

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

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2 lakes

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22

23 **Abstract**

24 Despite the increasing amount of knowledge available regarding the ecological interactions between species, the
25 dynamics of anurans in aquatic environments are little explored and understood. In this way, our work aims to
26 assess which factors influence the composition and the ecological interactions of hylid anurans in oxbow lakes
27 in the middle Purus River, Amazonas. We sampled three lakes with high, medium and low levels of
28 connectivity twice, once during the flood and then in drought hydrological regimes. Variations in the hylid
29 anuran assemblages and ecological interactions were tested as function of environmental niche, food resources,
30 level of connectivity and hydrological regime. The availability of environmental resources and the availability

31 of food resources were the best factors that explain the distribution of hylid anurans, which were also highly
32 dependent on the variations between the hydrological regimes. The interactions between anurans,
33 macroinvertebrates and macrophytes showed a modular and specialized structure, which varied according to the
34 connectivity and hydrological regime of the lakes. Connectance showed an increasing trend from high to low
35 connectivity lakes, suggesting that anurans had low trophic and environmental specialization in lakes with low
36 connectivity. Hylids found in the lake of medium connectivity had higher values of trophic specialization and
37 modularity. Our results illustrate the role of river-lake connectivity and annual hydrological cycle to maintain
38 the aquatic biota and their interactions, and highlight the importance of floating meadows for the maintenance of
39 biodiversity in floodplains.

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

42

43 **Introduction**

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

56 In tropical lakes (e.g., oxbow lakes) floating meadows are dominant floristic elements, which may be
57 composed mainly by amphibian and free-floating plant species commonly known as macrophytes (Moura Júnior
58 et al. 2015). The aquatic macrophytes tend to grow rapidly and undergo changes in their distribution due to the
59 spatial and seasonal dynamics of the flood pulses (Junk et al. 1989), which ultimately influence the structure of
60 aquatic communities (Junk et al. 1989). Such changes prompt the flow of nutrients and organisms, increasing

61 spatial heterogeneity and availability of niches and resources between lakes (Thomaz et al. 2007). Because of
62 these traits, floating meadows are ideal environments for reproduction, refuge and feeding of fauna species
63 (Luz-Agostinho et al. 2009), which are important in the maintenance of the diversity of both macroinvertebrates
64 (e.g., insects; Petry et al. 2003; Peiró and Alves 2006; Pelicice and Agostinho 2006) and vertebrates such as
65 amphibians (Upton et al. 2014; Ramalho et al. 2016, 2018; Ganança et al. 2021). Floating meadows hosted
66 unique communities of anurans (Ramalho et al. 2018), that use the floating environment for breeding, sheltering,
67 foraging and dispersal (Hodl 1977; Hoogmoed 1993; Schiesari et al. 2003; Upton et al. 2014; Böning et al.
68 2017). The complex environment created by the unstable movement of floating meadows also act as a filter for
69 anuran species, since the occurrence of anuran species is dependent on macrophyte composition and their
70 vertical and horizontal structure (Upton et al. 2011, 2014; Ganança et al. 2021). In this sense, anuran
71 communities in floating meadows are composed essentially by hylid (i.e., treefrogs) anurans (Upton et al. 2014;
72 Böning et al. 2017; Ramalho et al. 2018). However, the role of macrophyte species composition (i.e., as
73 potential environmental niche) and their associated macroinvertebrates (i.e., as potential food resource), as well
74 as other local predictors (e.g., river-lake connectivity and hydrological regime), in the variation of anuran
75 communities in floating meadows are still misunderstood, causing a gap in the knowledge as to the complex
76 biodiversity in floodplains.

77 The use of tools from the Theory of Complex Networks has been useful to understand new aspects of
78 the ecology and evolution of species assemblages. This is because these tools allow us to study how the species
79 and their interactions are structured and how such structures vary over ecological gradients (Tylianakis and
80 Morris 2017). Space may promote variation in network structure by affecting the likelihood of potential
81 interactions (Guimarães Jr. 2020). Changes in the relative abundance or quality of the interaction partners can be
82 explained by different factors, such as latitudinal patterns (Ceron et al. 2019). Tropical anuran-prey networks
83 have high connectance, low modularity, and complementary specialization that are explained by the generalist
84 diet of anurans (Ceron et al. 2019). However, despite the knowledge of the global pattern involving anuran
85 networks, the knowledge regarding the properties of ecological interactions at local freshwater communities is
86 still scarce. Indeed, we still lack theory and natural history to understand how the anuran assemblages interact
87 with macrophytes assemblages in floating meadows (i.e., as an environmental resource for anurans) and their
88 associated macroinvertebrates (i.e., as a part of the diet for anurans). Therefore, investigating how interactions
89 are affected by changes in river-lake connectivity and hydrological regimes will increase of understanding of
90 how freshwater communities are assembled and maintained.

