

1 | Land use effects on the structure of trophic networks from Neotropical stream fish
2 | assemblages

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Abstract

Rising human demands for goods and services have led to an intensification in land use and habitat fragmentation, posing threats to ecosystems. Despite growing evidence regarding the significance of these global change factors, we still do not understand how these human activities impact ecological interactions and food webs in freshwater habitats. To understand part of these effects, we conducted a literature review on Neotropical fish trophic webs between 1982 and 2019 in Brazilian streams. Specifically, we evaluated how land use influences the structure of trophic fish networks. We hypothesize that increasing land use reduces biodiversity and modularity in fish networks due to the loss of specialist species and faunal homogenization, resulting in nested networks. We quantified six network metrics based on the species richness and distribution of interactions (nestedness and modularity), trophic specialization, mean number of links per species, link density, and number of trophic links according to the number of nodes (number of links). We observed that the trophic networks are more nested than modular, thus supporting our hypothesis. However, we only observed a negative effect of land use on modularity, and the mean number of links per species, whereas other metrics such as nestedness, trophic specialization, number of species, and link density are not influenced by land-use. These findings highlight the relevance of preserving natural vegetation along watercourses and its key contribution to the functioning of aquatic ecosystems. Additionally, our results demonstrate that the interactions between consumer and resource represented by trophic network descriptors should also be considered in future studies on the importance of conservation of riparian forests.

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Abstract

In studies of fish trophic networks, one of the main gaps is how interactions between species respond to anthropogenic stressors. To understand the effects of land use on the structure of freshwater fish trophic networks, we compiled a dataset of 49 neotropical fish trophic webs sampled from 1982 to 2019 across Brazil. We hypothesize that increasing land-use intensity will change the structure of trophic networks, reducing modularity and trophic specialization, and increasing nestedness. We calculated nestedness, modularity, trophic specialization, number of links and link density from diet information. We assessed land use in a 500-meter buffer around each sampling point from MapBiomas information. Our analysis provides a comprehensive overview of the responses of trophic networks to land use and shows that variation in modularity was greater in pastures, while changes in network complexity were more evident in agriculture. We found a negative relationship between land-use gradient and modularity and links density. These findings highlight the relevance of preserving natural vegetation along watercourses and its key contribution to the functioning of aquatic ecosystems. Our results demonstrate that the interactions between consumer and resource represented by trophic network descriptors should also be considered in future studies on the importance of conservation of riparian forests.

Keywords: ecological networks, food web, Neotropical savanna, modularity, nestedness

Introduction

— Natural communities are composed of different species interacting with each other in different ways, which can be organized as ecological networks (Fortunato & Hric, 2016). A network can be represented by a graph where the species or individuals are nodes and the

biological interactions are the links between them (Boecaeletti, Latora, Moreno, Chavez & Hwang, 2006). The study of networks provides an efficient way of representing, characterizing and revealing the determinants of the structure of natural interaction systems. This approach has been successfully applied to understand complex interaction systems such as mutualism (Mougi & Kondoh, 2014), trophic interactions (Baumgartner & Robinson, 2016), neural or genetic networks (Roth et al., 2016) and how these structures changes over space and time (Warren, 1989; Pinter-Wollman, 2015). It provides new insights into the ecological and evolutionary processes in structuring and organizing biotic interactions (Tylianakis & Morris, 2017).

—— Recent research has been focused on the human effect on the dynamic and structure of networks. Authors have found that habitat degradation, for instance, promotes homogenization and a reduction in network complexity and stability (Ollerton, McCollin, Fautin & Allen, 2007; Sebastián-González et al., 2015; Song, 2017; Pellissier et al., 2017; Dáttilo & Vasconcelos, 2019; Felipe-Lucia et al., 2020). This nestedness pattern emerges when specialized species tend to interact with subsets of partners of most generalist species (Bascompte, Jordano, & Melia, 2003). It involves differences in the abundance of predator-prey interactions and higher rates of extinction of specialist species (Pires & Guimarães, 2013). On the other hand, modular networks are formed by subgroups of consumer species interacting more with one resource group than other resources outside its subgroup, hence forming many modules in the network (Olesen, Bascompte, Dupont, & Jordano, 2007; Dormann & Strauss, 2014). In trophic interactions, other network descriptors such as trophic specialization also enable the understanding of the organization of networks and its ecological drivers (Staudacher et al., 2017). This network metric indicates the degree of species consumption on exclusive food items. Investigations of how the properties of networks vary according to anthropic stressors have the potential to provide

insights into how the trophic networks may vary under the influences of processes such as environmental filtering, competition or facilitation (Pellissier et al., 2017).

———Trophic interactions are an essential component for understanding the dynamics of populations, and consequently the emerging patterns of coexistence and diversity in communities. Despite the increased interest in this field, the knowledge of how and why trophic networks vary along land-use gradients is elusive (Pellissier et al., 2017; Felipe-Lucia et al., 2020). Recently, theoretical studies have shown that the main determinants of network structure differentiation at different sites are variations in ecological and environmental factors (Emer, Venticinque, & Fonseca, 2013; Dugger et al., 2018). In studies of fish trophic interactions, one of the main gaps is how interactions between species respond to anthropogenic impact (Tylianakis et al., 2007). Based on local scale studies, it has been suggested that trophic networks in aquatic ecosystems under strong anthropogenic impact tend to present generalist species with greater connectivity among nodes and a high level of nestedness (Manoel & Uieda, 2017) compared to regions with preserved native vegetation (Thompson & Townsend, 2005). Recently, Felipe-Lucia et al. (2020) showed that increasing land use intensity resulted in homogeneous and less modular networks, while forest formations resulted in more complex networks. The integrity of riparian forest is crucial for the provision of food resources for aquatic communities and ecosystem change are threatening their supply (Zeni & Casatti, 2014; Carvalho et al., 2019). To understand these impacts, it is essential to investigate the trophic relationships between communities (Lobón-Cerviá, Mazzoni, & Rezende, 2016), and how the drivers of global change (ie, intensification of land use) affect these trophic relationships. Thus, understanding the variation of trophic structures at large scale and testing the generality of these predictions is important to build consistent knowledge of the effects of land use on trophic networks.

Most impacts on freshwater bodies are directly or indirectly related to the conversion of the adjacent vegetation to pasture or cropland (Vorosmarty et al., 2010). Croplands and pastures influence fish communities through multiple paths (Dala-Corte et al., 2016). Croplands cause increased siltation, nutrient input, increase the organic loading through fertilizers and homogenization of the stream substrate (Sutherland, Culp, & Benoy, 2012), and pastures also increase the dissolved organic matter into watercourses (Neill, Deegan, Thomas & Cerri, 2001). At the same time, local reduction in riparian vegetation cover reduce nutrient supply and the input of allochthonous material, increase autochthonous production and completely change the quality and quantity of available food resources (Bambi et al., 2016; Zeni & Casatti, 2014). As a consequence, fish species often change their resource use in response to changes in resource availability (Prejs & Prejs, 1987) and poor environmental conditions (Alonso, Carvalho, Alves, Moreira, & Pompeu, 2019). These modifications can increase niche overlap due to an expansion of generalist/opportunistic feeding strategy and a reduction in specialist species. Consequently, the structure of the trophic network (Pimm, Lawton, & Cohen, 1991) should vary according to the degree of land-use change (Winemiller, 1990).

