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Ecological drivers of multiple facets of beta diversity using disparate biological groups and different taxonomic level across hierarchical spatial and temporal scales

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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais do Departamento de Biologia, Centro de Ciências Biológicas da Universidade Estadual de Maringá, como requisito parcial para obtenção do título de Doutor em Ecologia e Limnologia.
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Preditores ecológicos de múltiplas facetas da diversidade beta usando grupos biológicos díspares e diferentes níveis taxonômicos em escalas espaciais e temporais hierárquicas

RESUMO

O conhecimento sobre padrões temporais e espaciais locais e regionais da biodiversidade, como base para modelos biogeográficos e planejamento de conservação, foi pouco explorado para dois componentes fundamentais da diversidade beta: substituição e diferença de riqueza. Avaliar até que ponto a variabilidade nesses componentes da diversidade *beta* é congruente no espaço e no tempo para grupos biológicos distintos, que possuem ampla variação em suas características funcionais (por exemplo, modo de dispersão) é, até agora, desconhecido. Ademais, um dos principais paradigmas da ecologia é entender se os padrões biogeográficos empíricos dos macrorganismos também se aplicam aos microrganismos. Assim, esta tese é composta por três segmentos. O primeiro teve como objetivo determinar se a congruência entre táxons da diversidade *beta* taxonômica e funcional e seus componentes variam ao longo do espaço e do tempo. Os resultados mostraram como análises hierárquicas detalhadas podem revelar padrões ocultos de congruência entre táxons. Foi apoiada parcialmente a hipótese de que a força da congruência entre táxons geralmente diminui com o aumento das distâncias funcionais entre pares de grupos biológicos. No segundo segmento, foram contrastados padrões longitudinais na diversidade *beta* total e seus componentes no último trecho não represado do rio Paraná para grupos biológicos de dispersão ativa (peixe) e passiva (fitoplâncton). Os resultados ratificam que os padrões de biodiversidade exibidos por grupos biológicos únicos não coincidem necessariamente com os de outros grupos que mostram grande variação nas características biológicas. Estas descobertas melhoram a compreensão da heterogeneidade induzida por tributários e destacam a importância dos trechos de rios livre de barramentos para preservar sua integridade. No terceiro segmento, foram utilizados dados morfológicos de organismos vivos e dados moleculares para verificar qual abordagem explica melhor o papel dos preditores ambientais e espaciais na estruturação de protistas ciliados, bem como tentar esclarecer sua biogeografia. Foi demonstrado que os filtros ambientais tiveram uma maior influência na dissimilaridade par a par baseada em dados morfológicos do que nas baseadas em dados moleculares. Entretanto, fatores biogeográficos, impostos pela distância entre os locais, limitam a distribuição da composição baseada em dados moleculares, resultando em composições de espécies significativamente distintas em cada um dos lagos associados às planícies de inundação analisadas. Em resumo, os resultados desta tese demonstram que a biologia da conservação e a avaliação ambiental precisam monitorar diferentes grupos biológicos, bem como levar em consideração a escolha da resolução taxonômica, pois cada grupo e abordagem fornecem *insights* exclusivos.

Palavras-chave: Congruência entre taxa. Traços funcionais. Sistema rio-planície de inundação. Substituição de espécies. Tecnologias de sequenciamento de alto rendimento (HTS).

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ABSTRACT

Our knowledge on temporal and fine- and broad-scale patterns of biodiversity, as a basis for biogeographical models and conservation planning, have been few explored to two fundamental components of beta diversity: replacement and richness difference. Whether variability in these components of beta diversity is congruent in space and time for disparate biological groups, which show wide variation in functional traits (e.g., dispersal mode), is, hitherto, unknown. Moreover, one of the main standing paradigms is to understand whether the empirical biogeographic patterns of macro-organisms also apply to micro-organisms. This thesis consists of three papers. The first one aimed to determine whether the cross-taxon congruence of taxonomic and functional beta diversity and its components varies across space, and time. Our results showed how detailed hierarchical analyses can reveal hidden patterns of cross-taxon congruence. We partly supported the hypothesis that the strength of cross-taxon congruence generally decreases with the increase of functional distances between pairs of biological groups. In the second paper, we contrasted longitudinal patterns in the total beta diversity and its components in the last non-dammed stretch of the Paraná River for actively (fish) and passively (phytoplankton) dispersing biological groups. The results ratify that biodiversity patterns exhibited by single biological groups do not necessarily match those of other groups that show wide variation in biological features. Our findings have improved understanding of tributary-induced heterogeneity and highlight the importance of dam-free stretches of rivers for preserving its integrity. In the third paper, we used morphological data from live organisms and molecular data to verify which approach better explain the role of environmental and spatial predictors on the ciliates structuration, as well as clarify their biogeography. We found that environmental filters had a greater influence on the morphological than on the molecular site-by-site dissimilarities. Meanwhile, biogeographic factors and the distance among sites limit the distribution of molecular-based composition, resulting in significantly different species compositions in each of the floodplain-associated lakes analyzed. In summary, the findings of this thesis suggest that conservation biology and environmental assessment need to monitor different biological groups, as well as take into account for the choice of taxonomic resolution, as each group and approach provides unique insights.

***Keywords*:** Cross-taxon congruence. Functional trait. Floodplain system. Replacement. High-throughput sequencing technologies (HTS).

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SUMMARY

1 GENERAL INTRODUCTION

Improving the knowledge about the distributions of species and the mechanisms that influence them are at the heart of biogeography, ecology and conservation biology (Cottenie, 2005). In order to understand species distribution patterns in structuring communities, it is pivotal to (1) evaluate how it vary across multiple scales (Alahuhta & Heino 2013; Gonçalves-Souza *et al.* 2014; Souffreau *et al.* 2015b; Heino *et al.* 2017a), (2) consider the importance of the temporal dynamics of the ecosystems studied (Langenheder *et al.*, 2012; Fernandes *et al.*, 2014; Heino *et al.*, 2015; Sarremejane *et al.*, 2017) (3) compare different groups of organisms showing potential differences in their functional characteristics and dispersal capacity (Beisner *et al.* 2006; De Bie *et al.* 2012; Padial *et al.* 2014; Heino *et al.* 2017a) and (4) analyze patterns of diversity and/or composition of the same biological group across different taxonomic resolutions (Landeiro *et al.*, 2012; Burrascano *et al.*, 2018; Xu *et al.*, 2019).

While most previous studies focused on patterns in alpha or gamma diversity (Hillebrand *et al.*, 2001), beta diversity has received considerable renewed interest in recent years (Socolar *et al.*, 2016). Beta diversity can be defined as the variation in assemblage composition among sampling units or the extent of change in assemblage composition along gradients (Anderson *et al.*, 2011), and it can further include different components (e.g., replacement and richness difference components; Podani & Schmera, 2011). Species replacement is related to factors affecting changes in species identities between sites, whereas richness difference informs about factors determining differences in the number of species (Cardoso *et al.*, 2014). Recently, studies have shown that decomposing beta diversity into their respective replacement and richness difference components (Podani & Schmera, 2011) facilitates the detection of more complex ecological patterns in space and time (Legendre, 2014a).

An intuitive short-cut to biodiversity conservation is to focus on how the occupancy and abundance of different groups of organisms co-vary in space and time (Legendre, 2014b), which we may refer to as cross-taxon congruence (Lovell *et al.*, 2007). For this endeavor, knowing the spatial and temporal variation in beta diversity allows for designing and implementing cost-effective management strategies, to preserve the integrity of ecosystems and their functions (Mori, Isbell & Seidl, 2018). Furthermore, functional beta diversity (i.e. sets of individual-level morphological, physiological or phenological characteristics) may reveal how environmental conditions filter species from the regional pool and how they share resources, potentially linking ecological processes to biodiversity patterns (Mouchet *et al.*, 2010). Therefore, an integrative congruence-based approach combining taxonomic and functional beta diversity may provide constructive insights into how biodiversity change can affect ecosystem functioning and, ultimately, the provision of ecosystem services (Xu *et al.*, 2019).

Patterns of cross-taxon congruence may be driven by three main non-exclusive mechanisms operating at different spatial scales (Gaston, 1996). The first one assumes parallel responses to environmental gradients and temporal dynamics of ecosystems, intrinsically led by similar environmental requirements (Vilmi *et al.*, 2016). Secondly, congruence may also emerge from common biogeographic history, whereby resident biological groups undergone similar dispersal constraints and/or evolutionary trajectories (Burrascano *et al.*, 2018). The third mechanism relies on the structuring role of biotic interactions (i.e., competition or predator-prey; Duan et al., 2016). Of these mechanisms, several studies aiming at improving the predictive ability of the cross-taxon congruence approach suggested that empirical patterns among taxa are mostly driven by different dispersal abilities (Velghe & Gregory-Eaves, 2013; Hájek *et al.*, 2014).

Dispersal mode (e.g., passive vs. active dispersers) can determine the dispersal potential of different biological groups (De Bie *et al.*, 2012; Soininen, 2016; Hill *et al.*, 2017). Comparative studies in aquatic systems have shown that dispersal limitation tends to be stronger for large (e.g. fish) than for small organisms (e.g. phytoplankton) (Beisner *et al.*, 2006; De Bie *et al.*, 2012; Padial *et al.*, 2014). For instance, small passive dispersers species are easily carried long distances by water flow, wind and animals, and may utilize dispersal strategies, such as the production of spores, cysts or drought resistance eggs, increasing their dispersal ability and overcoming geographic barriers more easily (Van der Gucht *et al.*, 2007). Although the dispersal of active dispersers, such as fishes, is restricted to via-watercourses routes, in connected systems, fishes are potentially good dispersers and may actively select sites for colonization (De Bie *et al.*, 2012; Erős *et al.*, 2017). given that actively and passively dispersing taxa may respond differently to ecological gradients, they are not likely to respond similarly to anthropogenic changes in aquatic ecosystems (Heino, 2010). Thus, the consideration of these different dispersal strategies of organisms is advisable for guiding biomonitoring and conservation (Vilmi *et al.*, 2016; Morais *et al.*, 2018).

In addition, hitherto, one of the main standing paradigms is to understand whether the empirical biogeographic patterns of macro-organisms also apply to micro-organisms (Shoemaker, Locey & Lennon, 2017). A central debate in microbial biogeography has contrasted species distributions as either ubiquitous or restricted in space and time, but the coexistence of both patterns is now well supported (e.g., van der Gast, 2015). Micro-organisms are small, numerous, and have high population densities (Fenchel & Finlay, 2004). In addition to their ability in producing cysts, this combination makes them less prone to local extinction and increase their potential for dispersal events (Astorga *et al.*, 2012). In the last two decades, a second biogeography perspective even suggests that some microbial taxa may be endemic (Martiny *et al.*, 2006; Green & Bohannan, 2006; van der Gast, 2015; Tessler *et al.*, 2017; Ribeiro, Duarte & Crossetti, 2018).

In microbial eukaryotes (i.e., protists), two main characteristics have been used to track taxon distributions: morphologies and molecules. Morphologically-defined species (morphospecies) always face some problematic issues. For instance, morphological analyses are frequently limited because some specimens are injured during fixation, the presence of cryptic and polymorphic species puzzle their diversity, and there are only a few specialized professionals for identification (Sáez & Lozano, 2005; Caron *et al.*, 2012). Therefore, biogeographical patterns may be obscured by cryptic and polymorphic species (Dunthorn *et al.*, 2014). Fortunately, the advent of new methods for sequencing the environmental RNA or DNA from ribosomal small sub-unit (SSU), such as high-throughput sequencing technologies (HTS), has thrown a new era in microbial ecology (Porter & Hajibabaei, 2018). HTS data is now fundamental for ecological studies on microbial organisms, especially those investigating biogeographic patterns (van der Gast, 2015).

According to the exposed, this thesis consists of three papers, all of which were conducted in river-floodplain systems and adjacent habitats. It was verified how patterns of different facets of beta diversity (including its components, taxonomic and functional data, as well as morphological and molecular approaches) from different biological communities. Specifically, the first one aimed to determine whether the cross-taxon congruence of taxonomic and functional beta diversity and its components varies across space, and time, using a comprehensive field dataset that encompasses almost a continental extent. In the second one, we investigated longitudinal patterns in the total beta diversity and its replacement and richness difference components in the last non-dammed stretch of the Paraná River in the Brazilian territory, for actively (fish) and passively (phytoplankton) dispersing biological groups. Finally, in the third one, we used morphological data from live organisms and molecular data to verify which approach better explain the role of environmental and spatial predictors on the ciliate structuration in the four Brazil’s greatest floodplains, as well as clarify their biogeography.

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2 CROSS-TAXON CONGRUENCE OF MULTIPLE BETA DIVERSITY FACETS ACROSS SPATIAL AND TEMPORAL SCALES

ABSTRACT

An intensively debated issue in ecology is whether variability in the patterns of diversity of different biological groups is congruent in space and time. Recently, ecologists have recognized the need of analyzing congruence in the light of multiple diversity facets (beta diversity, taxonomic, and functional). The aim of this study was to determine whether the cross-taxon congruence of taxonomic and functional beta diversity and its components varies across space, and time, using a comprehensive field dataset that encompasses almost a continental extent. Our general hypothesis was that the congruence across biological groups would increase with between-group similarity, whether for taxonomic or functional approaches. In deep, we examined how congruence patterns varied across spatial and temporal scales by focusing on how the cross-taxon congruence differs among floodplains and between dry/flood periods. Our surveys on floodplain lakes comprise information on eight biological groups from the four major Neotropical river-floodplain systems (Amazônia, Araguaia, Pantanal and Paraná). We analysed cross-taxon congruence in the different beta diversity facets and components using Procrustes analysis. Our results showed how detailed hierarchical analyses can reveal hidden patterns of cross-taxon congruence, and partly supported the hypothesis that the strength of cross-taxon congruence generally decreases with the increase of functional distances between pairs of biological groups, but this relationship is spatial and temporal variable.

Keywords: replacement; richness difference; aquatic communities; freshwater; concordance

2.1 Introduction

Biodiversity decline has been attributed to several anthropogenic impacts, including habitat fragmentation (Barlow et al., 2016), changes in the dynamics of ecosystems (Winemiller et al., 2016), overexploitation of resources (Barnes et al., 2014), introduction of alien species (Bellard et al., 2016), and climate change (Lourenço-de-Moraes et al., 2019). Scientists have thus been motivated to identify which factors are fundamental for the maintenance of biodiversity and which ecosystem functions are likely affected by biodiversity change (Brose and Hillebrand, 2016). Although there has been significant progress in biodiversity assessments, hitherto monitoring and conservation activities have often remained too complex and expensive (Butchart et al., 2010).

An intuitive short-cut to biodiversity conservation is to focus on how the occupancy and abundance of different groups of organisms co-vary in space and time (Legendre, 2014a), which we may refer to as cross-taxon congruence (Lovell et al., 2007). From an ecological view, we may evaluate the strength and significance of correlations in community-level biodiversity facets between pairs of biological groups, given a set of localities (Heino, 2010). Regarding financial resources, the congruence-based approach may be used to identify surrogates that portray fundamental aspects of biodiversity conservation and thus to reduce further investments on surveying many biological groups at multiple scales at the same time (Heino, 2010). However, the potential for the use of these surrogates relies on the strength of cross-taxon congruence within each context, and the existence of common patterns in spatial and temporal arrangements remains elusive (Westgate et al., 2014).

For this endeavor, knowing the spatial and temporal variation in community composition (i.e., beta diversity) allows for designing and implementing cost-effective management strategies, to preserve the integrity of ecosystems and their functions (Mori et al., 2018; Socolar et al., 2016). While the classical beta diversity approach is based on the taxonomic identity of species (i.e., genus and/or species), the functional beta diversity, defined as the variation in multiple functional traits (i.e. sets of individual-level morphological, physiological or phenological characteristics), has been suggested as an alternative or complementary approach (Braghin et al., 2018; Rocha et al., 2018; Violle et al., 2007). This is because traits often describe species characteristics that reflect adaptations to specific environmental conditions (Violle et al., 2007). Considering that some functional trait combinations can be expressed by only one or a couple of species sharing similar characteristics in a local community, the trait composition may thus exhibit a relatively high correspondence with environmental gradients regardless of the identity of species (Göthe et al., 2017). Consequently, functional beta diversity may reveal how environmental conditions filter species from the regional pool and how they share resources, potentially linking ecological processes to biodiversity patterns (Mouchet et al., 2010). Therefore, an integrative congruence-based approach combining taxonomic and functional beta diversity may provide constructive insights into how biodiversity change can affect ecosystem functioning and, ultimately, the provision of ecosystem services (Xu et al., 2019).

Both taxonomic and functional beta diversity can be decomposed into two additive components: replacement and richness difference (Cardoso et al., 2014). The replacement component accounts for changes in species or trait composition, whereas the richness difference component depicts the loss and gain of species or traits across sites (Cardoso et al., 2014). Moreover, a recent extension to this approach allows for partitioning beta diversity into the same additive elements using abundance instead of presence–absence data, which provides complementary information about variation of beta diversity patterns along environmental gradients (Legendre, 2014a). This extended approach is useful because, in many cases, considering the variation in the abundance of organisms in a set of habitats may better explain the relationships between community composition and the environment, whereas these relationships could be weaker using presence–absence data only (Heino, 2014). Although the partitioning of beta diversity can provide fundamental information on how biological communities vary across landscapes (Lansac-Tôha et al., 2019; Rocha et al., 2018; Yang et al., 2015), little is known about how cross-taxon congruence relates to each of these beta diversity components and how biodiversity patterns vary at different spatial and temporal scales.