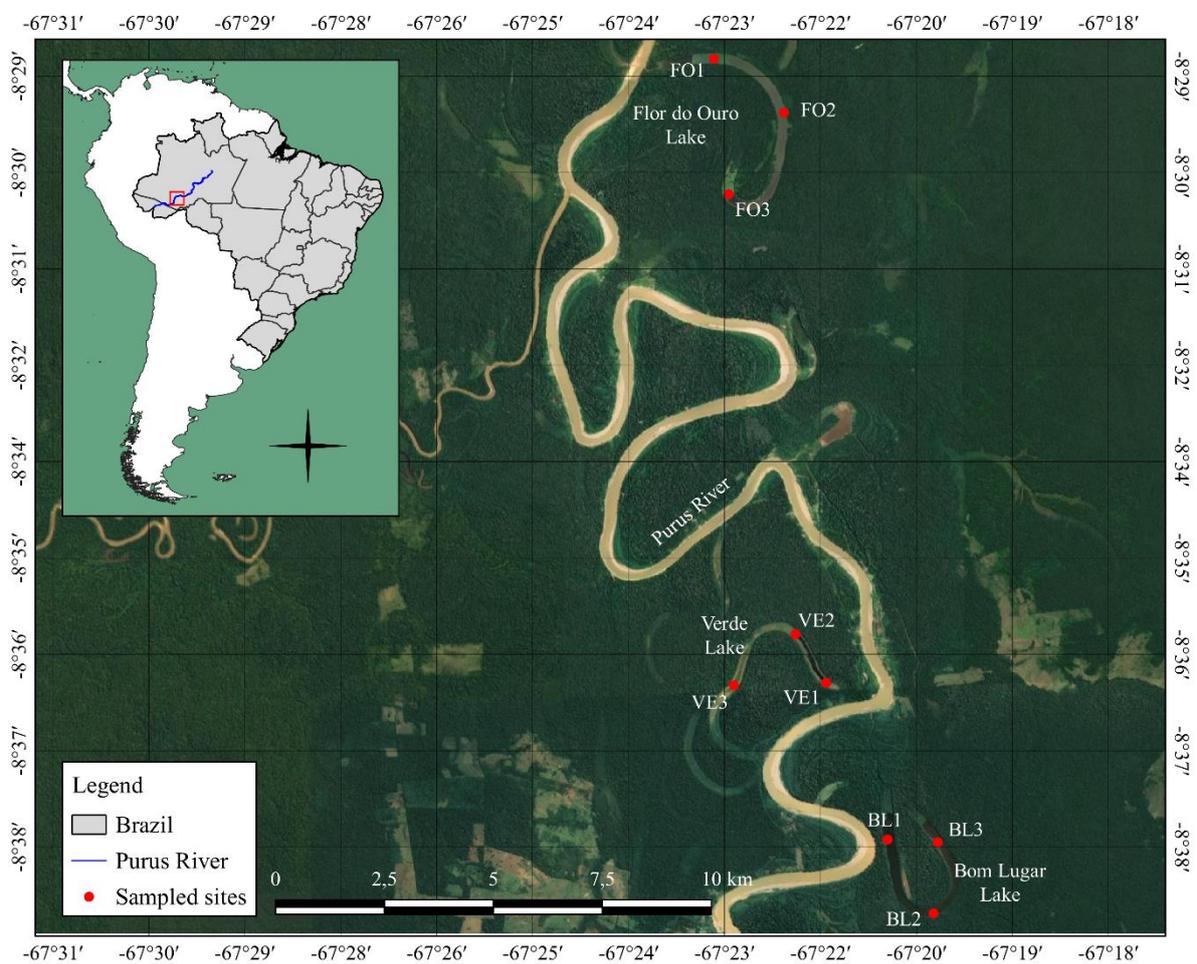
91 The aim of this study was to examine how the communities of hylid anurans can vary with macrophyte
92 assemblages in floating meadows and their associated macroinvertebrates, and how these interactions are
93 affected by changes in river-lake connectivity and hydrological cycle. Specifically, we tested the following
94 hypotheses: (i) the environmental niche and available food resources are the primary predictors explaining the
95 variation in composition of hylid anurans, although it should be dependent on both river-lake connectivity and
96 hydrological cycle. We do expect this relationship because anurans associated with floating meadows are
97 formed specially by species adapted to the flood pulse (Ramalho et al. 2018), which use the floating vegetation
98 as calling and breeding sites (Hödl 1977; Upton et al. 2014; Ramalho et al. 2016), dispersion vectors (Schiesari
99 et al. 2003; Böning et al. 2017) and potential source of food because they house a high diversity of
100 macroinvertebrates (St. Pierre and Kovalenko, 2014). Thus, we sought to confirm that floating meadows contain
101 enough environmental heterogeneity that induce to a non-random anuran assemblage structure (Ganança et al.
102 2021). If the environmental niche and food resource, as well as their variations throughout the hydrological
103 cycle and lake-river connectivity, are important components to structure anuran communities, (ii) we expect that
104 interactions between hylid anurans, macrophytes and macroinvertebrates vary in function of river-lake
105 connectivity and hydrological regime. To this end, we identified the macrophyte species where each specimen
106 was registered and analyzed its stomach content. According to the optimal foraging theory (OFT), when food is
107 scarce, individuals expand their diet width to include less-favored items, which may expand their trophic niches
108 and therefore affect their ecological networks (Emlen 1966; Robinson and Wilson, 1998). Thus, we predict that
109 the oxbow lake more isolated and with low connectivity level has a high number of interactions (i.e., high
110 connectance), in response to the lower supply of food, resulting in non-restrictive diets. In contrast, because
111 more connected lakes have higher migration taxes (e.g., macrophyte species; Mormul et al. 2013), they can
112 result in a great prey availability, leading to a maximum of prey selectivity and more specialized networks. We
113 expect also that interactions between anurans and invertebrates would display modularity as it has been shown
114 that such networks are not nested, but they show low levels of specialization and modularity and high
115 connectance (Ceron et al. 2019). Across the different hydrological regimes and river-lake connectivity, we
116 expect that such properties are going to vary, from more specialized interactions in the most connected lakes to
117 generalized interactions in the less connected lakes.

