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MARIANA NUNES MENEGAT

EFEITOS DA HETEROGENEIDADE DO HABITAT SOBRE COMUNIDADES DE INSETOS AQUÁTICOS: ABORDAGEM TAXONÔMICA E FUNCIONAL

ERECHIM, FEVEREIRO DE 2022.

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BANCA EXAMINADORA

ROZANE MARIA RESTELLO (Orientadora)
Universidade Regional Integrada do Alto Uruguai e das Missões

SILVIA VENDRUSCOLO MILESI (Orientadora)
Universidade Regional Integrada do Alto Uruguai e das Missões

DIEGO M. P. DE CASTRO
Universidade Federal de Minas Gerais

CRISTIANE BIASI
Universidade Regional Integrada do Alto Uruguai e das Missões

Erechim, Fevereiro de 2022.

Efeitos da heterogeneidade do habitat sobre comunidades de insetos aquáticos: abordagem taxonômica e funcional

Discente: Mariana Nunes Menegat

Orientadoras: Profa. Dra. Rozane Maria Restello e Profa. Dra. Silvia Vendruscolo Milesi

22 de fevereiro de 2022

Resumo

A biodiversidade dos ecossistemas aquáticos é influenciada por diversos fatores ambientais, e dentre eles, a heterogeneidade dos microhabitats. Estes se destacam como impulsionadores da diversidade taxonômica e funcional das comunidades de insetos aquáticos. O objetivo desta dissertação foi avaliar os efeitos da heterogeneidade do substrato sobre a diversidade taxonômica e funcional das comunidades de Trichoptera e Ephemeroptera, considerando a importância da disponibilidade de recursos alimentares, durante a colonização do substrato. Este estudo foi realizado em um riacho de pequena ordem na região Sul do Brasil. Para realizar o experimento, foram incubados 30 pares de amostradores artificiais que simulam substrato heterogêneo e homogêneo. Após 1, 3, 5, 10, 15 e 30 dias foram recolhidos cinco pares de substrato, para em cada um, quantificar os insetos aquáticos, clorofila-*a* e matéria orgânica. Foi observado que a disponibilidade de clorofila-*a* e matéria orgânica aumentou ao longo do tempo, mas não diferiu entre os substratos. A matéria orgânica foi um recurso alimentar importante para ambas as ordens, e influencia a diversidade funcional de Trichoptera e a abundância de Ephemeroptera. Trichoptera apresentou maior riqueza e diversidade taxonômica e funcional em substratos heterogêneos. A heterogeneidade do substrato mostrou maior influência sobre a ordem Trichoptera em comparação com a ordem Ephemeroptera, tanto taxonomicamente quanto funcionalmente. Os substratos heterogêneos conferem maior diversidade de microhabitats propiciando a coexistência de espécies e maior diversidade de características. De maneira geral, conclui-se que Trichoptera foi mais sensível aos filtros ambientais impostos por condições dos microhabitats em riachos.

Palavras-chave

Riachos. Ephemeroptera. Trichoptera. Diversidade taxonômica. Diversidade funcional.

Effects of habitat heterogeneity on aquatic insect communities: taxonomic and functional approach

Student: Mariana Nunes Menegat

Advisors: Dr. Rozane Maria Restello and Dr. Silvia Vendruscolo Milesi

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Abstract

The biodiversity of aquatic ecosystems is influenced by several environmental factors, and among them, the heterogeneity of microhabitats. These stand out as drivers of taxonomic and functional diversity of aquatic insect communities. The objective of this dissertation was to evaluate the effects of substrate heterogeneity on the taxonomic and functional diversity of Trichoptera and Ephemeroptera communities, considering the importance of food resources availability, during substrate colonization. This study was carried out in a small-order stream in southern Brazil. To carry out the experiment, 30 pairs of artificial samplers that simulate heterogeneous and homogeneous substrates were incubated. After 1, 3, 5, 10, 15 and 30 five pairs of substrates were collected to quantify aquatic insects, chlorophyll-a and organic matter in each one. It was observed that the availability of chlorophyll-a and organic matter increased over time, but did not differ between substrates. Organic matter was an important food resource for both orders, and influences the functional diversity of Trichoptera and the abundance of Ephemeroptera. Trichoptera showed greater richness and taxonomic and functional diversity in heterogeneous substrates. Substrate heterogeneity showed greater influence on the order Trichoptera compared to the order Ephemeroptera, both taxonomically and functionally. Heterogeneous substrates provide greater diversity of microhabitats that support species coexistence and greater diversity of characteristics. In general, it was concluded that Trichoptera was more sensitive to environmental filters imposed by microhabitat conditions in streams.

Keywords

Stream. Mayflies. Caddisflies. Taxonomic diversity. Functional diversity.

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1. INTRODUÇÃO GERAL

1.1 Insetos aquáticos

Os ecossistemas aquáticos continentais abrigam alta riqueza de espécies de insetos aquáticos, organismos dominantes nestes ambientes, e amplamente distribuídos em uma variedade de diferentes habitats (KOROIVA e PEPINELLI, 2019). Os insetos aquáticos estão envolvidos em processos ecológicos importantes para o funcionamento dos ecossistemas aquáticos, como a decomposição, ciclagem de nutrientes, fluxo de energia e cadeia alimentar (DEL-CLARO, 2019). Este grupo de organismos apresenta alta diversidade de espécies e capacidade de refletir as condições ecológicas do ambiente, apresentando um amplo espectro de tolerância às alterações ambientais (CALLISTO et al., 2001; DOMINGUEZ e FERNANDEZ, 2009). Reflexo disto, os insetos aquáticos são importantes indicadores da integridade ecológica dos ecossistemas aquáticos (HEPP et al., 2016; BREDA et al., 2018).

Dentre os diversos grupos de insetos aquáticos, as ordens Trichoptera, Ephemeroptera e Plecoptera são grupos sensíveis às alterações ambientais, especialmente aquelas causadas por atividades humanas (BISTPO et al., 2006). Estas ordens estão presentes em ambientes com boas condições ambientais, físicas e químicas, como a presença de vegetação ripária, boa oxigenação e alta velocidade da água (BREDA et al., 2018; HUIÑOCANA et al., 2020). Trichoptera é uma das ordens mais diversas de insetos aquáticos e possui representantes em diferentes grupos tróficos funcionais, sendo o hábito alimentar fragmentador constantemente relacionado a esta ordem (MORSE et al. 2019). O principal recurso alimentar dos fragmentadores é a matéria orgânica alóctone, como folhas, galhos e sementes, que além de fonte de energia representam abrigo para os Trichoptera (MORETTI et al., 2009; MORSE et al., 2019). Estes, possuem uma glândula produtora de seda, localizada no abdome, que auxilia na aderência de destes diferentes tipos de materiais envolta do corpo, como estratégia de proteção/sobrevivência (PES et al., 2018). Por sua vez, a ordem Ephemeroptera, em estágio larval, é caracterizada pela presença de três cercos caudais e brânquias abdominais (SALLES et al., 2018). Ephemeroptera é constantemente relacionada a hábitos alimentares raspadores, se alimentando preferencialmente de matéria orgânica autóctone (perifíton), e boa parte de seus representantes apresentam corpo achatado (MERRITT e CUMMINS, 1996; SALLES et al., 2018).

