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Species richness and functional structure of fish assemblages in three freshwater habitats: effects of environmental factors and management

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Abstract

In this study, the inverted trophic hypothesis was tested in the freshwater fish communities of a 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 multi-dimensional scaling (NMDS). The influence of environmental conditions for multiple fish assemblage response variables (richness, total abundance and abundance per trophic group) was tested using generalised linear mixed models (GLMM). The metric typically employed to describe diversity; that is, 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

1 | INTRODUCTION

There is increasing recognition, not least by the UN Convention on Biological Diversity, of a need for the management of the effects 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 (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 (Austen *et al.*, 1994; Noble *et al.*, 2007). The benefit of the functional aspects over the taxonomic diversity indices 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 & Watling, 1982). Another motive for use of functional structure analysis is that anthropogenic actions have a major influence on community biomass distributions (McCauley *et al.*, 2018). The measurement 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 examined using both traditional biodiversity indices (species richness) and the relative dominance of different trophic feeding groups as a proxy for the functional structure of the assemblage in an attempt to assess the applicability of these two measures in the assessment of the fish biodiversity.

The Jurumirim Reservoir consists of heterogeneous environments both in terms of structure and dynamics, for example, distinct lacustrine and riverine zones (Henry, 2014). Lacustrine sites are characterised by deep water, a vertically stratified water column and limited nutrient availability in the well-lit surface waters, which keeps primary production at a relatively low level (Zanata & Espíndola, 2002). Riverine sites, located in the tributaries, are usually limited in transparency of water; that is, sediment transport processes in these areas are affected by water flow, erosion and rains, and also have relatively low primary productivity (Wetzel, 2001). Marginal lagoons, located alongside the river channel, represent lentic waters with high rates of primary productivity and sediment deposition (Henry, 2014). Reservoirs, tributaries and marginal lagoons, in combination, represent a large range of environmental variability (Franklin, 2010; Hartley *et al.*, 2010). They can be well suited for elucidating studies about habitat filtering and species sorting (Erős *et al.*, 2017;

Vanschoenwinkel *et al.*, 2010), while fish species and community composition can be analysed in relation to environmental variables (O'Sullivan & Reynolds, 2008; Thornton *et al.*, 1990; Wetzel, 2001). These parameters are ideal for discerning the ecological preferences of the ichthyofauna, which are potentially exposed to distinct ranges of environments reflected in different community compositions and relative abundances. In other words, the fish are not simply found in a specific environment because they had no other choice of environment.

The reservoir examined in this study was created following the construction of a dam in the mid-20th Century. The changing habitat conditions following creation of the dam led to changes in fish distributions in the period immediately following dam construction. Since 1974, the upper Paranapanema Basin has been classified as having excellent water quality and resources when compared with other basins within industrial or agriculture regions of Brazil (Carvalho, 2009), which means it offers an interesting study system in which to explore variation in functional structure in relation to environmental conditions. Over the past three decades, the intensity of fishing, the fish stocking, the fish-cage farming and the introduction of non-native species have promoted changes in the fish composition, although physical conditions in the reservoir system have remained essentially unchanged (Nogueira *et al.*, 2014). Fishing in the Jurumirim Reservoir had been represented by a little subsistence and sport fishing, the latter being related to tourism in the area (Novaes & Carvalho, 2009). The intensity of fishing in the reservoir was previously estimated at 15.7 kg ha^{-1} year^{-1} with catch per unit effort (CPUE) values estimated at 10.5 kg fisherman^{-1} day^{-1} (Novaes & Carvalho, 2009; Schork *et al.*, 2013). The increase of fish-cage farming in Jurumirim is estimated at 2460 t year^{-1}, considering the current rate of production and growth potential relative to new aquaculture parks, in which the Nile tilapia *Oreochromus nilotucus* (L. 1758) is the main farmed species (Montanhini *et al.*, 2015). Data on intentional fish stocking indicate 7,102,057 individuals belonging to six non-native fish species (*Astronotus crassipinnis* (Heckel 1840), *Cyprinus carpio* L. 1758, *Sorubim lima* (Bloch & Schneider 1801), *Schizodon borellii* (Boulenger 1900), *Triportheus angulatus* (Spix & Agassiz 1829), *O. niloticus* and *Hoplias lacerdae* Miranda Ribeiro 1908) were released into the reservoir between 1978 and 1992 (Garcia *et al.*, 2017).

In the Jurumirim Reservoir system, alien fish species have been introduced for a variety of purposes; that is, enhancement of sport fishing, aquaculture, stock management and to support an aquarium trade. Yellow tucunare *Cichla kelberi* Kullander & Ferreira 2006 has been illegally released for sport fishing. This species is generally piscivorous and potentially influences ecosystems by increasing the predation pressure on lower trophic levels (Santos *et al.*, 1994). *Oreochromus nilotucus* has escaped from aquaculture facilities. This species normally occupies lower trophic levels and can influence ecosystems through changes in primary production and water transparency (Vitule *et al.*, 2009). These two species are examples of the fact that the functional types (sizes, dietary preferences, *etc.*) of introduced fish species can be quite different and can have distinct influences on

ecosystems and the diversity of native fish (Latini & Petrere, 2004; Pelicice & Agostinho, 2009; Vitule *et al.*, 2009).

These anthropogenic actions can facilitate the top-heaviness of trophic levels through the introduction of novel consumers (McCauley *et al.*, 2018). Piscivores and detritivores could be dominant in the reservoir as a whole, while herbivores could dominate in the riverine habitat. Thus, it is expected that the proportion of upper trophic levels is higher in the reservoir than in the riverine habitat, demonstrating a trophic inversion in the fish communities. Some studies have reported inverted trophic pyramids or inverted trophic biomass pyramids for fish groups (McCauley *et al.*, 2018). In this present study, the inverted trophic hypothesis was tested in the freshwater fish communities of the reservoir. The relative proportion of fish feeding at high and low trophic levels would differ in the different habitats of the Jurumirim Reservoir and that the proportion of fish from high–low trophic levels would be influenced by the physical conditions in the reservoir and by the presence of alien species. The aims of this study were to describe and compare the distribution of the fish communities in the different habitat types through NMDS and to explain these differences by analysing the effects of environmental and anthropogenic gradients.

