



## Environmental heterogeneity explains species turnover but not nestedness in fish assemblages of a Neotropical basin

A heterogeneidade ambiental explica o turnover de espécies, mas não seu aninhamento em assembleias de peixes de uma bacia Neotropical

Oscar Eduardo Peláez<sup>1\*</sup>, Filipe Manoel Azevedo<sup>2</sup> and Carla Simone Pavanelli<sup>1,3</sup>

<sup>1</sup>Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil

<sup>2</sup>Programa de Graduação em Ciências Biológicas, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil

<sup>3</sup>Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura – Nupélia, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil

\*e-mail: oscar\_pelaez@hotmail.com

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**Abstract: Aim:** Heterogenous environments can contribute to maintain biodiversity. Traditionally beta diversity studies have focused on determining the effect of environmental variables on the total dissimilarity of species composition. However, decomposing beta diversity in species replacement and nestedness could give new insights on mechanisms affecting spatial patterns of biodiversity. We aimed to answer two main questions about spatial patterns of fish diversity in a Neotropical basin: 1) whether some regions contribute differently to fish diversity, and 2) whether species turnover and nestedness are explained by environmental gradients. **Methods:** Sampling sites in the main channel and tributaries of the Upper Paraná River were sampled between 2013 and 2015. We partitioned beta diversity and tested the relationship of turnover and nestedness with environmental variables. **Results:** 74 species were captured. Some of these species were restricted to different sites, contributing to variation in species composition. Hill numbers showed a trend for higher diversity in the tributaries than in Paraná River sampling sites, and the partition of beta diversity revealed that species replacement drove dissimilarity in species composition. Only total beta diversity and turnover were related to environmental variables, mainly conductivity and turbidity. **Conclusions:** Species diversity and composition of fish assemblages in the Upper Paraná River could be related to environmental gradients. Overall, our results suggest that Paraná River tributaries contribute to increase environmental heterogeneity, and hence to maintain a high diversity and variation in species composition. For that reason, we strongly recommend preserving highly heterogeneous habitats in the region.

**Keywords:** species diversity; Hill numbers; beta diversity; environmental gradient; dBRDA.

**Resumo: Objetivo:** Ambientes heterogêneos podem contribuir para o sustento da biodiversidade. Tradicionalmente os estudos de diversidade beta foram focados no efeito do ambiente na dissimilaridade total da composição de espécies. Particionar a diversidade beta em *turnover* e aninhamento de espécies



poderia fornecer outras noções dos mecanismos que afetam os padrões espaciais de biodiversidade. Aqui almejamos responder duas perguntas sobre padrões espaciais em assembleias de peixes de uma bacia neotropical: 1) se algumas regiões contribuem diferentemente para a diversidade de espécies, e 2) se os componentes da diversidade beta são explicados por gradientes ambientais. **Métodos:** Locais na calha principal e tributários do alto rio Paraná foram amostrados entre 2013 e 2015. A diversidade beta foi particionada e testada a relação do *turnover* e aninhamento com variáveis ambientais. **Resultados:** Setenta e quatro espécies foram capturadas. Algumas espécies estiveram restritas a diferentes locais contribuindo para a variação na composição de espécies. Segundo os números de Hill, tributários tendem a apresentar maior diversidade que os locais do rio Paraná, enquanto a diversidade beta foi determinada principalmente por *turnover*. Somente a diversidade beta total e o *turnover* estiveram relacionados a variáveis ambientais, principalmente condutividade e turbidez. **Conclusões:** A diversidade de espécies e a composição nas assembleias de peixes no alto rio Paraná podem estar relacionadas a gradientes ambientais. Em síntese, nossos resultados sugerem que os tributários do rio Paraná contribuem para a heterogeneidade ambiental e, portanto, para manter alta diversidade e variação na composição de espécies. Assim, é fortemente ressaltada a necessidade de se preservar ambientes heterogêneos na região.

**Palavras-chave:** diversidade de espécies; números de Hill; diversidade beta; gradiente ambiental; dbRDA.

## 1. Introduction

Beta diversity is defined as the variation in the identities of species among sites (Heino et al., 2015). Over the past decade the variation in species composition was recognized as being not only a result of species replacement (turnover), but also of the contribution of differences in species richness among sites (nestedness). Consequently, it was proposed that measures of beta diversity based on dissimilarity could be partitioned to account for these two components of variation in species composition: dissimilarity among sites derived from species replacement and dissimilarity derived from nestedness (Baselga, 2010).

The relationship between beta diversity and environmental heterogeneity depends on the spatial scale and dispersal rates. Thus, a stronger environmental control on species composition is expected at intermediate spatial scales, where dispersal is neither too high to mask the effects of environmental variables (Heino et al., 2015) nor too low for the differences in species composition to be related to historical processes (e.g. Villéger et al., 2013). However, few studies distinguished the relationship between environmental heterogeneity and patterns of turnover and nestedness (Bishop et al., 2015; Boyero et al., 2015). Disentangling the mechanisms underlying beta diversity can help direct conservation strategies (Socolar et al., 2016). For instance, a high turnover can indicate that sites differ in environmental characteristics selecting different species. Therefore, a high diversity of species can be preserved when environmental heterogeneity at landscape scale is maintained. On the other hand, a high nestedness could show that sites with high

species richness should be a priority for conservation (Gianuca et al., 2017).