Patterns of cross-taxon congruence may be driven by three main non-exclusive mechanisms operating at different spatial scales (Gaston, 1996). The first one assumes parallel responses to environmental gradients and temporal dynamics of ecosystems, intrinsically led by similar environmental requirements (Vilmi et al., 2016). Secondly, congruence may also emerge from common biogeographic history, whereby resident biological groups undergone similar dispersal constraints and/or evolutionary trajectories (Burrascano et al., 2018). The third mechanism relies on the structuring role of biotic interactions (i.e., competition or predator-prey; Duan et al., 2016). Of these mechanisms, several studies aiming at improving the predictive ability of the cross-taxon congruence approach suggested that empirical patterns among taxa are mostly driven by different dispersal abilities, which mostly coincided with their body sizes (Hájek et al., 2014; Velghe and Gregory-Eaves, 2013). Simply put, we may expect that the potential for dispersion would decrease with body size (De Bie et al., 2012). In aquatic environments, for example, wind-based passive dispersers such as ciliates would drift away into floodplains further than fish, considering a regional scale (Incagnone et al., 2015).

Although these are important recent advances, many critical knowledge gaps related to the underlying ecological processes remain. For instance, differences in the body size of organisms can actually impose fundamental constraints on physiological parameters affecting habitat occupancy, such as life span, metabolic rate, and reproductive potential (Fenchel, 1974). However, body size-based general patterns of congruence may be only a surrogate representing essential functional differences among biological groups, such as cellular organization (i.e., uni- or multicellular), reproduction mode (i.e., parthenogenesis, sexual reproduction), dispersal mode (i.e., aerial, wind, water-based), nutrition (i.e., autotrophic, heterotrophic), and life-cycle strategy (i.e., r/K selection) (Barton et al., 2013; Browne and MacDonald, 1982; De Bie et al., 2012; Hillebrand et al., 2001; Lansac-Tôha et al., 2019). As an extended approach, we here considered whether dissimilarities between biological groups, based on the combination of some of these characteristics, are significant predictors of cross-taxon congruence using data from the four largest South American floodplains.

River-floodplains systems are suitable model environments to investigate the mechanisms influencing the patterns of biodiversity and cross-taxon congruence (Padial et al., 2012; Vieira et al., 2015). They are environmentally heterogeneous and typically host a high diversity of species, although are experiencing a rapid loss of biodiversity worldwide (Ward et al., 1999). The yearly hydrological regime, characterized by alternating floods and droughts, is a key factor influencing their structure and functioning (Junk et al., 1989). Flood pulses are of utmost importance, as they promote intensive biotic and abiotic exchange between the river and its surrounding landscape, affecting the structure of the aquatic communities and the availability of nutrients and resources (Junk et al., 1989). Floods also tend to produce the so-called "homogenization" phenomenon, reducing the spatial variability of biological and environmental factors and therefore the floodplain-scale beta diversity (Thomaz et al., 2007). In contrast, during droughts, many aquatic habitats are isolated from each other, and local communities are strongly influenced by local factors such as resources fluctuation, competition and predation, thus maximizing the floodplain-scale beta diversity (Lansac-Tôha et al., 2016; Thomaz et al., 2007). For this reason, we expect that the relative contributions of community–environment relationships, spatial dynamics, and biological interactions to the congruence patterns to vary between hydrological periods (Vieira et al., 2015), although it has barely been investigated (Lários et al., 2017).

Thus, the aim of this study was to determine whether the cross-taxon congruence of taxonomic and functional beta diversity and its components varies across space, and time, using a comprehensive field dataset that encompasses almost a continental extent. Our surveys on floodplain lakes comprise information on eight biological groups, which show high variation in species diversity and therefore functional traits. The general hypothesis was that the congruence across biological groups would increase with between-group similarity, whether for taxonomic or functional approaches. In deep, we examined how congruence patterns varied across spatial and temporal scales by focusing on how the cross-taxon congruence differs among floodplains and between dry/flood periods. To accomplish this task, we used a sequential scale-out perspective focusing on the strength of cross-taxon congruence (i) between dry and flood periods considering each floodplain, separately; (ii) among floodplains, grouping both dry and flood periods; and (iii) between periods, grouping all four floodplains. From our appraisal, hopefully the results found here give out an interesting tool in a conservation context. We also expect to highlight the importance of the context-dependent nature of using biological surrogates in ecological assessments. Moreover, to our knowledge, this study is the first investigation on how cross-taxon congruence vary across floodplain systems using multiple biological groups in a continent-wide scale.

2.2 Methods

2.2.1 Study area

We studied the four major Neotropical river-floodplain systems (Amazônia, Araguaia, Pantanal and Paraná) (Fig. 1). These floodplains are disposed from northern to southern Brazil, comprising a wide latitudinal gradient (3° to 23°S) at a continental scale of approximately 2,300 km (Fig. 1). Along this gradient, the Amazon and Araguaia floodplains (3° to 13°S) are located in northern and central Brazil, respectively, with an equatorial climate characterized by 25 to 29 ºC average air temperatures and high average annual precipitation (1,300 to 2,000 mm) (Irion et al., 1997). The Pantanal and Paraná floodplains, located southern at this latitudinal gradient (19° to 23°S), have tropical and subtropical climates, with lower average temperatures (between 16 and 28ºC) and lower annual precipitation (ca. 1,400 mm) (Stevaux, 1994). In terms of human influence on these environments, there is a gradient ranging from the Amazônia floodplain (which has relatively preserved forests and tributaries), through the Pantanal and Araguaia (with moderate to intense human activities), to the Paraná floodplain (which is located in the most economically developed Neotropical region) (Rocha et al., 2017).

The Amazônia floodplain system (3°02´–3°34´S and 59°38´–60°50´W; Fig. 1), is composed of a complex network and covers an area of 3,5 x 10^7 ha (Junk et al., 1989), considered as the largest basin in the world. This floodplain presents a remarkable flood period and supports high levels of biodiversity (Bozelli et al., 2015). The amplitude of water-level fluctuations varies extensively among the rivers of the Amazon basin, from year to year, with mean annual water-level fluctuations about 10 m (Amaral et al., 2018). The high-water period begins in November and is at its maximum in July, whereas October is normally the driest month (Irion et al., 1997).

The Araguaia floodplain system (12°49´-13°25´S and 50°36´–50°43´W; Fig. 1) is considered the fourth largest basin in South America, with an area of 7,8 x 10^7 ha. The floodplain is covered by the Brazilian savannah biome, with a small part of the lower basin being within the Amazon rainforest. This floodplain also presents different flood periods, of which the high-water period occurs between November and April, and the low-water period between May and October (Lininger and Latrubesse, 2016).

The Pantanal floodplain system (18°46´-19°34´S and 56°58´-57°46´W; Fig. 1) is also one of the largest wetlands in the world, located in the upper Paraguay River basin (Junk et al., 2006), covering approximately 1,4 x 10^7 ha. Flood pulse follows a unimodal annual cycle, the amplitude of which varies between two and five meters. The high-water period occurs between May and September and the low water period between June and September (Junk et al., 2006).

The Upper Paraná River floodplain system (22º40´-22º54´S and 53º13´-53º38´W; Fig.1) has a drainage area of 2.8 x 10^6 ha. The Paraná River is the major river of the La Plata Basin, considered the second longest in South America, has a multichannel pattern, varied width, and presence of islands and lakes (Angelo Antonio Agostinho et al., 2004). The Paraná floodplain is strongly influenced by an upstream cascade of reservoirs, which reduces the amplitude and duration of the flood pulse (Angelo A. Agostinho et al., 2004; Souza Filho, 2009).

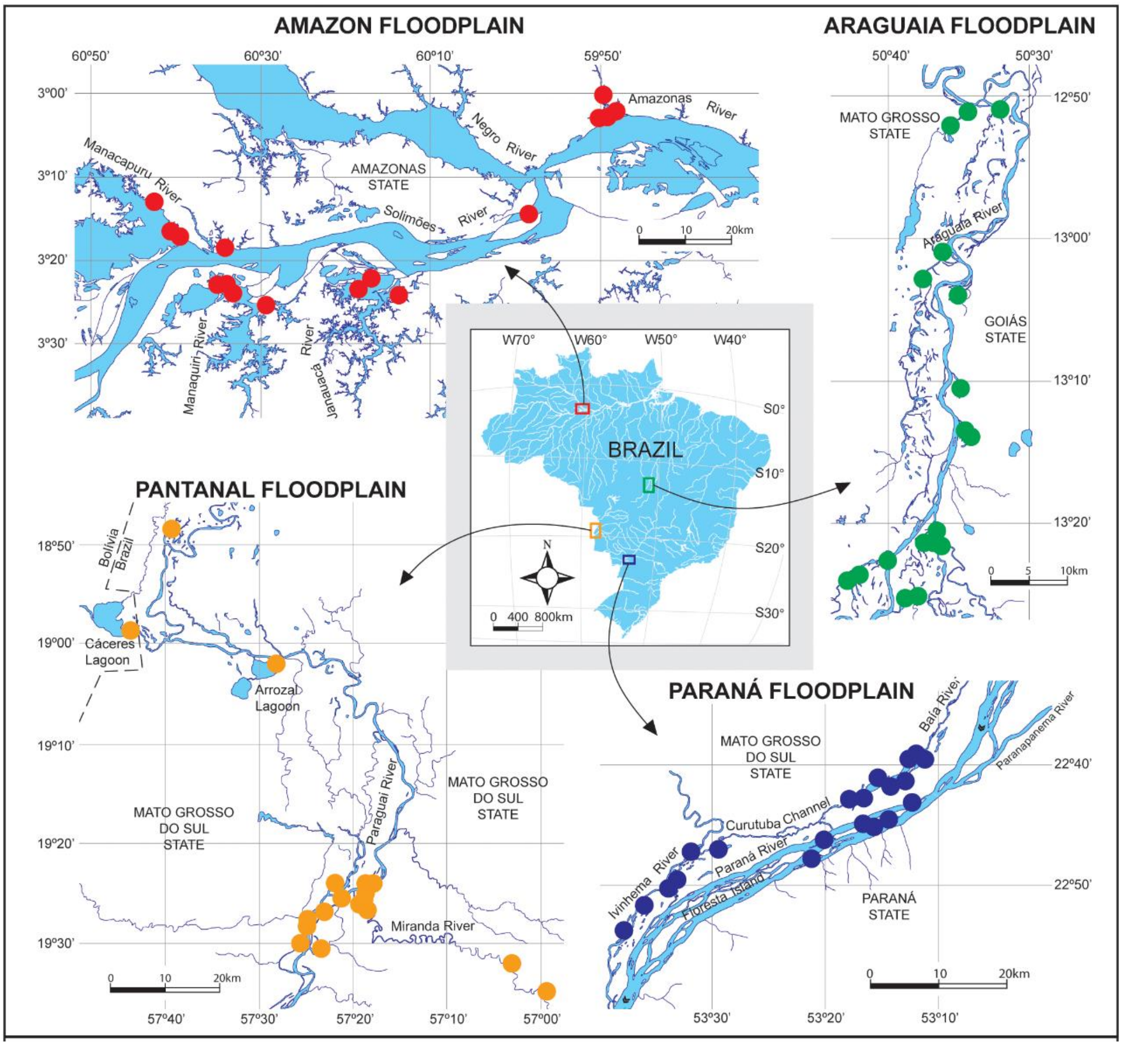


Fig. 1: Map of the study area showing the sampled floodplain-lakes at Amazonia (red circles), Araguaia (green circles), Pantanal (orange circles) and Paraná (blue circles)

2.2.2 Sampling periods

Two sampling campaigns, including dry- and flood-water periods, were conducted in the four floodplains. We sampled 66 and 71 lakes connected to the main river or tributaries in these four Brazilian floodplains in the dry- and flood-water periods, respectively. In the dry period, the samples were collected out in September 2011 (Paraná – 20 lakes), October 2011 (Amazonia – 16 lakes), November 2011 (Araguaia – 18 lakes) and March 2012 (Pantanal – 12 lakes). In the flood period, samples were taken in August 2011 (Pantanal – 18 lakes), February 2012 (Paraná – 20 lakes), March 2012 (Araguaia – 18 lakes) and May 2012 (Amazônia – 15 lakes) (Fig. 1).

2.2.3 Biological communities

We analyzed data from measurements for eight biological groups in all four floodplains during dry and flood periods. The methods of sampling and laboratory analysis for each group are summarized in Table 1; more details can be found in Appendix S1. Samplings were standardized for all environments, and counting and identification of species of each biological group were performed by the same team. All biological communities were properly collected with all required permissions from the Brazilian Environmental Ministry (Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Authorization system and information on Biodiversity (SISBIO)), under protocol number 29652.

Table 1. Summary of the methodology of sample collection and laboratory analysis used for each biological group**.** See Appendix S1 for more details.

Group	**Data type**	**Units**	**Sampling region**	**Sample collection**	**Sample analyses**
Phytoplankton	Abundance	ind.mL^{-1}	Limnetic	Directly with bottles	Counting randomly per field, using an inverted microscope
Ciliates	Abundance	cells.L^{-1}	Limnetic	Directly with bottles	*In vivo*, using sub-sampling technique
Testate amoebae, rotifers, microcrustacean	Abundance	ind.m^{-3}	Limnetic	Motorized pump and plankton net	Sedgewick-Rafter counting chamber under an optical microscope
Ostracods	Abundance	ind.g^{-1}dw	Littoral	Macrophytes were washed, and the residual with ostracods was filtered through a 160 µm mesh	Folsom fractioner, stereo- and transmission microscopes
Macrophytes	Presence / absence	NA	Littoral	Visual observations, and rake	NA
Fish	Abundance	CPUE (ind.m^{-2})	Littoral	Seine nets (20 m x 1.5 m) with 0.54 cm mesh size	Biometric analysis

2.2.4 Functional traits within biological groups

We gathered information on functional traits for eight biological groups. In order to facilitate cross-taxon comparisons of functional data, we chose traits that are intimately related to the spatial distribution patterns of each organism and an individual’s fitness, as well as to their effect on ecosystem processes (Violle et al., 2007; Weiss and Ray, 2019). The literature sources used for functional classification and the relationship between each trait and its corresponding ecosystem function can be found in Table S1.

2.2.5 Functional distance among biological groups

To investigate the effect of functional differences on the cross-taxon congruence, we also estimated the functional distances among biological groups. For this purpose, we considered biological characteristics that are commonly known to interfere with the distribution patterns of organisms, such as body size (De Bie et al., 2012), cellular organization (uni or multicellular) (Hillebrand et al., 2001), replication type (parthenogenesis, sexual or both) (Browne and MacDonald, 1982), dispersal mode (passive or active) (Lansac-Tôha et al., 2019) and nutrition (heterotrophic or autotrophic) (Barton et al., 2013) (Table 2).

Table 2: Cross-biological group traits.

Biological groups	**Body Size (cm)**	**Cellular organization**	**Replication type**	**Dispersal mode**	**Nutrition**
Phytoplankton	0.00396	unicellular	parthenogenesis	passive	autotrophic
Ciliates	0.008406	unicellular	parthenogenesis	passive	heterotrophic
Testate amoebae	0.009773	unicellular	parthenogenesis	passive	heterotrophic
Rotifers	0.03033	multicellular	parthenogenesis	passive	heterotrophic
Microcrustaceans	0.059988	multicellular	both	passive	heterotrophic
Ostracods	0.087824	multicellular	both	passive	heterotrophic
Fish	18.35	multicellular	sexual	active	heterotrophic
Macrophytes	50	multicellular	both	passive	autotrophic

2.2.6 Data analysis

We assessed cross-taxon congruence using the Procrustes analysis (Jackson, 1995) on data that representing three facets of beta diversity, under two ecological approaches (i.e., taxonomic and functional). To address each of the proposed objectives, three nested subsets of the full dataset were created: the first one considered the combinations between each floodplain (Amazônia, Araguaia, Pantanal and Paraná) and each period (dry and flood), separately (eight datasets); the second one, also considered each floodplain, but shared both periods (four datasets); and the third subset included all floodplains, but separate periods (two datasets). All data handling and statistical analyses were performed in the R environment (R Core Team, 2019) and each procedure is described below.

First, we computed taxonomic site-by-site dissimilarity matrices for each biological group and subsets by applying the Sørensen index on presence-absence and the Bray-Curtis index for abundance data (except for macrophytes) (Legendre, 2014b; Peres-Neto and Jackson, 2001). Following Podani and Schmera (2011), the total taxonomic beta diversity (β^T_{total}) was decomposed into replacement (β^T_{repl}) and richness/abundance difference (β^T_{Rdiff} / β^T_{ABdiff}) components, using the *beta* function from package "*BAT*" (Cardoso et al., 2015). Before calculating the total functional beta diversity (β^F_{total}) and decomposing into its components (β^F_{repl}, β^F_{Rdiff}, and β^F_{ABdiff}), we used information on traits of each biological group to calculate the functional resemblances among species based on Gower index (Gower, 1966), using the function *gowdis* in package "FD" (Laliberté, E., Legendre, P., Shipley, B., & Laliberté, 2014). Then, this species-by-species dissimilarity matrix was subjected to a hierarchical clustering using the function *hclust* from the package "*stats*". Finally, the generated cluster was used in the same *beta* function to calculate and decompose the functional beta diversity. After all these procedures, we produced 1,344 dissimilarity matrices representing the following combinations: [floodplain (4) + period (2) + floodplain * period (8)] * presence-absence/abundance (2) * taxonomic/functional (2) * beta diversity component (3) * biological group (8) (Fig. 2A).

Secondly, as the Procrustes analysis is flexible enough to deal with any ordination technique but requires the multivariate scores of each observation (Jackson, 1995), were first summarized each dissimilarity matrix in a reduced dimensional space using Principal Coordinates Analysis (PCoA; Gower, 1966); function *cmdscale* from "stats" package. We chose Procrustes instead of other usual methods (e.g., Mantel correlations) because it is more powerful to deal with spans large environmental gradients, despite being recognized as a suitable method for congruence-based approaches (Peres-Neto and Jackson, 2001). This is true in our case, especially when considering subsets two and three, which had remarkable quantitative differences between periods and among the floodplains, respectively. In this analysis, site scores from any pair of ordinations are compared by calculating the badness-of-fit statistic (m^2) that measures the mismatch between two ordination configurations (Jackson, 1995). The m^2 values were easily transformed into a goodness-of-fit Procrustes r statistic, where $r = \sqrt{1 - m^2}$ (Peres-Neto and Jackson, 2001), to quantify the congruence between ordinations. This transformed statistic varies between 0 (no congruence) and 1 (perfect congruence).

