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

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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 webs, 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 (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 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 (REF). 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) when 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) 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? 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 more complex (i.e., larger number of links, number of species and link density) and specialized (i.e., larger modularity and greater trophic specialization) networks. The second hypothesis is that basins with greater anthropogenic influence may decrease the diversity of food resources, resulting in the predominance of generalist species (i.e., more nested and less modular and less specialized trophic networks).

**Materials and methods**

*Dietary data base*

We searched for dietary studies with fish assemblages available in the literature, considering the Scopus, Web of Science and Google Scholar databases. Several combinations of keywords were used for the searches, namely: (fish\*) AND (stream) AND (feed\* OR diet) AND (other terms of interest). We only considered studies (articles) with more than five species in studies that represent the local community, because we were interested in describing the local community network structure. 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 (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 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. The studies diverge in their way to quantify consumed food items and these matrices served as the basis for building the trophic networks detailed below. Thus, we used information on the presence/absence of interactions (i.e., binary matrices) for calculating trophic network descriptors, except for the trophic specialization metric (H2’, considers interaction frequencies).

*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, such as? network size, robustness and sampling intensity (REF). 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) is 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 interaction specialization (H2’) 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, 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). 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 H2' 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. H2’ 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 H2’ value. In contrast, a species that feeds on only two rarer food items would have a very high H2’ value. The higher the level of selectivity of the species, the greater the H2’.

*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 & Vasconcelos, 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 R (Dormann, Fründ, Blüthgen, & Gruber, 2009). Then, we used the standardized effect size of each index (z transformations), calculated as (observed - μ) / σ, where ‘observed’ is the value of the focal network metric (e.g., Q, NODF, Link density and Number of links), μ is the mean value of focal metric over all null matrices, and σ is its standard deviation, and used it as the response variables. 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. For each local network, the probabilities of the empirical values under the null model are presented in the Supplementary Material (Table S2). Note that we did not use any standardization in H2' because a standardization is already performed when this network descriptor is calculated (Blüthgen, Menzel, & Blüthgen, 2006).

*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 10000 m in 500-m increments (500 – 10000 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. 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 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 network metric 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 (of Z-scores values for NODF, Q, and H2’, Link species, Number of links, and Number of species) of 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 (Borcard & 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 the we calculated the Cook's distance and removed outliers with cook's distance greater than 1 to correct the model (Supporting Information Figure S1). Analyzes 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).

**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 ± 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%). 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) then 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 2f), whereas the number of links was positively associated, but not significant (p> 0.05; Figure 2e). 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 areas showed low modularity values (p=0.04, Figure 2b). When evaluating which of the land uses influence the structure of the trophic network, cropland was positively associated with 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**

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 generalizes previous ones at local scale (Kortsch et al., 2019, Manoel & Uieda, 2017; Peterson, Keppeler, Saenz, Bower, & Winemiller, 2017), and shows evidence of land-use effects on the structure of trophic networks of freshwater fish. Trophic networks located in areas with intense land-use change had less species and less links involved, as well as less modular structure. Decomposing land-use into the two majors components, we observed that both the percentage of cropland and pasture dictated the structure of trophic networks, but their effects are mainly on the number of species and modularity, whereas we did not observe effects on nestedness, nor on the specialization index.

Disturbance in lotic ecosystems related to land-use change in surrounding terrestrial habitat often reduce the heterogeneity of microhabitats, increase siltation, and modify physico-chemical water conditions (Nessimian et al., 2008; Casatti et al., 2006; Almada et al., 2019). These overall changes in habitat structure contribute to simplifying fish assemblages by excluding habitat specialists, and increasing the abundance of generalist species (Winemiller 1990; Thompson & Townsend, 2005; Dala-Corte, Becker, & Melo, 2017; Arantes et al., 2018). This mechanism is in line with our results as we found that the link density and modularity were negatively related to the land-use gradient, supporting that the structure of trophic networks is simplified 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). On the other hand, two important metrics, nestedness and the degree of trophic specialization were not affected by the land-use gradient, although the first showed a positive, but not significant (Table 1, Figure 2a) effect, and an the second a negative effect, and not significant (Table 2).

Taken together, the lack of effect of land-use on nestedness and specialization, and the greater effect on modularity and link density suggest that the structure of trophic networks could be much more influenced by the loss of specialist species. In general, specialist species are lost as increases the disturbances in altered environments. 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 models indicate that the modularity and the number of species are determined by cropland and pasture (that is, of the most common classes of land-use change). According to previous studies, the decrease in the number of 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 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. 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 biodiverse 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 analysed the data with feedback from M.S.D.; D.M.A.S. wrote the manuscript with substantial contribution from M.S.D. and feedback from J.F.G.Jr. and A.A.R.

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**Data availability**

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

**Declarations**

**Confict 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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**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 (NODFzscore), b) Trophic specialization (H2'), c) Modularity (Qzscore); 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 (wNODFzscore), Modularity (Qzscore), Specialization (H2 '), Link density, Number of links (links por 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 | r2 adj | p-value |
| NODF | 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 (H2'), 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 |
| H2' |  |  |  |  |  |  |
|  | 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**.**