Despite the Upper Paraná River basin being a highly impacted system, more than 300 fish species occupy its habitats with 48% of these species being endemic to the basin, constituting a differentiated biogeographic province (Graça & Pavanelli, 2007; Langeani et al., 2007; Buckup, 2011). Moreover, almost every year the number of species is increased by descriptions of unknown fauna from the Paraná River and its tributaries (Tencatt et al., 2014; Serra & Langeani, 2015; Roxo et al., 2016). Due to its diversity, highly endemic species and disturbance intensity in the region, it is worth any effort to know the status of Paraná River fish species and which factors influence its assemblages.

Here we aim to describe the patterns of variation of species composition and to determine how much of the turnover and nestedness patterns of fish assemblages in the Upper Paraná river is explained by environmental heterogeneity. In this highly-impacted system (Barletta et al., 2010; Espínola et al., 2014; Daga et al., 2015) a stretch of approximately 210 km still remains undammed. This stretch is characterized by a high environmental variability with multiple channels, permanent and temporal lagoons, seasonal and daily changes in water level and heterogeneity in the confluence of the main channel of the Paraná River and its tributaries (Thomaz et al., 2007; Roberto et al., 2009). Tributaries may contribute for variation in species composition of aquatic communities, with tributaries themselves and their confluences, consisting of higher order streams, providing physical and chemical discontinuities

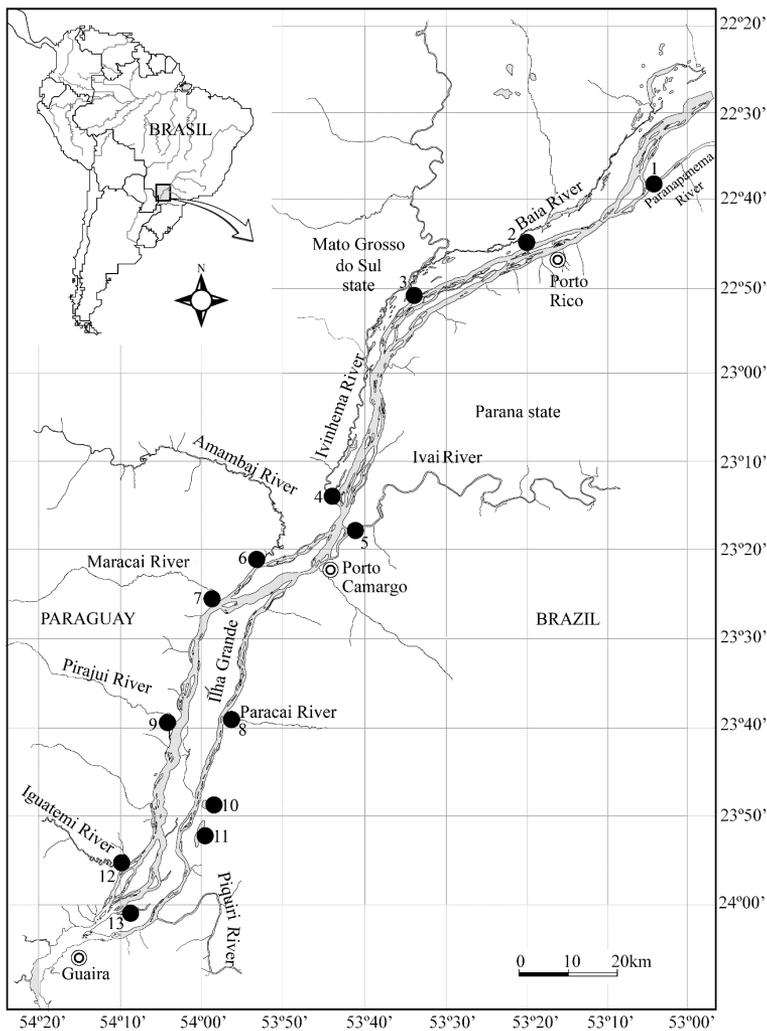
that can influence patterns of diversity and species composition (Benda et al., 2004; Heino et al., 2013; Czeplédi et al., 2016). Here, we give an overall description of the diversity and composition of fish assemblages and the contribution of the Paraná River and its tributaries to fish diversity in that region. We aimed to answer two main questions: 1) Do tributaries and river sites differ in patterns of turnover and nestedness? And 2) are turnover and nestedness related to environmental variables?

