Longitudinal patterns in distribution of native and non-native fish species in a regulated temperate Neotropical river

Padrões longitudinais na distribuição de espécies nativas e não-nativas de peixes em um rio Neotropical temperado regulado

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Abstract: Aim: We evaluated the longitudinal patterns in distribution of native and non-native fish species in a hydrologically fragmented and environmentally variable lowland temperate river. **Methods:** Four sites representing contrasting habitat and environmental conditions were sampled: a clear water reservoir, a turbid water lagoon and two river reaches with clear and turbid waters each. Environmental variables were measured *in situ* and in the laboratory. Fishes were sampled using trammel and beach seine nets. **Results:** Two main environmental scenarios were identified: the upstream reaches, with colder, clearer and nutrient-oxygen poor waters (reservoir and its downstream river) and the downstream reaches, where turbidity, dissolved oxygen, water temperature, conductivity and nutrients largely increased (lagoon and its downstream river). Fourteen species with a high non-native/native (4:10) ratio were collected. Non-native species (NNS) were confined to lentic conditions, where the silverside *Odontesthes bonariensis* dominated. Native species (NS) better thrive in lotic conditions where the turbid scenario further favored tolerant species. Environmental conditions also seemed to influence the distribution of NNS. Fish assemblage structure considering either, all species, NNS or NS significantly differed among sampled reaches and habitat (lentic-lotic) conditions. Total fish abundance was higher in lentic reaches. Species richness and diversity were favored by the turbid scenario. Beta diversity was mostly explained by the replacement component revealing the substitution of species as the main pattern of variation. Water conductivity, nitrates and dissolved oxygen were the most important predictor variables in the best and most frequent explanatory models of fish assemblage structures. **Conclusions:** Our results revealed that a low diversified Neotropical fish fauna is disrupted by habitat fragmentation due to the creation of artificial impoundments and the introduction of NNS. Environmental conditions further modulate the fish assemblage structure by affecting the distribution of species where tolerant species were favored by turbid, nutrient-rich waters with higher conductivity and pH.

Keywords: reservoir; eutrophication; non-native species; fishes; Sauce Grande river.

Resumo: Objetivo: Neste trabalho avaliamos os padrões longitudinais de distribuição de espécies nativas e não-nativas de peixes em um rio de planície fragmentado hidrologicamente e variável limnologicamente. **Métodos:** Quatro locais representando condições ambientais e de habitat contrastantes foram amostrados: um reservatório de águas claras, uma lagoa de águas turvas e dois trechos do rio, um de águas claras e outro de águas turvas. As variáveis ambientais foram medidas *in situ* e no laboratório. Os peixes foram amostrados com redes de arrasto e de espera. **Resultados:** Dois cenários ambientais foram identificados. Um à montante, com águas mais frias, claras e pobres em nutrientes e oxigênio dissolvido (o reservatório e o trecho do rio abaixo do mesmo) e outro, à jusante, onde a turbidez, oxigênio dissolvido, temperatura da água, condutividade e os nutrientes aumentaram consideravelmente (a lagoa e o trecho do rio abaixo da mesma). Quatorze espécies com uma alta proporção entre espécies não-nativas e nativas (4/10) foram coletadas. As espécies não-nativas (NNS) estiveram confinadas a condições lênticas, onde o peixe-rei *Odontesthes bonariensis* dominou as assembleias de peixes. As espécies nativas (NS) proliferaram melhor em condições lóticas onde o cenário de águas turvas favoreceu as espécies tolerantes. As condições ambientais também parecem ter influenciado a distribuição das NNS. A estrutura da assembleia de peixes considerando todas as espécies em conjunto ou NS e NNS em separado, foram significativamente diferentes entre os trechos amostrados e condições de habitat (lêntico-lótico). A abundância total de peixes foi maior em trechos lênticos. A riqueza de espécies e a diversidade foram favorecidas pelo cenário de turbidez. A análise da diversidade beta foi explicada em maior parte pelo *turnover* revelando a substituição de espécies como o principal padrão de variação. A condutividade elétrica da água, os nitratos e oxigênio dissolvido foram as variáveis preditivas mais importantes nos melhores e mais frequentes modelos explicativos das estruturas da assembleia de peixes. **Conclusões:** Nossos resultados revelaram que uma fauna de peixes Neotropicais pouco diversificada é alterada pela fragmentação do habitat devido à construção de barragens e pela introdução de NNS. As condições ambientais modularam ainda mais a estrutura da assembleia de peixes afetando a distribuição de suas espécies onde as espécies tolerantes foram favorecidas por aguas turvas, ricas em nutrientes, com maior condutividade e pH.

Palavras-chave: reservatório; eutrofização; espécies introduzidas; peixes; rio Sauce Grande.

1. Introduction

Lotic ecosystems in temperate regions are known to present a natural longitudinal gradient in environmental conditions and aquatic communities (Vannote et al., 1980). However, this natural scenario is commonly disrupted by a myriad of anthropic stressors. Particularly, freshwater ecosystems are increasingly affected by habitat fragmentation (Saunders et al., 1991), cultural eutrophication processes (Smith & Schindler, 2009) and introductions of non-native species (Cucherousset & Olden, 2011), affecting aquatic biota, including fishes (Guenther & Spacie, 2006; Granzotti et al., 2018). Under these circumstances, the evaluation of multiple-stressor effects on species populations, communities and ecosystems in freshwaters is a major challenge (Ormerod et al., 2010).

In river ecosystems, habitat fragmentation ranges from local incisions of riparian banks to large reservoirs. According to the Serial Discontinuity Concept (Ward & Stanford, 1983), dams result in upstream-downstream shifts in biotic and abiotic patterns and processes. Dam construction alters the natural dynamics of rivers, changes the environmental characteristics (lotic into a lentic environment), decreases nutrient concentrations (after filling process) and increases water transparency (Agostinho et al., 2007). These changes drastically impact on fish communities (Agostinho et al., 2016; Turgeon et al., 2019). Particularly, this scenario favors an abundance increase of limnetic native fish species (Johnson et al., 2008; Gubiani et al., 2018), obstructs the dispersal and migration of organisms (Penczak & Kruk, 2000) and can cause shifts in community structure (Liew et al., 2016; Smith et al., 2018). The disruption of natural scenario imposed by large dams and reservoirs also enhances the establishment non-native species (Johnson et al., 2008; Liew et al., 2016). Overall, a declining abundance of native endangered and threatened species and increasing the abundance of non-native species are expected in regulated rivers (Guenther & Spacie, 2006).

Non-native species are causing dramatic changes in many ecological systems worldwide, and are profoundly altering the natural communities (Cucherousset & Olden, 2011; Pyšek et al., 2020). Although not all introduced fishes become established, many exert significant ecological, evolutionary, and economic impacts (Jeschke & Strayer, 2005). Ecological effects have been shown to be severe and range from behavioral shifts of native species in the presence of invaders to changes in food webs and the extirpation of entire faunas

(Cucherousset & Olden, 2011). The presence of non-native fishes reduces richness and diversity of the native fish community (Pyšek et al., 2020), causes the disappearance of some species and a reduction in the abundance of young individuals of others (Godinho et al., 1994).

In addition to habitat fragmentation by dams and biological invasions (many often favored by habitat fragmentation) lowland rivers worldwide have experienced a marked eutrophication (Jarvie et al., 2002). Eutrophication generates, among many other changes, an increase in the turbidity of watercourses (Ansari et al., 2010). There is much evidence that the community composition of fish may change dramatically with the turbidity state of the ecosystems (Van de Bund & Van Donk, 2002; Granzotti et al., 2018). These differences have been largely attributed to the refuge provided by the aquatic vegetation in clear-water systems and by the negative effect of turbidity on fish species that use vision to detect their prey affecting predator-prey interactions (Chambers et al., 1999). Indeed, even narrow ranges in water transparency, traditionally neglected as important factors for fishes, may be still important for some species in highly turbid waters (Rosso et al., 2010).

