposição não é controlada apenas por fatores pontuais, como a qualidade da matéria orgânica ou eventos climáticos isolados, mas emerge da interação complexa e indireta entre clima, nutrientes, comunidades biológicas e o tempo.

Neste contexto, o estudo da comunidade de hifomicetos aquáticos revelou que a variação interanual teve uma influência mais pronunciada na estrutura da comunidade de hifomicetos do que a variação intra-anual. Este padrão, que contrastou com as expectativas de forte sazonalidade, indicou uma notável estabilidade funcional e resiliência temporal dessas comunidades fúngicas em riachos tropicais. Adicionalmente, a química da água e a qualidade da matéria orgânica foliar emergiram como os principais fatores ambientais que moldaram essa comunidade, sublinhando a relevância dos recursos e das condições ambientais de longo prazo na seleção e manutenção dos grupos de decompositores.

O principal avanço deste trabalho está em evidenciar que a escala temporal atua como um eixo estruturante da dinâmica ecológica, modulando os efeitos de outras variáveis ambientais e biológicas. A identificação de vias indiretas, por exemplo, a influência do tempo sobre a temperatura, que afeta a química da água e, por fim, a comunidade decompositora destaca a importância de abordagens integrativas e multivariadas na ecologia de ecossistemas.

Outro ponto relevante foi constatar a resiliência funcional da decomposição, mesmo diante de mudanças ambientais e biológicas. Isso sugere que, em ecossistemas tropicais diversos como a Mata Atlântica, há redundância funcional suficiente para manter o funcionamento ecossistêmico, apesar de flutuações intra e interanuais. Essa estabilidade é um indicativo da complexidade ecológica desses sistemas, mas também reforça a importância de mantê-los protegidos.

Os achados da tese contribuem com novas evidências para a ecologia de riachos tropicais, especialmente no contexto de mudanças climáticas. Eles reforçam a necessidade de estudos de longo prazo e fornece ferramentas para entender como processos fundamentais, como a decomposição, respondem a pressões ambientais ao longo do tempo.

Epílogo

Always stay gracious

your best revenge is your paper

- Beyoncé