Here, we aim to assess the anthropogenic effects on the trophic networks structure of Neotropical stream fish. We addressed the following questions: (a) are the structure of fish trophic networks related to land-use changes? and (b) which of the major land-use classes (i.e. pasture or cropland) has the greater effect on the structure of fish trophic networks? The first hypothesis is that basins with greater vegetation cover can increase the supply and diversity of food resources (terrestrial insects, terrestrial allochthonous resources) to streams, resulting in networks more complex (ie large number of links, species and link density) and specialized (ie larger modularity and greater trophic specialization). The second hypothesis is that basins with

~~greater anthropogenic influence may decrease the diversity of food resources, resulting in the predominance of generalist species (ie, more nested and less specialized trophic networks).~~

Introduction

Natural communities are composed of different species interacting with each other in different ways, which can be organized as ecological networks (Fortunato & Hric, 2016). A network can be represented by a graph where the species or individuals are nodes and the biological interactions are the links between them (Boccaletti et al., 2006). The study of networks provides an efficient way of representing, characterizing, and revealing the determinants of the structure of natural interaction systems. This approach has been successfully applied to understand complex interaction systems such as mutualism (Mougi & Kondoh, 2014), trophic interactions (Baumgartner & Robinson, 2016), neural or genetic networks (Roth et al., 2016). However, how these structures change over space and time is still a challenging (Warren, 1989; Pinter-Wollman, 2015). Thus, studies that explore these changes will provide new insights into the ecological and evolutionary processes in structuring and organizing biotic interactions (Tylianakis & Morris, 2017).

Recent research has been focused on the human actions on the dynamic and structure of networks (Wang et al., 2021; Effert-Fanta et al., 2023; Neves et al., 2024). For instance, habitat degradation promotes homogenization and reduction in network complexity, resulting in network more nested (i.e., species interactions are hierarchically organized, with a few species interacting with many others) than modular (i.e., species interactions are compartmentalized with some species interacting only within specific subsets) (Bascompte et al., 2003; Olesen et al., 2007; Pires & Guimarães, 2013; Dormann & Strauss, 2014). In trophic interactions, other network

descriptors, such as trophic specialization (a metric that indicates the degree of species consumption on exclusive food items), mean number of links per species, and number of trophic links according to the number of nodes (number of links given consumers and resources) also can be affected by human actions (Felipe-Lucia et al., 2020). For instance, human actions can reduce aquatic habitat heterogeneity and promote habitat fragmentation, disrupting the balance of species interactions within ecosystems (Staudacher et al., 2017). Thus, examining how the properties of networks are determined by anthropogenic stressors have the potential to provide insights into how the trophic networks are structured (Pellissier et al., 2017) and their consequences on ecosystem functioning.

Trophic interactions are an essential component for understanding the dynamics of populations, and consequently the emerging patterns of coexistence and diversity in communities (Pellissier et al., 2017; Dáttilo & Vasconcelos, 2019). Despite the increased interest in this field, the knowledge of how and why trophic networks vary along land-use gradients is elusive (Pellissier et al., 2017; Felipe-Lucia et al., 2020). Recently, theoretical studies have shown that the main determinants of network structure differentiation at different sites are variations in ecological and environmental factors (Emer, Venticinque & Fonseca, 2013; Dugger et al., 2018; Arruda et al., 2020). In studies of fish trophic interactions, one of the main gaps is how interactions between species respond to anthropogenic impact (Tylianakis et al., 2007). Based on local scale studies, it has been suggested that trophic networks in aquatic ecosystems under strong anthropogenic impact tend to favor generalist species with greater connectivity among nodes and a high nestedness level (Manoel & Uieda, 2018) when compared to regions with preserved native vegetation (Thompson & Townsend, 2005).

Most impacts on freshwater bodies are directly or indirectly related to the conversion of the adjacent vegetation to pasture or cropland (Vorosmarty et al., 2010). Croplands and pastures influence fish communities through multiple paths (Dala-Corte et al., 2016). For instance, croplands cause increased siltation, nutrient input, increase the organic loading through fertilizers and homogenization of the stream substrate (Sutherland et al., 2012), while pastures also increase the dissolved organic matter into watercourses (Neill et al., 2001). At the same time, local reduction in riparian vegetation cover reduces nutrient supply and the input of allochthonous material, increases autochthonous production, and completely changes the quality and quantity of available feeding resources (Bambi et al., 2023; Leal et al., 2023). Consequently, fish species often change their resource use in response to changes in resource availability (Prejs & Prejs, 1987) and poor environmental conditions (Alonso et al., 2019). These modifications can increase niche overlap due to an expansion of generalist/opportunistic feeding strategy and a reduction in specialist species. Thus, the structure of the trophic network (Pimm et al., 1991) should vary according to the degree of land-use change (Winemiller, 1990). In short, the integrity of riparian forests is crucial for the provision of food resources for aquatic communities and ecosystem changes are threatening their supply (Zeni & Casatti, 2014; Carvalho et al., 2019; Dolabela et al., 2022). To understand these impacts, it is essential to investigate the trophic relationships between communities (Lobón-Cerviá et al., 2016), and how the drivers of local change (i.e., intensification of land use) affect these trophic relationships. Thus, understanding the variation of trophic structures at large scale and testing the generality of these predictions is important to build consistent knowledge of the effects of land-use on trophic networks.

Here, we aim to assess the land use effects on the trophic networks structure of Neotropical stream fish assemblages. We addressed the following questions: (a) is the structure of fish trophic

networks related to land-use changes? and (b) which of the major land-use classes (*i.e.*, pasture or cropland) has the greater effect on the structure of fish trophic networks? We hypothesized that locations with high vegetation cover could increase the supply and diversity of food resources (e.g., terrestrial insects, terrestrial allochthonous resources) to streams, resulting in a high diversity of specialized fishes that form a network more modular than nested. Conversely, sites of intense land use values determine less specialized assemblages, more simplified (a small number of links), and more nested trophic networks. Our results will highlight the relevance of preserving natural vegetation along watercourses and its key contribution to the functioning of aquatic ecosystems.