The Pampa Plain is the most productive cultivated area of Argentina (Baldi et al., 2006). Prairie streams in this region have high levels of nutrients, low current velocity, fine bottom sediments, macrophytes as main type of primary producers and herbaceous riparian corridor (Feijoó et al., 1999). Patterns in land use (advance of the agricultural frontier and displacement of livestock to marginal areas), fluvial regulation through channelization and the creation of artificial impoundments are major threats to the integrity of lotic ecosystems in the Pampa Plain (Viglizzo et al., 2001; Rosso & Fernández Cirelli, 2013). This scenario of regional threats is further worsened by the occurrence of non-native fish species. Among them, the common carp, *Cyprinus carpio*, certainly represents one of the most pervasive introductions of exotic fish species (Maiztegui et al., 2016). However, many shallow lakes and reservoirs of the Pampa Plain are periodically stocked with inland silversides, *Odontesthes bonariensis,* the most emblematic and relevant species in lentic systems of central and northeast of Argentina (Mancini et al., 2016). In some southern drainages of the region, the criolle perch *Percichthys trucha* was stocked in the sixties for recreational purposes (Ringuelet, 1961).

Certainly, combined impacts of habitat fragmentation, eutrophication and non-native fish species on fish assemblages of the Pampa Plain represent a major threat to native fish fauna. The lowland rivers of this region are therefore a good opportunity to improve our understanding about patterns of native fish fauna under multiple stressors and the potential ecological impacts of non-native fishes. In this paper, a survey of fish assemblages in a hydrologically fragmented and environmentally variable temperate Neotropical river of the Pampa Plain, Argentina, was conducted. Particularly, the aim of this paper was to evaluate patterns in abundance and distribution of native and non-native fish species and its relationship with key limnological variables along several reaches of this river with contrasting habitat and environmental conditions.

It could be anticipated that habitat fragmentation imposed by dams will drastically affect fish abundance and distribution, particularly favoring non-native fishes in these environments. On the contrary, native reophilic species would hardly thrive in these modified conditions. Longitudinal variation in key environmental variables is also expected to affect fish assemblages. The magnitude and direction of these relationships are not easily anticipated other than the most tolerant fishes would be favored by the most detrimental environmental conditions. Overall, understanding the impact of multiple stressors on the fish assemblages would lead to thoughtful management and conservation actions that necessarily must be taken on strong ecological grounds about the target species.

2. Material and Methods

2.1. Study area

The Sauce Grande River belongs to a large hydrographic basin located in the south of Buenos Aires province, originated by small order streams that head in the Sierra de la Ventana, at 500 m above sea level. Shortly beyond its source, the river is artificially impounded by the Paso de las Piedras Reservoir. With a surface area rounding 3,600 hectares, this reservoir averages 8.2 m of depth with a maximum of 28 m (Fernández et al., 2009). Its main use is to provide drinking tap water to Bahía Blanca (around 300,000 inhabitants) and Punta Alta cities (around 60,000 inhabitants) and the industries of "Ingeniero White". This system is also used for recreational fishing of the inland silverside *O. bonariensis* (ADA, 2017). Downstream, river

flows with oligo-mesotrophic, hipohaline and clear waters (Cony, 2018) until it is naturally impounded by coastal sand dunes creating the Sauce Grande Lagoon. This lagoon has an area of 21.55 km², an average depth of 1.4 m and a maximum depth of 1.8 m (Fornerón et al., 2010). This Lagoon was defined as a eutrophic, oligohaline and turbid environment dominated by phytoplankton (Cony, 2018). As in the reservoir, the Sauce Grande Lagoon is periodically stocked with inland silversides to support recreational fisheries. Downstream to the Sauce Grande Lagoon, the river flows into the Atlantic Ocean after a meandering course of 30 km.

2.2. Field and laboratory activities

Samplings were conducted in four sites along the Sauce Grande River aimed to represent the contrasting habitat and environmental conditions to which fishes are exposed in this ecosystem. Sampling locations were placed in Paso de las Piedras Reservoir, an artificial impoundment with clear waters (labeled CwLe=clear water lentic conditions; 38°24'16.25" S, 61°44'38.87" W), Sauce Grande Lagoon, a natural impoundment with turbid waters (labeled TwLe=turbid water lentic conditions; 38°56'18.51" S, 61°22'56.02" W) and two reaches of Sauce Grande River, downstream to Paso de las Piedras Resevoir, a river reach with clear waters (labeled CwLo=clear water lotic conditions; 38°45'47.00" S, 61°42'43.09" W) and downstream to Sauce Grande Lagoon, a river reach with turbid

waters (labeled TwLo=turbid water lotic conditions; 38°57'5.94" S, 61°13'46.63" W) (Figure 1). Each sampling site was visited three times during spring (October), summer (March) and autumn (May) months.

Environmental variables were measured *in situ* including water temperature (°C), dissolved oxygen (mg/L), water conductivity (μS/cm), pH and turbidity (NTU) using a multiparameter probe (Horiba U-53G). Nitrate and total phosphorus (mg/L) were quantified after processing water samples in the laboratory according to standard methods (APHA, 2012). In Paso de las Piedras Reservoir, all these variables were gathered from the Autoridad del Agua de la Provincia de Buenos (ADA, 2018). Materials and methods for field and laboratory water analysis by ADA are the same as those employed in this study.

Fish sampling was performed using trammel and beach seine nets. Trammel nets were constructed with an outer mesh size of 80 mm between knots and an inner mesh size of 15 mm between knots. A total of 12 m were deployed at each river reach and 100 m in both lentic environments. Beach seine net was constructed with 15 m long wings (10 mm mesh) and a 2 m long bag (5 mm mesh). These gear devices were probed to successfully collect all fish species intended to be collected in this biogeographic region (Bertora et al., 2018a). Trammel nets were left overnight and 2 to 4 seining were performed at each site during each sampling
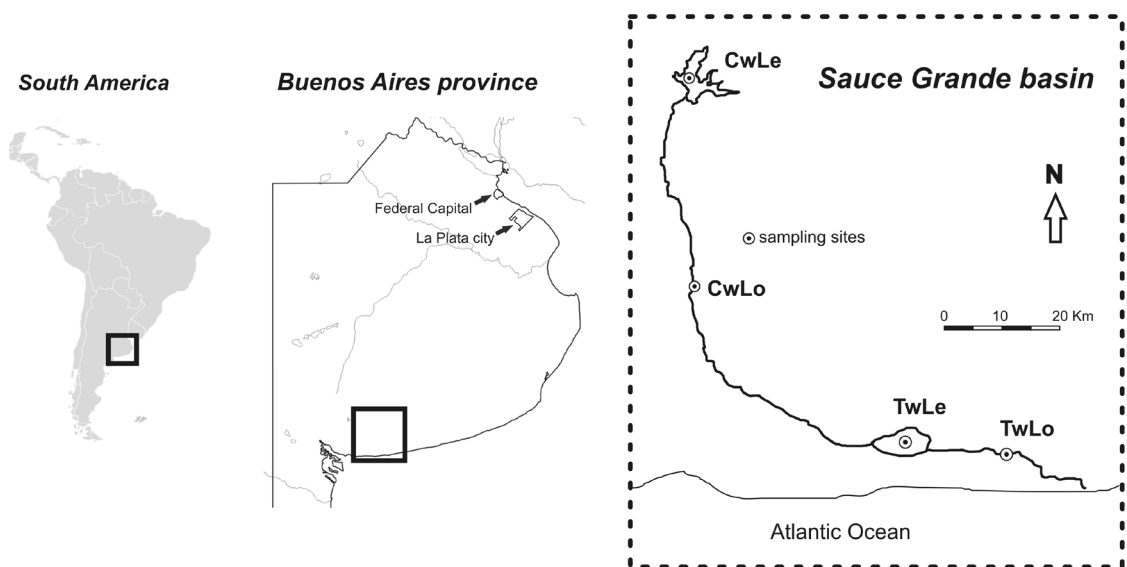
Figure 1. Location of sampling sites in the Sauce Grande River. CwLe = clear water lentic conditions at Paso de las Piedras Reservoir; CwLo = clear water lotic conditions at reach of Sauce Grande River downstream of the reservoir; TwLe = turbid water lentic conditions at Sauce Grande Lagoon; TwLo = turbid water lotic conditions at reach of Sauce Grande River downstream of the lagoon.

date. No additional species was caught beyond the third seining. Fish sampling and handling protocols followed during the course of our surveys were evaluated and approved by the Ethics Comitee of the 'Facultad de Ciencias Exactas y Naturales' of the 'Universidad Nacional de Mar del Plata' (RD-2018-126). Fish captured were euthanized by an overdose in benzocaine solution as suggested by international guidelines (Barker et al., 2002). Fish species were identified following Ringuelet et al. (1967) and Rosso (2006).