Because our goal here was restricted to understand how the strength of congruence varies according to the dataset and the approach, we did not test their significances. We evaluated the congruence between (i) taxonomic *versus* taxonomic beta diversity among biological groups and (ii) functional *versus* functional beta diversity among biological groups. In all cases, Procrustes analysis was performed with respect to the same data types (presence-absence or abundance) and the same subsets, using the function *protest* from package "*vegan"* (Oksanen et al., 2018) (Fig. 2B).

Finally, to assess the relationship between the congruence patterns and functional distances among biological groups, we fitted linear models using the function *lm* from package "stats". Models considered the Gower-based functional dissimilarities among biological groups as predictor variable, as previously calculated, and pairwise congruence as response variables. In practice, we used the slope of the best-fitting line, which, in our case, indicated how much congruence values changed as a function of the cross-taxon functional differences. For instance, under our prediction, a negative slope of the fitted model would indicate a negative relationship between cross-taxon congruence and their functional distance (Fig. 2C).

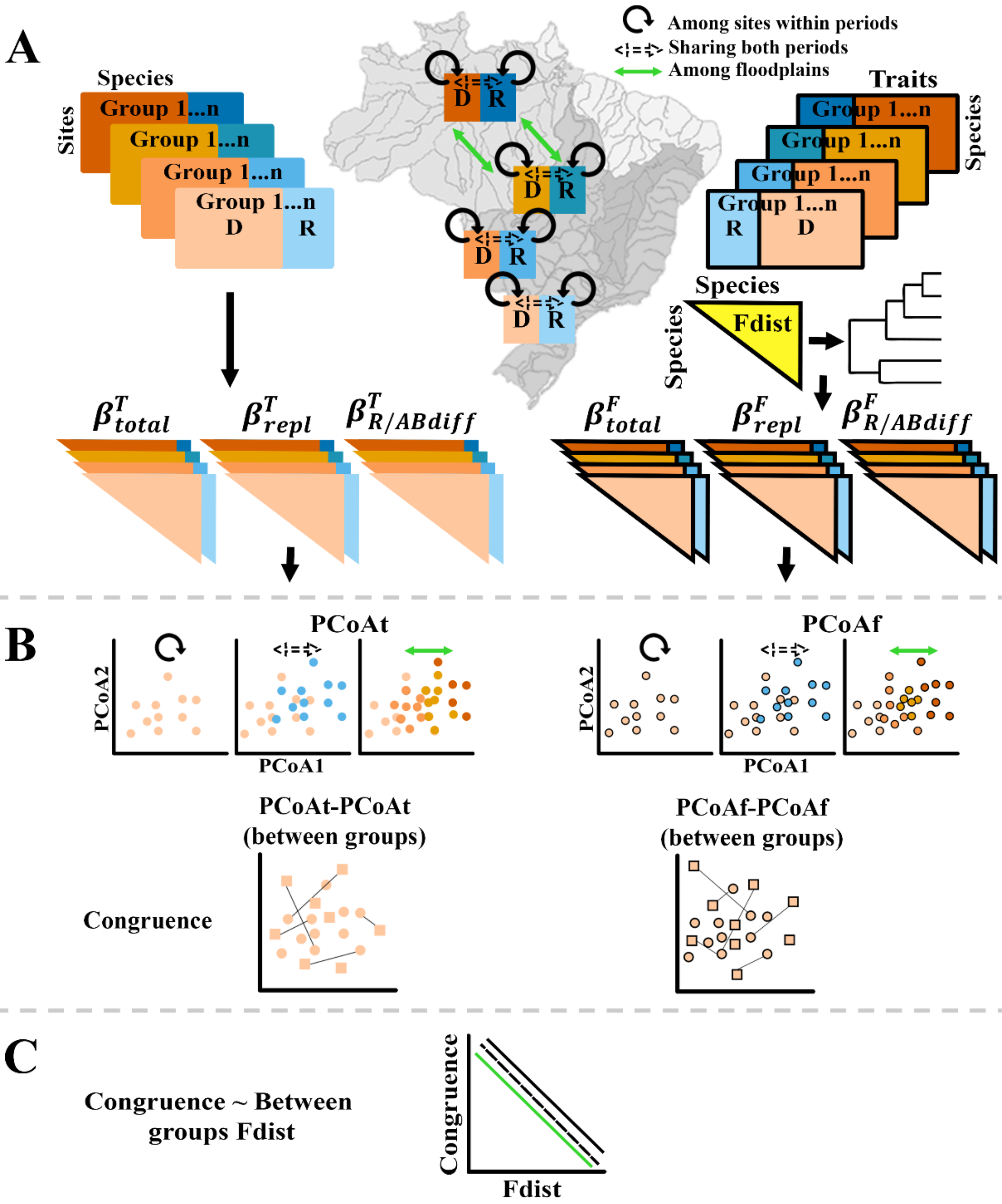


Fig. 2: A summary of the analytical approach. A: this shows the combinations of the three nested subsets, how the taxonomic and functional datasets are organized, and calculation of each beta diversity component. B: shows the steps to obtain congruence values. First, we performed a PCoA ordination and, then, the Procrustes correlations. C: Linear regression was conducted between congruence values and functional dissimilarities among biological groups.

2.3 Results

2.3.1 Cross-taxon congruence patterns across spatial and temporal scales

When each hydrological period and floodplain was analyzed individually, the cross-taxon congruence based on presence-absence data showed, little variation between dry and flood periods (Fig. 3). However, the Paraná floodplain stood out in relation to the other floodplains, showing a higher strength of congruence for the β_{total} and β_{diff}. An inverse pattern was found when the data involved the two hydrological periods together, with the lowest values of taxonomic and functional congruence for β_{repl} and mainly for β_{total} being observed for the Paraná floodplain. At the continental scale, there was a slight increase in general congruence patterns, regardless of the hydrological period, especially for β_{total}. Moreover, in general, similar patterns were found between both taxonomic and functional approaches. However, it was possible to verify a marked differentiation when dry and flood periods were analyzed together, and the differences were even more pronounced at the continental scale, with higher means of all pairs of congruence for the taxonomic, especially for β_{total}^{T} and β_{repl}^{T} beta diversity components (Fig. 3).

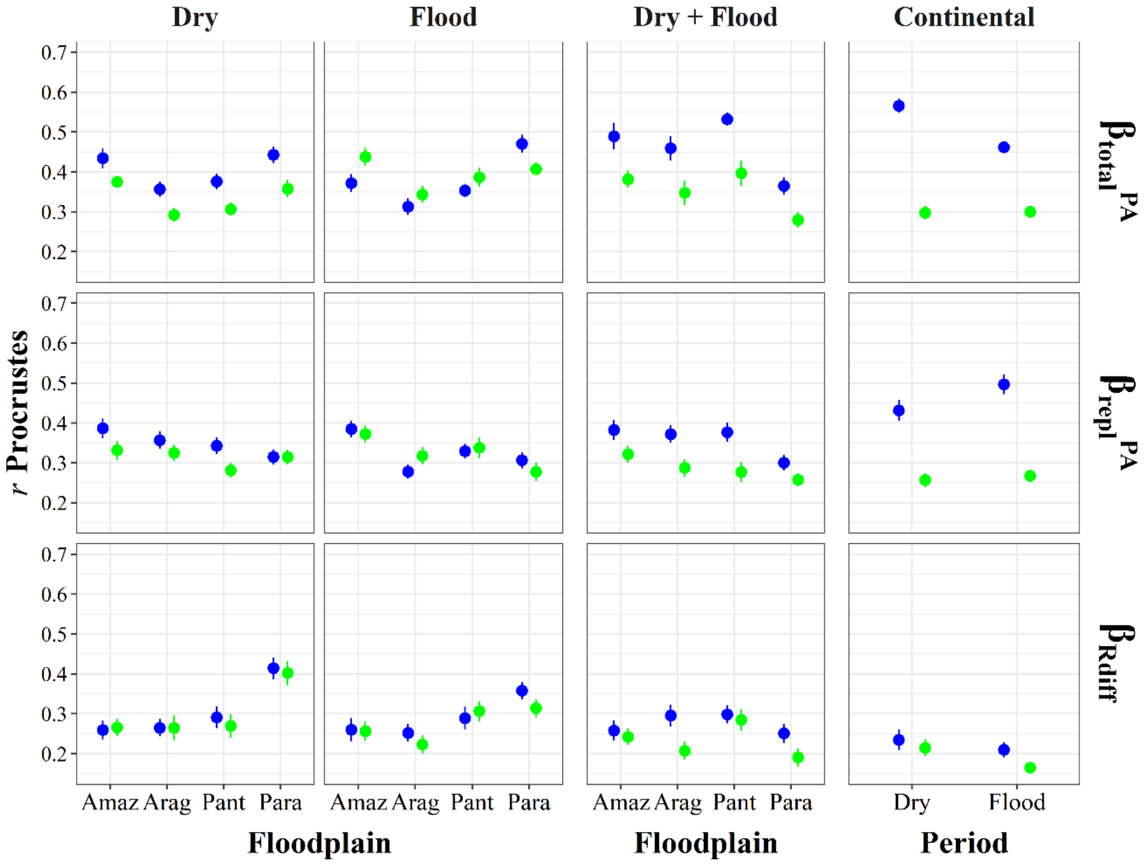


Fig. 3: Mean and standard deviation of strength of congruence calculated from all pairs of combinations between biological groups for presence-absence data. Blue = Taxonomic approach; Green = Functional approach; Amaz = Amazonia; Arag = Araguaia; Pant = Pantanal; Para = Paraná.

When the strength of congruence was calculated based on abundance data, similar patterns as above were found (Fig. 4). Both periods of dry and flood also differed little from each other, and the Paraná floodplain, although less intense, showed higher values for β_{total} and β_{ABdiff}. However, the highest averages of congruence occurred when dry and flood periods were analyzed together. In addition, for the same scale, it is possible to observe a clear downward trend in the congruence values based on β_{total} and β_{ABdiff} from the Amazon floodplain to Paraná. As with presence-absence data, the highest congruence values were found for β_{total} and β_{repl}, with the strength of congruence also being lower for these two components in the functional approach at the continental scale. It is noteworthy that for the β_{ABdiff}component, the congruence between the taxonomic and functional approaches was extremely similar at all scales (Fig. 4). The strength of congruence of all pairs of combinations between biological groups based on data presence-absence and abundance data for all nested subsets are provided in Figs. S1-S8.

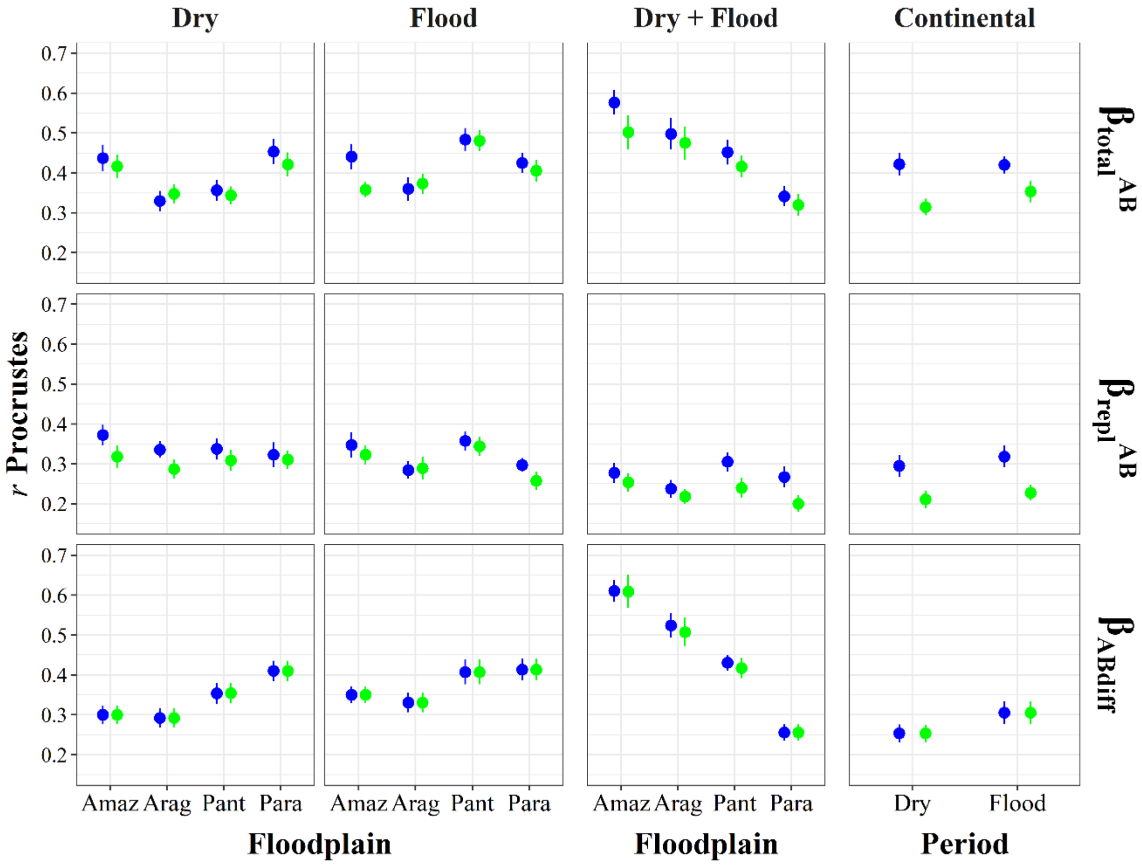
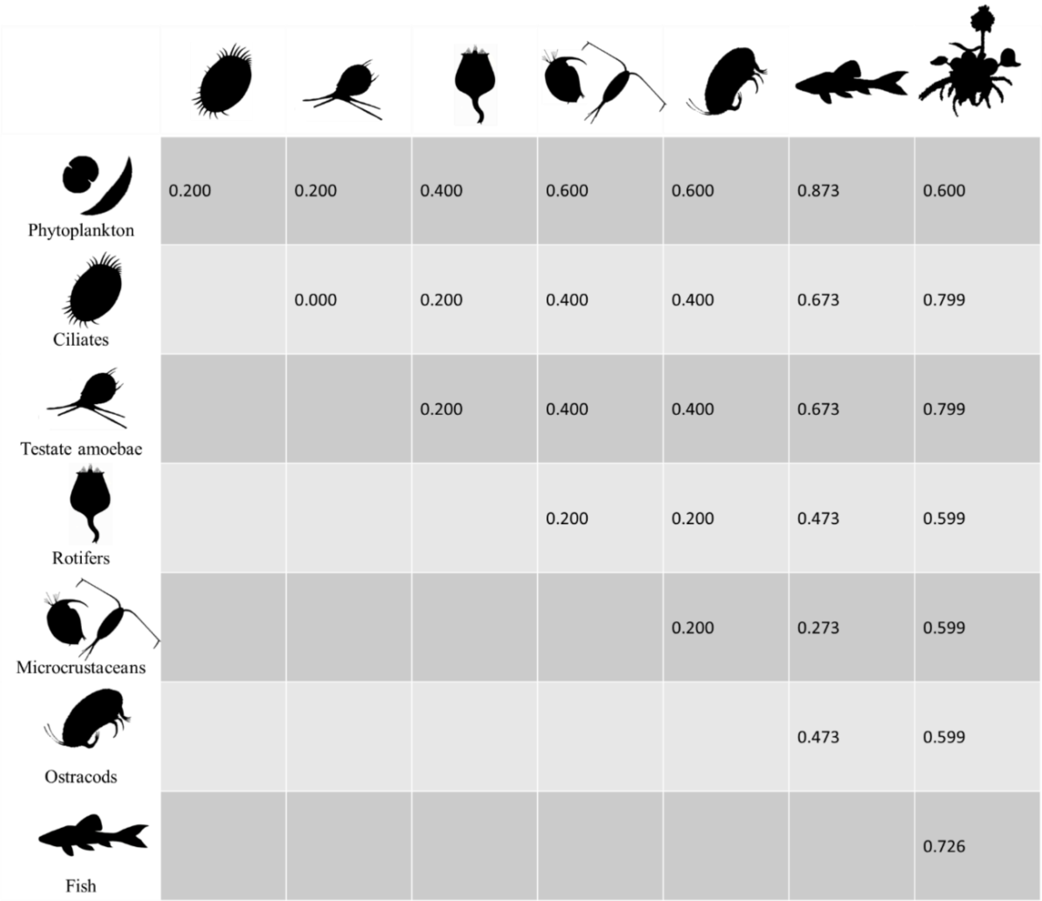


Fig 4: Mean and standard deviation of the strength of congruence calculated from all pairs of combinations between biological groups for abundance data. Blue = Taxonomic approach; Green = Functional approach; Amaz = Amazonia; Arag = Araguaia; Pant = Pantanal; Para = Paraná.

2.3.2 Relation between congruence and functional distances among biological groups

Based on the biological characteristics of each individual biological group, higher functional distances were verified for combinations of phytoplankton and fish, ciliates and macrophytes, testate amoebae and macrophytes. In contrast, lower distances were found for combinations of ciliates and testate amoebae, microcrustaceans and ostracods, ciliates and phytoplankton. The values of all generated distances are provided in Fig. 5.