Materials and methods

Data sampling

Dietary data base

We conducted a systematic literature review of articles published from 1982 to 2021 from electronic databases and search engines, including searched for dietary studies with fish assemblages available in the literature, considering the Scopus, Web of Science and Google Scholar. Our focus was on studies examining the diet of freshwater fish assemblages in Brazil. Our search focuses on several combinations of keywords: ~~databases. Several combinations of keywords were used for the searches, containing~~ (fish*) AND (stream*) AND (feed*). The literature survey returned many studies, but ~~wefeeding OR diet) AND (other terms of interest).~~ We only considered ~~articlesstudies (artieles)~~ articles with more than five species ~~in studies~~ that represent the local community; because we were interested in describing the local community network structure. ~~Additionally. The study site samples covered large reaches of rivers (rivers and streams) in multiple habitats located in natural, pasture and agricultural areas. In addition, we~~

focused on the papers expressing the diet of species as the feeding index (IAi) or numeric or volume percentage of the food item in the diet of each individual ~~species (Bonato~~(Santos et al., 2012; Peressin2021; Souza et al., 2018; Santos2020; Peressin et al., 2021; Souza2018; Bonato et al., 2022; Caldatto et al., 20232012), to make sure they were fully characterizing feeding habitats. We also considered thesis and gray literature reporting fish trophic networks with the same condition described above (N=18). In total, we compiled 49 trophic networks across Brazil (~~compiled 49 peer-reviewed articles covering dietary data and study location coordinates~~ (Table S1). We extracted information from the dietary tables of the papers (row food items and column species) that included different food items represented by different families of terrestrial and aquatic insects, algae, plant material, crustaceans, and mollusks. As these published studies may ~~The studies~~ diverge in their way to quantify consumed food items and sampling efforts~~these~~ ~~matriees served as the basis for building the trophic networks detailed below. Thus, we preferred~~ using ~~used~~ information on the presence/absence of interactions (*i.e.*, binary matrices) for focusing mostly on the incidence, rather than strength of the interaction, and avoid biases regarding items quantification and sampling effort~~calculating trophic network descriptors,~~ ~~except for the trophic specialization metric (H2', considers interaction frequencies).~~

Network metrics

We built bipartite networks in which the nodes represent the fish species (consumers) and food items (resources), while the links between them represent the items consumed by each species (Dormann & Strauss, 2014). Specifically, we used each interaction matrix to quantify network metrics, such as fish species richness, nestedness, modularity, trophic specialization, number of links, and the mean number of link per species. The number of fish species (*i.e.*, nodes) is defined by the total number of consumers within each matrix (May 1973; Tilman

1996). We quantified nestedness with the *NODF* metric, which is a widely-used network metric and based on the concepts of overlap and decreasing fill of the adjacency matrix (Almeida-Neto et al., 2008). We quantified modularity with the *Q* metric that measures the difference between the observed fraction of links connecting species in the same module and the fraction expected by chance (Newman, 2006) using an algorithm modified for two-mode networks (Dormann & Strauss, 2014). A modular network consists of interconnected modules, each module being a group of species more closely connected to each other than to species in other modules. (e.g., Olesen et al., 2007).

Trophic specialization was quantified by the H_2' index, which is based on the deviation of the number of interactions performed by a species and the expected total number of interactions per species. H_2' is a two-dimensional index derived from the Shannon index used to compare different networks, and ranges from 0 (no specialization, highly generalist) to 1 (complete specialization) (Blüthgen et al., 2006). The metric is calculated by a comparison between observed and expected interaction frequencies, based on the species marginal totals (Blüthgen et al., 2006). As it is based on frequencies of interactions, this was the only metric calculated using relative abundance consumed items (i.e., the strength of interactions). In the case of a food web, a species may be feeding only on a particular food item, but if this item presents a higher frequency of interactions in the system, it may limit the specialization degree and therefore the species would receive a low H_2' value. In contrast, a species that feeds on only two rarer food items would have a very high H_2' value. The higher the level of selectivity of the species, the greater the H_2' . On the other hand, we estimated the link density which is defined as the number of trophic links (*L*) divided by the total number of nodes (consumers and resources, *S*) in a food web (*L/S*). This metric is related to the number of trophic interactions in a food web, providing

information on the complexity of the food web and the number of pathways along which energy can flow (Dunne et al., 2002). Lastly, we also estimated the mean number of links per species, which informs how connected species are within the food web (Bersier et al., 1994; Dunne et al., 2002).

Null model of trophic network structure

When calculating network descriptors, it is important to control for a possible sampling bias related to network dimensions (*i.e.*, number of species and trophic links), which could prevent comparing descriptors among networks. Therefore, we compared three main (NODE, Q_1 and H_2') observed descriptors from individual networks to those calculated under null models with the same randomized matrix (Kortsch et al., 2019; Quimbayo et al., 2018; Dáttilo & Vasconcelos, 2019). We randomized the observed trophic networks over 499 matrices for each network descriptor, using a null model that fixes both marginal totals and connectivity ('swap.web' null model), *i.e.*, maintaining constant the number of interactions (and therefore connectivity), as implemented in the "bipartite" package in R (Dormann et al., 2009). Then, we quantified the Standardized Effect Size (SES) of each observed network metric (*i.e.*, NODE, Q_1 and H_2') as the difference between observed and null estimated values of network metrics using the following equation: $(\text{observed} - \mu) / \sigma$, where 'observed' is the value of the focal network metric, μ is the mean value of focal metric over all null matrices, and σ is its standard deviation of all null matrices. Negative and positive SES values indicate observed values that are lower and higher, respectively, than the expectation, given the number of species and trophic links. Empirical values of trophic network descriptors were considered to deviate strongly from the randomized food webs if these were outside the 0.05 to 0.95 quantile range of the null distribution.

299

300 *Anthropogenic impact in streams*

301 We have used geographical coordinates of sampling sites from each study to quantify the
302 anthropogenic impact, and calculated the average land use over multiple sites. As geographical
303 coordinates of each sampling site is not always provided in published papers or gray literature,
304 we have also calculated the anthropogenic impact over the region of each study to account for
305 the influence of land-use on the structure of fish trophic networks. In both cases, we have created
306 overlapping concentric buffers around sites or sampling regions with a 500 m radius, and
307 calculated the percentage area of each land-use class (Figure 1) using ArcMap 10.6.1 (ESRI,
308 2018). The form and extent of buffers to characterize local scale impacts is largely heterogeneous
309 over studies, ranging from circular to riparian buffers of 50 - 500 m (Brejão et al. 2021; Pessoa et
310 al. 2024). We opt for 500m circular buffers as it captures at the same time local and regional
311 scale changes, and is large enough to deal with major land-use changes over distinct Brazilian
312 biomes.

313 We used land-use data from the Brazilian Annual Land-use and Land Cover Mapping
314 Project (MapBiomas, Collection 4.1, MapBiomas, 2020). This project produces 30-m pixel
315 resolution digital annual maps of land-use in Brazil based on random forest and machine learning
316 automatic classification processes applied to Landsat Data Collection satellite images (from 1985
317 until 2018). We retrieved MapBiomas land use layer information for the respective sampling year
318 reported in each individual study. The corresponding year was not possible only for a sample
319 obtained in 1982 and another in 2019, for which MapBiomas information was not available;
320 then, we used the closest available information in the time series (1985 and 2018, respectively).
321 The 18 land-use and land-cover classes occurring in the evaluated sites were consolidated into

two broader categories of natural and non-natural land-cover. Natural land-cover encompasses forest formation, savanna formation, mangrove, wetland, grassland, salt flat, rocky outcrop, and other non-forest natural formations (such as beach and dune, river, lake, and ocean). The overall anthropogenic impact group includes forest plantation, pasture, annual and perennial crop, semi-perennial crop (sugarcane), mosaic of cropland and pasture, urban infrastructure, mining, and other non-vegetated areas. Using these categories, we were able to create a gradient of natural land-cover loss across sites, ranging from completely natural to most-modified land cover. After the broad land-cover classification, we represented cropland by the sum of the classes related to agricultural use (annual and perennial crop, and semi-perennial crop – sugarcane –), while pasture metric included the pasture class as they are the most frequent land use types in Brazil. This was useful to evaluating the individual effects of these two land-use type on trophic networks.