2.3. Data analyses

2.3.1. Spatial autocorrelation test

In ecological studies, where the sampling sites are arranged along the same longitudinal gradient, the spatial auto-correlation of the data must be tested. Therefore the influence of the longitudinal position of sites along the main stem of the river on environmental variables, fish species abundance and assemblage attributes were analyzed to identify if our results reflect the patterns of studied variables rather than geographic distance between sampled reaches. So, two RELATE routines (Clarke & Gorley, 2015) were performed to verify the correlation between the serial model and the faunal (abundances and attributes) and environmental dissimilarity matrices. The faunal matrix was constructed using Bray-Curtis similarity and the environmental matrix was constructed using Euclidean distance. This analysis determines the level of association between two resemblance matrices, in this case, the serial model matrix (linear distance between sampled sites in km) and the faunal Bray-Curtis similarity matrix or the environmental Euclidean distance matrix. The linear distances between sampled sites were as follows: CwLe-CwLo 40 km, CwLo-TwLe 35 km and TwLe-TwLo 11 km. All data were previously standardized (to zero mean and unit variance). Spearman correlation was used and the permutation tests were performed with 9999 random permutations. The null hypothesis postulating that there is no spatial autocorrelation of the data was tested, that is no tendency for variables to be similar at nearby localities.

2.3.2. Environmental conditions

A Principal Component Analysis (PCA) was conducted with all environmental variables measured at each sampling site. This analysis orders and represents continuous multivariate data in a smaller dimension (standardized orthogonal linear combinations of the variables) that explain the data variability (proportion of total variability explained). The biplot allows visualizing observations and variables in the same scatterplot, thus it is possible to identify associations between observations, between variables and between variables and observations. To perform this analysis data were standardized and correlation matrix was used. Statistical significance in longitudinal and habitat (lentic vs. lotic) variation of environmental conditions were tested by means of an ANOSIM procedure (Clarke & Green, 1988) conducted on the Euclidean similarity matrix of measured variables.

2.3.3. Fish assemblages

Fish species abundances were expressed as capture per unit of effort (CPUE total). The unit of effort was standardized to an overnight deployment of 12 m of trammel nets and one seining of beach seine net averaging 10 m long. Relative specific abundances were transformed to square root to reduce the weight of the dominant species. In addition, different fish assemblage attributes were estimated. Abundance of non-native species (CPUE NNS) was calculated including exotic (*C. carpio*) and allochthonous (*O. bonariensis*, *Cyphocharax voga* and *P. trucha*) species. Exotic species were those considered phylogenetically and biogeographical distant that are introduced, typically from other continents. Conversely, allochthonous species were Neotropical or Austral fish fauna without evidence of being naturally present in the studied basin. Abundance of native species (CPUE NS) was estimated including the remaining captured species. Species richness and Shannon-Weaver diversity were calculated for each site. A one way Kruskal-Wallis ANOVA and Mann-Whitney tests were used to test for significance in differences of fish assemblages attributes (CPUE NNS, CPUE NS, species richness and Shannon-Weaver diversity) among sites and between habitats (lentic vs. lotic) respectively. In order to determine if fish assemblage structure in contrasting river reaches significantly differ considering the abundances of all fishes, abundances of NS or abundances of NNS, three separate one-way ANOSIM analyses were performed, using different sites as factors. These analyses were conducted on the Bray-Curtis similarity matrix generated with the specific abundances. ANOSIM analyses were also used to evaluate the differences in fish assemblage structure between lotic (CwLo and TwLo) and lentic conditions (CwLe and TwLe), using the habitat as a factor. All the similarity matrices generated in ANOSIM tests

were used to perform the analysis of non-metric multidimensional scaling (nMDS; Clarke & Green, 1988) in order to visually inspected dissimilarities. To further explore structural resemblance between fish assemblages among different environmental and habitat conditions, a similarity percentages analysis (SIMPER; Clarke, 1993) was conducted. This test highlights those species that contribute most to explain the dissimilarities between observed assemblages. In addition, beta diversity (β diversity) was calculated to explore patterns in composition of the fish communities along the longitudinal gradient (Carvalho et al., 2012). The total beta diversity based on Jaccard dissimilarity coefficient was partitioned into the replacement (β repl.) and richness difference (β rich.) components (Baselga, 2010).

2.3.4. Relationships between environmental conditions and fish assemblages

The PCA scores were used as an integration of the environmental variables to determinate possible associations between this environmental scenario and the fish community. Spearman rank correlation coefficients were estimated to explore the empirical relationships between fish assemblage attributes and specific abundances with PCA scores of environmental variables.

Distance-based linear models (DistLM) were performed to achieve a direct quantitative partitioning of the multivariate variability that is explained by each of several environmental variables. DistLM is a routine for analyzing and modeling the relationship between a response multivariate data cloud (biological variables) and one or more predictor variables (environmental variables) (Anderson et al., 2008). This tool does a partitioning of variation in a data cloud described by a resemblance matrix according to a regression model. We used the same response matrices included in the nMDS-ANOSIM protocol: the abundances of all fish species combined, abundances of NS and abundances of NNS. Abundance data was square-root transformed prior to analyses. Draftsman plots were performed to check for skewness and redundancy among predictor variables. Then, environmental variables were log transformed and the turbidity was excluded from the analysis, as it was highly correlated with other variables. Models including all possible combinations of predictor variables were generated using the BEST procedure. Modified Akaike's Information Criterion (AICc) was used to identify the best model. Models with the

lowest AICc are considered the most parsimonious. All DistLMs were run with 9999 permutations. The difference between the AICc value of the best model and each of the other models (ΔAICc) was calculated and the Akaike weights of models (Burnham & Anderson, 2002) with values of these differences less than 2 were estimated. Burnham & Anderson (2002) suggested that models having AICc values within 2 units of the best model should be examined more closely to see if they differ from the best model by 1 variable. Thus, those models that showed a ΔAICc <2, differed from the best model by a single variable and obtained an increase of R^2 were selected to complement the best model in explaining the relationships between environmental variables and fish assemblages. In these models (ΔAICc <2), the relative importance of each predictor variable (Wi, predictor weight, Symonds & Moussalli, 2011) was calculated. For each predictor variable, the Akaike weights of all the models containing that predictor were summed. Those predictors that frequently occur in the most likely models (ΔAICc <2) have an Akaike weight close to 1 whereas variables that are absent from most likely models or are only present in less likely models (high AICc values) have an Akaike weight close to 0.

Statistical analyses were performed with PRIMER.5 (Plymouth Routines In Multivariate Ecological Research) with the add-on package PERMANOVA+, PAST 4.01 (Paleontological Statistics software package for education and data analysis) and InfoStat packages.

3. Results

3.1. Spatial autocorrelation test

The spatial autocorrelation analyses showed that there was no tendency for fish assemblage (R= 0.062, *p* value= 0.473) nor environmental variables (R= 0.031, *p* value= 0.572) to be more similar at nearby localities in the Sauce Grande River.

3.2. Environmental conditions

Sampled sites showed significant differences in their main environmental attributes (ANOSIM: R= 0.756, *p* value= 0.0002, Table 1). Along the longitudinal gradient of the river, different reaches displayed a progressive increase in dissolved oxygen and temperature. Although all sampled sites had alkaline waters, river reaches with more turbid waters had the highest pH values. In addition to

their higher turbidity, these sites also showed higher conductivity and nutrient concentrations. No significant differences were found in environmental variables according to the habitat condition of the sites (lentic vs. lotic, ANOSIM: R= 0.059, *p* value= 0.226).

The first two axes of the Principal Component Analysis cumulatively explained 86.8% of the total variation in environmental conditions along the sampling sites of the Sauce Grande River (Figure 2). This analysis showed a marked spatial ordination of samples along the first component. The CwLe and CwLo samplings were closely grouped in the negative end of the first component, while TwLo samples were located around the centroid of the ordination. The TwLe samples were confined to the positive extreme of the first component. This spatial arrangement allowed discriminating sites along a gradient of progressive increase in pH, turbidity, conductivity and nutrient concentrations (Table 1). In the second principal component, sites were located from negative to positive end according to a progressive increase in water temperature and dissolved oxygen concentration. Clear water reaches (CwLe and CwLo) with less nutrient concentrations and water conductivity (negative end of CP1) also showed colder and less oxygenated waters. The warmer and more oxygenated waters (positive end of CP2) were only observed under turbid and nutrient-rich conditions, a situation more variable in lentic turbid reaches.

Table 1. Environmental variables measured in different sampling sites of the Sauce Grande River.

