1 **SPECIES RICHNESS AND FUNCTIONAL STRUCTURE OF FISH ASSEMBLAGES**

2 **IN THREE FRESHWATER HABITATS: EFFECTS OF ENVIRONMENTAL**

3 **FACTORS AND MANAGEMENT**

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ABSTRACT

Anthropogenic actions can facilitate the top-heaviness of trophic levels through the introduction of novel consumers. In this present study, the inverted trophic hypothesis was tested in the freshwater fish comunities of reservoir. The distribution of fish species in three freshwater habitats in the Jurumirim Reservoir, Brazil, was examined using both species richness and the relative proportions of different trophic groups. These groups were used as a proxy for functional structure in an attempt to test the ability of these measures to assess fish diversity. Assemblage structures were first described using non-metric multidimensional scaling (NMDS). The influence of environmental conditions for multiple fish assemblage response variables (richness, total abundance and abundance per trophic group) was tested using Generalized Linear Mixed Models (GLMMs). The metric typically employed to describe diversity, i.e., species richness, was not related to environmental conditions. However, absolute species abundance was relatively well explained with up to 54% of the variation in the observed data accounted for. Differences in the dominance of trophic groups were most apparent in response to the presence of introduced fish species: the iliophagous and piscivorous trophic groups were positively associated, while detritivores and herbivores were negatively associated, with the alien species. This suggests that monitoring functional diversity might be more valuable than species diversity for assessing effects of disturbances and managements policies on the fish community.

Keywords: mixed effects models, nutrients, reservoir, sedimentation, trophic level.

INTRODUCTION

There is increasing recognition (e.g. UN Convention on Biological Diversity) of a need for the management of the impacts of human activities on the abundance and distribution of the non-human organisms in the environment. Such management requires an understanding of the factors controlling the distributions of species (biodiversity) in nature. Traditionally, the baseline for assessing biodiversity has been metrics related to species richness (e.g., Chaudhary *et al.*, 2016; Pianka, 1966; Tittensor *et al.*, 2010). The main problem of assessing taxonomic diversity alone is the fact that the species is only one unit against a set of all the characteristic, functional and genetic variations that ultimately control the ecological functions (Griggs *et al.*, 2013). More recently, however, the need to consider the functional diversity of the biosphere has been highlighted (Steffen *et al.*, 2015) and a number of studies have turned attention to the assessment of the "functional" structure of ecosystems (e.g. Austen *et al.,* 1994; Noble *et al.*, 2007). The benefit of the functional aspects over the taxonomic diversity indexes is the use of groups with functionally similar species (functional groups) that occupy similar adaptive zones (Stanley, 1979) - although they are geographically and evolutionarily distinct. The functional groups can predict the outcome of interspecific interactions and interpret patterns in the community structure (Steneck and Watling, 1982). Another motive for use of functional structure analysis is that anthropic actions have a major impact on community biomass distributions (McCauley *et al.*, 2018). The optical of the loss of diversity richness cannot explain it. The descriptions of biomass and abundance distributions in trophic boundaries and within communities helps elucidate fundamental mechanisms that shape the architecture of ecological communities (McCauley *et al.*, 2018). In this study, the distribution of fish species in the Jurumirim Reservoir, Brazil, was

66 examined using both traditional biodiversity indices (species richness) and the relative

67 dominance of different trophic feeding groups as a proxy for the functional structure of the

68 assemblage in an attempt to assess the applicability of these two measures in the assessment

69 of the fish biodiversity.

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72   The Jurumirim Reservoir consists of heterogeneous environments both in terms of

73 structure and dynamics, for example, distinct lacustrine and riverine zones (Henry, 2014).

74 Lacustrine sites are characterised by deep water, a vertically stratified water column and

75 limited nutrient availability in the well-lit surface waters, which keeps primary production at

76 a relatively low level (Zanata and Espíndola, 2002). Riverine sites, located in the tributaries,

77 are usually limited in transparency of water, i.e. sediment transport processes in these areas

78 are affected by water flow, erosion and rains; and also have relatively low primary

79 productivity (Wetzel, 2001). Marginal lagoons, located alongside the river channel, represent

80 lentic waters with high rates of primary productivity and sediment deposition (Henry, 2014).

81 Reservoir, tributary, and marginal lagoon, in combination, represent a large range of

82 environmental variability (Franklin 2010; Hartley *et al*., 2010). They can be well suited for

83 elucidating studies about habitat-filtering and species-sorting (Vanschoenwinkel *et al*., 2010;

84 Erös *et al*., 2017), while fish species and community composition can be analysed in relation

85 to environmental parameters (O'Sullivan and Reynolds, 2004; Thornton *et al*., 1990; Wetzel,

86 2001). These parameters are ideal for discerning the ecological "preferences" of the

87 ichthyofauna, which are potentially exposed to distinct ranges of environments reflected in

88 different community compositions and relative abundances. In other words, the fish are not

89 simply found in a specific environment because they had no other choice of environment.