118

119 **Material e methods**

120 *Study area*

121 The study was conducted in lakes located in the floodplain of the middle Purus River, in the municipality of
122 Boca do Acre, State of Amazonas, Brazil (Figure 1). The Purus River basin is located in the northeast region of
123 the Amazon, where the Purus River is one of the greatest tributaries of the Solimões-Amazonas system. This
124 river is one of the longest rivers in South America, covering approximately 3,380 km, entering Brazil through
125 the State of Acre, with its mouth in the river Solimões, state of Amazonas. It is classified as a white-water river
126 (Sioli 1991) with meandering pattern and water rich in Andean sediments (Ríos-Villamizar et al. 2011). The
127 climate of the region is tropical rainy monsoon type (Köppen 1948; Projeto RadamBrasil 1976). The rainfall has
128 an annual cycle marked by a rainy season, between November and March, and a dry season, between May and
129 September, while April and October are considered transition months (Angelis et al. 2008).
130



131
132 Figure 1. Oxbow lakes sampled in the middle Purus River, Amazon basin, Brazil. Yellow circles indicate the
133 location of the transects sampled in the Flor do Ouro Lake (FO1, FO2, FO3), Verde Lake (VE1, VE2, VE3) and
134 Bom Lugar Lake (BL1, BL2, BL3).

135

136 *Lake and connectivity categorization*

137 We surveyed the anuran assemblages, macrophytes and macroinvertebrates in three oxbow lakes in the middle
 138 Purus River (Figure 1). The lakes were selected based on the connectivity criteria, in which we used the
 139 parameters of lake depth (m), connectivity depth (m), connectivity profile (terrain elevation in meters),
 140 connectivity length (m) and permanence of connection of the lake-river over the hydrological cycle. The depth
 141 of each lake and its connectivity was measured every 50 m using an echo-sounder model Eagle Cuda 168. The
 142 connectivity profile and connectivity length were obtained using a portable GPS tool. For the connectivity
 143 profile, the elevation was measured every 50 m to find a proxy of the terrain' variation close to the confluence
 144 with the Purus River. These measures were obtained during flood and drought hydrological season for the lakes
 145 of high and medium connectivity, and during the flood for the lakes of low connectivity. The oxbow lake
 146 categorized as high connectivity (Bom Lugar lake) presented an average depth of 19.1 ± 6.1 m, connectivity
 147 depth of 6.9 ± 3.8 m, connectivity profile with elevation of 337.4 ± 18.1 m asl and connectivity length of 2.172
 148 m, remaining connected with the Purus River throughout the flood and drought hydrological cycle. The lake of
 149 medium connectivity (Flor do Ouro lake) presented an average depth of 17 ± 5.4 m, connectivity depth of $7.4 \pm$
 150 3.6 m, connectivity profile with elevation of 319.4 ± 6.1 m asl and connectivity length of 456 m, remaining
 151 partially connected with the river during the drought. The lake of low connectivity (Verde lake) presented an
 152 average depth of 8.8 ± 3.6 m, connectivity depth of 3.8 ± 5.8 m, connectivity profile with elevation of $371.2 \pm$
 153 20.6 m asl and connectivity length of 305 m, remaining disconnected from the river during the drought
 154 hydrological regime (Table 1). Thus, our observations in the field allowed us to infer that the connectivity
 155 profile (variation of terrain elevation) is directly related to the degree of connectivity. For example, although the
 156 high connectivity lake has longer connectivity and depth of connectivity similar to that of medium connectivity,
 157 the lower profile of the terrain along connectivity allows it to remain connected with the river during all
 158 hydrological regimes.

159
 160 Table 1. Characterization of the oxbow lakes sampled in the middle Purus River, Amazon basin, Brazil, and its
 161 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	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

162

163 ***Data collection***

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

169

170 ***Environment and food resource availability***

171 We evaluated the available environmental resources through the abundance of the macrophytes species in the
172 floating meadows sampled in each transect. The abundance of the macrophyte was visually evaluated by the
173 counting of the coverage percentage of each species within a 0.5 x 0.5 m quadrat. Within each 200 m transect,
174 we conducted a boat sampling at a distance of approximately 10 m from the edge of the lake and delimited five
175 equidistant points (every 50 m) to throw the quadrat, where we throw it five times per point in each survey,
176 totalizing 25 quadrats in each transect. The abundance of macrophyte species obtained for each point were
177 summed up to estimate the total covering in each transect. Macrophyte species were identified according to
178 Guterres et al. (2008), Thiers (2018), SPLink (2018) and Flora do Brasil (2020). The availability of food
179 resources was evaluated through the collection of macroinvertebrates in floating meadows at the same time and
180 at the same points where macrophyte species were sampled along the 200 m transect. The samplings were
181 carried out using a 4m² seine floating net, formed by two cables of 220cm length connected to a net of 200cm
182 width and 200cm length, handled by two researchers. The floating net was pulled in the floating meadows, from
183 the bottom to the surface, seeking the maximum capture of individuals for 10 minutes every 50 m. The

184 invertebrate specimens were euthanized with a lethal chamber, using 58% acetone and fixed in 70% alcohol.
185 The highest possible taxonomic level was identified using the aquatic insect guide of Hamada et al. (2014).