Environmental variables	Code	CwLe		CwLo		TwLe		TwLo		PC1	PC2
		avg	SD	avg	SD	avg	SD	avg	SD	(ρ)	(ρ)
dissolved oxygen (mg/L)	DO	6.58	0.98	6.88	0.29	8.61	2.34	11.33	0.93	0.5	0.76
nitrate (mg/L)	NO$_3$	1.14	0.41	0.63	0.12	3.7	0.73	2.41	0.87	0.9	0.04
pH		8.21	0.27	8.56	0.51	9.97	0.04	9.06	0.62	0.93	-0.03
temperature (°C)	temp	15.06	5.39	18.53	1.23	20.87	3.8	21.47	3.68	0.56	0.64
total phosphorus (mg/L)	TP	0.23	0.16	0.87	0.12	3.43	0.99	1.77	0.15	0.93	-0.28
turbidity (NTU)	turb	8.15	1.1	5.33	1.53	453.33	159.48	196.67	35.47	0.93	-0.29
water conductivity (µS/cm)	WC	411.78	22.28	1680	216.56	7143.33	442.3	2846.67	335.61	0.96	-0.23

CwLe = clear water lentic conditions; CwLo = clear water lotic conditions; TwLe = turbid water lentic conditions; TwLo = turbid water lotic conditions; avg = average; SD = standard deviation; PC1 and PC2: correlation coefficients between environmental variables and the first two principal components.
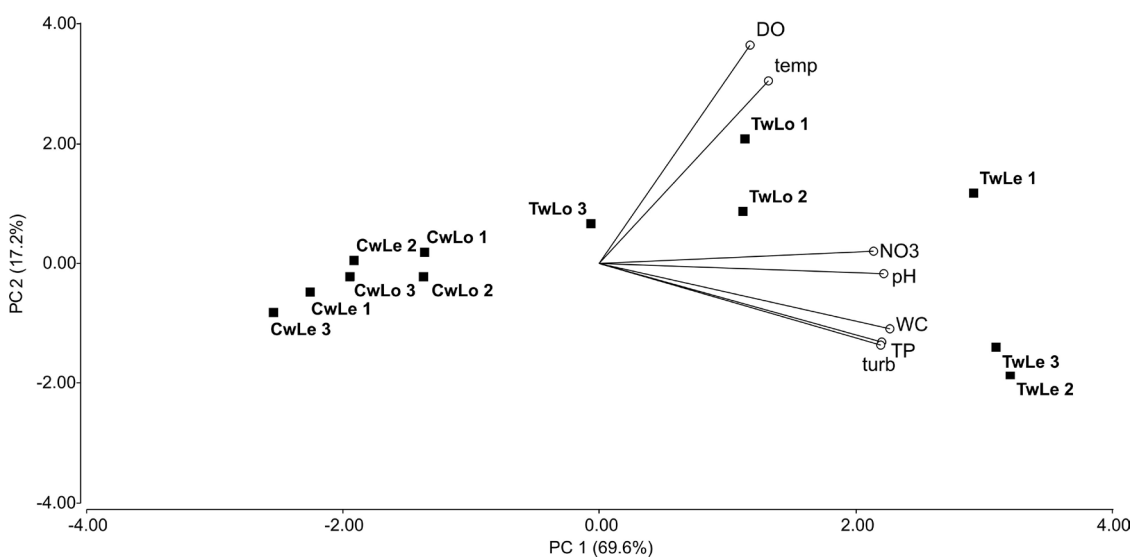
Figure 2. Biplot of the first two PCA axes based on environmental data of the Sauce Grande River (CwLe = clear water lentic conditions; CwLo = clear water lotic conditions; TwLe = turbid water lentic conditions; TwLo = turbid water lotic conditions; DO = dissolved oxygen; temp = temperature; NO3 = nitrate; WC = water conductivity; TP = total phosphorous; turb = turbidity; CP1= First Principal Component; CP2 = Second Principal Component).

3.3. Fish assemblages

The samplings yielded 14 species belonging to 7 orders and 10 families (Table 2). Characiformes and Siluriformes were the most represented orders with 5 and 3 species respectively. All families but Characidae and Heptapteridae presented one single species. Non-native species (NNS) like *C. carpio*, *C. voga*, *O. bonariensis* and *P. trucha* were recorded. Overall, the most abundant species were *O. bonariensis*, *O. jenynsii*, *C. interruptus* and *J. lineata* (Table 2). Eight species showed a widespread distribution, being collected in all sampling sites along the study river: *B. iheringii*, *C. interruptus*, *C. paleatus*, *J. lineata*, *O. jenynsii*, *P. laticeps*, *P. pampa* and *R. quelen* (Table 2). However, their spatial patterns in abundance distribution were highly variable (Figure 3). The small piscivorous *O. jenynsii* showed similar abundances in different sites, while the abundance distribution of *P. pampa* and *P. laticeps* was highly skewed to lotic conditions and *J. lineata* mostly occurred in lentic conditions. Species like the small characids *B. iheringii* and *C. interruptus* and three Siluriformes, *C. paleatus*, *P. laticeps* and *R. quelen*, presented a minimum abundance in the reservoir (CwLe). In turn, the two more distant downstream reaches accounted for the largest abundances of *B. iheringii*, *C. interruptus* and *C. paleatus* (Table 2, Figure 3). In contrast to the widespread species, there were some species confined to a single sampling site, two NNS, *P. trucha* and *C. carpio* in

CwLe and the cichlid *A. facetus* in TwLo. The inland silverside *O. bonariensis* although it was collected in all sites except CwLo, it was noticeably more abundant in lentic reaches. The same was observed for the detritivorous *C. voga*, a species only found in lentic environments, being most abundant in the lagoon. *C. decemmaculatus* was the only species being preferentially collected in the lotic reach downstream of the reservoir (CwLe).

Due to the spatially variable abundance and distribution of fish species along sampling sites, significant differences were found in the structure of fish assemblages in different reaches of the Sauce Grande River (ANOSIM: R= 0.614, *p* value= 0.001, Figure 4a). In the reservoir (CwLe) the fish community was dominated by the inland silverside *O. bonariensis*, followed by the small piscivore *O. jenynsii* and the one-sided livebearer *J. lineata* (Figure 4b). However, in lotic reaches downstream to the reservoir (CwLo and TwLo), the proportion of the inland silverside sharply decreased and the contribution of *C. interruptus*, *B. iheringii*, *C. decemmaculatus*, *C. paleatus* and *P. pampa* to the fish community structure was more noticeably. In the lagoon (TwLe), *O. bonariensis* was again the most represented species and the contributions of the remaining species closely resembled those observed in lotic reaches.

Significant differences were also observed in the structure of fish assemblages (Figure 4a) between the studied sites if the abundances
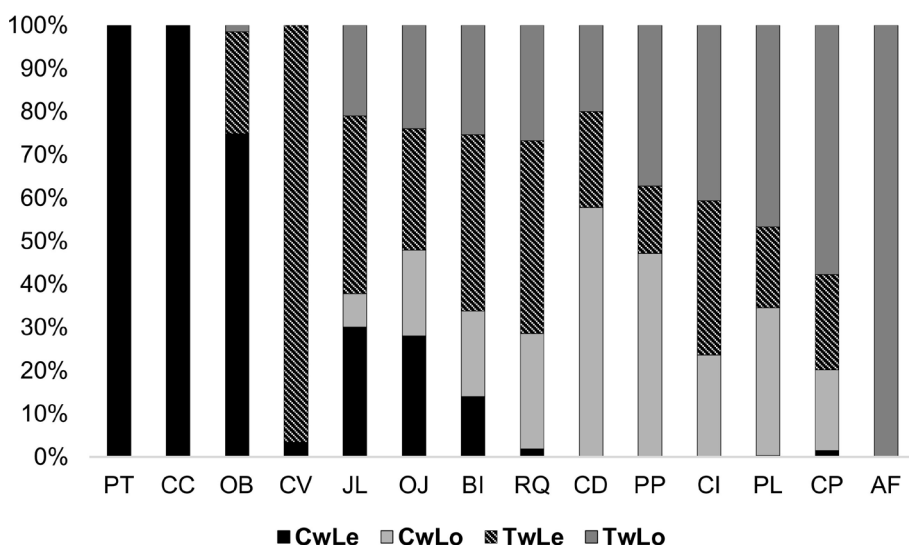

Figure 3. Bar chart showing the distribution of total fish collected of each species within the Sauce Grande River (CwLe = clear water lentic conditions; CwLo = clear water lotic conditions; TwLe = turbid water lentic conditions; TwLo = turbid water lotic conditions). Species are intentionally sorted by means of their spatial distributions to ease the interpretation. Species codes as listed in Table 2.

