Untangling the complex food webs of tropical rainforest streams

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Conflict of Interest

The authors declare no conflict of interest.

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Statement on Inclusion

Our study brings together authors from Brazil and the UK, led by a scientist based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. This study includes undergraduate, graduate and established researchers from the region where the study was carried out.

Data availability statement

Data will be publicly available in a repository after publication.

UNTANGLING THE COMPLEX FOOD WEBS OF TROPICAL RAINFOREST STREAMS

ABSTRACT

1. Food webs depict the tangled web of trophic interactions associated with the functioning of an ecosystem. Understanding the mechanisms providing stability to these food webs is therefore vital for conservation efforts and management of natural systems.

2. Here, we first characterised a tropical stream meta food web and five individual food webs using a Bayesian Hierarchical approach unifying three sources of information (gut content analysis, literature compilation, stable isotope data). With data on population-level biomass and individually measured body mass, we applied a bioenergetic model and assessed food web stability using a Lotka-Volterra system of equations. We then assessed the resilience of the system to individual species extinctions using simulations and investigated the network patterns associated with systems with higher stability.

3. The model resulted in a stable meta food web with 307 links among the 61 components. At the regional scale, 70% of total energy flow occurred through a set of ten taxa with large variation in body masses. The remaining 30% of total energy flow relied on 48 different taxa, supporting a significant dependency on a diverse community. The meta food web was stable against individual species extinctions, with a higher resilience in food webs harbouring omnivorous fish species able to connect multiple food web compartments via weak, non-specialized interactions. Moreover, these fish species contributed largely to the spatial variation among individual food webs, suggesting that these species

could operate as mobile predators connecting different streams and stabilising variability at the regional scale.

4. Our results outline two key mechanisms of food web stability operating in tropical streams: (i) the diversity of species and body masses buffering against random and size-dependent disturbances (ii) high regional diversity and weak omnivorous interactions of predators buffering against local stochastic variation in species composition. These mechanisms rely on high local and regional biodiversity in tropical streams, which is known to be strongly affected by human impacts. Therefore, an urgent challenge is to understand how the ongoing systematic loss of diversity jeopardises the stability of stream food webs in human-impacted landscapes.

Key words: Food Webs, Metabolic Theory, Stability, Macroinvertebrates, Stable Isotopes.

RESUMO

1. As teias alimentares representam um emaranhado de interações tróficas associadas ao funcionamento de um ecossistema. Compreender os mecanismos que proporcionam estabilidade a estas teias alimentares é, portanto, vital para os esforços de conservação e gestão dos sistemas naturais.

2. Aqui, primeiro caracterizamos uma meta teia alimentar de riachos tropicais e cinco teias alimentares individuais usando uma abordagem hierárquica Bayesiana unificando três fontes de informação (análise de conteúdo

estomacal, compilação de literatura, dados de isótopos estáveis). Com dados sobre biomassa em nível populacional e massa corporal medida individualmente, aplicamos um modelo bioenergético e avaliamos a estabilidade da cadeia alimentar usando um sistema de equações Lotka-Volterra. Em seguida, avaliamos a resiliência do sistema às extinções de espécies individuais usando simulações e investigamos os padrões de rede associados a sistemas com maior estabilidade.

3. O modelo resultou em uma meta teia alimentar estável com 307 ligações entre os 61 componentes. Na escala regional, 70% do fluxo total de energia ocorreu através de um conjunto de dez taxa com grande variação nas massas corporais. Os restantes 30% do fluxo total de energia dependiam de 47 taxa diferentes, apoiando uma dependência significativa de uma comunidade diversificada. A meta teia alimentar foi estável contra extinções de espécies individuais, com uma maior resiliência em teias alimentares que abrigam espécies de peixes onívoros capazes de conectar múltiplos compartimentos da teia alimentar através de interações fracas e não especializadas. Além disso, estas espécies de peixes contribuíram amplamente para a variação espacial entre as cadeias alimentares individuais, sugerindo que estas espécies poderiam operar como predadores móveis conectando diferentes riachos e estabilizando a variabilidade à escala regional.

4. Nossos resultados descrevem dois mecanismos principais de estabilidade da cadeia alimentar operando em riachos tropicais: (i) a diversidade de espécies e massas corporais que protegem contra distúrbios aleatórios e dependentes do

tamanho (ii) alta diversidade regional e fracas interações onívoras de predadores que protegem contra a variação estocástica local na composição de espécies. Estes mecanismos dependem de uma elevada biodiversidade local e regional em riachos tropicais, que são conhecidos por serem fortemente afetados pelos impactos humanos. Portanto, um desafio urgente é compreender como a contínua perda sistemática de diversidade põe em risco a estabilidade das teias alimentares em paisagens impactadas pelo homem.

Palavras-chave: Teias alimentares, Teoria Metabólica, Estabilidade, Macroinvertebrados, Isótopos Estáveis.

INTRODUCTION

Food webs depict the tangled web of trophic interactions associated with the transfer of energy within an ecosystem. These ecological networks offer mechanistic insights into energy flow, nutrient cycling, and population dynamics, highlighting critical links that influence the stability and resilience of natural ecosystems. Consequently, food webs provide a vital tool for conservation efforts and ecosystem management, allowing better-informed decisions about how to protect and preserve the functioning of natural systems (Giakoumi et al., 2015). Therefore, understanding the mechanisms that govern food web stability with precision and detail is pivotal to improve our understanding of ecosystem functioning in the face of the current environmental crisis (Yodzis, 1981; Ives & Carpenter, 2007).

Despite decades of research on food web stability, the topic is still highly debated, especially concerning whether higher biodiversity confers higher resilience to disturbance (Hatton et al., 2024; McCann, 2000). While classic theories emphasise the destabilising role of diversity given a higher connectance among multiple nodes increasing chances of cascade extinctions (May, 1973), contemporary theory suggests a stabilising role of diversity when this is associated with weak interactions among predators and multiple prey, creating negative covariance between different resources buffering the system against extinctions (McCann, 2000). Despite the large and growing body of theoretical studies on these ideas, empirical evaluations are still lagging behind, as appropriate and detailed data for rigorously testing these theoretical advances are not widely available (Ives & Carpenter, 2007).

Describing food webs in streams and rivers is particularly challenging due to the inherent complexity and dynamics of these ecosystems (Winemiller, 1990). The continuous flow of water combined with the spatio-temporal heterogeneity of resources create a constantly changing environment, making it difficult to capture the food web in full detail. Tropical streams particularly pose a challenge as they are highly diverse and knowledge of trophic interactions is rare for many taxonomic groups (Motta & Uieda, 2005; Reboredo Segovia et al., 2020), resulting in few isolated food web descriptions (Ceneviva-Bastos et al., 2012; Motta & Uieda, 2005) that we know little about their stability in the face of disturbance. Among these understudied ecosystems, streams of Brazilian Atlantic Rainforest are highly threatened by human land-use intensification and the substitution of forests for pasture and monoculture plantations (Siqueira et al., 2015). Since these ecosystems provide a myriad of services to human society, from fresh water and recreation to nutrient cycling (Meyer, 1997; Palmer et al., 2014), understanding the stability of their food webs in well-preserved regions is the first step in predicting their response to human impacts (Collyer et al., 2023).

