Land-use intensification systematically alters the size structure of aquatic communities in the Neotropics

Running title: land-use changes and size spectra

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Abstract

Land-use and land-cover transitions can affect biodiversity and ecosystem functioning in a myriad of ways, including how energy is transferred within food-webs. Size spectra (i.e. relationships between body size and biomass or abundance) provide a means to assess how food-webs respond to environmental stressors by depicting how energy is transferred from small to larger organisms. Here, we investigated changes in the size spectrum of aquatic macroinvertebrates along a broad land-use intensification gradient (from Atlantic Forest to mechanized agriculture) in 30 Brazilian streams. We expected to find a steeper size spectrum slope and lower total biomass in more disturbed streams due to higher energetic expenditure in physiologically stressful conditions, which has a disproportionate impact on large individuals. As expected, we found that more disturbed streams had fewer small organisms than pristine forest streams, but, surprisingly, they had shallower size spectra slopes, which indicates that energy might be transferred more efficiently in disturbed streams. Disturbed streams were also less taxonomically diverse, suggesting that the potentially higher energy transfer in these webs might be channeled via a few efficient trophic links. However, because total biomass was higher in pristine streams, these sites still supported a greater number of larger organisms and longer food chains (i.e. larger size range). Our results indicate that land-use intensification decreases ecosystem stability and enhances vulnerability to population extinctions by reducing the possible energetic pathways while enhancing efficiency between the remaining food-web linkages. Our study represents a step forward in understanding how land-use intensification affects trophic interactions and ecosystem functioning in aquatic systems.

Keywords: metabolic theory, benthic macroinvertebrates, freshwater ecosystems, individual size distributions, aquatic insects, macroecology, energy transfer, food web, land-use intensification, length-mass equation

1 | INTRODUCTION

Ecosystem vulnerability to land-use and land-cover transitions is a worldwide concern (Arowolo et al., 2018; Mendoza-Ponce et al., 2018; El-Hamid et al., 2020). In the Neotropical

realm, where a large proportion of the world's biological diversity remains, conversion of forests to pastures and agricultural lands is the main driver of deforestation (Andrade de Sá et al., 2013), with a loss of over 100 million ha of primary tropical forests in the last 40 years (Nunes et al., 2022). Despite the impacts associated with the ongoing expansion of croplands and pastures, little is known about how aquatic food-web structure and energy flow are affected by land-use intensification (Reum et al., 2020).

Food-webs in forest headwater streams are fuelled by allochthonous litter inputs, which support most of the secondary production in these 'brown' food-webs (Wallace et al., 1997; Hall et al., 2000). Land-use intensification, particularly from primary forests to pasture and agriculture, has direct and indirect effects on the quantity and quality of this main energy source and, consequently, on the structure and functioning of the ecosystem (Piggott et al., 2015; Martínez et al., 2016). Specifically, agriculture practices can directly reduce allochthonous litter inputs, while also increasing water nutrients and pollutant concentrations due to the use of pesticides and fertilizers, and indirectly increase temperature due to the removal of the riparian vegetation, all affecting stream primary production (Tanaka & Santos, 2017). This may lead to a complex change from brown (based on detritus) to green (based on primary production) energy pathways in food-webs (Zou et al., 2016). Thus, to comprehend the effects of land-use intensification on stream ecosystems, ongoing research needs to examine trophic responses along an impact gradient (Mor et al., 2021).

Environmental change influences the body size of individuals within communities (Brose et al., 2017; Merckx et al., 2018). Body size is widely recognized as one of the most important biological characteristics to explain metabolism, trophic interactions, and distribution of abundance in food-webs (Brown et al., 2004; Chang et al., 2014). Therefore, changes in the relationship between body size and biomass or abundance (i.e. size spectrum) can be used to evaluate the responses of food-webs across environmental gradients (Petchey & Belgrano, 2010; Perkins et al., 2018; Potapov et al., 2019a; 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. In closed systems, a negative linear association should emerge from small numerous individuals to larger, but rarer, consumers (Brown et al., 2004; White et al., 2007; Saito et al., 2021). Coefficients of the size spectrum (intercept and slope) can differ among communities or even within a single community over time, and their variation can be used to evaluate ecological predictions (Rice & Gislason, 1996; Petchey & Belgrano, 2010; Perkins et al., 2018; Potapov et al., 2019a; Pomeranz et al.,

2021). The size spectra intercept at x = 0 (henceforth, intercept) represents the quantity of smaller organisms (e.g. at lower trophic levels, Martínez et al., 2016). In size-structured food-webs, the size spectra slope (hereafter, slope) indicates the rate of biomass reduction, with less energy available at higher trophic levels due to energy loss (respiration) and inefficient transfer of biomass (Brown et al., 2004). For example, shallow slopes (less negative) indicate efficient energy transfer by supporting a greater proportion of larger individuals, while steeper slopes indicate low energy transfer efficiency, with fewer large individuals being supported by smaller 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 understanding predator-prey dynamics, interaction strengths, trophic position, and the size 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). Generalized size spectrum theory states that variation in PPMR can lead to systematic deviations from linear size spectra (henceforth, secondary structure), with a higher or lower number of individuals than expected by a linear fit, for a given size class (Chang et al., 2014). Thus, in disturbed streams where the energy demand might be higher (Petchey & Belgrano, 2010), changes in PPMR might result in a more pronounced secondary structure. Secondary structure in size spectra is a widely observed phenomenon and could also be driven by habitat complexity (Rogers et al., 2014), omnivory (Chang et al., 2014), trophic cascades (Rossberg et al., 2019), the narrow range of prey size (Plank & Law, 2011), dynamic or long-term seasonal cycles (Datta & Blanchard, 2016), and organisms feeding on allochthonous resources (Perkins et al., 2018).