## 2. Material and Methods

### 2.1. Sampling

Sampling sites were located in a stretch of approximately 210 km between Porto Primavera and Itaipu reservoirs in the Upper Paraná River,

including some of its main tributaries (between 22°28'S - 52°56'W and 24°4'S - 54°14'W). Samplings were carried out in 23 sampling sites, 10 sites located in main tributaries: Paranapanema, Baía, Ivinhema, Ivinheminha, Ivaí, Amambai, Maracaí, Paracaí, Pirajuí and Iguatemi; 10 sites located in the main channel of the Paraná River, 2km upstream the confluence of each tributary with the Paraná River; and three adjacent lagoons: Saraiva, São João and Xambrê. Considering that Ivinhema River has several mouths flowing into the Paraná River, here we separated its sampling sites into Ivinhema (sites close to Baía River) and Ivinheminha (sites close to Ivaí River) (Figure 1). Since two of the three lagoons (Saraiva, São João) likely only receive individuals from adjacent sites in the Paraná River, and the other lagoon (Xambrê)



**Figure 1.** Sampling sites in the Upper Paraná River floodplain. Paraná River in grey. (1) Paranapanema; (2) Baía; (3) Ivinhema; (4) Ivinheminha; (5) Ivaí; (6) Amambai; (7) Maracaí; (8) Paracaí; (9) Pirajuí; (10) São João lagoon; (11) Xambrê lagoon; (12) Iguatemi; (13) Saraiva lagoon. Sampling sites in the main channel of the Paraná River were located upstream from each point in the map (except for 10 and 11).

only recently lost its connection with the main river channel, they were considered as sites belonging to the Parana River. Fishes were sampled quarterly from August 2013 to May 2015 using a seine (20 m × 1.5 m; 0.5 cm mesh). Nets were operated by sweeping semi-circles next to the shore and species abundances were expressed as catch per unit effort (individuals · m<sup>-2</sup> of net). Fish samples were fixed in formalin (10%) and identified based on specialized bibliography (e.g. Graça & Pavanelli, 2007; Britski et al., 2012). Voucher specimens were deposited at the fish collection of the Research Nucleus in Limnology, Ichthyology and Aquaculture (Nupélia), Maringá State University, Brazil. Classification of species followed Eschmeyer et al. (2016). Additionally, we considered six environmental variables at each site: conductivity (µS cm<sup>-1</sup>), dissolved oxygen (mg L<sup>-1</sup>), pH, turbidity (NTU), water temperature (°C) and mean depth (m).

## 2.2. Species diversity

We first described some aspects of  $\alpha$  diversity of tributaries and the main channel of the Paraná River. For this, we used Hill numbers to calculate “true” species richness ( $q = 0$ ), Shannon diversity ( $q = 1$ ) and Simpson diversity ( $q = 2$ ) (Chao et al., 2014). Hill numbers are expressed in units of effective number of species: how many species with similar abundances are needed for two communities to have the same value of a diversity measure. Due to physical limitations for accessing some sites every month, we finally obtained 168 samples instead of 176 (8 for each site). Thus, sites varied in sampling effort and sample size. These variations in sampling effort can influence the number of species that can be detected in an assemblage (Chao & Jost, 2012; Colwell et al., 2012). Therefore, sample-size-based rarefaction and extrapolation of Hill numbers were used to estimate diversity curves according to Chao et al. (2014). These curves show the expected diversity as a function of sample size and were used to compare diversity indices for most commonly used Hill numbers ( $q = 0, 1$  and  $2$ ). Comparisons were performed using the smaller sample as reference and extrapolating diversity to twice the size of the reference sample. 95% confidence intervals for those curves were computed by a bootstrap method based on 999 iterations. iNEXT package (Hsieh et al., 2016) in R 3.2.4 was used to estimate rarified Hill numbers.

## 2.3. Assemblage composition

To explore spatial patterns in species composition we used two approaches. First, a non-metric multidimensional scaling analysis – NMDS – was employed to display Bray Curtis dissimilarity among sites in portions of the sampled region. As some species were present in most sites and other restricted to certain regions, sites were grouped in northern, southern, right and left portions.

Then, partition of beta diversity (Baselga, 2013) was used to separate the two components of Bray Curtis dissimilarity among assemblages: i) abundance gradients, equivalent to species nestedness, when individuals are lost from one site to the other but without species loss or when species disappear from one site; ii) balanced variation in abundance, when species composition changes through species replacement. It occurs when the number of individuals remains almost equal from one site to another but the individuals of a species are replaced by a similar number of individuals of another species. Beta diversity partition was performed with ‘betapart’ package (Baselga & Orme, 2012) in R software.

## 2.4. Statistical analyses

PERMDISP analysis (Anderson et al., 2006) was used to test the homogeneity in multivariate dispersions of Bray Curtis dissimilarity matrix and answer our first question (whether tributaries and river sites varied in patterns of turnover and nestedness). Regarding the second question (whether turnover and nestedness are explained by environmental heterogeneity), we used distance-based linear models (dbRDA) to explore the relationship between Bray Curtis dissimilarity and environmental variables (Legendre & Anderson, 1999; Anderson, 2001). To test the significance of these relationships, P-values were obtained by Monte Carlo permutations (999 permutations). The multivariate ordination analysis and distance based linear models were performed using ‘Vegan’ package (Oksanen et al., 2016).