2 | MATERIALS AND METHODS

The sampling programme, including the capture of live fish, was reviewed and authorised by the animal ethics committee, Sistema de Autorização e Informação em Biodiversidade (SISBIO) linked to Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA), a Brazilian governmental entity that deals with environmental policies; the SISBIO licence has the registration number: 15549Q1.

2.1 | Study area

The dam for the Jurumirim hydroelectric plant was built on the upper Paranapanema River in the late 1950s near the convergence of the Paranapanema and Taquari Rivers (Carvalho, 2009). The associated Jurumirim Reservoir, which is under state protection, is fed by 10 tributaries and has a flooded area of 484 km^2 with a perimeter of 1115 km. Its volume is 7.2 billion m^3 and it has a mean depth of 12.90 m (maximum 40 m), with a drainage area of *c.* 17,800 km^2. Twenty-eight municipalities are situated within the basin catchment with a combined population of over 2.5 million inhabitants (Nogueira *et al.*, 1999). Therefore, this area is of high importance for providing ecosystem services to the local region, for example, hydropower, quantity and quality of clean water, food supply and recreation potential.

2.2 | Data collection and preparation

Fish and environmental samples were collected at 13 sites throughout the Jurumirim Reservoir system (Figure 1; 23–24°S, 48–49°W) every 3 months from April 2011 to January 2013, generating a total of 104 sample sets. Sites were selected to represent the heterogeneity of limnological habitats found in the reservoir system. Another condition used in site selection was that the sites should meet the requirements for effective and reliable gillnet capture. Environmental conditions monitored at these sites included physical and chemical properties, nutrient concentrations and the characterisation of bottom sediments (Supporting Information Table S1 in File S1). Temperature, conductivity, dissolved oxygen, nutrients and chlorophyll concentration were measured at a depth of 1 m. Fish gillnets were retrieved after a fishing period of 18 h. Catches were identified and weighed following the taxonomy of Graça and Pavanelli (2007). Based on these data, species richness and total number of individuals were calculated for each site (Krebs, 1989).

In order to explore the functional structure of the species assemblages, each species was assigned to a trophic group according to the following trophic categories: detritivorous (Mérona & Rankin-de-Mérona, 2004), herbivorous (Castro, 1997) insectivorous, piscivorous (Williams *et al.*, 1998), omnivorous (Mérona & Rankin-de-Mérona, 2004) and iliophagous (*i.e.*, a diet of microorganisms and organic matter within muddy substrate; Hahn *et al.*, 1998). The digestive tract of each captured fish was examined and the stomach contents were analysed using a stereo-optic microscope. Food items were weighed and classified according to the alimentary index (I_A%) proposed by Kawakami and Vazzoler (1980): I_A% = $100(F_i M_i)(\Sigma F_i M_i)^{-1}$, where: i = 1, 2 ... n, F_i is the frequency of occurrence of food item i (%); M_i is the wet mass of item i (%). The dominant group of food items (highest I_A%) was used to define the trophic group for all species for which this study had a sample size of at least four individuals (60% of the species). For the 40% of species with too few samples (< four individuals with stomach contents) to establish the trophic group from gut contents, trophic group classification was based on published data (published before March 8th 2019; *e.g.*, journal articles, university theses, books and FishBase; Supporting Information Table S2 in File S1).

2.3 | Statistical analysis

In order to describe the similarity in fish assemblages among the sites visually, non-metric multidimensional scaling (NMDS) was used in two dimensions with 999 permutations. This allowed us to find the optimal placement of sites and species, so that the more similar two species assemblages are, the closer the sites are the in two-dimensional plot of the NMDS (Oksanen *et al.*, 2015). Similarity was calculated from the species composition data using Bray-Curtis distance because it is robust with respect to bias induced by differences in sampling effort (Faith *et al.*, 1987). Sites that were most similar to one another in species composition are closest together on the NMDS plot (Figure 2; Oksanen *et al.*, 2015).

The trophic inversion hypothesis (McCauley *et al.*, 2018) for fish community structure in reservoirs was tested by comparing the ratios of the distributions of biomass and the abundance of fishes occupying higher and lower trophic levels, where predatory and detritivorous fish species (piscivorous, omnivorous and detritivorous), were defined as eating at the higher trophic levels. Fish belonging to the remaining