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92   The reservoir examined in this study was created following the construction of a dam

93   in the middle of the 20th Century. The changing habitat conditions following creation of the

94   dam led to changes in fish distributions in the period immediately following dam

95   construction. Since 1974, the Upper Paranapanema basin has been classified as having

96   excellent water quality and resources when compared to other basins within industrial or

97   agriculture regions in Brazil (Carvalho, 2009), which means it offers an interesting study

98   system in which to explore variation in functional structure in relation to environmental

99   conditions. Over the past three decades, the intensity of fishing, the fish stocking, the fish

100   cage farming and the introduction of non-native species have promoted changes in the fish

101   composition, although physical conditions in the reservoir system have remained essentially

102   unchanged (Nogueira *et al.*, 2014). Fishing in Jurumirim Reservoir had been represented by a

103   little subsistence and sport fishing, the latter being related to tourism in the area (Novaes and

104   Carvalho, 2009). The intensity of fishing in the reservoir was previously estimated at 15.7 kg

105   ha^{-1} $year^{-1}$ with CPUE values estimated at 10.5 kg $fisherman^{-1}$ day^{-1} (Novaes and Carvalho,

106   2009; Schork *et al.*, 2013). The increase of fish cage farming in Jurumirim is estimated at

107   2460 t yr^{-1}, considering the current rate of production and growth potential relative to new

108   aquaculture parks, in which the Nile tilapia *Oreochromus nilotucus* (L. 1758) is the main

109   farmed species (Montanhini *et al.*, 2015). Data on intentional fish stocking indicate 7,102,057

110   individuals belonging to six non-native fish species (*Astronotus crassipinnis* (Heckel 1840),

111   *Cyprinus carpio* Linnaeus 1758, *Sorubim lima* (Bloch and Schneider 1801), *Schizodon*

112   *borellii* (Boulenger 1900), *Triportheus angulatus* (Spix and Agassiz 1829), *O. niloticus*, and

113   *Hoplias lacerdae* Miranda Ribeiro 1908) were released into the reservoir between 1978 and

114   1992 (Garcia *et al.*, 2017).

115

116   In the Jurumirim Reservoir system, alien fish species have been introduced for a

117   variety of purposes, i.e. enhancement of sport fishing, aquaculture, stock management and to

118   support an aquarium trade. Yellow tucunare *Cichla kelberi* Kullander and Ferreira 2006 has

119   been illegally released for sport fishing. This species is generally piscivorous and potentially

120   influences ecosystems by increasing the predation pressure on lower trophic levels (Santos *et*

121   *al.*, 1994). *Oreochromus nilotucus* has escaped from aquaculture facilities. This species

122   normally occupies lower trophic levels and can influence ecosystems through changes in

123   primary production and water transparency (Vitule *et al.*, 2009). These two species are

124   examples of the fact that the functional types (sizes, dietary preferences, etc.) of introduced

125   fish species can be quite different and can have distinct influences on ecosystems and the

126   diversity of native fish (Latini and Petrere, 2004; Pelicice and Agostinho, 2009; Vitule *et al.*,

127   2009).

128   These anthropogenic actions can facilitate the top-heaviness of trophic levels through

129   the introduction of novel consumers (McCauley *et al.*, 2018). Piscivores and detritivores

130   could be dominant in the reservoir as a whole, while herbivores could dominate in the

131   riverine habitat. Thus, it is expected that the proportion of upper trophic levels is higher in

132   the reservoir than in the riverine habitat, demonstrating a trophic inversion in the fish

133   comunities. Some studies have reported inverted trophic pyramids or inverted trophic

134   biomass pyramids for fish groups (McCauley *et al.*, 2018 and references therein). In this

135   present study, the inverted trophic hypothesis was tested in the freshwater fish comunities of

136   reservoir. The relative proportion of fish feeding at high and low trophic levels would differ

137   in the different habitats of Jurumirim Reservoir and that the proportion of fish from high/low

138   trophic levels would be influenced by the physical conditions in the reservoir and by the

139   presence of alien species. The aims of this study were to describe the distribution of the fish

140   communities: 1) comparing communities in the different habitat types through NMDS and 2)

141 explaining these differences by analysing the effects of environmental and anthropogenic

142 gradients.

143

144 **MATERIAL AND METHODS**

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147 STUDY AREA

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150 The dam for the Jurumirim Hydroelectric Plant was built on the upper Paranapanema River

151 in the late 1950s near the convergence of the Paranapanema and Taquari Rivers (Carvalho,

152 2009). The associated Jurumirim Reservoir, which is under state protection, is fed by ten

153 tributaries and has a flooded area of 484 km^2 with a perimeter of 1,115 km. Its total water

154 volume is 7.2 billion m^3 and it has a mean depth of 12.90 m (maximum 40 m), with a

155 drainage area of approximately 17,800 km^2. Twenty-eight municipalities are situated within

156 the watershed of the basin with a combined population of over 2.5 million inhabitants

157 (Nogueira *et al.*, 1999). Therefore, this area is of high importance for providing ecosystem

158 services to the local region, for example, hydropower, quantity and quality of clean water,

159 food supply and recreation potential.

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161 DATA COLLECTION AND PREPARATION

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163

164 Fish and environmental samples were collected at 13 sites throughout the Jurumirim reservoir

165 system (Fig. 1; 23°-24° S/48°-49° W) every three months from April 2011 to January 2013,

166   generating a total of 104 sample sets. Sites were selected to represent the heterogeneity of

167   limnological habitats found in the reservoir system. Another condition used in site selection

168   was that the sites should meet the requirements for effective and reliable gillnet capture.