## 3. Results

Over the two years of sampling, 32351 individuals were captured, representing 74 species, 25 families and eight orders, that is approximately 24% of fish species registered at the Upper Paraná River basin. As most Neotropical basins, Characiformes (35 species), Siluriformes (17 species) and Perciformes (9) were the orders with the highest number of species. It is important to notice that 32% (24 species) of the captured species are

non-native. Almost all of these non-native species (22 species) expanded their distribution ranges from the lower Paraná basin after the Itaipu construction. Additionally, 66 individuals of *Platanichthys platana* (Regan, 1917), species of recent occurrence in the region were captured, mostly in sites of the Paraná River (Table 1).

### 3.1. Species diversity

Considering all sites, 57 species were registered in the main channel of the Paraná River and 61 species were captured in the Paraná River tributaries. Ivinhema, Baía and Iguatemi showed the highest number of species for tributaries (38, 30 and 26 species respectively), and São

**Table 1.** Fish species from the upper Paraná River, collected between August 2013 and May 2015. Abbreviations as in NMDS ordination (Figure 3). NA: Not analyzed (species with only one individual, generally a juvenile). Classification follows Eschmeyer & Fong (2017), excepting Characidae subfamilies, which follow Miranda (2010).

MYLIOBATIFORMES	CHARACIFORMES
<b>Potamotrygonidae</b> <i>Potamotrygon amandae</i> Loboda & Carvalho, 2013 (P.AMA)	<b>Tetragonopterinae</b> <i>Hyphessobrycon eques</i> (Steindachner, 1882) (H.EQU)
<b>CLUPEIFORMES</b>	<i>Hemigrammus ora</i> Zarske, Le Bail & Géry, 2006 (H.ORA)
<b>Clupeidae</b>	<i>Moenkhausia bonita</i> Benine, Castro & Sabino, 2004 (M.BON)
<i>Platanichthys platana</i> (Regan, 1917) (P.PLA)	<i>Moenkhausia forestii</i> Benine, Mariguela & Oliveira, 2009 (M.FOR)
<b>CHARACIFORMES</b>	<i>Moenkhausia gracilima</i> Eigenmann, 1908 (M.GRA)
<b>Crenuchidae</b>	<i>Moenkhausia aff. intermedia</i> Eigenmann, 1908 (M.INT)
<i>Characidium aff. zebra</i> Eigenmann, 1909 (C.ZEB)	<b>Clado Astyanax</b>
<b>Erythrinidae</b>	<i>Astyanax aff. fasciatus</i> (Cuvier, 1819) (A.FAS)
<i>Hoplias mbigua</i> Azpelicueta, Benítez, Aichino & Mendez, 2015 (H.MBI)	<i>Astyanax lacustris</i> (Lütken, 1875) (A.LAC)
<i>Hoplias</i> sp. ( <i>Hoplias</i> sp.)	<i>Psellogrammus kennedyi</i> (Eigenmann, 1903) (P.KEN)
<i>Hopleryrhinus unitaeniatus</i> (Spix & Agassiz, 1829) (NA)	<b>Stevardiinae</b>
<b>Parodontidae</b>	<i>Diapoma guarani</i> Mahner & Géry, 1987 (D.GUA)
<i>Apareiodon affinis</i> (Steindachner, 1879) (A.AFI)	<i>Bryconamericus stramineus</i> Eigenmann, 1908 (B.STR)
<b>Cynodontidae</b>	<i>Knodus moenkhausii</i> (Eigenmann & Kennedy, 1903) (K.MOE)
<i>Rhaphiodon vulpinus</i> Spix & Agassiz, 1829 (NA)	<b>SILURIFORMES</b>
<b>Serrasalmidae</b>	<b>Auchenipteridae</b>
<i>Mylossoma duriventre</i> (Cuvier, 1818) (M.DUR)	<i>Parauchenipterus galeatus</i> (Linnaeus, 1766) (P.GAL)
<i>Metynnis lippincottianus</i> (Cope, 1870) (M.LIP)	<i>Auchenipterus osteomystax</i> (Miranda Ribeiro, 1918) (A.OST)
<i>Serrasalmus maculatus</i> Kner, 1858 (S.MACU)	<b>Doradidae</b>
<i>Serrasalmus marginatus</i> Valenciennes, 1837 (S.MAR)	<i>Trachydoras paraguayensis</i> (Eigenmann & Ward, 1907) (T.PAR)
<b>Hemiodontidae</b>	<b>Heptapteridae</b>
<i>Hemiodus orthonops</i> Eigenmann & Kennedy, 1903 (H.ORT)	<i>Pimelodella avanhandavae</i> Eigenmann, 1917 (P.AVA)
<b>Anostomidae</b>	<i>Pimelodella gracilis</i> (Valenciennes, 1835) (P.GRA)
<i>Leporinus friderici</i> (Bloch, 1794) (L.FRI)	<i>Pimelodella taenioptera</i> Miranda Ribeiro, 1914 (NA)
<i>Megaleporinus piavussu</i> (Britski, Birindelli & Garavello, 2012) (L.PIA)	<b>Pimelodidae</b>
<i>Schizodon borellii</i> (Boulenger, 1900) (S.BOR)	<i>Sorubim lima</i> (Bloch & Schneider, 1801) (S.LIM)
<b>Curimatidae</b>	<i>Hemisorubim platyrhynchos</i> (Valenciennes, 1840) (H.PLA)
<i>Steindachnerina brevipinna</i> (Eigenmann & Eigenmann, 1889) (S.BRE)	<i>Pimelodus maculatus</i> Lacepède, 1803 (P.MAC)
<i>Steindachnerina insculpta</i> (Fernández-Yépez, 1948) (S.INS)	<i>Pimelodus misteriosus</i> Azpelicueta, 1998 (P.MYS)
<b>Prochilodontidae</b>	<i>Pimelodus ornatus</i> Kner, 1858 (NA)
<i>Prochilodus lineatus</i> (Valenciennes, 1837) (P.LIN)	<i>Iheringichthys labrosus</i> (Lütken, 1874) (I.LAB)
<b>Bryconidae</b>	<b>Loricariidae</b>
<i>Salminus hilarii</i> Valenciennes, 1850 (NA)	<i>Loricariichthys platymetopon</i> Isbrücker & Nijssen, 1979 (L.PLA)

