Environmental Drivers and Network Structure of Hylid Anurans in Floating Meadows From Amazonian Oxbow Lakes

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Abstract

Despite the increasing amount of knowledge available regarding the ecological interactions between species, the dynamics of anurans in aquatic environments are little explored and understood. In this way, our work aims to assess which factors influence the composition and the ecological interactions of hylid anurans in oxbow lakes in the middle Purus River, Amazonas. We sampled three lakes with high, medium and low levels of connectivity twice, once during the flood and then in drought hydrological regimes. Variations in the hyloid anuran assemblages and ecological interactions were tested as function of environmental niche, food resources, level of connectivity and hydrological regime. The availability of environmental resources and the availability
of food resources were the best factors that explain the distribution of hylid anurans, which were also highly
dependent on the variations between the hydrological regimes. The interactions between anurans,
macroinvertebrates and macrophytes showed a modular and specialized structure, which varied according to the
connectivity and hydrological regime of the lakes. Connectance showed an increasing trend from high to low
connectivity lakes, suggesting that anurans had low trophic and environmental specialization in lakes with low
connectivity. Hylids found in the lake of medium connectivity had higher values of trophic specialization and
modularity. Our results illustrate the role of river-lake connectivity and annual hydrological cycle to maintain
the aquatic biota and their interactions, and highlight the importance of floating meadows for the maintenance of
biodiversity in floodplains.

Keywords: Floodplain, macroinvertebrates, ecological interactions, nestedness, modularity, river-lake
connectivity

Introduction

In aquatic environments, changes in community structure are attributed to the sum of multiple processes,
including limiting and homogenizing effects of the species dispersion (Junk et al. 1989). Hydrological variation
caused by the flood pulse in floodplains is a primary factor responsible for the ecological changes in aquatic
biota (Junk et al. 2014), mainly mediated by the connectivity of river-lake systems (Thomaz et al. 2007). Floods
create temporary connections between rivers and lakes which promote biological homogenization, through
dispersion of biota and dilution of chemical components (Thomaz et al. 2007; Petsch 2016). When lakes are
totally or partially isolated, local factors tend to influence variations in communities, including a reduction in
depth, lake area, water transparency and dissolved oxygen content, as well as increase in nutrient concentration,
electrical conductivity, pH and predation pressure (Thomaz et al. 2007; Scarabotti et al. 2011). Community
structure therefore is influenced by how individuals from different species are filtered by the environmental
constraints imposed by isolation, which may affect their ecological interactions and the dispersal capacity of
each species (Hubbel 2001; Begon et al. 2006).

In tropical lakes (e.g., oxbow lakes) floating meadows are dominant floristic elements, which may be
composed mainly by amphibian and free-floating plant species commonly known as macrophytes (Moura Júnior
et al. 2015). The aquatic macrophytes tend to grow rapidly and undergo changes in their distribution due to the
spatial and seasonal dynamics of the flood pulses (Junk et al. 1989), which ultimately influence the structure of
aquatic communities (Junk et al. 1989). Such changes prompt the flow of nutrients and organisms, increasing
spatial heterogeneity and availability of niches and resources between lakes (Thomaz et al. 2007). Because of these traits, floating meadows are ideal environments for reproduction, refuge and feeding of fauna species (Luz-Agostinho et al. 2009), which are important in the maintenance of the diversity of both macroinvertebrates (e.g., insects; Petry et al. 2003; Peiró and Alves 2006; Pelicice and Agostinho 2006) and vertebrates such as amphibians (Upton et al. 2014; Ramalho et al. 2016, 2018; Ganança et al. 2021). Floating meadows hosted unique communities of anurans (Ramalho et al. 2018), that use the floating environment for breeding, sheltering, foraging and dispersal (Hodl 1977; Hoogmoed 1993; Schiesari et al. 2003; Upton et al. 2014; Böning et al. 2017). The complex environment created by the unstable movement of floating meadows also act as a filter for anuran species, since the occurrence of anuran species is dependent on macrophyte composition and their vertical and horizontal structure (Upton et al. 2011, 2014; Ganança et al. 2021). In this sense, anuran communities in floating meadows are composed essentially by hylid (i.e., treefrogs) anurans (Upton et al. 2014; Böning et al. 2017; Ramalho et al. 2018). However, the role of macrophyte species composition (i.e., as potential environmental niche) and their associated macroinvertebrates (i.e., as potential food resource), as well as other local predictors (e.g., river-lake connectivity and hydrological regime), in the variation of anuran communities in floating meadows are still misunderstood, causing a gap in the knowledge as to the complex biodiversity in floodplains.