Diante da estreita relação entre as diferentes espécies e componentes do ambiente, as alterações nas variáveis ambientais podem afetar os insetos aquáticos, bem como os processos ecológicos que são dependentes destes. As variáveis ambientais da paisagem (e.g uso e cobertura do solo) e físico químicas da água (e.g. teor de nutrientes, condutividade elétrica, oxigênio e carbono orgânico dissolvido) são alteradas em decorrência de impactos naturais, e antropogênicos, principalmente. Por exemplo, a vegetação nativa nas áreas adjacentes aos riachos, que é uma das principais fontes de energia para as comunidades aquáticas, tem sido frequentemente convertida em áreas destinadas a atividades agrícolas e agropecuárias (ESTEVES e GONÇALVES, 2011; SIEGLOCH et al., 2016). Estas atividades representam aumento no aporte de nutrientes e contaminantes (e.g., metais pesados oriundos de agroquímicos) que podem diminuir a riqueza de insetos (HEPP et al., 2010; CASTRO et al., 2018; LOUREIRO et al., 2018). Em contraponto, riachos com maior integridade ecológica apresentam maior heterogeneidade ambiental, e consequentemente, diversidade de espécies (BARNES et al., 2013).

1.2 Heterogeneidade do habitat

A ocorrência e distribuição dos insetos aquáticos é influenciada por diversos fatores que atuam em diferentes escalas espaciais e temporais (MATTHEWS, 1998). Em escalas espaciais mais amplas, fatores históricos (e.g especiação, extinção e dispersão) e climáticos (e.g temperatura e precipitação), e em escalas locais, fatores como a heterogeneidade do habitat e condições bióticas e abióticas são determinantes na distribuição e diversidade de insetos aquáticos (KOROIVA e PEPINELLI, 2019). A heterogeneidade do habitat é um dos principais fatores que influenciam a diversidade biológica nos ecossistemas aquáticos (HYNES, 1970). Nos riachos, os substratos heterogêneos caracterizam-se pela superfície complexa, com diferentes tipos, tamanhos e texturas e presença de espaços intersticiais/cavidades (BOYERO, 2003). Estes substratos favorecem maior abundância e riqueza de insetos pois possibilitam maior disponibilidade de habitat, refúgio e recursos alimentares (GRAÇA et al., 2004; MILESI et al., 2016). As irregularidades e diferenças estruturais nos substratos heterogêneos tornam esses locais adequados para serem usados como refúgio dos insetos contra predação e/ou eventos de distúrbios ambientais. Além disso, a presença de matéria orgânica grossa, como galhos e folhas, é responsável pelo aumento da complexidade dos substratos heterogêneos, que permitem, devido a estrutura irregular maior disponibilidade de material autóctone e alóctone (BROWN, 2003). Estudos mostram que características de habitats heterogêneos tendem a refletir em maior abundância e riqueza taxonômica e funcional de insetos (HEPP et al., 2012; MILESI et al., 2016).

Por outro lado, a homogeneização dos habitats, que ocorre principalmente em riachos impactados, pode levar a comunidades similares taxonômica e funcionalmente. Os substratos homogêneos, caracterizados por uma estrutura lisa e uniforme, reduzem a disponibilidade de habitats, refúgios e recursos alimentares, expondo os insetos a perturbação e interações competitivas (MILESI et al., 2016). Por exemplo, a riqueza e abundância de insetos é afetada negativamente em substratos homogêneos, quando comparadas a substratos heterogêneos (HEPP et al., 2012; MILESI et al., 2016). Com isso, a homogeneização dos habitats, leva, consequentemente, a homogeneização das comunidades aquáticas e perdas de funções ecossistêmicas. Assim, a heterogeneidade do substrato é um importante fator impulsionador da biodiversidade, pois permite a coexistência de espécies e maior riqueza taxonômica e funcional (TOWNSEND et al., 1997).

Além disso, ao longo do tempo, diversos fatores (e.g. colonização, processo de sucessão ecológica) devem influenciar o desenvolvimento e composição das comunidades (CARDINALE et al., 2001; RICKLEFS, 2008). A colonização de um novo substrato é um conceito chave na ecologia, e é bem difundido que ao longo do tempo de colonização a abundância e riqueza das comunidades deve aumentar e se desenvolver à medida que avançam os estágios sucessionais (MATHOOKO, 1995; CARVALHO e UIEDA, 2004; MILESI et al., 2019). Conforme colonizam, os insetos aquáticos selecionam locais com base nas características e composição do habitat, como a qualidade e quantidade de recursos, competidores/predadores e refúgios (MILESI et al., 2019; PINTAR E RESETARITS, 2017; 2021). Demonstrando que a heterogeneidade do substrato está diretamente associada a colonização do substrato.

Nesse contexto, os substratos homogêneos e heterogêneos podem influenciar espécies de insetos aquáticos através da seleção de características funcionais. Nos substratos heterogêneos são encontrados insetos com maior tamanho do corpo (MILESI et al., 2016), em resposta a maior disponibilidade de recursos alimentares, e possivelmente, a maior estabilidade do habitat que reduz as interações competitivas, podendo ainda estar relacionado com um ciclo mais longo de vida. Enquanto que, nos substratos homogêneos, os insetos tendem a apresentar tamanho menor e corpo achatado, que atribui resistência ao arrasto e redução do deslocamento (MILESI et al., 2016). Quanto ao hábito alimentar, os substratos heterogêneos suportam insetos pertencentes a diferentes grupos tróficos, e fragmentadores (e.g. *Phylloicus* sp., Trichoptera: Calamoceratidae) estão constantemente associados a estes devido ao acúmulo de matéria orgânica (MILESI et al., 2016). Em contrapartida, os substratos homogêneos são a preferência de insetos raspadores (e.g *Baetodes* sp., Ephemeroptera: Baetidae), que se alimentam de perifíton e possuem capacidade de fixação no substrato (MILESI et al., 2016). A superfície lisa dos substratos homogêneos favorece o desenvolvimento de alta biomassa de perifíton (BIGGS e HICKEY, 2000). Estas variações nas características funcionais das espécies, que são utilizadas para colonizar e permanecer em diferentes ambientes aquáticos, reforçam a estreita relação entre os insetos aquáticos e o ambiente em que vivem, principalmente o substrato. As características funcionais (e.g fisiológicas, morfológicas e comportamentais) refletem as estratégias ecológicas e aptidão individual das espécies (VIOLLE et al., 2007; DEZERÁLD et al., 2015), que podem estar relacionadas a história evolutiva ou adaptação ao ambiente.