Phytoplankton	0.200	0.200	0.400	0.600	0.600	0.873	0.600
Ciliates		0.000	0.200	0.400	0.400	0.673	0.799
Testate amoebae			0.200	0.400	0.400	0.673	0.799
Rotifers				0.200	0.200	0.473	0.599
Microcrustaceans					0.200	0.273	0.599
Ostracods						0.473	0.599
Fish							0.726

Fig. 5. Cross-biological group functional distances based on Gower´s index.

In general, taxonomic and functional approaches showed similar relationship between congruence patterns and functional distances among biological groups, with a stronger relationship for β_{total} and β_{repl}, regardless of the numerical resolution used (Figs. 6-7). In the case of the subset comprising each floodplain and period separately, while weaker relationships were found in the flood period for all floodplains, this relationship was more accentuated in the drought period. However, the slope ranged from negative (as in the Araguaia and Paraná floodplains) to positive (more intense in the Amazonia floodplain). This inverse pattern of the expected for Amazonia was mainly due to the great strength of congruence based on

β_{repl} between phytoplankton and fish in the dry period (Fig. S1). For the subset that comprised the four floodplains separately, including both periods, the slope was always negative towards β_{total} and β_{repl}, although the relationships were generally weak. Finally, at the continental scale, the most negative β_{total} and β_{repl} relationships were found, mainly for abundance data. β_{Rdiff} and β_{ABdiff} showed no relationship between congruence and among-group functional distances.

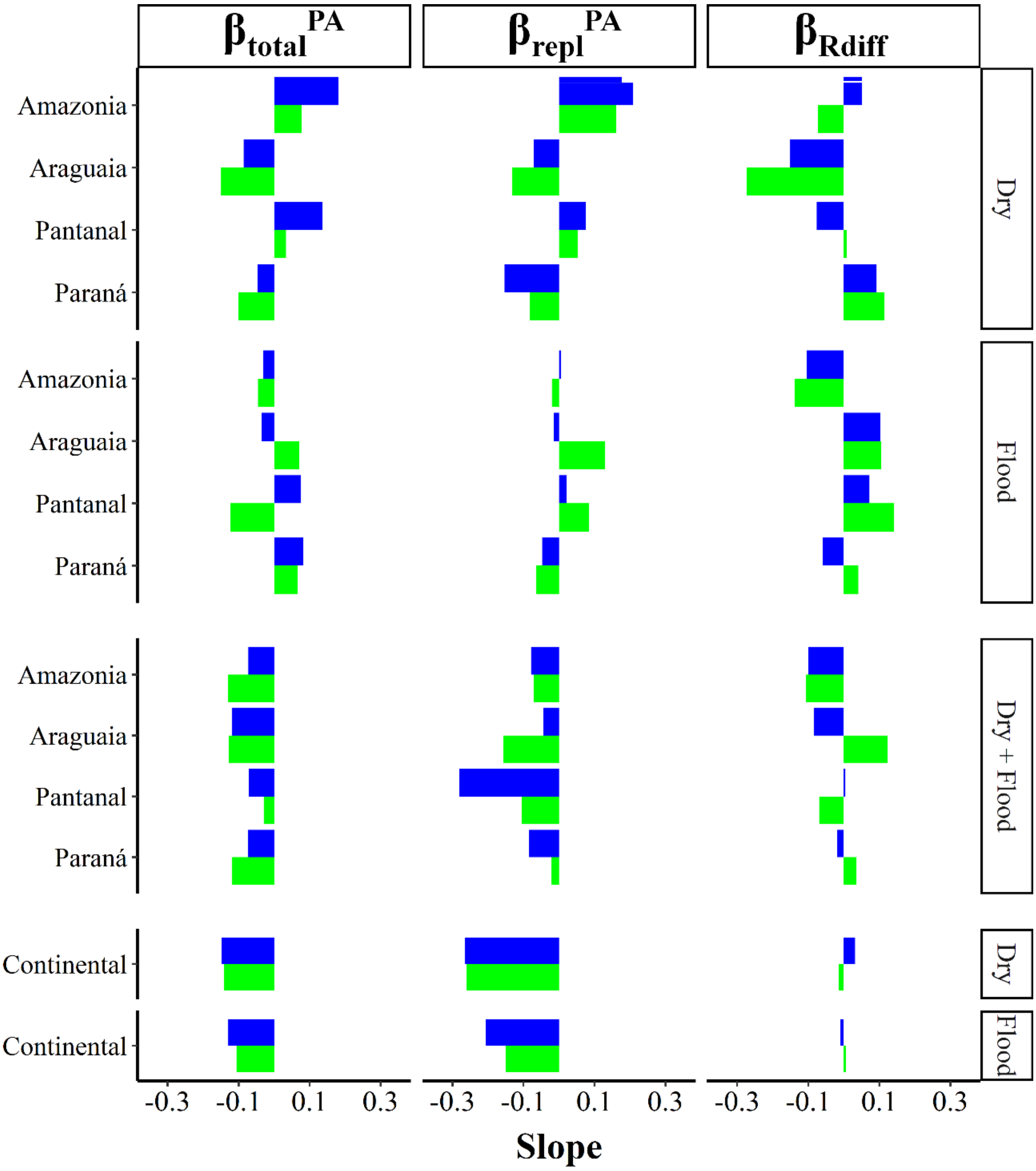


Fig. 6: Relationship between the congruence patterns observed with the functional distances between biological groups for presence-absence data.

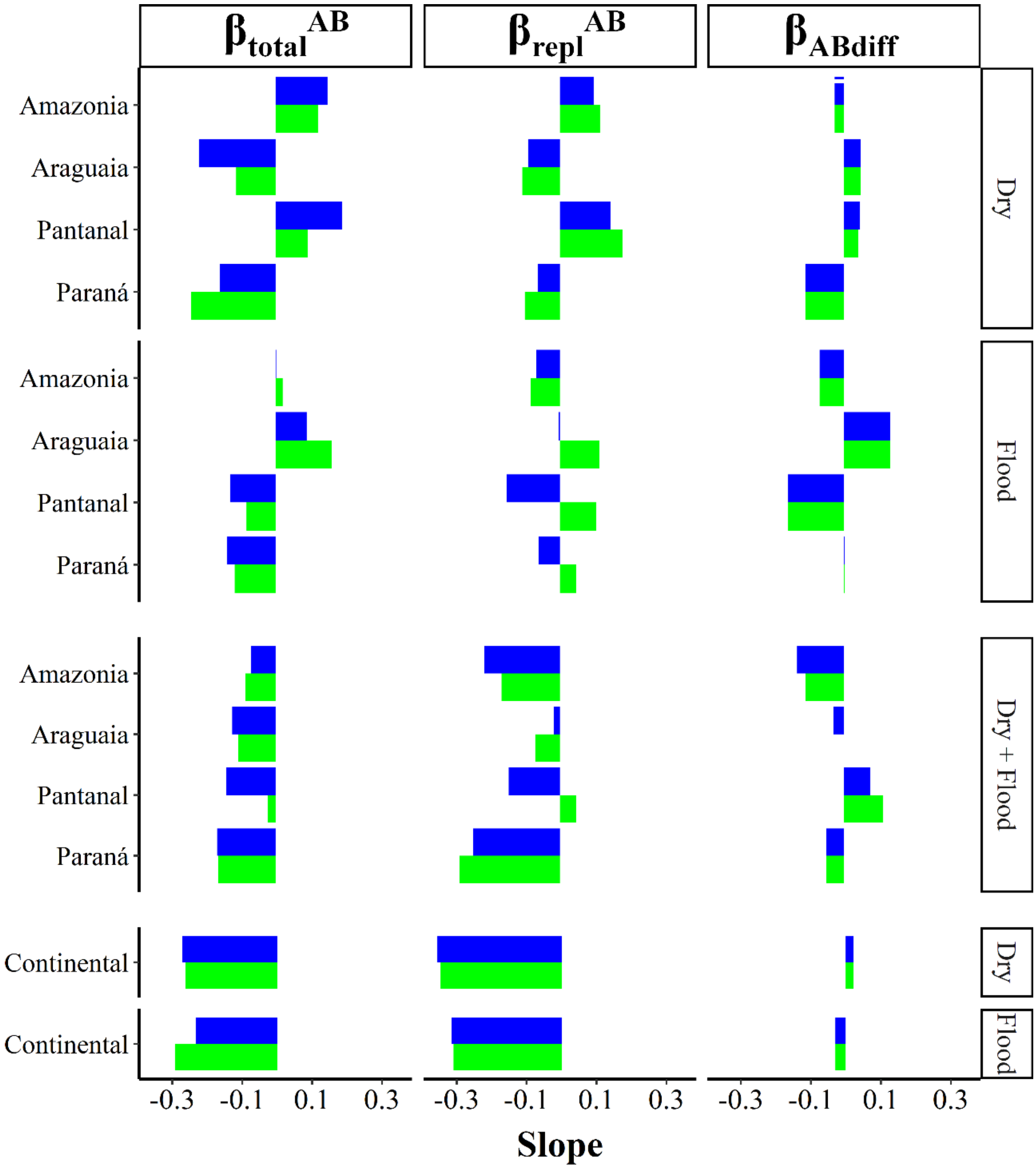


Fig. 7: Relationship between the congruence patterns observed with the functional distances between biological groups for abundance data.

2.4 Discussion

The analysis of taxonomic and functional beta diversity, along with their replacement and richness difference components, adds novel insights into previous studies analyzing patterns of taxonomic cross-taxon congruence. Moreover, this approach may result in potential differences between the facets, thus being an important tool for global conservation planning. Our results showed how detailed hierarchical analyses can reveal hidden patterns of cross-taxon congruence, which depends on an interactive effect of environmental conditions, biotic interactions, temporal dynamics, dispersal limitations and broad-scale historical processes. Our study partly supported the hypothesis that the strength of cross-taxon congruence generally decreases with the increase of functional distances between pairs of biological groups, but this relationship is spatial and temporal variable.

2.4.1 Analyzing individual floodplains and each period separately

The mean congruence considering each floodplain and hydrological period individually was low for all beta diversity components regardless of the taxonomic or functional approach. Indeed, studies conducted at small scales usually have found weak cross-taxon congruence (Heino, 2010; Westgate et al., 2014). This is because for localized studies, the absence of strong environmental gradients should lead to a weak association between environmental conditions and community structure (Heino et al., 2015b), thereby obscuring patterns of congruence caused by similar environmental filtering among multiple biological groups. However, in river-floodplain systems, the low level of connectivity among habitats during the dry period produces high environmental heterogeneity and may limit the dispersal of aquatic organisms, contributing to increased importance of environmental filters (Bozelli et al., 2015). For this reason, Padial *et al.* (2012) predicted that the strength of cross-taxon congruence should be higher during the dry periods than during the flooding, but their results did not support this assumption. However, that study was carried out only in the Upper Paraná River floodplain, which has a series of dams upstream that regulate water flow, reducing the intensity and duration of floods and, consequently, the differences between periods (Angelo A. Agostinho et al., 2004). Here, we built on these findings, including other three floodplains with much more contrasting hydrological periods, showing little evidence that the strength of the congruence changes according to the variation of the hydrological regime.

It is interesting to highlight that both β_{Rdiff} and β_{ABdiff} cross-taxon congruencies were higher in the Paraná floodplain. This can be explained by the peculiarities of the study area, which encompass three distinct subsystems (Paraná, Ivinhema and Baía) associated with the three large rivers of the region. The Paraná subsystem is directly affected by a cascade of upstream reservoir. The Baia River, which follows a course parallel to the Paraná River, is also influenced by the operation of upstream reservoir, but yet it preserves a pristine system of wetlands. The Ivinhema subsystem is located in a dam-free region in the Ivinhema River State Park. Studies have shown that changes involving reduction in nutrients and an increase in water transparency were evident in the Paraná River, less obvious in the Baía River (which is only partially influenced by the dam) but largely indistinguishable in the unimpounded Ivinhema River (Granzotti et al., 2018; Roberto et al., 2009). Thus, the higher strength of congruence in this floodplain may be explained by similar responses in terms of abundance difference and functional richness difference for different biological groups among the lakes, which are generally higher in the Ivinhema subsystem and lower in the Paraná subsystem for many biological groups (Braghin et al., 2018; Granzotti et al., 2018; Rodrigues et al., 2015).

Low cross-taxon congruence in small-scale studies may also be caused by a strong influence of biotic interactions differentially determining diversity patterns at fine scales (Duan et al., 2016). Although we may not necessarily have measured the impact of biotic interactions on congruence patterns, our results are indicative of a highly complex and variable interplay of potential biotic interaction in explaining cross-taxon congruence in the beta diversity patterns of the investigated pairs of biological groups. For instance, even though functionally-related biological groups may be similarly structured by the environment, they may also have a higher competition / predation ratio, which directly interferes with congruence patterns (Oliveira et al., 2019). Phytoplankton and ciliates could be expected to show similar community variation across sites, as they have similar body size, reproduction mode and potential for dispersal. However, the strength of congruence between these groups generally did not follow this presumption. This is in agreement with Allen *et al*. (1999), who found that strong distributional congruence among closely-related biological groups occurred at broad scales, but they showed little or no significant relationship when subregions were examined separately. Several studies conducted all over the world have been found that predation exercised by ciliates can limit phytoplankton development (Šimek et al., 1995; Zingel et al., 2007) and, consequently, weaken the spatial congruence between these two biological groups. In the same way, opposing patterns of zooplankton diversity across a natural landscape is also common in nature (Horváth et al., 2014; Vieira et al., 2017). For instance, rotifers and microcrustacean possess distinct reproductive strategies and life cycles (Allan, 1976), as well as differences in their dispersal ability (Dias et al., 2016). Consequently, they respond differently to underlying environmental gradients (Bini et al., 2008), which may explain the weak relationship detected between these biological groups in this study.

In addition, indirect biotic interactions may cause strong congruence between functionally distinct biological groups. For example, the greatest functional distance between the biological groups evaluated was between phytoplankton and fish. In the Amazonia floodplain during dry period, the strongest congruence among all pairs of comparisons was exactly between these two groups when assessed based on β_{repl}. Although this strong congruence of community replacement between phytoplankton and fish was a surprising outcome, other studies have been found similar results (Padial et al., 2012). Planktivorous fish are known to produce strong effects on the structure and dynamics of the zooplankton community through the control exercised by predation (Lazzaro et al., 2003). These changes can reach lower trophic levels, through an effect known as "trophic cascade" (Carpenter et al., 1985). In this sense, reductions in zooplankton abundance, especially microcrustacean, can positively influence the phytoplankton community, due to decreased predatory pressure on them (Attayde and Hansson, 2001; Lacerot et al., 2013). Therefore, the combination of direct and indirect trophic interactions may be important processes driving cross-taxon congruence at small scales (Duan et al., 2016; Padial et al., 2012). This may, in part, explain why the results of the regression between the strength of cross-taxon congruence and the functional distance between biological groups varied from negative to positive in each floodplain, especially in the dry period.

2.4.2 Analyzing both periods together

Temporal variations in community composition are ubiquitous in nature, and different responses have been documented in aquatic ecosystems for community–environment relationships. In terms of cross-taxon congruence, common patterns of temporal beta diversity for different communities are expected in ecosystems showing strong seasonal environmental variations (Allen *et al.*, 2017). Regardless of the approach utilized, our results showed that when both hydrological periods were included in the analysis, the congruence in the beta diversity components was relatively low when only the presence-absence was taken into account. Conversely, the variation in abundance (β_{ABdiff}) between both periods was quite congruent among biological groups, which also reflected in high values of β_{total}. This result reinforces the idea that, in many cases, taking into account the variation in the abundance of organisms in a set of habitats may better explain the relationships between biological communities and the environment, whereas this relationship may be weaker for presence-absence data (Heino, 2014).

In the case of this study, when periods changed and community abundance changed accordingly, there was a higher strength of congruence. For instance, Vieira *et al.* (2015), using a similar statistical approach and data gathered in the nearly pristine Araguaia River floodplain, showed that zooplankton communities were able to represent the changes caused by seasonal flooding, exhibiting different community structures between hydrological periods. Similarly, in a recent study involving long-term sampling sites in the Pantanal floodplain system, Lários *et* *al*. (2017) showed that communities exhibited high levels of congruence in general and attributed these patters to the temporal dynamics of that system, dictated by alterations between dry and flood periods. The only exception in this study was registered in the Paraná River floodplain system, where the responses of the different groups in terms of abundance were less congruent according to the change of the hydrological period. As previously discussed, the hydrological regime of this floodplain is strongly regulated by upstream dams, thus reducing the duration and intensity of flood periods (Angelo A. Agostinho et al., 2004). Thus, in the absence of a major factor driving communities similarly through the time, changes in biological communities tend to be more stochastic over hydrological periods. This is consistent with the theory that increasing stochastic drift in community structure is expected in the absence of strong environmental filters (Chase et al., 2009).

For beta diversity calculated from presence-absence matrices, the congruence of taxonomic and functional Brich was low, even for floodplains with marked changes between hydrological cycles, as is the case of the Amazonian floodplain. The variation in species richness between hydrological periods varies greatly from study to study. Often, the greater stability and availability of food during periods of drought, contribute to greater species/functional richness in that period (Schöll et al., 2012). On the other hand, during this period, biotic interactions are more intense, and certain communities can be suppressed by predators, thus reducing their richness, especially in a prolonged dry season (Bortolini et al., 2016a). In addition, during the flood periods, there may be a greater contribution of species adapted to other compartments of the water column, such as species from the littoral and benthic region (Lansac-Tôha et al., 2009). Thus, even though the abundance of most groups is lower in the flood period, the taxonomic and functional richness may be higher than in the dry season, which leads to low congruence values.

Contrary to the findings when the periods were analyzed separately, we found that the relationship between the strength of congruence and the functional dissimilarity of biological groups tended to be negative for the components Btotal and Brepl, although in most cases weak. The magnitude of the temporal replacement likely depended on the sampling interval relative to the length of the generation cycle or developmental periods of species within a community (Allen *et al.*, 2017). For instance, microbial communities can show complete turnover in minutes (Fenchel, 1974), while microinvertebrate communities vary within days or months (Allan, 1976). Furthermore, the seasonal dynamics of river-floodplain fish communities in relation to flood pulses may exhibit a lag of roughly two or three years, depending on a species' longevity (Isaac et al., 2016).

