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GIOVANNA COLLYER RESENDE

SIZE SPECTRA IN TROPICAL STREAMS: effects of land use changes

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Dissertação apresentada ao Programa de Pós-Graduação em Ciências Ambientais da Universidade Federal de São Carlos, como parte dos requisitos para a obtenção do título de Mestre em Ciências Ambientais[1].

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O Relatório de Defesa assinado pelos membros da Comissão Julgadora encontra-se arquivado junto ao Programa de Pós-Graduação em Ciências Ambientais.

Dedico este trabalho ao meu Avô.

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Ea quae scimus sunt pars minima eorum quae ignoramus.

("The things we know are the smallest part of the things we don't know.")

Carl Linnæus, 1758

RESUMO

As mudanças no uso do solo alteraram a estrutura e o funcionamento dos ecossistemas, incluindo interações tróficas que controlam o fluxo de matéria e energia. Nós investigamos as diferenças entre a relação log10-biomassa e log10-classes de tamanho corporal (*size spectrum*) de riachos impactados e preservados ao longo de um gradiente de uso do solo, indo desde cobertura quase completa por floresta nativa até agricultura completa de monoculturas. O *size spectrum* caracteriza quantos organismos de cada classe de tamanho são mantidos nas comunidades e, portanto, é uma forma de acessar o fluxo de energia entre os níveis tróficos. Utilizamos dados de macroinvertebrados de 30 riachos, localizados no sudeste do Brasil. Previmos que os riachos impactados poderiam ter mais ou menos recursos basais disponíveis (ou seja, intercepto do *size spectrum* é maior ou menor, respectivamente), e em ambos os casos esperávamos um custo energético mais alto, sustentando menos biomassa em classes de tamanho grande (ou seja, inclinação do *size spectrum* mais íngreme). Também esperávamos mais desvios no modelo em riachos impactados (menor regressão R^2), devido à alta demanda de energia e baixa eficiência de transferência energética, fazendo com que os organismos se alimentassem fora de sua proporção ideal de massa predador-presa. Nossos resultados demonstraram que riachos impactados têm menos organismos pequenos disponíveis em níveis tróficos mais baixos (menores interceptos) do que riachos preservados, mas com uma transferência de energia mais eficiente (inclinações mais rasas). Isso pode ser devido aos poucos elos de interação fortes relacionados a comunidades com menor diversidade e à simplificação da teia alimentar em ambientes impactados, o que tende a diminuir a estabilidade e aumentar a vulnerabilidade a eventos estocásticos. Os riachos preservados são mais complexos e têm mais caminhos de energia possíveis, resultando em forças de interação mais fracas, o que leva a uma maior estabilidade da comunidade. Também demonstramos que os desvios no modelo não variam sistematicamente ao longo do gradiente de uso do solo, assim como sua estrutura não é definida pelo tipo de uso do solo. Nosso estudo representa um passo adiante para entender como os impactos antrópicos afetam as interações tróficas e o funcionamento dos ecossistemas em riachos tropicais.

ABSTRACT

Changes in land use have altered the structure and functioning of ecosystems, including trophic interactions that control the flow of matter and energy. We investigated the differences between the relationship of log10-biomass and log10-body size classes (size spectrum) of impacted and preserved streams along a land use gradient, going from almost complete coverage by native forest to complete agriculture of monocultures. The size spectrum characterizes how many organisms of each size class are maintained in the communities and is therefore a way of accessing the energy flow between trophic levels. We used data from macroinvertebrates of 30 streams, located in southeastern Brazil. We predicted that impacted streams could have more or less basal resources available (i.e. higher or lower size spectra intercept, respectively), and in both cases we expected a higher energetic cost, sustaining less biomass in large size classes (i.e. steeper size spectra slope). We also expected more deviations in the model in impacted streams (lower regression R^2), due to the high energy demand and low energy efficiency transfer, causing organisms to feed outside their ideal predator–prey mass ratio. Our results demonstrated that impacted streams have fewer small organisms available at lower trophic levels (lower intercepts) than preserved streams, but with a more efficient energy transfer (shallower slopes). This may be due to few strong interaction links related to communities with less diversity and the simplification of the food web in impacted environments, which tends to decrease stability and enhance vulnerability to stochastic events. Preserved streams are more complex and have more energy pathways possible, resulting in weaker interaction strengths, which leads to a higher community stability. We also demonstrated that deviations in the model do not vary systematically across the land use gradient, as well as its structure is not defined by the land use type. Our study represents a step forward to understand how anthropogenic impacts affect trophic interactions and ecosystem functioning in tropical streams.

Keywords: Energy transfer; Food webs; Tropical streams; Body size; Community stability.

SUMÁRIO

Apresentação

Este trabalho está redigido conforme o Regimento Interno de 2020 do Programa de Pós-Graduação em Ciências Ambientais da Universidade Federal de São Carlos. Nela constam a Introdução Geral em português com o embasamento teórico necessário para a compreensão da dissertação; o Artigo redigido em inglês contendo introdução, métodos, resultados e discussão; a Conclusão Geral em português com o destaque dos principais resultados da pesquisa; e o Material Suplementar. Tanto a Introdução Geral como a Conclusão Geral possuem uma linguagem menos técnica, de forma a facilitar a compreensão do artigo para todos os leitores, da área ou não.

Iniciei esse mestrado em abril/2021, e sua conclusão ocorreu em menos de um ano. O motivo se deu pela minha aprovação como *Research Student* na bolsa de pesquisa oferecida pelo MEXT (Ministério da Educação, Cultura, Esporte, Ciência e Tecnologia), a ser realizada no Japão com início em abril/2022, podendo ser estendida para um mestrado e doutorado. Com essa possibilidade, tomei a decisão de concluir o mestrado no Brasil em tempo recorde em conjunto com o meu orientador, que desde o início apoiou e incentivou a realização desse sonho, até quando eu mesma duvidava que era possível. Deixo registrada a minha eterna gratidão pelo seu suporte e ensinamentos, professor Victor. Evolui imensamente ao longo desse ano, e tenho muito orgulho do resultado do nosso esforço! Esse é apenas o começo.

Meu interesse em ecologia começou desde o início da minha graduação, com a vontade de estudar sobre "bichos" (apesar de ter dedicado o início do meu curso ao direito ambiental). De certa forma, continuo assim. Nesse início de minha trajetória como pesquisadora, já tenho a convicção de que quero responder perguntas ecológicas, independente do sistema e dos organismos, e, seguindo meu mestre, me tornar uma *"question based researcher"*.

Introdução Geral

Os trópicos abrigam grande parte da diversidade biológica terrestre e são de extrema importância para a manutenção da vida na Terra, comportando mais de ¾ (78%) das espécies do mundo (Barlow et al., 2018). Apenas no Brasil, que é a nação com o maior volume de água doce do planeta, 15% de todas as espécies de plantas e animais residem no território brasileiro (Barlow et al., 2018; Mello et al., 2020). Esses dados não incluem a quantidade de organismos que são descritos anualmente, sendo esse valor estimado em quase 20.000 (Tancoigne & Dubois, 2013; Barlow et al., 2018). Essa discussão facilmente percorre o debate sobre a dificuldade em se catalogar dados no Brasil, seja devido à extensão do território ou à falta de incentivo aos pesquisadores, o que não é o foco do presente trabalho. Aqui discutiremos sobre a biodiversidade tropical, especificamente brasileira, e como nossos ecossistemas são afetados pelas mudanças de uso no solo.

O termo biodiversidade refere-se à diversidade biológica das diferentes formas de vida, desde microrganismos até os seres humanos (Alho, 2012). Trazendo a biodiversidade no contexto dos ecossistemas, consideramos não apenas a diversidade entre os organismos, mas também a interação dos seres vivos entre si e com o meio ambiente. Isso inclui o entendimento do fluxo de energia dentro do ecossistema, com as plantas sendo a fonte primária de energia. As plantas absorvem energia solar, e parte dessa energia é consumida pelos herbívoros, que são consumidos por carnívoros, que por sua vez podem ser consumidos por outros carnívoros, e assim até que parte da energia seja transferida aos organismos decompositores. Os resultados dessa decomposição (partículas menores e nutrientes) podem ainda ser absorvidos novamente pelas plantas, recomeçando o ciclo da matéria, uma vez que a energia, utilizada pelos organismos ao longo desse caminho, é dissipada para sempre. A energia é convertida pelos organismos em outras formas dentro de seus corpos e utilizada durante o seu ciclo de vida, como para se alimentar, reproduzir e crescer (metabolismo) (Brown et al., 2004). Esse sistema natural é considerado dinâmico, holístico e complexo, pois considera os organismos, suas interações e seus habitats de forma integrada, compondo o sistema dinâmico da natureza.

Nesse contexto, ações antrópicas podem afetar negativamente os ecossistemas de diversas formas. Em locais de clima tropical, por exemplo, um impacto comumente observado é a mudança de uso do solo de floresta para agricultura (Andrade de Sá et al., 2013), o que pode gerar perda ou alteração de habitats, perda da biodiversidade, contaminação dos recursos naturais, mudanças climáticas, entre diversas consequências que podem influenciar outros sistemas em escala local, regional e até mesmo global (Chivian & Bernstein, 2008). Há inúmeras formas de

estudar como os impactos antrópicos afetam os sistemas naturais, sendo uma delas a análise da interação entre os organismos baseado no fluxo de energia, como descrito anteriormente.