Table 1. Continued...

<b>Characidae</b>	<i>Loricariichthys rostratus</i> Reis & Pereira, 2000 (L.ROS)
<b>Aphyocharacinae</b>	<i>Loricaria proluxa</i> Isbrücker & Nijssen, 1978 (L.PRO)
<i>Aphyocharax anisitsi</i> Eigenmann & Kennedy, 1903 (A.ANI)	<i>Pterygoplichthys ambrosettii</i> (Holmberg, 1893) (P.AMB)
<i>Aphyocharax dentatus</i> Eigenmann & Kennedy, 1903 (A.DEN)	<i>Hypostomus ancistroides</i> (Ihering, 1911) (NA)
<b>Cheirodontinae</b>	<i>Hypostomus commersoni</i> Valenciennes, 1836 (NA)
<i>Serrapinnus calliurus</i> (Boulenger, 1900) (S.CAL)	<b>GYMNOTIFORMES</b>
<i>Serrapinnus heterodon</i> (Eigenmann, 1915) (S.HET)	<b>Rhamphichthyidae</b>
<i>Serrapinnus notomelas</i> (Eigenmann, 1915) (S.NOT)	<i>Gymnorhamphichthys britskii</i> Carvalho, Ramos & Albert, 2011 (G.HYP)
<b>GYMNOTIFORMES</b>	<b>PERCIFORMES</b>
<b>Rhamphichthyidae</b>	<b>Sciaenidae</b>
<i>Ramphichthys hahni</i> (Meinken, 1937) (R.HAH)	<i>Plagioscion squamosissimus</i> (Heckel, 1840) (P.SQU)
<b>Sternopygidae</b>	<b>Cichlidae</b>
<i>Eigenmannia guairaca</i> Peixoto, Dutra & Wosiacki, 2015 (E.TRIL)	<i>Cichla kelberi</i> Kullander & Ferreira, 2006 (C.KEL)
<i>Eigenmannia virescens</i> (Valenciennes, 1836) (E.VIR)	<i>Geophagus sveni</i> Lucinda, Lucena & Assis, 2010 (G.PRO)
<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801) (S.MACR)	<i>Satanoperca pappaterra</i> (Heckel, 1840) (S.PAP)
<b>Apterodontidae</b>	<i>Apistogramma cf. commbrae</i> (Regan, 1906) (A.COM)
<i>Apterodontus ellisi</i> (Alonso de Arámburu, 1957) (A.ELL)	<i>Aequidens plagiozonatus</i> Kullander, 1984 (A.PLA)
<b>CYPRINODONTIFORMES</b>	<i>Laetacara araguaiaae</i> Ottoni & Costa, 2009 (NA)
<b>Poeciliidae</b>	<i>Crenicichla britskii</i> Kullander, 1982 (C.BRI)
<i>Pamphorichthys</i> sp. (PAMPH)	<b>PLEURONECTIFORMES</b>
<i>Phalloceros harpagos</i> Lucinda, 2008 (NA)	<b>Achiridae</b>
	<i>Catathyridium jenynsii</i> (Günther, 1862) (C.JEN)

João was the lagoon with highest richness (28 species). On the other hand, at sites near Rosana and Porto Primavera reservoirs, the lowest species richness were registered (20 species). Rarefaction/extrapolation curves for Hill numbers showed that sites in the main channel of the Paraná River and its tributaries have similar species richness ( $q = 0$ ). In contrast, for Shannon diversity ( $q = 1$ ) and Simpson diversity ( $q = 2$ ) tributaries showed a higher diversity, although 95% intervals overlap (shaded-color area) (Figure 2).