The use of tools from the Theory of Complex Networks has been useful to understand new aspects of the ecology and evolution of species assemblages. This is because these tools allow us to study how the species and their interactions are structured and how such structures vary over ecological gradients (Tylianakis and Morris 2017). Space may promote variation in network structure by affecting the likelihood of potential interactions (Guimarães Jr. 2020). Changes in the relative abundance or quality of the interaction partners can be explained by different factors, such as latitudinal patterns (Ceron et al. 2019). Tropical anuran-prey networks have high connectance, low modularity, and complementary specialization that are explained by the generalist diet of anurans (Ceron et al. 2019). However, despite the knowledge of the global pattern involving anuran networks, the knowledge regarding the properties of ecological interactions at local freshwater communities is still scarce. Indeed, we still lack theory and natural history to understand how the anuran assemblages interact with macrophytes assemblages in floating meadows (i.e., as an environmental resource for anurans) and their associated macroinvertebrates (i.e., as a part of the diet for anurans). Therefore, investigating how interactions are affected by changes in river-lake connectivity and hydrological regimes will increase of understanding of how freshwater communities are assembled and maintained.
The aim of this study was to examine how the communities of hylid anurans can vary with macrophyte assemblages in floating meadows and their associated macroinvertebrates, and how these interactions are affected by changes in river-lake connectivity and hydrological cycle. Specifically, we tested the following hypotheses: (i) the environmental niche and available food resources are the primary predictors explaining the variation in composition of hylid anurans, although it should be dependent on both river-lake connectivity and hydrological cycle. We do expect this relationship because anurans associated with floating meadows are formed specially by species adapted to the flood pulse (Ramalho et al. 2018), which use the floating vegetation as calling and breeding sites (Hödl 1977; Upton et al. 2014; Ramalho et al. 2016), dispersion vectors (Schiesari et al. 2003; Böning et al. 2017) and potential source of food because they house a high diversity of macroinvertebrates (St. Pierre and Kovalenko, 2014). Thus, we sought to confirm that floating meadows contain enough environmental heterogeneity that induce to a non-random anuran assemblage structure (Ganança et al. 2021). If the environmental niche and food resource, as well as their variations throughout the hydrological cycle and lake-river connectivity, are important components to structure anuran communities, (ii) we expect that interactions between hylid anurans, macrophytes and macroinvertebrates vary in function of river-lake connectivity and hydrological regime. To this end, we identified the macrophyte species where each specimen was registered and analyzed its stomach content. According to the optimal foraging theory (OFT), when food is scarce, individuals expand their diet width to include less-favored items, which may expend their trophic niches and therefore affect their ecological networks (Emlen 1966; Robinson and Wilson, 1998). Thus, we predict that the oxbow lake more isolated and with low connectivity level has a high number of interactions (i.e., high connectance), in response to the lower supply of food, resulting in non-restrictive diets. In contrast, because more connected lakes have higher migration taxes (e.g., macrophyte species; Mormul et al. 2013), they can result in a great prey availability, leading to a maximum of prey selectivity and more specialized networks. We expect also that interactions between anurans and invertebrates would display modularity as it has been shown that such networks are not nested, but they show low levels of specialization and modularity and high connectance (Ceron et al. 2019). Across the different hydrological regimes and river-lake connectivity, we expect that such properties are going to vary, from more specialized interactions in the most connected lakes to generalized interactions in the less connected lakes.

Material e methods

Study area
The study was conducted in lakes located in the floodplain of the middle Purus River, in the municipality of Boca do Acre, State of Amazonas, Brazil (Figure 1). The Purus River basin is located in the northeast region of the Amazon, where the Purus River is one of the greatest tributaries of the Solimões-Amazonas system. This river is one of the longest rivers in South America, covering approximately 3,380 km, entering Brazil through the State of Acre, with its mouth in the river Solimões, state of Amazonas. It is classified as a white-water river (Sioli 1991) with meandering pattern and water rich in Andean sediments (Ríos-Villamizar et al. 2011). The climate of the region is tropical rainy monsoon type (Köppen 1948; Projeto RadamBrasil 1976). The rainfall has an annual cycle marked by a rainy season, between November and March, and a dry season, between May and September, while April and October are considered transition months (Angelis et al. 2008).

Figure 1. Oxbow lakes sampled in the middle Purus River, Amazon basin, Brazil. Yellow circles indicate the location of the transects sampled in the Flor do Ouro Lake (FO1, FO2, FO3), Verde Lake (VE1, VE2, VE3) and Bom Lugar Lake (BL1, BL2, BL3).
Lake and connectivity categorization

We surveyed the anuran assemblages, macrophytes and macroinvertebrates in three oxbow lakes in the middle Purus River (Figure 1). The lakes were selected based on the connectivity criteria, in which we used the parameters of lake depth (m), connectivity depth (m), connectivity profile (terrain elevation in meters), connectivity length (m) and permanence of connection of the lake-river over the hydrological cycle. The depth of each lake and its connectivity was measured every 50 m using an echo-sounder model Eagle Cuda 168. The connectivity profile and connectivity length were obtained using a portable GPS tool. For the connectivity profile, the elevation was measured every 50 m to find a proxy of the terrain’ variation close to the confluence with the Purus River. These measures were obtained during flood and drought hydrological season for the lakes of high and medium connectivity, and during the flood for the lakes of low connectivity. The oxbow lake categorized as high connectivity (Bom Lugar lake) presented an average depth of 19.1 ± 6.1 m, connectivity depth of 6.9 ± 3.8 m, connectivity profile with elevation of 337.4 ± 18.1 m asl and connectivity length of 2.172 m, remaining connected with the Purus River throughout the flood and drought hydrological cycle. The lake of medium connectivity (Flor do Ouro lake) presented an average depth of 17 ± 5.4 m, connectivity depth of 7.4 ± 3.6 m, connectivity profile with elevation of 319.4 ± 6.1 m asl and connectivity length of 456 m, remaining partially connected with the river during the drought. The lake of low connectivity (Verde lake) presented an average depth of 8.8 ± 3.6 m, connectivity depth of 3.8 ± 5.8 m, connectivity profile with elevation of 371.2 ± 20.6 m asl and connectivity length of 305 m, remaining disconnected from the river during the drought hydrological regime (Table 1). Thus, our observations in the field allowed us to infer that the connectivity profile (variation of terrain elevation) is directly related to the degree of connectivity. For example, although the high connectivity lake has longer connectivity and depth of connectivity similar to that of medium connectivity, the lower profile of the terrain along connectivity allows it to remain connected with the river during all hydrological regimes.