Importantly, tropical stream ecosystems are likely to differ in their structure and functioning compared to their better-studied temperate counterparts (Saito, Perkins, et al., 2021). In terms of food webs, warmer tropical streams should be composed of species with fast life cycles, accelerated biomass turnover, and lower local densities (Saito, Stoppa, et al., 2021), resulting in highly variable composition (Siqueira et al., 2020) and species interactions (Saito, Perkins, et al., 2021). A recent study hypothesised that such highly dynamic food webs, embedded in a high regional diversity, should be stable due to the weak interaction effects among multiple interacting species (Collyer et al., 2023), where the functioning of a diverse, generalist community would be buffered against disturbances by interchanges of trophic interactions (Kratina et al., 2012; Rooney & McCann, 2012). In that case, we should expect pristine tropical stream food webs to depict two patterns. First, local food webs should be composed of predator-prey interactions that deviate from optimal predator-prey mass ratios (Collyer et al., 2023; Kratina et al., 2012). Aquatic food webs are commonly size-structured, meaning that predators are consistently and systematically larger than their prey, and yet, under warmer tropical conditions, we should have a higher prevalence of omnivory because high energetic demands can force organisms to feed up and down the food web (González-Bergonzoni et al., 2012). Therefore, we hypothesise that pristine food webs will be composed of weakly size-structured interactions, with predators feeding on both large and small prey due to their high metabolic requirement. Second, these tropical food webs should also be characterised by high local diversity, buffering predators from extinctions due to the possibility of prey switching and stabilising dynamics between resources. Since these tropical communities are prone to random variations in composition (Siqueira et al., 2020), a high diversity of possible interactions should enhance the stability of these systems, as redundant predators and prey can buffer the system against the loss of energetic channels.

In addition, local food webs are always exchanging energy and matter within a regional meta food web (Winemiller, 1990). As such, the realisation of potential trophic interactions is constrained by the dispersal processes of predators and prey (Rooney & McCann, 2012; Winemiller, 1990). Similar to the role of predators dampening variation at the bottom of food webs (Rooney & McCann, 2012), mobile predators coupling sub-food webs can stabilise metacommunities by buffering variability among communities (Rooney et al., 2008; Siqueira et al., 2024). This should increase spatial asynchrony among communities entailing high food web dissimilarity in space, mostly due to changes in predator frequency. Considering the expected high local dynamism of Atlantic Forest stream communities due to faster metabolism, we hypothesise a high dissimilarity of local food webs in space, being stabilised by predator coupling at the regional scale (Rooney et al., 2008).

Despite the dozens of methods developed to characterise food webs in nature, the use of individual methods to estimate trophic interactions commonly results in incomplete or simplified characterizations (Layman et al., 2012). Fortunately, the combination of recent theoretical and methodological advances gives us new tools to describe patterns of energy fluxes at the population level with high precision. First, a new method unifying multiple sources of information within a singular analytical Bayesian framework provides an excellent opportunity to untangle undescribed food webs, while overcoming problems of individual sources of information (Hernvann et al., 2022). This method integrates information taken from the literature, from direct observations and extracted from stable isotope analyses to infer the most likely diet proportion of each consumer and the likelihood of these interactions. Second, advances in metabolic scaling theory allow us to infer the energy requirements of populations based on their individual body masses and their total population sizes (Brown et al., 2004). Together with information about diet proportions, we can now estimate the required energy potentially flowing from prey to predators, quantifying the food web in a general ecological currency (Gauzens et al., 2019).

Leveraging a suite of advances in food web ecology, we evaluate how stable the pristine ecosystems of the Brazilian Atlantic Rainforest should be in face of disturbances. We first characterise a well-resolved meta food web of streams from Atlantic Forest through the integration of node properties (body mass and abundance) and various sources of feeding link information. Second, we applied recent methods for calculating the stability of the food web to disturbances within an energetic framework (Gauzens et al., 2019; Moore & de Ruiter, 2012). We hypothesised that 1) due to the elevated metabolic demands in warm conditions, invertebrates and fish assemblages would be weakly size-structured, characterised by predators feeding at multiple trophic levels, with with a weak association between individual body mass and trophic level within invertebrate and fish assemblages, as well as across the whole food web. 2) Given the high species diversity in tropical streams, we anticipated that energy flow within the food webs would involve a multitude of links. Predators would engage in a range of non-specialized interactions with prey resulting in bioenergetically stable food webs (Kratina et al., 2012). 3) The simulated removal of individual taxa from a complex tropical food web would not significantly disrupt its stability, as it would not heavily rely on key strong interactions. 4) Finally, we expected that the spatial variation in the composition of local food webs would be associated with compositional changes in large predators, indicating that mobile predators enhance spatial asynchrony among communities entailing regionally stable meta food webs (Siqueira et al., 2024).

METHODS

We sampled food web components (basal resources, invertebrate and vertebrate consumers) in relatively pristine streams in Southeast Brazil. We then applied a Bayesian framework to describe a regional meta food web and five individual food webs integrating data from gut contents analysis, published studies and stable isotope analysis of consumers and resources (Hernvann et al., 2022). Finally, we applied an energetic model using body masses, energy efficiencies estimates and the network topology to describe the amount of energy fluxes and the food web stability (Gauzens et al., 2019).

Field and laboratory protocols

We sampled five (2nd to 3rd orders) stream stretches within the Cananeia catchment (state of São Paulo, Brazil) to collect high-resolution community data for food web reconstruction. We sampled three streams (S1, S6 & S8) which were less than 3 km apart, and in one stream (S8) we sampled three different stretches along an altitudinal gradient (with 24, 45 and 88 metres of altitude). The vegetation at the studied sites is predominantly formed by Ombrophilous Dense Atlantic Forest, mostly well-preserved stretches and few sections of secondary forest (Schaeffer-Novelli et al., 1990). The climate is humid subtropical (Alvares et al., 2013), with mean annual rainfall above 2,200 mm (Schaeffer-Novelli et al., 1990). There are two main seasons: summers (November - April) have mean air temperature of approximately 27° C, whereas mild winters (May - October) have a mean temperature of approximately 22° C. The five stream sites were sampled in October 2019 and had a mean water temperature of 22°C (SD=0.68), pH of 5.7 (SD=0.66) and oxidation-reduction potential (mv) of 381 (SD=111) (see Table S1).

The field protocol encompassed standard sampling techniques for surveying stream food webs. First, we performed 3-pass quantitative depletion electrofishing at each site (up to 100 m) using a Smith-Root LR-24 backpack electrofisher with the boundary of survey reaches enclosed by stop nets. We identified most captured fish to species level and measured (fork length) in the field (SISBIO ethical approval number 72482-1). We sampled macroinvertebrates (>250 μm) using 10 replicate Surber samples (30 cm X 30 cm) randomly positioned in the stream benthos. We sorted these samples live at the host laboratory using a transilluminated tray and identified them to the lowest possible taxonomic level without preparing slices (e.g. Chironomidae were identified to family level). We took measurements of individual linear dimensions (e.g. head-capsule width or body length) with a calibrated ocular micrometre allowing individual dry mass to be calculated from published regression equations (Collyer et al., 2023). We sacrificed a subsample of all captured fish (n = 142) and fixed them in 99,3% Isopropyl alcohol for subsequent gut content analysis in the laboratory. We extracted guts and examined under a stereomicroscope (Leica EZ4, 40x maximum magnification). We identified all diet items found (n = 502) to the lowest possible taxonomic level (28 categories).