Table 2. Site-specific and cumulative (Total) abundance (in CPUE, SD = standard deviation) of fish species collected, richness and diversity of sampled sites in Sauce Grande River.

Order	Family	Species	Code	CwLe total	CwLe mean	CwLe SD	CwLo total	CwLo mean	CwLo SD	TwLe total	TwLe mean	TwLe SD	TwLo total	TwLo mean	TwLo SD	Total
Atheriniformes	Atherinopsidae	Odontesthes bonariensis*	OB	123.61	41.2	43.94				39	13	2.6	2.5	0.83	0.76	165.11
Characiformes	Characidae	Psalidodon pampa	PP	0.04	0.01	0.02	12	4	2.18	4	1.33	1.15	9.5	3.17	1.04	25.54
		Bryconamericus iheringii	BI	6.33	2.1	2.8	9	3	1	18.5	6.17	0.76	11.5	3.83	1.61	45.33
		Cheirodon interruptus	CI	0.04	0.01	0.02	16.5	5.5	2.18	25	8.33	2.08	28.5	9.5	3.04	70.04
		Oligosarcus jenynsii	OJ	20.43	6.8	7.1	14.5	4.83	0.76	20.5	6.83	1.76	17.5	5.83	2.57	72.93
	Curimatidae	Cyphocharax voga*	CV	0.35	0.12	0.07				10	3.33	1.53				10.35
Cichliformes	Cichlidae	Australoheros facetus	AF										3	1	1	3
Cypriniformes	Cyprinidae	Cyprinus carpio*	CC	0.16	0.05	0.05										0.16
Cyprinodontiformes	Anablepidae	Jenynsia lineata	JL	19.33	6.44	10.03	5	1.67	1.53	26.5	8.83	1.26	13.5	4.5	1.32	64.33
	Poeciliidae	Cnesterodon decemmaculatus	CD				13	4.33	1.26	5	1.67	1.53	4.5	1.5	1.8	22.5
Perciformes	Percichthyidae	Percichthys trucha*	PT	0.08	0.03	0.02										0.08
Siluriformes	Callichthyidae	Corydoras paleatus	CP	0.42	0.1	0.2	5.5	1.83	1.61	6.5	2.17	1.53	17	5.67	0.29	29.42
	Heptapteridae	Pimelodella laticeps	PL	0.04	0.01	0.02	5.5	1.83	1.26	3	1	1	7.5	2.5	1.8	16.04
		Rhamdia quelen	RQ	0.2	0.07	0.03	3	1	1	5	1.67	1.53	3	1	0	11.2
Richness					8.33	0.58		8	1		9.67	0.58		10	1	
Diversity					0.65	0.14		1.95	0.12		2.05	0.05		2.05	0.18	

CwLe = clear water lentic conditions; CwLo = clear water lotic conditions; TwLe = turbid water lentic conditions; TwLo = turbid water lotic conditions; *non-native species.
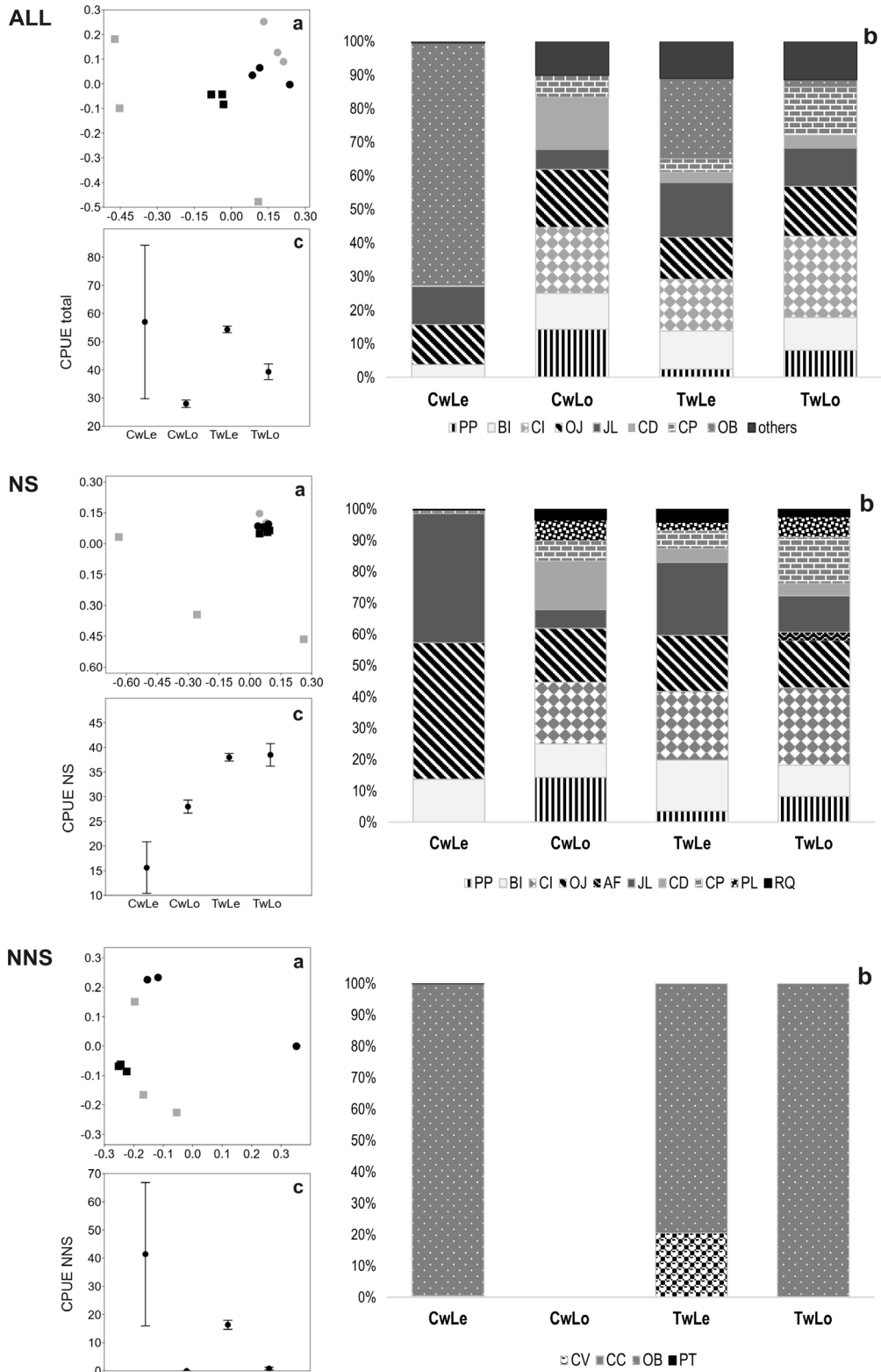
Figure 4. (a) Non-metric multidimensional scaling of the abundances of all fish species (ALL), only native species (NS) and only non-native species (NNS) in sampled sites (CwLe = clear water lentic conditions; CwLo = clear water lotic conditions; TwLe= turbid water lentic conditions; TwLo = turbid water lotic conditions) of the Sauce Grande River (lentic sites: squares, lotic sites: dots; CwLe = gray square; CwLo = gray dot; TwLe = black square; TwLo = black dot); (b) Percentage contribution of specific abundances for the same three data sets (ALL, NS and NNS). The species codes as listed in Table 2. "Others" category in abundances of all fish species (ALL) corresponds to species whose abundance was less than 6.5% at all sites; (c) Mean abundances and standard deviations of fish species for the three data sets.

of native species (ANOSIM: R= 0.3858, p value= 0.0006) are discriminated from those of non-native species (ANOSIM: R= 0.591, p value= 0.0029). Moreover, if sites are compared in terms of habitat (lentic versus lotic) conditions, the structure of the fish community showed significant differences (Figure 4a), considering all the collected species (ANOSIM: R= 0.5481, p value= 0.0029), only the native ones (ANOSIM: R= 0.2389, p value= 0.0049) and only non-native ones (ANOSIM: R= 0.5907, p value= 0.002). Lotic reaches were almost devoid of NNS, except for the record of some specimens of *O. bonariensis* collected in TwLo (Figure 4b). All NNS inhabiting the Sauce Grande River were collected in CwLe (reservoir) and two of them, *C. voga* and *O. bonariensis*, were also found (Table 2, Figure 3) in TwLe (lagoon). In CwLe the combined abundance of NNS accounted for the 75% of the overall fish abundance, while in TwLe it slightly surpassed the 25% of total fish abundance (Figure 4b). Overall, the species that contributed most to explain these dissimilarities in different habitat and environmental conditions were the inland silverside *O. bonariensis*, *C. decemmaculatus*, *C. interrupts*, *C. paleatus* and *J. lineata* (Table 3). The same patterns were observed when native and non-native species were considered separately.