Table 1. Characterization of the oxbow lakes sampled in the middle Purus River, Amazon basin, Brazil, and its respective degree of connectivity.

| Parameters       | Oxbow lake            |
|------------------|-----------------------|
|                  | Bom Lugar | Flor do Ouro | Verde     |
| Latitude         | 8.38515  | 8.28393  | 8.44361  |
| Longitude        | 67.20373 | 67.23290 | 67.22490 |
### Parameters

| Parameters                      | Oxbow lake          |
|--------------------------------|---------------------|
|                                | Bom Lugar           | Flor do Ouro       | Verde            |
| Lake depth (m)                 | 19.1±6.1            | 17±5.4             | 8.8±3.6          |
| Connectivity depth (m)         | 6.9±3.8             | 7.4±3.6            | 3.8±5.8          |
| Connectivity profile (m asl)   | 337.40±18.08        | 319.40±6.08        | 371.2±20.64      |
| Connectivity length (m)        | 2.172               | 459                | 305              |
| Time of connectivity           | Flood and drought   | Flood and early drought | Flood          |
| Degree of connectivity         | High                | Medium             | Low              |

### Data collection

In each lake, we surveyed the anuran assemblages, floating meadows and macroinvertebrates along three transects, totalizing nine transects in the middle Purus River (Figure 1). The transects were standardized in 200 m length, with a minimum distance of 1000 m among them in each lake and chosen according to the availability of floating meadows. We surveyed each transect twice, once during the hydrological regime of drought (8-17 July 2017) and once during the flood season (17-25 January 2018).

### Environment and food resource availability

We evaluated the available environmental resources through the abundance of the macrophytes species in the floating meadows sampled in each transect. The abundance of the macrophyte was visually evaluated by the counting of the coverage percentage of each species within a 0.5 x 0.5 m quadrat. Within each 200 m transect, we conducted a boat sampling at a distance of approximately 10 m from the edge of the lake and delimited five equidistant points (every 50 m) to throw the quadrat, where we throw it five times per point in each survey, totalizing 25 quadrats in each transect. The abundance of macrophyte species obtained for each point were summed up to estimate the total covering in each transect. Macrophyte species were identified according to Guterres et al. (2008), Thiers (2018), SPLink (2018) and Flora do Brasil (2020). The availability of food resources was evaluated through the collection of macroinvertebrates in floating meadows at the same time and at the same points where macrophyte species were sampled along the 200 m transect. The samplings were carried out using a 4m$^2$ seine floating net, formed by two cables of 220cm length connected to a net of 200cm width and 200cm length, handled by two researchers. The floating net was pulled in the floating meadows, from the bottom to the surface, seeking the maximum capture of individuals for 10 minutes every 50 m. The
invertebrate specimens were euthanized with a lethal chamber, using 58% acetone and fixed in 70% alcohol. The highest possible taxonomic level was identified using the aquatic insect guide of Hamada et al. (2014).

### Anuran surveys and stomach contents analysis

The hylid anuran surveys were carried out at the same transects and at the same time of the surveys of macrophytes and macroinvertebrates. We performed the anuran sampling using the active and auditory search methods (Crump and Scott Jr. 1994), always carried out by two researchers on a boat, approximately 10 m from the edge of the lake. For each anuran individual visualized, the macrophyte species where it was found calling or foraging at the time of collection was registered and named as environmental resource used. The individuals sampled were anesthetized and euthanized with 5% xylocaine, fixed in 10% formalin and stored in 70% alcohol. The stomachs of the collected specimens were removed, the contents were scattered in a Petri dish, counted and analyzed using a stereomicroscope, and subsequently preserved in 1μl microtubes (Eppendorf) with 70% alcohol. Food items were identified and categorized to the lowest possible taxonomic level (Hamada, et al. 2014), named as a food resource consumed and used in the following interaction analysis.

### Data analysis

We focused our hypothesis in a limited number of species because most species were not prevalent throughout the samples. To test whether the variations in the hylid anuran assemblages are explained mainly by environmental niche and food availability, we built four models referring to each group of predictor variables that could influence the species composition variation in the floating meadows. Thus, models included the environmental niche, available food resources, level of connectivity and hydrological regime. Firstly, in the model of environmental niche we included only macrophyte species that (i) occurred in at least three samples or (ii) showed a coverage percentage ≥ equal to or greater than 5% in at least one sample. For the models of food availability resources, only taxa of macroinvertebrates that (i) occurred in at least three samples or (ii) had total abundance ≥ equal to or greater than 20 were considered. Anuran abundance was standardized through Hellinger's transformation (Legendre & Legendre, 2012). Percentage values of available environmental resources and abundance of available food resources were transformed by calculating the square root and logarithmic function, respectively. The levels of connectivity and hydrological regime were rank-categorized (connectivity: low = 1, medium = 2, high = 3; hydrological regime: drought = 1, flood = 2). In order to avoid overestimation of the models, the influence of environmental niche and available food resources on the anuran
communities were evaluated by the forward selection procedure, and only the significant variables were selected and included in the RDA (Blanchet et al., 2008). This procedure was performed with 999 iterations for each model and the selection was finalized when the variables had a $P$ value greater than $\alpha=0.05$ (Peres-Neto et al., 2006). We tested the models’ significance using a Redundancy Analysis (RDA) with 999 Monte Carlo iterations. Moreover, we performed a Partial Redundancy Analysis (pRDA) with variance partitioning to evaluate the pure and shared relative contribution of sets of variables to the variation in the hylid anuran assemblages (Dray et al. 2012). Every procedure was performed using the functions available in the packfor (Dray et al. 2013), vegan (Oksanen et al. 2017) and adespatial (Dray et al. 2020) packages in R software (R Core Team 2020).

