Land use effects on the structure of trophic networks from Neotropical fish

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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 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, number of links per species (links 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 number of links, whereas other metrics such as nestedness, trophic specialization, number os 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.

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, 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 actions on the dynamic and structure of networks. For instance, habitat degradation promotes homogenization and a reduction in network complexity, resulting in more nested network (i.e., species interactions are hierarchically organized, with a few species interact with many others) than modular (i.e., species interactions are compartmentalized with some species interacting only within specific subsets) (Bascompte, Jordano, & Melia, 2003, Pires & Guimarães, 2013, Olesen, Bascompte, Dupont, & Jordano, 2007; Dormann & Strauss, 2014). In trophic interactions, other network descriptors such as trophic specialization (metric that indicates the degree of species consumption on exclusive food items), number of links per species (links density), 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. 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 to ecossystem functioning.

Trophic interactions are an essential component for understanding the dynamics of populations, and consequently the emerging patterns of coexistence and diversity in communities (Dáttilo & Vasconcelos, 2019; Pellissier et al., 2017). 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 present generalist species with greater connectivity among nodes and a high level of nestedness (Manoel & Uieda, 2017) 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). 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 reduces nutrient supply and the input of allochthonous material, increase autochthonous production and completely change the quality and quantity of available feeding resources (Bambi et al., 2016; Zeni & Casatti, 2014). Consequently, 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. Thus, the structure of the trophic network (Pimm, Lawton, & Cohen, 1991) should vary according to the degree of land-use change (Winemiller, 1990). In short, the integrity of riparian forest 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; Dolobela et al., 2022). To understand these impacts, it is essential to investigate the trophic relationships between communities (Lobón-Cerviá, Mazzoni, & Rezende, 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. 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, high land use values determine less specialized assemblages, more simplified (less number of links) and more nested trophic networks. Our results will provide highlight the relevance of preserving natural vegetation along watercourses and its key contribution to the functioning of aquatic ecosystems.

Materials and methods

Data sampling

We conducted a systematic literature review of articles published from 1982 to 2021 from electronic databases and search engines, including 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: (fish*) AND (stream*) AND (feed*). The literature survey returned many studies, but we only considered articles with more than five species that represent the local community because we were interested in describing the local community network structure. Additionally, 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 (Santos et al., 2021; Souza et al., 2020; Peressin et al., 2018; Bonato et al., 2012), to make sure they were fully characterizing feeding habitats. We also considered thesis, masters and gray literature reporting fish trophic network with the same condition described above (N=18). In total, we compiled 49 trophic networks across Brazil (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 diverge in their way to quantify consumed food items and sampling efforts, we preferred using information on the presence/absence of interactions (i.e., binary matrices) for focusing mostly on the incidence, rather then strength, of the interaction and avoid biases regarding items quantification and sampling efforts.

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 average of links. 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 based on the concepts of overlap and decreasing fill of the adjacency matrix (Almeida-Neto, Guimaraes, Guimaraes, Loyola, & Ulrich, 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, in which 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).

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, 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). 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 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, Williams, & Martinez, 2002). Lastly, we estimate the average number of links per species, which informs how connected species are within the food web (Dunne, Williams, & Martinez, 2002; Bersier, Dixon, & Sugihara, 1994).

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 all observed index values in individual networks to those calculated under null models with the same randomized matrix (Dáttilo & Vasconcelos, 2018; Kortsch et al., 2018; Quimbayo et al., 2018). 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, Fründ, Blüthgen, & Gruber, 2009). Then, we quantified the Standardized Effect Size (SES) of each observed network metric (i.e., NODF, Q, and H_2') as the difference between observed and null estimate values of network metrics using the following equation: (observed - μ) / σ, 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. Scripts for calculating all those metrics can be found on github repository .