| 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
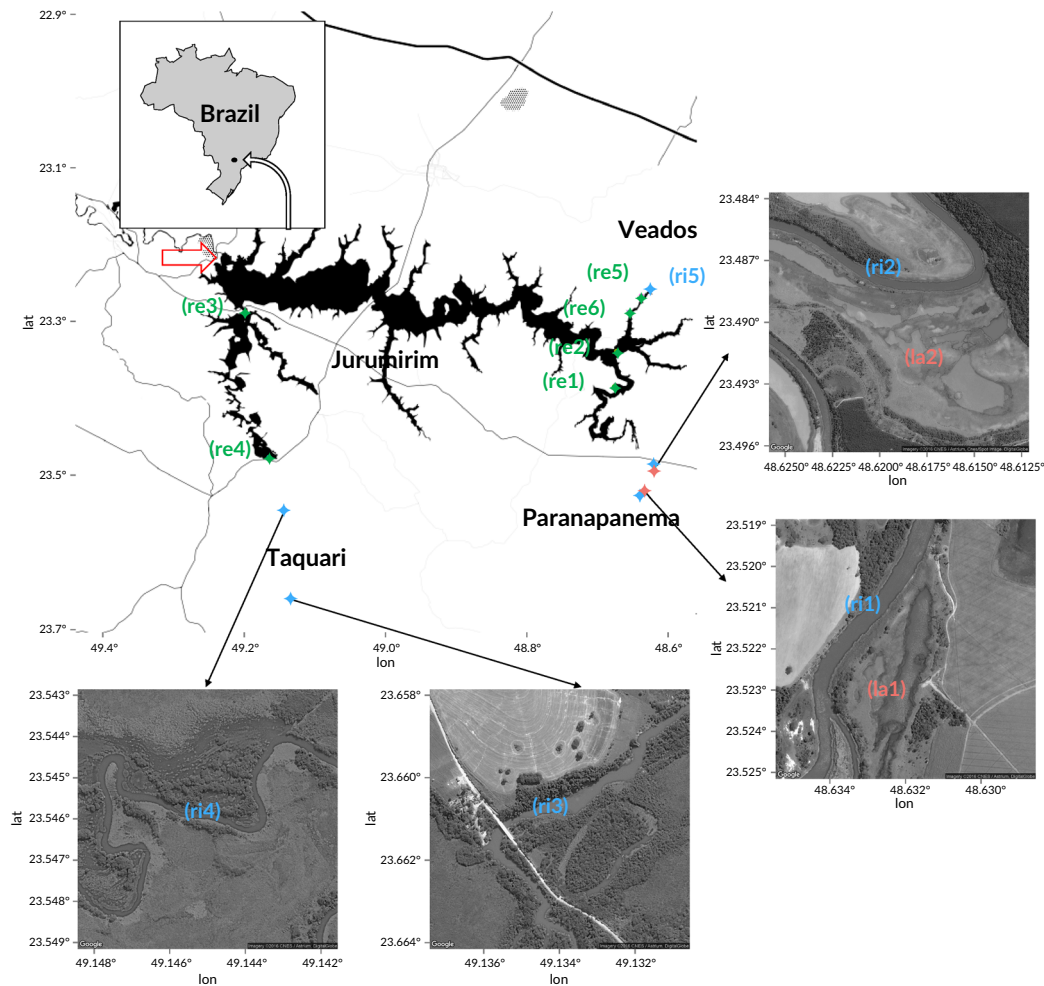
FIGURE 1 Sampling locations and qualitative description of all sites on Jurumirim Reservoir, Brazil: ⇩, The dam of the hydroelectric plant

groups (herbivores, iliophages and insectivores) were considered to be eating at lower trophic levels. Ratios approaching 1 indicate a balanced distribution in the community between higher and lower trophic groups. The fish trophic levels ratio across different habitat types were compared using the Kruskal-Wallis test.

Based on previous analyses that identified important environmental conditions for predicting fish species richness and abundance (Griffiths, 2012), 11 abiotic variables from the set of 21 variables collected were selected as predictors (Table 1). Broadly speaking, these variables represent changes in limnological conditions associated with damming. Using them therefore enables us to identify the importance of limnological gradients for determining species assemblages. Because the presence of non-native fish species can strongly influence the structure of resident fish assemblages (Britton & Orsi, 2012; Vitule *et al.*, 2009), the presence of *C. kelberi*, the jewel tetra *Hyphessobrycon eques* (Steindachner 1882), the silver dollar *Metynnis maculatus* (Kner 1858), *O. nilotucus*, the catfish *Pterygoplichthys ambrosetti* (Holmberg 1893) or the red-breasted tilapia *Coptodon*