Regarding the attributes of the fish community some general patterns were observed (Table 2, Figure 4c). Overall, abundances of NS (Kruskal-Wallis H= 9.35, p value= 0.0247) and NNS (Kruskal-Wallis H= 8.88, p value= 0.0267), species richness (Kruskal-Wallis H= 6.67, p value= 0.0683) and assemblage diversity (Kruskal-Wallis H= 7.31, p value= 0.0627) were significantly (some marginally) different among sites. The abundances of NS and diversity showed a certain longitudinal tendency, being highest in the most downstream reaches, TwLe and TwLo. The reservoir showed the less diversified community and the species richness was higher in sites with turbid, nutrient-rich waters. Total fish abundance was considerably higher in lentic reaches albeit the wide dispersion of values observed in the reservoir precludes a significance in tested differences (Mann-Whitney W= 49, p value= 0.1212). Instead, when considering only the NNS, abundance was significantly higher in lentic reaches (Mann-Whitney W= 57, p value= 0.0022).

The analysis of beta diversity showed that lotic reaches were fairly similar (β diversity average CwLo-TwLo= 0.25, Figure 5) whereas the largest difference was found between CwLe and the lotic reach downstream to reservoir (β diversity average CwLo-CwLe= 0.67). The similarity found between the lotic reaches and the lagoon (CwLo-TwLe= 0.39, TwLo-TwLe= 0.26) is greater than that found with the reservoir (CwLo-CwLe= 0.67, TwLo-CwLe= 0.58). Their beta diversity patterns were mostly explained by the replacement component. However, assemblage dissimilarities between lotic reaches were mainly due to the richness differences component (absolute gain or loss of species).

Table 3. Contribution percentage of specific abundances to different sampling sites in the Sauce Grande River using SIMPER analysis.

Species	Contribution percentage (%)					
	CwLe vs. CwLo	CwLe vs. TwLe	CwLe vs. TwLo	CwLo vs. TwLe	CwLo vs. TwLo	TwLe vs. TwLo
A. facetus	<1	<1	3.87	0	9.46	6.41
B. iheringii	5.62	8.63	5.67	5.66	4.95	4.75
C. carpio	<1	1.06	<1	0	0	0
C. decemmaculatus	11.03	6.12	4.99	7.55	13.63	7.14
C. interruptus	12.02	16.41	15.24	4.76	9.65	3.81
C. paleatus	5.24	6.33	10.45	5.59	16.02	8.17
C. voga	1.7	8.64	1.61	13.33	0	14.8
J. lineata	9.4	11.9	9.1	14.45	13.22	7.17
O. bonariensis	27.65	18.17	22.75	26.76	8.74	23.8
O. jenynsii	5.02	6.36	5.46	3.2	5.91	4
P. laticeps	6.56	4.55	6.96	5.25	7.14	7.37
P. pampa	10.3	5.41	8.57	7.63	5.58	6.7
P. trucha	<1	<1	<1	0	0	0
R. quelen	3.83	5.69	3.77	5.81	5.7	5.89

CwLe = clear water lentic conditions; CwLo = clear water lotic conditions; TwLe = turbid water lentic conditions; TwLo = turbid water lotic conditions.
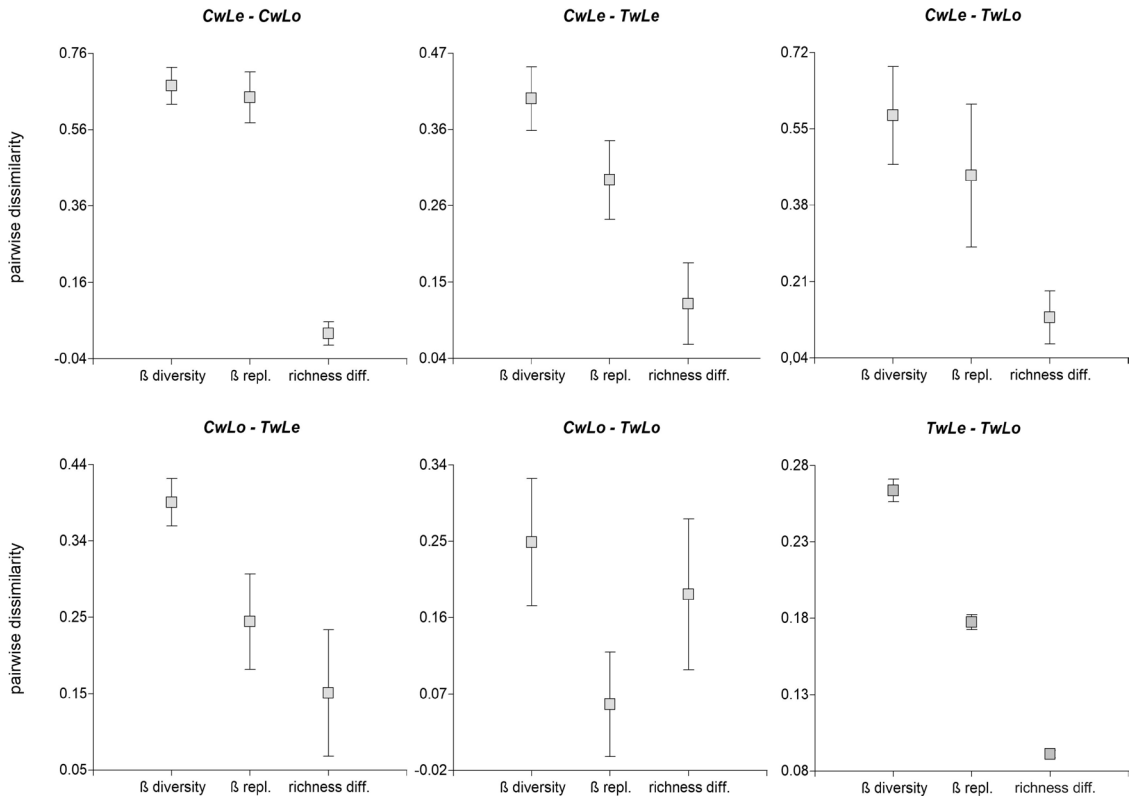
Figure 5. Means and standard deviation of beta diversity (β diversity) and its components (β repl.= replacement, β rich.= richness differences) calculated for different pairs of sampled sites of the Sauce Grande River (CwLe = clear water lentic conditions; CwLo = clear water lotic conditions; TwLe = turbid water lentic conditions; TwLo = turbid water lotic conditions).

3.4. Relationships between environmental conditions and fish assemblages

Different fish assemblage attributes and specific abundances were intimately associated with particular environmental conditions (Table 4). The total fish and NS abundances, species richness, assemblage diversity and the abundance of some species such as *B. iheringii* and *C. interruptus* seemed to be favored by environments with high pH, turbidity, conductivity and nutrient concentrations, as summarized by the first component. In turn, *A. facetus*, *C. paleatus* and *P. pampa* were most abundant in warmer, oxygen-rich waters.

For the fish assemblage structure considering all fish species, the best explanatory model (lowest value of AICc) had two environmental variables: nitrates and water conductivity (Table 5). With the inclusion of dissolved oxygen, the second best model substantially improved its explanation power (47.9 to 62.7%) with a minimum increase (0.71) in the AICc. These three variables also composed the best model (72.8%) for the fish assemblages considering the abundances of NNS. Instead, when only NS abundances were considered, the best model incorporated water conductivity as the unique variable with a small R^2 (29.7%). With the inclusion of total phosphorous, its explanatory power accounted for 45.8% of the observed variation. Given its frequency of occurrence in models proposed and the weight of these models, the nitrate ($Wi_{all\,species}= 0.595$, $Wi_{NNS}= 1$) and water conductivity ($Wi_{all\,species}= 0.733$, $Wi_{NNS}= 0.680$) were the most important predictor variables for the fish assemblages considering the abundance of all fish species, adding dissolved oxygen ($Wi= 0.727$) for the abundances of NNS. For fish assemblages of NS abundances, the water conductivity ($Wi_{NS}= 0.675$) was the most frequently predictor variable occurring in the models.