During fieldwork we also collected material for subsequent stable isotope analysis (SIA). We obtained fish tissue from fin clips for a subset of individuals of each species caught during electrofishing surveys. We performed kick net sampling qualitatively in all microhabitats (mostly gravel and boulder riffles and some leaf litter pools) to collect macroinvertebrates which were processed whole for stable isotope analysis. We sampled basal resources from each stream by collecting allochthonous leaf packs, mosses attached to the substrate and scrapes of biofilm from stones and boulders. We froze all samples in the host laboratory in liquid nitrogen (at -80 °C) in individually labelled tubes until subsequent analysis. Back to the laboratory, we stored all samples at 60° C in an oven until total dry mass was achieved. We grinded the tissues to a fine powder. Subsequently, 1 mg +/- 0.2 mg of fish and macroinvertebrate samples, and 2.5 mg ±0.2 mg of basal resources were weighed into tin capsules (Elemental Microanalysis® 8×5mm) prior to isotopic analysis. For small invertebrate taxa that potentially weighed less than 1 mg individually (e.g. Chironomidae, Simuliidae), we pooled 6-20 individuals of similar size together to reach the minimum weight expected for each sample (Perkins et al., 2018). We analysed samples of macroinvertebrates (n=139), fishes (n=160) and basal resources (n=30) for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios at an analytical laboratory at Queen Mary University of London, UK using a continuous flow isotope ratio mass spectrometer (SerCon Integra 2, Stable Isotope Analyser, Crewe, UK). Protein IRMS Standard (Elemental Microanalysis® OAS/Isotope 5g) encapsulated like the other samples was used as a standard and inserted in each run after every ten samples. We then applied an ANOVA comparing the $\delta^{15}N$ of basal resources (biofilm, moss and leaves) among stretches and found that they were not distinct (ANOVA, F = 0.35, P = 0.84) indicating that δ^{15}N baselines among stream sites were comparable.

Food web reconstruction

We applied the Ecodiet approach to derive a well-resolved meta food web (Hernvann et al., 2022). This Bayesian hierarchical model jointly considers three sources of information: direct observations (e.g. gut content analysis) including the potential proportion of different diet items, literature information describing putative feeding links based on interactions described in other sites, and data from stable isotope analysis, derived from a Bayesian mixing model to estimate the likelihood of the interactions and the diet proportions inferred from the two first sources of information. Here, we integrated data from the five stream sites including 329 δ^{15}N and δ^{13}C values of basal resources, macroinvertebrates and fish; 502 diet items identified from fish gut content analysis and; 226 potential feeding interactions for Neotropical stream communities derived from a literature search including bibliometric analysis of 52 references (see Supplementary Material). This hierarchical model generated the probabilities of trophic links and provided the proportions of diet items for each taxon. The key strengths of this framework included the quantification of i) the reliability of individual published datasets (i.e. different values range between 0 and 1 depending on the methods used in a published study for each interaction) and ii) the relative importance of gut vs. literature data to define the food web topology to be investigated in the mixing model. For this last comparison, a parameter was set to define how equivalent literature and gut content data are (e.g. setting the parameter value to 50 indicates that literature data are equivalent to analyses of 50 new stomach contents). In our case, all studies in the literature search were set to 1 (reliable) and the literature data were given equal weight compared to gut content data. We assessed the performance of the model using Gelman-Rubin test of MCMC convergence. Variables (links) with Rhat > 1.1 failed to converge and we removed them from the model. This method was implemented using the Ecodiet package in R (Hernvann et al., 2022).

Using the estimated food web topology and the diet proportions, we applied the fluxweb approach, which infers the amount of energy flowing through each population considering a steady-state system (Gauzens et al., 2019). This method was applied to both the meta food web and each of the five individual food webs. The approach requires the average species body mass and population density information to estimate the total biomass of each population and their energetic requirements.

The fluxweb method considers a top-down perspective where the energetic requirement of each consumer species is calculated from the mean body mass of that species, and its population density, balanced against the population biomasses of their prey. In this balanced system, gains G_i are balanced with losses L_i which are calculated as

$$L_i = X_i \ + \ \sum_j F_{ij} , \qquad \text{(eq. 1)}$$

where X_i defines species losses (e.g. metabolic costs or death rates) and F_{ij} is the flux of energy from species *i* to predator *j*. In this case, gain G_i is defined as

$$G_i = \sum_j F_{ji} e_{ij} , \qquad \text{(eq. 2)}$$

where F_{ji} defines the influx coming from other species depending on a diet proportion (estimated with Ecodiet in our study) and e_{ij} denotes the efficiency in energy uptake given the prey identity (see below). In our study, the metabolic cost X_i was defined from the allometric equations (Brown et al. 2004)

$$X_i = X_0 M_i^b, \qquad \text{(eq. 3)}$$

where X_0 and *b* are constants related to organismal physiologies and M_i is a given body mass. We defined X_0 equal to 18.18 for fishes, 17.17 for invertebrates, and *b* equal -0.29 for all organisms following Brown et al. (2004). Efficiencies were defined at prey level and set to 0.906, 0.545 and 0.158 for animals, plants and detritus, respectively (i.e. consumers feeding on animals have higher efficiencies per unit of mass consumed) (Gauzens et al., 2019). We additionally applied different values for *b* and efficiencies to understand the sensitivity of our analyses to specific input parameters. For the metabolic exponent *b*, we considered the values from a review of metabolic rates across organisms and ontogenetic development (Glazier, 2005). In this study he identified that metabolic rate exponents are commonly ⅔, ¾ and 1 (isometric scaling). Therefore, to consider such variation we also used the values of *b* considering these three different exponents. For the efficiency values, we considered the minimum and maximum values of the 95% confidence interval modelled in a systematic assessment of efficiencies and respiration in natural communities (Lang et al., 2017). In this assessment, they found that carnivores had the highest assimilation efficiency (ε0,carnivores = 0.906, CI 0.95 = 0.88-0.927), herbivores had an intermediate assimilation efficiency (ε0,herbivores = 0.545, CI 0.95 = 0.466-0.621), and detritivores had the lowest assimilation efficiency (ε0,detritivores = 0.158, CI 0.95 = 0.108-0.227).

Data analysis

Hypothesis 1: Due to the elevated metabolic demands in warm conditions, tropical food webs should be weakly size-structured, with variable size differences between predators and prey.

To test our first hypothesis and to determine the relationship between body mass and trophic position, we related δ^{15}N tissue values (a proxy for trophic position) and body mass by applying linear mixed effects models for the isotopic values of consumers. Log-transformed mean consumer body mass (mg of dry mass) was treated as a fixed effect while taxonomic identity was treated as random intercept and random slope, separately. We also ran models that included the group (fish or invertebrate) as a fixed effect with interaction with body mass to account for a potential relationship that is dependent on the organism group. We could not apply a single model with both random intercept and slope due to the large number of samples and taxa in our dataset (lack of sufficient degrees of freedom). Models with and without organism group as a fixed effect were compared based on their marginal R^2, AIC, and a Chi-Squared test.

We then determined size-density relationships regressing species' mean body mass and population density on double-log axes. These relationships depict how energy is shared among species with different body masses, providing information about species that have higher or lower densities than expected based on allometric scaling principles (White et al., 2007). We applied this method for the meta food web and each of the five individual food webs. These empirical relationships were contrasted against the theoretical allometric expectation considering a slope of -1, or

Sheldon's rule that considers that despite the scaling of -¾ of metabolic rates with increasing body sizes, there are consistent energetic losses among trophic levels (Brown et al., 2004). Therefore, a theoretical relationship with slope-1 for the best-fit model (we found the intercept considering minimum least-square criteria) was fitted together with the empirical linear model.

Hypothesis 2: Given the high species diversity in tropical streams, energy flow within food webs would be characterised by weak interactions between predators and prey resulting in bioenergetically stable food webs.