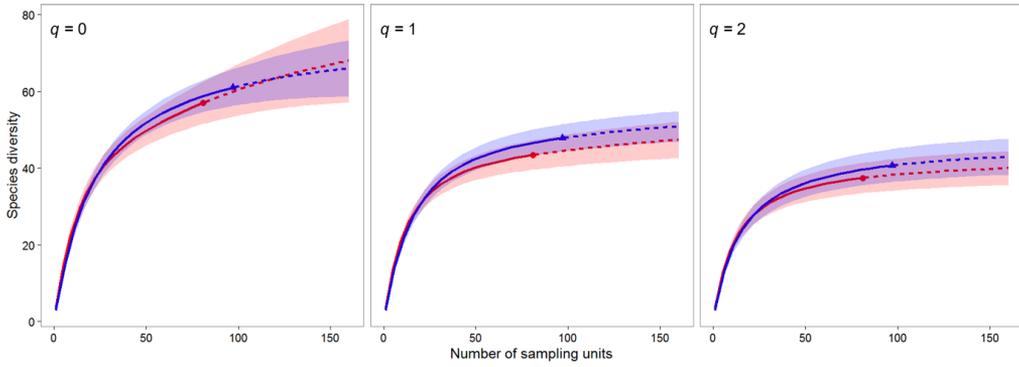
### 3.2. Assemblages composition

Non-metric multidimensional ordination conserved 89% of the original distances among sites. NMDS scatterplot describes how regions differed in species composition and abundance. For instance, *Apareiodon affinis*, *Mylossoma duriventre* and *Crenicichla britskii* were more abundant in sites in the northern portion of the sampled region (Parapanema, Baía and Ivinhema rivers), while other species (*Hemiodus orthonops*, *Prochilodus lineatus*, *Megaleporinus piavussu*) have higher abundances in the southern and left side of the sampled region (Iguatemi, Pirajuí and Maracáí rivers) (Figure 3).

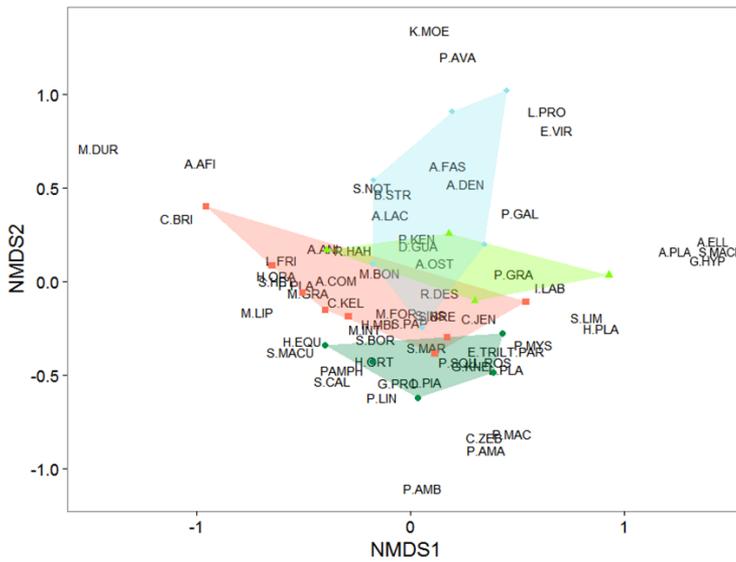
PERMDISP analysis showed that total beta diversity in the tributaries and Paraná River did not differ in its variation ( $F=0.411$ ,  $P=0.533$ ). However, species turnover was higher between tributaries than between Paraná River sites ( $F=5.47$ ,  $P=0.03$ ), whereas species nestedness was higher between Paraná River sites ( $F=5.05$ ,  $P=0.04$ ). Dissimilarity in assemblage composition (mean:  $0.71 \pm 0.18$ ) was driven in a similar proportion by turnover and nestedness. However, the turnover component indicated that replacement of species tended to be higher (turnover:  $0.41 \pm 0.19$ ; nestedness:  $0.30 \pm 0.22$ ). When only Paraná River sites were included, the pattern was reversed (turnover:  $0.27 \pm 0.20$ ; nestedness:  $0.38 \pm 0.24$ ): the turnover component decreases and beta diversity is driven mainly by a change in richness or abundance of species occupying many sites (Table 2).

### 3.3. Relationship between beta diversity and environmental variables

Changes in species composition were associated with environmental variables (Table 2). dbRDA analyses explained between 25.6% to 73.6% of dissimilarity in species composition when all