186

187 *Anuran surveys and stomach contents analysis*

188 The hylid anuran surveys were carried out at the same transects and at the same time of the surveys of
189 macrophytes and macroinvertebrates. We performed the anuran sampling using the active and auditory search
190 methods (Crump and Scott Jr. 1994), always carried out by two researchers on a boat, approximately 10 m from
191 the edge of the lake. For each anuran individual visualized, the macrophyte species where it was found calling
192 or foraging at the time of collection was registered and named as environmental resource used. The individuals
193 sampled were anesthetized and euthanized with 5% xylocaine, fixed in 10% formalin and stored in 70% alcohol.
194 The stomachs of the collected specimens were removed, the contents were scattered in a Petri dish, counted and
195 analyzed using a stereomicroscope, and subsequently preserved in 1µl microtubes (Eppendorf) with 70%
196 alcohol. Food items were identified and categorized to the lowest possible taxonomic level (Hamada, et al.
197 2014), named as a food resource consumed and used in the following interaction analysis.

198

199 **Data analysis**

200 We focused our hypothesis in a limited number of species because most species were not prevalent throughout
201 the samples. To test whether the variations in the hylid anuran assemblages are explained mainly by
202 environmental niche and food availability, we built four models referring to each group of predictor variables
203 that could influence the species composition variation in the floating meadows. Thus, models included the
204 environmental niche, available food resources, level of connectivity and hydrological regime. Firstly, in the
205 model of environmental niche we included only macrophyte species that (i) occurred in at least three samples or
206 (ii) showed a coverage percentage \geq equal to or greater than 5% in at least one sample. For the models of food
207 availability resources, only taxa of macroinvertebrates that (i) occurred in at least three samples or (ii) had total
208 abundance \geq equal to or greater than 20 were considered. Anuran abundance was standardized through
209 Hellinger's transformation (Legendre & Legendre, 2012). Percentage values of available environmental
210 resources and abundance of available food resources were transformed by calculating the square root and
211 logarithmic function, respectively. The levels of connectivity and hydrological regime were rank-categorized
212 (connectivity: low = 1, medium = 2, high = 3; hydrological regime: drought = 1, flood = 2). In order to avoid
213 overestimation of the models, the influence of environmental niche and available food resources on the anuran

214 communities were evaluated by the forward selection procedure, and only the significant variables were selected
215 and included in the RDA (Blanchet et al., 2008). This procedure was performed with 999 iterations for each
216 model and the selection was finalized when the variables had a P value greater than $\alpha=0.05$ (Peres-Neto et al.,
217 2006). We tested the models' significance using a Redundancy Analysis (RDA) with 999 Monte Carlo
218 iterations. Moreover, we performed a Partial Redundancy Analysis (pRDA) with variance partitioning to
219 evaluate the pure and shared relative contribution of sets of variables to the variation in the hylid anuran
220 assemblages (Dray et al. 2012). Every procedure was performed using the functions available in the *packfor*
221 (Dray et al. 2013), *vegan* (Oksanen et al. 2017) and *adespatial* (Dray et al. 2020) packages in R software (R
222 Core Team 2020).

223 In order to examine the interactions between macrophytes, anurans and macroinvertebrates, we used
224 the data obtained from the macrophyte species in which the anuran was collected calling or foraging (the
225 environmental resource used) and the quantitative data on stomach content (food resources consumed), using an
226 approach based on the Theory of Complex Networks. For this, interaction matrices A were constructed, where
227 a_{ij} was the number of interactions of an anuran, with macrophyte or macroinvertebrate and 0 where there were
228 no interactions. We obtained 12 matrices corresponding to the interactions of hylid anurans observed in each
229 lake for the attributed category (high, medium and low connectivity) over two different hydrological regimes
230 (flood and drought). Each matrix was divided by the type of interactions, anurans with environmental resources
231 used (macrophyte) or food resource consumed (stomach content; i.e., macroinvertebrates); this for all oxbow
232 lakes and hydrological regimes. Finally, twelve matrices were obtained per lake, six with all interactions
233 between the anurans and macrophytes (environmental resource) in both hydrological regimes (drought and
234 flood), and six with macroinvertebrates (food resource) consumed in both hydrological regimes. For the
235 description of the interactions, we used the following network descriptors: connectance, weighted nestedness
236 (wNODF), modularity and complementary specialization (H_2'), similar to the approach used by Ceron et al.
237 (2019).

238 Connectance describes the ratio between the total number of realized links and the maximum
239 theoretical number of links. This d gives a description of how many interactions are not realized based in the
240 total possible (Jordano 1987). Its values range from 0 to 1, 0 indicates that all of potential interactions are not
241 realized and 1 indicates that all the potential interaction in the network is realized. Weighted nestedness, based
242 on the Nestedness Metric, Based on Overlap and Decreasing Fill (NODF), describes the extent to which
243 interactions of specialist species correspond to a subset of generalist interactions (Bascompte et al. 2003). We

244 calculated the weighted nestedness (wNODF), which is based on the overlap and decreasing fill in the weighted
245 matrix (Almeida-Neto and Ulrich 2011). Nestedness values range from 0 (non-nested network) to 100 (perfect
246 nesting). We also calculated modularity, which measures how groups of species are densely connected and
247 present only sparser connections with other groups of interacting species. We analyzed modularity using the
248 recently implemented LPAwb + algorithm (Liu and Murata 2010; Beckett 2016). Finally, we calculated
249 complementary specialization (H_2'), which is a network-wide index of specialization for quantitative interaction
250 matrices. It describes how species restrict their interactions from those randomly expected based on partner's
251 availability (Blüthgen et al., 2006). The assumption is that if species have preferences for specific interaction
252 partners, these preferences would be captured as a deviation from random encounters given by partner
253 availability (Blüthgen et al. 2006). Values of H_2' range from 0 to 1 indicating the extremes of generalization and
254 specialization, respectively. The significance of wNODF, modularity, and H_2' were assessed by comparing them
255 with those obtained for randomized networks generated by a null model based on Patefield's algorithm
256 (Patefield 1981). We generated 1,000 randomized matrices to estimate the significance of nestedness and
257 complementary specialization and 100 matrices to estimate modularity. To quantify the departure of the
258 observed network values from null expectation, we calculated null-model corrected values by subtracting
259 observed metric value from mean value across all randomized networks (Δ – transformation). Then, the Δ –
260 transformed value was divided by the standard deviation of values across all randomized networks (z –
261 transformation; Dalsgaard et al. 2017; Zanata et al. 2017). All network metrics and null models were calculated
262 with the 'bipartite' ver. 2.08 package (Dormann et al. 2008) in R software (R Core Team 2020).