To test this hypothesis, first, we characterised the meta food web and each individual food web by calculating the number of nodes (number of taxa in each food web), number of links (number of trophic interactions), link density (mean number of links per node), connectance (the ratio between the number of links and all possible links), compartmentalization (measures the degree of connectedness of subsystems within a network, with higher values of connectance indicating more discrete subsystems), mean trophic position (mean trophic position of nodes within a food web with basal resources set to 1) and omnivory (the mean degree of variation in the trophic position of consumed resources) (Kones et al., 2009; Kratina et al., 2012; Latham, 2006; Pimm & Lawton, 1980). Indices were calculated using the package *NetIndices* in R (Kones et al., 2009).

Then, we tested the hypothesis by using the estimated energy fluxes from the fluxweb analysis and calculating the stability of food webs (stability of their Jacobian matrices) considering a Lotka-Volterra model of consumers and resources (Moore & de Ruiter, 2012). The stability of a food web can be measured using a Jacobian interaction matrix concerning the partial derivatives of the equations for each species with respect to all species in the food web near equilibrium (May, 1973; Neutel et al., 2002). A food web is therefore considered stable when the Jacobian matrix has negative real parts eigenvalues for every interaction - i.e., all consumers can be sustained based on the biomasses of their resources (see Supplementary Material from Gauzens et al. 2019).

Hypothesis 3: Local extinctions of individual taxa from a complex tropical food web would not significantly disrupt its stability, as it would not heavily rely on key strong interactions.

To test the third hypothesis, we simulated multiple species extinction scenarios to determine the consequences of individual species loss for the stability of the meta food web. Here, in each scenario we individually removed one species at a time, recalculating energy fluxes and stability using fluxweb in R (Gauzens et al., 2019). We performed this species removal procedure for all species in our meta food web. Secondary extinctions could happen in our model after species removal, if a given species has a positive eigenvalue in the new Jacobian matrix after calculating stability. In this case, the food web would be termed unstable. To understand which network aspect is associated with higher food web stability, we calculated the network indices described above (number of taxa in each food web, number of links, link density, connectance, compartmentalization, mean trophic position, and omnivory) for each simulated food web after each species extinction. With these values, we applied a Pearson correlation matrix between them with the inclusion of the maximum eigenvalue of the Jacobian matrices (the stability measure).

Hypothesis 4: Spatial dissimilarity of local food webs would be associated with changes in large predators, indicating that mobile predators enhance spatial asynchrony among communities entailing regionally stable meta food webs.

To test the last hypothesis we calculated compositional and network dissimilarity using the Bray-Curtis index (Legendre, 2014). Whereas the compositional dissimilarity is based on differences in the relative species abundances, the network dissimilarity also accounts for the presence or absence of species interactions following species addition - e.g. one species can add multiple interactions to a food web, while another species can add only one interaction. We decomposed the network beta diversity into the components of ‘changes caused by the absence of predator’, ‘changes caused by the absence of prey’, or ‘changes caused by mutual absences’ (Novotny, 2009). We did not calculate the components of network dissimilarity associated with rewiring and turnover, as our interactions are defined at the meta food web level, preventing our assessment of rewiring - i.e. species always interact with the same species once they are present. Beta diversity indices were calculated using the bipartite package (Dormann et al. 2008).

RESULTS

Food web components

We identified 1352 invertebrates from 54 different taxonomic groups. From this, 313 individuals were *Macrobrachium* (Paleomonidae, Decapoda) collected through both Surber sampling and electrofishing, while the others mostly included insects, with a small proportion (<1%) of Oligochaeta, Platyhelminthes and Gastropoda collected by Surber sampling (0.9 m^2 in total). The insects with the highest abundances were *Macrostemum* (Hydropsychidae, Trichoptera, n = 170), *Gripopteryx* (Gripopterygidae, Plecoptera, 118), *Simulium* (Simuliidae, Diptera, 95), Chironomidae (Diptera, 92), *Chimarra* (Philopotamidae, Trichoptera, 79), *Smicridea* (Hydropsychidae, Trichoptera, 60), *Helicopsyche* (Helichopsychidae, Trichoptera, 46), *Farrodes* (Leptophlebiidae, Ephemeroptera, 30), Baetidae (Ephemeroptera, 26) and Belostomatidae (Hemiptera, 20). We also captured 332 fish from 12 species (413,5 m^2 sampled). Two fish species were found across all sites: catfish *Acentronichthys leptos* Eigenmann & Eigenmann, 1889 (66), and knifefish *Gymninotus pantherinus* Steindachner, 1908 (32). Other abundant (but less widespread) fish species included the lambari *Deuterodon iguape* Eigenmann, 1907 (71) and the characids *Hollandichthys multifasciatus* Eigenmann & Norris, 1900 (61), *Characidium lanei* Travassos, 1967 (34) and *Mimagoniates microlepis* Steindachner, 1877 (34).

Relationship between trophic position and body mass

We analyzed 329 samples for stable isotopes that were categorized into 42 groups, including basal resources, macroinvertebrates and fish. Fish generally has the highest δ^{15}N values (i.e. occupied the highest trophic positions), but there was a considerable overlap with many macroinvertebrates and shrimps. The relationship between δ^{15}N and individual body masses suggested that fishes are more strongly size structured than macroinvertebrates, only partly supporting our first hypothesis (Figure 1B). Macroinvertebrates had high isotopic variability with large overlap in bi-dimensional space between species with different body masses (Figure 1C), although some taxa were clearly distinct (e.g. *Macrobrachium* and damselflies with high δ^{15}N values and grazers *Psephenus* and *Gripopteryx* with the lowest δ^{15}N values).

Our mixed effects models supported this visual inspection with models with both random slopes and intercepts (species) returning associations with body sizes (estimate = 0.45, SE = 0.08, t = 5.38 and estimate = 0.39 SE = 0.08, t = 4.57, respectively) that depended on the group (fish or invertebrate) (interaction effect, estimate from model with random slope = -0.31, SE = 0.11, t = -2.86 and estimate from model with random intercept = -0.27, SE = 0.11, t = - 2.47). Overall, this means that there is a general association between trophic level and body sizes, where fishes are strongly size structured, but invertebrates are not. Considering groups as a fixed effect interacting with body size is important for the relationship as a comparison with a model without groups renders only half of the marginal R^2 (marginal $R^2 = 0.64$ vs. marginal $R^2 = 0.31$) and a significantly higher AIC (AIC = 788 vs. AIC = 802, Chi square = 17.33, $P < 0.001$). Moreover, separate models for only fish and only invertebrates return significant slopes only for fish (body mass fixed effect estimates = 0.60, SE = 0.09, t-value = 6.44, species as random slopes). The patterns in community-level isotopic composition for individual sites were largely similar to those observed for the regional meta food web (Figure S1).