Here, for the first time, we quantified the relationship between macroinvertebrate size structure and land-use intensification in subtropical Brazilian streams. Land-use intensification from forest to pasture and ultimately to mechanized agriculture should lead to a gradual increase in water nutrient concentrations and temperatures, a decrease in the shading of streams due to vegetation removal, and an increase in fine sediments because of erosion (Martínez et al., 2016; Poeppl et al., 2019). With these stream modifications, we expected that macroinvertebrate size spectra would change in a systematic manner. Specifically, we hypothesize that land-use intensification would limit the number of small macroinvertebrates,

such as primary consumers (e.g. due to a reduction in allochthonous litter inputs, which results in nutritional constraints on secondary production, Martínez et al., 2016), resulting in a lower intercept. Furthermore, energetic costs could be higher in disturbed streams due to the degradation of water quality leading to harsher physiological conditions. We therefore hypothesize that this should lead to a reduction in total community biomass and less efficient energy transfer to larger macroinvertebrate predators – i.e. a more negative size spectrum slope (Petchey & Belgrano, 2010; García et al., 2017). Finally, we hypothesized that these higher energetic constraints (i.e. less energy available at lower trophic levels to sustain the next levels) in metabolically stressful conditions would influence organisms' foraging behaviors. Specifically, we expected a more pronounced secondary structure (i.e. systematic curvature in the size spectrum) in impacted streams due to deviations in prey preferences of predators (e.g. specializing, selecting more or less nutritious prey, or generalizing) through the reduction of the quality and quantity of resources (Saito et al., 2021).

2 | METHODS

Study area and sampling

We used data collected from 100 streams 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. 1, see also Heino et al., 2018; Siqueira et al., 2020; and Petsch et al., 2021). Streams were located within a strong land-use intensification 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 pastures, mechanized agriculture (mainly sugar cane monocultures), and commercial forestry such as *Eucalyptus* and *Pinus* plantations. To quantitatively characterize the land-use-intensification gradient (expected to be from forest to agriculture), we applied a Principal Component Analysis (PCA) using standardized environmental and land-use data (see the description of variables below). The PCA was also used to select 30 out of the 100 sampled streams to conduct the subsequent laboratory procedures and analyses. The criterion for the selection of streams was their relationship with the land-use gradient of interest, depicted by the PCA first axis (see Results). The climate in the region is characterized by two seasons: dry season from April to August, and wet season from September to March. At the time of sampling (September and November of 2015), there were no recent floods or droughts. Stream order was 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).
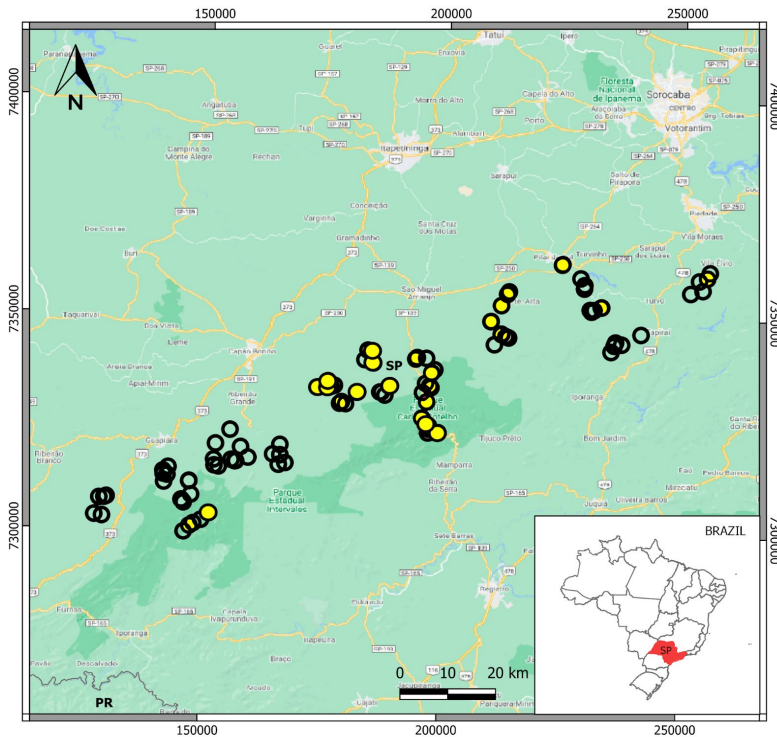
Figure 1. Location of the 100 streams sampled in southeastern Brazil. Black circles refer to each stream sampled, and yellow circles represent the 30 streams selected for this study. Darker green area indicates preserved streams, with natural vegetation (e.g. state parks).

For sampling macroinvertebrates, a 2-minute kick-net sample (net mesh size: 0.250 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, considering variations in velocity, depth, macrophyte cover and benthic particle size. The four sample units were pooled, all organisms were separated from debris and preserved in alcohol in the field.

Land-use gradient

To characterize the stream's environment, 15 physical and chemical variables 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. pH and conductivity were also measured in each stream using

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the Horiba U-50 series device, and water samples were collected to analyze total nitrogen and total phosphorus. Land-cover and land-use were estimated by satellite images from orthorectified RapidEye (Berlin, Germany) multispectral imagery (Planet, 2016), within a 400 m buffer along tracts of the streams and grouped into the following categories: native forest, secondary/managed forest, commercial forestry, pasture, agriculture, urban, mining, wetland, bare soil, water and mixed. Further details regarding methodological procedures can be found in Heino et al. (2018), Siqueira et al. (2020) and Petsch et al. (2021).