Podemos acessar o fluxo energético em ecossistemas por meio da relação entre tamanho corporal e abundância ou biomassa dos organismos. Na natureza, o tamanho do corpo é reconhecido como uma das dimensões mais importantes para explicar as interações tróficas e a distribuição da abundância em teias alimentares (Chang et al., 2014). Grande parte da variação entre os organismos (e.g. história de vida, funções ecológicas) depende do tamanho corporal, que é um dos principais determinantes do metabolismo (Brown et al., 2004; Heneghan et al., 2019). Na teoria, os predadores buscam se alimentar de presas que estão dentro de uma proporção de tamanho ótima, para que seu ganho energético seja otimizado. Ou seja, os organismos buscam encontrar, capturar, manipular, consumir e ingerir o alimento de forma a obterem o máximo de calorias enquanto gastam menos energia e tempo possível (Schoener, 1971). Essa teoria é conhecida como Teoria do Forrageamento Ótimo, e esse comportamento de alimentação varia conforme as alterações na abundância e nos ganhos energéticos dos recursos (MacArthur & Pianka, 1966). Dessa forma, espera-se que organismos maiores se alimentem de organismos menores dentro da proporção ótima, gerando assim uma relação previsível entre o tamanho do corpo e a abundância de organismos dentro de um ecossistema, com o fluxo de energia decaindo de um nível para o outro, devido a subtração decorrente dos gastos metabólicos.

Aqui exploramos a relação do tamanho do corpo e biomassa de macroinvertebrados aquáticos em 30 riachos localizados no sudeste brasileiro, os quais encontram-se dentro de um gradiente de uso do solo que varia de locais com florestas bem preservadas até ambientes dominados pela agricultura. Ao analisarmos os insetos aquáticos, temos uma variação de tamanho que representa parte da teia alimentar do ecossistema, onde há indivíduos maiores que se alimentam de organismos menores, demonstrando o fluxo de energia, a estrutura e o funcionamento dos ecossistemas no contexto de mudanças no uso do solo. Além disso, os insetos aquáticos são comumente utilizados em estudos semelhantes por diversas razões, por exemplo: são ubíquos, geralmente sensíveis às mudanças ambientais, apresentam curto ciclo de vida, há várias metodologias de coleta de baixo custo, são relativamente fáceis de identificar, entre outras vantagens (Buss, 2008). Nossos resultados trazem informações sem precedentes sobre os impactos antrópicos no funcionamento dos ecossistemas aquáticos em regiões tropicais.

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1 | INTRODUCTION

Ecosystem vulnerability to land use changes is a worldwide concern (Meyer & Turner II, 1992; Metzger et al., 2006). In tropical countries, where a large proportion of the world's biological diversity remains, agriculture is one of the main drivers of deforestation (Andrade de Sá et al., 2013), with a loss of approximately 12.3 million ha per year of tropical forest during the 1990s (Benhin, 2006). These changes increase mean temperatures, decrease mean rainfall (spatially and temporally) and intensify forest fires (Lawrence & Vandecar, 2015; Silva Junior et al., 2020), which directly modify the structure and functioning of several ecosystems (Zhang et al., 2019; Bai et al., 2019). Despite these impacts, little is known about how aquatic food web structures and energy flow are affected by land use changes, especially in tropical climates (Reum et al., 2020). Hence, studies focusing on trophic interactions and energy flow can elucidate the effects of environmental changes on ecosystems (Petchey & Belgrano, 2010; Heneghan et al., 2019).

Food webs of forested headwater streams are mostly based on allochthonous litter inputs from surrounding forests, which supports most of the secondary production in these environments (Wallace et al., 1997; Hall et al., 2000). Therefore, land use changes, in particular for agriculture, have direct and indirect effects on the quantity and quality of the main energy source, and thus on the structure and functioning of the ecosystem (Piggott et al., 2015; Martínez et al., 2016). While deforestation can increase nutrient and pollutant concentrations, it can also increase temperature and primary production (Tanaka & Santos, 2017), which may affect the complex interaction between brown (based on detritus) and green (based on primary production) food webs (Zou et al., 2016). Therefore, in order to comprehend the effects of land use changes in stream food webs, ongoing research needs to examine trophic responses along an impact gradient (Mor et al., 2021).

In food webs, anthropogenic impacts influence the body size of individuals within communities (Brose et al., 2017), which is widely recognized as one of the most important dimensions to explain metabolism, trophic interactions, and distribution of abundance in food webs (Brown et al., 2004; Chang et al., 2014). Changes in the relationship between body size and abundance or biomass (i.e. size spectrum) can be used to evaluate communities responses to environmental stressors, assessing the structure and dynamics of ecological communities (Petchey & Belgrano, 2010; Perkins et al., 2018; Potapov et al., 2019; Pomeranz et al., 2021). The size spectrum is usually represented by a linear regression of $\log_{10}$-number of individuals (or summed biomass) by $\log_{10}$-body size classes in relation to the midpoint of each size class. It is expected that, in closed systems, the direction of energy flow from small numerous individuals to larger but rarer consumers should be a negative and linear association (Figure 1; Brown et al., 2004; White et al., 2007; Saito et al., 2021). Coefficients of the size spectrum (intercept and slope) can inform

about the energy flow in the food web (Perkins et al., 2018). These coefficients can differ among communities or even within a single community over time, and their variation can be used to test ecological predictions (Rice & Gislason, 1996; Petchey & Belgrano, 2010). For example, shallow slopes (less negative) may indicate efficient energy transfer by supporting a greater proportion of larger individuals, while steeper slopes may indicate low energy transfer efficiency, with fewer large individuals being supported by smaller organisms (Pomeranz et al., 2021).
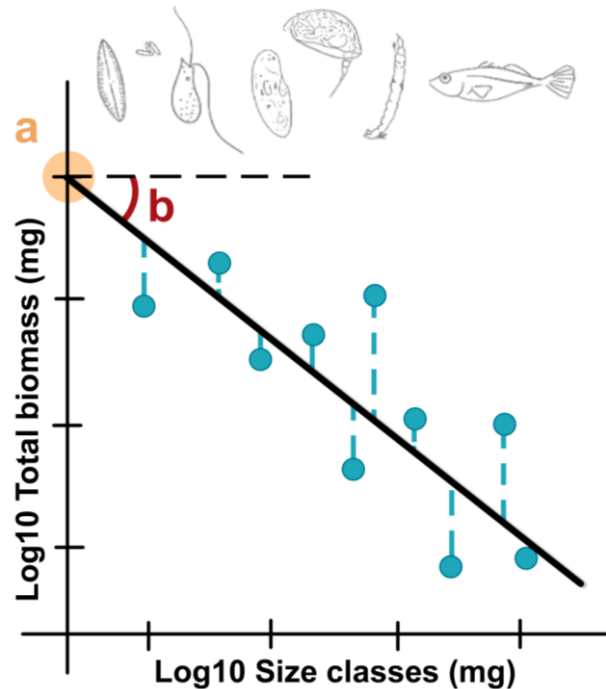
Figure 1. Representation of the size spectrum (black line) relating size bins and total biomass (blue dots). The intercept (a) indicates the amount of energy available in the system (small organisms at the base of the food web). The slope (b) indicates the energy efficiency of the ecosystem, as high efficiency implies the maintenance of larger organisms being sustained in greater biomass. The model fit informs how the biomass of organisms is controlled by metabolic constraints. Model deviations (i.e. variation around the slope, indicated by blue dotted lines) can indicate alternative energy pathways in the maintenance of organisms.

The size structure of food webs is determined by size-dependent trophic interactions between predators and prey (Brose et al., 2006). The predator–prey mass ratio (PPMR) is essential for predator-prey dynamics, interaction strengths, trophic position, size and structure of food webs (Chang et al., 2014; Gibert & Delong, 2014). The Optimal Foraging Theory assumes that predators' feeding decisions differ according to changes in the abundance and energy gains from resources (Emlen, 1966; MacArthur & Pianka, 1966). Therefore, foraging outside the optimal PPMR would mean feeding on organisms that cost more energy to capture and consume, with lower energy gains (Stephens & Krebs, 1987). Since streams are open systems and impacted streams demand more energy for organisms to survive (Petchey & Belgrano, 2010; Perkins et al., 2018), there can be variation to the linear fashion of size spectra (henceforth, secondary structure), with systematic deviations driven by higher or lower number of individuals than expected by a linear fit for a given size class. There are some hypotheses that try to explain this event

(Blanchard et al., 2017), such as complexity of habitats (Rogers et al., 2014), omnivory (Chang et al., 2014), the narrow range of prey size (Plank & Law, 2011), dynamic or long-term seasonal cycles (Datta & Blanchard, 2016), and organisms feeding of allochthonous prey (Perkins et al., 2018). Nonlinear size spectra and secondary structure are still poorly explored but could explain the variations in community structure across different environmental gradients.

Although size spectrum is an emerging topic in literature, there are more studies in marine environments (e.g. Law et al., 2012; Blanchard et al., 2017; Heneghan et al., 2019; Reum et al., 2020) than in freshwater sites (Petchey & Belgrano, 2010). Besides, more is known about temperate systems (e.g. Martínez et al., 2016; Perkins et al., 2018; Pomeranz et al., 2021; Mor et al., 2021) than tropical systems (e.g. Benejam et al., 2016; Potapov et al., 2019), with virtually no studies about the effects of land use changes on size spectra of tropical streams, as those in Brazil. The lack of research in this area is worrying, as Brazil is a developing country with the highest amount of freshwater resources in the world (Mello et al., 2020) and, historically, has disordered and accelerated land use changes with the increase of urban areas (Benejam et al., 2016).

Here, for the first time we analyzed the effects of land use changes at the catchment scale (forest to agriculture gradient) on macroinvertebrate community size structure of southeastern Brazilian streams. We tested the overall prediction that the size spectra differ between impacted and preserved environments. We hypothesized that decreasing vegetation in impacted streams could influence the quantity of basal energy available as a consequence of decreasing allochthonous resources (e.g. leaf litter), resulting in a lower intercept (basal energy available) due to nutritional constraints on secondary production (Martínez et al., 2016). However, deforestation could also lead to a higher primary production as a result of higher incidence of sunlight and enhanced nutrient loads (Benstead & Pringle, 2004), leading to a higher intercept in impacted streams. Furthermore, the energetic costs should be higher in impacted streams due to the degradation of water quality leading to harsher physiological conditions which would increase metabolic costs and decrease biomass (Petchey & Belgrano, 2010; García et al., 2017). Therefore, we found potential explanations to expect that the intercept should be both higher (more energy via green pathways) or lower (less energy via brown pathways) in impacted streams, but the slope should be steeper (more negative) in both cases, with lower energy efficiency transfer due to increase in metabolic costs (Brown et al., 2004; Petchey & Belgrano, 2010). Finally, this higher energetic constraints in impacted sites would influence organisms' foraging behaviors, leading to a more evident secondary structure (deviations in the size spectrum) in impacted streams due to deviations from the PPMR. By characterizing the size spectra along a land use gradient, we take a step towards understanding how these impacts can alter trophic interactions and energy use in tropical streams.