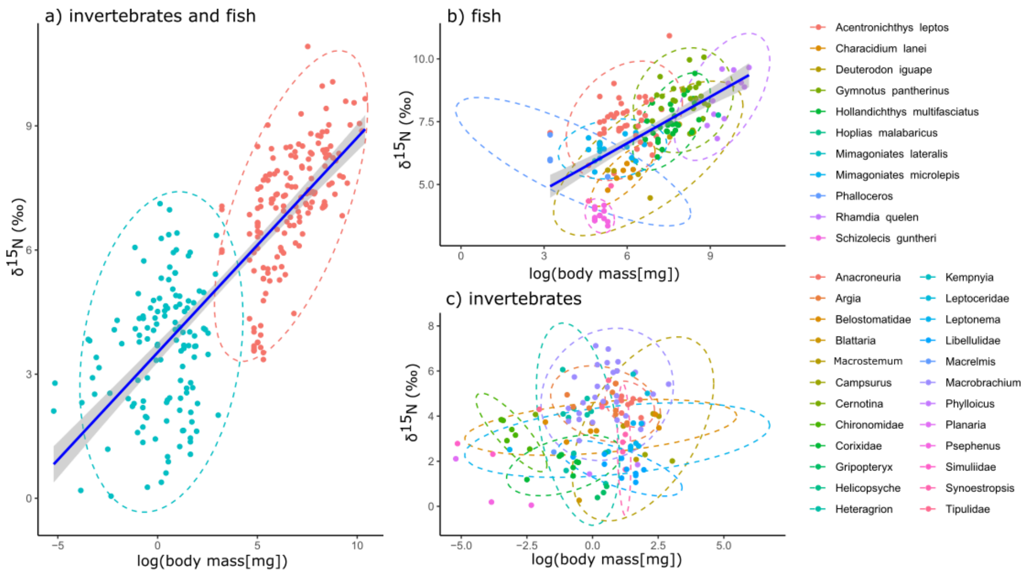

Figure 1. Isotopic composition of fish and macroinvertebrates from Atlantic Forest streams (Cananeia, Brazil). a) General association between mean body mass (mg) and $\delta^{15}N$ values (relative trophic position) of organisms (some isotopic samples encompass multiple individuals, e.g. Chironomidae). Individual associations for fish (b) and invertebrates (c). Ellipses correspond to 95% confidence level for a multivariate t-distribution. The line in the (a) panel indicates the fitted linear mixed effects model with body mass as fixed effect and species as random slope (estimate = 0.45, SE = 0.08, t = 5.38). The model in the fish panel indicates the fitted linear mixed effects model with body mass as fixed effect and species as random slope (body mass fixed effect estimates = 0.60, SE = 0.09, t-value = 6.44).

Food web construction

The EcoDiet model identified a high link probability for most of the analysed interactions with link probabilities within two groups: 14% had probabilities between 0.2 and 0.18, but all the other 86% had probabilities higher than 0.82. The diagnostics of the whole model resulted in Gelman-Rubin statistics higher than 1.1 for 54 links (~16% of the links), indicating a lack of convergence in the MCMC algorithm (Hernvann et al. 2022). The final meta food web after removing these links contained 307 links, including the likelihood of diet proportion for each consumer. The number of nodes in each site ranged between 28 and 41 while the number of interactions ranged between 73 and 171, with a positive trend between the two characteristics - more diverse sites had more links and also occurred in wider and shallower stretches of streams (e.g. S1 and S8C). Consequently, connectance was similar between stretches with a mean of 10% of all possible links actually realised (see Table S2 for other network metrics).

Energy fluxes

For the meta food web, the 10 populations with highest energetic demands were composed of six Trichoptera genera *Macrostemum*, *Leptonema*, *Synoestropsis*, *Helicopsyche*, *Cernotina* and *Phylloicus*, one Ephemeroptera (*Campsurus*), one Diptera (Chironomidae), one Plecoptera (*Gripopteryx*) and one Palaemonidae (*Macrobrachium*). In sum, these species account for 70% of total energy flux in these ecosystems. Yet, a considerable 30% of the energy flow is shared between the remaining 48 consumers, which is partially in agreement with the second hypothesis (Figure 2). The biofilm was the main basal resource that mostly contributed to food web energy flows, followed by moss and leaves (Figure S3).

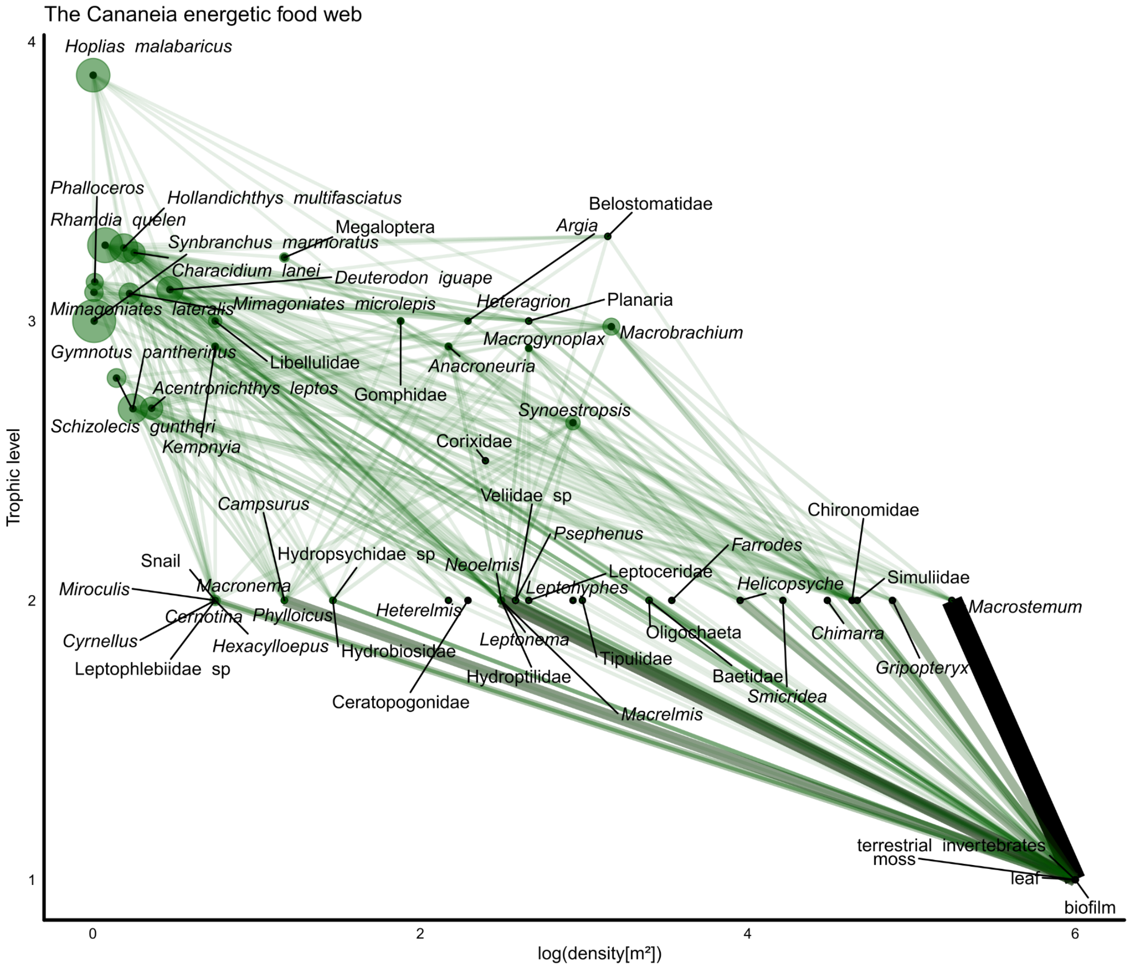

Figure 2. Regional meta food web with energy fluxes from Atlantic Forest streams (Cananeia, São Paulo, Brazil). Width of links are proportional to differences in the amount of energy flowing (J/year/m²) at the population level estimated by the *fluxweb*

energetic model. Position along the y axis represents the trophic position of each taxon. Node sizes are proportional to species average body masses (mg).

Some invertebrates (e.g. *Macrostemum*, *Macrobrachium*) were disproportionately abundant (Figure 3). The relationship between body mass and population density showed that these taxa tended to be regionally more abundant than expected from their mean body masses (i.e. they were above the regression model, Figure 3), especially compared to the empirical model, but also to the theoretical expectation with slope = -1. This pattern was also evident at the local scale, but the species above the regression model varied from site to site (Figure S2). Moreover, the empirical relationship was shallower than the theoretical expectation with exponent -1.