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, Hamada & Couceiro (2003) and Novaes (2014) for Perlidae (Plecoptera), Segura et al. (2011) for Elmidae (Coleoptera), and finally, Azevêdo & Hamada (2008) for Megaloptera.

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. We measured body length in insects from the distance between the anterior part of the head and the posterior part of the last abdominal segment (excluding cerci and appendices), while 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, we measured the height of the shell along its longest axis (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 a compiled list of published length-mass relationship equations (Tables S1, S2 and S3). When more than one length-mass equation was found for the same taxa, we selected the one with the higher R^2 and higher sample size. 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

For each stream, we constructed the normalized biomass spectrum (e.g. Platt & Denman, 1978; Blanchard et al., 2005; Roy et al., 2011) using a maximum likelihood method provided by Edwards et al. (2017), implemented in R programming language (function *LBNbiom.method*, package 'sizeSpectra'). This method fits the regression between the accumulated biomass within a size bin - normalized by dividing by the width of that bin - against the midpoint of the size bin, on log-transformed axes (Edwards et al., 2017). The LBNbiom method has been widely used (Blanchard et al., 2005; Roy et al., 2011; Foo & Asner, 2021) and is one of the methods that can accurately estimate the size spectrum slope according to a systematic comparison of approaches (Edwards et al., 2017). The number of size bins was between three and nine (except for stream '24' which had two size bins) and varied according to the body size range observed in each stream and were sufficient to show linear relationships in our data.

Data analyses

To investigate changes in size spectra coefficients in relation to the environmental gradient, we performed linear regressions using the PCA first axis as explanatory variable (see below) and the values of intercept, slope, R^2, 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' (Hothorn et al., 2015) in R version 4.0.5 (R Core Team, 2021), 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 land-use intensification 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.

Finally, since land-use intensification is notable for altering community composition and diversity (Siqueira et al., 2015; Petsch et al., 2021), we additionally calculated the correlation between the abundance of families and the first axis of PCA using the Pearson coefficient. This complementary analysis was conducted to help explain possible deviations from linear size spectra. Then, we used a permutational multivariate analysis of variance (PERMANOVA), using the *adonis* function available in the 'vegan' package (Oksanen et al., 2013). When *adonis* is used

with a continuous explanatory variable, it is analogous to a linear regression where each point is associated with its own centroid which is the best fit to a linear approximation. To assess changes in taxonomic local diversity along the environmental gradient, we used a linear regression of the Chao1 index and the PCA first axis.

3 | RESULTS

The first two axes of the PCA explained 24.88% of the variation in our environmental and land-use data, which also encompasses variation in chemical and physical factors inherent to stream dynamics. The first axis was negatively associated with forest cover, but positively associated with agriculture and secondary managed forest; this was the main gradient in our data. Contrary to our expectations, temperature and nutrient concentration (i.e. nitrogen) were not strongly associated with agricultural streams, and forest streams were not strictly associated with shading. As expected, agricultural streams had substrate composed mainly of sand, while forest streams were composed of boulders. Pasture was not identified as an intermediate land-use within the gradient of forest-agriculture, instead its variation was related to the PCA second axis indicating that pasture and agriculture modify streams in distinct ways. The 30 streams distributed along the PCA first axis (14.77% of variation represented, Fig. 2) were, therefore, selected according to the land-use intensification gradient from forest cover to agriculture dominated watersheds.

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).
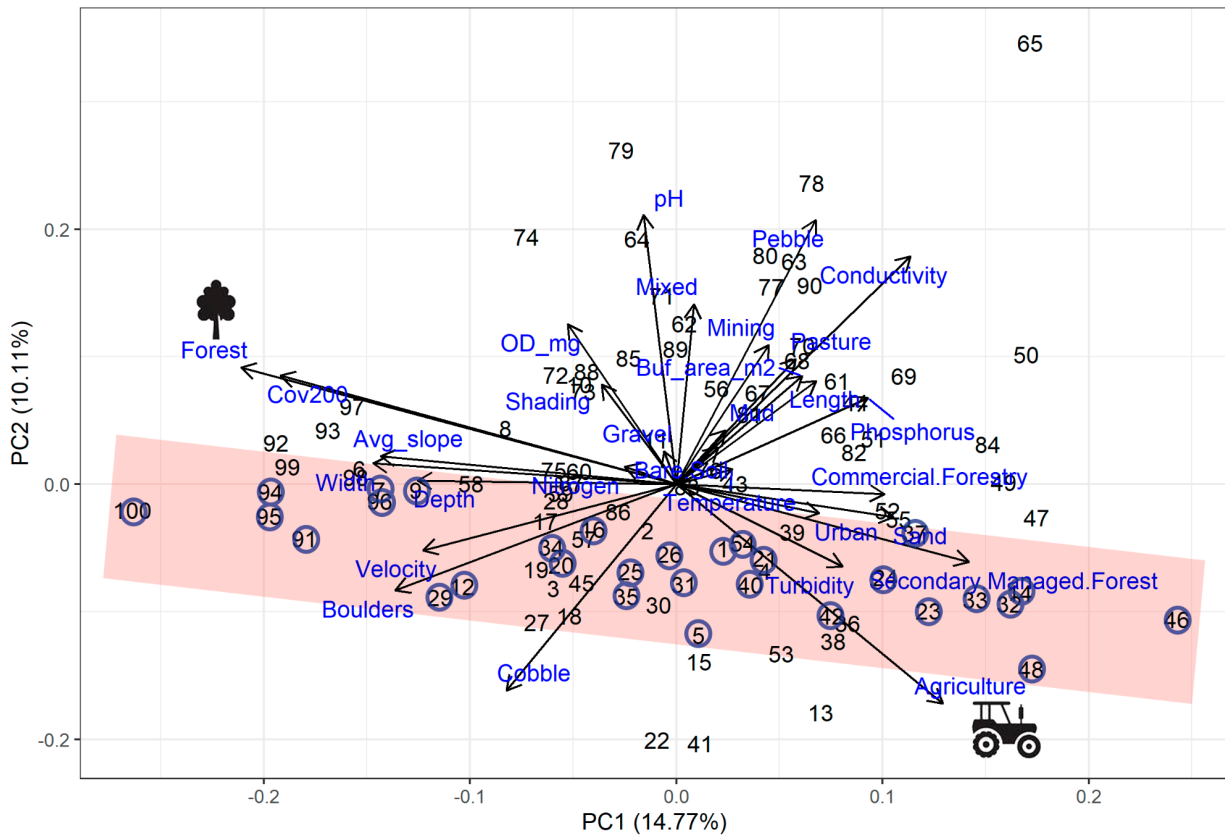
Figure 2. Principal Component Analysis (PCA) of environmental variables associated with 100 subtropical streams. The red area represents streams associated with the environmental gradient from forest (marked with a tree symbol) to agriculture (marked with a tractor symbol). Blue circles inside the red area indicate the 30 streams chosen in this study. 'Cov200': percentage of forest in an area with a radius of 200 m; and 'Buf_area_m2': percentage of forest cover along a 400 m buffer.