1.3 Abordagens taxonômicas e funcionais em comunidades

A diversidade biológica pode ser medida de várias formas e reflete a conservação dos ambientes, sendo tema recorrente em estudos de ecologia de comunidades, principalmente diante de um cenário de aumento constante da intensidade de perturbações antrópicas. Valores mais altos de diversidade taxonômica e funcional de insetos aquáticos descrevem ambientes com melhor funcionamento ecossistêmico (SOBRAL e CIANCIARUSO, 2012; HUIÑOCANA et al., 2020). Integrar abordagens taxonômicas e funcionais têm revelado a importância de analisar por meio de diferentes perspectivas os efeitos de filtros ambientais sobre os insetos aquáticos. O componente taxonômico é uma medida simples que fornece informações sobre a riqueza, composição e abundância das espécies (SHIMANO et al. 2012). Quantificar medidas taxonômicas é uma das maneiras mais bem difundidas e consolidadas na ecologia, que consiste basicamente em identificar o número de espécies em uma determinada comunidade ou área de interesse (MAGURRAN, 2004). A diversidade taxonômica, por exemplo, pode ser mensurada através da riqueza e equabilidade das espécies (SHANNON e WEAVER, 1949). No entanto, abordar apenas medidas taxonômicas pode não ser suficiente para compreender padrões de organização das comunidades em relação ao funcionamento do ecossistema (DOLÉDEC et al., 2011).

Integrar abordagens baseadas em características funcionais fornece uma estrutura mecanicista para a interpretação de padrões de distribuição das espécies, e reflete a estrutura da comunidade e a função do ecossistema (HEINO et al., 2005; VIEIRA et al., 2006).

O componente funcional representa as características funcionais das espécies (CIANCIARUSO et al., 2009), sendo medida pela variação e distribuição destas. A diversidade funcional, baseada na variabilidade de características funcionais que representam o *fitness* das espécies, revelam a conexão entre a comunidade e o ecossistema relacionando a dissimilaridade de funções ecológicas (TILMAN, 2001; HEINO, 2005; VIOLLE, et al., 2007). Pioneiro no uso da abordagem funcional, Cummins (1973), descreveu grupos funcionais para invertebrados aquáticos (e.g predadores, coletores, raspadores, filtradores e fragmentadores) baseados em relações tróficas. A teoria do rio contínuo proposta por Vannote et al., (1980) descreve a distribuição de grupos tróficos funcionais ao longo do gradiente fluvial longitudinal, e mostra que a estrutura taxonômica e funcional das comunidades, se ajusta as mudanças no ambiente ao desenvolver estratégias biológicas. Tanto que, também foram relatados na literatura os efeitos negativos dos usos da terra sobre as características funcionais dos insetos (DOLÉDEC et al., 2011; CASTRO et al., 2018; LIU et al., 2021). Introduzindo o uso de substratos artificiais, estudos observaram as estratégias ecológicas das espécies e revelaram a existência de filtros ambientais que selecionam espécies com características funcionais adequadas a determinadas condições ambientais (MILESI et al., 2016; MILESI et al., 2019; GODOY et al., 2021).

Em razão do aumento dos impactos por causas naturais, e principalmente, antrópicas e consequente perda gradual da diversidade biológica, é importante integrar métricas taxonômicas e funcionais para fornecer dados fundamentais para a conservação da biodiversidade e funcionamento de ecossistemas aquáticos. Os impactos geram alterações de fatores ambientais que podem afetar direta e indiretamente os processos ecológicos e as comunidades de insetos em riachos (HEEP et al., 2010, AGRA et al., 2020). Nesta dissertação, abordamos dois componentes da biodiversidade, taxonômico e funcional, para avaliar os efeitos da heterogeneidade do habitat sobre a composição e estrutura das comunidades de insetos aquáticos. Além de, ampliar as discussões acerca da estreita relação entre o substrato, recursos alimentares e a organização das comunidades aquáticas.

A dissertação apresenta uma Introdução Geral, com informações conceituais sobre o tema do estudo, um Capítulo na forma de manuscrito e uma Conclusão Geral com perspectivas de desdobramento do estudo. No manuscrito intitulado "Substrate heterogeneity as a predictor of taxonomic and functional structure of stream insects communities" foram utilizados amostradores artificiais de substrato heterogêneo e homogêneo com o objetivo de avaliar os efeitos da heterogeneidade do substrato sobre a diversidade taxonômica e funcional das comunidades de Ephemeroptera e Trichoptera ao longo da colonização, considerando a distribuição dos recursos alimentares (clorofila-*a* e matéria orgânica). O manuscrito foi preparado e submetido ao periódico Aquatic Ecology (Qualis/CAPES A3), e é apresentado aqui em acordo com as normas do periódico.

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SUBSTRATE HETEROGENEITY AS A PREDICTOR OF TAXONOMIC AND FUNCTIONAL STRUCTURE OF STREAM INSECT COMMUNITIES

Mariana Nunes Menegat[1,*], Silvia Vendruscolo Milesi[1,2], Luiz Ubiratan Hepp[1,2] e Rozane Maria Restello[1]

[1] Programa de Pós-Graduação em Ecologia, Universidade Regional Integrada do Alto Uruguai e das Missões, Avenida Sete de Setembro, 1621, Erechim, RS, Brasil, CEP 99709-910.
[2] Universidade Federal de Mato Grosso do Sul, Campus de Três Lagoas, Unidade II, Av. Ranulpho Marques Leal, 3484, Três Lagoas, MS, Brasil, CEP 79.613-000.

*Autor correspondente: marianamenegat@outlook.com

Abstract

Substrate heterogeneity is an important environmental factor that regulates biodiversity, influencing the distribution and occurrence of aquatic communities. In small streams heterogeneity is an environmental predictor that increases the taxonomic and functional diversity of aquatic insects. However, this relationship can be mediated by temporal factors associated with the assemblies succession patterns. In this study, we used artificial samplers (i.e. heterogeneous and homogeneous) to assess the effects of substrate heterogeneity on taxonomic and functional diversity of Ephemeroptera and Trichoptera communities considering the importance of food resource availability during colonization. After this period, all substrates were washed to remove insects and returned to the stream for another 30 days. After 1, 3, 5, 10, 15 and 30 we removed five pairs to quantify aquatic insects, chlorophyll-a content and organic matter in each substrate. The availability of chlorophyll-a and organic matter increased over time, but did not differ between substrates. We observed greater taxonomic and functional richness and diversity for Trichoptera assemblages in heterogeneous substrates. We observed the influence of organic matter on the Trichoptera functional diversity and Ephemeroptera abundance. Caddisflies demonstrate greater taxonomic and functional sensitivity to substrate heterogeneity. In addition, the organic matter associated with the substrates was the most relevant food resource for both insect orders.

Keywords

Functional diversity. Taxonomic diversity. Caddisflies. Mayflies. Chlorophyll-*a*. Organic Matter.