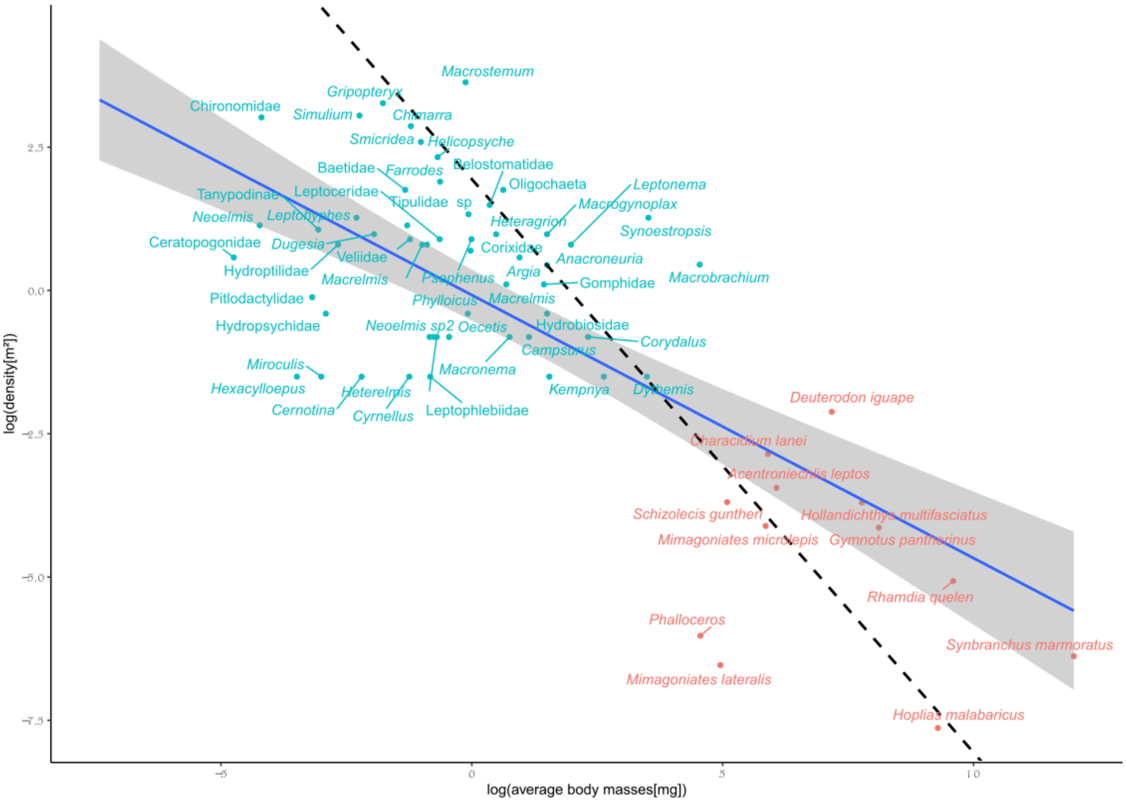

Figure 3. Species size-density relationship for Cananeia streams (density relationship for the regional meta-web). Log-transformed density of individuals in the regional

species pool is regressed against log-transformed mean body masses of each taxonomic group (slope = -0.45, $R^2 = 0.48$, $P < 0.001$). Species above or below the regression line indicate species with relatively more or less individuals than expected based upon their body size. The dashed line indicates the least-square best fit model for a slope=-1, an empirical benchmark predicted by allometric scaling theory.

For individual stream sites, some species were important contributors across all sites while some of them were only important for some specific ones (Figure 4). For instance, *Macrostemum*, Chironomidae, *Gripopteryx* and *Macrobrachium* were widespread and abundant in the regional species pool and contributed strongly to the energy flux in all five stream food webs. In contrast, *Campsurus*, *Farrodes*, *Deuterodon iguape*, *Helicopsyche*, *Macrelmis* and *Synoestropsis* were only important in one or two sites (Figure 4).

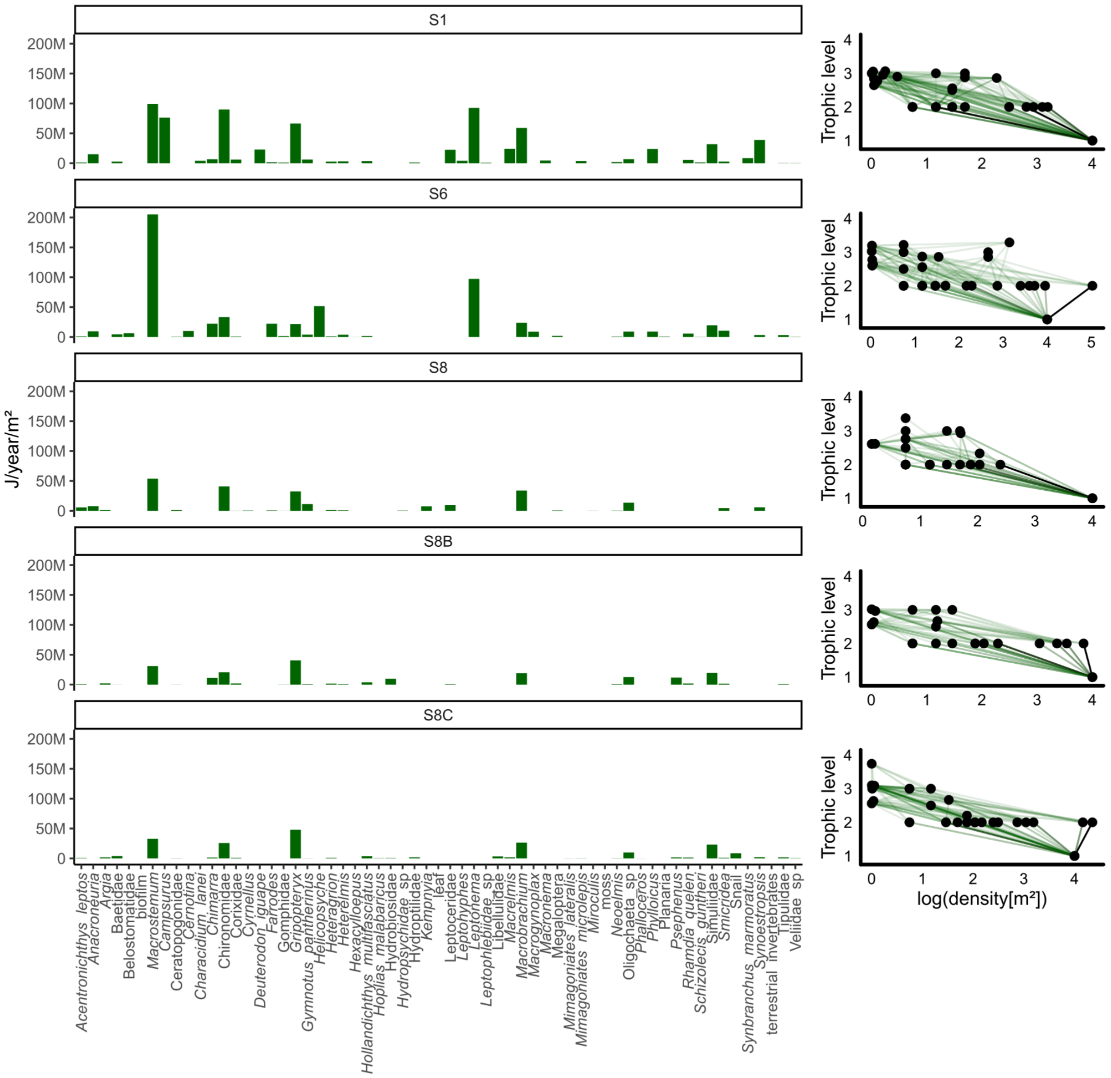

Figure 4. Energy fluxes (J/year/m²) from individual nodes and the five food webs from Atlantic Forest streams from Cananeia (São Paulo, Brazil). Position along the y axis in the individual food webs represent the trophic position of each taxon. Darker link colours represent interactions of higher energy fluxes.