FIGURE 2 Ordination of fish species composition by nonmetric multi-dimensional scaling (NMDS) of Bray-Cutis distances (k = 2, stress = *c.* 10%). The ordination is based on 31 fish species abundance sampled from 100 observations in the Jurumirim Reservoir, upper Paranapanema River, São Paulo, Brazil. Confidence interval (95%) ellipses are shown for each group, Aaff, *Apareiodon affinis*; Aalt, *Astyanax altiparanae*; Aboc, *Astyanax bockmanni*; Afas, *Astyanax fasciatus*; Ccal, *Callichthys callichthys*; Ckel, *Cichla kelberi*; Cmod, *Cyphocharax modestus*; Cren, *Coptodon rendalli*; Etri, *Eigenmannia trilineata*; Gbra, *Geophagus brasiliensis*; Gkne, *Galeocharax knerii*; Gsyl, *Gymnotus sylvius*; Hanc, *Hypostomus ancistroides*; Hequ, *Hyphessobrycon eques*; Hint, *Hoplosternum littorale*; Hlit, *Hoplosternum littorale*; Hmal, *Hoplias malabaricus*; Hmar, *Hypostomus margaritifer*; Hnig, *Hypostomus* cf. *nigromaculatus*; Hpau, *Hypostomus aff. Paulinus*; Hreg, *Hypostomus regain*; Ilab, *Iheringichthys labrosus*; Lamb, *Leporinus amblyrhynchus*; Lfri, *Leporinus friderici*; Lobt, *Leporinus obtusidens*; Loct, *Leporinus octofasciatus*; Lstr, *Leporinus striatus*; Mmac, *Metynnis maculatus*; Onil, *Oreochromis niloticus*; Opar, *Oligosarcus paranensis*; Pamb, *Pterygoplichthys ambrosetti*; Pava, *Pimelodella avanhandavae*; Plin, *Prochilodus lineatus*; Pmac, *Pimelodus maculatus*; Pmes, *Piaractus mesopotamicus*; Rdor, *Rhinodoras dorbignyi*; Rque, *Rhinodoras dorbignyi*; Rque, *Rhamdia quelen*; Shil, *Salminus hilarii*; Sins, *Steindachnerina insculpta*; Sint, *Schizodon intermedius*; Smac, *Serrasalmus maculatus*, Snas, *Schizodon nasutus*. Groups (●) Lagoon, (●) Reservoir, and (●) River
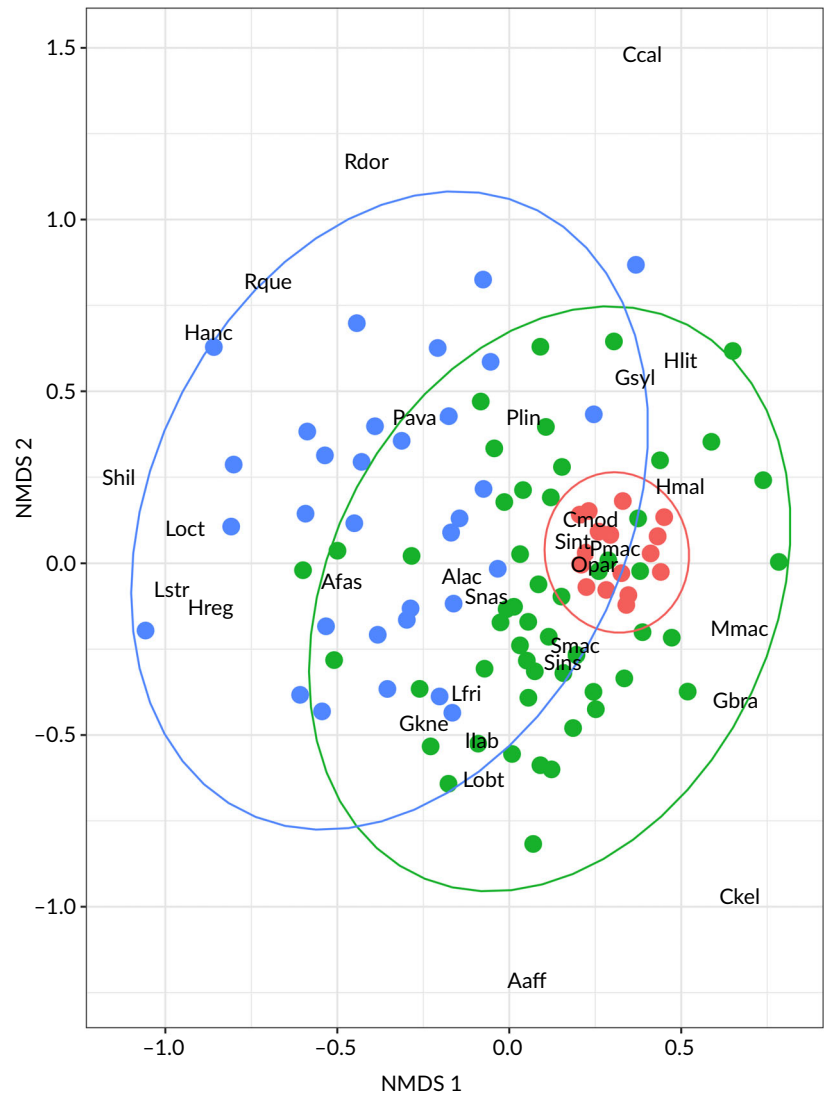
rendalli (Boulenger 1897) was also included as a binary predictor variable (Supporting Information Table S2 in File S1).

Generalised linear mixed models (GLMM; Logan, 2011) were generated to determine the potential for these variables to predict multiple aspects of the assemblage (species richness, abundance of individuals across all species and abundance of individuals within trophic groups), which resulted in eight models. Month and site were included as random effects to account for spatial and temporal autocorrelation (Zuur *et al.*, 2009). To meet the conditions of multiple regression, data were checked for normality and homogeneity of variance and then transformed with log (x + 1). Outliers were checked for using Cook's distance for each variable (Logan, 2011); the outliers were deleted so that the resulting data matrix had the same number of observations for each variable but no outliers. To ease the comparison of coefficients among the predictor variables, those measured on a continuous scale were normalised to be centred at zero with a SD = 1 (Bolker, 2008). Pearson and Spearman correlations were generated to test for multicollinearity of predictor variables, which was considered problematic if r > 0.6 (Bolker, 2008). In the case of collinearity, the

variable presenting the clearest *a priori* biological meaning was included in the model while the other was excluded. All variables were tested for linear and quadratic relationships and those with a quadratic variable that reduced the Bayesian information criterion (ΔBIC) by >3 in comparison with the linear model were included as quadratics. The full model included all biologically plausible interactions between factors.

Following model selection, models within 3 ΔBIC of the top ranked model were considered equivalent and model-averaged (Bolker, 2008; Burnham & Anderson, 2003). Model averaging of this top-model set can provide a robust means of obtaining parameter estimates (both point and uncertainty estimates) and making predictions (Burnham & Anderson, 2003). Confidence intervals (95%) were calculated for the model-averaged coefficients (Zuur *et al.*, 2009). For testing the significance of the parameters, variables were defined as contributing significantly to the predictive model if their confidence intervals did not overlap zero. The variation in the data explained by random effects was considered as significant if 95% confidence intervals for the estimated intercept for individual groups (*i.e.*, months or

TABLE 1 Equipment and methodology used to obtain quantitative environmental data

Environmental factors	Measurement		
	Equipment or methodology	Location	Measure Unit
Abiotic			
Physico-chemical parameters of the water			
Transparency	Secchi disk	Field	m
Dissolved oxygen	HORIBA multiparameter sensor	Field	Mg l^{-1}
Temperature	HORIBA multiparameter sensor	Field	°C
Electric conductivity	HORIBA multiparameter sensor	Field	μS cm^{-1}
pH	HORIBA multiparameter sensor	Field	pH
Nutrients dissolved in water			
Total phosphorus	Golterman et al., 1978	Laboratory	μg l^{-1}
Total nitrogen	Golterman et al., 1978	Laboratory	μg l^{-1}
Suspended material	Teixeira et al., 1965	Laboratory	mg l^{-1}
Chlorophyll-a	Golterman et al., 1978	Laboratory	μg l^{-1}
Bottom sediment			
Granulometry (fine grain size)	Wentworth (1922), Suguio and Suguio (1973)	Laboratory	%
Organic matter	Wentworth (1922), Suguio and Suguio (1973)	Laboratory	%
Biotic			
Non-native fish	Species identification Langeani et al. (2007), Reis et al. (2003)	Field	Binary (Presence (1) and absence (0))

sites) overlapped the mean intercept value (Supporting Information Figure S1). The marginal coefficient of determination ($R^2_{\text{GLMM}(m)}$), which indicates the variance explained by fixed factors and conditional coefficient of determination ($R^2_{\text{GLMM}(c)}$), which indicates the variance explained by both fixed and random factors (Nakagawa & Schielzeth, 2013), were estimated. If the values of $R^2_{\text{GLMM}(c)}$ were equal to or less than $R^2_{\text{GLMM}(m)}$, the random effects model was simplified to a GLM to minimise problems of over-parameterisation (Zuur et al. 2009).