Anthropogenic impact in watersheds

We calculated anthropogenic impact surrounding each sampling site to account for the influence of land-use on the structure of fish trophic networks. We created overlapping concentric buffers around each sampling site, with 500 meters radius, and calculated the percentage area of each land-use class (Figure 1) using ArcMap 10.6.1 (ESRI, 2018). We tested several buffer sizes from 500 to 10,000 m in 500-m increments (500 – 10,000 m) and the 500 m buffer was best suited to our models. In addition, at sampling sites where fish sampling was carried out over more than one stream reach, we calculated the average land use over multiple sites. We used land-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 layer information for the respective sampling year reported in each individual study. The corresponding year was not possible only for a sample obtained in 1982 and another in 2019, for which MapBiomas information was not available; then, 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 (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 (100%) to no-remaining natural cover. After the broad 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 S2) as they are the most frequent laduse types in Brazil.

Linear modelsNODF, Q, and H_2'

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 $NODF_{SES}$, Q_{SES}, and $H_2'_{SES}$ metrics were standardized effect sizes, we also previously rescaled (zero mean and unity standard deviation) the response variables Link density, Number of links and Number of fish species (log10-transformed) between all observed matrix values in order to get comparable scale estimates and model coefficients. Then, we used simple linear regressions to assess whether the impact in a 500-meter buffer influences the $NODF_{SES}$, Q_{SES}, Link density, Number of links, as well as species richness and $H2'_{SES}$ (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 one, 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 outlier in model residuals based on high Cook's distance values and removed the a few largest one in order 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 global 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. XXX) and select (using forward.sel function) the most important spatial filters (Borcard et al. 2011) to control for spatial autocorrelation in our models. Coefficients, p values, Moran’s I and selected MEMs from spatial models are provided in Result outputs.

Analyzes were performed in R v. 3.5.3 (R Core Team, 2016), using ‘networklevel’ (Dormann, Fründ, Blüthgen, & Gruber, 2009), ‘nested’ and ‘metaComputeModules’ functions from ‘bipartite’ package (Marquitti et al., 2014). (codes and procedures are available online; GitHub)

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 fish species (mean ± 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% ± 28.72%), followed by cropland (14.73% ± 27.81%) in the 500m 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).

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 effect of land use on Q_{SES} and a positive effect on Number of links (Table 1; Figure 2b, and d). Lastly, when discriminating land use in two major categories of pasture and cropland, we observed that pasture had a negative effect on Q_{SES} and on Link density (Table 2). On the other hand, cropland had a negative effect on Number of fish species (Table 2). We did not observe any effect of those categories on network metrics nor spatial autocorrelation on the multiple regression models (Table 2).

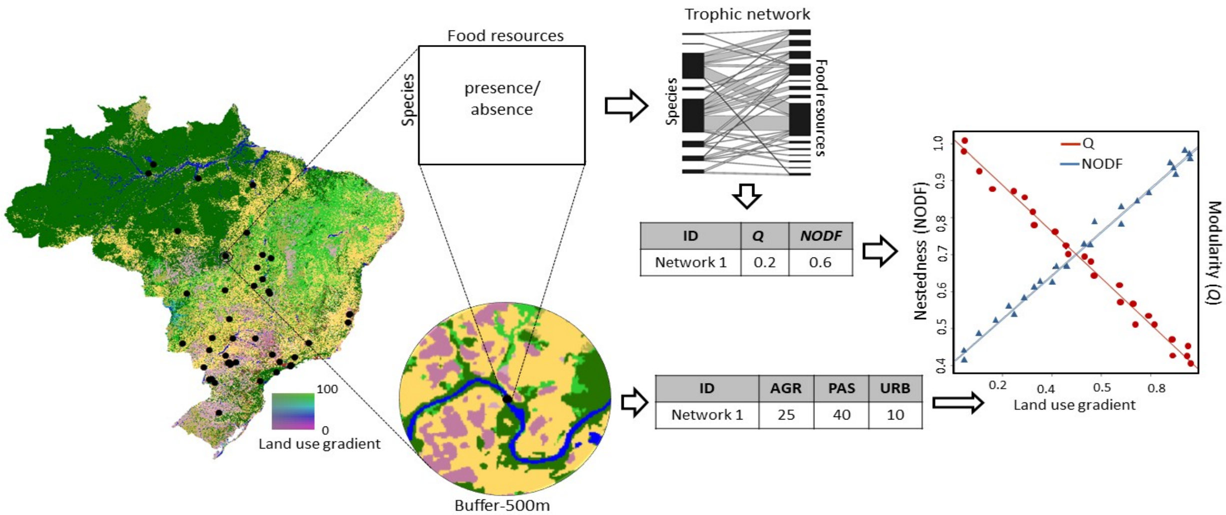

Figure 1. Description of the procedure of sampling the trophic network. We quantified land-use information around a 500-m radius buffer at each sampling point, obtaining data from the year the study was conducted. Diet data were used to generate food webs within each sub-basin. We calculated the indexes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