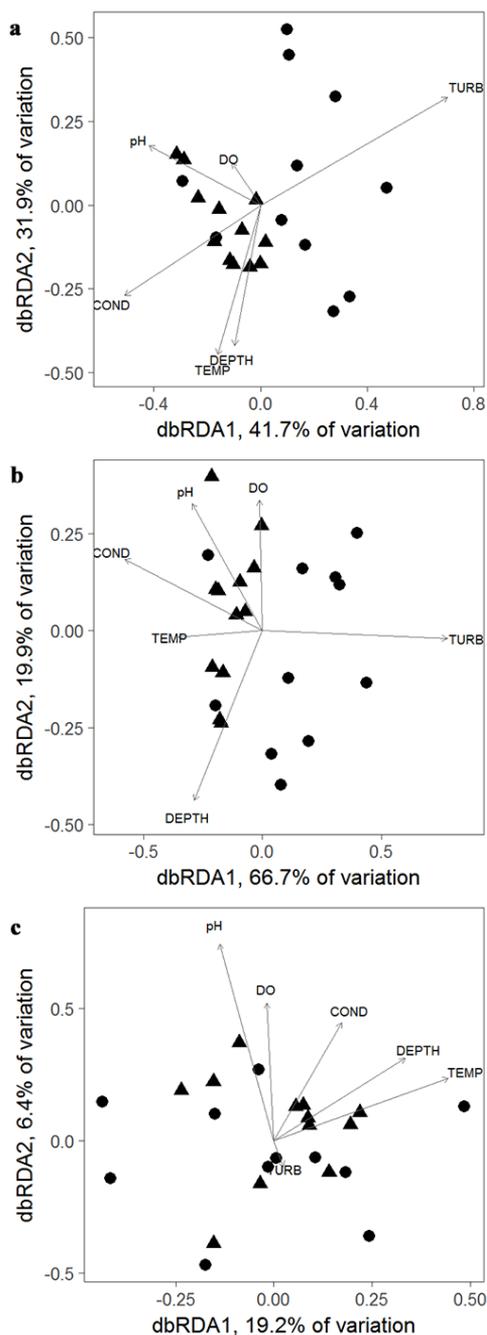
**Figure 2.** Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines) of fish diversity at the Upper Paraná River (Hill numbers of order 0, 1 and 2).  $q = 0$ : species richness;  $q = 1$ : Shannon diversity;  $q = 2$ : inverse of Simpson's concentration. Blue: tributaries; red: Paraná River.



**Figure 3.** Non-metric multidimensional ordination of species composition of fish assemblages at the Upper Paraná River. Stress = 0.1495. Squares: sites in the northern portion of the sampled region (Parapanema, Baía and Ivinhema rivers); triangles: sites in the middle portion of the sampled region (Ivinheminha, Ivaí and Amambai rivers); diamonds: sites on the left side of the sampled region (Paracá, São João and Xambê); circles: sites in the southern and right side of the sampled region (Maracá, Pirajuí and Iguatemi rivers). See species names in Table 1.

**Table 2.** Partition of beta diversity (mean and standard deviation of Bray Curtis dissimilarity) for fish assemblages and its relationship with environmental variables ( $R^2$  and P-values) in the Upper Paraná River. TEMP: water temperature; DO: dissolved oxygen; COND: conductivity; DEPTH: mean depth. Significant relationships in bold.

	Bray Curtis	TEMP	DO	COND	TURB	pH	DEPTH
	<b>Total</b>			<b><math>R^2</math> (P values)</b>			
<b>All sites</b>	0.71 ± 0.18	0.06 (0.07)	0.04 (0.33)	0.07 (0.05)	<b>0.10 (0.01)</b>	<b>0.08 (0.04)</b>	0.05 (0.19)
<b>Paraná River</b>	0.66 ± 0.25	0.15 (0.27)	0.07 (0.58)	0.20 (0.18)	0.06 (0.75)	0.04 (0.85)	0.02 (0.95)
<b>Tributaries</b>	0.72 ± 0.14	0.11 (0.09)	0.09 (0.18)	0.08 (0.27)	<b>0.14 (0.03)</b>	<b>0.13 (0.04)</b>	0.11 (0.07)
	<b>Turnover</b>						
<b>All sites</b>	0.41 ± 0.19	0.06 (0.16)	0.02 (0.59)	<b>0.18 (&lt;0.01)</b>	<b>0.15 (&lt;0.01)</b>	0.03 (0.46)	<b>0.10 (0.03)</b>
<b>Paraná River</b>	0.27 ± 0.20	0.07 (0.54)	0.04 (0.62)	0.19 (0.34)	0.03 (0.65)	0.08 (0.54)	0.07 (0.55)
<b>Tributaries</b>	0.47 ± 0.20	0.10 (0.11)	0.10 (0.12)	0.12 (0.07)	<b>0.22 (0.01)</b>	0.07 (0.21)	<b>0.20 (0.02)</b>
	<b>Nestedness</b>						
<b>All sites</b>	0.30 ± 0.22	0.08 (0.22)	0.06 (0.34)	0.05 (0.98)	0.08 (0.22)	0.13 (0.11)	0.02 (0.94)
<b>Only Paraná</b>	0.38 ± 0.24	0.15 (0.32)	0.11 (0.41)	0.16 (0.32)	0.10 (0.48)	0.01 (0.92)	0.04 (0.68)
<b>Tributaries</b>	0.23 ± 0.18	0.15 (0.27)	0.09 (0.43)	0.01 (0.81)	0.11 (0.35)	0.23 (0.18)	0.01 (0.92)



**Figure 4.** Distance-based Redundancy Analysis (dbRDA) of species assemblages and environmental variables in the Upper Paraná River. (a) Total Bray Curtis; (b) Turnover and (c) Nestedness. Circles: Paraná River sites; Triangles: Tributaries. TEMP: water temperature; DO: dissolved oxygen; COND: conductivity; DEPTH: mean depth.

sites and the different components of Bray Curtis (total, turnover and nestedness) were considered (Figure 4). Considering the total Bray Curtis, the first axis (41.7% of variation) was highly correlated with turbidity ( $F = 2.81$ ;  $P = 0.01$ ) and pH ( $F = 2.21$ ;  $P = 0.04$ ), whereas the turnover

was related to conductivity ( $F = 6.12$ ;  $P < 0.01$ ) (first axis 66.7% of variation). Conversely, for changes in species composition related to nestedness, the first two axes of the dbRDA only explained 25.6% of variation and did not show a significant relationship with the environmental variables considered here (Figure 4, Table 2).