4. Discussion

4.1. Environmental conditions

Environmental conditions significantly differed among sampled reaches. In this context, two main environmental scenarios can be roughly identified in the Sauce Grande River. One is composed by the

upstream, less alkaline, clearer, colder and nutrient-oxygen-poor waters represented by the reservoir and its downstream lotic reach. The other, is composed by the more distant downstream Sauce Grande Lagoon and its downstream lotic reach, where turbidity, nutrients, oxygen, water conductivity and temperature largely increases. Indeed, reaches with colder, clearer and nutrient-oxygen poor waters grouped tightly at one extreme of the ordination irrespective of their lentic or lotic conditions. The lower values of conductivity, turbidity and nutrient concentrations in the reservoir closely resemble a pattern recurrently observed in these artificial water bodies (Agostinho et al., 2007). Similar

abiotic conditions in the river reach downstream to the reservoir were observed. About this, Baxter (1977) postulated that heat, silt and nutrients retained in reservoirs are lost to the streams. On the other hand, the enhanced productivity commonly incorporated by floodplain lagoons to lowland river ecosystems (Junk et al., 1989) may largely explain the eutrophic conditions observed in downstream reaches. The more eutrophic downstream reaches of this river were also characterized by higher dissolved oxygen concentration, pH, turbidity and water conductivity. The eutrophication is an inevitable process given in a course from the source to mouth caused by drainage from cultivated and inhabited districts (Butcher, 1947). In this respect, changes in land-uses could be considered as one of the main drivers for the observed deterioration of water quality in Argentina (Rosso & Fernández Cirelli, 2013; Amuchástegui et al., 2016) as in many parts of the world (Allan, 2004). The impact on the thermal condition and oxygenation of waters seemed evident in the reservoir and its downstream river reach, where the lowest temperatures and dissolved oxygen concentrations were recorded. Under natural conditions, the small volume of water in a river reach and turbulent mixing ensure that river water responds to changes in the meteorological conditions and incorporate atmospheric oxygen (McCartney, 2009). In contrast, large masses of still water in reservoirs allow thermal stratification and the occurrence of cold, deoxygenated waters in the hypolimnion (Beutel & Horne, 1999). Nevertheless, dissolved oxygen concentration in the lower layer of Paso de las Piedras Reservoir is close to the saturation value almost throughout all the year (Estrada et al., 2011) due to the lack of stratification (Intartaglia & Sala, 1989). Therefore, reservoir-derived reduction of dissolved oxygen is less likely and its increase by enhanced primary

Table 4. Spearman rank correlation coefficients between fish assemblage attributes and specific abundances with PCA scores of environmental variables.

	PCA axis 1	PCA axis 2
AF abundance	0.25	0.57*
BI abundance	0.81*	0.13
CC abundance	-0.46	-0.15
CD abundance	0.11	-0.16
CI abundance	0.71*	0.02
CP abundance	0.51	0.66*
CV abundance	0.37	-0.47
JL abundance	0.47	-0.2
OB abundance	0.08	-0.23
OJ abundance	0.51	0.39
PL abundance	0.32	0.12
PP abundance	0.2	0.57*
PT abundance	-0.45	-0.13
RQ abundance	0.43	0.41
total abundance	0.62*	0.11
NS abundance	0.89*	0.25
NNS abundance	0.08	-0.23
richness	0.78*	0.23
diversity	0.74*	0.32

*p value<0.05. prop. NNS = proportion of non-native species. Species codes as listed in Table 2.

Table 5. First 10 best overall models found for fish assemblages of Sauce Grande River using the AICc criterion.

Abundances of all species				Abundances of native species				Abundances of non-native species			
N	Variables	AICc	R²	N	variables	AICc	R²	N	variables	AICc	R²
2	NO₃, WC	84.48	0.479	1	WC	82.83	0.297	3	NO₃, DO, WC	93.18	0.728
3	NO₃, DO, WC	85.19	0.627	1	TP	83.16	0.278	2	NO₃, WC	93.98	0.569
1	WC	85.56	0.226	2	TP, WC	83.38	0.458	2	NO₃, DO	94.99	0.531
1	TP	85.67	0.219	2	NO₃, WC	83.53	0.451	3	NO₃, TP, DO	95.09	0.68
2	pH, WC	85.85	0.416	1	temp	83.88	0.233	4	temp, NO₃, DO, WC	95.39	0.806
3	NO₃, TP, WC	85.94	0.603	2	pH, WC	84.35	0.412	2	NO₃, TP	95.39	0.515
4	NO₃,TP, DO, WC	86.31	0.757	2	temp, WC	84.48	0.406	1	NO₃	95.4	0.341
2	NO₃, TP	86.35	0.391	3	NO₃, TP, WC	84.53	0.597	3	NO₃, pH, WC	96.14	0.652
1	Temp	86.36	0.173	2	NO₃, TP	84.73	0.393	4	NO₃, TP, DO, WC	97.41	0.771
4	temp, NO₃, DO, WC	86.97	0.744	3	TP, pH, WC	85.24	0.573	4	temp, NO₃, TP, DO	97.62	0.767

N = number of variables.

production in downstream reaches is perhaps a more plausible reason for observed differences.

4.2. Fish assemblages in the context of a fragmented habitat and variable environmental conditions

The fish fauna inhabiting the Sauce Grande River represents one of the southernmost occurrences of Brazilian taxa in the continent and it is composed by a very impoverished fraction of the paranoplatense fish fauna (Ringuelet, 1961). All species previously known from the Sauce Grande River basin (Casciotta et al., 1999; Grosman et al., 2017) were collected in our surveys. Four non-native species were collected but only *O. bonariensis* developed well established populations (Grosman et al., 2017).

Some general patterns in fish assemblage attributes were observed. Total fish abundance and abundance of NNS were higher in lentic conditions when compared with lotic reaches. In reservoirs, fish abundance is usually higher than that observed in the river before the dam was constructed (Agostinho et al., 2016). This is mostly explained by the development of lacustrine species that take the opportunity of the new created lentic conditions (Johnson et al., 2008; Smith et al., 2018). On the other hand, a lacustrine environment created by a lagoon within the river network enhances the primary productivity (Junk et al., 1989) which certainly may support larger fish populations (Petrere, 1983), including the non-native species. Fish assemblage diversity was extremely low (a third of the lowest value in other reaches) in the reservoir. Artificially impounded habitats worldwide typically develop disparate divergent biological communities from those that originally occurred in the river (Freedman et al., 2014; Perônico et al., 2020). The effects brought by dams, change according to the inherent adaptability of fish communities to respond to the physico-chemical and biological changes (Rosenberg et al., 1997). Neotropical fishes evolved predominantly in flowing waters, and only few species have adaptations to inhabit in lentic environments, such as those created by impoundments (Gomes & Miranda, 2001). Such a lack of traits and plasticity may partly explain the decrease in richness and diversity observed in Sauce Grande reservoir. Similar findings were reported for reservoirs in temperate regions (Turgeon et al., 2019) and in the main river basins in Brazil (Agostinho et al., 2007; Perônico et al., 2020). Total fish abundance, species richness, the abundance of NS and assemblage diversity also seemed to be influenced by environmental conditions since they were all high, positive and significantly related with a gradient of increasing turbidity, water conductivity and nutrient concentrations. An increase in assemblage diversity and species richness is expected in fluvial ecosystems as habitat diversity (Lowe-McConnell, 1975) but also eutrophication (Butcher, 1947) increases. Given the nature of the Pampean lotic ecosystems, with high nutrients concentration and sediment loads (Feijoó et al., 1999), it is expected that the native fish species are adapted and favored by these conditions which could be detrimental for non-native fish species. Indeed, our results revealed that both NS and NNS were influenced by major environmental gradients where water conductivity, nitrates and dissolved oxygen turned to be the most important predictor variables in the best and most frequent explanatory models of the fish assemblage structures.