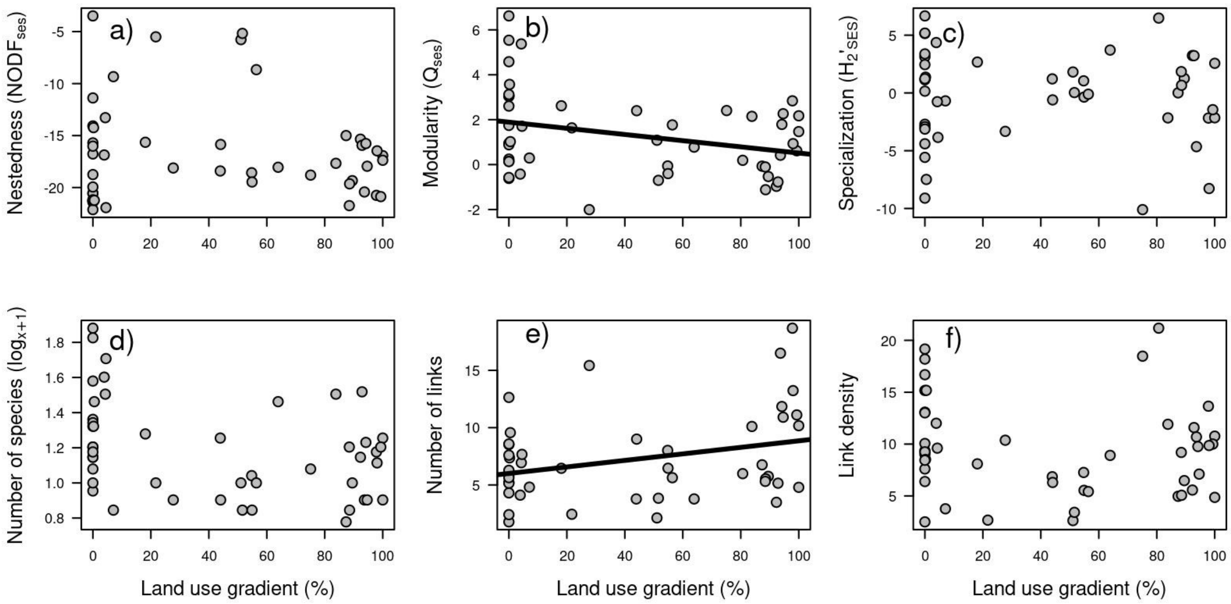

Figure 2. Simple relationships between land-use gradient on watersheds and the trophic network descriptors and food-web complexity metrics. a) Nestedness ($NODF_{SES}$), b) Trophic specialization ($H_2'{}_{SES}$), c) Modularity (Q_{SES}); d) Density of link, e) Link per species and f) Numbers of species ($\log_{10}[x + 1]$). 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 ($NODF_{SES}$), Modularity (Q_{SES}), Specialization ($H_2'_{SES}$), Link density, Number of links and Number of species in fish communities. Trophic Specialization, Link density, Number of links no need for transformation and the Number of species was $log_{10}(x+1)$ transformed. We also report Moran' I values 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; only outputs for land-use is shown.

Network descriptor	Estimate	SE	t-value	R^2 adj	p-value	Moran's I without Spatial Filters	Moran's I with Spatial Filters
$NODF_{SES}$	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	-
Number of links	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 ($_{SES}$), Modularity (Q_{SES}), Specialization ($H_2'_{SES}$), Number of links, Link density and Number of fish species. We also report Moran' I values 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; only outputs for land-use is shown.