2 | METHODS

Study area and sampling

We use data taken between September and November of 2015 from 30 streams out of 100 distributed in 20 watersheds (i.e. 5 streams per watershed) in southeastern Brazil, with a spatial extent of 70 km in north-south and 120 km in east-west directions (Fig. 2, see also Heino et al., 2018; Siqueira et al., 2020; and Petsch et al., 2021). Streams were located within a strong land use gradient, going from complete coverage by Atlantic Forest (running through 3 major protected areas: Carlos Botelho, Intervales, and Alto Ribeira state parks; State of São Paulo) to areas dominated by agriculture, such as pastures, *Eucalyptus* and *Pinus* plantations. The climate is characterized by two seasons: dry season from April to August, and wet season from September to March. At the time of sampling, there were no recent floods or droughts. Streams' orders were generally the same within watersheds, but varied among watersheds (e.g. 2nd- and 3rd-order). The maximum distance between pairs of streams within watersheds ranged from 2.48 to 8.86 km. More details about the study area can be found in Heino et al. (2018), Siqueira et al. (2020) and Petsch et al. (2021).
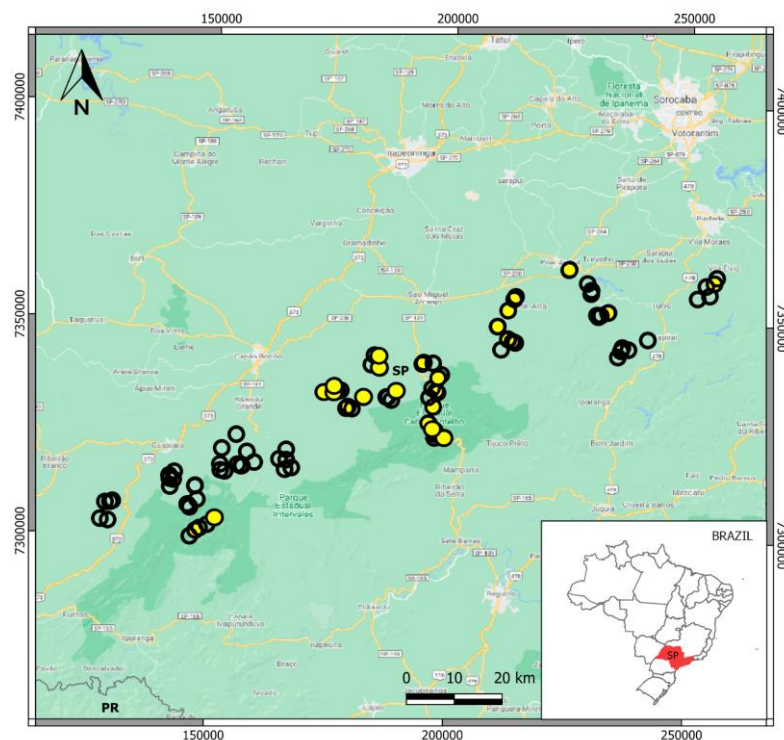
Figure 2. Location of the 100 streams sampled in southeastern Brazil. Black circles refer to each stream sampled and yellow circles represent the 30 streams selected for this study. Darker green area indicates preserved streams, with natural vegetation (e.g. state parks).

A 2-minute kick-net sample (net mesh size: 0.5 mm) was used in each stream, with four 30-second sample units obtained in the main microhabitats at a riffle site of c. 25–50 m², taking into account variations in velocity, depth, macrophyte cover and benthic particle size. The four

sample units were pooled, all insects were separated from debris and preserved in alcohol in the field.

Land use gradient and selection of streams

For the environmental data, 15 important physical and chemical variables for the distribution of insects in lotic environments were measured. The variables measured consisted of velocity (m/s) and depth (cm) in nine random points of each stream; particle size classes (%) visually estimated in 0.25 m² sections in 3 random locations, using a modified Wentworth's (1922) scale of particle sizes: sand (0.25–2 mm), gravel (2–16 mm), pebble (16–64 mm), cobble (64–256 mm), and boulder (256–1,024 mm); mean stream width based on three cross-channel measurements and visually estimated shading using riparian vegetation at each site. Native forest cover was estimated by satellite images within a 400 m buffer along tracts of the streams. pH and conductivity were also measured in each stream using the Horiba U-50 series device; water samples were collected to analyze total nitrogen and total phosphorus. Land use cover data was also characterized for each watershed and resulted in the categories of native forest, secondary/managed forest, exotic/planted forest, pasture, agriculture, urban, mining, wetland, bare soil, water, and mixed.

Because the size spectra approach used in this study is highly time demanding and many streams are not strongly associated with the land use gradient of interest, we selected 30 streams out of the 100 sampled streams to carry out our subsequent analyses. To select these streams, we characterized the environmental gradient of interest (forest to agriculture), using a Principal Component Analysis (PCA), reducing the environmental data in two main dimensions that represent part of the original information. In general, the PCA transforms a group of correlated variables into a group of orthogonal uncorrelated axes known as principal components (Janžekovič & Novak, 2012). To select the 30 streams, we considered mainly the first axis, which was strongly associated with forest and agriculture (see Results).

Identification, measurement, and body mass estimation of organisms

All organisms from the 30 selected streams were identified to the lowest taxonomic level possible. Most insects were identified to genus level, since species-level identification is, for the most part, not feasible for tropical aquatic insects due to the lack of description for many species, especially in immature stages (Cruz et al., 2013). The keys used to identify each organism were: Mugnai et al. (2010) and Hamada et al. (2014) for general identification of all groups, Novaes (2014) for Perlidae (Plecoptera) and Hamada & Couceiro (2003) for Plecoptera, Segura et al.

(2011) for Elmidae (Coleoptera), Azevêdo & Hamada (2008) for Megaloptera, and Edwards et al. (2009) for Hirudinea.

Each organism was positioned in a petri dish, with 70% alcohol (except for Coleoptera adults, which were identified while dry). We used a LEICA EZ4 stereomicroscope, with a millimetric paper under the Petri dish for measurement. Body length in insects was measured from the distance between the anterior part of the head and the posterior part of the last abdominal segment (excluding cerci and appendices), head width was measured across the widest part of the head; and for Helicopsychidae (Trichoptera), we measured the widest portion of the case (Towers et al., 1994). For Gastropoda, height of the shell along its longest axis was measured (Méthot et al., 2012). Lastly, for Trichodactylidae (Decapoda, Crustacea), we measured carapace width by the largest distance between the lateral edges of the carapace (Ferreguetti, 2018).

With measurements of body length, head width, carapace width and shell height, we estimated individual dry mass (mg) using published length-mass relationship equations (Tables S1, S2 and S3). When more than one equation was found for the same taxa, we selected the one with higher R². Organisms ≤ 0.0026 mg were excluded from the analysis to avoid the inclusion of size classes that may be affected by under-sampling (Perkins et al., 2018).

Size spectra

The size spectrum for each stream was calculated using the maximum likelihood method LBNbiom (e.g. Platt & Denman, 1978; Blanchard et al., 2005; Roy et al., 2011), adapting the code provided by Edwards et al. (2017) using R programming language (function LBNbiom.method, package 'sizeSpectra'). This method fits the regression of log10(accumulated normalised biomass within a size bin divided by the width of that bin) against log10(midpoint of the size bin) (Edwards et al., 2017). That is, in the y-axis we have log10 of the sum of all organisms present in each specific size bin, divided by its respective size bin width. In the x-axis, we have log10 of the size bin midpoint. The number of size bins was between two and nine, which were sufficient to show linear relationships in our data.

Data analyses

To investigate the behavior of size spectra coefficients in relation to the environmental gradient, we performed linear regressions using the PCA first axis as explanatory variable and the values of intercept, slope, R², heteroscedasticity, total biomass and size range from each stream as response variables. For total biomass, we summed dry masses of all organisms in each stream. To access the secondary structure, we calculated heteroscedasticity (the structure of residuals in size spectra models) applying the Breusch-Pagan test using the function *bptest* in the package 'lmtest'

in R v. 0.9-39, with Kendall's rank correlation method. For the size range, we subtracted the highest value with the lowest value of individual dry mass from each stream. To understand how larger and smaller organisms were affected by the gradient, we performed two quantile regressions of the 95th and 5th percentile using data from individual body masses (log$_{10}$ mg) in each site, with the '*quantile*' function available in base R. In order to understand changes in composition along the gradient, we calculated correlation between abundance of families and the first axis of PCA, using the Pearson method. Finally, we calculated the Shannon-Weaver diversity index to assess changes in diversity along the environmental gradient using a linear regression.