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1. Introduction

The occurrence and distribution of aquatic insect communities is influenced by environmental heterogeneity (Downes et al. 2000; Milesi et al. 2016). According to the ecological niche theory (Hutchinson, 1959), environmental heterogeneity may represent an increase in biological diversity permiting niches with a greater species number and allowing the coexistence of these in the same area (Milesi et al. 2016). The streams substrate heterogeneity reflects the habitat physical structure and the spatial variability in aquatic communities, ecological processes and patterns, being an important predictor of their taxonomic and functional structure (Kolasa e Rollo 1991; McIntosh 1991; Palmer 1997; Bilia et al. 2015; Ferreira et al., 2017). The increase in insect richness and density is determined by substrate heterogeneity (Lamberti e Resh 1979, Erman e Erman 1984, Poff et al. 2006, Palmer et al. 2010; Milesi et al. 2016). Heterogeneous substrates provide different conditions for the establishment of organisms, whether due to the irregular configuration of their surface or the greater capacity to retain food resources that may be used by associated insects (Hepp et al., 2012).

Heterogeneous substrates are characterized by irregular structure and presence of cavities, comprising different types of sediments, sizes and textures (O'Connor 1991; Boyero 2003; Brown 2003). These heterogeneous substrates have greater availability of food resources, habitat and interstitial spaces, which serve as a refuge for aquatic insects (Graça et al. 2004; Hepp et al., 2012; Milesi et al. 2019). On the other hand, homogeneous substrates have a smooth and structurally similar surface, exposing insects to predation and environmental disturbances. (Gallardo et al. 2009). Homogeneous substrates can act as an environmental filter on insects, producing characteristics adapted to resistance under adverse conditions (Milesi et al., 2016). In addition, throughout the colonization process, the substrate complexity can increase due to organic matter accumulation (O'Connor 1991; Boyero 2003; Brown 2003).

Periphyton and allochthonous organic matter are two important food sources for aquatic insects in small-order streams (Ferreira et al., 2017; Tonin et al., 2018). Periphyton is a source of autochthonous organic matter which comprises a complex community of organisms (including bacteria, fungi and algae) (Wetzel 1983). On the other hand, allochthonous organic matter (e.g. leaves, branches and seeds) corresponds to coarse and fine particulate matter (CPOM and FPOM, respectively) that comes from stream adjacent vegetation. Scraper insects such as *Itaura* sp. (Trichoptera: Glossossomatidae) and *Baetodes* sp. (Ephemeroptera: Baetidae) feed preferentially by scraping the periphyton (Merritt e Cummins, 1996; Wallace e Webster 1996). On the other hand, shredding insects such as *Nectopsyche* sp. (Trichoptera: Leptoceridae) and *Phylloicus* sp. (Trichoptera: Calamoceratidae) feed on the CPOM, converting it into FPOM that serves as food for the filter feeders (e.g. *Chimarra* sp., Trichoptera: Philopotamidae; e *Smicridea* sp., Trichoptera: Hydropsychidae) (Merritt e Cummins, 1996; Wallace e Webster 1996). In this sense, the availability of different food resources can influence the taxonomic and functional diversity of insects (Gallardo et al. 2009; Milesi et al. 2016).

Classic taxonomic characteristics (e.g. diversity indexes, composition, abundance and species richness) assess biological diversity through quantitative perspectives (Shimano et al. 2012). On the other hand, the functional characteristics (e.g. physiological, morphological and behavioral) are able to reflect the ecological strategies and individual species aptitude (Violle et al. 2007; Dezérald et al. 2015), contributing to the understanding of the ecological services provided by aquatic communities (Morse et al. 2019). For example, abundance and richness of aquatic insect assemblages tend to increase over time of colonization, particularly due to habitat heterogeneity and availability of food resources. (Mathooko 1995; Carvalho e Uieda 2004; Milesi, et al. 2019). Likewise, richness and functional diversity increase in heterogeneous substrates (Milesi et al. 2016). On the other hand, the insect functional characteristics, such as the flattened body shape, which contribute to locomotion and ability to attach on substrates, and the small body size, which provides drag resistance, are mainly found associated with homogeneous substrates (Milesi et al. 2016; Milesi et al. 2019). Thus, the functional characteristics have greater peculiarities due to the substrate heterogeneity of the environment (Milesi et al. 2016).

Aquatic insects represent a group of great importance in ecological processes, participating in the nutrient cycling and food chain (Callisto et al., 2001; Yang e Gratton, 2014). These organisms are widely distributed in aquatic environments and colonize a variety of habitats under different environmental conditions (eg landscape and water physical-chemical characteristics) (Clarke et al., 2008; Ferreira et al., 2017; Breda et al. 2018). In headwater streams in subtropical regions, the insect orders Trichoptera and Ephemeroptera show high abundance and diversity, standing out for their sensitivity to environmental changes at different levels of anthropization (Ongaratto et al. 2018; Milesi e Melo 2014; Huiñocana et al., 2020). Trichoptera is one of the most diverse aquatic insect orders distributed in almost all known aquatic habits and with representants in all functional trophic groups (Morse et al. 2019). Trichoptera are considered “habitat engineers” as they use different types of materials (eg leaves, branches and sand) to build shelters as a survival strategy (Moretti et al. 2009; Morse et al. 2019). In turn, Ephemeroptera colonize different habitats and belong to distinct functional trophic groups, presenting incomplete metamorphosis with a nymphal stage (immature) (Merritt e Cummins 1996; Salles et al. 2004). Despite being considered sensitive organisms to impacted environments, some mayflies (i.e., Baetidae) showed variation in the requirement for areas of greater environmental integrity (Buss e Salles 2007; Souza et al. 2011).

The positive relationship between environmental heterogeneity and species diversity is an established pattern in ecology. Here, we intend to understand the effects of substrate heterogeneity on the aquatic insect assemblages, considering the food resources availability (i.e. periphyton and allochthonous organic matter) associated with the substrates. For this, we used artificial samplers to evaluate the effects of heterogeneous and homogeneous substrates on the taxonomic and functional diversity of Trichoptera and Ephemeroptera assemblages during substrate colonization. We expect that substrate heterogeneity will positively influence the taxonomic and functional diversity of Trichoptera and Ephemeroptera assemblages during colonization. Furthermore, we expect that food resources positively influence Trichoptera and Ephemeroptera taxonomic and functional diversity, enhancing the colonization of organisms on substrates.