Linear models NODF, Q, and H₂'

We constructed models in which the response variables were the Standardized Effect Size (SES) of each network metric, and the predictors were the proportional area of anthropogenic land-use, cropland, and pasture. As only NODF_{SES}, Q_{SES}, and H₂'_{SES} metrics were standardized effect sizes and the other metrics could not be compared via null models, we also previously rescaled (zero mean and unity standard deviation) the response variables Link density, Mean Number of links per species and Number of fish species (Log10-transformed) between all observed matrix values to get comparable scale estimates and model coefficients among metrics. Then, we used simple linear regressions to assess whether the impact in a 500-meter buffer influences the NODF_{SES}, Q_{SES}, H₂'_{SES}, Link density, Mean Number of links per species, as well as species richness (Figure 1). We also used multiple linear regressions with the same response

variables to estimate cropland and pasture individual effects on each network metric; this strategy was useful to decompose the broad land-use index in two most common land use type in Brazil. It is important to note that Variance Inflation Factor (VIF) using cropland and pasture was low, enabling their use in the same model. We checked for normality of the residuals of all models using the Shapiro test, and the assumption of normality was met in most model residuals. We also checked outliers in model residuals based on high Cook's distance values and removed the few largest ones to correct model assumptions. This procedure greatly improved normality assumptions after a few outlier remotion.

Based on the geographic coordinates of sampling sites informed in the published papers, we finally tested for spatial autocorrelation in all model residuals using Moran's I index. We often found no evidence of positive spatial autocorrelation in most of them and reported them here (see Results). In the cases we detected spatial autocorrelation even after outlier remotion, we used coordinates to create Moran Eigenvector Maps (MEMs) using 'dbmem' function from 'adespatial' package (Dray et al., 2006; Dray et al., 2012) and select (using forward.sel function) the most important spatial filters (Borcard et al. 2011) to control for spatial autocorrelation in our models. Corrected coefficients, p values, Moran's I and the selected MEMs from spatial models are provided in outputs when necessary.

Analyzes were performed in R v. 3.5.3 (R Core Team, 2016), using 'networklevel' (Dormann et al., 2009), 'nested' and 'metaComputeModules' functions from 'bipartite' package (Marquitti et al., 2014). All code and procedures are available online in the GitHub repository.

Results

Overall, we recorded 24,214 trophic interactions involving 608 fish species and 185 food items (mainly invertebrates, plant material, detritus, and algae). Locally, we registered between five to 99 fish species (mean \pm SD, 20.93 ± 20.04) and five to 58 consumed items (15.55 ± 10.62). Regarding land use, we found a more significant proportion of pasture ($19.81\% \pm 28.72\%$), followed by cropland ($14.73\% \pm 27.81\%$) in the 500 m buffer of sampling sites. Most species had an overall invertivore diet (49% aquatic or terrestrial invertebrates), while 18% were detritivores, 10% were omnivorous, 9% were herbivorous, and about 7% consumed mainly fish and 4% consumed algae (Table S3). Networks in general were more nested (0.33 ± 0.13) than modular (0.24 ± 0.11), with high trophic specialization (0.59 ± 0.16 ; Table S4). Simple correlations among response metrics showed that networks with high nestedness presented low modularity, low specialization, and high modularity (Table S5).

Contrary to our expectation, we did not find land use effects in the $NODF_{SES}$, $H_2'_{SES}$, species richness, and Link density (Table 1; Figure 2a, c, d, and f, respectively). However, we observed a negative land use effect on Q_{SES} and a positive effect on the mean number of links per species (Table 1; Figure 2b and d). Lastly, when discriminating land use in two major categories of pasture and cropland, we observed that % pasture negatively influenced Q_{SES} and Link density (Table 2). Besides, cropland had a negative effect on the number of fish species (Table 2). We did not observe any effect of those categories on network metrics or spatial autocorrelation on the multiple regression models (Table 2).

Network Structure

We built the bipartite networks in which the nodes represent the fish species (consumers) and food items (resources), while the links between them represent the items consumed by each species. We used each interaction matrices to calculate independent trophic network descriptors.

There are many network indices, and they differ in sensitivity to detect the property in question, network size robustness and sampling intensity. To understand how land-use intensity modifies food webs, we chose metrics that represent the overall network structure, such as network nestedness, modularity, trophic specialization, and food-web complexity metrics (Number of species, Link density and Number of links). The number of species (nodes), defined by the total number of consumers and resources (May 1973; Tilman 1996). The link density is defined as the number of trophic links (L) divided by the total number of nodes (consumers and resources, S) in a food web (L/S). The average number of links per species informs about how connected species are within the food web (Dunne, Williams, & Martinez, 2002; Bersier, Dixon, & Sugihara, 1994). The number of links is related to the number of trophic interactions in a food web. Number of links has implications for the complexity of the food web, and the number of pathways along which energy can flow (Dunne, Williams, & Martinez, 2002). We quantified nestedness with the nestedness metric based on overlap and decreasing fill (NODF), which is based on the concepts of overlap and decreasing fill of the adjacency matrix (Almeida-Neto, Guimaraes, Guimaraes, Loyola, & Ulrich, 2008). Nestedness describes webs with overlapping interactions, where in a perfectly nested network all interactions must be subsets of generalist interactions (Bascompte, Jordano, & Melia, 2003).—

We calculate specialization of trophic networks by quantifying the Modularity and Trophic specialization (H_2') indices. We quantified the modularity with the metric Q that measures the difference between the observed fraction of links connecting species in the same module and the fraction expected by chance using an algorithm modified for two-mode networks (Dormann, & Strauss, 2014). A modular network consists of interconnected modules. Each module is a group of species, which are more closely connected to each other than to species in

other modules. (e.g., Olesen, Bascompte, Dupont, & Jordano, 2007) and here it is an indicator of the degree of specificity of trophic interactions, representing sets of species specialized in a resource type or resource subset. Network specialization was quantified by the H_2' index, which is based on the deviation of the number of interactions performed by a species and the expected total number of interactions per species. H_2' is a two-dimensional index derived from the Shannon index used to compare different networks, and ranges from 0 (no specialization, highly generalist) to 1 (complete specialization) (Blüthgen, Menzel, & Blüthgen, 2006). The metric is calculated by a comparison between observed and expected interaction frequencies, based on the species marginal totals (Blüthgen et al., 2006). In the case of a food web, a species may be feeding only on a particular food item, but if this item presents higher frequency of interactions in the system, it may limit the specialization degree and therefore the species would receive a low H_2' value. In contrast, a species that feeds on only two rarer food items would have a very high H_2' value. The higher the level of selectivity of the species, the greater the H_2' .