In order to examine the interactions between macrophytes, anurans and macroinvertebrates, we used the data obtained from the macrophyte species in which the anuran was collected calling or foraging (the environmental resource used) and the quantitative data on stomach content (food resources consumed), using an approach based on the Theory of Complex Networks. For this, interaction matrices $A$ were constructed, where $a_{ij}$ was the number of interactions of an anuran, with macrophyte or macroinvertebrate and 0 where there were no interactions. We obtained 12 matrices corresponding to the interactions of hylid anurans observed in each lake for the attributed category (high, medium and low connectivity) over two different hydrological regimes (flood and drought). Each matrix was divided by the type of interactions, anurans with environmental resources used (macrophyte) or food resource consumed (stomach content; i.e., macroinvertebrates); this for all oxbow lakes and hydrological regimes. Finally, twelve matrices were obtained per lake, six with all interactions between the anurans and macrophytes (environmental resource) in both hydrological regimes (drought and flood), and six with macroinvertebrates (food resource) consumed in both hydrological regimes. For the description of the interactions, we used the following network descriptors: connectance, weighted nestedness (wNODF), modularity and complementary specialization ($H_2'$), similar to the approach used by Ceron et al. (2019).

Connectance describes the ratio between the total number of realized links and the maximum theoretical number of links. This gives a description of how many interactions are not realized based in the total possible (Jordano 1987). Its values range from 0 to 1, 0 indicates that all of potential interactions are not realized and 1 indicates that all the potential interaction in the network is realized. Weighted nestedness, based on the Nestedness Metric, Based on Overlap and Decreasing Fill (NODF), describes the extent to which interactions of specialist species correspond to a subset of generalist interactions (Bascompte et al. 2003).
calculated the weighted nestedness (wNODF), which is based on the overlap and decreasing fill in the weighted matrix (Almeida-Neto and Ulrich 2011). Nestedness values range from 0 (non-nested network) to 100 (perfect nesting). We also calculated modularity, which measures how groups of species are densely connected and present only sparser connections with other groups of interacting species. We analyzed modularity using the recently implemented LPAwb + algorithm (Liu and Murata 2010; Beckett 2016). Finally, we calculated complementary specialization (H$_2'$), which is a network-wide index of specialization for quantitative interaction matrices. It describes how species restrict their interactions from those randomly expected based on partner’s availability (Blüthgen et al., 2006). The assumption is that if species have preferences for specific interaction partners, these preferences would be captured as a deviation from random encounters given by partner availability (Blüthgen et al. 2006). Values of H$_2'$ range from 0 to 1 indicating the extremes of generalization and specialization, respectively. The significance of wNODF, modularity, and H$_2'$ were assessed by comparing them with those obtained for randomized networks generated by a null model based on Patefield´s algorithm (Patefield 1981). We generated 1,000 randomized matrices to estimate the significance of nestedness and complementary specialization and 100 matrices to estimate modularity. To quantify the departure of the observed network values from null expectation, we calculated null-model corrected values by subtracting observed metric value from mean value across all randomized networks (Δ – transformation). Then, the Δ – transformed value was divided by the standard deviation of values across all randomized networks (z – transformation; Dalsgaard et al. 2017; Zanata et al. 2017). All network metrics and null models were calculated with the ‘bipartite’ ver. 2.08 package (Dormann et al. 2008) in R software (R Core Team 2020).

**Results**

**Environmental and available food resources**

We identified 32 species of macrophytes in the floating meadows, 25 in lakes of high-level connectivity, 20 in medium and 16 in low connectivity. The most abundant macrophyte species were *Pistia stratiotes* (Araceae) (21%), *Eichhornia crassipes* (Pontederiaceae) (16%) and *Ludwigia helminthorrhiza* (Onagraceae) (11%). During the flood, the more abundant macrophyte species were *P. stratiotes* in lakes of high and medium connectivity (42% and 35%, respectively) and *E. crassipes* (34%) in low connectivity. During the hydrological regime of drought, the more abundant species were *P. stratiotes* (25%) in lakes of high connectivity, *E. crassipes* (44%) in medium, and *L. helminthorrhiza* (38%) in low connectivity lakes (Table S1).
We sampled 4041 individuals of macroinvertebrates. Individuals not identified or in the larval stage were not used in the statistical analyzes. The more abundant invertebrate taxons were Hemiptera (18%), Orthoptera (17%) and Diptera (Culicidae, 15%). The more abundant taxon during the flood hydrological regime in the lake of high connectivity was Hemiptera (24%), while Orthoptera was more abundant in lakes of medium (32%) and low (19%) connectivities. During the drought, the more abundant taxons were Hemiptera in lakes of high (25%) and low connectivities (27%) and Orthoptera in the lake of medium (35%) connectivity (Table S2).

Effects of environment and available food resources on species abundance

We observed and recorded 741 individuals of five most prevalent hylid anurans in the floating meadows: Boana punctata (129 individuals), Dendropsophus reticulatus (408), Sphaenorhynchus carneus (52), S. dorisae (34) and S. lacteus (118; Table S3). Based on pre-established criteria, we selected 20 macrophyte species (available environmental resource) and 18 macroinvertebrate taxa (available food resource) to compose the RDA models. The model with macrophytes was the most explanatory (72%) and includes the species Pistia stratiotes, Ceratopteris pteridoides, Lemna minuta and Utricularia gibba. Available food resources explained 57% of the anuran variation and included the taxa Gastropoda, Odonata, Araneae and Orthoptera. The hydrological regime and connectivity explained 37% and 16% of the variation, respectively. In general, the greatest explanation was shared between macrophyte models, food resources and hydrological regime (78%), where the three groups combined were explained better than individually. The pure explanations were 9% for macrophytes, 8% for food resources and 1% for hydrological regime (Figure 2).
Figure 2. Variation in anuran abundance explained by environmental resources (macrophyte species), lake connectivity, available food resources (macroinvertebrate taxons) and hydrological regime.