3 | RESULTS

The 30 selected streams distributed along the PCA first axis (14,77% explained of the total variation, Fig. 3) were associated with a land use gradient from Forest cover to Agriculture dominated basins. The first two axes of PCA explained 24.88% of the variation in our data, which also encompasses variation in chemical and physical factors inherent to natural environments. From these 30 streams, we measured and identified 15,410 individuals within 14 Orders, 58 families and 73 genera. The five Orders with the highest abundance were Diptera (n=6,612), Ephemeroptera (3,499), Coleoptera (1,766), Trichoptera (1,423) and Plecoptera (1,075).
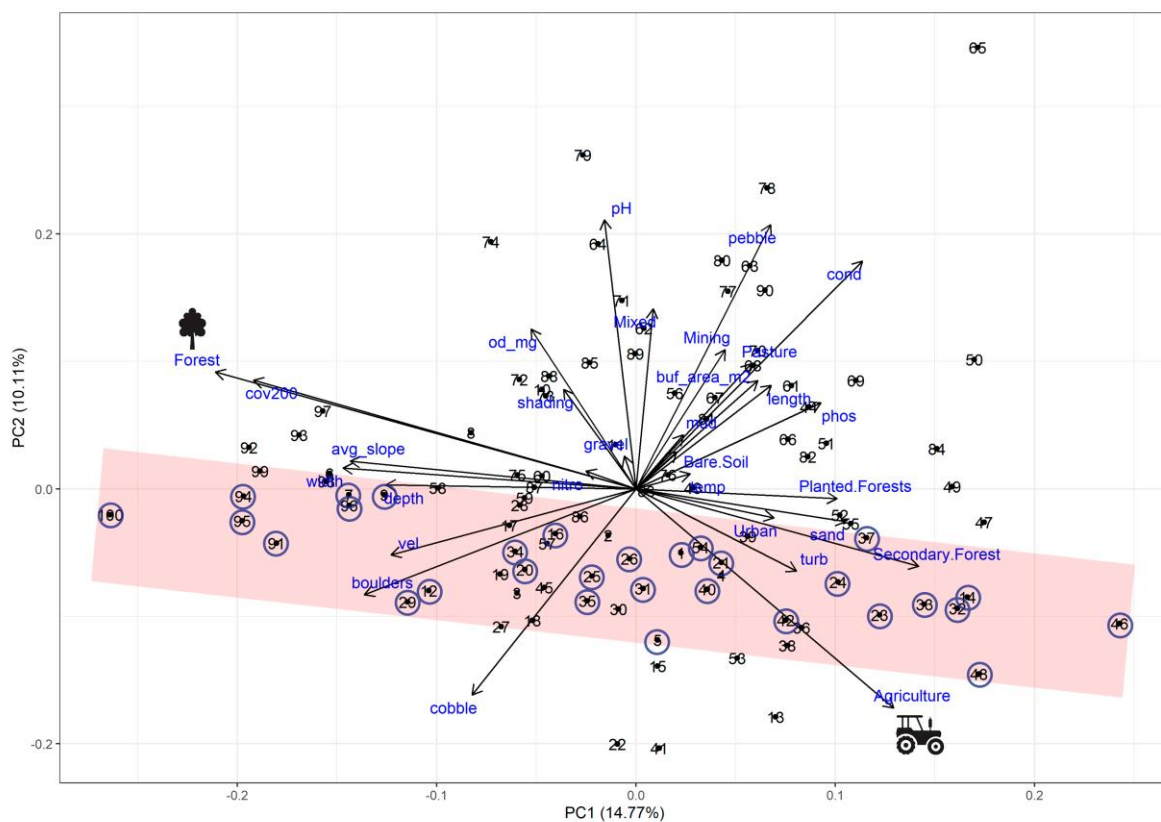
Figure 3. Principal Component Analysis (PCA) of environmental variables associated with 100 tropical streams. The red area represents streams associated with the environmental gradient from forest (marked with a tree symbol) to agriculture (marked with a tractor symbol). Blue circles inside the red area indicate the 30 streams chosen for this research.

Size spectra from the 30 streams were characterized in terms of the intercept, slope, model fit and heteroscedasticity. The intercept of all streams varied from 3.2 to 0.48, and the slope varied from -0.23 to -1.25. Figure 4 depicts the size spectrum from 30 streams, showing that preserved areas have higher intercepts, but a steeper slope. In more impacted streams, the slope becomes shallower and the intercept, lower. All 30 representations of size spectra are available in the Supplementary Material (Figure S1).
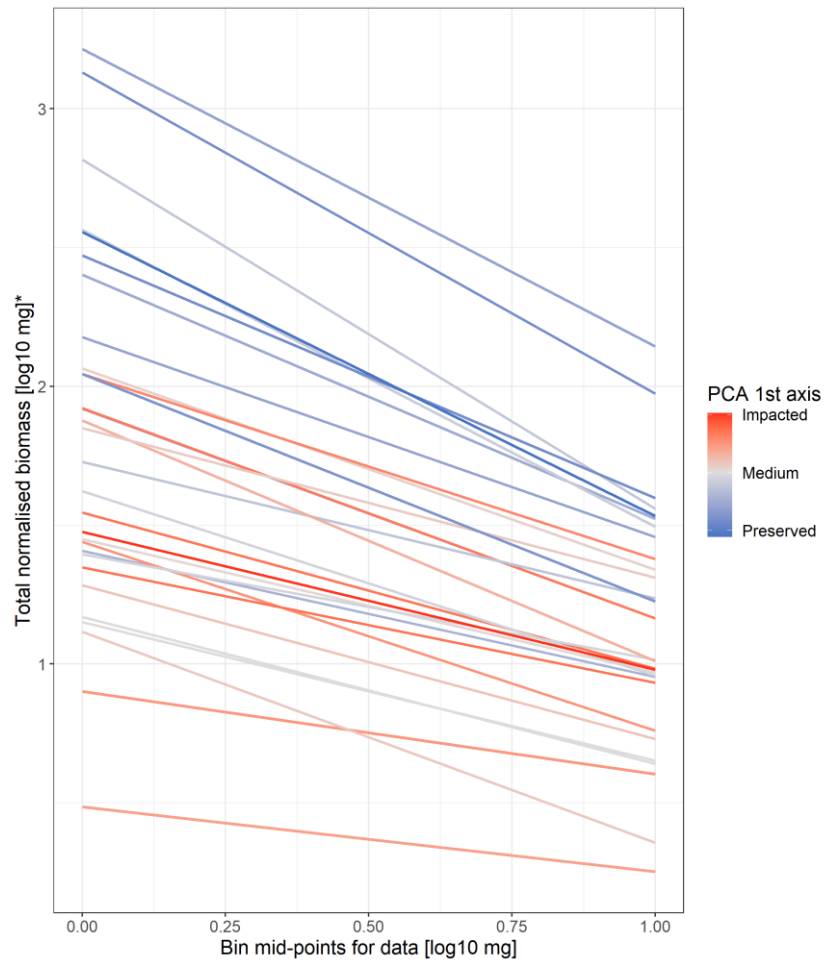
Figure 4. Patterns in the size spectrum of 30 tropical streams along a land use gradient. The lines were plotted using individual values of intercept and slope from each stream. Body mass range (0 to 1) was set to avoid regressions ending at different size bins. The color gradient considers the position of streams in the PCA first axis. Blue lines represent streams with prevalence of forest, and red lines streams with prevalence of agriculture. *Total normalized biomass (see "Methods" for details).

The intercept decreased with increasing land use intensification (PCA first axis) ($R^2 = 0.34$, $p < 0.001$; Fig. 5a). The size spectra slope, on the other hand, was less negative (shallower) in impacted streams ($R^2 = 0.28$, $p < 0.01$; Fig. 5b). The model fit (R^2) of the size spectra did not change systematically along the gradient ($p > 0.05$; Fig. 5c) and was consistently high, with a mean value of 0.71 and a standard deviation of 0.23. Heteroscedasticity also did not differ along the gradient ($p > 0.05$; Fig. 5d) and varied from 0.01 to 3.35 (Breusch-Pagan value). Beside these measurements from the size spectra, total biomass (Fig. 5e) decreased in more impacted streams ($R^2 = 0.22$, $p < 0.01$) and was positively correlated with the intercept as shown by the Kendall