2. Metodology

2.1 Study area

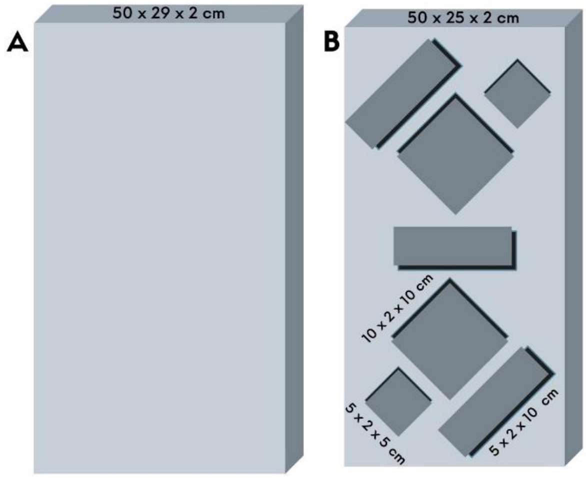
We carried out this study on a third-order stretch of the Rio Dourado, located in southern Brazil (29°31'57" S, 50°14'55" W). The stream is located in a region that has a temperate subtropical climate (Köppen Cfb type) (Alvares et al. 2013). The region is part of the Atlantic Forest Biome and presents vegetation consisting of a mixture of Subtropical Forest, composed of species with tropical-subtropical distribution from Alto Uruguai and Mixed Ombrophilous Forest (Oliveira-Filho et al. 2015). The stream drainage area has low human intervention with low percentages of agricultural use (Decian et al. 2010). The stream has pools and rapids with presence of rocks, stones, gravel and vegetal debris banks deposited in the streambed, with riparian vegetation on both sides. During the experiment period (about 30 days), the stream water remained well oxygenated (~ 9 mg L^{-1}), slightly acidic (pH ~ 6.4) and with low electrical conductivity (< 30 μS cm^{-1}) (see Milesi et al. 2016).

2.2 Field Procedures

We carried out the experiment between May and June of 2015 (austral autumn and winter), installing artificial samplers made on metamorphic rock blocks (slate stone type) simulating the homogeneous and heterogeneous substrates. The homogeneous substrate samplers consisted of a smooth and unmodified surface block (50 × 29 × 2 cm) and the heterogeneous ones consisted of a block on stone with pieces of different sizes (but same stone type) fixed on the upper and lower surfaces (two pieces of 5 × 2 × 5 cm, three pieces of 5 × 2 × 10 cm and two pieces of 10 × 2 × 10 cm). To standardize the sampled area on both substrates, the heterogeneous substrate samplers had a smaller size (50 × 25 × 2 cm) (Figure 1).

We installed 30 pairs of artificial substrates (one homogeneous and one heterogeneous), ~2 m apart, along a ~500 m stretch in the stream. The substrates remained for 30 days in the stream to allow periphyton colonization. Afterwards, we wash the substrates and remove the insects and put them back in the stream to start the colonization experiment for another 30 days. We removed five substrate pairs after 1, 3, 5, 10, 15 and 30 days and with a Surber sampler (250 μm mesh) we collected the insects which were fixed in situ with 70% ethanol. We collected the organic matter adhered to the samplers substrates with a Surber sampler (250 µm mesh). We performed three periphyton sub-sampling obtained by scraping (area of 4.7 cm^2) the upper surface of each substrate.

Fig. 1 Representative schematic drawing of the artificial samplers used in the experiment. (A) Homogeneous substrate with smooth surface and, (B) heterogeneous substrate with pieces of different sizes fixed to increase heterogeneity.



2.3 Laboratory procedures

In the laboratory, we washed the material from the field under 250 µm mesh sieves for complete separation of organisms and inorganic and inorganic debris. We identified aquatic insects of the orders Trichoptera and Ephemeroptera up to the taxonomic level of the genus using the identification keys of Merritt and Cummins (1996), Fernández and Domínguez (2001), Salles et al. (2004) and Pes et al. (2005).

To estimate the amount of organic matter adhered to the substrates, we dried the collected material in an oven (60°C/72 h) for subsequent weighing. From the periphyton samples, we estimated the concentration of chlorophyll-a using the spectrophotometric method (Biggs and Kilroy 2000). We used organic matter and chlorophyll-a as proxies for food resources available in the substrates (homogeneous and heterogeneous) throughout colonization.

2.4 Functional traits

We considered four insects functional characteristics (food habits, body size, body shape and locomotion) distributed in 14 categories (Table 1). We obtained information on functional characteristics from the available literature on neotropical streams (Baptista et al. 2006; Tomanova and Usseglio-Polatera 2007; Reynaga and Santos 2012). For body size, we performed direct measurements of all insects (head-to-abdomen measurements). We synthesized the data of functional characteristics compensating the different types and levels of information available using the fuzzy code approach, which quantifies the affinity of each taxon belonging to each category, ranging from zero (no affinity) to three (strong affinity) (Chevenet et al. 1994; see Milesi et al. 2016) (Supplemental Material, Table 1S).

Table 1 Aquatic insects functional characteristics and their categories.

Functional characteristics	Categories
Feeding habitats	Filterer
	Collector
	Shredder
	Scraper
	Predator
Body size (mm)	<0.25
	25-0.50
	0.50-1
	>1
Body shape	Cylindrical
	Flattened
Locomotion	Crawler
	Swimmer
	Case build

2.5 Data Analysis

We calculate taxonomic diversity using Simpson diversity index, which indicates the probability that two individuals randomly removed from a community belong to different species (Magurran, 2014). We calculate functional richness and diversity using the “dbFD” function in the FD package (Laliberté et al. 2014). For functional diversity we used Rao's quadratic entropy (Rao 1982), which generally represents the classic Simpson diversity index and is based on specific abundance and functional differences between pairs of individuals in a community (Botta-Dukát 2005). Thus, we constructed an association matrix (Euclidean distance) from the fuzzy code values of each characteristic category (Chevenet et al. 1994). For functional richness we use the combinations of values of unique characteristics in the community (Villéger 2008).

We used linear regressions to evaluate chlorophyll-a concentrations and amount of organic matter over time and between substrates. We used an analysis of covariance to assess differences in abundance, taxonomic richness (number of genera), taxonomic diversity (Simpson index), functional richness and functional diversity (Rao index) of Trichoptera and Ephemeroptera between substrates (homogeneous and heterogeneous) over time (covariate). Finally, we performed correlations of the amount of organic matter and concentration of chlorophyll-a with each metric (abundance, richness and taxonomic and functional diversity) for the heterogeneous and homogeneous substrate, considering time. We performed all analyzes in the R software (R Core Team, 2019).

3. Results

The chlorophyll-a concentration in the substrates ranged from 0.001 to 29.3 µg g^{-1}, while the amount of organic matter adhered to the substrates ranged from <0.001 to 165.3 g $stone^{-1}$. We observed 2.2±1.0 µg g^{-1} of chlorophyll-a in heterogeneous substrates and 3.2±1.2 µg g^{-1} in homogeneous ones. On the other hand, we observed 23.5±4.2 g $stone^{-1}$ of organic matter in homogeneous substrates and 33.3±7.2 g $stone^{-1}$ in heterogeneous substrates. The chlorophyll-a and organic matter concentrations were similar among the substrates, but they increased over time ($F_{(1,58)}$= 21.3, p<0.001 e $F_{(1,58)}$=8.2, p=0.005, respectively).

Over 30 days of colonization we collected a total of 3,449 aquatic insects. Of this total, 1,736 Ephemeroptera (50.3% of the total), distributed in 4 families and 8 genera and 1,713 Trichoptera (49.7%) distributed in 8 families and 18 genera of Trichoptera (Table 2).