169   Environmental conditions monitored at these sites included physical and chemical properties,

170   nutrient concentrations and the characterization of bottom sediments (see full list in Table

171   S1). Temperature, conductivity, dissolved oxygen, nutrients and chlorophyll concentration

172   were measured at a depth of 1 meter. Fish gillnets were retrieved after a fishing period of 18

173   hours. Catches were identified and weighed following the taxonomy of Graça and Pavanelli

174   (2007). Based on these data, species richness and total number of individuals were calculated

175   for each site (Krebs, 1989).

176

177

178   In order to explore the functional structure of the species assemblages, each species

179   was assigned to a trophic group according to the following trophic categories: detritivorous

180   (Mérona and Rankin-de-Mérona, 2004), herbivorous (Castro, 1997) insectivorous,

181   piscivorous (Williams *et al.*, 1998), omnivorous (Mérona and Rankin-de-Mérona, 2004), and

182   iliophagous (i.e., a diet of microorganisms and organic matter within muddy substrate, Hahn

183   *et al.*, 1998). The digestive tract of each captured fish was examined and the stomach

184   contents were analysed using a stereo- and an optic microscope. Food items were weighed

185   and classified according to the Alimentary Index (AI%) proposed by Kawakami & Vazzoler

186   (1980), following the equation: $AI\% = F_i W_i \times 100 \times / \Sigma F_i \times W_i$, where: AI = food index; i =

187   1, 2 ... n, food, F_i = frequency of occurrence of item i (%); W_i = wet weight of item i (%).

188   The dominant group of food items (highest AI%) was used to define the trophic group for all

189   species for which this study had a sample size of at least four individuals (60% of the

190   species). For the 40% of species with too few samples (<four individuals with stomach

191 contents) to establish the trophic group from gut contents, trophic group classification was

192 based on published data (published before March 8th 2019 e.g., journal articles, university

193 theses, books and FishBase – Table S2).

194

195 STATISTICAL ANALYSIS

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197

198 In order to describe the similarity in fish assemblages among the sites visually, Non-Metric

199 Multidimensional Scaling (NMDS) was used in two dimensions with 999 permutations. This

200 allowed us to find the optimal placement of sites and species, so that the more similar two

201 species assemblages are, the closer the sites are the in two-dimensional plot of the NMDS

202 (Oksanen 2015). Similarity was calculated from the species composition data using Bray-

203 Curtis distance because it is robust with respect to bias induced by differences in sampling

204 effort (Faith *et al.*, 1987). Sites that were most similar to one another in species composition

205 are closest together on the NMDS plot (Fig.2; Oksanen *et al.*, 2015).

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207

208   The trophic inversion hypothesis (McCauley *et al.*, 2018) for fish community

209 structure in reservoirs was tested by comparing the ratios of the distributions of biomass and

210 the abundance of fishes occupying "higher" and "lower" trophic levels, where predatory and

211 detritivorous fish species (piscivorous, omnivorous and detritivorous), were defined as eating

212 at the higher trophic levels. Fish belonging to the remaining groups (herbivores, iliophages

213 and insectivores) were considered to be eating at lower trophic levels. Ratios approaching 1

214 indicate a balanced distribution in the community between higher and lower trophic groups.

215   The fish trophic levels ratio across different habitat types were compared using the Kruskal-

216   Wallis test.

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219   Based on previous analyses that identified important environmental conditions for

220   predicting fish species richness and abundance (Griffiths, 2011), 11 abiotic variables from the

221   set of 21 variables collected were selected as predictors (Table I). Broadly speaking, these

222   variables represent changes in limnological conditions associated with damming. Using them

223   therefore enables us to identify the importance of limnological gradients for determining

224   species assemblages. Because the presence of non-native fish species can strongly influence

225   the structure of resident fish assemblages (e.g., Britton and Orsi, 2012; Vitule *et al.*, 2009),

226   the presence of *C. kelberi*, the jewel tetra *Hyphessobrycon eques* (Steindachner 1882), the

227   silver dollar *Metynnis maculatus* (Kner 1858), *O. nilotucus*, the catfish *Pterygoplichthys*

228   *ambrosetti* (Holmberg 1893) or the red-breasted tilapia *Coptodon rendalli* Boulenger 1897

229   was also included as a binary predictor variable (Table S2).

230

231

232   Generalized Linear Mixed Models (GLMM; Logan, 2011) were generated to

233   determine the potential for these variables to predict multiple aspects of the assemblage -

234   species richness, abundance of individuals across all species, and abundance of individuals

235   within trophic groups - resulting in eight models. Month and site were included as random

236   effects to account for spatial and temporal autocorrelation (Zuur *et al.*, 2009). To meet the

237   conditions of multiple regression, data were checked for normality and homogeneity of

238   variance, and then transformed with log $(x + 1)$. Outliers were checked for using Cook's

239   distance for each variable (Logan, 2011); the outliers were deleted so that the resulting data

240 matrix had the same number of observations for each variable, but no outliers. To ease the

241 comparison of coefficients among the predictor variables, those measured on a continuous

242 scale were normalized to be centered at zero with a standard deviation of one (Bolker, 2008).

243 Pearson and Spearman correlations were generated to test for multicollinearity of predictor

244 variables, which was considered problematic if $r > 0.6$ (Bolker, 2008). In the case of

245 collinearity, the variable presenting the clearest *a priori* biological meaning was included in

246 the model while the other was excluded. All variables were tested for linear and quadratic

247 relationships, and those with a quadratic variable that reduced the Bayesian Information

248 Criterion (ΔBIC) by > 3 in comparison with the linear model were included as quadratics.

249 The full model included all biologically plausible interactions between factors.

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251

252   Following model selection, models within 3 ΔBIC of the top ranked model were

253 considered equivalent and model-averaged (Burnham and Anderson, 2002; Bolker, 2008).