Food items consumed by anurans

Among the individuals registered and collected in the floating meadows, 334 had their had empty stomachs and 407 were used in our analysis, including 47 individuals of Boana punctata, 217 of Dendropsophus reticulatus, 41 of Sphaenorhynchus carneus, 81 of Sphaenorhynchus lacteus and 21 of Sphaenorhynchus dorisae. In relation to food items consumed, Formicidae was the most frequent prey group (29.5%), followed by Aranea (14.5%), and Culicidae (7.2%). During the rainy season, Formicidae was the most frequent prey in lakes of high (69.1%), medium (42.0%), and low (69.6%) connectivity. However, during the dry season, the most consumed prey changed among lakes with different connectivities: Araneae was the most frequent prey consumed in lakes of high (22.1%) and medium (28.0%) connectivity, while Isoptera was most frequent in lakes of low connectivity (25.0%) (Table S4).

Ecological interactions

Network metrics according to regime, connectivity and by the interaction type are shown in Table 2. Connectance showed an increasing trend from high to low connectivity lakes in both interaction types. The higher connectance values were recorded in macrophyte networks during the hydrological regime of drought in lakes with low connectivity (C = 0.8; Figure 3). Networks did not show a nested pattern (p > 0.05 for all networks). All networks (macrophytes and diet) showed higher trophic specialization and a modular structure, with the exception of the macrophyte network in a flooded lake with low connectivity, and in a lake with medium connectivity during the drought (Figure 3 and Figure 4). The most specialized interactions were recorded in diet networks in the hydrological regime of flood in lakes with medium connectivity (H2’ = 0.85; Figure 4). For macrophytes networks, the most specialized interactions were recorded in the hydrological regime of flood in lakes with medium connectivity (H2’ = 0.41). Specialization and modularity showed a decrease during the drought for both network types. Modularity was higher in diet networks during flood in lakes with medium connectivity (M = 0.42). For macrophytes networks, modularity was absent or low both in flood or drought (Figure 3 and Figure 4).
Table 2. Descriptors of networks divided by regime, connectivity and by the interaction between anurans, macrophytes and macroinvertebrates. Z-scores values are in parentheses. M = microhabitat use and D = diet. Values significantly (P <0.05) are in bold.

|            | Flood       | Medium | Low  |
|------------|-------------|--------|------|
| Connectance| 0.34 M 0.38 | 0.32 M 0.56 | 0.61 M 0.77 |
| Nestedness | 18.18 43.83 | 0 32 | 16.62 66.67 |
| Modularity | 0.39 (9.63) 0.27 (6.52) | 0.42 (7.13) 0.33 (9.2) | 0.4 (7.55) 0.01 (-1.12) |
| Specialization | 0.67 (9.47) 0.22 (5.68) | 0.85 (10.58) 0.41 (13.34) | 0.71 (11.36) 0.03 (-0.66) |

|            | Drought     | Medium | Low  |
|------------|-------------|--------|------|
| Connectance| 0.47 M 0.5  | 0.5 M 0.66 | 0.61 M 0.8 |
| Nestedness | 28.12 41.4 | 34.21 83.33 | 29.37 33.75 |
| Modularity | 0.25 (4.08) 0.07 (-0.02) | 0.22 (4.04) 0.01 (-0.91) | 0.22 (7.25) 0.28 (7.82) |
| Specialization | 0.46 (5.38) 0.11 (1.89) | 0.32 (3.03) 0.02 (-0.18) | 0.42 (8.87) 0.27 (9.9) |

Figure 3. Graphs showing modules (colors) in anuran-macrophyte interactions by lake connectivity (high, medium and low) during the hydrological periods of flood and drought. Circles represent macrophyte (orange) and anuran (green) species.
Discussion

Our results support our first hypothesis, by showing that the availability of environmental resources (i.e., species of macrophytes) and the availability of food resources (i.e., macroinvertebrates) are the best factors that explain the distribution of hylid anurans. In addition, a high percentage of explanation indicates that the variation in abundance of hylid anurans is highly dependent on the variation in the macrophytes and macroinvertebrates composition between the hydrological regimes. Moreover, our results support the second hypothesis as we found that the connectance, modularity and specialization of anuran, macrophytes and macroinvertebrates networks varies depending on the connectivity and the hydrological regime.

We found that the abundance of the hylid species is influenced by all the factors that we measured (i.e., availability of environment, connectivity, food resource and hydrological regime). However, the availability of the environmental and food resources was the best factor explaining the variation in the abundance of anuran species. Anurans that occur in floating meadows are highly adapted to the open and unstable environment (Ramalho et al., 2018), where species are segregated horizontally and vertically according to their reproductive and foraging requirements (Hödl 1977; Hoogmoed 2013; Upton et al. 2011; Upton et al. 2014). For example, studies in other regions of the Amazon have found that *Sphaenorhynchus carneus*, *S. dorisae* and *S. lacteus* may
occupy lower vegetation in the floating meadows (e.g., in *Salvinia* spp., *Eichhornia* spp. and *Pistia* spp.), while larger species such as *Boana punctata* and *Dendropsophus reticulatus* occupy higher strata in the floating vegetation (e.g., in *Paspalum repens*) (Hödl 1977; Upton et al. 2011; Upton et al. 2014). These relationships have shown that environmental characteristics of floating meadows (e.g., macrophyte height, macrophyte morphotype composition and water depth) creates a gradient of environmental heterogeneity that acts as a filter in anuran communities (Ganança et al. 2021). Our results indicate that the importance of macrophytes as environmental resources for anurans is complex and varies in space and time, as indicated by the fractions shared between environmental resources, lake-river connectivity and hydrological cycle.