All analyses were performed in R 3.1.1 (www.r-project.org) with vegan (Oksanen et al., 2015), lme4 (Bates et al., 2014), Mumin (Bartón, 2014), visreg (Breheny & Burchett, 2012), effects (Fox, 2003), car (Fox & Weisberg, 2010), plotrix (Lemon, 2006) and ggplot2 (Wickham, 2009) packages.

3 | RESULTS

The composition of fish assemblages grouped according to habitat type (lagoon, reservoir and river) when compared using the Bray–Curtis similarity metric, indicated by the proximity of sites in the NMDS plot (Figure 2). Species associated with river sites included the Cascarudo Callichthys callichthys (L. 1758), the catfishes Hypostomus ancistroides (Ihering 1911) and Hypostomus regani (Ihering 1905), the headstanders Leporinus octofasciatus Steindachner 1915 and Leporinus striatus Kner 1858, the three-barbelled catfish Rhamdia quelen (Quoy & Gaimard, 1824), the thorny catfish Rhinodoras dorbignyi (Kner 1855) and the golden dorado Salminus hilarii Valenciennes, 1850. All

other species were more closely associated with dam and marginal lagoon sites, suggesting a preference among these species for lentic conditions.

Each trophic group was sampled at all sites and on all days, although some species were locally restricted in their distributions. For example the characin Astyanax bockmanni Vari & Castro 2007, the catfish Hypostomus nigromaculatus (Schubart 1964) and the pacu Piaractus mesopotamicus (Holmberg 1887) are omnivorous species that were not found in reservoir sites (Supporting Information Table S3 in File S1). Similarly, the piscivorous C. kelberi and trahiras Hoplias intermedius (Günther 1864), the iliophagous catfish Hypostomus margaritifer (Regan 1908) and the omnivorous headstander Leporinus amblyrhynchus Garavello & Britski 1987 were all absent from marginal lagoons and river sites (Supporting Information Table S3 in File S1).

Communities dominated by fish occupying higher trophic levels (piscivores, omnivores and detritivores) were more strongly associated with the reservoir (mean > 1), while communities dominated by lower trophic levels were associated with the river (mean < 1; K-W test: $\chi^2 = 36.65$, df = 7, P < 0.001; Figure 3).

Species richness was poorly predicted by the selected explanatory variables, underperforming relative to the intercept-only model (species richness $R^2 = 0.08$). Month and site did not capture any additional variance in the data and therefore the species richness model was simplified to a GLM. In contrast, the total number of individuals was better predicted, with 38% of the variation in the data explained by environmental conditions, increasing to 54% with the inclusion of month and site as random effects ($R^2_{\text{GLMM}(m)} = 0.38$, $R^2_{\text{GLMM}(c)} = 0.54$).

FIGURE 3 Box plots (——, median; □, 25–75th percentiles; |, 95% range; ●, outliers) of the ratio of (a) number of individuals and (b) biomass to higher and lower trophic groups to each habitat type and over the months. Lower trophic groups are herbivores, iliophagous, insectivores; higher trophic groups are piscivores, omnivores, detritivores
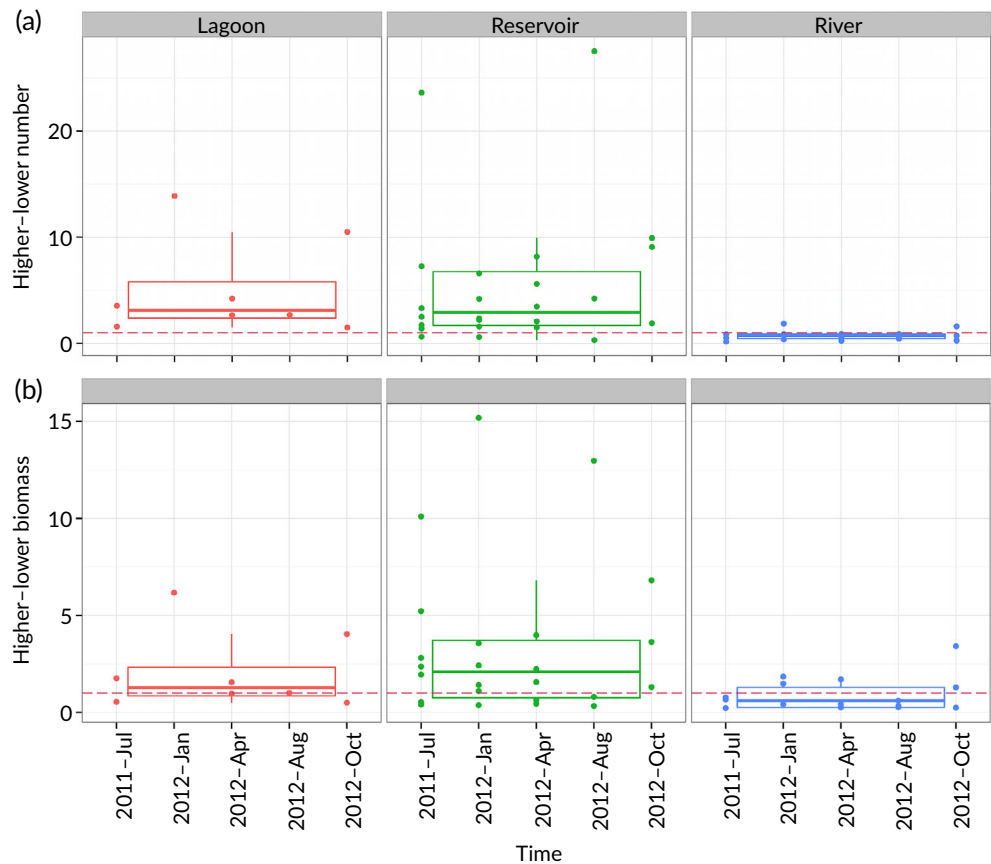
Specifically, the total abundance was predicted to decrease with increased temperature, smaller sediment grain size, lower concentration of organic matter and decreasing pH (Table 2). Interactions among the predictor variables indicated that, with low concentrations of nitrogen and phosphorous, the number of individuals decreases with increasing chlorophyll-*a*, while at high concentrations of these nutrients, the relationship switches to an increase in individuals with increasing chlorophyll-*a* (Figure 4a,b). The presence of non-native fish species did not contribute significantly in any of these models.