The intercept of the size spectra of all streams varied from 0.48 to 3.2 (log10 mg), and the slope varied from -0.23 to -1.25. Streams in watersheds with high forest cover had higher intercepts but steeper slopes, while streams in agricultural watersheds had shallower slopes and lower intercepts (Fig. 3). Individual plots showing the 30 size spectra using the Log Cumulative Distribution (Edwards et al. 2017) can be found in Supplementary Material (Fig. S1).
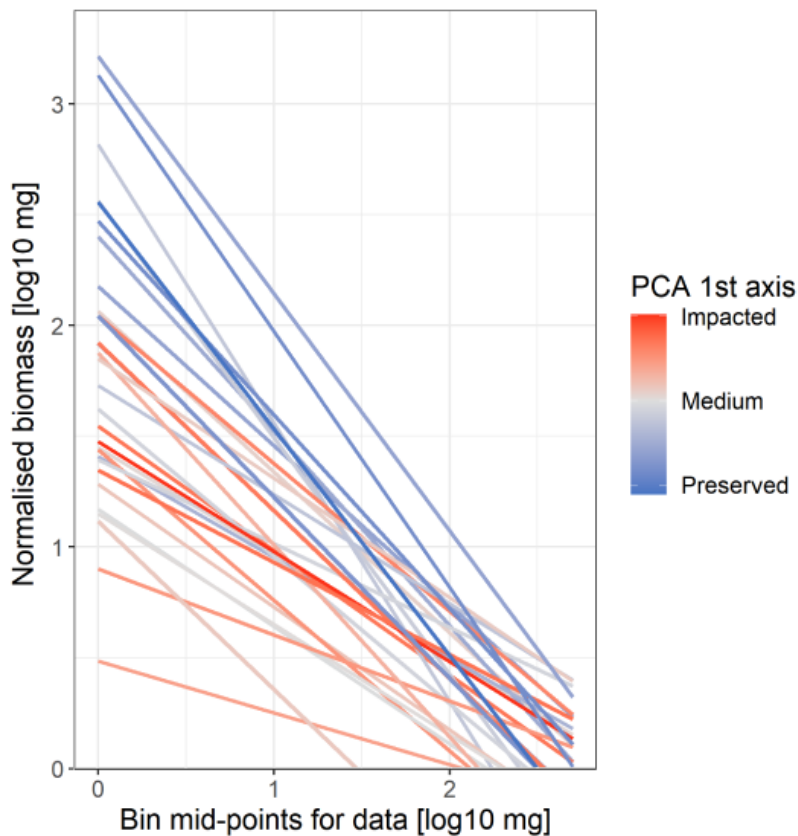
Figure 3. Patterns in the size spectrum of 30 subtropical streams along a land-use gradient. The linear model was plotted using individual values of intercept and slope from each stream. Color gradient considers the position of streams in the PCA first axis. Blue lines represent streams with prevalence of forest, and red lines streams with prevalence of agriculture. *Total normalized biomass (see "Methods" for details).