rank correlation coefficient ($\tau = 0.80$; Fig. 5f). Moreover, the intercept and total biomass were negatively correlated with the slope ($\tau = -0.70$ and $\tau = -0.50$, respectively; Fig. 5f).
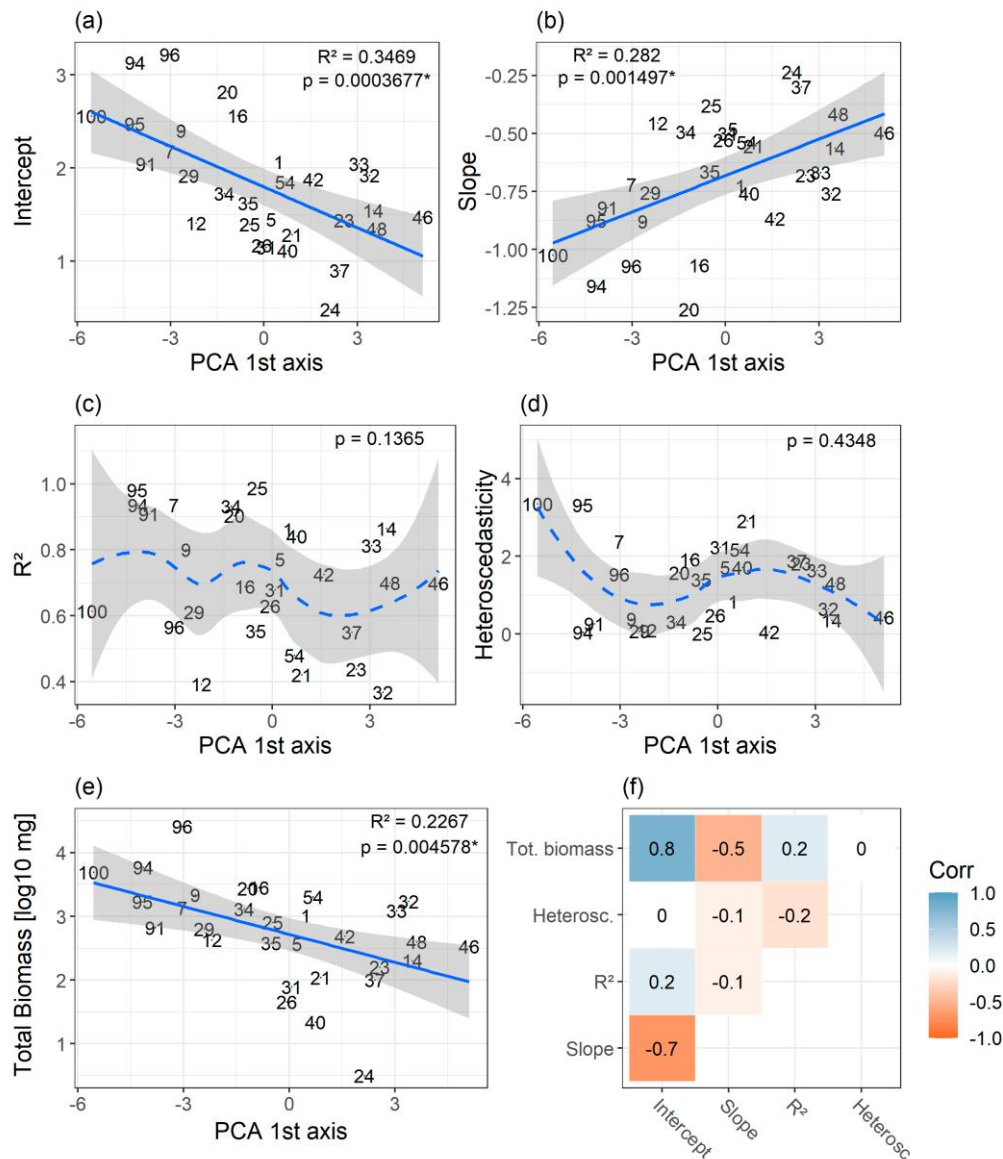
Figure 5. Relationship between land use changes and size spectra coefficients, model fit, heteroscedasticity and total biomass. Land use intensification increases from left to right on x-axes of panels a-e. Grey shading in figures (a) to (e) represents a 95% confidence interval. Blue straight lines show a significant linear pattern, and dashed lines show non-significant linear pattern. Along the gradient, the intercept (in mg) decreases (a) and the slope become shallower (b). The model fit (c) and heteroscedasticity (Breusch-Pagan test) were not significantly different in preserved and impacted streams. Total biomass (in mg) (e) was higher in preserved streams. The Kendall rank correlation coefficient (f) depicts that total biomass is positively correlated with intercept, and both are negatively correlated with the slope.

Size range (max(M) - min(M), in $\log_{10}$ mg) of organisms decreases with increasing land use intensification, varying from 0.05 to 3.45 $\log_{10}$ mg ($R^2 = 0.25$, $p < 0.01$; Fig. 6a). Larger organisms were more affected in impacted streams (95% Quantile regression, $R^2 = 0.09$, $p < 0.01$, slope = -0.06; 5% Quantile regression, $R^2 = 0.06$, $p < 0.01$, slope = -0.01; Fig. 6b), indicating that along the gradient, communities have smaller organisms in impacted streams. Figure 6c depicts

the size range for different taxa, indicating that larger organisms consisted mainly of Decapoda, Megaloptera, Trichoptera, Plecoptera and Odonata.
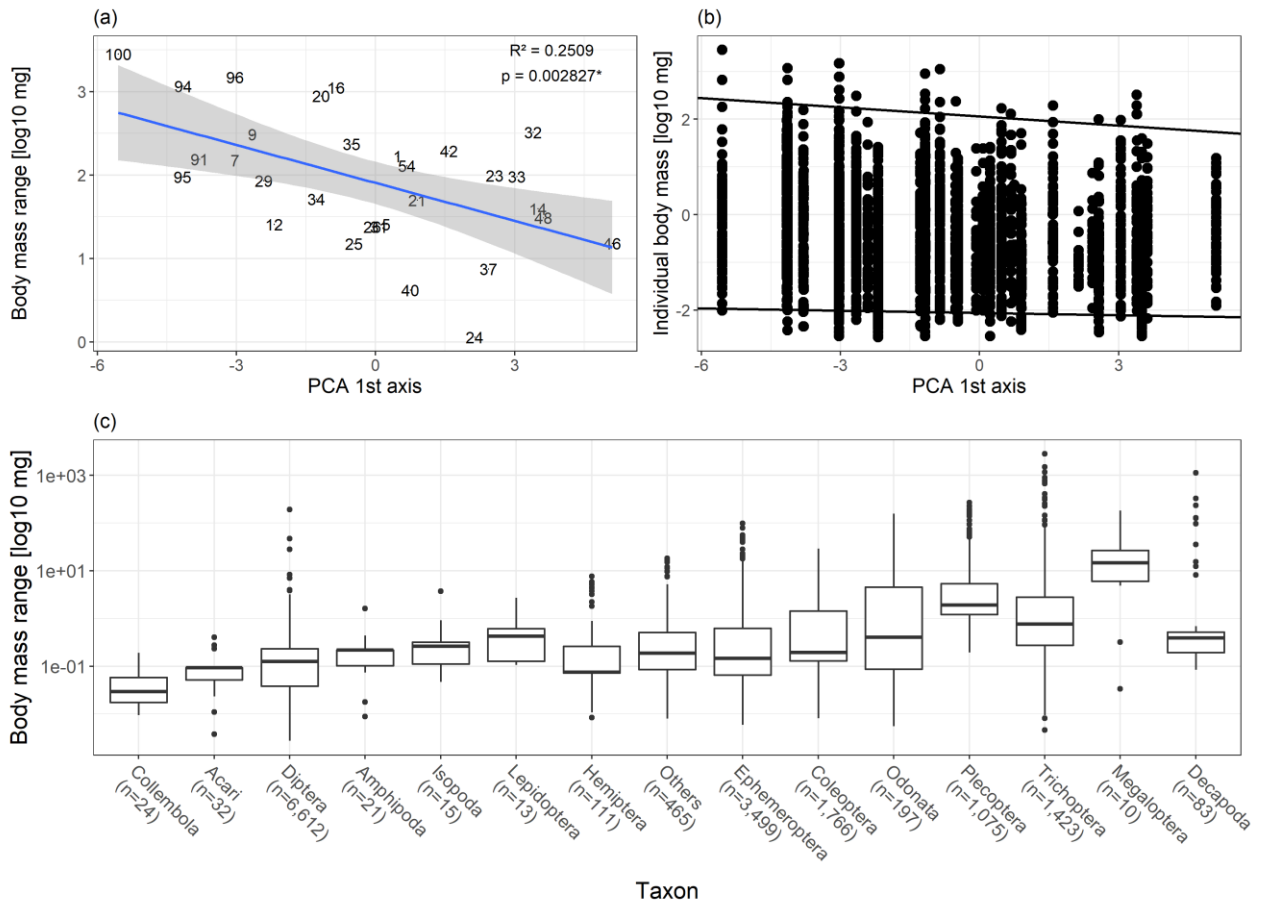
Figure 6. Size range analysis. Land use intensification increases from left to right in (a) and (b). (a) Range of body size (log10 [max(M) − min(M)], in mg) decreases along the gradient (grey shading indicates a 95% confidence interval). (b) Quantile regressions of the 95th and 5th percentile (top and bottom lines, respectively) of body size (log10 mg) across the environmental gradient. (c) Boxplot of range size (log10 mg) for each taxon, showing that larger organisms consisted mostly of Decapoda, Megaloptera, Trichoptera, Plecoptera and Odonata. The group classified as "Others" was composed of Gastropoda, Hirudinea, Oligochaeta and Turbellaria.

We found that all identified families from Trichoptera, Plecoptera and Megaloptera orders were positively associated with preserved streams, indicating once again that larger organisms are more abundant in less impacted areas. In general, most taxa were associated with preserved streams (74%), with few families more abundant in impacted streams (26%) (Figure 7). Diptera was the order with more representatives positively related to agriculture, with Simuliidae most associated with impacted streams (Figure 7). Furthermore, Perlidae (Plecoptera) was the family with the strongest association with preserved areas (Figure 7).
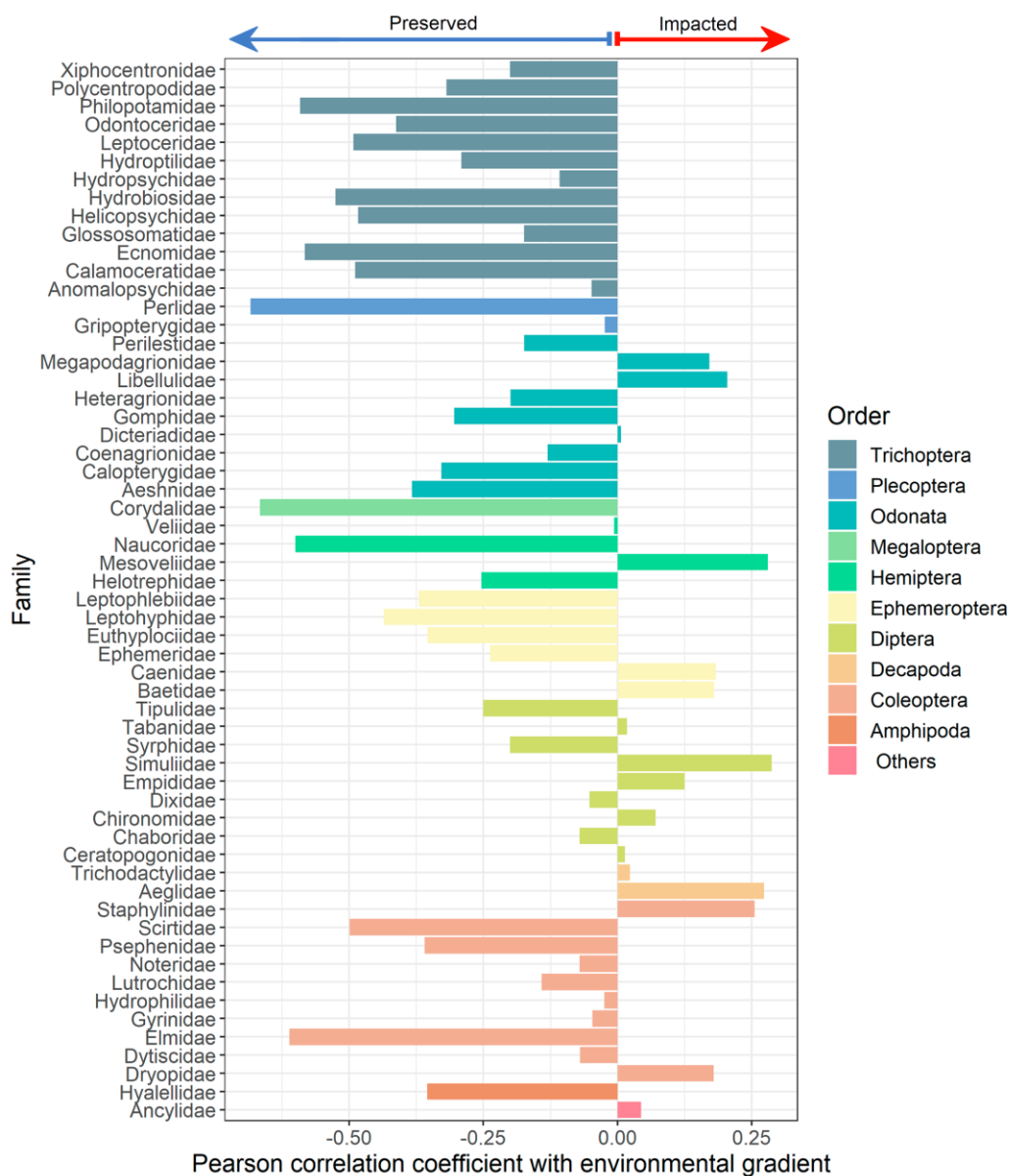
Figure 7. Abundance of families in relation to the gradiente. Values more negative indicate preserved areas (left), as well as positive values represent impacted areas (right). Colors represent the correspondent order from each family. Preserved and impacted limits consisted of the Pearson correlation coefficient of abundance value from each family with the PCA 1st axis. The order classified as "Others" was composed of Gastropoda, Hirudinea, Oligochaeta and Turbellaria.