Besides these differences among individual food webs, supporting our second hypothesis, all food webs and the meta food web were stable, i.e. had negative values for the maximum eigenvalue of the Lotka Volterra Jacobian matrices. This analysis considered that stream food webs are in a stable state if the real parts of eigenvalues from the Jacobian are all negative (between -4.9 and -13.5). This means that the population energy demands are consistent with the amount of energy available at lower trophic levels, meaning that there is no population too large that cannot be sustained by the amount of energy from prey. The sensitivity analyses, changing the values of *b* and efficiencies, also returned stable meta food webs in except for when $b = 1$, which is the isometric scaling where metabolic rate is constant. The results of the sensitivity analyses can be found in Supplementary Material and the results using the original values of *b* (-0.29) and mean efficiencies from Lang *et al.* (2017) are reported in following.

In agreement with our third hypothesis, the simulation extinction resulted in food webs that remained stable after the removal of individual species each at a time (maximum Jacobian eigenvalues ranging between -14.60 and -7.41). That is, after species removal, no secondary extinctions were observed (all species had negative eigenvalues after calculating stability in the resulting food webs). We found that, despite the consistent stability of the food web to species removal, and lack of secondary extinctions, there are network patterns associated with the variation in the stability values (Figure 5). Higher stability (the inverse of the maximum eigenvalue) was related to greater omnivory in the food web ($r=0.27$, $p<0.05$), lower levels of network compartmentalization ($r=-0.32$, $p<0.05$), and lower average link weights ($r= -0.40$, $p<0.05$) (Figure 5 and Figure S4). Thus, removing omnivorous species that connect different sub-webs with multiple weak interactions is detrimental to ecosystem stability. When looking into the species that have the highest impact on food web stability, we can also observe that many fish species were of high importance, especially considering how little they contribute to the total energy fluxes (e.g. the knifefish *Gymnotus pantherinus* that eats 22 different food items and the tetrafish *Deuterodon iguape* with 19 food items, Figure 5).

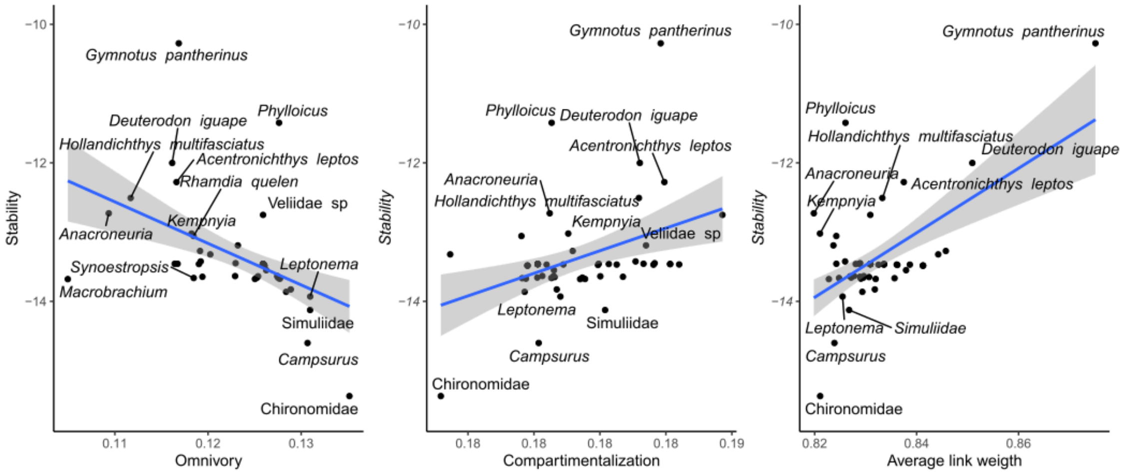

Figure 5. Associations between the stability of simulated meta food webs and network metrics. Each point in each scatterplot represents a simulated meta food web after the extinction of a given species (labelled). The stability was estimated as the maximum eigenvalue of the Jacobian matrix using a Lotka-Volterra system of equations. More negative values indicate higher system stability to disturbances. Lower stability was associated with simulations that reduced omnivory and increased compartmentalization and average link weight. The models in each plot represent linear regressions with the following results: Omnivory ($R^2 = 0.07$, $P = 0.04$), Compartmentalization ($R^2 = 0.10$, $P = 0.01$), Average link weight ($R^2 = 0.15$, $P = 0.001$).

Food web dissimilarity

As predicted by the fourth hypothesis, the dissimilarity of the network was higher than the compositional dissimilarity (Figure 6). Approximately 40% of interactions changed from one food web to another, while pure compositional dissimilarities among stream communities were approximately 25%. These compositional changes were strongly associated with the absence of predators when prey taxa were present, with a much smaller contribution of the component of prey absence and mutual absence (less than 10%, Figure 6).

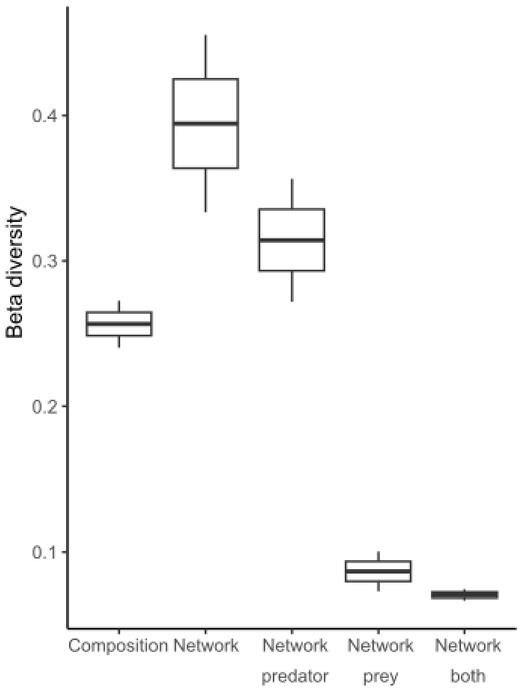

Figure 6. Compositional and network dissimilarity among local streams from the Cananeia watershed (São Paulo, Brazil) based on Bray-Curtis index. Composition = compositional beta diversity, Network = network beta diversity, Network predator = network dissimilarity caused by the absence of predator, Network prey = network dissimilarity caused by the absence of prey, Network both = network dissimilarity caused by the absence of both predators and prey.

DISCUSSION

Untangling a network of trophic interactions through integration of energetic principles has been proposed as a key new approach to understand ecosystem functioning under a comparable currency (Barnes et al., 2014). Here, we combined recently advanced methods and theories (Gauzens et al., 2019; Hernvann et al., 2022) to derive a well-resolved energetic food web from tropical rainforest and investigate the mechanisms behind its stability. By doing so, we found locally and regionally stable networks, where energy was channelized through a taxonomically diverse set of organisms, such as chironomids and stoneflies, and from small to large taxa (e.g. from chironomids to palaemonid shrimps). These food webs were stable in the face of simulated individual species extinctions with an evidenced importance of omnivorous fishes interconnecting different food web compartments at local scales and different communities at regional scales. These characteristics potentially govern food web stability at local and regional scales highlighting the roles of omnivory and alpha and beta diversity. Below, we explain these new insights for understanding the dynamics of tropical stream ecosystems and how important these mechanisms could be for anticipating the impacts of the current environmental crisis.