The intercept of the size spectra decreased with increasing land-use intensification (PCA first axis) (R^2 = 0.34, $p < 0.001$; Fig. 4a). The slope, on the other hand, was less negative (shallower) in disturbed streams (R^2 = 0.28, $p < 0.01$; Fig. 4b). The model fit (R^2) of the size spectra did not change systematically along the gradient ($p > 0.05$; Fig. 4c) and was consistently high (0.71 ± 0.23; mean ± standard deviation). Heteroscedasticity did not differ along the gradient ($p > 0.05$; Fig. 4d) and varied from 0.01 to 3.35 (Breusch-Pagan value). Besides these measurements from the size spectra, total biomass (Fig. 4e) was lower in more disturbed streams (R^2 = 0.22, $p < 0.01$) and was positively correlated with the intercept as shown by the Kendall rank correlation coefficient (τ = 0.80; Fig. 4f). The intercept and total biomass were negatively correlated with the slope of the size spectra (τ = - 0.70 and τ = - 0.50, respectively; Fig. 4f).
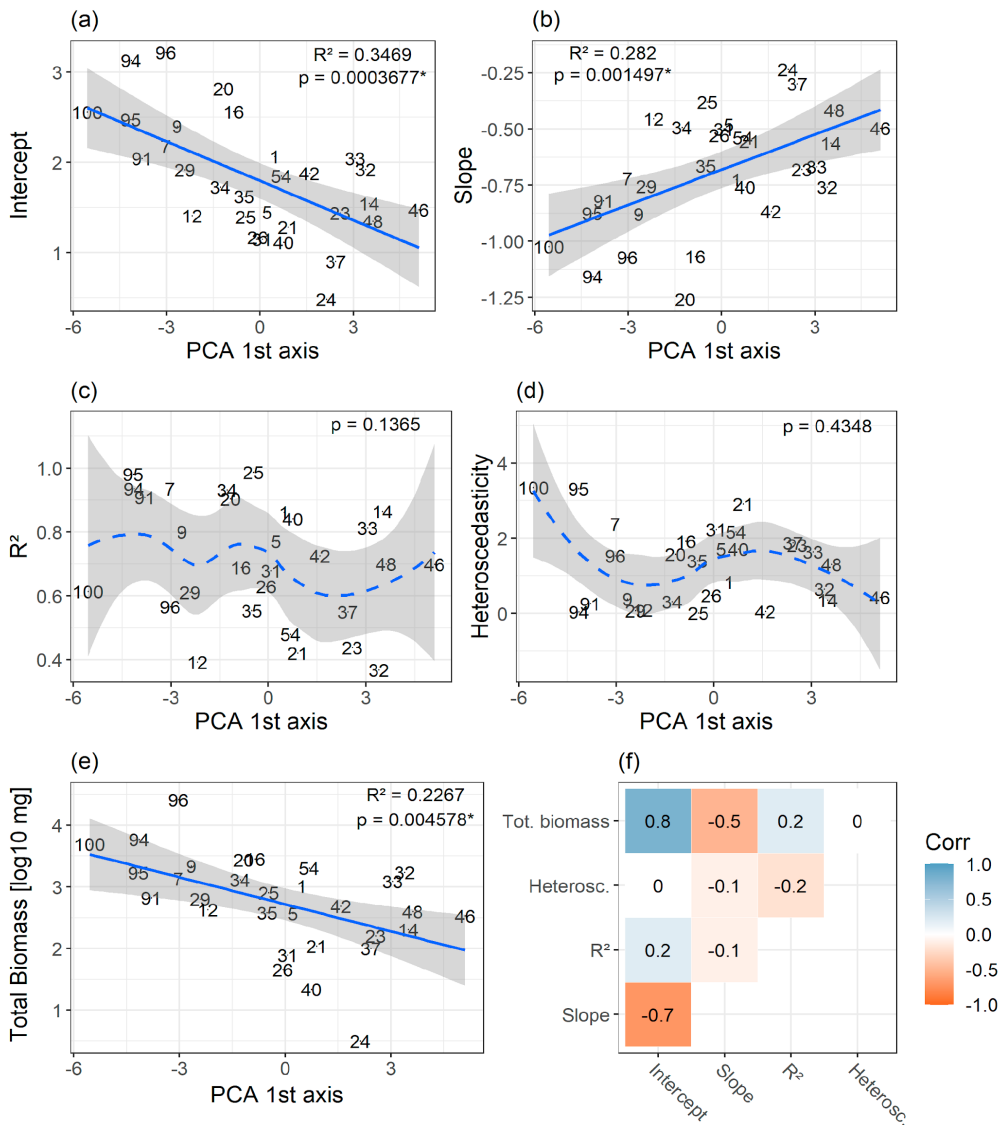
Figure 4. Relationship between land-use change and size spectra coefficients, model fit, heteroscedasticity and total biomass. land-use intensification increases from left to right on x-axes of panels a-e. Grey shading in figures (a) to (e) represents a 95% confidence interval. Blue straight lines show a significant linear pattern and dashed curved lines (fitted using locally weighted smoothing technique) show non-significant linear pattern. Along the gradient, the intercept (in mg) decreases (a) and the slope becomes 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 size spectrum slope.

Size range (maximum - minimum body mass, in $\log_{10}$ mg) of organisms decreased with increasing land-use intensification, varying from 0.05 to 3.45 $\log_{10}$ mg (R^2 = 0.25, p < 0.01; Fig. 5a). The abundance of larger organisms was more associated with land-use intensification in comparison to smaller organisms (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. 5b), indicating that along the gradient, communities had smaller organisms in disturbed streams. Larger organisms consisted mainly of predators, such as Decapoda, Megaloptera, Trichoptera, Plecoptera and Odonata (Figure 5c),