263

264 **Results**

265 ***Environmental and available food resources***

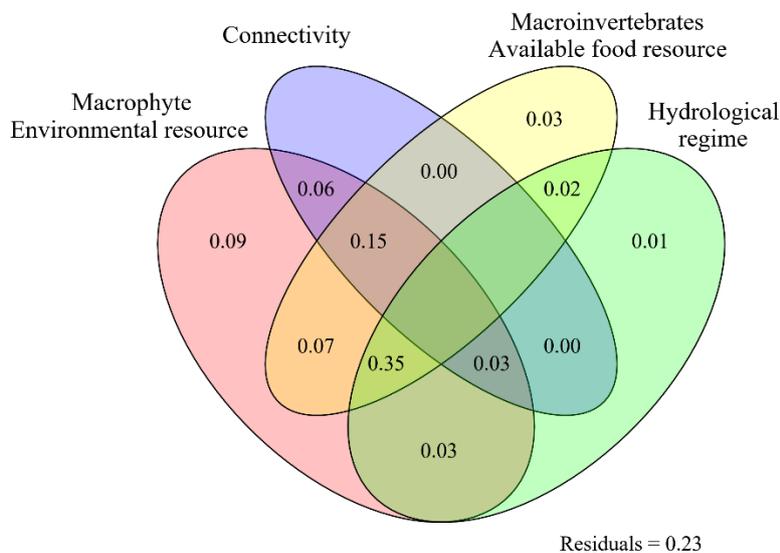
266 We identified 32 species of macrophytes in the floating meadows, 25 in lakes of high-level connectivity, 20 in
267 medium and 16 in low connectivity. The most abundant macrophyte species were *Pistia stratiotes* (Araceae)
268 (21%), *Eichhornia crassipes* (Pontederiaceae) (16%) and *Ludwigia helminthorrhiza* (Onagraceae) (11%).
269 During the flood, the more abundant macrophyte species were *P. stratiotes* in lakes of high and medium
270 connectivity (42% and 35%, respectively) and *E. crassipes* (34%) in low connectivity. During the hydrological
271 regime of drought, the more abundant species were *P. stratiotes* (25%) in lakes of high connectivity, *E.*
272 *crassipes* (44%) in medium, and *L. helminthorrhiza* (38%) in low connectivity lakes (Table S1).

273 We sampled 4041 individuals of macroinvertebrates. Individuals not identified or in the larval stage
 274 were not used in the statistical analyzes. The more abundant invertebrate taxons were Hemiptera (18%),
 275 Orthoptera (17%) and Diptera (Culicidae, 15%). The more abundant taxon during the flood hydrological regime
 276 in the lake of high connectivity was Hemiptera (24%), while Orthoptera was more abundant in lakes of medium
 277 (32%) and low (19%) connectivities. During the drought, the more abundant taxons were Hemiptera in lakes of
 278 high (25%) and low connectivities (27%) and Orthoptera in the lake of medium (35%) connectivity (Table S2).
 279

280 ***Effects of environment and available food resources on species abundance***

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

292



293

294 Figure 2. Variation in anuran abundance explained by environmental resources (macrophyte species), lake
295 connectivity, available food resources (macroinvertebrate taxons) and hydrological regime.

296

297 *Food items consumed by anurans*

298 Among the individuals registered and collected in the floating meadows, 334 had their had empty stomachs and
299 407 were used in our analysis, including 47 individuals of *Boana punctata*, 217 of *Dendropsophus reticulatus*,
300 41 of *Sphaenorhynchus carneus*, 81 of *Sphaenorhynchus lacteus* and 21 of *Sphaenorhynchus dorisae*. In
301 relation to food items consumed, Formicidae was the most frequent prey group (29.5%), followed by Aranea
302 (14.5%), and Culicidae (7.2%). During the rainy season, Formicidae was the most frequent prey in lakes of high
303 (69.1%), medium (42.0%), and low (69.6%) connectivity. However, during the dry season, the most consumed
304 prey changed among lakes with different connectivities: Aranae was the most frequent prey consumed in lakes
305 of high (22.1%) and medium (28.0%) connectivity, while Isoptera was most frequent in lakes of low
306 connectivity (25.0%) (Table S4).