From all Trichoptera, 819 individuals (47.8%) colonized the heterogeneous substrate and 894 individuals (52.2%) colonized the homogeneous substrate. In both substrates, the genera *Itaura* sp. and *Smicridea* sp. showed greater abundance (Table 2). *Marilia* sp. and *Leucotrichia* sp. colonized only the heterogeneous substrate, while *Cernotina* sp. and *Helycopsyche* sp. exclusively colonized the homogeneous substrate (Table 2). In turn, from Ephemeroptera, we observed that

1,012 individuals (58.3%) colonized the heterogeneous substrate and 724 individuals (41.7%) colonized the homogeneous substrate. In the heterogeneous substrate, *Baetodes* sp. was the most abundant, while *Caenis* sp. was the most abundant in the homogeneous substrate (Table 2). *Tricorythode*s sp. colonized exclusively the heterogeneous substrate and *Camelobaetidius* sp. the homogeneous substrate (Table 2).

Table 2 Genera abundance of Ephemeroptera and Trichoptera order found in homogeneous and heterogeneous substrates after 30 days of experiment.

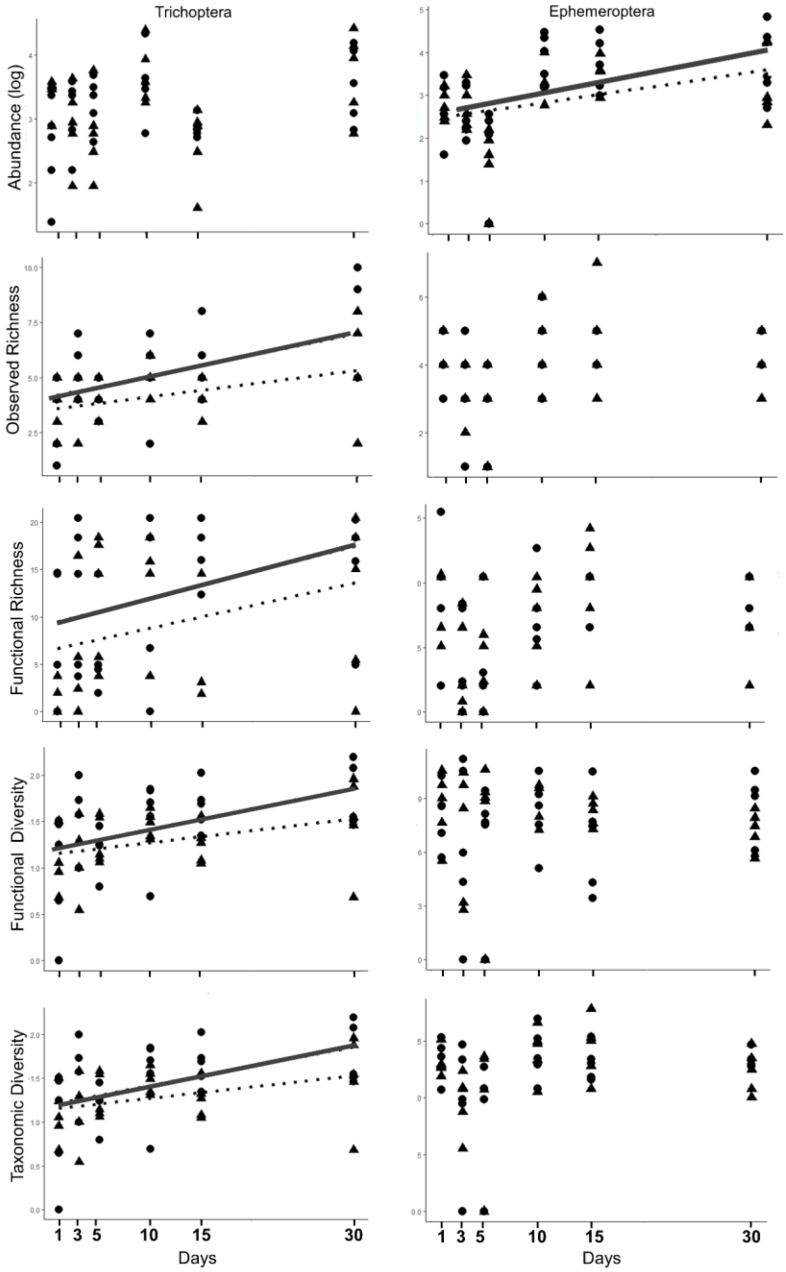
		Abundance	
		Substrate	
		Homogeneous	Heterogeneous
EPHEMEROPTERA			
Baetidae	*Baetodes* Needham e Murphy, 1924	237	488
	Camelobaetidius Demoulin, 1966	6	0
	Americabaetis Kluge, 1992	65	79
Caenidae	*Caenis* Stephens, 1835	353	362
Leptophlebiidae	*Farrodes* Peters, 1971	27	46
	Thraulodes Ulmer, 1920	20	14
Leptohyphidae	*Tricorythopsis* Traver, 1958	16	21
	Tricorythodes Ulmer, 1920	0	2
TRICHOPTERA			
Calamoceratidae	*Phylloicus* Müller, 1880	44	44
Glossosomatidae	*Itaura* Müller, 1888	372	304
	Protoptila Banks, 1904	51	29
Helicopsychidae	*Helycopsyche* Siebold, 1856	2	0
Hydropsychidae	*Leptonema* Guérin, 1843	3	6
	Smicridea Pictet, 1836	322	304
Hydroptilidae	*Hydroptila* Dalman, 1819	2	7
	Leucotrichia Mosley, 1934	0	3
	Metrichia Ross, 1938	12	41
	Neotrichia Morton, 1905	62	56
	Oxyethira Eaton, 1873	3	4
Leptoceridae	*Oecetis* McLachlan, 1877	5	5
	Nectopsyche Müller, 1879	1	2
	Triplectides Kolenati, 1859	2	2
Odontoceridae	*Marilia* Müller, 1880	0	3
Philopotamidae	*Chimarra* Stephens, 1829	5	7
	Worlmaldia McLachlan, 1865	2	2
Polycentropodidae	*Cernotina* Ross, 1938	6	0

Among the metrics used for the Ephemeroptera order, abundance was the only one that showed variation among substrates (Figure 2; Table 3). However, this variation was mediated by colonization time (30 days). On the other hand, among the metrics used with the Trichoptera order, the only one that did not show influence by the substrate was the abundance metric. The Trichoptera taxonomic richness and diversity and functional richness and diversity were higher in the heterogeneous substrate, especially over time (Figure 2; Table 3).

Table 3 Results of univariate analyzes (ANCOVA) for abundance, taxonomic richness and diversity, richness and functional diversity of Trichoptera and Ephemeroptera, using substrate and time (covariate) as predictive factors.