while smaller organisms were mostly detritivores, such as Collembola, Acari, Diptera, Amphipoda and Isopoda.
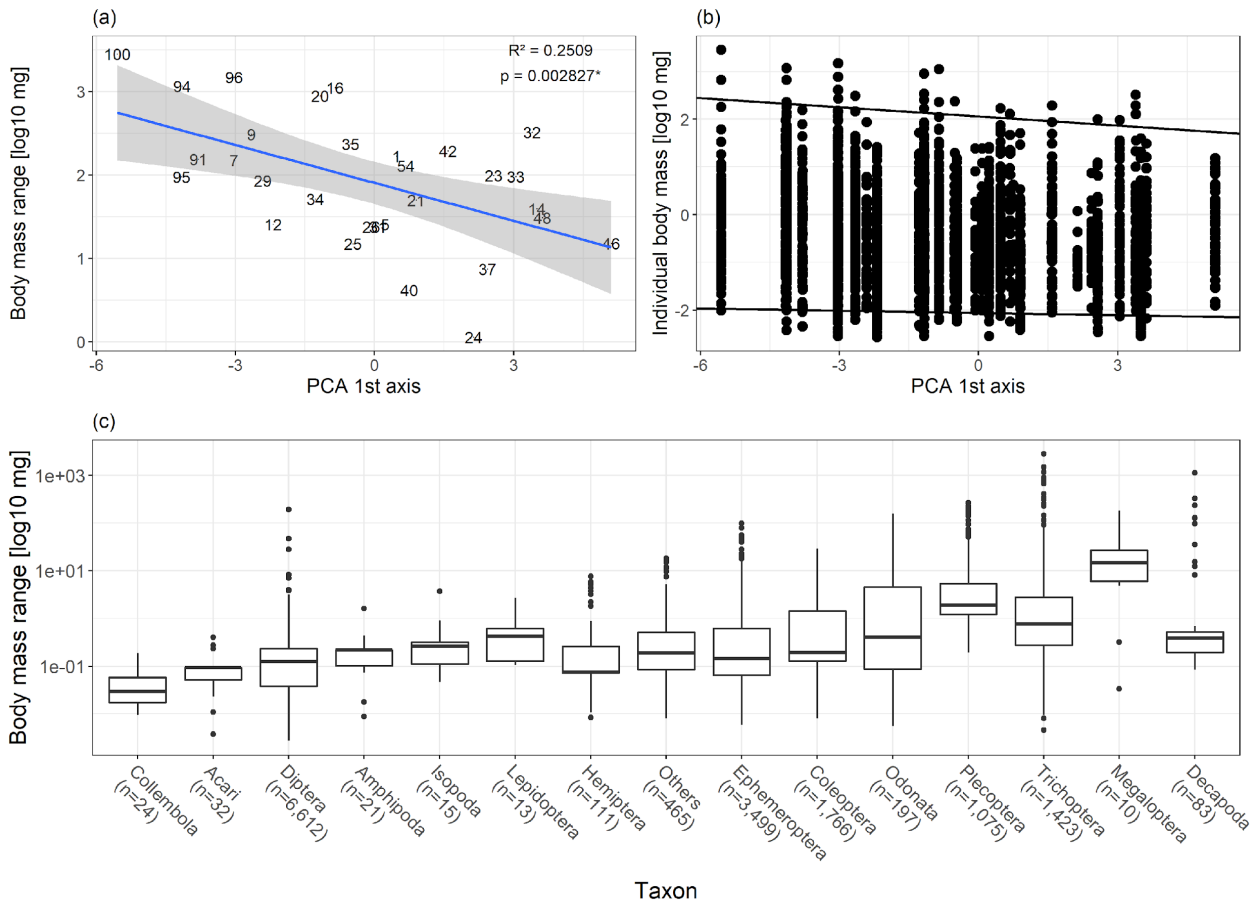
Figure 5. Size range analysis. land-use intensification increases from left to right in (a) and (b). (a) Range of body size ($\log_{10}$ [max(body mass) – min(body mass)], in mg) decreases along the gradient (gray shading indicates a 95% confidence interval). (b) Quantile regressions of the 95th and 5th percentile (top and bottom lines, respectively) of body size ($\log_{10}$ mg) across the environmental gradient. (c) Boxplot of range size ($\log_{10}$ mg) for each taxon, showing that larger organisms consisted mostly of Decapoda, Megaloptera, Trichoptera, Plecoptera and Odonata. The group classified as "Others" included Gastropoda, Hirudinea, Oligochaeta and Turbellaria.

We found that all identified families of Trichoptera, Plecoptera and Megaloptera (composed mainly of large insects) were positively correlated (Pearson correlations) with preserved streams, indicating once again that larger organisms were more abundant in more preserved streams. In general, most taxa were correlated with preserved streams (74%), with few families more abundant in impacted streams (26%) (Fig. 6). Diptera was the order with more taxa positively correlated to agriculture, with Simuliidae most correlated with impacted streams (Fig. 6). Furthermore, Perlidae (Plecoptera) was the family with the strongest correlation with preserved streams (Fig. 6). These patterns in community composition in preserved and disturbed streams were concordant with results obtained from the PERMANOVA using the PCA first axis and the abundance of genera from the 30 streams (R^2 = 0.32, p < 0.001).
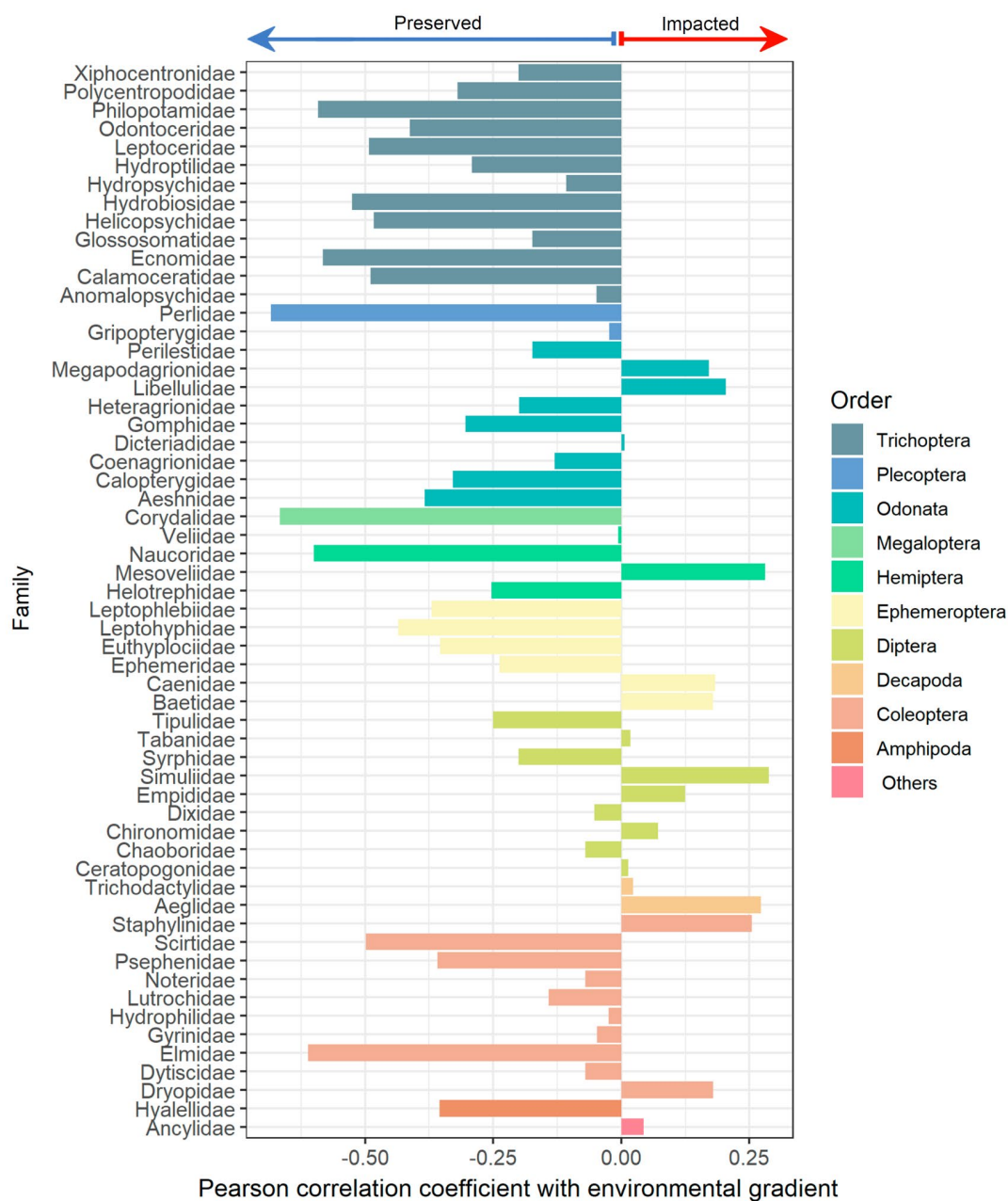
Figure 6. Abundance of families in relation to the land-use intensification. Negative values indicate preserved streams (left), whilst positive values represent impacted streams (right). Color shading represents the correspondent order for each macroinvertebrate family. Preserved and impacted limits consisted of the Pearson correlation coefficient of abundance value from each family with the PCA 1st axis. The group classified as "Others" included Gastropoda, Hirudinea, Oligochaeta and Turbellaria.