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	-
	Cropland	-0.02	0.018	-1.18	0.25		
	Pasture	0.017	0.018	0.98	0.33		
Q_{SES}						0.01	-
	Cropland	-0.006	0.008	-0.75	0.46		
	Pasture	-0.022	0.008	-2.84	**0.001****		
$H_2'_{SES}$						0.04	-
	Cropland	-0.035	0.021	-1.67	0.10		
	Pasture	0.009	0.018	0.51	0.61		
Link density						0.01	-
	Cropland	-0.01	0.02	-0.47	0.64		
	Pasture	-0.05	0.02	-2.23	**0.03***		
Number of links						-0.03	-
	Cropland	0.023	0.02	1.16	0.25		
	Pasture	0.002	0.018	0.11	0.91		
Number of species ($\log_{10}$[x+1])						0.06	-
	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

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 number of links, resulting in a network less modular. This result supported our initial hypothesis and may be due to changes in surrounding terrestrial habitats reducing the heterogeneity of microhabitats, increasing siltation, and modifying physico-chemical water conditions (Nessimian et al., 2008; Casatti et al., 2006; Almada et al., 2019).

Overall, changes in habitat structure can contribute to simplifying fish assemblages by excluding habitat specialists, resulting in an increase in generalist species (Winemiller, 1990; Thompson & Townsend, 2005; Dala-Corte, Becker, & Melo, 2017; Arantes et al., 2018) or forcing species to amplify their trophic niche and increase the consume of previously unavailable resources. This last mechanism is in line with our results as we found that the number of links and modularity were positively and negatively, respectively, related to the land-use gradient, supporting that the structure of trophic networks is simplified and more connected under an intense disturbance regime as reported also by other aquatic groups (Pellissier et al., 2017; Lara et al., 2020; Mokross, Ryder, Côrtes, Wolfe & Stouffer, 2014; Sebastián-González et al., 2015). The lack of effect of land use on nestedness and specialization, and strong effect on modularity and number of links suggest that trophic stream networks of fish assemblages are modulated by specialist species, which are firstly affected due to environmental disturbances.

Previous assessments have addressed the effects of environmental gradients on network ecology (Pellissier et al., 2017; Tylianakis & Morris, 2017), concluding that these are primarily related to changes in species composition and relative abundances. A recent study on spatial patterns in the food web associated with environmental gradients (Kortsch et al., 2019) showed that the spatial variation in the structure of the fish food web is related to turnover in species composition. As a result, the structure of the trophic network became more connected and less modular. However, the turnover in species composition alone should not be the main cause of the lower modularity of the networks. The decrease in modularity can be linked to the reduction in the diversity of trophic groups, generating changes in the composition of the module. This is expected when each trophic group feeds on a wide range of resources (Felipe-Lucia, 2020). Therefore, the decrease in modularity indicates that species trophic interactions are being driven by a small number of less specialized trophic groups. Our results also indicated that the modularity, link density and the number of species are reduced due cropland and pasture (that is, of the most common classes of land-use change). According to previous studies, the decrease in the number of fish species with high levels of local farming practices suggests that these activities around the streams simplify aquatic trophic networks (Bonato, Delariva, & Silva, 2012; Zeni & Casatti, 2014; Santos, Ferreira, & Esteves, 2015).

The maintenance of the riparian and natural vegetation cover influences the supply of allochthonous material (fruits, leaves and insects) and increases the physical heterogeneity of the channel, providing different feeding habitats for the species. In 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 opportunist species to deal with changes in the availability of food resources, particularly low-quality food items (Dala-Corte, Becker & Melo, 2017; Ferreira et al., 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 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 on 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 expanded to include data from other highly diverse tropical regions facing similar pressures from land-use and land-cover change.

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Author contributions

D.M.A.S.N compiled the database and managed the data; A.A.R. obtained the land use data and made the land use map; D.M.A.S.N and M.S.D. analysed the data with feedback from J.P.Q.; D.M.A.S. wrote the manuscript with substantial contribution from M.S.D. and feedback from

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Data availability

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

Conflict of interest

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

Authorship statement

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this material or similar material has not been and will not be submitted to or published in any other publication before its appearance in the Hydrobiologia Journal.

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