Spatial patterns in fish species distribution were reflected in the beta diversity analysis. The similarity found between both lotic reaches and the lagoon was greater than that found with the reservoir. This suggests that the marked changes imposed by the reservoir against the natural conditions of the lagoon and lotic reaches, generated drastic changes in the fish communities. Indeed, the highest dissimilarity in fish assemblage composition was found between the reservoir and the lotic reach downstream to the dam. As the similarity between reservoir and its downstream reach regarding environmental conditions was high, the observed differences in beta diversity patterns can be mostly attributed to the fragmented habitat conditions imposed by the dam. In our study, beta diversity patterns were mostly explained by species replacement along the longitudinal river axis, a pattern also observed in several tributaries of the upper Paraná River (Peláez et al., 2017). Species replacement refers to the simultaneous gain and loss of species along ecological gradients, when species tend to replace each other (Legendre, 2014). In regulated rivers it is expected that damming-induced changes affect beta diversity components downstream of the reservoir, contributing to the dominance of species replacement component (Lansac-Tôha et al., 2019). In this context, the increase of the abundance of non-native species is also a well-known consequence of reservoirs in the Neotropical region (Guenther & Spacie, 2006; Liew et al., 2016) and worldwide (Han et al., 2008; Jellyman & Harding, 2012).

The Sauce Grande River showed a high non-native/native species ratio, more noticeably in lentic reaches. Non-native species such as *C. carpio* and

P. trucha were only collected in the reservoir. The low number of specimens of these species collected in the Sauce Grande, together with their narrow distribution suggests a recent entrance of these species in this basin. Paradoxically, the presence of both species in the Pampa Plain is known from many decades ago. The exotic *Cyprinus carpio* was introduced in Argentina in 1925 (Baigún & Quirós, 1985) and its distribution has expanded significantly in the last three decades (Maiztegui et al., 2016). Similarly, *P. trucha* was intentionally stocked in the Sauce Grande Basin, more than five decades ago (Ringuelet, 1961). This historical context suggests that some local constraints could be hampering the successful establishment of these NNS in this river ecosystem. *Cyprinus carpio* was intentionally stocked in the reservoir and it is quite probable that only the physical barrier imposed by the dam is confining this species. *Cyprinus carpio* has a broad tolerance to different environmental factors, including eutrophication and turbidity (Zambrano et al., 1998) that characterize the downstream reaches of the Sauce Grande River. In contrast, the restriction of *P. trucha* in clear waters would probably also obey to the fact that this environment more closely resembles the natural habitats (low water conductivity and turbidity, low amounts of nutrients) of this species in freshwater ecosystems of Patagonia (Macchi et al., 2007). Non-native Neotropical allochthonous species, *C. voga* and *O. bonariensis* were largely confined to lentic reaches, but their local abundances in these environments were contrasting. Whereas the inland silverside presented its largest population in the reservoir, the detritivorous *C. voga* was more abundant in the turbid, eutrophic conditions lagoon. The trophic ecology of these species together with the preferential route of energy and food webs in each habitat could help to explain the observed patterns. *C. voga* is an iliophagous detritivorous fish species (Corrêa & Piedras, 2013). Turbid and productive lakes are more likely to sustain a detritivore assemblage of consumers (Vanni et al., 2006). In contrast, the preferential food web dynamic in reservoirs derived from pelagic nutrients (Freedman et al., 2014) would explain the outstanding abundance of *O. bonariensis* which fed on the zooplankton of Paso de las Piedras Reservoir (Fritz, 2018).

Whereas some native species were widely and equally distributed along the different sampled reaches, others where restricted or skewed to a particular habitat (lotic or lentic reaches) or environmental (clear or turbid waters) conditions. *O. jenynsii* was less responsive to environmental and habitat factors, a pattern also observed for this species in another riverine-lentic ecosystem of the Pampa Plain (Rosso & Quirós, 2009). Riverine habitat fragmentation likely more markedly influenced *A. facetus* since it was only found in lotic conditions. Nevertheless, some major patterns in other NS respective to habitat were observed. Species preferently collected in riverine natural conditions of the Sauce Grande River, as *P. pampa*, *C. decemmaculatus* and the small Siluriformes *P. laticeps*, are considered intolerant to environmental degradation (Hued & Bistoni, 2005; Bertora et al., 2018b). The number of intolerant species is considered an exclusive metric of the fish assemblages living in healthy riverine conditions (de Freitas Terra & Araújo, 2011). *C. decemmaculatus* is the most frequent and abundant Cyprinodontiformes in lotic ecosystems of the Pampa Plain being comparatively less common in lentic conditions (Rosso, 2006). Conversely to these species, the one-sided livebearer *J. lineata* was largely confined to lentic conditions. This species is commonly found as one of the most abundant accompanying species of *O. bonariensis* in shallow lakes (Rosso, 2006).

Native species responsive to environmental gradient were *B. iheringii*, *C. interruptus*, *A. facetus, C. paleatus* and *P. pampa*. Turbid reaches, with nutrient-rich waters and higher conductivity were dominated by eurioic species as *B. iheringii* and *C. interruptus*. Eutrophication is as a strong driver for fish assemblage structure in freshwater ecosystems (Van de Bund & Van Donk, 2002; Granzotti et al., 2018). Generally, it could be expected that vision oriented fishes prevail in clear oligotrophic waters, as most Characiformes, whereas chemo or tactile-oriented fishes, as most Siluriformes, domain in turbid eutrophic conditions (Pouilly & Rodriguez, 2004; Rosso et al., 2010). Both *B. iheringii* and *C. interruptus* are small invertivorous Characiformes usually consumed by larger fish. The food intake of small invertivorous fishes decreased in turbid water due to anti-predator behavior resulting in higher prey survival (Figueiredo et al., 2016). This may partially explain the positive association of small Characiformes and water turbidity in the Sauce Grande Basin. A similar result was observed for *Serrapinnus notomelas*, other small invertivorous Characiformes inhabiting the upper Paraná River (Piana et al., 2006). Concomitantly, the enhanced primary productivity that can be associated to

turbid, eutrophic reaches of this system, also would favor the establishment of large populations of these small Characiformes. *Corydoras paleatus* presents a wide environmental plasticity which explains its wide distribution in South American (Tencatt et al., 2016). In our study, the abundance of this small armored catfish was higher in turbid conditions and further favored by warmer waters with higher concentrations of dissolved oxygen. A positive relationship between abundance of Siluriformes species and water turbidity was also found in temperate shallow lakes of Argentina (Rosso et al., 2010) and in several freshwater ecosystems of Bolivia, Venezuela and Brazil (Pouilly & Rodríguez, 2004).

4.3. Aspects of management and conservation

Reservoirs affect the natural river conditions, causing deep changes in biological communities, so management actions are usually not simples. In this respect, efficient management and conservation of Neotropical fish in reservoirs are currently constrained by the incipient knowledge about the Neotropical fish fauna, the absence or inadequate monitoring of the results of the implemented actions, insufficient knowledge about the problems to be solved, and the superfluous management of impoundments impacts (Agostinho et al., 2016). In addition, reservoirs are also linked with the establishment of many non-native fish species in Neotropical river ecosystems (Daga et al., 2015). It is therefore necessary to prevent the arrival of potentially non-native species, the timely management of incursions, effective management of those already established and promote a deep social awareness engaging volunteers in surveillance and monitoring (key role of citizen science; Pyšek et al., 2020). The absence of non-native species is the first step towards conservation of freshwater ecosystems as, ideally, freshwater protected areas should contain no non-native species (Saunders et al., 2002). This claims for a thoughtful and more careful management of surface waters in Neotropical ecosystems regarding stocking programs for non-native fish farming, an inconvenient common practice in many tropical reservoirs of South America (Ortega et al., 2015).

5. Conclusions

Our results revealed that a low diversified Neotropical fish fauna is modulated both, by habitat fragmentation imposed by the creation of artificial impoundments and by major environmental variables. Water temperature seemed to be further affected by the presence of the reservoir. In consequence, reservoir affected fish assemblages directly by habitat fragmentation and the enhancement of non-native species and indirectly by its effects on environmental variables as water temperature. In this scenario, native reophilic species better thrive in lotic reaches but once there, environmental conditions were important in regulating the expression of fish assemblage structure. Tolerant species were favored by turbid, nutrient-rich waters with higher conductivity, pH and dissolved oxygen. Altogether, habitat disruption and limnological variables related with eutrophication and water quality (water conductivity, nutrient concentrations, pH, dissolved oxygen and turbidity) as well as those affected by disruption of natural conditions imposed by the reservoir (water temperature) shaped observed differences between fish assemblage structures in the spatially fragmented and environmentally variable Sauce Grande River basin.

Acknowledgements

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