Null model of trophic network structure

When calculating network descriptors, it is important to control for a possible sampling bias related to network dimensions (i.e. number of species and number of trophic links), which could prevent comparing descriptors among networks. Therefore, we compared all observed index values in individual networks to those calculated under null models (Dáttilo & Vaseonecelos, 2018; Kortsch et al., 2018; Quimbayo et al., 2018). We randomized the observed trophic networks over 1,000 matrices for each network descriptor, using a null model that fixes both marginal totals and connectivity (swap web null model), i.e., maintaining constant the number of interactions (and therefore connectivity), as implemented in the “bipartite” package in

436 R (Dormann, Fründ, Blüthgen, & Gruber, 2009). Then, we used the standardized effect size of
437 each index (z transformations), calculated as $(\text{observed} - \mu) / \sigma$, where observed is the value of
438 the focal index (e.g. Q, NODF, Link density and Number of links), μ is the mean value of focal
439 index over all null matrices and σ is its standard deviation, and used it as the response variables.
440 Empirical values of trophic network descriptors were considered to deviate strongly from the
441 randomized food webs if these were outside the 0.05 to 0.95 quantile range of the null
442 distribution. For each local network, the probabilities of the empirical values under the null
443 model are presented in the Supplementary Material (Table S2). Note that we did not use any
444 standardization in H_2' because a standardization is already performed when this network
445 descriptor is calculated (Blüthgen, Menzel, & Blüthgen, 2006).

use data from the Brazilian Annual Land-use and Land Cover Mapping Project (MapBiomas, Collection 4.1, MapBiomas, 2020). This project produces 30-m pixel resolution digital annual maps of land-use in Brazil based on random forest and machine learning automatic classification processes applied to Landsat Data Collection satellite images (from 1985 until 2018). We retrieved MapBiomas land use information for the respective sampling year reported in each study. The year correspondence was not possible only for a sample obtained in 1982 and another in 2019, for which MapBiomas information was not available then, so we used the closest available information in the time series (1985 and 2018, respectively). The 18 land-use and land-cover classes occurring in the evaluated sites were consolidated into two broader categories of natural and non-natural land-cover. Natural land-cover encompasses forest formation, savanna formation, mangrove, wetland, grassland, salt flat, rocky outcrop, other non-forest natural formation, beach and dune, river, lake and ocean. The overall anthropogenic impact includes forest plantation, pasture, annual and perennial crop, semi-perennial crop (sugarcane), mosaic of cropland and pasture, urban infrastructure, mining and other non-vegetated areas. Using these categories, we were able to create a gradient of natural land-cover loss across sites, ranging from completely natural (100%) to no remaining natural cover. After the classification of the areas, we represented cropland by the sum of the classes related to agricultural use (annual and perennial crop, and semi-perennial crop—sugarcane—), while pasture metric included the pasture class (Table S3).

Linear models

We constructed models in which the response variables were the standardized z value of each index and the predictors were the proportional area of anthropogenic land-use, cropland and

pasture. We used simple linear regressions to assess whether the impact in a 500-meter buffer influences the structure (values using Z-scores to NODF, Q, and H_2^2 ; Link species, Number of links and Number of species) of the trophic networks (Figure 1). Based on the geographic coordinates of sampling sites, we tested for spatial autocorrelation in the residuals of our models using global Moran's I and found no evidence of positive spatial autocorrelation in most of them, except for the link density and species number (Table S4). For this, we used spatial models to control these variations and to correct the degrees of freedom of our models, using 'dbmem' function from 'adespatial' package (Boreard & Legendre, 2011).

We checked for normality of the residuals of the models using the Shapiro test. The assumption of normality was met in all cases, except for the density of link, for which we calculated the Cook's distance and removed outliers with cook's distance greater than 1 to correct the model (Supporting Information Figure S1). Analyses were performed in R v. 3.5.3 (R Core Team, 2016), using 'networklevel' function (Dormann, Fründ, Blüthgen, & Gruber, 2009), 'nested' function and 'metaComputeModules' function, all from 'bipartite' package (Marquitti et al., 2014).

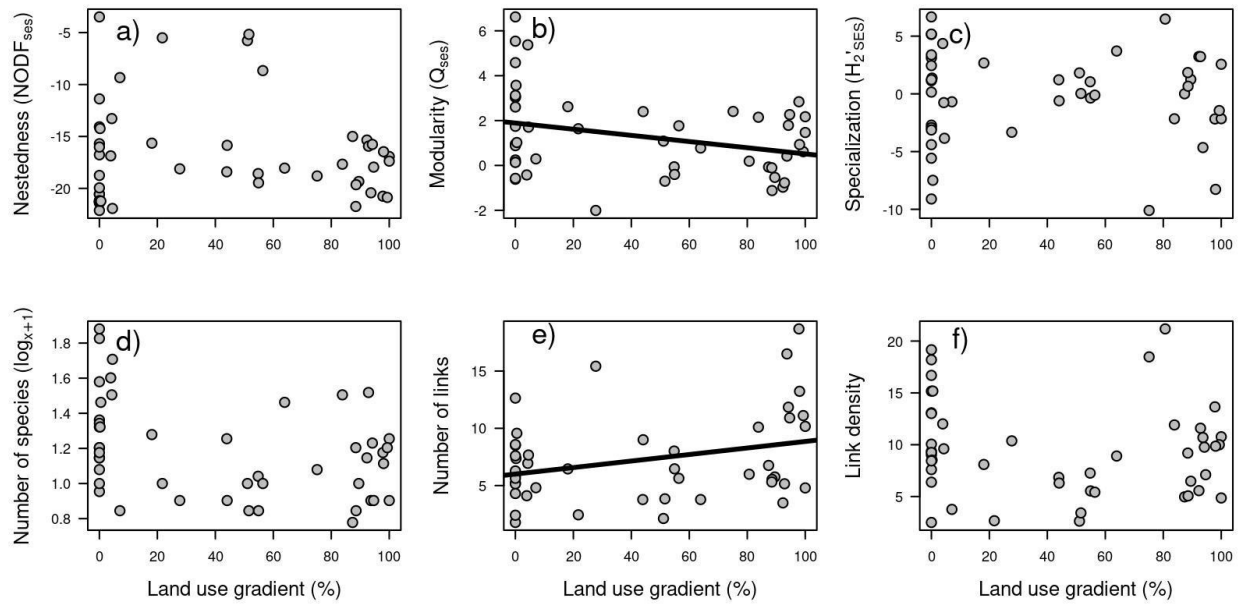


Figure 2. Simple relationships between land-use gradient on watersheds and the trophic network descriptors and food-web complexity metrics. a) Nestedness (NODF_{Ses}), b) Trophic specialization (H₂'_{Ses}), c) Modularity (Q_{Ses}); d) Density of link, e) Link per species and f) Numbers of species (log₁₀[x + 1]). Each point represents a sampling site with independent trophic fish networks). Linear regression coefficients are shown in table 1.