Further evidence of changes in community composition along the gradient is supported by the proportion of organisms from different orders in each stream (Fig. S2). A decrease in Coleoptera was observed in more disturbed streams, as well as fewer taxa from other orders (e.g. Odonata and Plecoptera). The proportion of Diptera increased towards more disturbed streams (Fig. S2). The result of the linear regression applied to the Chao1 index of estimated richness indicated that species richness decreased towards more impacted sites (R^2 = 0.40, $p <$ 0.001).

4 | DISCUSSION

Our study indicates that the conversion of native forest into agricultural lands affects the biomass of macroinvertebrates and the size structure of stream food-webs. We show that the size spectra coefficients and community composition varied along the gradient of land-use intensification. In streams surrounded by agricultural lands, there was less biomass of small organisms at lower trophic levels (lower intercept), flatter size-spectrum slope, and a lower proportion of larger organisms. Size spectra were well characterized by a linear relationship in each stream and deviations from a linear fit did not change according to the environmental gradient. We also show that most macroinvertebrate families were more abundant in forest streams, while less than 30% of the families, represented mostly by Diptera, were more abundant in impacted agricultural streams. Likewise, our analysis of community composition also indicates a dominance of Chironomidae as the main energy source for higher trophic levels, with less diversity in disturbed streams. In the following, we describe how our results elucidate that land-use changes can alter trophic interactions and energy use, with potential negative consequences for stability and ecosystem vulnerability.

The low biomass of small organisms at lower trophic levels in non-forest streams is in line with our hypotheses and has been predicted and documented in many studies (Petchey & Belgrano, 2010; Pomeranz et al., 2018), with few exceptions (e.g. Martínez et al., 2016). This low biomass suggests that more disturbed ecosystems sustain low population densities, which could arise because deforestation decreases the input of detritus into streams, affecting the total biomass fluxing through brown food-webs (Martínez et al., 2016). We also expected that disturbed streams would have more negative slopes (steeper) than preserved streams (Petchey & Belgrano, 2010). Surprisingly, we found the opposite. Size spectra slopes were shallower in non-forest streams. As evidenced in our work and supported by the literature (e.g. Arim et al., 2010; Perkins et al., 2018; O'Gorman et al., 2019; Potapov et al., 2019b; Fraley et al., 2020), the food-webs in our study are size-structured, meaning that larger organisms are feeding upon the smaller ones. For instance, the largest organisms found (i.e. Decapoda, Megaloptera, Trichoptera, Plecoptera and Odonata) consisted predominantly of predators, feeding mostly from organisms from the lower trophic level instead of from the base of the food-web (Stewart et al., 1973; Galbreath & Hendricks, 1992; Bueno & Bond-Buckup, 2004; Gamboa et al., 2009; Williner et al., 2014). Moreover, we found that the slope of the normalized size spectrum was approximately -1 for 'pristine' streams (Figure 4b). This value is similar to the value typically reported for marine food-webs (Kerr & Dickie, 2001) and consistent with that predicted by

allometric theories in ecology (Brown & Gillooly, 2003). As the slope can be seen as a proxy of energy flux through trophic levels in size-structured communities (Brown et al., 2004; Woodward et al., 2005), the most intuitive conclusion then is, assuming no systematic change in the predator-prey mass ratio between sites, that energy transfer efficiency is simply greater in disturbed streams, which is conflicting with theoretical predictions that environmental impacts increase energetic costs (Petchey & Belgrano, 2010).