#### 4. Discussion

The Upper Paraná River basin holds a high fish diversity (Langeani et al., 2007). However, despite long term researches in the Paraná River floodplain which have surveyed different aspects of fish assemblages (e.g. Agostinho et al., 2001; Daga et al., 2009; Gubiani et al., 2010; Padial et al., 2014), the stretch between Porto Primavera Reservoir and the transition zone of the Itaipu Reservoir in its entire longitude had not been extensively studied before. Only Baumgartner et al. (2010) had described diversity patterns in fish assemblages in approximately half of the longitude of this stretch (three sites in tributaries and four in the Paraná River). They sampled similar sites at the Ilha Grande National Park and found similar results to the ones observed here regarding the total number of species (74 species) and the proportion of non-native species (32% of species). It is worth to mention the capture of *P. platana*, a clupeid fish registered mainly in the La Plata basin and brackish lagoons of the coastal region of Brazil, Uruguay and Argentina. *Platanichthys platana* was registered in previous surveys in headwaters of the Tiête river (Langeani et al., 2007; Marceniuk et al., 2011; Furlan et al., 2013), but only recently was captured in the Paraná River floodplain and it is unknown whether this species is successful and established in this region.

We observed that patterns of  $\alpha$  diversity in tributaries and Paraná River sample sites were similar for species richness ( $q = 0$ ), however tributaries tended to have a higher Shannon ( $q = 1$ ) and Simpson ( $q = 2$ ) diversity (Figure 2). This indicates that tributaries tended to hold a higher diversity when dominant species become more relevant and when neither rare nor common species are favored. That pattern could be a consequence of the use of tributaries as route for migration and spawning sites for long-migratory species (Agostinho et al., 2001; Fernandes et al., 2009). We observed that species with opportunistic strategies - sedentary, generalist without parental care (Winemiller, 1989) - showed a higher abundance in the Paraná River, whereas seasonal species - migratory, without parental care

- and equilibrium - sedentary with parental care  
- species were captured mainly in the tributaries.

These differences in species composition among tributaries and the Paraná River were disentangled by partition of beta diversity in a balanced component, representing turnover, and a gradient component, equivalent to nestedness. By using this procedure, we noticed that different mechanisms could be driving dissimilarity patterns of fish assemblages. While species turnover was higher among tributaries, river sites showed a compositional dissimilarity drove by nestedness. Turnover, when all sites were considered, was related to environmental variables while nestedness was not. Species turnover along environmental gradients have also been reported for other communities (Rouquette et al., 2013; Bishop et al., 2015). Contrary to species replacement, nestedness can be low and unrelated to environmental variables when dispersal is high, or be high when environmental variables filter out species from one site to another and dispersal is limited (Gianuca et al., 2017). However, although species can be filtered out from some sites, when dispersal is not limited they are rescued by individuals from other sites and the pattern can shift from nestedness to turnover.

Species sorting by environmental filtering could result in differences in species composition between Paraná River and its tributaries and between the tributaries themselves. Hence, species filtering may account for the relationship between species replacement and environmental variables (Ferrareze et al., 2014; Heino et al., 2015). In addition, the detection of this relationship may be a consequence of the size of the sample area. The spatial extent of the surveyed region also exerts an important influence on the variation in species composition and its relationship with environmental variables. When spatial extent is increased, the environmental variation or length of environmental gradients also could increase, and the influence of environmental variables in species composition is more likely to be detected (Chase & Leibold, 2003; Heino et al., 2015).

However, species sorting is not just the result of species filtering by environmental variables, but also their filtering by species interactions (Chase & Leibold, 2003; Winegardner et al., 2012). Although we detected a significant relationship between variation in species composition and environmental variables, mainly turbidity, it is possible that this variable itself do not affect species turnover or nestedness, but facilitated mechanisms

doing that. Recent studies demonstrated that turbidity has an effect on species interactions, either reducing or increasing the intensity of predation (Pelicice & Agostinho, 2009; Petry et al., 2010; Figueiredo et al., 2013, 2016). In addition, the effects of visual predators on fish assemblages (Pelicice & Agostinho, 2009; Petry et al., 2010) and the effects of habitat complexity in fish diversity (Gomes et al., 2012) have also been reported. Consequently, the observed relationship between dissimilarity in species composition with environmental variables can be a result of the combined effects of species interaction, habitat heterogeneity and habitat complexity (Petry et al., 2010; Gomes et al., 2012; Figueiredo et al., 2013).

Ecologically, this means that environmental heterogeneity could increase the variability in environmental conditions to which different species are adapted. Thus, environmental heterogeneity can contribute to maintain a higher species diversity or variation in species composition between habitats through species replacement. Overall, our results suggest that the Upper Paraná River tributaries make an important contribution to environmental variation, dissimilarity in species composition and species diversity, a contribution that must be of importance to be preserved.

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