Table 1. Linear regression coefficients between the land-use across sites and the trophic network descriptors Nestedness ($NODE_{SES}$), Modularity (Q_{SES}), Specialization (H'_2_{SES}), Link density, Mean Number of links per species and Number of species in fish communities. Trophic Specialization, Link density, Mean Number of links per species no need for transformation and the Number of species was $\log_{10}(x+1)$ transformed. We also report Moran' I value to evaluate spatial autocorrelation in all models; when it was present, we rerun the same models including selected Moran Eigenvector Maps (MEMs) based on forward selection; when including land-use metrics and selected MEMs, spatial autocorrelation disappeared.

| Network descriptor | Estimate | SE | t-value | R ² adj | p-value | Moran's I without Spatial Filters | Moran's I with Spatial Filters |
|--|----------|-------|---------|--------------------|--------------|-----------------------------------|--------------------------------|
| $NODE_{SES}$ | 0.006 | 0.005 | 1.19 | 0.009 | 0.23 | -0.10 | = |
| Q_{SES} | -0.01 | 0.007 | -2.03 | 0.06 | 0.05* | -0.02 | = |
| H'_2_{SES} | -0.003 | 0.015 | -0.21 | 0.00 | 0.83 | 0.006 | = |
| Link density | -0.01 | 0.016 | -0.82 | 0.00 | 0.41 | -0.03 | = |
| Mean Number of links per species | 0.03 | 0.01 | 2.15 | 0.07 | 0.04* | -0.04 | = |
| Number of species ($\log_{10}[x+1]$) | 0.000 | 0.001 | 0.368 | 0.43 | 0.71 | = | -0.014 (MEMs 5, 1, 7, 6, 4) |

SE: Standard error. * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$

Table 2. Regression coefficients of two land-use variables (cropland and pasture) explaining variation in Nestedness ($NODF_{SES}$), Modularity (Q_{SES}), Specialization ($H_2'_{SES}$), Mean Number of links per species, Link density and Number of fish species. We also report Moran' I value to evaluate spatial autocorrelation in all models; when it was present, we rerun the same models including selected Moran Eigenvector Maps (MEMs) based on forward selection, but this procedure was not necessary in any of these models.

| Network descriptor | Predictors | Coefficients | SE | t-value | p-value | Moran's I without Spatial Filters | Moran's I with Spatial Filters |
|--|------------|--------------|-------|---------|----------------|-----------------------------------|--------------------------------|
| $NODF_{SES}$ | | | | | | 0.04 | = |
| Q_{SES} | Cropland | -0.02 | 0.018 | -1.18 | 0.25 | 0.01 | = |
| | Pasture | 0.017 | 0.018 | 0.98 | 0.33 | | |
| $H_2'_{SES}$ | Cropland | -0.006 | 0.008 | -0.75 | 0.46 | 0.04 | = |
| | Pasture | -0.022 | 0.008 | -2.84 | 0.001** | | |
| Link density | Cropland | -0.035 | 0.021 | -1.67 | 0.10 | 0.01 | = |
| | Pasture | 0.009 | 0.018 | 0.51 | 0.61 | | |
| Mean Number of links per species | Cropland | -0.01 | 0.02 | -0.47 | 0.64 | -0.03 | = |
| | Pasture | -0.05 | 0.02 | -2.23 | 0.03* | | |
| Number of species ($\log_{10}[x+1]$) | Cropland | 0.023 | 0.02 | 1.16 | 0.25 | 0.06 | = |
| | Pasture | 0.002 | 0.018 | 0.11 | 0.91 | | |
| | Cropland | -0.12 | 0.05 | -2.19 | 0.03* | | |
| | Pasture | -0.075 | 0.06 | -1.34 | 0.19 | | |

SE= Standard error. * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$

Results

Overall, we recorded 24,214 trophic interactions involving 608 species of fish and 185 food-items (mainly invertebrates, plant material, detritus and algae). Locally, we registered between 5 to 99 species of fish (mean \pm SD, 20.93 ± 20.04) and 5 to 58 consumed items (15.55 ± 10.62). In relation to land-use, we found a greater proportion of pasture ($19.81\% \pm 28.72\%$) and followed by cropland ($14.73\% \pm 27.81\%$). Most species had an overall invertivore diet (49% aquatic or terrestrial invertebrates), while 18% were detritivores, 10% were omnivorous, 9% were herbivorous, and about 7% consumed mainly fish and 4% consumed algae (Table S5). Networks in general were more nested (0.33 ± 0.13) than modular (0.26 ± 0.11), with high trophic specialization (0.58 ± 0.15) (Table S6). Sites with greater number of species presented greater number of links, lower nestedness and higher modularity (Table S7).

In terms of food-web complexity, the link density of local networks was negatively associated with the land-use gradient ($p=0.02$; Figure 2), whereas the number of links was positively associated, but not significant ($p>0.05$; Figure 2). We did not find land-use effects in the degree of specialization, number of species and nestedness of network ($p=0.67$; $p=0.31$; $p=0.23$, respectively), however, sites located in impacted locations showed low modularity values ($p=0.04$). When evaluating which of the land uses influence the structure of the trophic network, cropland was positively associated with the food-web complexity metrics (number of species). We found no individual influence of cropland and pasture on nestedness nor on specialization degree of trophic networks (Table 2). The pasture was negatively related to modularity, on the other hand, cropland was negatively related to the number of species (Table 2).

Discussion

Our regional study reveals that food networks of stream fish assemblages in Brazil are modulated by land use, supporting results observed in marine ecosystems and other regions (Kortsch et al., 2019, Peterson, Keppeler, Saenz, Bower, & Winemiller, 2017). Additionally, we observed that trophic networks located in areas with intense land use exhibited high mean number of links per species, resulting in a network less modular. This result supported our initial hypothesis and may be due to changes in surrounding terrestrial habitats that reduce the heterogeneity of microhabitats, increasing siltation, and modifying physico-chemical water conditions (Nessimian et al., 2008; Casatti et al., 2006; Almada et al., 2019).

By gathering data from stream fish assemblages, we studied trophic network descriptors and assessed the extent to which the structure of networks was determined by land-use gradient across Brazil. Our study over a large spatial scale generalize previous ones at local scale (Kortsch et al., 2019, Manoel & Uieda, 2017; Peterson, Keppeler, Saenz, Bower, & Winemiller, 2017), and shows evidence

556 of land-use effects on the structure of trophic networks of freshwater fish. Sites located in areas with
557 intense land-use change had less species and less links involved, as well as less modular trophic
558 networks. Decomposing land-use into the two major land-uses in Brazil shows that both the percentage
559 of cropland and pasture dictated the structure of trophic networks, but their effects are mainly on the
560 number of species and modularity, whereas we did not observe effects on nestedness, nor the
561 specialization index.