254 Model averaging of this 'top model set' can provide a robust means of obtaining parameter

255 estimates (both point and uncertainty estimates) and making predictions (Burnham and

256 Anderson, 2002). Confidence intervals (95%) were calculated for the model-averaged

257 coefficients (Zuur *et al.*, 2009). For testing the significance of the parameters, variables were

258 defined as contributing significantly to the predictive model if their confidence intervals did

259 not overlap zero. The variation in the data explained by random effects was considered as

260 significant if 95% confidence intervals for the estimated intercept for individual groups (i.e.,

261 months or sites) overlapped the mean intercept value (Figure S1). The marginal coefficient of

262 determination ($R^2_{GLMM(m)}$), which indicates the variance explained by fixed factors, and

263 conditional coefficient of determination ($R^2_{GLMM(c)}$), which indicates the variance explained

264 by both fixed and random factors (Nakagawa and Schielzeth, 2013), were estimated. If the

265 values of $R^2_{GLMM(c)}$ were equal to or less than $R^2_{GLMM(m)}$, the random effects model was

266 simplified to a GLM to minimise problems of over-parameterisation (Zuur *et al.*, 2009).

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268

269   All analyses were performed in R version 3.1.1 (R Development Core Team) with

270 vegan (Oksanen *et al.*, 2015), lme4 (Bates *et al.*, 2012), Mumin (Bartoń, 2012), visreg

271 (Breheny and Burchett, 2013), effects (Fox, 2003), car (Fox and Weisberg, 2011), plotrix

272 (Lemon, 2006) and ggplot2 (Wickham, 2009) packages.

273

274

275 **RESULTS**

276

277

278 The composition of fish assemblages grouped according to habitat type (lagoon, reservoir and

279 river) when compared using the Bray-Curtis similarity metric, indicated by the proximity of

280 sites in the NMDS plot (Figure 2). Species associated with river sites included the Cascarudo

281 *Callichthys callichthys* (L. 1758), the catfishes *Hypostomus ancistroides* (Ihering 1911) and

282 *Hypostomus regani* (Ihering 1905), the headstanders *Leporinus octofasciatus* Steindachner

283 1915 and *Leporinus striatus* Kner 1858, the three-barbeled catfish *Rhamdia quelen* (Quoy &

284 Gaimard, 1824), the thorny catfish *Rhinodoras dorbignyi* (Kner 1855) and the golden dorado

285 *Salminus hilarii* Valenciennes, 1850. All other species were more closely associated with

286 dam and marginal lagoon sites, suggesting a preference amongst these species for lentic

287 conditions.

288

289

290   Each trophic group was sampled at all sites and on all days, although some species

291   were locally restricted in their distributions. For example the characin *Astyanax bockmanni*

292   Vari & Castro 2007, the catfish *Hypostomus nigromaculatus* (Schubart 1964) and the pacu

293   *Piaractus mesopotamicus* (Holmberg 1887) are omnivorous species that were not found in

294   reservoir sites (Table S3). Similarly, the piscivorous *C. kelberi* and trahiras *Hoplias*

295   *intermedius* (Günther 1864), the iliophagous catfish *Hypostomus margaritifer* (Regan 1908)

296   and the omnivorous headstander *Leporinus amblyrhynchus* Garavello & Britski 1987 were all

297   absent from marginal lagoons and river sites (Table S3).

298

299

300   Communities dominated by fish occupying higher trophic levels (piscivores,

301   omnivores and detritivores) were more strongly associated with the reservoir (mean > 1),

302   while communities dominated by lower trophic levels were associated with the river (mean <

303   1) (K-W test: chi-squared = 36.65, df = 7, p-value < 0.001; Fig. 3).

304

305

306   Species richness was poorly predicted by the selected explanatory variables,

307   underperforming relative to the intercept-only model (species richness $R^2 = 0.08$). Month

308   and site did not capture any additional variance in the data and therefore the species richness

309   model was simplified to a GLM. In contrast, the total number of individuals was better

310   predicted, with 38% of the variation in the data explained by environmental conditions,

311   increasing to 54% with the inclusion of month and site as random effects ($R^2_{GLMM(m)}= 0.38$,

312    $R^2_{GLMM(c)} = 0.54$). Specifically, the total abundance was predicted to decrease with increased

313   temperature, smaller sediment grain size, lower concentration of organic matter and

314   decreasing pH (Table II). Interactions among the predictor variables indicated that, with low

315   concentrations of nitrogen and phosphorous, the number of individuals decreases with

316   increasing chlorophyll a, while at high concentrations of these nutrients, the relationship

317   switches to an increase in individuals with increasing chlorophyll a (Fig. 4a, b). The presence

318   of non-native fish species did not contribute significantly in any of these models.

319

320

321   Contrary to the whole assemblage metrics, the presence of non-native fish played a

322   important role in predicting the abundance of four of the six trophic groups: detrivores,

323   herbivores, omnivores and piscivores (Table II). Across the models, the environmental

324   conditions and the presence of non-native fish together explained 13% to 64% ($R^2_{\text{GLMM}(m)}$)

325   and, when random effects were also included, explained 35% to 89% ($R^2_{\text{GLMM}(c)}$) of the

326   variation in the data (Table II). The contribution of environmental predictors varied

327   substantially among groups but all models included a significant contribution from at least

328   one environmental predictor. Interactive effects between chlorophyll-a and nitrogen (Fig.