We found high congruence for microbial communities which suggest that these communities have changed spatially more when compared to other biological groups. The patterns identified should apply to a range of systems, although the time scale at which they are manifested can vary among systems. However, our sampling interval in each sampled floodplain was about one year. This does not allow us, for example, to accurately assess how micro-organisms and micro-invertebrates, for example, vary in terms of community composition over time, since for all of these groups, a large number of generations have succeeded the second sampling. Therefore, possible differences in the patterns of the beta diversity components may have been masked.

2.4.3 Broad-scale cross-taxon congruence patters

We found that the most negative correlations between the strength of the congruence and functional distances among biological groups were found at continental scale, regardless of the hydrological period or numerical resolution used. At broader spatial scales, cross-taxon congruence in the patterns of replacement and richness difference might reflect biogeographical factors, such as speciation, extinction and historical dispersal events (Burrascano et al., 2018; Pawar et al., 2007). Therefore, a common biogeographic history could lead to the increase of cross-taxon congruence. Recent studies have shown that cross-taxon congruency is strongest between biological groups with similar body size (Hájek et al., 2014; Velghe and Gregory-Eaves, 2013). Our results add to this conclusion and provide a more robust approach, including other traits that may interfere with the potential for dispersal and colonization of new habitats and, therefore, are closely related to the biogeographic patterns shown by an organismal group.

For both taxonomic and functional approaches, this relationship was verified only for the Btotal and Brepl components. Contrasting results were found by Allen *et al.*, (1999), which found that the relationship between congruence and biological groups size was more related to the difference in species richness than to the changes in species composition. The greater relationship with Brepl can be explained due to the fact that the biological groups considered in this study have marked differences in their dispersal ability, which gives them quite different distribution patterns on a broad-scale. For instance, micro-organisms such as ciliates, phytoplankton and testate amoebae share a suite of common functional traits, such as small size, reproduction mode and dispersal, which contribute to low dissimilarity with each other. Compared to large bodied organisms, these micro-organisms achieve high population densities, which make them less prone to local extinction events (Wilkinson, 2002), allowing higher propagule numbers and increasing their potential for dispersal events (Fenchel and Finlay, 2004). In contrast, spatial patterns are commonly found for zooplankton communities, mainly at broad spatial scales (Declerck et al., 2011; Mazaris et al., 2010; Viana et al., 2016).

An excellent example of how functional dissimilarity can be a better predictor of the spatial distribution of organisms instead of body size is the comparison between macrophytes and fish. These two biological groups are by far the largest in terms of size in this study. However, they showed high functional dissimilarity and low congruence at continental scale. This is probably because of their potential differences in dispersal ability. If, on the one hand, fish dispersal is restricted via watercourses, which in turn may have a series of physical barriers that prevent their free movement (De Bie et al., 2012), macrophytes have several strategies, such as fragmentation and seeds release, which enhance their effectiveness in dispersing across a long distance (Alahuhta et al., 2017). Thus, studies have shown that fish can exhibit strong biogeographic patterns (Beisner et al., 2006; Mazaris et al., 2010), while macrophytes may have low species turnover even at intercontinental scales (Alahuhta et al., 2017). We thus propose that the interaction of dispersal limitation and the importance of local barriers such as river basin divide in speciation events partly accounted for the patterns of congruence we detected.

Here, we expanded the concept of cross-taxon congruence to comprise afunctional approach. However, it should be noted that while the relationship found was negative for functional beta diversity, the mean degree of congruence between all pairs of comparisons was markedly lower compared to the taxonomic approach at broad scale. Recent studies have acknowledged that regions of high taxonomic diversity may be incongruent with regions of high functional diversity, particularly if one community is composed of a combination of functionally different species and the other one is not (Mason et al., 2005; Mouchet et al., 2010). Moreover, functional diversity may not vary as much across the landscape such as taxonomic diversity, especially if species replacements are mostly between functionally redundant species (Braghin et al., 2018; Villéger et al., 2012). Therefore, as environmental changes may have an impact on functional diversity and alter species interactions and ecosystem functioning regardless of the change in taxonomic diversity, different biological groups may show contrasting functional beta diversity patterns even if taxonomic beta diversity varies similarly across the landscape.

2.5 Conclusion

Here, we showed how cross-taxon congruence is highly dependent on the spatial and temporal context. At broad scales, the results suggest that taking into account the functional distance between biological groups is essential, and the choice of the better surrogate group for biomonitoring depends on the question and aims of the project. Moreover, if hydrological regime is not regulated by dam´s operation, our results suggest the potential for use of the cross-taxon surrogacy approach in the monitoring of hydrological periods. However, the strength of cross-taxon congruence was higher when the datasets included the species relative abundances, suggesting that considering quantitative protocols may be essential to answer certain objectives. More interestingly, we found that functional congruence is weaker than taxonomic congruence in many cases. This finding leads us to conclude that different organismal groups may be governed by different environmental factors and ecological processes.

Considering that both conservation of biodiversity and sustainable use of natural resources requires planning, enhancing the efficiency of monitoring programs can be more cost-effective if only one or a few biological groups can predict distributions patterns of other biological groups. However, the strength of community congruence was weak and rarely exceeded 0.7, which is often recommended for one biological group to predict well enough the spatial patterns of others (Heino, 2010; Lovell et al., 2007). Furthermore, even when the degree of congruence between two biological groups was high at a certain scale, the same pattern was not repeated in space or time, making it difficult to directly suggest any specific surrogate taxon.

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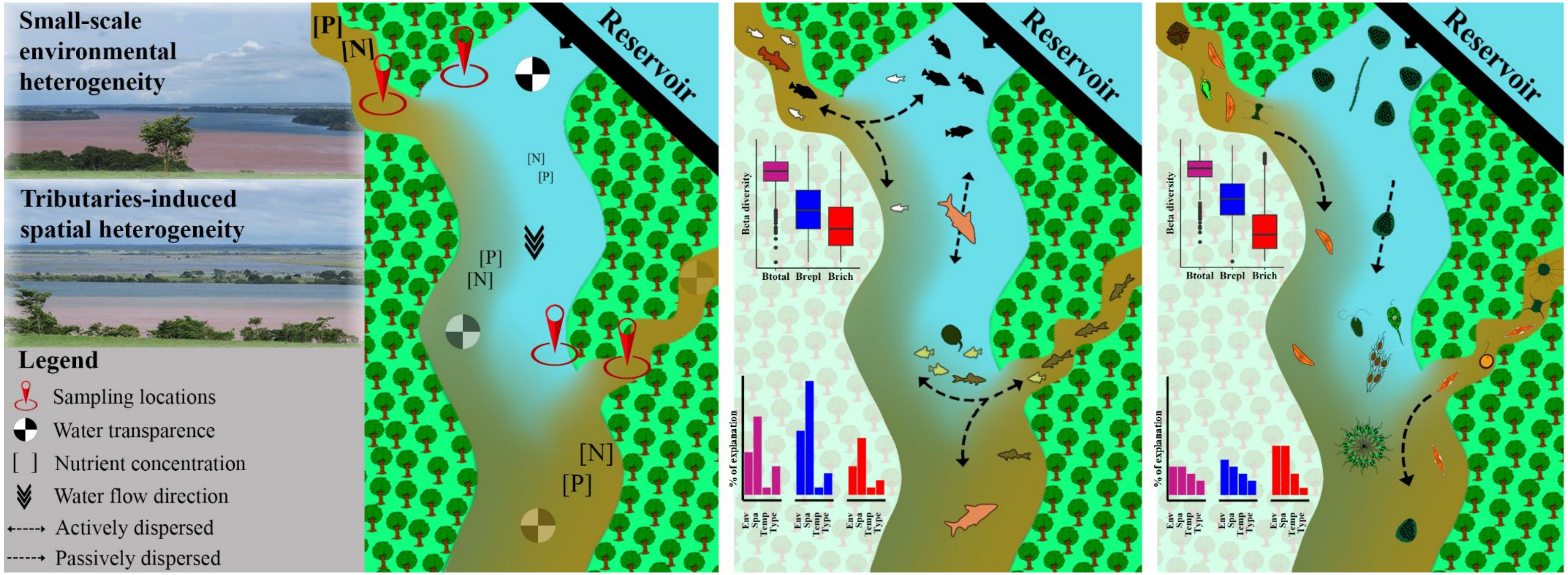
3 DIFFERENTLY DISPERSING ORGANISM GROUPS SHOW CONTRASTING BETA DIVERSITY PATTERNS IN A DAMMED SUBTROPICAL RIVER BASIN

ABSTRACT

Although it is widely known that dams can have large impacts on the environmental and biological characteristics of downstream rivers, there is a substantial lack of studies focusing on which ecological processes cause longitudinal changes in biological communities downstream of reservoirs. We investigated longitudinal patterns in the total beta diversity and its replacement and richness difference components for actively (fish) and passively (phytoplankton) dispersing biological groups. Our results, obtained from a 230 km sampling stretch, demonstrated the key role played by tributaries in the downstream direction from main river impoundment, which influenced local environmental conditions and beta diversity patterns of each biological group. Both replacement and richness difference contributed to high values of total beta diversity for fish (average = 0.77) and phytoplankton (average = 0.79), but their relative importance was more associated with the replacement component for both biological groups (average = 0.45 and 0.52, respectively). Moreover, we observed clear differences between fish and phytoplankton in beta diversity patterns operating at small and broad scales, as well as in the mechanisms driving each beta diversity component. Directional dispersal-related processes and environmental filtering played a major role in shaping total beta diversity and its components for fish, while temporal factors explained considerable parts of phytoplankton beta diversity. Our findings contributed to understanding of tributary-induced heterogeneity and highlight the importance of dam-free stretches of rivers for preserving the integrity of dammed river basins.

Keywords: dam impacts, impoundment, replacement, fish, phytoplankton, tributary influences

Graphical abstract



Highlights

1. We investigated longitudinal patterns of fish and phytoplankton in a dammed river.
2. Beta diversity was mostly contributed by species replacement for both biological groups.
3. Tributaries tended to be environmentally and compositionally different from main river sites.
4. Differences found showed that multiple taxa are recommended in assessing human disturbance.
5. Preserving dam-free stretches of rivers should be a priority for the integrity of dammed rivers.

3.1 Introduction

Improving the knowledge about the distributions of species, how they vary across spatial and temporal scales, and the mechanisms that influence them are at the heart of ecological research (Cottenie, 2005). In addition to local scale diversity (alpha-diversity), variation in community composition among sites and in time (beta diversity) is an important determinant of regional diversity (Baselga, 2010). Recently, studies have shown that decomposing beta diversity into their respective replacement and richness difference components (Podani and Schmera, 2011) facilitates the detection of more complex ecological patterns in space and time (Legendre, 2014b). The replacement component reflects the substitution of species in one site by different species, whereas the richness difference component derives from the loss or gain of species (Carvalho et al., 2012). These two beta diversity components are complementary and both often contribute to total dissimilarity between sites, but their relative importance can be different depending on the local and regional factors structuring communities (Heino et al., 2018; Victorero et al., 2018).

In nature, beta diversity is often thought to be driven by environmental heterogeneity (Alahuhta et al., 2017; Soininen et al., 2018). This relationship is expected because more heterogeneous conditions in a region provide more niche opportunities, allowing species to track environmental variation among sites when dispersal is sufficient (Heino et al., 2015b). However, dispersal limitation may restrict the species occurrence at different localities, resulting in spatially structured beta diversity patterns, regardless of environmental variation (Viana et al., 2016). In addition, in light of the high temporal variability in environmental factors, dispersal rates and levels of connectivity between local habitats in any freshwater ecosystem, assessing the temporal dynamics is also important for understanding beta diversity patterns (Bozelli et al., 2015; Wojciechowski et al., 2017). Therefore, as environmental, spatial and temporal factors interact and influence each beta diversity component, their relative importance may vary even within the same system, depending on the organism groups that differ in their specific ecological and biological characteristics (De Bie et al., 2012; Heino et al., 2017).

One potential driver for such differences is the organisms' potential for among-site dispersal (Padial et al., 2014), as limited, sufficient and excessive dispersal may differentially alter the community dynamics (Heino et al., 2015b). For instance, small passive dispersers species are easily carried long distances by water flow, wind and animals, and may utilize dispersal strategies, such as the production of spores, cysts or drought resistance eggs, increasing their dispersal ability and overcoming geographic barriers more easily (Van der

Gucht et al., 2007). Although the dispersal of active dispersers, such as fishes, is restricted to via-watercourses routes, in connected systems, fishes are potentially good dispersers and may actively select sites for colonization (De Bie et al., 2012; Erős et al., 2017). Hence, local environmental conditions are usually expected to be the main regulators of passive dispersers, while spatial processes are considerate to be more important for active dispersers (De Bie et al., 2012; Padial et al., 2014; Viana et al., 2016). However, studies have also frequently shown opposite results (Grönroos et al., 2013; Heino et al., 2017; Hill et al., 2017). The absence of a clear overall pattern is mainly because of the fact that studies varied in spatial extent and type of environment, which, in turn, directly influence the main mechanisms driving spatial variation of communities (Heino et al., 2015b). However, given that actively and passively dispersing taxa may respond differently to ecological gradients, they are not likely to respond similarly to anthropogenic changes in aquatic ecosystems (Heino, 2010). Thus, the consideration of these different dispersal strategies of organisms is advisable for guiding biomonitoring and conservation (Morais et al., 2018; Vilmi et al., 2016).

Dam construction is one of the main threats to freshwater ecosystem and has been responsible for causing major environmental modifications, which contribute to changes in species composition and result in an alteration of biodiversity (Abati et al., 2016; Ceschin et al., 2015; Tombolini et al., 2014; Winemiller et al., 2016). In river–floodplain systems, the construction of dams alters the natural dynamics of rivers owing to the control of water flow from upstream reservoirs, resulting in a great reduction in the amplitude of floods as well as changes in environmental characteristics, such as decrease in nutrients and increase in water transparency (Agostinho et al., 2008; Santos et al., 2017). In this context, the importance of undammed tributaries for the longitudinal gradient of the main river is relevant, considering that those tributaries contribute to the input of organic and inorganic particulate matter, thus minimizing the effects of dam control and increasing the environmental heterogeneity along this gradient (Stanford and Ward, 2001). Consequently, it is expected that damming-induced changes affect beta diversity components downstream of the reservoir, which has implications for guiding practical management decisions (Braghin et al., 2018; Chaparro et al., 2019). For example, species may track the environmental gradient along the river, contributing to the dominance of species replacement. In contrast, localities closer to the dam may have lower species diversity when compared to more distant ones, since the particular environmental conditions imposed by the impoundment may be unsuitable for many species. Therefore, studies based on beta diversity partitioning approach (Carvalho et al., 2012; Podani and Schmera, 2011; Rocha et al., 2018) may provide a useful tool for mapping biodiversity and implementing different conservation strategies to preserve regional species diversity downstream of reservoirs.

The main aim of this study was to investigate potential drivers of the replacement and richness-difference beta diversity components in the last non-dammed stretch of the Paraná River in the Brazilian territory. We analyzed a dataset for two biological groups (i.e. fish and phytoplankton), which show wide variation in body size, dispersal mode (active versus passive disperser), generation time and tolerance to the physical characteristics of lotic environments (Padial et al., 2014). We expected that the relative roles of environmental, spatial, and temporal processes, as well the type of river (main channel or tributaries), should differ between the beta diversity components of fish and phytoplankton. Thus, the relative contribution of each component of beta diversity could be different between these biological groups, or even different ecological processes could control similar beta diversity patterns. More specifically, we predicted that i) the active dispersers (i.e. fish) would be more related to the local environment factors (i.e. species-sorting mechanisms along environmental gradients) than the passive dispersers (i.e. phytoplankton). Such patterns are expected to happen because the spatial extent of the studied area and the associated spatial gradients do not contain any natural barriers (e.g. waterfalls and intermittent river channels) that may prevent dispersal among localities. Thus, fish can freely disperse in the river network, allowing species to track more suitable environmental conditions, as compared to passively dispersing phytoplankton (Erős et al., 2017). Consequently, we predicted that ii) phytoplankton would show the prevalence of spatial processes, regardless of the environmental variation. This is due to the unidirectional downstream water flow along the longitudinal gradient of the river, in association with the influence of river confluence effects and through the influx of species into the main channel, would result in variations in community composition from upstream to downstream direction (Bortolini et al., 2017; Liu et al., 2013). Although this process may also occur for fish (Erős et al., 2012), since upstream dispersal is more difficult than downstream dispersal for any aquatic organisms (Blanchet et al., 2011), we expected that its importance would be more pronounced for phytoplankton, since they are dispersed mainly passively following the river flow (Dong et al., 2016). Finally, we predicted that iii) the temporal dynamics would be important to explain beta diversity patterns for both biological groups, since changes in precipitation, temperature and hydrological regime are key factors structuring physical, chemical and biological aspects in river floodplain systems (Junk et al., 1989; Thomaz et al., 2007).