Contrary to the whole assemblage metrics, the presence of non-native fish played an important role in predicting the abundance of four of the six trophic groups: detrivores, herbivores, omnivores and piscivores (Table 2). Across the models, the environmental conditions and the presence of non-native fish together explained 13% to 64% ($R^2_{GLMM(m)}$) and, when random effects were also included, explained 35% to 89% ($R^2_{GLMM(c)}$) of the variation in the data (Table 2). The contribution of environmental predictors varied substantially among groups but all models included a significant contribution from at least one environmental predictor. Interactive effects between chlorophyll-*a* and nitrogen (Figure 4d,f,h) and between temperature and nitrogen (Figure 4c,e,g) were extremely weak, with large confidence intervals, so we will not discuss them further in this paper.

Iliophagous, herbivores and detritivores were well predicted with more than 30% of the variation in the data ($R^2_{GLMM(m)}$ = 0.64,

$R^2_{GLMM(m)}$ = 0.32, $R^2_{GLMM(m)}$ = 0.31). Herbivores and detritivores had their habitat characterised by smaller sediment grain size and was less likely to harbour non-native fish. Detritivores were associated with water that was more saline (higher conductivity), more acidic (lower pH) and lower in chlorophyll-*a* concentration. Herbivores were primarily associating abundance with lower conductivity, higher pH, more phosphorous and lower chlorophyll-*a* concentrations. Iliophagous species were specifically associated with higher temperatures and lower productivity, indicated by negative coefficients of phosphorous and organic matter and tended to be found in sites with non-native fish. Omnivores and piscivores were better predicted (omnivore $R^2_{GLMM(m)}$ = 0.40, piscivore $R^2_{GLMM(m)}$ = 0.59) in habitats with smaller grain sizes but otherwise showing little overlap in association. Piscivores were more likely to be found in waters with higher likelihood for the presence of non-native fish (Table 2). Insectivores were poorly predicted ($R^2_{GLMM(m)}$ = 0.13) by environmental conditions and the presence of non-native fish; their only association was with less saline waters.

Including random effects in these models had different effects across trophic groups. Detritivore, insectivore and omnivore abundances were much better predicted by the inclusion of month and site, increasing the variation explained by 23%, 22% and 49%, respectively. Herbivore abundance was not improved at all by adding random effects, while amount of variation explained in the iliophage and piscivore abundance data was increased by 11% and 9%, respectively.

TABLE 2 Relationship beweeen environmental conditions and species richness, number of individuals, and the abundance of individuals within trophic groups. Generalised linear models (GLM), some including mixed effects (GLMM) were used to quantify these relationships. Only those environmental variables included in the model averaged over the best model set following model selection are presented. Months and sites were included as random effects in the GLMMs

	Species richness	Number of individuals	Detritivores	Herbivores	Iliophagous	Insectivores	Omnivores	Piscivores
Averaged model coefficients								
Intercept	**2.62**	**4.78**	**3.28**	**3.54**	−0.28	**0.60**	**2.91**	**2.64**
Temperature	0.06	**−0.09**	0.25	−0.07	**0.38**	0.24	**−0.43**	0.13
Conductivity	0.02		**0.31**	**−0.33**		**−0.54**	−0.09	0.12
pH	−0.02	**0.09**	**0.57**	**−0.17**		−0.02	**−0.37**	**0.24**
Nitrogen	−0.02	**−0.33**	0.10	−0.19	0.25		−0.72	−0.27
Phosphorus	−0.03	0.02	0.01	**0.15**	**−0.75**	−0.01		0.05
Chlorophyll-a	−0.05	**−0.05**	**−0.37**	−0.08	−0.48	0.08	0.12	
Fine grain size		**−0.27**	**−0.28**	**−0.56**			**−0.33**	**−0.12**
Organic matter	0.02	**−0.20**		**−0.33**	**−0.78**	−0.05		0.09
Non-native fish	−0.07	0.08	**−0.22**	**−0.30**	**1.55**			**0.32**
Chlorophyll-a × phosphorus		**0.15**						
Chlorophyll-a × nitrogen		**0.35**		**0.57**	**0.68**		**0.48**	
Nitrogen × temperature			**0.50**	**−0.18**				−0.05
Averaged model statistics								
Month	0.02	0.37	0.51	0.23	0.88		0.94	0.45
Sites		0.42	1.44	0.49	2.16	0.83	0.51	0.38
$R^2_{GLMM(m)}$	0.08	0.38	0.31	0.32	0.64	0.13	0.40	0.59
$R^2_{GLMM(c)}$		0.54	0.54		0.75	0.35	0.89	0.68
BIC	292.76	955.19	616.54	792.71	280.88	277.3	524.7	461.87

BIC, Bayesian information criterion; $R^2_{GLMM(m)}$, Percentage of marginal explained variance; $R^2_{GLMM(c)}$, percentage of conditional explained variance. Values in bold, $P < 0.05$.