Another evidence of changes in community composition along the gradient is the proportion of organisms from different Orders in each stream (Figure 8). A decrease in Coleoptera is observed in more impacted streams, as well as less representatives from other Orders (e.g. Odonata and Plecoptera). A predominance of Diptera in impacted streams is also evident in Figure 8 (the proportion of Diptera increases towards more impacted streams, right sided). The result of the linear regression applied to the Shannon index indicated that diversity decreased towards more impacted sites ($R^2 = 0.27$, $p < 0.01$). This suggests that food webs in impacted streams are less diverse and thus simpler.
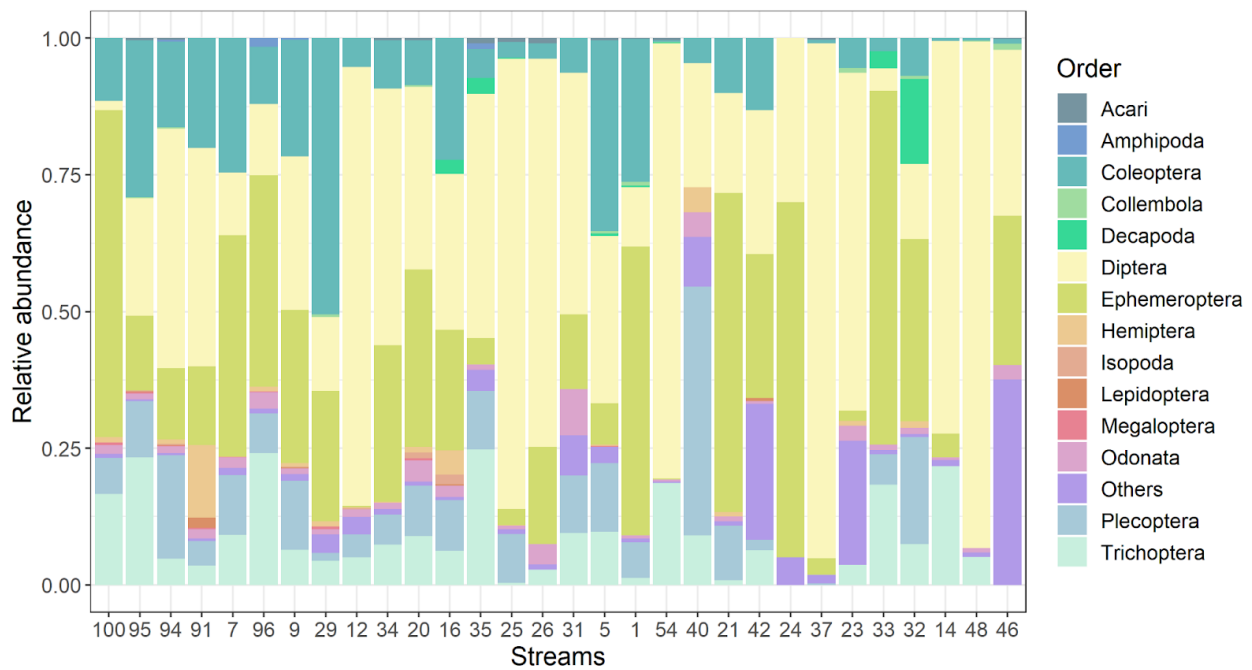
Figure 8. Proportion of orders for each stream representing changes in community assemblage along the gradient (land use intensification increases from left to right).

4 | DISCUSSION

By analyzing 30 tropical streams in southeastern Brazil, we found empirical evidence that the conversion of forest into agricultural systems interferes in the biomass and energy flow of aquatic macroinvertebrates, altering the structure and functioning of ecological communities. These streams encompass a large environmental gradient in terms of land use, going from almost complete coverage by forest to complete agriculture of monocultures, and demonstrated that the size spectra coefficients and community composition differ along the gradient. In impacted environments (prevalence of agriculture), a decrease in the biomass of small organisms at lower trophic levels (lower intercept) and a flatter size-spectrum slope were observed in comparison with preserved environments (prevalence of forest), with lower proportion of larger organisms. In addition, size spectra were fairly linear in all systems (the model fit and heteroscedasticity does not change according to the environmental gradient) depicting how energetic constraints are overarching drivers of community patterns in systems under different land use contexts. We also show that most macroinvertebrate families were more abundant in preserved streams, while less than 30% of the families, represented mostly by Diptera, were more abundant in impacted streams. Likewise, community composition also indicates a dominance of Chironomidae as energy sources for higher trophic levels, with less diversity in impacted environments. In the following, we describe how our results elucidate that land use changes can alter trophic interactions and energy use, decreasing stability and enhancing ecosystems vulnerability.

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The decreased biomass of small organisms at lower trophic levels with increasing environmental impacts is in line with one of our hypotheses and has been predicted and documented in many studies (Petchey & Belgrano, 2010; Pomeranz et al., 2018; Saito et al., 2021), with few exceptions (e.g. Martínez et al., 2016 and Pomeranz et al., 2021). These studies suggest that more impacted environments affect population density and community biomass due to a high metabolic demand (Petchey & Belgrano, 2010; Martínez et al., 2016; Pomeranz et al., 2018). Also, deforestation should impact resource supply by decreasing detrital resources entering stream webs, affecting community's biomass (Martínez et al., 2016). We also expected that impacted systems would have slopes more negative (steeper) than preserved environments (Petchey & Belgrano, 2010; Saito et al., 2021). Yet, we found the opposite, size spectra slope was shallower in impacted streams. The size spectra slope (hereafter, slope) is a coefficient that indicates the rate of biomass reduction, with less energy available at higher trophic levels due to energy loss (heat production and respiration) and to inefficient transfer of biomass (Brown et al., 2004), which causes the slope to be a proxy of energy flux through the trophic levels (Woodward et al., 2005; Perkins et al., 2018). The most intuitive conclusion is that energy transfer efficiency is simply greater in impacted systems, which is conflicting with theoretical predictions that impacts increase energetic costs (Petchey & Belgrano, 2010).

An alternative explanation lies in the arguments of the diversity-stability debate. According to McCann (2000), increasing diversity, on average, increases stability of an ecosystem. This happens when higher diversity entails an average weaker consumer-resource interaction strength (weak-interaction effect) (McCann, 2000). Increasing richness enables different possibilities of consumer–resource interactions, making them more general and less specialized and with mostly weak interactions. With weaker interactions, the food web should be more stable in terms of variations due to loss of interactions, and less likely to undergo chaotic dynamics (McCann et al., 1998). On the other hand, an ecosystem with low diversity probably has less and strong interactions possible, making the system more oscillatory and susceptible to loss. In this sense, how species interact must be important to maintain persistence in different communities in face of the variability that underlies ecosystems (McCann, 2000). Therefore, we can expect that decreasing biodiversity and restricting basal resources supply, driven by deforestation, will reduce possible energetic pathways, and thus increase, on average, the interaction strength, enhancing ecosystem instability and its potential to collapse (Hall et al., 2000; McCann, 2000). Even though we did not analyze the distribution of interaction strengths, our results suggest that the shallower slope in impacted environments may be due to the loss of diversity (or the capability of the ecosystem to sustain different species), that potentially simplifies the trophic system (Schuldt et al., 2018) and reduces possible energy pathways while

likely increasing interaction strengths. We can justify that the energy transfer appears to be less efficient in preserved streams probably because food webs in preserved environments are more diverse and complex with have many energetic pathways that can protect communities to collapse in face of stochastic events (McCann, 2000). That is, supporting more variations and enhancing stability due to the weak-interaction effect. The results are surprisingly aligned with an experimental study that examines effects of leaf litter exclusion on predator-prey interactions (Hall et al., 2000). The authors empirically observed that excluding leaf litter leads to fewer energetic pathways from preys to predators, but with strong interactions among the observed taxa, supporting our inference that removing allochthonous inputs can end negative consequences to ecosystem stability.