307

308 *Ecological interactions*

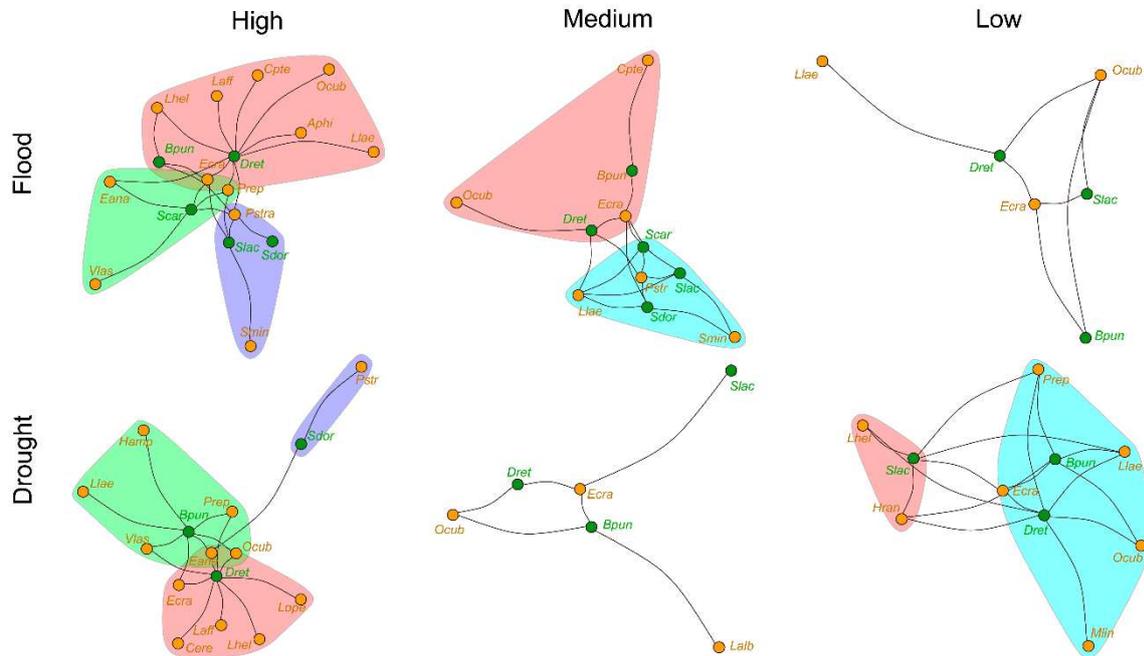
309 Network metrics according to regime, connectivity and by the interaction type are shown in Table 2.
310 Connectance showed an increasing trend from high to low connectivity lakes in both interaction types. The
311 higher connectance values were recorded in macrophyte networks during the hydrological regime of drought in
312 lakes with low connectivity ($C = 0.8$; Figure 3). Networks did not show a nested pattern ($p > 0.05$ for all
313 networks). All networks (macrophytes and diet) showed higher trophic specialization and a modular structure,
314 with the exception of the macrophyte network in a flooded lake with low connectivity, and in a lake with
315 medium connectivity during the drought (Figure 3 and Figure 4). The most specialized interactions were
316 recorded in diet networks in the hydrological regime of flood in lakes with medium connectivity ($H_2' = 0.85$;
317 Figure 4). For macrophytes networks, the most specialized interactions were recorded in the hydrological
318 regime of flood in lakes with medium connectivity ($H_2' = 0.41$). Specialization and modularity showed a
319 decrease during the drought for both network types. Modularity was higher in diet networks during flood in
320 lakes with medium connectivity ($M = 0.42$). For macrophytes networks, modularity was absent or low both in
321 flood or drought (Figure 3 and Figure 4).

322

323 Table 2. Descriptors of networks divided by regime, connectivity and by the interaction between anurans,
 324 macrophytes and macroinvertebrates. Z-scores values are in parentheses. M = microhabitat use and D = diet.
 325 Values significantly ($P < 0.05$) are in bold.

	High		Medium		Low	
Flood	D	M	D	M	D	M
Connectance	0.34	0.38	0.32	0.56	0.61	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	D	M	D	M	D	M
Connectance	0.47	0.5	0.5	0.66	0.61	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)

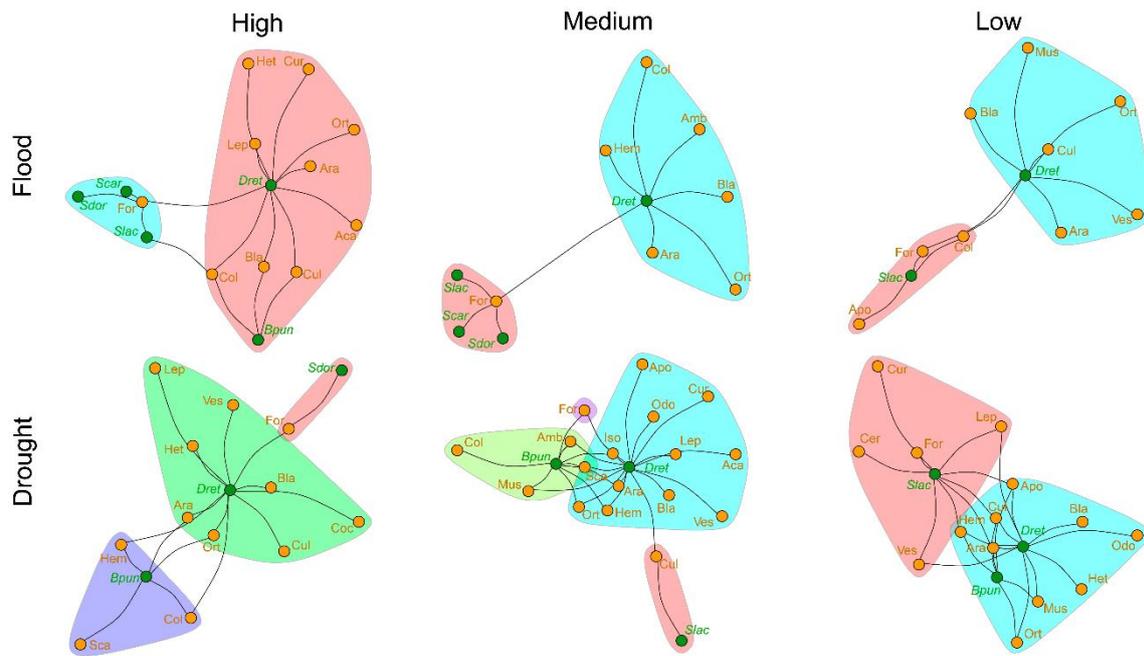
326



327

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

331



332

333 Figure 4. Graphs showing modules (colors) in anuran-macroinvertebrate interactions by lake connectivity (high,
 334 medium and low) during the hydrological periods of flood and drought. Circles represent prey categories
 335 (orange) and anuran species (green).