562 Overall, Disturbance in lotic ecosystems related to land-use change in surrounding terrestrial
563 habitat often reduce the heterogeneity of microhabitats, increase siltation, and modify physico-chemical
564 water conditions (Nessimian et al., 2008; Casatti et al., 2006; Almada et al., 2019). These overall
565 changes in habitat structure can contribute to simplifying fish assemblages by excluding habitat
566 specialists, resulting in an increase in and increasing the abundance of generalist species (Winemiller,
567 1990; Thompson & Townsend, 2005; Dala-Corte, Becker, & Melo, 2017; Arantes et al., 2018) or
568 forcing species to amplify their trophic niche and increase the consume of previously unavailable
569 resources. This last mechanism is in line with our results as we found that the mean number of links per
570 species link density and modularity were positively and negatively, respectively, negatively related to
571 the land-use gradient, supporting that the structure of trophic networks is simplified and more
572 connected under an intense disturbance regime as reported also by other aquatic groups (Pellissier et
573 al., 2017; Lara et al., 2020; Mokross, Ryder, Côrtes, Wolfe & Stouffer, 2014; Sebastián-González et al.,
574 2015). The lack of effect of land use on ~~On the other hand, two important metrics,~~ nestedness and
575 specialization, and strong effect on modularity and mean number of links per species suggest that
576 trophic stream networks of fish assemblages are modulated by specialist species, which are firstly
577 affected due to environmental disturbances ~~the degree of trophic specialization were not affected by the~~
578 ~~land-use gradient, although the first showed a positive, but not significant (Table 1, Figure 2) effect,~~
579 ~~and an the second a negative effect, and not significant (Table 2).~~

580 ~~Taken together, the lack of effect of land-use on nestedness and specialization, and the greater~~
581 ~~effect on modularity and link density suggest that the structure of trophic networks could be much more~~
582 ~~influenced by the loss of specialist species. In general, specialist species are lost as increases the~~
583 ~~disturbances in altered environments.~~ Previous assessments have addressed the effects of
584 environmental gradients on network ecology (Pellissier et al., 2017; Tylianakis & Morris, 2017),
585 concluding that these are primarily related to changes in species composition and relative abundances.
586 A recent study on spatial patterns in the food web associated with environmental gradients (Kortsch et
587 al., 2019) showed that the spatial variation in the structure of the fish food web is related to turnover in
588 species composition. As a result, the structure of the trophic network became more connected and less
589 modular. However, the turnover in species composition alone should not be the ~~leading main~~ cause of
590 the lower modularity of the networks. The decrease in modularity can be linked to the reduction in the
591 diversity of trophic groups, generating changes in the composition of the module. This is expected
592 when each trophic group feeds on a wide range of resources (Felipe-Lucia, 2020). Therefore, the
593 decrease in modularity indicates that species trophic interactions are ~~being~~ driven by a small number of
594 less specialized trophic groups. Our ~~results also indicated models indicate~~ that the modularity, ~~link~~
595 ~~density and~~ ~~and the~~ number of species are ~~reduced due to determined by~~ cropland and pasture (that is,
596 of the most common classes of land-use change). According to previous studies, the decrease in the
597 number of ~~fish~~ species with high levels of local farming practices suggests that these activities around
598 the streams simplify aquatic trophic networks (Bonato ~~et al., Delariva, & Silva~~, 2012; Zeni & Casatti,
599 2014; Santos ~~et al., Ferreira, & Esteves~~, 2015).

600 The maintenance of the riparian ~~natural~~ vegetation cover influences the supply of allochthonous
601 material (fruits, leaves and insects), ~~and increases and increas~~ the physical heterogeneity of the channel,
602 providing different feeding habitats for the species ~~corroborating findings from Nuven et al. (2022).~~ –In
603 fact, in highly impacted environments, the supply of autochthonous and allochthonous resources

decreases dramatically due to the absence of riparian vegetation and, consequently, to the availability of terrestrial insects and plant material for fish (Zeni & Casatti, 2014). Previous studies have shown that fish in agricultural landscapes can increase the consumption of low-protein and indigestible foods, such as detritus, sediments and organic waste (Dala-Corte et al., 2016). This is associated with the ability of ~~opportunists~~ opportunists species to deal with changes in the availability of food resources, particularly low-quality food items (~~Ferreira et al., 2012; Dala-Corte, Beeker & Melo, 2017; Ferreira et al., 2017~~ 2012).

Conclusions

Our study indicates that habitat degradation by land-use change affects the structure of trophic interactions, resulting in large-scale variation in the food web structure throughout an anthropogenic impact gradient. There is a trend towards simplification of aquatic environments influenced by cropland and pasture in ~~Neotropical~~ neotropical aquatic environments, often resulting in less complex and less modular networks. Moreover, cropland and pasture showed more pronounced changes in food-web complexity metrics than ~~in~~ non structural attributes of networks. In sum, our findings highlight the importance of riparian vegetation modulating the trophic structure of fish communities. Since the trophic structure of fish communities responds to the degree of land-use change, restoring the integrity of landscapes, even partially, could improve the functioning of aquatic systems and their biodiversity. Further developments to quantify the land-use at a finer scale, the degree of native vegetation integrity, the time since the land-cover change, the spatial pattern of fragments in the landscape, in addition to local environmental characteristics such as the input of organic matter, and limnological and structural measures at the study sites will help to capture more subtle differences and better understand the influence of riparian forest removal on trophic networks. Our work could be replicated and further

628 | expanded to include data from other highly ~~diverse~~biodiverse tropical regions facing similar ~~pressures~~
629 | ~~from~~ land-use and land-cover change pressures.

630 |

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648 | declare.

649 | **Author contributions**

650 | M.S.D., D.D.M.A.S.N., and J.F.G.Jr developed the idea of the manuscript; D.M.A.S.N. -

651 compiled the database and managed the data; A.A.R. obtained the land use data and made the land use
652 map; D.M.A.S.N. and M.S.D. -analysed the data with support from J.P.Q~~feedback from M.S.D.~~;
653 D.M.A.S.N. and M.S.D. -wrote the manuscript with substantial contributions and feedbacks from
654 J.P.Q.~~contribution from M.S.D. and feedback from~~ J.F.G.Jr. and A.A.R..

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668 **Data availability**

669 A summary of the data used in this paper is available as Supporting Information.

671 **Declarations**

672 **ConflictConflict of interest**

673 The authors declare that they have no known competing financial interests or personal
674 relationships that could have appeared to influence the work reported in this paper.