329   4d,f,h) and between temperature and nitrogen (Fig. 4c,e,g) were extremely weak, with large

330   confidence intervals, so we will not discuss them further in this paper.

331

332

333   Iliophagous, herbivores and detritivores were well predicted with more than 30% of

334   the variation in the data ($R^2_{\text{GLMM}(m)}$ = 0.64, $R^2_{\text{GLMM}(m)}$ = 0,32, $R^2_{\text{GLMM}(m)}$ = 0.31). Herbivores

335   and detritivores had their habitat characterised by smaller sediment grain size and was less

336   likely to harbour non-native fish. Detritivores were associated with water that was more

337   saline (higher conductivity), more acidic (lower pH), and lower in chlorophyll-a

338   concentrations. Herbivores were primarily associating abundance with lower conductivity,

339   higher pH, more phosphorous and lower chlorophyll-a concentrations. Iliophagous species

340   were specifically associated with higher temperatures and lower productivity, indicated by

341   negative coefficients of phosphorous and organic matter, and tended to be found in sites with

342   non-native fish. Omnivores and piscivores were better predicted (omnivore $R^2_{GLMM(m)}$ =

343   0.40, piscivore $R^2_{GLMM(m)}$ = 0.59) in habitats with smaller grain sizes but otherwise showing

344   little overlap in association. Piscivores were more likely to be found in waters with higher

345   likelihood for the presence of non-native fish (See Table II for coefficient values).

346   Insectivores were poorly predicted ($R^2_{GLMM(m)}$ = 0.13) by environmental conditions and the

347   presence of non-native fish; their only association was with less saline waters.

348

349

350   Including random effects in these models had different impacts across trophic groups.

351   Detritivore, insectivore and omnivore abundances were much better predicted by the

352   inclusion of month and site, increasing the percent of variation explained by 23%, 22% and

353   49% respectively. Herbivore abundance was not improved at all by adding random effects,

354   while amount of variation explained in the iliophage and piscivore abundance data was

355   increased by 11% and 9% respectively.

356

357

358   **DISCUSSION**

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360

361   This study presents species and community metrics comparing the lagoon, reservoir and

362   tributaries in the Jurumirim Reservoir. The results obtained by NMDS analysis suggest that

363   species are segregated into these different habitats. The results of the GLMM models

364   furthermore suggest trophic level is a more appropriate monitoring tool for describing

365 ecological status than species richness. While no significant relationship was found between

366 species richness and the abiotic factors considered here, trophic level did correlate with the

367 different conditions. This suggests that more information relevant to understanding and

368 describing the ecological status of the different fish communities in the reservoir system is

369 contained in the trophic level metrics than in species richness. Specifically, differences in the

370 relative abundances of fish were found (Fig. 3), highlighting different trophic structures

371 among the different habitats identified. Predators from higher trophic niches and detritovores

372 dominated in lentic habitats (reservoir), while fishes occupying lower trophic levels

373 dominated in other habitats and thus, the inverted trophic hypothesis (McCauley *et al.*, 2018)

374 was supported.

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377 RELATIONSHIP BETWEEN FISH DISTRIBUTIONS AND ENVIRONMENTAL

378 PARAMETERS:

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381 The interaction analyses reported indicate possible relationships between some

382 environmental parameters and different fish groups. We consider here to what degree these

383 relationships might be causal. When there is a pattern, we justified the distribution of trophic

384 groups considering the variation of environmental parameters that respond quantitatively the

385 anthropic actions, impoundment and fish introductions.

386

387

388 Total nitrogen concentration was found to be a better predictor of herbivorous,

389 iliophagous and omnivorous fish than it was of phytoplankton biomass (chlorophyll-a

390 concentration). As there is no *a priori* reason to expect total nitrogen to directly influence the

391 abundance of these fish groups, it is assumed that high concentrations of total nitrogen serve

392 here as a proxy for identifying habitats with a high abundance of organic material and/or high

393 remineralization rates of nitrogen, i.e. conditions that would be attractive for all three trophic

394 groups, which appeared to increase in habitats with high total nitrogen, i.e. typically lotic

395 conditions (Table S1).

396

397

398   A decrease in iliophagous fish (but a slight increase in herbivores) was detected in

399 relation to increased phosphorous concentrations. Generally, higher phosphorous

400 concentrations were noted under river as compared to reservoir conditions. The release or

401 uptake of phosphorous into the water column in the river channel is associated with biotic

402 components of the system (periphyton and vascular plants) and bottom sediments (Correll,

403 1998). Once delivered to a reservoir, phosphorous is usually stored in the bottom sediments.

404 The results of the current study are consistent with previous work which has shown that the

405 phosphorous-fish relationship can be the result of changes occurring at the base of the food

406 web (i.e., primary production) in response to changed nutrient conditions in an oligotrophic

407 system (Karlsson *et al.*, 2009), as in Jurumirim.