The available food resources are good predictors of the variation in hylid abundance. The results reinforce that variation in macroinvertebrates along with the environmental gradient of floating meadows may exert a profound influence on the associated organisms (Poi de Neiff 2003; Peiró and Alves 2006; Upton et al. 2014; Hill et al. 2016). The main macroinvertebrates that explained the variation in hylids were Gastropoda, Odonata, Araneae and Orthoptera, which apparently also interact in a complex way and mediated by specific condition imposed by lake-river connectivity and hydrological cycle. Floating meadows, and macrophyte species as well (as discussed in detail below), are then important foraging sites for anurans, although the complexity of the interactions (e.g., if anurans are predator or prey) still needs to be more explored. Thus, variations in the environmental and food resources directly influence anuran assemblage in floating meadows, indicating a complex structuring by the niche and a non-random pattern in species distribution in space and time.

As expected, the aquatic interactions between anurans, macroinvertebrates and macrophytes showed a modular and specialized structure with no nestedness. Our results showed that the network descriptors among anurans, macroinvertebrates and macrophytes networks vary according to the connectivity and hydrological regime of the lake. Connectance showed an increasing trend from high to low connectivity lakes in both interaction types. This result suggests that anurans are tend to establish more interactions with macrophytes and macroinvertebrates when resources are expected to be more abundant (Thomaz et al. 2009). For specialization, higher values were found in medium connectivity and had a decrease during the drought, both to diet and macrophytes networks. During the drought, when resources are reduced, it is expected that anurans eat and use the resources that are available, reducing specialization and increasing connectance (Emlen 1966; Robinson and Wilson 1998). On the other hand, specialization may be especially favored when resource availability increases, according to predictions of optimal foraging theory (Robinson and Wilson 1998). Therefore, in the flood season,
when resources are supposedly more abundant in the floodplain, the species of hylids were more selective in
terms of food selection and habitat use, so that each species tended to consume specific foods and occupy
macrophytes with specific structures.

Macrophyte networks presented modular interactions both in flood and drought, which demonstrates
that anurans interact more often with some species of macrophyte. The formation of cohesive groups between
anurans and resources could indicate that anurans select the plant where they live and the resources they
consume. Therefore, it seems that anurans select fluctuant plants to use, which favors diet and breeding, but the
identity of these macrophytes did not strongly interfere with their choices. It is worth to note that the lack of
modularity or nestedness in some of the studied networks does not indicate that there could be other interactions
pattern within the networks (Guimarães Jr. 2020). The higher values of specialization in diet and macrophytes
networks and the high modularity in diet networks, all in medium connectivity, resemble how alpha diversity
changes in floodplain systems. Ward and Rockner (2001) proposed that the alpha diversity of several groups
reaches a peak in habitats with an intermediate degree of connectivity. This is because the excessive
connectivity may keep all communities in pioneer stages or may reduce species diversity if excessive nutrient
loading in the river leads to eutrophication of connected floodplain water bodies (Van den Brink et al. 1996;
Ward and Tockner, 2001). Thus, in intermediate levels of connectivity the local diversity of macrophytes and
preys probably influences the ecological interactions of anurans derived from them. In fact, it has been shown
that the main factors structuring ecological networks are the local abundances of interacting species (neutral
factors) (Guimarães Jr. 2020).

The primary prey of anurans is insects, as well as other arthropods, such as spiders and mites (Simon
and Toft 1991; Duellman and Trueb 1994). Each anuran species tended to prefer certain food items and most of
the food items consumed by the anurans were available in the floating meadows. The items consumed by the
anuran species in this study corroborates the diet described for the species (Duellman 1978, 2005; Lopez et al.
2009). However, by implementing a network approach we were able to assess the changes in diet of anurans by
changes in habitat connectivity. In this case, we found that in lakes with low connectivity, anurans had a less
diversified diet. This evidence suggests that dispersion and therefore habitat connectivity are factors that
structure the anuran and its partners in all lakes, as expected by the Neutral theory of diversity (Hubbel 2001), in
which the movement of species is one of the factors explaining species local abundance, for example.

Variations in the availability of environmental resources (macrophytes) and food resources
(macroinvertebrates) were influenced by the connectivity of the lakes and hydrological regimes, affecting the
abundance and structure of interactions of hylid anurans. The interactions found showed that the species use the
same resources, which are available in the floating meadows for their consumption, and although they are more
generalist, some species use resources more specifically than others. These results show that the hylids
associated with floating meadows in this study have their distribution affected by the interaction to both
macrophyte and macroinvertebrate species, as well as to lake connectivity level and hydrological regimes. These
alterations in the environmental niche affect the anurans associated with floating meadows and show the
importance of this environment for biodiversity.

Declarations

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Availability of data and materials – All data produced from this study are provided in this manuscript.