An alternative explanation lies in the arguments of the diversity-stability hypothesis, which suggests that higher diversity, on average, leads to higher ecosystem stability (McCann, 2000). High species richness enables different possibilities of consumer–resource interactions, making them more general, weak, and less specialized. 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 fewer and stronger interactions, making the system more oscillatory and susceptible to the loss of few interactions. Therefore, we can expect that decreasing biodiversity and restricting basal resources supply, two common consequences of deforestation, might reduce possible energetic pathways, and thus increase, on average, the strength of interactions (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 non-forest streams 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) resulting in relatively greater energy transfer channeled via few efficient trophic links. We also found that the energy transfer appears less efficient in preserved streams, probably because food-webs are more diverse and complex, with many energetic pathways that can buffer food-web functioning from local extinctions (McCann, 2000). That is, supporting more variations and enhancing stability due to the weak-interaction effect. Our results are surprisingly aligned with an experimental study that showed that excluding leaf litter leads to fewer but stronger energetic pathways from prey to predators (Hall et al., 2000), supporting our inference that reduced allochthonous inputs can have consequences on interaction strengths. In the context of land-use intensification, together with the loss of diversity, this should enhance ecosystem instability and its potential to collapse.

Larger organisms tend to be more affected by environmental impacts than smaller organisms (Cardillo et al., 2005; Sodhi et al., 2009). These larger organisms (Decapoda, Megaloptera, Trichoptera, Plecoptera and Odonata in our study) were more abundant in more forest streams and are known to have more impact-sensitive species (Docile et al., 2016), which

causes changes in the community composition, with fewer taxa in impacted streams (Bonada et al., 2006). Stream macroinvertebrate communities composed of small populations are more likely affected by demographic stochastic events (Siqueira et al., 2020), which may play an important role in how communities are structured in disturbed streams. Therefore, if communities with low species abundance (in our case, in disturbed streams) are more affected by demographic stochasticity and have few strong interaction strengths (efficient energy flow), it is possible that the loss of important species and thus ecological functions can lead to abrupt changes of the whole ecosystem. Thus, if biodiversity loss increases interaction strengths, land-use intensification may alter how species interact, and trigger a cascade effect that may scale to the entire ecosystem (McCann, 2000; Dala-Corte et al., 2020).

In addition to changes in standing biomass at lower trophic levels and energy transfer, we expected more deviations in the model fit (lower R^2) in disturbed streams due to the high energy demand and the predicted less efficient energy transfer. Organisms might then seek alternatives for maintenance and growth, feeding on larger or smaller prey than expected by the Optimal Foraging Theory. However, we observed that size spectra model fit and heteroscedasticity values did not vary according to the land-use intensification gradient, meaning that the degree of secondary structure (more or less organism biomass than expected based upon body size, represented by R^2) was independent of the environmental change we focused on. The results support our assumption that the studied streams are size-structured, since the few representatives of the largest organisms that may include omnivores able to feed down in the food-web did not systematically affect the linear fashion of the size spectra (Chang et al., 2014). The model fit was mostly high along the gradient (R^2 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 power-law theory (White et al., 2007). Moreover, linear size spectra suggest that the metabolic rules underpinning the assembly of ecological communities (i.e. the number of organisms from the previous trophic level restricting the number of organisms from the next trophic level; Brown et al., 2004; Saito et al., 2021) appear relevant, independently of the environmental context.

Even though our study provides insights into trophic interactions of freshwater food-webs in the neotropics, it is important to acknowledge certain caveats. Firstly, inferences about energy transfer using a size spectrum approach are based on allometric models, which assume that larger organisms feed on smaller prey with an optimal body size (Blanchard et al., 2009). However, this assumption may not hold true in many natural ecosystems, as factors such as

parasitism, omnivory, and allochthonous resources can influence organisms' behavior (Perkins et al., 2018). Thus, body size alone may not accurately indicate an organism trophic level, and this could be especially true in the tropics, which are believed to have higher prominence of generalist consumers, both large and small (Blanchette et al. 2014, but see also Dudgeon et al. 2010). Ongoing research in the tropics using biotracers such as stable isotope data and gut content analyses are still rare compared to temperate systems but should be a promising avenue for refining trophic levels in tropical ecosystems (Hernvann et al., 2022). Secondly, our study only considered macroinvertebrates, which encompassed a range of body mass from 0.0027 mg to 2,821 mg and trophic groups: from primary consumers to predators. Therefore, the patterns in size spectra we show could change when considering a wider range of body masses and trophic levels (e.g. periphyton and fishes). As we do not have data on fish and other groups that could modify the size spectrum patterns, and we do not have clear information on the trophic position of the organisms, we suggest caution in extrapolating the observed patterns for the entire size spectrum. Yet, considering that macroinvertebrates are mostly at an intermediate position in the food chain, this gives us information about how energy from the allochthonous material or primary producers are being used, as well as how much of this energy will remain available for higher trophic levels.

Our study represents the first regional-scale characterization of size-spectrum in tropical streams. The results provide new insights into how land-use intensification can affect the structure and functioning of tropical stream communities. We show that agricultural streams have lower total biomass available at lower trophic levels, but perhaps more efficient energy transfer to higher trophic levels , probably due to strong interaction links, which also influence their vulnerability to extinction events. More preserved forest streams have more organisms at lower trophic levels and higher diversity, which can result in weaker interaction links, making communities in these streams more stable. Our study adds to mounting evidence that worldwide land-use intensification impacts go far beyond biodiversity loss and modify food-web size structure and energy transfer within ecosystems.

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