3.2 Methods

3.2.1 Study area

This study was carried out in the Upper Paraná River floodplain system (22°400-22°500S; 53°100-53°240W), the last non-dammed stretch of the Paraná River, restricted to 230 km between the Porto Primavera dam (São Paulo State, Brazil) (22º 37´S, 53º 6´W) and Itaipu reservoir (Paraná State, Brazil) (23º 55´S, 54º 8´W) (Fig. 1). This area has great ecological, social and economic importance, since it is protected by three conservation units (Protected Area of the Islands and Várzeas of the Paraná River, National Park of Ilha Grande, and the State Park of Ivinhema), containing high biodiversity of both aquatic and terrestrial organisms (Agostinho et al., 2004). The floodplain is characterized by seasonal hydrological periods, with alternate events of flood (October-February) and drought (June-September). However, a series of upstream impoundments have largely controlled the river discharge, affecting several hydrological attributes (e.g. period, amplitude, duration and frequency of floods) (Agostinho et al., 2008) and, consequently, the structure and dynamics of communities located downstream (Braghin et al., 2018; Granzotti et al., 2018; Oliveira et al., 2018). Moreover, in the last decades, the Upper Paraná River has faced a substantial reduction of the amount of nutrients (Roberto et al., 2009), but the presence of a large number of undammed tributaries flowing into the main channel is fundamental to mitigate dams' negative impacts through the input of nutrients and organic matter (Jati et al., 2017; Santana et al., 2017).

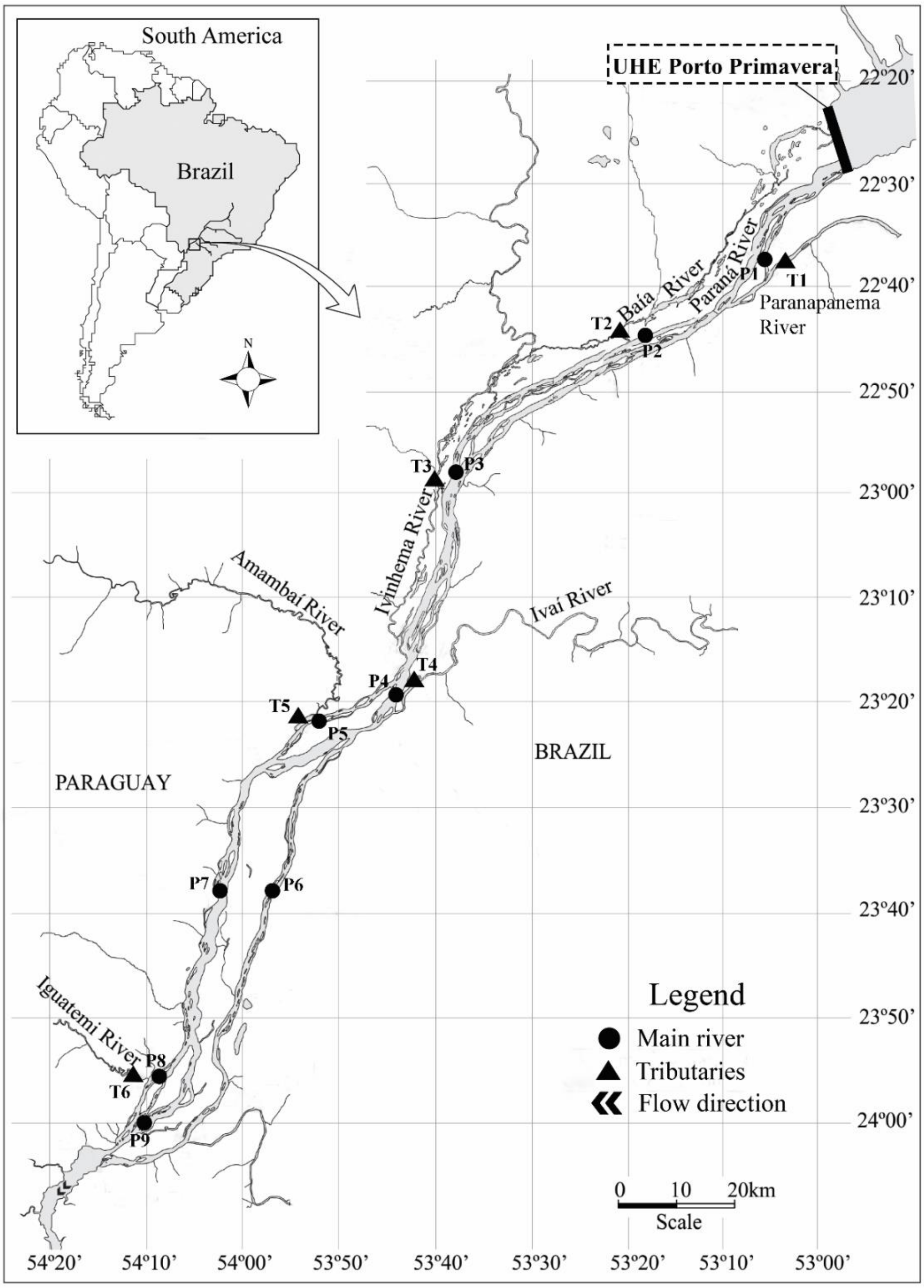


Fig. 1: Upper Paraná River floodplain showing the sampling sites.

3.2.2 Sampling and laboratory analysis

Field surveys were performed encompassing different phases of the region hydrological cycle, being four campaigns in the rainy period (October 2013, February and November 2014, and February 2015) and four in the dry period (August 2013, May and August 2014, and May 2015) (Supplementary Material Fig. S1). Although a clear pattern in the fluviometric level of the Paraná River can be observed between rainy and dry periods, floods only occur when the water level of the Paraná River reaches 3.5 m (Souza Filho, 2009). Because the water level was above 3.5 m for just a few days (Fig. S1), it was not sufficiently long enough to be characterizes as a flood period. Thus, samples in this study did not represent differences between flood and drought periods, as the environments were connected to the main river exclusively by permanent channels. We conducted nine transects at the longitudinal gradient of the Paraná River, and at six tributaries (Paranapanema, Baía, Ivinhema, Ivaí, Amambai and Iguatemi rivers), resulting in a total of 120 samples (15 sites × 8 campaigns). Sites were selected searching for independent sampling locations over the main tributaries of the Parana River. Sampling sites in the Paraná River were always located upstream of the mouths of the main tributaries, to avoid sample dependency. From all of these six tributaries, only the Paranapanema River is impacted by damming.

For fish capture were used 20 m trawls (20 m x 1.5 m) and with standardized effort of 3 drag per site. Fish were anesthetized with benzocaine diluted and fixed in 10% formalin and later identified at species level. Phytoplankton were sampled directly at the subsurface (10–20 cm below the water–air interface) with bottles and fixed in situ with acetic Lugol solution (Bicudo and Menezes, 2006). Phytoplankton were identified using an inverted microscope, following the Utermohl (1958) method. Our sample design was approved by the Ethic Committee on Animal Use of the State University of Maringá (CEUA/UEM), according the rules issued by the National Council for Control of Animal Experimentation (CONCEA).

Physical and chemical variables were measured simultaneously with the fish and phytoplankton sampling and included a total of 16 environmental variables: water temperature (°C), depth (m), width (m), Secchi transparency (m), turbidity (NTU), dissolved oxygen (mgL^{-1}), pH, conductivity (μScm^{-1}), alkalinity ($mEqL^{-1}$), nitrate (μgL^{-1}), ammonium (μgL^{-1}), total nitrogen (μgL^{-1}), phosphate (μgL^{-1}), total phosphorus (μgL^{-1}), organic suspension material (mgL^{-1}) and inorganic suspension material (mgL^{-1}). For a detailed description of the analytical protocol processed for each environmental variable, please see Santana et al. (2017).

3.2.3 Predictor variables

Environmental matrix was composed of the standardized environmental variables described a bove. We checked the multicollinearity among environmental variables using variance inflation factors (VIF) and removed variables that were strongly correlated with other variables (VIF > 10) before statistical analyses (Oksanen et al., 2018). Spatial and temporal variables were derived from asymmetric eigenvector maps (AEM) (Blanchet, Legendre & Borcard 2008), in which the eigenvectors are proxies for spatial dispersal (Blanchet et al., 2011) and temporal processes (Legendre and Gauthier, 2014). For spatial AEM, first we constructed a site-by-edge binary matrix, considering a set of sites coordinates and the directional flow of main river. As the present study area comprises a large number of islands (Fig. 1), which can considerably increase the watercourse distance between sampling sites, we assigned weights to the links between sites, weighting the connectivity by the watercourse distances (Dray et al., 2006). This procedure allows the detection of patterns that can be disregarded using only geographical coordinates (Dray et al., 2006). For temporal AEM, we started from the eight sampling dates created a new matrix with seven eigenvectors that represent forms of directional stochastic process, including patterns at fine and broad temporal scales (Legendre and Gauthier, 2014). For both spatial and temporal AEMs, we decided to use the whole set of AEM eigenvectors in the forward selection procedure, because we were expecting that in addition to eigenvectors with positive Moran's I autocorrelation coefficients, negative autocorrelation could also be important in this study (see Supplementary Material Fig. S2-S3 for details of the selected spatial and temporal AEMs, which show positive and negative correlation between them). Negative autocorrelation for spatial eigenvectors can be important when neighboring sites have different composition (Blanchet *et al.* 2008). As our samplings include sites in tributaries flowing into the main river and sites upstream geographically very close (less than 1 Km in some cases), negative eigenvectors could be important in this study. In the case of temporal eigenvectors, the negative correlation model is interesting because it may show an important alternation in community structure between seasons (Legendre and Gauthier, 2014). Finally, our fourth predictor variable was composed of a dummy variable, differentiating the sampled sites in the channel of the main river from those in the tributaries.

3.2.4 Data analysis

All statistical analyses were performed in the R environment. For details about the the R packages and the respective R functions, see Fig. 2.

We first calculated beta diversity components (site-by-site dissimilarity matrices) for fish and phytoplankton communities based on Jaccard dissimilarity coefficient using incidence data. We applied the approach independently proposed by Podani & Schmera (2011) and Carvalho, Cardoso & Gomes (2012), where total beta component (Btotal) is partitioned into the replacement (Brepl) and richness difference (Brich) components. Of the two main ways of beta diversity partitioning (Baselga 2010 vs Podani & Schmera 2011), we chose to use the latter approach because we were interested in all kinds of richness differences between sites and not only nestedness, which is a special case of richness difference (Legendre, 2014b). We also did this decision because the nestedness component based on local community datasets is typically very low (Alahuhta et al., 2017; Soininen et al., 2018). We thus generated three dissimilarity matrices for each biological group. Each of these three pairwise matrices for each biological group was used in distance-based redundancy analysis (db-RDA, Legendre & Anderson 1999). We applied a forward selection with two stopping rules to identify the final sets of environmental variables (Env), spatial variables (Spa), temporal variables (Temp) influencing the replacement component, richness difference and total beta diversity. Subsequently, to examine the relative contribution of pure and shared effects of Env, Spa, Temp and also type of river (dummy variable) to explain beta diversity variation, variance partitioning (Peres-Neto et al., 2006) was performed. Statistical significance of the four pure fractions was tested using ANOVA. We used the square-root transformation to account for negative eigenvalues in all db-RDA and variance partitioning analyses (Legendre, 2014b).

In order to investigate environmental and biological dissimilarity patters operating at small and broad scales, we produced RGB colour maps. We conducted the environmental analysis based on Euclidean distances on logarithmically-transformed (except pH) and standardized environmental variables. Then, we used principal component analysis (PCA) to ordinate the variation in environmental dissimilarity among the sites. For biological dataset, nonmetric multidimensional scaling (NMDS) were performed separately based on Btotal, Brepl and Brich site-by-site dissimilarity matrices for each biological group. Prior the PCA and NMDS analyses, we calculated the mean of each pairwise dissimilarity matrices among all sampling times. We assumed that dissimilarity patterns can vary over time, and mean results may hide some important finding. Thus, we also performed the same procedures separately for each sampling time and the results of these individual analysis can be found in Figs. S4-S6. RGB colour maps projects a two-dimensional matrix into a red-green-blue space, being such that similar colours represent low dissimilarity between sites. Then, we plotted the RGB dots on the original coordinates of sites and the results were plotted on the maps of the study area to facilitate visual inspections.

Finally, to assess the concordance between fish and phytoplankton beta diversity patterns, we used Procrustes rotation analyses on each beta diversity component (Btotal, Brepl and Brich), separately for each sampling time. This method is powerful in the detection of matrix associations (Peres-Neto and Jackson, 2001). To perform this analysis, we used the same biological ordinations (i.e. NMDS) described above. In the Procrustes analysis, axis scores from two ordinations (e.g. one for fish Btotal and another for phytoplankton Btotal at sampling time 1) were compared using a rotational-fit algorithm that minimizes the sum of squared residuals between the ordinations. The statistic value generated (m^2) reflects such residuals, such that low values indicate high association and higher values indicate low association. To facilitate comparisons between the ordinations in a meaningful way, "protest" function transform the Procrustes m^2 statistic to the r statistic according to the equation $r = \mathrm{sqrt}(1-m^2)$ (Peres-Neto and Jackson, 2001). The significance of the congruence between any two ordinations was tested by a Monte Carlo procedure with 999 permutations.

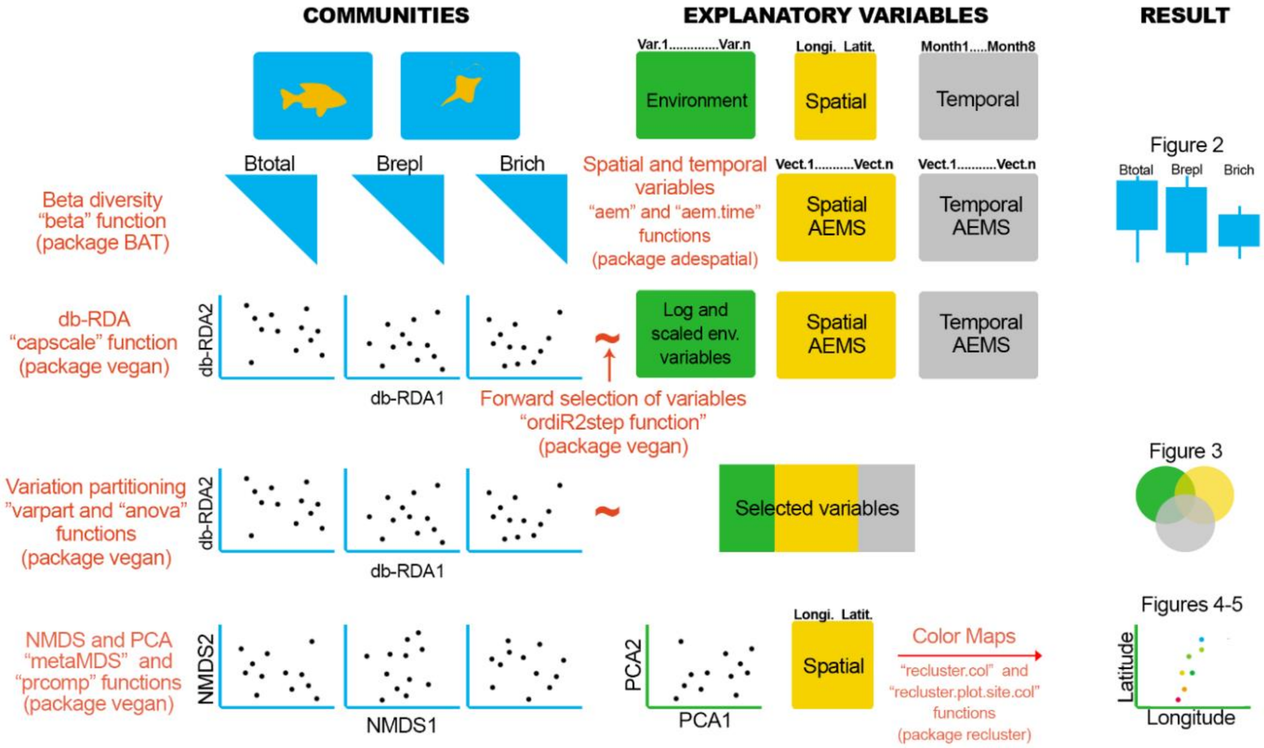


Fig. 2. A flow-chart of beta-diversity analyses. Names in red depicts the function and the respective R-package.

3.3 Results

3.3.1 Biodiversity features of the fish faunas and phytoplankton floras

A total of 63 fish and 118 phytoplankton taxa were recorded from the 120 data sites examined. The average, maximum and minimum species richness present at each sampling site (alpha diversity) were respectively 9, 19 and 1 for fish and 10, 27 and 2 for phytoplankton. For details about the species richness recorded for each biological group along the channel of the main river and its tributaries, see Table S1 and Data S1. We found that there were no clear differences between fish and phytoplankton beta diversity (Fig. 3). Both organism groups displayed high levels of Btotal and were driven mainly by Brepl, but Brich also had a high contribution to Btotal values. However, while Brepl was slightly higher for phytoplankton than for fish, the opposite was true for Brich (Fig. 3).