4 | DISCUSSION

This study presents species and community metrics comparing the lagoon, reservoir and tributaries in the Jurumirim Reservoir. The results obtained by NMDS analysis suggest that species are segregated into these different habitats. The results of the GLMM models furthermore suggest trophic level is a more appropriate monitoring tool for describing ecological status than species richness. While no significant relationship was found between species richness and the abiotic factors considered here, trophic level did correlate with the different conditions. This suggests that more information relevant to understanding and describing the ecological status of the different fish communities in the reservoir system is contained in the trophic level metrics than in species richness. Specifically, differences in the relative abundances of fish were found (Figure 3), highlighting different trophic structures among the different habitats identified. Predators from higher trophic niches and detritovores dominated in lentic habitats (reservoir), while fishes occupying lower trophic levels dominated in other habitats and thus, the inverted trophic hypothesis (McCauley *et al.*, 2018) was supported.

4.1 | Relationship between fish distributions and environmental variables

The interaction analyses reported indicate possible relationships between some environmental variables and different fish groups. We consider here to what degree these relationships might be causal. When there is a pattern, we justified the distribution of trophic groups considering the variation of environmental variables that respond quantitatively the anthropic actions, impoundment and fish introductions.

Total nitrogen concentration was found to be a better predictor of herbivorous, iliophagous and omnivorous fish than it was of phytoplankton biomass (chlorophyll-*a* concentration). As there is no *a priori* reason to expect total nitrogen to directly influence the abundance of these fish groups, it is assumed that high concentrations of total nitrogen serve here as a proxy for identifying habitats with a high abundance of organic material or high remineralisation rates of nitrogen; that is, conditions that would be attractive for all three trophic groups, which appeared to increase in habitats with high total nitrogen, conditions that are typically lotic (Supporting Information Table S1 in File S1).

A decrease in iliophagous fish (but a slight increase in herbivores) was detected in relation to increased phosphorous concentrations.
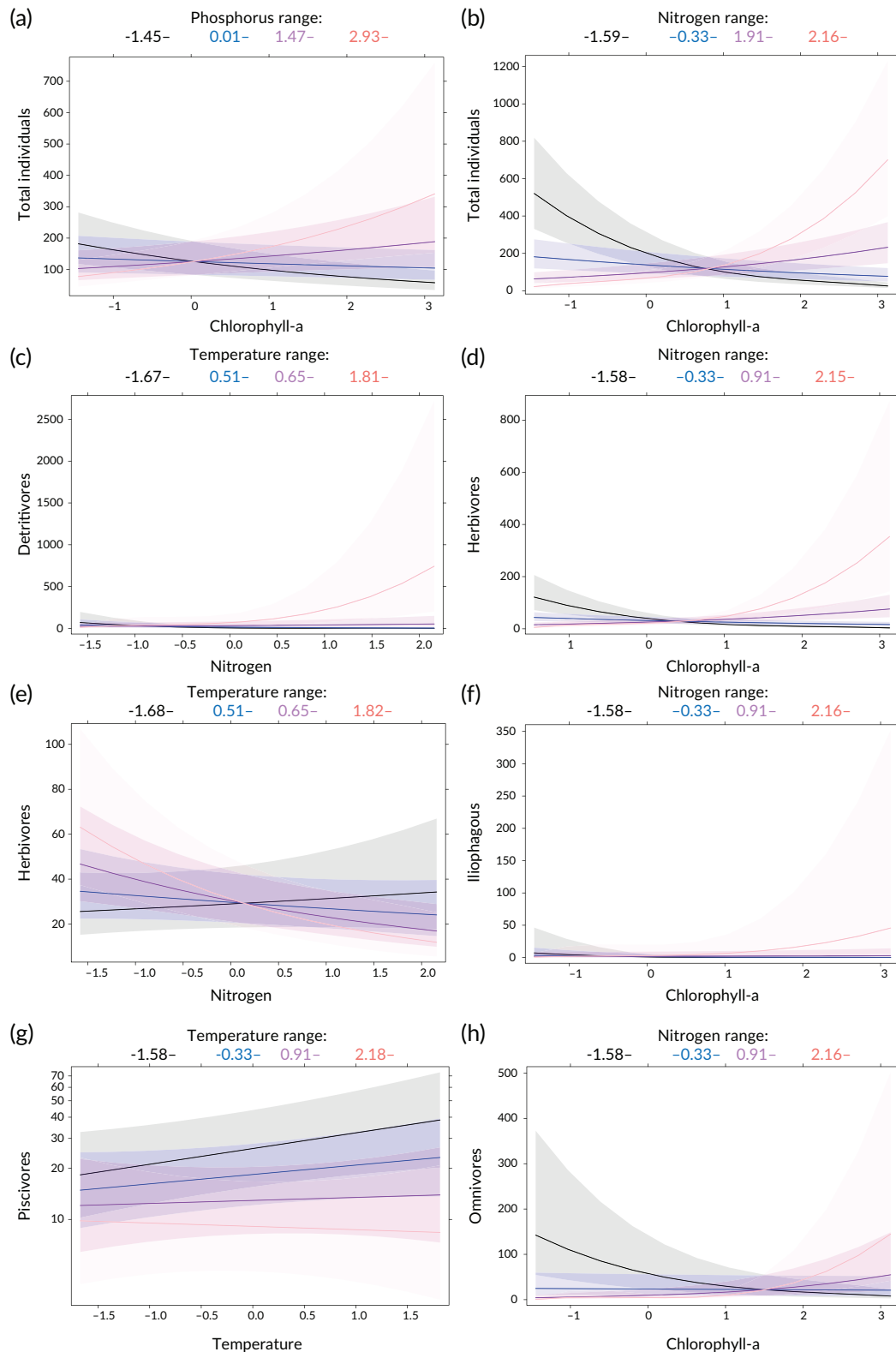
FIGURE 4 The interaction effect of explanatory variables (x-axes) for the response variables (y-axes). The range of variables was fixed at four constants to visualise the interactions: ——, small; ——, small–mid; ——,- mid–large; ▨, large values. The interaction values were centered and scaled as all numerically predicted variables