Our results show a reduction of the size range and total biomass across the gradient, with a decrease in larger macroinvertebrates in impacted streams, as expected since larger-bodied organisms are more affected by environmental impacts than smaller organisms (White et al., 2007; Brose et al., 2017). Larger organisms (Decapoda, Megaloptera, Trichoptera, Plecoptera and Odonata) were more abundant in preserved areas and are known to have more impact-sensitive representatives (Docile et al., 2016). This causes changes in the community composition, with fewer taxa in impacted streams (Bonada et al., 2006). According to Siqueira et al. (2020), communities with lower abundance are more likely affected by demographic stochastic events (neutral process), which may play an important role on how these communities are structured. Therefore, if communities with lower abundance (in our case, in impacted streams) become more stochastic and are potentially more unstable with few strong interaction strengths (efficient energy flow), it is possible that the loss of important species and thus ecological functions can lead to the collapse of the whole ecosystem. This reinforces the argument that biodiversity loss can strengthen interaction strengths and raises awareness that land use changes can possibly alter how species interact and thus trigger a cascade effect that may scale to the entire ecosystem (McCann, 2000; Dala-Corte et al., 2020).

In addition to changes in biomass at lower trophic levels and energy transfer, we expected more deviations in the model fit (lower R^2) in impacted environments due to the high energy demand and the predicted less efficient energy transfer (Brown et al., 2004), leading organisms to seek alternatives for maintenance and growth, feeding on larger or smaller prey than expected by the Optimal Foraging Theory. Moreover, making an analogy with environments with higher temperatures and impacted streams, Saito et al. (2021) predicted that the secondary structure could vary with temperature, which similarly could happen with impacted environments. However, we observed that energy transfer is linearly predictable, and the model fit and heteroscedasticity values in each stream are not affected by land use changes, meaning that the secondary structure

(more or less organisms than expected, represented by R²) is present regardless of the degree of impact. The location of the secondary structure represented by heteroscedasticity (e.g. more large organisms than expected) also does not have a pattern along the gradient. Nevertheless, the model fit was mostly high along the gradient (R² mainly from 0.5 to 0.9), indicating that the size spectrum is a good model to explain the relationship between log-biomass and log-body mass, in accordance with the power-law theory (White et al., 2007), but most importantly, that the metabolic rules underpinning the assembly of ecological communities are relevant independently of the environmental context.

Our study represents the first regional-scale characterization of tropical streams size-spectrum. The results elucidate unprecedented information on how changes in land use can affect the structure and functioning of tropical aquatic communities. We argue that impacted streams have fewer small organisms available at lower trophic levels, but an efficient energy transfer, probably due to strong interaction links, which also influence their vulnerability to stochastic events. At the same time, preserved streams have more organisms at lower trophic levels available and higher diversity, which can result in weaker interaction links, making these communities more stable. More studies on tropical streams size-spectrum could provide further understanding on how anthropogenic impacts affect the size structure of these ecosystems.

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Considerações Finais

Ao longo do nosso artigo exploramos o comportamento da relação tamanho corporal e biomassa de ecossistemas aquáticos tropicais dentro de um gradiente de uso do solo (floresta-agricultura). Dentre os principais resultados, observamos indícios de que ambientes impactados (associados à agricultura) são possivelmente mais instáveis, onde há menos diversidade biológica, restringindo potenciais caminhos para que a energia flua entre os níveis tróficos. Com menos possibilidades do direcionamento de energia, pode-se ter relações fortes entre os organismos. Dessa forma, caso um evento que não era esperado aconteça (e.g. grande seca na região, exploração de um recurso, poluição), pode causar um efeito em cascata em todo o ecossistema. Esses links fortes de energia tornam os ecossistemas mais suscetíveis à eventos estocásticos, o que pode direcioná-los ao colapso, resultando na perda de importantes espécies (talvez algumas nem descobertas ainda) que são de extrema importância para a sociedade e o meio ambiente. Um forte indício dessa teoria é uma inclinação do size spectra menos acentuada nos riachos impactados em comparação com os preservados, indicando uma transferência de energia mais eficiente. Por outro lado, locais preservados possuem uma maior biodiversidade, maior biomassa e uma maior variação no tamanho dos organismos. Isso pode contribuir para que haja diversas espécies com diferentes funções e comportamentos, ampliando assim as possibilidades do fluxo de energia. Desse modo, tem-se possivelmente links de energia mais fracos, tornando o ecossistema mais estável e menos sensível a eventos estocásticos.

No contexto atual, onde um dos *hot topics* na área ambiental refere-se às mudanças climáticas, cujo interesse tem se tornado cada vez mais frequente dentro e fora da academia, o nosso artigo contribui de forma inédita não apenas com o entendimento sobre o comportamento dos ecossistemas aquáticos brasileiros, mas também com a divulgação de dados sobre a biodiversidade tropical. Entendo que este trabalho é apenas mais um passo para a contribuição da compreensão sobre o funcionamento e a estrutura dos ecossistemas aquáticos tropicais, e que pouco sabemos frente ao que ainda há de ser explorado e descoberto.

Supplementary Material

Figure S1. Individual size spectrum for 30 streams along the land use gradient based on values from the PCA first axis (impact increases from left to right, top to bottom). Points represent each size bin with the normalized body mass from individual organisms in the fitted regression (line).
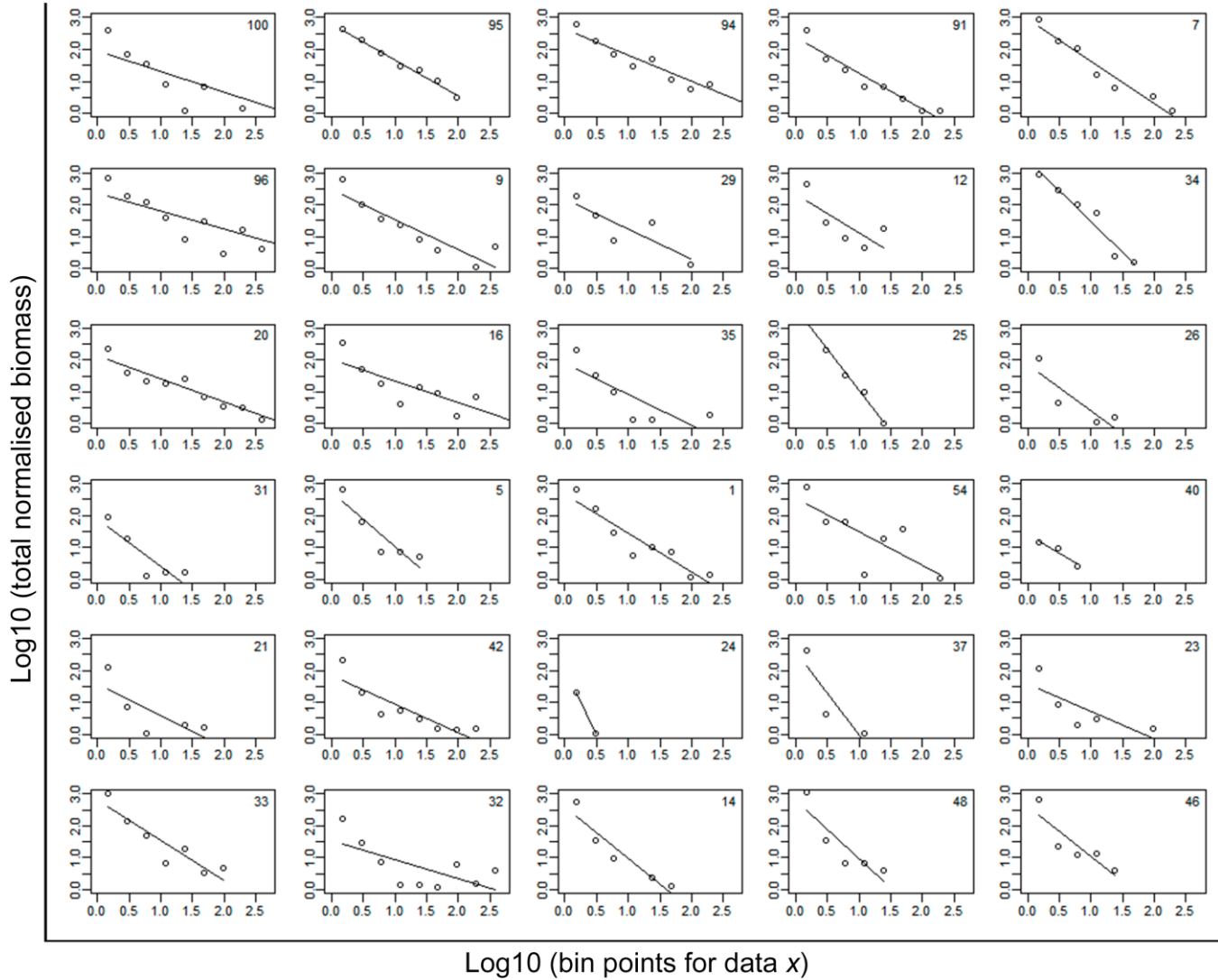
Table S1. Length-mass relationship equations for Power model (DM = a * x ^ b). TBL = Total Body Length (mm) in insects included the distance between the anterior part of the head and the posterior part of the last abdominal segment, HW = Head Width (mm) included the widest part of the head, for Helicopsychidae (Trichoptera), BW = Body Width (mm) consisted in the widest portion of the case (Towers et al., 1994). DM = Dry Mass (mg). BL = Body Length (mm). (*) Ash-free dry mass (AFDM) was used instead of DM, apply the equation DM = AFDM*100/(100 - % ash) to convert (Benke et al., 1999). When the species/genus used for the equations did not belong to the observed genera, the one with the highest R^2 or the one most similar in shape was chosen. (†) Equations were chosen considering the family/order most similar in shape. For Diptera and Hemiptera, (a) and (b) are means calculated from individual taxa within a group, and R^2 value is the range of R^2 (Benke et al., 1999).