Author contributions – All authors contributed to the conceptualization and design of the project. LRAM and
WPR collected the data, performed the data analysis, and led the writing of the text. FVA, KC, and PL provided
additional expertise on interaction network, performed the data analysis, and wrote the text. LRV provided
additional expertise on hydrology and river-lake connectivity. LJSV assisted with data interpretation and
writing, and supervised this research. All authors critiqued the manuscript and gave final approval for
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Table S1. Relative abundance of macrophyte species found in three oxbow lakes of different connectivity during the flood and drought hydrological regime in the middle Purus River, Amazon basin, Brazil.

| Taxon               | High connectivity | Medium connectivity | Low connectivity | Relative abundance |
|---------------------|-------------------|---------------------|------------------|--------------------|
|                     | Flood | Drought | Flood | Drought | Flood | Drought | |
| **Amaranthaceae**   |       |         |       |         |       |         | |
| *Alternanthera philoxeroides* | 0.25  | 0.19    |       |         |       |         | 0.08  |
| **Araceae**         |       |         |       |         |       |         | |
| *Lemna minuta*      | 7.80  | 3.89    | 5.89  | 10.98   | 0.17  | 0.96    | 4.78  |
| *Pistia stratiotes* | 42.28 | 24.73   | 34.55 | 11.24   | 4.94  |         | 20.86 |
| *Wolffiela lingulata* | 0.15  | 0.17    | 0.19  |         | 2.03  |         | 0.42  |
| **Araliaceae**      |       |         |       |         |       |         |       |
| *Hydrocotyle ranunculoides* |       |         | 1.69  | 0.67    | 4.51  | 28.00   | 5.58  |
| **Asteraceae**      |       |         |       |         |       |         |       |
| *Eclipta prostrata* | 0.70  | 0.67    |       |         |       |         | 0.26  |
| *Enydra anagallis*  | 5.35  | 22.94   | 0.60  |         | 0.12  |         | 5.54  |
| *Gymnocoronis spilanthoides* | 0.48  |         |       |         |       |         | 0.08  |
| *Mikania scandens*  |       |         | 2.64  | 2.32    |       |         | 0.80  |
| **Commelinaceae**   |       |         |       |         |       |         |       |
| *Commelina erecta*  | 0.19  |         |       |         |       |         | 0.04  |
| **Cucurbitaceae**   |       |         |       |         |       |         |       |
| *Luffa operculata*  | 0.29  |         |       |         |       |         | 0.06  |
| **Cyperaceae**      |       |         |       |         |       |         |       |
| *Oxycaryum cubense* | 1.28  | 2.27    | 7.35  | 20.66   | 17.14 | 6.99    | 8.42  |
| **Euphorbiaceae**   |       |         |       |         |       |         |       |
| *Caperonia castaneifolia* | 0.40  |         |       |         |       |         | 0.07  |
| **Fabaceae**        |       |         |       |         |       |         |       |
| *Mimosa pigra*      | 0.19  |         |       |         |       |         | 0.02  |
| Taxon                        | High connectivity | Medium connectivity | Low connectivity | Relative abundance |
|-----------------------------|-------------------|---------------------|------------------|--------------------|
|                             | Flood  | Drought | Flood  | Drought | Flood  | Drought |                |
| Vigna lasiocarpa             | 0.73   | 4.10    | 0.95   |          |          |          | 1.10           |
| Hydrocharitaceae             |        |         |        |          |          |          |                |
| Limnobium laevigatum         | 2.69   | 7.84    | 5.51   | 2.81     | 4.00    |          | 4.08           |
| Lentibulariaceae             |        |         |        |          |          |          |                |
| Utricularia gibba            | 2.06   | 1.48    | 3.63   | 0.04     | 8.75    | 4.38     | 3.42           |
| Onagraceae                   |        |         |        |          |          |          |                |
| Ludwigia affinis             | 1.10   | 0.38    |        |          |          |          | 0.28           |
| Ludwigia helminthorrhiza     | 6.10   | 8.77    |        | 16.07    | 37.94   |          | 11.49          |
| Ludwigia leptocarpa          |        | 0.42    |        |          |          |          | 0.07           |
| Passifloraceae               |        |         |        |          |          |          |                |
| Passiflora sp                | 1.03   | 0.16    |        |          |          |          | 0.22           |
| Phyllanthaceae               |        |         |        |          |          |          |                |
| Phyllanthus fluitans         | 0.10   |        |        |          |          |          | 0.02           |
| Poaceae                      |        |         |        |          |          |          |                |
| Bracharia purpurascens       | 0.40   |        |        |          |          |          | 0.07           |
| Hymenachne amplexicaulis     |        | 0.36    |        |          |          |          | 0.07           |
| Panicum aquaticum            |        |         |        |          | 0.46    |          | 0.07           |
| Paspalum repens              | 5.45   | 3.89    | 0.21   | 2.32     | 7.88    |          | 3.43           |
| Pontederiaceae               |        |         |        |          |          |          |                |
| Eichhornia crassipes         | 13.65  | 0.72    | 10.25  | 43.73    | 34.18   | 5.22     | 16.25          |
| Pteridaceae                  |        |         |        |          |          |          |                |
| Ceratopteris pteridoides     | 1.13   | 6.03    | 0.48   | 4.88     |          |          | 2.07           |
| Ricciaceae                   |        |         |        |          |          |          |                |
| Ricciocarpus natans          |        | 2.77    |        | 0.03     |          |          | 0.54           |
| Salviniauriculata            |        |         |        |          |          |          |                |
| Salvinia minima              | 5.60   | 7.34    | 18.03  | 7.00     | 1.26    |          | 6.69           |
Table S2. Abundance of macroinvertebrates found in three oxbow lakes of different connectivity during the flood and drought hydrological regime in the middle Purus River, Amazon basin, Brazil.