The relationship between organism body mass and their trophic position provides a measure of food web size structure (i.e. the extent to which larger consumers feed on small prey and whether this is at a constant ratio) (Perkins et al. 2021). Partially in contrast to our first hypothesis, there was a strong association between δ^{15}N values and body mass for fish, both within and across species, indicating that larger fish are commonly higher up the food chain. This suggests that fish predators interact within a well-defined prey size spectrum to fulfil their energetic demands, a pattern expected in simple food web compartments comprising only a limited number of functional groups (Keppeler et al., 2020). However, this pattern did not hold for invertebrates where there was no relationship, more in agreement with our second hypothesis. This lack of association indicates that invertebrate consumers feed plastically up and down the food web to meet their metabolic requirements (i.e. feeding on larger or smaller prey than expected based on their optimum predator-prey mass ratio, (Potapov et al., 2021). It has been suggested that tropical streams have a greater prevalence of omnivorous and generalist feeding than in their temperate counterparts that have proportionally more taxa from delimited trophic groups like shredders and obligatory predators (Boyero et al., 2011). This generalist feeding strategy decreases energy transfer efficiency along the food chain due to a decrease in net gains when feeding upon proportionally small or large prey (Brose et al., 2005; Stephens & Krebs, 2019). Our findings add mounting evidence that generalist macroinvertebrates at intermediate trophic positions are likely inefficient, but represent diverse conduits of energy that potentially enhance the stability of these complex systems (Collyer et al., 2023).

At the meta food web scale, 70% of the total energy flux depended on a subset of ten taxa spread over orders of magnitude in body masses (from chironomids with an average 0.2 mg per individual to large shrimps with an average of 1060 mg per individual). This may have consequences for the stability of the food web as different body masses are associated with differences in life cycles and environmental responses such as size-selective predation, size-related risks of dislodgement by hydraulic forces, and use of size-related refugia in streambeds to counter these risks (Woodward et al., 2005). Indirectly, body mass is closely related to other traits, with smaller species often exhibiting population resilience with short life cycles, rapid growth, high reproductive rates and high number of dispersal events in time (Brown et al., 2004; Saito et al., 2015). We hypothesise that having a set of invertebrates with a wide range of body masses contributing strongly to energy flow could enhance resilience to local perturbations in tropical streams. Environmental changes negatively affecting specific size classes could be compensated by organisms with different body masses, which could sustain energy flows through the food webs.

Despite the subset of macroinvertebrates that were important for energy flows in all five streams, some taxa were only important in one or two sites. This diverse set of taxa constituted approximately 30% of the total energy flow, regionally. Moreover, three key results highlight the importance of the local and regional diversity for the functioning of tropical stream food webs, where energy flows do not rely strongly on specific trophic interactions. First, we found that simulating individual extinctions did not destabilise the meta food web, nor caused any immediate secondary extinctions. However, there were associations between more stable food webs and higher prevalence of omnivory, weaker trophic interactions and lower compartmentalization. Altogether this is a direct support that omnivorous species that connect multiple compartments with weak interactions are key in sustaining stable food webs (Kratina et al., 2012). As such, we indeed found that some fish species are relatively more important for the maintenance of food web stability, which is interesting as this describes different roles a species can have in the food web. On one hand, a species can contribute highly to the total energy flux and productivity linking terrestrial and aquatic compartments through the emergence of adults, while not being strongly pivotal for the network stability (e.g. Chironomidae). On the other hand, proportionally low amounts of energy can flow through other species, but these may connect different food web compartments, allowing for higher ecosystem resilience o (e.g. omnivorous fish that connect basal resources, macroinvertebrates and other fish).

Second, local food webs were approximately 40% dissimilar among each other. A high regional diversity coupled with high spatial variation can assure that multiple species can contribute a little to the energy flow, but also that a diverse pool of potential colonisers would be able to compensate for the eventual loss of species. Indeed, we found that several size classes were regionally composed by multiple taxa that could potentially compensate for species losses. For instance, *Macrostemum* (a net-spinning caddisfly) is the main contributor to energy fluxes, that regionally have at least three other genera from the same family with fairly similar sizes co-occurring in the watershed on different densities (*Leptonema*, *Macronema*, *Smicridea*). Intriguingly, *Leptonema* and *Smicridea* were found to be the most abundant taxa in the presence of *Macrostemum* in other well preserved Atlantic Forest streams (Saito, Stoppa, et al., 2021; Siqueira et al., 2020). Tropical stream communities have been suggested to be more stochastic in terms of colonizations and demography in comparison to temperate systems due to an accelerated pace of life that leads to more dispersal events and smaller population sizes (Saito, Perkins, et al., 2021; Siqueira et al., 2020). The greater contribution of stochastic processes should render spatial and temporal variation in the relative abundance of these taxa but with potentially weak impacts for patterns of energy flow.

Third, the dissimilarity of the food webs were associated to changes in predators, rather than prey, suggesting that spatial asynchrony of mobile predators dampens variability of prey communities and stabilises food webs regionally. We found that most of the fish species sampled were only present in one or two sites out of five, while most of the smaller invertebrates were common in four to five sites. Together with the importance of omnivorous fish evidenced by our extinction simulations, we can outline a regional effect of fish beta diversity in the stability of food webs. This should happen because omnivorous fish should feed upon productive patches when resources are high and move to other patches when resources get lower, allowing recovery of resources (i.e. invertebrates) from low densities. As an example, the catfish *Rhamdia quelen*, was one of the most important taxa for food web stability and was found to move more than 300 m in two hours of observation, indicating that one individual can effectively forage across multiple stream stretches within days (Schulz &

Leuchtenberger, 2006). This spatial asynchrony in the community of larger predators within a metacommunity of small spatial extent and little environmental heterogeneity suggests that these species could operate as mobile predators connecting the different streams stabilising the meta-food web.

Despite the evidence outlining the mechanisms supporting the stability of tropical stream food webs, we describe two key limitations of our work. 1) Our study was conducted in one tropical region using five individual food webs composing one meta food web and therefore, we do not have a strong empirical gradient to test the influence of variations in species diversity, omnivory and beta diversity on stability patterns. We emphasise the need for future studies to try to disentangle such effects in studies comparing food webs across gradients using empirical data (e.g. across latitude) or experiments (mesocosm experimentations). 2) Our modelling exercise took into account the extinction of singular species and its potential effects on secondary extinctions caused by the loss of energy sources and how this could echo to destabilising the network. While accounting for realistic interactions in terms of energy flow, our simulation could not account for known mechanisms associated with secondary extinctions such as higher order interactions (Fowler, 2010) and behavioural changes with predator release (Hammerschlag et al., 2022). We emphasise how our study gives only the first steps in understanding tropical stream stability, as all these complex responses could modify real food web responses.

In summary, we found that all five tropical stream sites have energetic food webs that are stable to small perturbations. We observed two important associations: 1) diversity increases the total energy flowing up to the apex predators, 2) The presence and beta diversity of omnivorous fish stabilises local and regional food webs.

These lead us to two important mechanisms for the functioning of tropical stream food webs: (i) the diversity of body masses should buffer against size-dependent disturbances allowing high rates of productivity with higher diversity and (ii) high regional diversity and weak, non-specialized interactions buffering against local stochastic variation in species composition. These two mechanisms critically depend on the maintenance of local and regional biodiversity in tropical streams, which is known to be strongly affected by human land use intensifications from forests to monoculture plantations in different ways (Neves et al., 2023; Siqueira et al., 2015). Therefore, an urgent challenge is to understand how the systematic loss of diversity jeopardises the stability of stream food webs under human impacts and what could be the consequences for a sustainable use of resources.

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