336

337 **Discussion**

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

345 We found that the abundance of the hylid species is influenced by all the factors that we measured (i.e.,
 346 availability of environment, connectivity, food resource and hydrological regime). However, the availability of
 347 the environmental and food resources was the best factor explaining the variation in the abundance of anuran
 348 species. Anurans that occur in floating meadows are highly adapted to the open and unstable environment
 349 (Ramalho et al., 2018), where species are segregated horizontally and vertically according to their reproductive
 350 and foraging requirements (Hödl 1977; Hoogmoed 2013; Upton et al. 2011; Upton et al. 2014). For example,
 351 studies in other regions of the Amazon have found that *Sphaenorhynchus carneus*, *S. dorisae* and *S. lacteus* may

352 occupy lower vegetation in the floating meadows (e.g., in *Salvinia* spp., *Eichhornia* spp. and *Pistia* spp.), while
353 larger species such as *Boana punctata* and *Dendropsophus reticulatus* occupy higher strata in the floating
354 vegetation (e.g., in *Paspalum repens*) (Hödl 1977; Upton et al. 2011; Upton et al. 2014). These relationships
355 have shown that environmental characteristics of floating meadows (e.g., macrophyte height, macrophyte
356 morphotype composition and water depth) creates a gradient of environmental heterogeneity that acts as a filter
357 in anuran communities (Ganança et al. 2021). Our results indicate that the importance of macrophytes as
358 environmental resources for anurans is complex and varies in space and time, as indicated by the fractions
359 shared between environmental resources, lake-river connectivity and hydrological cycle.

360 The available food resources are good predictors of the variation in hylid abundance. The results
361 reinforce that variation in macroinvertebrates along with the environmental gradient of floating meadows may
362 exert a profound influence on the associated organisms (Poi de Neiff 2003; Peiró and Alves 2006; Upton et al.
363 2014; Hill et al. 2016). The main macroinvertebrates that explained the variation in hylids were Gastropoda,
364 Odonata, Araneae and Orthoptera, which apparently also interact in a complex way and mediated by specific
365 condition imposed by lake-river connectivity and hydrological cycle. Floating meadows, and macrophyte
366 species as well (as discussed in detail below), are then important foraging sites for anurans, although the
367 complexity of the interactions (e.g., if anurans are predator or prey) still needs to be more explored. Thus,
368 variations in the environmental and food resources directly influence anuran assemblage in floating meadows,
369 indicating a complex structuring by the niche and a non-random pattern in species distribution in space and
370 time.

371 As expected, the aquatic interactions between anurans, macroinvertebrates and macrophytes showed a
372 modular and specialized structure with no nestedness. Our results showed that the network descriptors among
373 anurans, macroinvertebrates and macrophytes networks vary according to the connectivity and hydrological
374 regime of the lake. Connectance showed an increasing trend from high to low connectivity lakes in both
375 interaction types. This result suggests that anurans are tend to establish more interactions with macrophytes and
376 macroinvertebrates when resources are expected to be more abundant (Thomaz et al. 2009). For specialization,
377 higher values were found in medium connectivity and had a decrease during the drought, both to diet and
378 macrophytes networks. During the drought, when resources are reduced, it is expected that anurans eat and use
379 the resources that are available, reducing specialization and increasing connectance (Emlen 1966; Robinson and
380 Wilson 1998). On the other hand, specialization may be especially favored when resource availability increases,
381 according to predictions of optimal foraging theory (Robinson and Wilson 1998). Therefore, in the flood season,

382 when resources are supposedly more abundant in the floodplain, the species of hylids were more selective in
383 terms of food selection and habitat use, so that each species tended to consume specific foods and occupy
384 macrophytes with specific structures.

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

401 The primary prey of anurans is insects, as well as other arthropods, such as spiders and mites (Simon
402 and Toft 1991; Duellman and Trueb 1994). Each anuran species tended to prefer certain food items and most of
403 the food items consumed by the anurans were available in the floating meadows. The items consumed by the
404 anuran species in this study corroborates the diet described for the species (Duellman 1978, 2005; Lopez et al.
405 2009). However, by implementing a network approach we were able to assess the changes in diet of anurans by
406 changes in habitat connectivity. In this case, we found that in lakes with low connectivity, anurans had a less
407 diversified diet. This evidence suggests that dispersion and therefore habitat connectivity are factors that
408 structure the anuran and its partners in all lakes, as expected by the Neutral theory of diversity (Hubbel 2001), in
409 which the movement of species is one of the factors explaining species local abundance, for example.

410 Variations in the availability of environmental resources (macrophytes) and food resources
411 (macroinvertebrates) were influenced by the connectivity of the lakes and hydrological regimes, affecting the

412 abundance and structure of interactions of hylid anurans. The interactions found showed that the species use the
413 same resources, which are available in the floating meadows for their consumption, and although they are more
414 generalist, some species use resources more specifically than others. These results show that the hylids
415 associated with floating meadows in this study have their distribution affected by the interaction to both
416 macrophyte and macroinvertebrate species, as well as to lake connectivity level and hydrological regimes. These
417 alterations in the environmental niche affect the anurans associated with floating meadows and show the
418 importance of this environment for biodiversity.