	Caddisflies			Mayflies		
	F	df	p-value	F	df	p-value
Abundance (log)	2.6	2.57	0.077	7.8	2.57	**<0.001**
Observed Richness	10.5	2.57	**<0.001**	1.0	2.57	0.369
Taxonomic Diversity	7.2	2.57	**0.001**	1.3	2.57	0.28
Functional Richness	4.3	2.49	**0.018**	0,.2	2.53	0.844
Functional Diversity	3.3	2.57	**0.041**	0.3	2.57	0.722

Fig. 2 Influence of substrates (homogeneous and heterogeneous) during colonization on (A) abundance, (B) richness, (C) taxonomic diversity, (D) functional richness and (E) functional diversity of the order Trichoptera, and (F) abundance, (G) richness, (H) taxonomic diversity, (I) functional richness and (J) functional diversity of the order Ephemeroptera. Dashed line and triangle represent homogeneous substrate and solid line and circle represent homogeneous substrate.



Chlorophyll-a concentrations were not related with any of the quantified metrics. On the other hand, the amount of organic matter was correlated with the Ephemeroptera abundance in the homogeneous substrate (r=0.53, p=0.002). In addition, the organic matter amount was correlated with the Trichoptera functional diversity in the homogeneous (r=0.36, p=0.04) and heterogeneous substrate (r=0.42, p=0.01).

4. Discussion

In this study we evaluated the effects of substrate heterogeneity on the taxonomic and functional characteristics of Trichoptera and Ephemeroptera assemblages, considering substrate colonization time and availability of allochthonous and autochthonous food resources. We observed that the effect of substrate heterogeneity is mediated by colonization time, especially for Trichoptera assemblages. Furthermore, the amount of organic matter adhered to the substrates (allochthonous resources) is associated with the abundance of Ephemeroptera and with the functional diversity of Trichoptera.

The heterogeneous substrate supported greater taxonomic and functional richness and diversity of Trichoptera. Structural irregularities and cavities on the surfaces of heterogeneous substrates increase species richness (Downes et al. 2000; Schneck et al. 2011), as they serve as a refuge for aquatic insects, protecting against possible predation and natural and anthropogenic disturbances (Brown al. 2003; Boyero et al. 2003). Caddisflies are very diverse aquatic insects, with organisms that have functional characteristics in several categories (e.g. feeding habits, locomotion, shape and body size). This demonstrates that diversification of microhabitats and food resources is important for the Trichoptera assemblage. Niche diversification through the increase of microhabitats providing greater living spaces, allows the resources partition and, therefore, the species coexistence with different biological characteristics (Downes et al. 2000; Schoener 1974). These more stable habitat conditions, observed in heterogeneous substrates, may favor the presence and maintenance of species and can represent a reduction in the effects of biotic interactions, such as predation and competition.

According to the Habitat Templet Model (Townsend and Hildrew, 1994), specific combinations of traits determine the species coexistence under specific environmental conditions. *Itaura* sp. and *Smicridea* sp. (Trichoptera) and *Baetodes* sp. and *Caenis* sp. (Ephemeroptera) shares a common characteristic, the cylindrical body form and were more abundant in the heterogeneous substrate. The cylindrical body shape confers low mobility, and is associated with greater environmental heterogeneity. Still, these genres have different eating habits and types of locomotion, which allows the coexistence and reduction of negative interaction effects. In agreement with other studies, heterogeneous substrates allow the organisms coexistence with different functional characteristics and are responsible for the expression of greater species richness and diversity (Downes et al. 2000; Gallardo et al. 2009; Milesi et al. 2016). Substrate heterogeneity has implications for species distribution and acts as an abiotic filter on the taxonomic and functional characteristics of insects (Milesi et al. 2016).

Contrary to our expectations, the taxonomic and functional richness and diversity of Ephemeroptera were not influenced by substrate heterogeneity. The Ephemeroptera genera are specialists in terms of eating habits and body size. For example, all genera observed in this study show predominantly collector feeding habits, with *Baetodes* sp., *Camelobaetidius* sp. and *Tricorythopsis* sp. being collector and scrapers. Collectors feed on MOPF deposited on the substrate surface or in deposition areas, whereas scrapers feed preferentially on periphyton (Wallace and Webster 1996). The reduced body size in Ephemeroptera (<0.25 mm) is a characteristic associated with homogeneous substrates, being an adaptation to altered environments that confers stress tolerance (Milesi et al. 2016). Although they are considered sensitive to environmental changes, some studies have reported a positive relationship between altered environments and Ephemeroptera richness (Siegloch et al. 2008; Souza et al. 2011). Although, taxonomically and functionally, Ephemeroptera does not differ between homogeneous and heterogeneous substrates, the habitats homogenization may favor the presence of these organisms, supposedly being less sensitive to low resources. Furthermore, homogeneous habitats can lead to biotic homogenization, making communities more similar to each other, especially regarding functional characteristics.

We expected hat food resources of autochthonous (i.e. periphyton) and allochthonous (i.e. organic matter) origin would be important for the taxonomic and functional characteristics of Ephemeroptera and Trichoptera assemblages. However, we observed relationships only with Ephemeroptera abundance and Trichoptera functional diversity. According to Milesi et al. (2019), the richness and functional diversity of aquatic insects can be influenced by the availability of food resources. We observed that organic matter was positively correlated with the functional diversity of Trichoptera. Organic matter is one of the main food sources of several Trichoptera genera (e.g. *Phylloicus* sp., *Triplectides* sp. and *Nectopsyche* sp.). Furthermore, the MOPF available in suspension is a food resource for filter filters (e.g. *Chimarra* sp., *Worlmaldia* sp., *Helycopsyche* sp., *Leptonema* sp., *Smicridea* sp. and *Leucotrichia* sp.), and deposited on the substrate surface is a food resource for collectors (e.g. *Hydroptila* sp., *Meritrichia* sp.). Furthermore, in addition to being a food resource, organic matter is used for shelter construction, which refers to the locomotion characteristics by several Trichoptera genera (e.g. *Itaura* sp. and *Proptila* sp.; Morse, et al. 2019).

The Ephemeroptera abundance was positively associated with the organic matter availability in the substrates. The amount of resources available from the initial decomposition process from allochthonous organic matter may be related to the dominance of collector habit in insects (Tomanova et al. 2006). The Ephemeroptera found in this study have a predominantly collector feeding habit, feeding on MOPF. Despite the Ephemeroptera affinity with the scraper habit (according to the fuzzy code), this result may demonstrate that mayflies tend to be experts in terms of feeding habits, especially in favorable habitat conditions, directly reflecting on the organisms abundance.

In this study, colonization time, considered as a covariate, was shown to exert an important effect on the distinction in taxonomic and functional characteristics of Trichoptera and Ephemeroptera assemblages. Furthermore, the food resources availability increased over the time, corroborating some studies (Hepp et al. 2012; Milesi et al. 2019). While substrate proved to be an important predictor for Trichoptera, food resources availability was important for Ephemeroptera abundance. Taxonomic diversity demonstrates patterns of species distribution while functional diversity demonstrates ecological differences between species (Tilman et al. 1997). Thus, the association between substrate, food resources and aquatic insects, mediated by time, are important environmental predictors for the structuring of aquatic insect assemblages (Hepp et al., 2012). Thus, the taxonomic and functional characteristics provide complementary information, making it possible to elucidate the effects of environmental factors, such as substrate heterogeneity on aquatic insect communities.