675

676 **Authorship statement**

677 All persons who meet authorship criteria are listed as authors, and all authors certify that they
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 679 participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each
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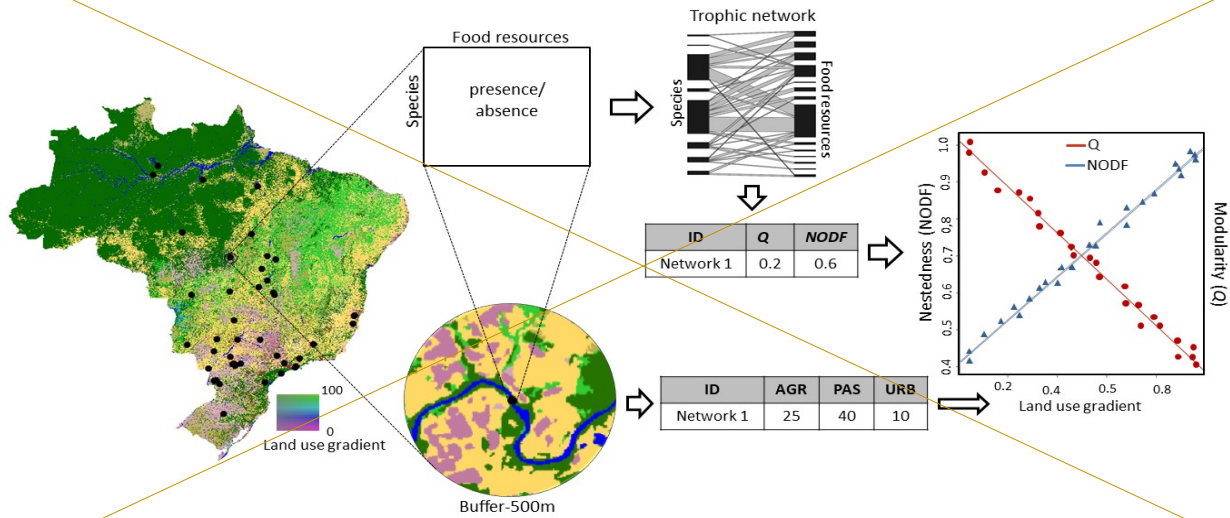
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Fig

Figure 1. Description of the procedure of sampling the trophic network. We quantified land-use information around a 500-m radius buffer at each sampling point, obtaining data from the year the study was conducted. Diet data were used to generate food webs within each sub-basin. We calculated the indexes of modularity, nestedness, trophic specialization and food-web complexity metrics (Number of species, Link density and Number of links) for each trophic network.

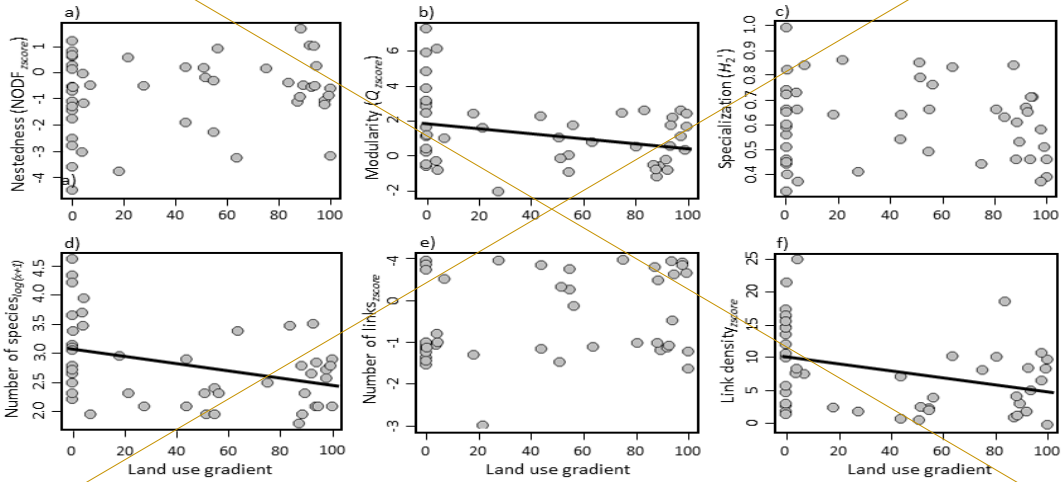


Figure 2. Scatterplots of the relationships between land-use gradient on watersheds and trophic network descriptors and food-web complexity metrics. a) Nestedness ($NODF_{zscore}$), b) Trophic specialization (H_2'), c) Modularity (Q_{zscore}); d) Density of link (zscore), e) Link per species (zscore) and f) Numbers of species ($\log(x+1)$). Each point represents a sampling site ($n = 49$ independent fish networks). Linear regression coefficients are shown in table 1.

Table 1. Linear regression coefficients between the natural land-use across sites and trophic network descriptors (Nestedness ($wNODF_{zscore}$), Modularity (Q_{zscore}), Specialization (H_2'), Link density, Number of links (links per species) and Number of species) of communities of fish. We use Z-

scored values for all metrics, except for number of species, in which log was used ($x + 1$) and Trophic specialization.

| Network descriptor | Estimate | SE | t-value | r ² adj | p-value |
|--------------------|----------|-------|---------|--------------------|---------|
| NODE | 0.006 | 0.005 | 1.19 | 0.009 | 0.23 |
| H_2' | -0.000 | 0.000 | -0.42 | -0.01 | 0.67 |
| Q | -0.01 | 0.006 | -2.03 | 0.06 | 0.04* |
| Link density | -0.08 | 0.03 | -2.36 | 0.09 | 0.01* |
| Number of links | 0.008 | 0.003 | 0.26 | 0.25 | 0.14 |
| Number of species | 0.000 | 0.00 | 1.01 | 0.00 | 0.31 |

SE= Standard error. Asterisk (*) denotes statistical significance, *p<.05. **p<.01. ***p<.001

Table 2. Regression coefficients of two land-use variables (cropland and pasture) in explaining the observed variation in nestedness (NODF), modularity (Q), Specialization (H_2'), Number of links, Link density and Number of species. We use Z-scored values for all metrics, except for number of species, in which log was used ($x + 1$) and Trophic specialization.

| Network descriptor | Predictor variables | Averaged coefficients | SE | t-value | p-value | Moran's I |
|--------------------|---------------------|-----------------------|-------|---------|---------|-----------|
| NODF | | | | | | |
| | Cropland | 0.008 | 0.007 | 1.04 | 0.30 | -0.02 |
| | Pasture | 0.001 | 0.007 | 0.17 | 0.86 | -0.02 |
| Q | | | | | | |
| | Cropland | -0.009 | 0.010 | -0.88 | 0.38 | -0.04 |
| | Pasture | -0.019 | 0.010 | -1.93 | 0.05* | -0.03 |
| H_2' | | | | | | |
| | Cropland | -0.000 | 0.000 | -0.54 | 0.58 | -0.01 |
| | Pasture | 0.000 | 0.000 | 0.44 | 0.65 | -0.02 |
| Link density | | | | | | |
| | Cropland | -0.06 | 0.03 | -1.65 | 0.10 | -0.09* |
| | Pasture | -0.05 | 0.03 | -1.72 | 0.09 | -0.11* |
| Number of links | | | | | | |
| | Cropland | 0.006 | 0.005 | 1.20 | 0.23 | -0.02 |
| | Pasture | 0.001 | 0.005 | 0.32 | 0.74 | -0.04 |
| Number of species | | | | | | |
| | Cropland | -0.006 | 0.003 | -2.01 | 0.04* | -0.10* |
| | Pasture | -0.006 | 0.005 | -1.84 | 0.07 | -0.12* |

SE: standard error; t-value: test statistic; asterisk (*) denotes statistical significance, * $p < .05$. ** $p < .01$. *** $p < .001$.