Generally, higher phosphorous concentrations were noted under river as compared with reservoir conditions. The release or uptake of phosphorous into the water column in the river channel is associated with

biotic components of the system (periphyton and vascular plants) and bottom sediments (Correll, 1998). Once delivered to a reservoir, phosphorous is usually stored in the bottom sediments. The results of the

current study are consistent with previous work, which has shown that the phosphorous–fish relationship can be the result of changes occurring at the base of the food web (*i.e.*, primary production) in response to changed nutrient conditions in an oligotrophic system (Karlsson *et al.*, 2009), as in Jurumirim Reservoir.

We found that not only the increase of conductivity is associated with sedimentation and reduced nutrient cycling (Dunlop *et al.*, 2005) but also the pH and organic matter. With respect to the latter two variables, the variations of values might be explained as being a consequence of the sedimentation in tributaries and the buffering nature of the reservoir. The flow of water influences fluvial erosion, which promotes sedimentation (Henry, 2014). The deposition of fine sediment and organic matter in the lentic regions is greater than that in lotic regions (Supporting Information Table S1 in File S1). The deposition of fine sediment on the substrate in a habitat affects all trophic levels. The river acidity levels were associated with sedimentation rates. However, the differences in acidity were not high enough to affect the abundance of herbivorous and omnivorous fish. In case of a more accentuated acidification, the phytoplankton biomass could be low, which could lead to a simplification of the zooplankton association, which, in turn, could limit many fish species (Hendrey *et al.*, 1976).

Piscivores and non-native fishes have earlier been reported, as was also observed in this study, to be dominant in deeper zones and in lentic environments (Matthews, 1998). Non-native fishes were not a variable exclusively pertinent to piscivorous fishes. They may also be omnivorous, iliophagous and herbivorous. In case of the trophic interactions of native and introduced piscivorous fish, Fugi *et al.* (2008) noted coexistence between these groups. They argued that this was due to prey and resource overlap being small between the introduced and the native species.

Iliophagous fish were found in our study to be more likely to coexist with non-native fish than detritivores. The detritivorous and iliophagous categories were separated in the analysis because different factors may influence the feeding by grazers that live on algae and consumers of detritus (Bowen, 1983; Flecker, 1996). In the case of the relationship between iliophagous and non-native fish in our study, however, the iliophagous fish are all represented by loricariids with scutes and they are harder to prey upon than naked or scale-covered fish. The occurrence of non-native fishes may be an important predictor of abundance and diversity of other species but the knowledge of potential effects of these non-native species is still limited.

4.2 | Implication for using trophic levels as a measure of stock management

The upper Paranapanema River basin has experienced the introduction of lacustrine species through fish stocking (Miranda, 2001). Native and non-native fish stocking has occurred since the 1980s in the Jurumirim Reservoir (CESP, 1996). Between 1999 and 2012, a Duke Energy Company stocking programme added more than 19 million young fish representing the native species *P. mesopotamicus*, *S. hilarii*, *Prochilodus lineatus* (Valenciennes 1837), *Leporinus friderici* (Bloch, 1794), *Leporinus obtusidens* (Valenciennes 1837) and *Brycon*

orbignyanus (Valenciennes 1850) to the reservoirs and tributaries of the Paranapanema River with the aim of building sustainable populations fully adapted to life in the river (Duke Energy, 2013). It is shown by our study that, with the exception of *B. orbignyanus* (Figure 2), these species are now widely distributed. *L. friderici* for example, was found in high abundances in the reservoir, where most other herbivores were not as frequent. The success of these populations might, therefore, be due to the stocking programme. The non-native fish stocking is not authorised, but such introductions are still occurring. It is not by chance that our study identified the occurrence of six non-native species.

If a trophic-level ratio metric becomes adopted as a management tool, it might be possible to use the ratio to identify the trophic profile of species most likely to succeed in potential stocking initiatives in different areas. The choice of species for fish stocking programmes should respect the habitat preferences of different trophic groups in order to avoid changing natural community structure. A fish index developed based on the distribution of different trophic levels might serve as a practical tool in relation to fish stock management for reservoirs with a similar range of environmental conditions as those in the range as in the Jurumirim reservoir system. However, the use of secondary data on trophic information of the fish species should be limited seeking local veracity due to the existence of a trophic plasticity. In our case, it was valuable to use data already published, since they would complement the information gap of the empirical analysis, being a literature with the area of study of the same hydrographic basin or approximations and the trophic plasticity occurring within the spectrum that defines each group.

The data presented here suggest that fish management in freshwaters (reservoirs and tributaries) should ideally be designed to deal with each habitat type individually. The trophic level (as a proxy for functional index) may be a more practical and appropriate tool for monitoring the local fish communities when traditional species-based diversity metrics, for example species richness, do not respond. In this study, we found that a substantial portion of the variation in abundances of individuals and trophic groups was explained by environmental conditions or the presence or absence of alien fish species. Thus, the simple trophic metric describing the relative proportion of fish from the highest trophic levels in the community used here provides a useful tool for monitoring changes in the functional structure of the communities present.

AUTHOR CONTRIBUTIONS

This study was designed by J.Q., H.B., G.S., R.S. and R.H. Field and laboratory data were obtained by J.Q., H.B., A.N., J.P., C.S., FL and R.S. J.P., C.S., F.L. conducted trophic analysis. J.Q., H.B., A.N., J.P. and R.S. conducted limnological analysis. S.K. and K.R. contributed with the model's analysis. J.Q., S.K. and K.R. conducted the statistical

analyses. J.Q., SK, G.S., R.H. and K.R. wrote the paper with input from all co-authors.

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