5. Conclusion

Substrate heterogeneity influenced the taxonomic and functional diversity of Trichoptera assemblage during colonization. Trichoptera followed the pattern of greater taxonomic and functional richness and diversity in heterogeneous substrates over time of colonization. On the other hand, Ephemeroptera demonstrated that its taxonomic and functional characteristics are independent of substrate heterogeneity. However, the food resources availability is the environmental factor that enables the mayflies colonization on stream substrates. Therefore, substrate heterogeneity proved to be an important predictor of aquatic insect structure, especially associated with the availability of allochthonous resources during colonization.

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7. Supplementary material

Table S1 Fuzzy code for each taxon belonging to each characteristics category and their respective functional characteristics (body size, feeding habits, locomotion and body shape) (0 = no affinity, 1 = weak affinity, 2 = moderate affinity, and 3 = strong affinity).

	Body size				**Feeding habits**					**Locomotion**			**Body shape**	
	<0.25	**0.25_0.5**	**0.5_1.0**	**>1.0**	**Colector**	**Shredder**	**Scraper**	**Filterer**	**Predator**	**Swimmer**	**Crawler**	**Case build**	**Flattened**	**Cylindrical**
Ephemeroptera														
Baetodes	2	1	0	0	3	0	3	0	0	3	2	0	0	3
Camelobaetidius	3	0	0	0	3	0	3	0	0	2	3	0	0	3
Americabaetis	1	1	0	0	3	1	2	0	0	3	2	0	0	3
Caenis	0	2	1	0	3	1	1	0	0	1	3	0	2	2
Farrodes	3	0	0	0	2	1	1	1	0	1	2	0	2	2
Thraulodes	0	1	0	0	3	0	2	1	0	1	3	0	3	0
Tricorythopsis	3	0	0	0	3	1	3	0	0	0	3	0	1	3
Tricorythodes	3	0	0	0	3	0	1	0	0	0	3	0	3	0
Trichoptera														
Phylloicus	0	0	0	1	1	3	0	0	0	0	3	2	0	3
Itaura	1	2	0	0	3	0	3	0	0	0	3	3	1	3
Protoptila	1	2	0	0	3	0	3	0	0	0	3	3	1	3
Helycopsyche	3	0	0	0	0	0	2	3	0	0	3	2	0	3
Leptonema	0	0	0	3	0	1	0	3	1	1	2	3	0	3
Smicridea	0	1	1	0	0	1	0	3	1	1	2	3	0	3
Hydroptila	3	1	0	0	3	2	2	0	0	0	2	1	3	3
Leucotrichia	3	0	0	0	2	2	2	3	0	1	2	2	1	3
Metrichia	3	0	0	0	3	0	2	0	0	0	3	1	2	3
Neotrichia	3	0	0	0	1	1	3	0	0	0	3	1	0	1
Oxyethira	3	0	0	0	3	1	1	2	0	1	2	3	0	1
Oecetis	3	1	0	0	2	2	1	0	1	2	2	0	0	3
Nectopsyche	1	2	1	0	2	3	1	0	0	0	3	0	0	3
Triplectides	0	0	2	2	2	3	0	0	0	0	3	0	0	3
Marilia	0	1	0	3	3	1	3	0	1	0	3	0	0	3
Chimarra	0	0	2	0	0	1	0	3	0	0	3	3	0	3
Worlmaldia	2	2	1	0	0	1	1	3	0	1	3	3	0	3
Cernotina	3	0	0	0	0	1	0	0	3	0	3	3	0	3

3 CONSIDERAÇÕES FINAIS

Nesta dissertação avaliamos os efeitos da heterogeneidade do substrato sobre a diversidade taxonômica e funcional das comunidades de Trichoptera e Ephemeroptera, considerando a importância da disponibilidade de recursos alimentares, durante a colonização. Pudemos observar que a heterogeneidade do substrato influencia a diversidade taxonômica e funcional, uma vez que os substratos heterogêneos contêm maior riqueza e diversidade taxonômica e funcional das assembleias de Trichoptera. Por outro lado, as métricas taxonômicas e funcionais de Ephemeroptera não foram influenciadas diretamente pela heterogeneidade do substrato. Concluindo que, em relação a heterogeneidade do substrato, os Trichoptera são mais sensíveis taxonômica e funcionalmente do que os Ephemeroptera.

Grupos de insetos com características (e.g formato cilíndrico do corpo, hábito fragmentador) que descrevem ecossistemas aquáticos com maior integridade ambiental e equilíbrio de funcionamento, foram observados em maior abundância em substratos heterogêneos. Quanto a disponibilidade de recursos alimentares, pudemos constatar que, principalmente no que se refere a matéria orgânica, é um fator que afeta positivamente o processo de colonização de Trichoptera e Ephemeroptera nos riachos. Isso mostra a importância da manutenção da vegetação ripária para a manutenção do funcionamento destes ecossistemas aquáticos.

Em relação ao uso dos amostradores artificias para a colonização e coleta dos insetos aquáticos, ressaltamos a efetividade em simular os substratos homogêneo e heterogêneo. As irregularidades e diferentes tamanhos dos substratos heterogêneos são características importantes para a colonização e permanência dos insetos aquáticos. Além disso, destacamos a importância da heterogeneidade do substrato na organização taxonômica e funcional dos insetos aquáticos.

As perspectivas de continuidade deste estudo, se concentram em abordar de maneira integrada a abordagem funcional e filogenética, com enfoque nos efeitos da heterogeneidade ambiental em escalas espaciais mais amplas, como o uso da terra. O constante aumento das atividades antrópicas que alteram a paisagem no entorno dos ecossistemas aquáticos, estão associados com as mudanças que ocorrem nos habitats e microhabitats dos insetos aquáticos. A abordagem funcional se mostrou importante para compreender a relação dos insetos aquáticos com os ambientes, e com o intuito de ampliar o conhecimento, o uso de abordagens filogenéticas é um importante aliado. A filogenia permite compreender a história evolutiva das espécies e suas características funcionais. Por exemplo, quanto menor a distância filogenética entre as espécies e mais similares forem as características funcionais, podemos buscar evidências de conservadorismo de nicho em resposta, provavelmente, a ambientes com menos influência de impactos antrópicos. Ou, podemos buscar evidências de convergência de características funcionais em função de filtros ambientais impostos por ambiente impactados. Por fim, a filogenia das espécies seria de grande valia, também no intuito de ampliar as informações disponíveis acerca das características funcionais em si, permitindo maior compreensão dos padrões ecológicos das comunidades de insetos aquáticos.