419

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433

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435

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

437

438 Author contributions – All authors contributed to the conceptualization and design of the project. LRAM and
439 WPR collected the data, performed the data analysis, and led the writing of the text. FVA, KC, and PL provided
440 additional expertise on interaction network, performed the data analysis, and wrote the text. LRV provided
441 additional expertise on hydrology and river-lake connectivity. LJSV assisted with data interpretation and

442 writing, and supervised this research. All authors critiqued the manuscript and gave final approval for
443 submission.

444

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446

447 Consent for Publication – Not applicable.

448

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451

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597 Supplementary Information

598 Table S1. Relative abundance of macrophyte species found in three oxbow lakes of different
 599 connectivity during the flood and drought hydrological regime in the middle Purus River,
 600 Amazon basin, Brazil.

Taxon	High connectivity		Medium connectivity		Low connectivity		Relative abundance
	Flood	Drought	Flood	Drought	Flood	Drought	
Amaranthaceae							
<i>Alternanthera philoxeroides</i>	0.25	0.19					0.08
Araceae							
<i>Lemna minuta</i>	7.80	3.89	5.89	10.98	0.17	0.96	4.78
<i>Pistia stratiotes</i>	42.28	24.73	34.55	11.24	4.94		20.86
<i>Wolffiella lingulata</i>	0.15	0.17	0.19			2.03	0.42
Araliaceae							
<i>Hydrocotyle ranunculoides</i>			1.69	0.67	4.51	28.00	5.58
Asteraceae							
<i>Eclipta prostrata</i>	0.70	0.67					0.26
<i>Enydra anagallis</i>	5.35	22.94		0.60		0.12	5.54
<i>Gymnocoronis spilanthoides</i>			0.48				0.08
<i>Mikania scandens</i>					2.64	2.32	0.80
Commelinaceae							
<i>Commelina erecta</i>		0.19					0.04
Cucurbitaceae							
<i>Luffa operculata</i>		0.29					0.06
Cyperaceae							
<i>Oxycaryum cubense</i>	1.28	2.27	7.35	20.66	17.14	6.99	8.42
Euphorbiaceae							
<i>Caperonia castaneifolia</i>			0.40				0.07
Fabaceae							
<i>Mimosa pigra</i>				0.19			0.02

Taxon	High connectivity		Medium connectivity		Low connectivity		Relative abundance
	Flood	Drought	Flood	Drought	Flood	Drought	
<i>Vigna lasiocarpa</i>	0.73	4.10	0.95				1.10
Hydrocharitaceae							
<i>Limnobium laevigatum</i>	2.69	7.84	5.51		2.81	4.00	4.08
Lentibulariaceae							
<i>Utricularia gibba</i>	2.06	1.48	3.63	0.04	8.75	4.38	3.42
Onagraceae							
<i>Ludwigia affinis</i>	1.10	0.38					0.28
<i>Ludwigia helminthorrhiza</i>	6.10	8.77			16.07	37.94	11.49
<i>Ludwigia leptocarpa</i>			0.42				0.07
Passifloraceae							
<i>Passiflora sp</i>	1.03		0.16				0.22
Phyllanthaceae							
<i>Phyllanthus fluitans</i>	0.10						0.02
Poaceae							
<i>Bracharia purpurascens</i>	0.40						0.07
<i>Hymenachne amplexicaulis</i>		0.36					0.07
<i>Panicum aquaticum</i>					0.46		0.07
<i>Paspalum repens</i>	5.45	3.89	0.21		2.32	7.88	3.43
Pontederiaceae							
<i>Eichhornia crassipes</i>	13.65	0.72	10.25	43.73	34.18	5.22	16.25
Pteridaceae							
<i>Ceratopteris pteridoides</i>	1.13	6.03	0.48	4.88			2.07
Ricciaceae							
<i>Ricciocarpus natans</i>		2.77				0.03	0.54
Salviniaceae							
<i>Azolla filiculoides</i>	1.13	0.14	8.29	0.04	4.74	0.14	2.48
<i>Salvinia auriculata</i>	1.03	0.86	1.54				0.63
<i>Salvinia minima</i>	5.60	7.34	18.03	7.00	1.26		6.69

601

602

603 Table S2. Abundance of macroinvertebrates found in three oxbow lakes of different
 604 connectivity during the flood and drought hydrological regime in the middle Purus River,
 605 Amazon basin, Brazil.

Taxon	High connectivity		Medium connectivity		Low connectivity		Relative abundance
	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

606

608 Table S3. Hylid species collected in three oxbow lakes of different connectivity during the
 609 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	
<i>Boana punctata</i>	6	39	8	26	16	34	129
<i>Dendropsophus reticulatus</i>	54	106	78	55	33	82	408
<i>Sphaenorhynchus carneus</i>	31	0	0	0	21	0	52
<i>Sphaenorhynchus dorisae</i>	10	2	0	0	22	0	34
<i>Sphaenorhynchus lacteus</i>	20	0	48	33	16	1	118
Total abundance	121	147	134	114	108	117	741

610

611

612 Table S4. Food items consumed by five hyliid species in three oxbow lakes of different
613 connectivity during the flood and drought hydrological regime in the middle Purus River,
614 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
Amblyptgi	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
Cerambycidae	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

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