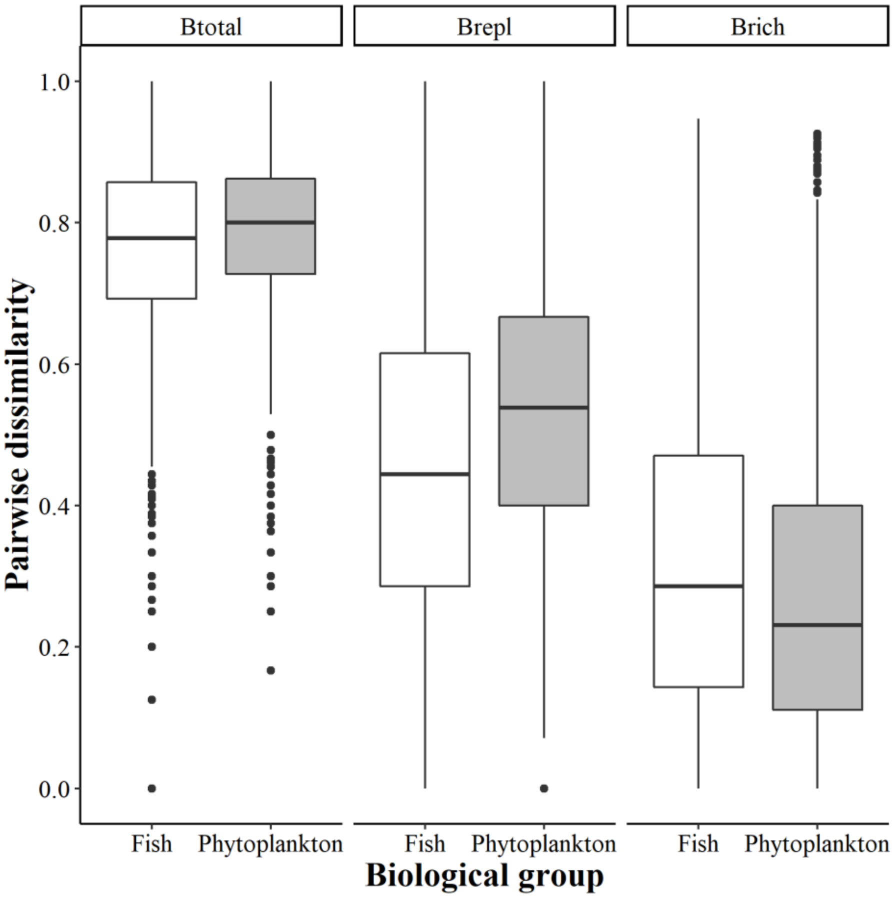


Fig. 3: Boxplots of pairwise dissimilaties for the total (Btotal), replacement (Brepl) and richness diference (Brich) of fish and phytoplankton communities. The central lines denote the median value, box denotes 25th and 75th percentiles, whiskers represent respectively the smallest and largest value within 1.5 times interquartile range below and above percentiles, and dots indicate outliers.

3.3.2 Contribution of environmental, spatial and temporal factors to beta diversity variation of fish and phytoplankton communities

For the environmental predictor variable group (Env), variables typically included by forward selection for fish were related to variation in turbidity, Secchi, conductivity, width and depth, whereas for phytoplankton, selected variables mostly denoted variation in nutrient concentrations (i.e. total phosphorous, nitrate, total nitrogen, and ammonium). Among spatial variables, both AEM eigenvectors with positive and negative spatial correlation were selected to compose the spatial predictor variable set (Spa) for fish and phytoplankton, indicating the importance of broad and fine scale spatial structuring. Similarly, the temporal predictor (Temp) included AEM which model positive and negative temporal correlation. For details about selected variables in the forward selection and the total adjusted R^2 values of each component, see Tables S2-S3.

Regarding the factors shaping fish and phytoplankton beta diversity, all explanatory variables explained, respectively, a total of 16.5% and 8.4% for Btotal, 22% and 10.1% for

Brepl and 10% and 12.4% for Brich (Fig. 4). For fish (Fig. 4a, c, e), Spa substantially explained the variation for all components of beta diversity. The shared fraction between Env and Spa was the second most important factor for Btotal and Brepl. River type was also important for Btotal and Brepl, but it was not statistically significant for Brich. Env explained part of Brepl and Brich, but had less importance for Btotal. Although usually less important, Temp also accounted for statistically significant fractions of variation in all fish beta diversity components. For phytoplankton (Fig. 4b, d, f), Temp was the main factor to explain the variation of Btotal and Brepl. Both Env and Spa increased in importance from Btotal and Brepl to Brich, being that the second one was the factor that most explained phytoplankton species richness differences. River type did not significantly influence any phytoplankton beta diversity component.

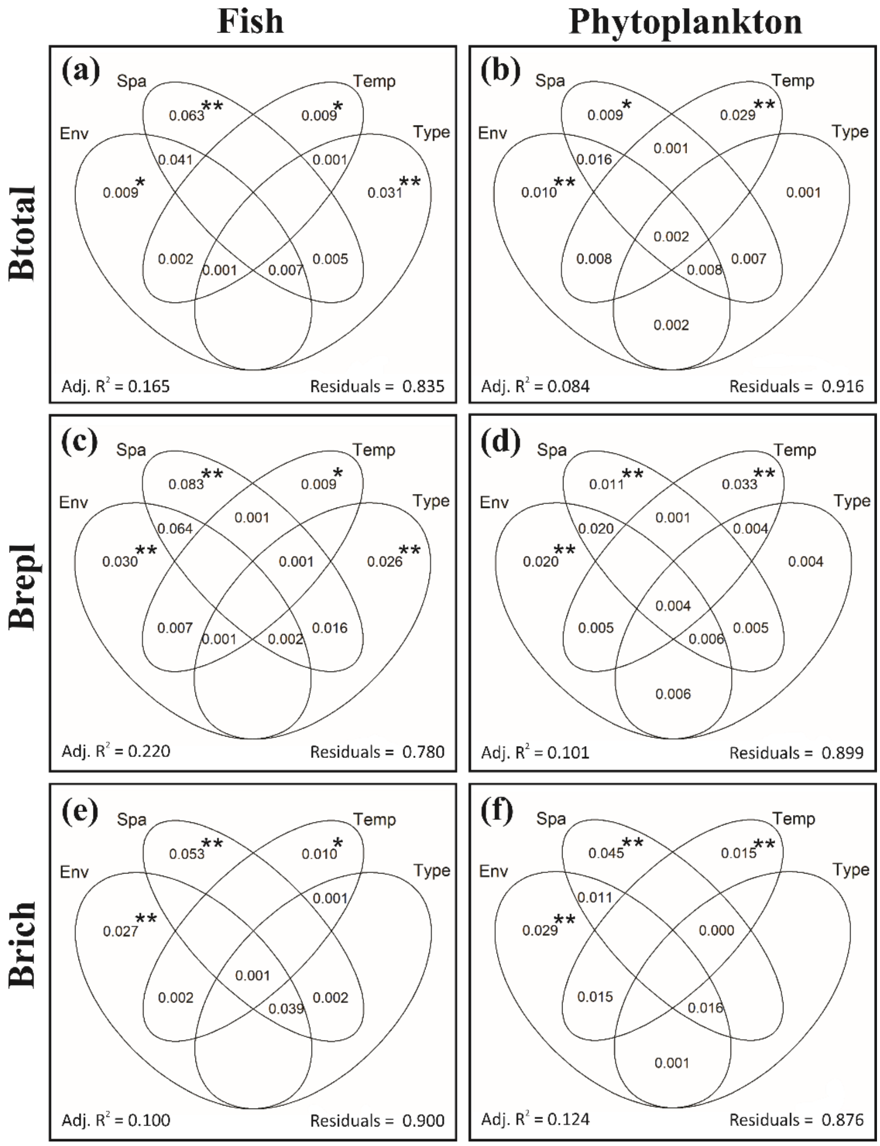


Fig. 4: Variation partitioning-based Venn diagrams showing the relative contribution of environmental variables (Env), spatial AEM eigenvectors (Spa), temporal AEM eigenvectors (Temp) and dummy variable separating the group of sites sampled in the main river of their respective tributaries (Type) to

fish (a, c, e) and phytoplankton (b, d, f) beta diversity variation. For acronyms see caption of Fig. 2. Values represent the adjusted R^2-values. Negative fraction values are not presented. Two asterisks represent significant results $p<0.01$; one asterisk $p<0.05$.

3.3.3 Spatial patterns of the environmental and biological dissimilarity variation

The PCA-based maps on Euclidean distances on environmental variables showed a marked distinction in the environmental conditions between the Paraná River and its tributaries (Figs. 5, S4). These differences reflected strong gradients in turbidity, water transparency, conductivity and nutrient concentration forms (Table. S1). In general, tributaries showed higher nutrient concentration and turbidity than the main dammed river, while the opposite was true for Secchi transparence and conductivity (Table S1). We also observed an increase in turbidity and nutrient concentrations with the increase in the distance from Porto Primavera reservoir (Table S1), which contributed to the highest environmental dissimilarity found for the first two upstream in comparison with other main river localities (Fig. 5). The only exception was recorded for the first tributary (Paranapanema River, T1), the only dammed tributary in the study area. In this way, its environmental conditions were more similar to the stretches upstream of the main river than the other tributaries studied.

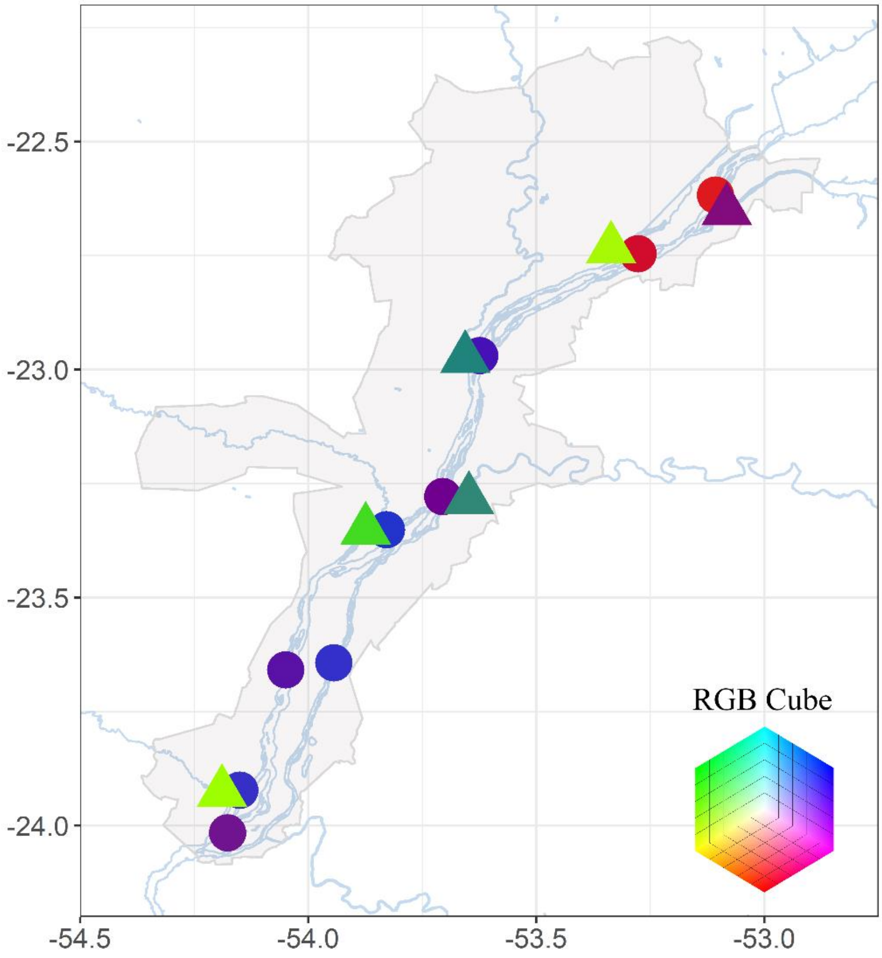


Fig. 5: RGB colour maps based on principal component analysis on the environmental variables along the longitudinal gradient of the last non-dammed stretch of the Paraná River. The RGB cube shows the distances between colours, where the higher distance represents the higher dissimilarity. Triangle = tributaries; circles = Paraná River.

The NMDS-based maps of Btotal and its Brepl and Brich components showed clear differences among them, and also between fish and phytoplankton patterns (Fig. 6). In general, the Btotal and Brepl components showed lower variation at small scales and an increase in dissimilarity along the longitudinal gradient of the river for fish, while some striking differences for these beta diversity components occurred even at very small scales for phytoplankton (e.g. the lateral gradient among the dammed main river and the closest tributaries) (Fig. 6). For the Brich component, both biological groups showed more pronounced differences at small scales, whereas no clear longitudinal gradients were observed at broad scale along the river course (Fig. 6).

The individual results for each sampling time for environmental and biological dissimilarities followed the same general trends, with some rare exceptions (Figs. S4-S6).

3.3.4 Concordance between actively and passively dispersing biological groups

The results from Procrustes analysis corroborated the differences found in the visual inspections of fish and phytoplankton dissimilarity patterns, showing a low and non-significant concordance between these biological groups for Btotal and its Brepl and Brich components at all sampling times (Table 1).

Table 1. Procrustes tests showing the concordance between fish and phytoplankton beta diversity patterns in each sampled time. Btotal = total beta diversity, Brepl= replacement, Brich= richness-difference.

Matrices compared	**Btotal**		**Brepl**		**Brich**	
	r	*P*	*r*	*P*	*r*	*P*
Fish and Phytoplankton						
Time 1	0.46	0.102	0.46	0.071	0.12	0.937
Time 2	0.25	0.654	0.42	0.167	0.16	0.879
Time 3	0.31	0.459	0.26	0.686	0.23	0.612
Time 4	0.44	0.132	0.22	0.806	0.17	0.822
Time 5	0.41	0.164	0.19	0.859	0.25	0.570
Time 6	0.32	0.420	0.30	0.492	0.28	0.519
Time 7	0.42	0.087	0.26	0.694	0.32	0.310
Time 8	0.29	0.564	0.33	0.418	0.27	0.475

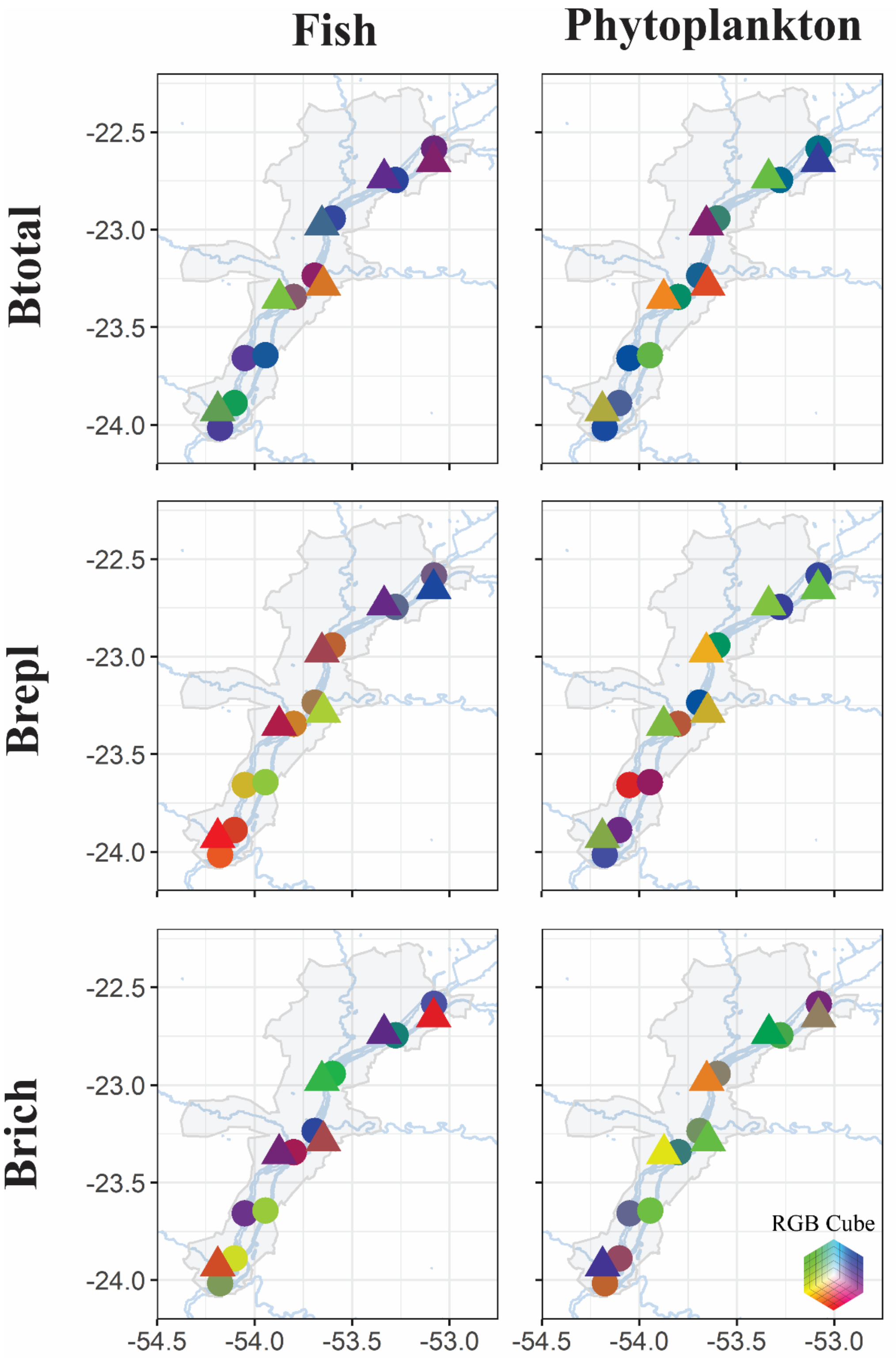


Fig. 6: RGB color maps based on non-metric multidimensional scaling for Btotal (first row), Brepl (second row) and Brich (third row) components along the longitudinal gradient of the last non-dammed stretch of the Paraná River. First column: fish. Second column: phytoplankton. The RGB cube shows the distances between colours, where the higher distance represents the higher dissimilarity.

3.4 Discussion

3.4.1 Patterns and dispersal mechanisms of fish communities

We predicted that the actively dispersing fish would be more strongly related to the environmental gradients than to spatial location across the study area. However, our results showed that directional spatial factors (AEM) affected all beta diversity components of fish. Indeed, river ecosystems are the prime example of environments where unidirectional flow influences the dispersal of species (Blanchet et al., 2011, 2008). However, in these systems, due to high connectivity between river networks, environmental factors are often more important than spatial location in determining fish distribution patterns (Erős et al., 2012, 2017; Heino et al., 2017). Some aspects should be highlighted by this relatively high importance of spatial factors. First, the spatial extent of our study area, although it does not contain any natural barriers that may prevent dispersal among localities, the longitudinal gradient of 230 km along the main river cannot be considered a local scale. In addition, the fish community was composed predominantly of small-sized species and the fact that these fishes move only short distances (Giam and Olden, 2018), dispersal limitation may drive the variation in fish beta diversity to some extent in the river longitudinal gradient. Although migratory fish usually travel long distances upstream or downstream and are thought to show little dispersal limitation (Padial et al., 2014), we only recorded the occurrence of six fish species that conduct long migrations in this study (*Megaleporinus piavussu* (Britski, Birindelli and Garavello, 2012), *Prochilodus lineatus* (Valenciennes, 1837), *Hemisorubim platyrhynchos* (Valenciennes, 1840), *Pimelodus maculatus* Lacepède, 1803, *Pimelodus mysteriosus* Azpelicueta, 1998 and *Sorubim lima* (Bloch and Schneider, 1801)).