| Taxon           | High connectivity | Medium connectivity | Low connectivity | Relative abundance |
|-----------------|-------------------|---------------------|-----------------|--------------------|
|                 | Flood  | Drought | Flood  | Drought | Flood  | Drought | Flood  | Drought |
| Acarina         | 1      | 10      | 3      | 5       | 1      |          | 0.49   |          |
| Araneae         | 44     | 109     | 32     | 95      | 25     | 95       | 9.90   |          |
| Blattodea       | 14     | 11      | 2      | 4       | 15     |          | 1.14   |          |
| Coccinellidae   | 4      | 2       | 2      | 2       |          |          | 0.25   |          |
| Coleoptera      | 47     | 22      | 58     | 25      | 119    | 16       | 7.10   |          |
| Curculionidae   | 11     | 32      | 7      | 7       | 64     | 21       | 3.51   |          |
| Diptera (Culicidae) | 90     | 67      | 10     | 66      | 149    | 211      | 14.67  |          |
| Diptera (Muscidae) | 85     | 39      | 6      | 16      | 61     | 69       | 6.83   |          |
| Gastropoda      | 11     | 4       | 17     | 18      | 9      |          | 1.46   |          |
| Gerridae        | 4      |          |        |          |        |          | 0.10   |          |
| Hemiptera       | 170    | 195     | 7      | 20      | 86     | 237      | 17.69  |          |
| Heteroptera     | 61     | 75      | 25     | 13      | 78     | 40       | 7.23   |          |
| Hymenoptera (Apoidea) | 1      | 1       | 1      | 2       |        |          | 0.12   |          |
| Hymenoptera (Formicidae) | 105    | 40      | 24     | 12      | 17     | 4        | 5.00   |          |
| Larva           | 9      |          |        | 36      | 7      |          | 1.29   |          |
| Lepidoptera     | 6      | 9       | 1      | 3       | 3      | 3        | 0.62   |          |
| Mantodea        | 4      |          |        |        |        |          | 0.10   |          |
| Odonata         | 1      | 2       | 1      | 7       | 10     |          | 0.52   |          |
| Orthoptera      | 42     | 141     | 102    | 178     | 163    | 60       | 16.98  |          |
| Scarabaeidae    | 9      | 19      | 61     | 14      | 62     |          | 4.08   |          |
| Trichoptera     | 8      |          |        |        |        |          | 0.20   |          |
| Vespidae        | 8      | 3       | 4      | 3       | 2      | 9        | 0.72   |          |
| **Total Geral** | 709    | 777     | 318    | 506     | 850    | 881      | 100.00 |          |
Table S3. Hylid species collected in three oxbow lakes of different connectivity during the flood and drought hydrological regime in the middle Purus River, Amazon basin, Brazil.

| Species                        | High connectivity | Medium connectivity | Low connectivity | Total abundance |
|--------------------------------|-------------------|---------------------|------------------|-----------------|
|                                | Flood  | Drought | Flood  | Drought | Flood  | Drought | abundance |
| Boana punctata                 | 6      | 39      | 8      | 26      | 16      | 34       | 129       |
| Dendropsophus reticulatus      | 54     | 106     | 78     | 55      | 33      | 82       | 408       |
| Sphaenophryncus carneus        | 31     | 0       | 0      | 0       | 21      | 0        | 52        |
| Sphaenophryncus dorisae        | 10     | 2       | 0      | 0       | 22      | 0        | 34        |
| Sphaenophryncus lacteus        | 20     | 0       | 48     | 33      | 16      | 1        | 118       |
| Total abundance                | 121    | 147     | 134    | 114     | 108     | 117      | 741       |
Table S4. Food items consumed by five hylid species in three oxbow lakes of different connectivity during the flood and drought hydrological regime in the middle Purus River, Amazon basin, Brazil.

| Taxon          | High connectivity | Medium connectivity | Low connectivity | Total frequency |
|----------------|-------------------|---------------------|------------------|-----------------|
|                | Flood             | Drought             | Flood           | Drought         | Flood | Drought |               |
| Acari          | 1                 | 0                   | 0               | 0               | 0     | 1       | 2              |
| Amblypgi       | 0                 | 0                   | 0               | 0               | 2     | 9       | 11             |
| Apoidae        | 0                 | 0                   | 3               | 4               | 0     | 1       | 8              |
| Araneae        | 3                 | 15                  | 3               | 26              | 5     | 13      | 65             |
| Blattodea      | 3                 | 8                   | 2               | 3               | 2     | 4       | 22             |
| Cerambicidae   | 0                 | 0                   | 0               | 2               | 0     | 0       | 2              |
| Coccinellidae  | 0                 | 1                   | 0               | 0               | 0     | 0       | 1              |
| Coleoptera     | 3                 | 3                   | 8               | 0               | 1     | 1       | 16             |
| Curculionidae  | 1                 | 0                   | 0               | 1               | 0     | 1       | 3              |
| Culicidae      | 3                 | 3                   | 10              | 13              | 0     | 3       | 32             |
| Elateridae     | 0                 | 0                   | 0               | 0               | 0     | 0       | 0              |
| Formicidae     | 47                | 8                   | 21              | 21              | 32    | 3       | 132            |
| Heteroptera    | 1                 | 5                   | 0               | 3               | 0     | 0       | 9              |
| Hemiptera      | 0                 | 7                   | 0               | 6               | 3     | 5       | 21             |
| Isoptera       | 0                 | 0                   | 0               | 0               | 0     | 23      | 23             |
| Lepidoptera    | 5                 | 1                   | 0               | 2               | 0     | 4       | 12             |
| Muscidae       | 0                 | 0                   | 1               | 6               | 0     | 3       | 10             |
| Odonata        | 0                 | 0                   | 0               | 1               | 0     | 3       | 4              |
| Orthoptera     | 1                 | 12                  | 1               | 3               | 1     | 4       | 22             |
| Scarabaeidae   | 0                 | 2                   | 0               | 0               | 0     | 13      | 15             |
| Vespidae       | 0                 | 3                   | 1               | 2               | 0     | 1       | 7              |