408

409

410   We found that not only the increase of conductivity is associated with sedimentation

411 and reduced nutrient cycling (Dunlop *et al.*, 2005) but also the pH and organic matter. With

412 respect to the latter two parameters, the variations of values might be explained as being a

413 consequence of the sedimentation in tributaries and the buffering nature of the reservoir. The

414 flow of water influences fluvial erosion, which promotes sedimentation (Henry, 2014). The

415 deposition of fine sediment and organic matter in the lentic regions is greater than that in lotic

416 regions (Table S1). The deposition of fine sediment on the substrate in a habitat affects all

417 trophic levels. The river acidity levels were associated with sedimentation rates. However,

418 the differences in acidity were not high enough to affect the abundance of herbivorous and

419 omnivorous fish. In case of a more accentuated acidification, the phytoplankton biomass

420 could be low, which could led to a simplification of the zooplankton association, which, in

421 turn, could limit many fish species (Hendrey et al., 1976).

422

423

424   Piscivores and non-native fishes have earlier been reported, as was also observed in

425 this study, to be dominant in deeper zones and in lentic environments (Matthews, 1998).

426 Non-native fishes was not a variable exclusively pertinent to piscivorous fishes. They may

427 also be omnivorous, iliophagous and herbivorous. In case of the trophic interactions of native

428 and introduced piscivorous fish, Fugi et al. (2008) noted coexistence between these groups.

429 They argued that this was due to prey and resource overlap being small between the

430 introduced and the native species.

431

432

433   Iliophagous fish were found in our study to be more likely to coexist with non-native

434 fish than detritivores. The detritivorous and iliophagous categories were separated in the

435 analysis because different factors may influence the feeding by grazers that live on algae and

436 consumers of detritus (Bowen, 1984; Flecker, 1996). In the case of the relationship between

437 iliophagous and non-native fish in our study, however, the iliophagous fish are all represented

438 by loricariids with scutes and they are harder to prey upon than naked or scale-covered fish.

439 The occurrence of non-native fishes may be an important predictor of abundance and

440   diversity of other species but the knowledge of potential effects of these non-native species is

441   still limited.

442

443

444   IMPLICATION FOR USING TROPHIC LEVELS AS A MEASURE OF STOCK

445   MANAGEMENT:

446

447

448   The Upper Paranapanema River basin has experienced the introduction of lacustrine species

449   through fish stocking (Miranda, 2001). Native and non-native fish stocking has occurred

450   since the 1980s in the Jurumirim Reservoir (CESP, 1996). Between 1999 and 2012, a Duke

451   Energy Company stocking program added more than 19 million young fish representing the

452   native species *P. mesopotamicus*, *S. hilarii*, *Prochilodus lineatus* (Valenciennes, 1837),

453   *Leporinus friderici* (Bloch, 1794), *Leporinus obtusidens* (Valenciennes, 1837), and *Brycon*

454   *orbignyanus* (Valenciennes, 1850) to the reservoirs and tributaries of the Paranapanema River

455   with the aim of building sustainable populations fully adapted to life in the river (Duke

456   Energy, 2013). It is shown by our study that, with the exception of *B. orbignyanus* (Fig 2),

457   these species are now widely distributed. *L. friderici* for example*,* was found in high

458   abundances in the reservoir, where most other herbivores were not as frequent. The success

459   of these populations might, therefore, be due to the stocking program. The non-native fish

460   stocking is not authorized; however introductions are still occurring. It is not by chance that

461   our study denounces the occurrence of 6 species.

462

463   If a trophic level ratio metric becomes adopted as a management tool, it might be

464   possible to use the ratio to identify the trophic profile of species most likely to succeed in

465   potential stocking initiatives in different areas. The choice of species for fish stocking

466   programs should respect the habitat preferences of different trophic groups in order to avoid

467   changing natural community structure. A fish index developed based on the distribution of

468   different trophic levels might serve as a practical tool in relation to fish stock management

469   for reservoirs with a similar range of environmental conditions as those in the range as in the

470   Jurumirim reservoir system. However, the use of secondary data on trophic information of

471   the fish species should be limited seeking local veracity due to the existence of a trophic

472   plasticity. In our case, it was valuable to use data already published, since they would

473   complement the information gap of the empirical analysis, being a literature with the area of

474   study of the same hydrographic basin or approximations and the trophic plasticity occurring

475   within the spectrum that defines each group.

476

477

478   The data presented here suggest that fish management in freshwaters (reservoirs and

479   tributaries) should ideally be designed to deal with each habitat type individually. The trophic

480   level (as a proxy for functional index) may be a more pratical and appropriate tool for

481   monitoring the local fish communities when traditional species-based diversity metrics, for

482   example species richness, do not respond. In this study, we found that a substantial portion of

483   the variation in abundances of individuals and trophic groups was explained by

484   environmental conditions or the presence/absence of alien fish species. Thus, the simple

485   trophic metric describing the relative proportion of fish from the highest trophic levels in the

486   community used here provides a useful tool for monitoring changes in the functional

487   structure of the communities present.

488

489

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691

692   SUPPORTING INFORMATION

693

694

695   Additional Supporting Information is found in the online version of this article:

696   Environmental variation analysis include Table S1; List of fish species include Table S2 and

697   Table S3; Confidence intervals of model-average coefficients for interception of random

698   variables in Figure S1.

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709   Figure 1. Sampling locations and qualitative description of all sites on Jurumirim Reservoir,

710   Brazil: red arrow indicates the dam of the hydroelectric plant.

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712   Figure 2. Ordination of fish species composition by Nonmetric Multi-Dimensional Scaling

713   (NMDS) of Bray-Cutis distances (k = 2, stress ≈ 10%). The ordination is based on 31 fish

714   species abundance sampled from 100 observations in the Jurumirim Reservoir, Upper

715   Paranapanema River, São Paulo, Brazil. Fish species are plotted in blue. Confidence ellipses

716   are shown for each group at a confidence interval of 95%. Acronyms for the respective

717   species are represented in Table S2.