Taxa	Measure (x)	a	b	r²	% ash	Source	Comments
COLEOPTERA							
Psephenidae*	BL	0.0077	2.883	0.95	5.5	Benke et al. (1999)	Original for *Psephenus sp.*
DIPTERA	TBL	0.0025	2.692	0.66 - 0.99		Benke et al. (1999)	
Ceratopogonidae	TBL	0.00022	2.871	0.91		Benke et al. (1999)	
Dixidae	HW	0.111	3.775	0.63		Miyasaka et al. (2008)	
Empididae*	BL	0.004	2.655	0.93	2.5	Benke et al. (1999)	
Tabanidae	BL	0.005	2.591	0.81		Benke et al. (1999)	Original for *Chrysops/Tabanus spp.*
EPHEMEROPTERA							
Caenidae							
Caenis sp.	HW	0.2667	2.764	0.96		Benke et al. (1999)	Original for *Caenis diminuta*
Ephemeridae							
Hexagenia sp.	TBL	0.0025	2.718	0.94		Benke et al. (1999)	Original for *Hexagenia limbata*
HEMIPTERA	TBL	0.0108	2.734	0.74 - 0.83		Benke et al. (1999)	
Veliidae	TBL	0.0083	2.777	0.74		Benke et al. (1999)	Original for *Rhagovelia obesa*
LEPIDOPTERA*	TBL	0.0027	2.918	0.97	17.7	Benke et al. (1999)	Original for *Petrophila sp.*
MEGALOPTERA							
Corydalidae							
Corydalus sp.	HW	0.321	3.256	0.97		Benke et al. (1999)	Original for *Corydalus cornutus*
NEMATODA †	BL	0.008	1.888	0.90		Miyasaka et al. (2008)	Original for Oligochaeta

Table S1. Continued.

			Power model (DM = a * x ^ b) [continued]				
Taxa	Measure (x)	a	b	r²	% ash	Source	Comments
ODONATA							
Anisoptera							
Gomphidae	TBL	0.0025	3.474	0.95		Dekanová et al. (2021)	
Libellulidae	TBL	0.0081	2.94	0.95		Dekanová et al. (2021)	
Zygoptera	HW	0.1189	3	0.97		Benke et al. (1999)	Original for *Ischnura sp.*
Calopterygidae	TBL	0.005	2.742	0.87		Benke et al. (1999)	Original for *Calopteryx sp.*
Coenagrionidae	HW	0.4727	2.455	0.85		Benke et al. (1999)	Original for *Argia spp.*
Argia sp.	HW	0.4727	2.455	0.85		Benke et al. (1999)	Original for *Argia spp.*
OLIGOCHAETA	BL	0.008	1.888	0.90		Miyasaka et al. (2008)	
TRICHOPTERA							
Glossosomatidae*	TBL	0.0092	2.888	0.96	6.6	Benke et al. (1999)	Original for *Glossosoma sp.*
Helicopsychidae							
Helicopsyche sp. (case width)	BW	0.0120	3.096	0.96	4.3	Benke et al. (1999)	
Leptoceridae							
Nectopsyche sp.	HW	2.644	3.297	0.74		Benke et al. (1999)	
Oecetis sp.	TBL	0.0034	3.212	0.71		Benke et al. (1999)	Original for *Oecetis spp.*
Odontoceridae*	TBL	0.0064	3.241	0.99	11.3	Benke et al. (1999)	Original for *Psilotreta sp.*
Philopotamidae							
Chimarra sp.	TBL	0.0044	2.652	0.97	12.1	Benke et al. (1999)	
Polycentropodidae	HW	1.568	3.302	0.90		Benke et al. (1999)	Original for *Polycentropus spp.*
TURBELLARIA	BL	0.0089	2.145	0.81		Benke et al. (1999)	Original for *Dugesia tigrina*

Table S2. Length-mass relationship equations for Linear model (ln(DM) = ln(a) + b * ln(x)). TBL = Total Body Length (mm) in insects included the distance between the anterior part of the head and the posterior part of the last abdominal segment, HW = Head Width (mm) included the widest part of the head (Towers et al., 1994). DM = Dry Mass (mg) (except for Trichodactylus sp. [g]). BL = Body Length (mm). CW = Carapace Width (cm). When the species/genus used for the equations did not belong to the observed genera, the one with the highest R² or the one most similar in shape was chosen. (†) Equations were chosen considering the family/order most similar in shape.

	Linear model (ln(DM) = ln(a) + b * ln(x))					
Taxa	Measure (x)	ln a	b	r²	Source	Comments
ARTHROPODA	TBL*BW	-2.3762	1.33	0.89	Gruner (2003)	
ACARI †	TBL*BW	-2.3762	1.33	0.89	Gruner (2003)	Original for Arthropoda
COLEOPTERA (A)	TBL	-2.0076	3.2271	0.97	Towers et al. (1994)	
Dryopidae (L) †	HW	2.2581	3.5741	0.86	Towers et al. (1994)	Original for Elmidae (L)
Dytiscidae (L) †	TBL	-4.0399	2.58	0.90	Mroczyński & Daliga (2016)	Original for Hydrophilidae (L)
Elmidae (L)	HW	2.2581	3.5741	0.86	Towers et al. (1994)	
Gyrinidae (L) †	TBL	-4.0399	2.58	0.90	Mroczyński & Daliga (2016)	Original for Hydrophilidae (L)
Hydrophilidae (L)	TBL	-4.0399	2.58	0.90	Mroczyński & Daliga (2016)	
Scirtidae (L) †	TBL	-6.4378	3.28	0.97	Mroczyński & Daliga (2016)	Original for Staphylinidae (L)
Staphylinidae (L)	TBL	-6.4378	3.28	0.97	Mroczyński & Daliga (2016)	
COLLEMBOLA	TBL	-5.185	2.809	0.92	Gruner (2003)	
DIPTERA						
Chironomidae	TBL	-6.311	2.435	0.90	Dekanová et al. (2021)	
Simuliidae	TBL	-3.79	1.78	0.81	Miserendino (2001)	Original for *Simulium spp.*
Tipulidae	TBL	-7.74	3.29	0.84	Miserendino (2001)	Original for *Hexatoma sp.*
EPHEMEROPTERA	TBL	-5.294	2.618	0.91	Dekanová et al. (2021)	
Baetidae	TBL	-5.392	2.654	0.84	Dekanová et al. (2021)	
Leptohyphidae	TBL	-2.13	2.753	0.84	Paciencia (2012)	Original for *Leptohyphes sp.*
Leptohyphes sp.	TBL	-2.13	2.753	0.84	Paciencia (2012)	
Leptophlebiidae	TBL	-5.073	2.564	0.92	Dekanová et al. (2021)	Original for *Atalophebia sp.*

		Linear model (ln(DM) = ln(a) + b * ln(x)) [continued]				
Taxa	Measure (x)	ln a	b	r²	Source	Comments
ODONATA						
Anisoptera						
Aeshnidae	TBL	-6.04	3.18	0.91	Miserendino (2001)	Original for *Aeshna sp.*
PLECOPTERA						
Gripopterygidae	TBL	-2.065	2.278	0.74	Paciencia (2012)	
Tupiperla sp.	TBL	-1.839	1.899	0.73	Paciencia (2012)	
Perlidae	TBL	-1.78	2.543	0.91	Paciencia (2012)	
Anacroneuria sp.	TBL	-1.789	2.555	0.91	Paciencia (2012)	
TRICHOPTERA	TBL	-5.857	2.549	0.76	Dekanová et al. (2021)	
Calamoceratidae						
Phylloicus sp.	TBL	-1.844	2.075	0.81	Paciencia (2012)	
Ecnomidae	TBL	-5.672	2.433	0.80	Dekanová et al. (2021)	Original for *Ecnomus sp.*
Hydrobiosidae	TBL	-4.70	2.37	0.99	Miserendino (2001)	Original for *Rheochorema sp.*
Hydropsychidae	TBL	-1.843	2.102	0.90	Paciencia (2012)	
Leptonema sp.	TBL	-3.209	3.19	0.81	Paciencia (2012)	
Smicridea sp.	TBL	-4.77	2.79	0.88	Miserendino (2001)	
Leptoceridae	TBL	-1.73	2.126	0.82	Paciencia (2012)	
Triplectides sp.	TBL	-1.712	2.109	0.80	Paciencia (2012)	

	Linear model (ln(DM) = ln(a) + b * ln(x)) [continued]					
Taxa	Measure (x)	ln a	b	r²	Source	Comments
CRUSTACEA						
Amphipoda	TBL	-4.733	2.682	0.99	Gruner (2003)	
Decapoda						
Aeglidae	TBL	-5.08	3.76	0.80	Miserendino (2001)	Original for *Aegla neuquensis*
Trichodactylidae						
Trichodactylus sp.	CW (cm)	-0.46	2.29	0.94	Ferreguetti (2018)	Original for *Trichodactylus fluviatilis* CW is in (cm) and DM is in (g)
Isopoda	TBL	-4.1865	2.77	0.97	Gruner (2003)	
HIRUDINEA	BL	-2.12	2	0.64	Edwards et al. (2009)	

Table S3. Length-mass relationship equations for Linear model (log10(DM) = log10(a) + b * log10(x)). SH = Shell Height (mm) along its longest axis (Méthot et al., 2012). DM = Dry Mass (mg).

	Linear model (log10(DM) = log10(a) + b * log10(x))					
Taxa	Measure (x)	log10 a	b	r²	Source	Comments
MOLLUSCA						
Ancylidae	SH	-1.01	3.13	0.95	Méthot et al. (2012)	