718

719   Figure 3. Box-plots of the ratio of biomass (a) and number of individuals (b) to higher and

720   lower trophic groups to each habitat type and over the months. Lower trophic groups =

721   herbivores, iliophagous, insectivores; higher trophic groups = piscivores, omnivores,

722   detritivores.

723

724   Figure 4. The interaction effect of explanatory variables (x-axes) for the response variables

725   (y-axes). The range of variables was fixed at four constants to visualize the interactions:

726   black - small, blue - small/mid, purple - mid/large and orange - large values. The interaction

727   values were centered and scaled as all numerically predicted variables.

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736   Figure 1

Localization	Limnologic aspect	Habitat type	Code
Paranapanema	lotic	main channel / rectilinear margin	ri1
Paranapanema	lotic	main channel / meandering margin	ri2
Sete Ilhas	lentic	marginal lagoon/circular margin	la1
Poço das Pedras	lentic	marginal lagoon/irregular margin	la2
Jurumirim	lentic	reservoir/upper	re1
Jurumirim	lentic	reservoir/middle	re2
Jurumirim	lentic	reservoir/lower (next to hydrelectric plan)	re3
Taquari	lotic	tributary, rectilinear and shallow margin with forest fragment	ri3
Taquari	lotic	tributary, meandering and deep	ri4
Taquari	lentic	tributary, beginning of the flood plain	re4
Veados	lentic	tributary, meandering and shallow	ri5
Veados	lentic	tributary, beginning of the flood plain	re5
Veados	lentic	tributary, flood plain and wide	re6
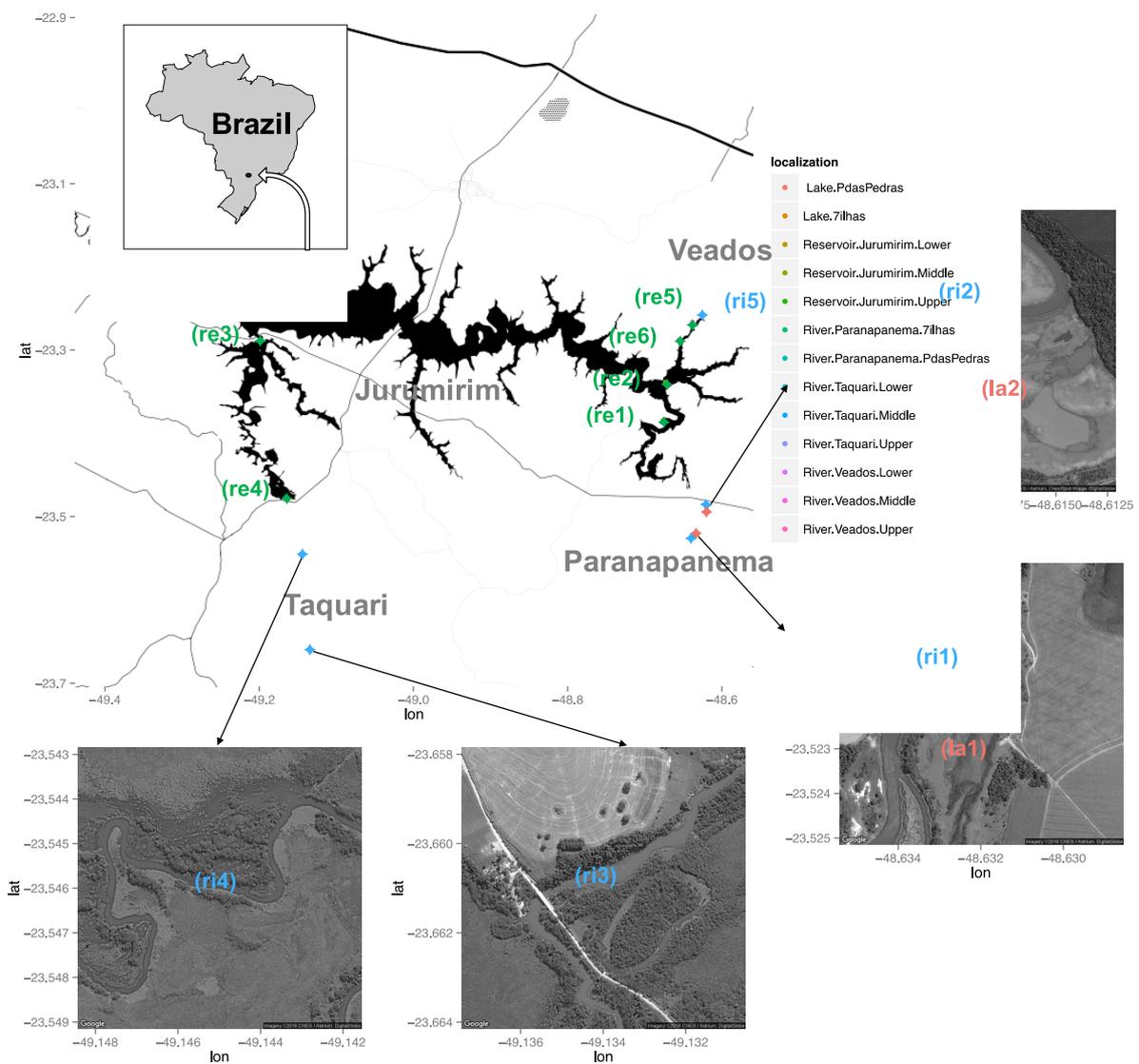
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741   Figure 2
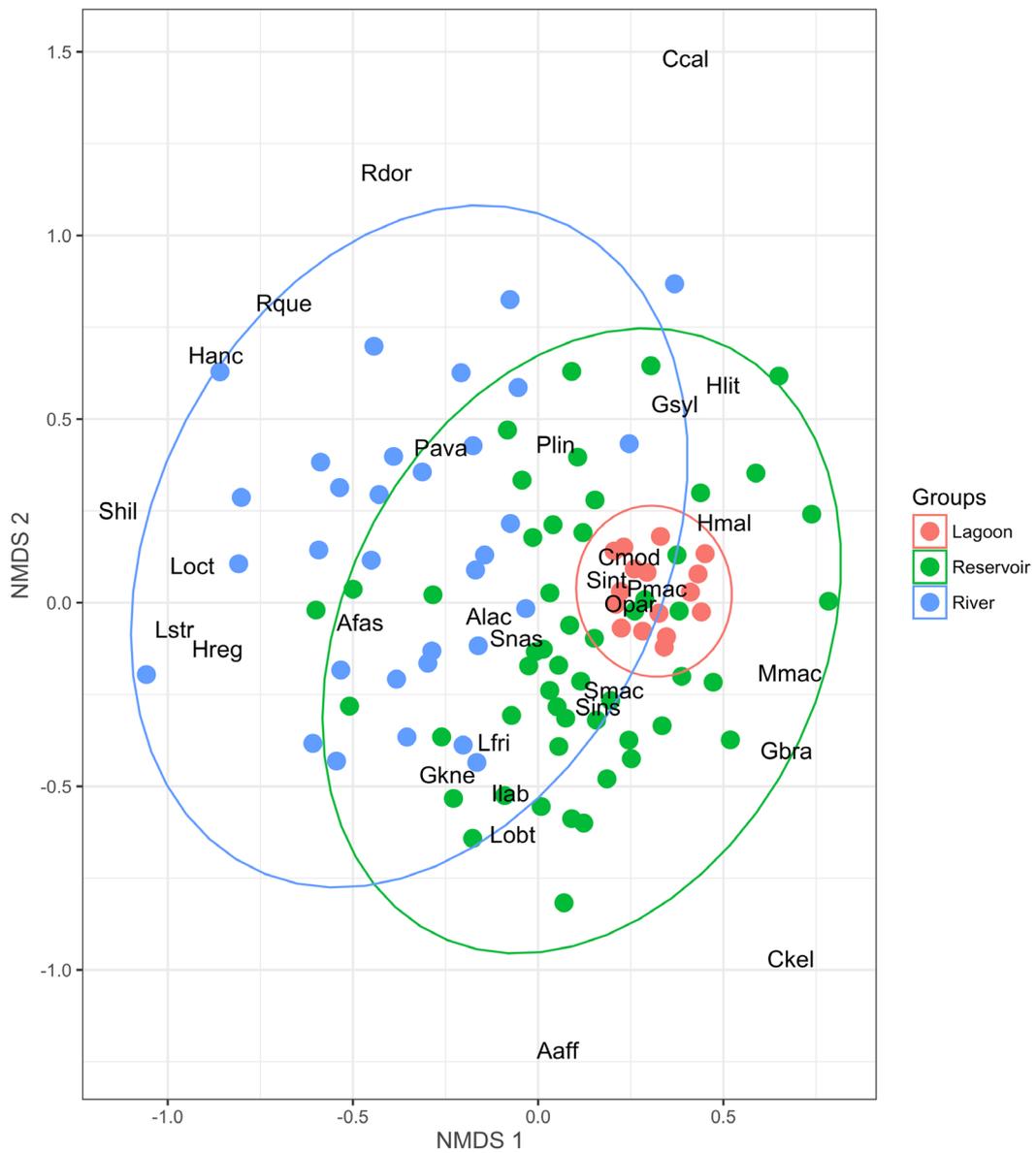
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752   Figure 3
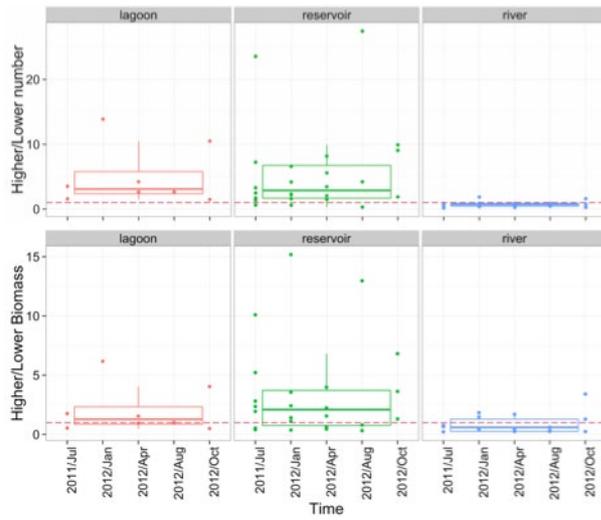
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Figure 4