Because spatial AEMs showing positive and negative autocorrelation were important, our findings point to a complex ecological phenomenon regarding the mechanisms influencing fish communities. In fact, a significant effect of pure spatial factors is frequently misunderstood, as it may be indicative of broad-scale dispersal limitation as well as small-scale dispersal surplus (Cottenie, 2005). In our study design, the lateral gradient among the dammed main river and the closest tributaries were marked by considerable variability in the environmental conditions between them and, in addition, they were located extremely close to each other (1-5 km). At such very small distances, the possible effects of dispersal limitation on beta diversity should be minor (Heino et al., 2013). The RGB colour maps showed that despite the profound environmental differences, pairwise dissimilarities of fish communities were low in the lateral gradient among the main river and closest tributaries, especially for Btotal and Brepl, probably due to high dispersal rates and frequent species exchange between these sites. Thus, dispersal surplus may have allowed species more adapted to the environmental conditions of the tributaries to persist in the less suitable dammed river and vice versa. This could have happened through source-sink dynamics, resulting in a significant spatial effect on fish communities (Heino et al., 2015b). The opposite pattern observed for the Brich component on a small scale (a high dissimilarity between neighboring sites) may also be interpreted as dispersal surplus, as a consequence of the dispersal of taxa from a highly populated source habitat to a less suitable sink habitat. In this case, the dissimilarity observed among these sites is a consequence of species richness difference among them. Nevertheless, this suggestion is speculative, and more specific studies are needed to assess the role of dispersal surplus on the beta diversity of riverine fish.

The directional spatial factors (AEM) not only uniquely explained the largest fraction of fish beta diversity variation, but also contributed substantially to shared explained fractions with environmental factors for the Btotal and Brepl components. This may reflect the fact that environmental variables were spatially structured (Cottenie, 2005). Thus, the use of spatial eigenfunction-based variables may have led to underestimation of the pure environmental influence on community structure (Gilbert and Bennett, 2010), which imply that the fish community's response to environmental variations along the last non-dammed stretch of the Paraná River cannot be discarded. The environmental variables were more strongly related to Brepl than Brich, and the main environmental variables responsible for such changes were turbidity or Secchi transparency, depth, and conductivity, which commonly explain variation in fish community structure (Rodríguez and Lewis, 1997; Santos et al., 2017). Specifically, Granzotti et al. (2018) showed that changes in water transparency, caused by impoundment, directly or indirectly affected fish community structure in the dammed Paraná River, but not in the non-dammed Ivinhema River.

Variations in Btotal and Brepl that were driven by local environmental conditions are particularly interesting, since they reflect tributary-induced environmental changes along the longitudinal gradient of the dammed river. These changes, in turn, can positively or negatively influence individual fish species (Rosso et al., 2010). Negative effects of the upstream reservoir are expected for fish species that use sensory organs other than visual detection to search and capture food in turbid waters or to perceive the presence of potential predators (Rodríguez and Lewis, 1997; Santos et al., 2018). The high water transparency caused by dam construction may also have positive influence on the occurrence of some alien piscivorous fish, which are often restricted to low-turbidity water stretches, as a result of their increased predation efficiency and decreased biotic resistance under these environmental conditions (Santos et al., 2018). We found some evidence supporting this reasoning. For instance, *Cichla kelberi* (Kullander & Ferreira, 2006), an invasive species, typically a diurnal, voracious and visual predator and responsible for fish fauna destruction in Paraná River basin (Pelicice and Agostinho, 2009), occurred only in the upstream stretch of the Paraná River, with only one occurrence of this species in the tributaries. Thus, since fish can actively disperse in the river network, allowing species to track more suitable environmental conditions (Erős *et al.*, 2012), changes caused by dams can act as strong environmental filters (Santos et al., 2017). These filters may select the sets of species that are better adapted to particular environmental conditions. This may also explain why part of the changes in the fish species composition was related to the type of river (main channel vs. tributaries).

Temporal factors had consistently less influence than the other predictors on the variation of Btotal (and their respective Brepl and Brich components) of fish communities. This result is rather unexpected, since in floodplain systems, temporal dynamics, characterized by alternating floods and droughts, are generally responsible for changes in fish communities (Padial et al., 2014). The lack of a clear flood period during this study may be linked to these findings. For instance, Fernandes et al. (2014) detected significant changes in the structure of fish communities, where species dispersal were limited at the beginning of the flooding, whereas this mechanism was not important at the end of the flood period. This is because connectivity is essentially dictated by the hydrological regime, with floods decreasing the environmental heterogeneity and favoring among-sites dispersal of species (Thomaz et al., 2007). Furthermore, the absence of floods prevents the occurrence of environmental cues used by some fish species to trigger gonad maturation, migration and spawning (Agostinho et al., 2004). The lack of floods may also have contributed to weakening the relationship between fish beta diversity and temporal dynamics related with reproductive strategies (Gutiérrez et al., 2018).

3.4.2 Patterns and dispersal mechanisms of phytoplankton communities

For phytoplankton beta diversity, we expected that these passive dispersers would be more strongly related to the spatial factors than environmental conditions. This is because both lateral connectivity and unidirectional flow through the Paraná River could favor downstream dispersal of species derived from tributaries and the upstream reservoir (Bortolini et al., 2017; Bovo-Scomparin et al., 2013). Our analysis showed that, although all beta diversity components were significant, only Brich was mostly driven by these processes. Dissimilarity in composition owing to Brich were high in the longitudinal gradient and were explained mainly by directional spatial processes, which could be related to the directional passive dispersal of species from tributaries and upstream sites (Dong et al., 2016; Liu et al., 2013). As far as we know, this is the first study that assessed the influence of spatial directional processes on different beta diversity components for phytoplankton. Therefore, more studies are necessary to evaluate if these processes are indeed more related to the variations of Brich than Brepl. In addition, despite the weak spatial influence shaping Btotal and Brepl, there is some field evidence to support that the spatial mechanisms driving these beta diversity components is different from those for fish. Dispersal limitation imposed by river networks may be evident at very small spatial extents for passive dispersers, owing to the restricted upstream movements (Göthe et al., 2013b). Our findings demonstrated that the greatest variations of Btotal and Brepl for phytoplankton occurred between the tributaries and the nearest upstream point in the main river. Thus, because phytoplankton communities of these nearby sites are not connected via water flow, we suggest that a portion of small-scale dissimilarity between the tributaries and the main river may be related to dispersal limitation rather than dispersal surplus.

Our results showed that local environmental variables had little influence on Btotal and its Brepl and Brich components of phytoplankton communities. Following our expectation, this suggests that continuous downstream passive dispersal through water flow limited the ability of phytoplankton to effectively track environmental variation along the main river. Although we cannot rule out the possibility that unmeasured ecological variables are influential (Peres-Neto and Legendre, 2010), such as grazing by both zooplankton (Verreydt et al., 2012) and benthic invertebrates (Vilmi et al., 2017), this was probably not the case in our study for three reasons.

First, previous studies have shown that the selected environmental variables, such as phosphorus and nitrogen forms, as well as water transparence and turbidity, were the main drivers influencing phytoplankton communities (Gillett et al., 2016; Jamoneau et al., 2018; Qu et al., 2018). Indeed, nutrient and light availability are considered primary elements for phytoplankton development (Reynolds, 2002). In addition, although light does not constrain phytoplankton development in sites associated with the Paraná River, low nutrient concentrations, especially phosphorus forms, might negatively affect phytoplankton diversity (Bovo-Scomparin et al., 2013). Rodrigues et al. (2015) suggested that site-by-site species richness variation of phytoplankton could be used as an indicator of environmental changes caused by the upstream reservoir in the Paraná River, which may explain the slight increase in the influence of environmental variables on the Brich component. Second, the relatively low total proportion of explained variation has been a typical finding in studies of phytoplankton (e.g. Nabout *et al.*, 2009), especially in a long-term dataset (Thomas et al., 2018), which suggests that the community structure of these small passive dispersers shows low predictability. Third, in systems showing high environmental harshness, neither species sorting nor dispersal mechanisms may shape aquatic communities (Datry et al., 2016). Rather, community structure may display a high degree of stochasticity caused by random colonization and extinction events (Hubbell, 2001).

This is likely to be the case of phytoplankton inhabiting lotic systems, where the recurrent instability of the water column, continuous downstream flow and high turbulence may impose limits on their colonization, establishment and development (Bovo-Scomparin et al., 2013; Jati et al., 2017). This may, in turn, lead to unexpected absences at sites that are otherwise environmentally suitable, consequently weakening the action of environmental filtering (Heino et al., 2015a). It is interesting to highlight that, in the same study area, Bortolini et al. (2017) found that phytoplankton community structure was strongly related with the environmental gradients. However, their study also included lentic environments, such as lakes adjacent to rivers, which may explain these contrasting findings (Qu et al., 2018). Due to the higher stability of lakes, species or propagules, once dispersed, may have time to colonize and develop under suitable conditions, increasing the match of species with local environmental conditions (Van der Gucht et al., 2007). Moreover, in studies strictly focusing on river networks, the influence of local environmental conditions may also be high, but generally at much broader spatial extents (Göthe et al., 2013a; Huszar et al., 2015; Jamoneau et al., 2018). Increasing spatial extent generally intensifies environmental filtering through increasing environmental gradient length, especially if this mechanism is not constrained by dispersal limitation, thereby allowing species composition to reflect the differences in environmental conditions among regions, basins or localities (Heino et al., 2017).

According our findings, phytoplankton beta diversity can vary temporally, especially the Btotal and Brepl components, which were mainly driven by this factor in this study. It is difficult to decipher how different mechanisms within the same region change over time and how this affects beta diversity (Langenheder et al., 2012). In dynamic systems such as rivers, temporal variability in environmental conditions is high and may result in high beta diversity. In the Paraná River floodplain system, temporal variation in phytoplankton community structure is thought to be related to the temporal dynamics of water temperature, turbidity and the concentrations of nitrogen and phosphorus forms (Bortolini et al., 2016b; Rodrigues et al., 2015). However, we found little support for this reasoning, as evidenced by the low contribution of the shared fraction between environmental and temporal factors, indicating that the measured environmental variables are not temporally structured and exert little influence on phytoplankton beta diversity. Therefore, other factors such as biological interactions or stochasticity in dispersal, which vary over time (Heino et al., 2015b), may explain the temporal variation of phytoplankton communities. For instance, Wojciechowski et al. (2017) showed high temporal variation in phytoplankton beta diversity patterns across subtropical reservoirs. Considering that part of the species pool of dammed rivers derives from the daily dispersal of propagules from upstream reservoirs (Bortolini et al., 2017; Gillett et al., 2016), temporal changes in phytoplankton composition in the reservoir may have influenced the temporal variation of phytoplankton beta diversity in the river downstream.

3.4.3 Implications for conservation and management

We found substantial differences in the main factors driving beta diversity of fish and phytoplankton communities. This finding suggests that the characteristics of each biological group, such as dispersal mode, probably influenced beta diversity patterns in different ways, which was reflected in the weak congruence observed between these two biological groups. Thus, our findings supported previous studies indicating that freshwater biological groups cannot be reliable surrogates for each other (Heino, 2010; Morais et al., 2018; Vilmi et al., 2016), and more than one biological group is recommended in the bioassessments of human disturbance and natural environmental variability of ecosystems.

It is noteworthy that homogenization of river dynamics by dams is a global trend (Poff et al., 2007). In the last decades, several studies have illustrated the biological consequences of long-term effects of flow regulation by dams in the Paraná River, including community structural and functional homogenization (Braghin et al., 2018; Granzotti et al., 2018; Oliveira et al., 2018). Therefore, the high beta diversity found for both fish and phytoplankton communities demonstrates the crucial role of tributary-induced spatial and temporal heterogeneity in mitigating the effects of anthropogenic activity on the ecosystem dynamics. We thus strongly reinforce the necessity of keeping such tributaries free of dams, in order to avoid biotic homogenization processes and the consequent loss of aquatic biodiversity (Gámez-Virués et al., 2015). Moreover, our results expand the biological effects of upstream reservoir to a new beta diversity approach, showing that not only substitution of species in one site by different species (Brepl), but also loss or gain of species between sites (Brich) may contribute to total beta diversity (Podani & Schmera, 2011). This information is extremely valuable in guiding conservation and management.

3.5 Conclusions

In general, directional dispersal-related processes played a major role in shaping total beta diversity and its replacement (Brepl) and richness difference (Brich) components for fish, while only Brich was driven by these factors for phytoplankton. Our findings suggest that more than one dispersal-related mechanism may occur at the same time, but at different spatial scales and probably in the opposite direction for the two biological groups analyzed. Environmental filtering and type of river were more important for Btotal and Brepl among actively dispersing fish than among passively dispersing phytoplankton, reflecting the inadequacy of passively-dispersing organisms to track suitable environmental conditions. In contrast, temporal factors explained considerable parts of Btotal and Brepl of phytoplankton communities, while temporal factors were negligible for fish.

In conclusion, in agreement with our hypothesis, this study ratifies the idea that even within the same study area, biodiversity patterns exhibited by single biological groups do not necessarily match those of other groups that show wide variation in biological features, such as body size and dispersal mode. In addition, by demonstrating the conditions under which tributaries reduce the cumulative impacts of multiple dams on river-floodplain systems (Winemiller et al., 2016), our findings have improved understanding of tributary-induced heterogeneity and highlight the importance of dam-free stretches of rivers for preserving the integrity of dammed river basins.

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4 PREDICTING MORPHOLOGICAL AND MOLECULAR STRUCTURE OF PROTIST CILIATES COMMUNITY ACROSS FLOODPLAIN SYSTEMS: SEPARATING THE ROLES OF ENVIRONMENTAL FILTERS AND SPATIAL PROCESSES

ABSTRACT

Hitherto, one of the main standing paradigms is to understand whether the empirical biogeographic patterns of macro-organisms also apply to micro-organisms. Here, we used morphological data from live organisms and molecular data from HTS to investigate the importance of spatial factors and environmental variables on structuring ciliate communities from floodplain-associated lakes. Our main goal is to verify which approach better explain the role of environmental and spatial predictors on the ciliate structuration in the four Brazil’s greatest floodplains, as well as clarify their biogeography. Planktonic waters were gathered from 33 lakes associated with four different river-floodplain systems in Brazil. We analyzed ciliates *in vivo* and also sequenced the DNA using a metabarcoding approach with general eukaryotic primers. We found striking evidences about the underlying mechanisms of community assembly, whether considering morphological or molecular approaches to identify ciliates from floodplain-associated lakes. Our results showed that the diversity of OTUs was much higher than that of morphospecies. Despite the method of identification, we found a consistent spatial assembly pattern of ciliates communities across the four floodplains systems. We found that environmental filters had a greater influence on the morphological than on the molecular site-by-site dissimilarities. Meanwhile, biogeographic factors and the distance among sites limit the distribution of morphological-based composition, resulting in significantly different species compositions in each of the floodplain-associated lakes analyzed. This finding suggests that ecological researches and biomonitoring activities needs to find a counter-balance, as each approach provides unique insights.

Keywords*:* Microbial biogeography. OTUs. DNA metabarcoding. Dispersal limitation. Metacommunity.

4.1 Introduction

One of the main questions in ecology is the distribution of species. Since the eighteenth century, many studies have been trying to understand how organisms are distributed in space and time (Isbell et al., 2018), which addressed the biogeographic patterns to factors such as speciation, extinction and dispersal events (Heino et al., 2017). Because the core of theoretical ecology is centered on the biology of plants and animals, applying these concepts in microbial communities is currently a major challenge for microbial ecologists. The main gaps between traditional and microbial approaches rely on obvious differences in scale and physiologies between macro- and micro-organisms (Martiny et al., 2006a), as well as among types of microorganisms (van der Gast, 2015).

The viewpoint that micro-organisms would have so high dispersal rates that they would not be restricted by geographic barriers supports the traditional hypothesis proposed by Baas-Becking (1934) that "Everything is everywhere, but the environment selects". His main argument presumes that local environmental conditions and biotic interactions, such as competition and predation, would be the main responsible for determining the local composition of species. However, micro-organisms are small, numerous, and have high population densities (Fenchel & Finlay, 2004a). In addition to their ability in producing cysts, this combination makes them less prone to local extinction and increase their potential for dispersal events (Astorga et al., 2012). In the last two decades, a second biogeography perspective even suggests that some microbial taxa may be endemic (Green & Bohannan, 2006; Martiny et al., 2006a; van der Gast, 2015; Tessler et al., 2017; Ribeiro et al., 2018). Hitherto, one of the main standing paradigms is to understand whether the empirical biogeographic patterns of macro-organisms also apply to micro-organisms (Shoemaker et al., 2017).

Microbial ecologists have to deal with many adaptations in their studies in order to test ecological theory in such a small scale (Prosser et al., 2007). Traditional methods applied in ecological studies on microbial eukaryotes (i.e., protists) always face some problematic issues. For instance, morphological analyses are frequently limited because some specimens are injured during fixation, the presence of cryptic and polymorphic species puzzle their diversity, and there are only a few specialized professionals for identification (Sáez & Lozano, 2005; Caron et al., 2012). There is also a bias toward identifying only the most abundant species thus ignoring most of the rare ones (Dunthorn et al., 2014; Logares et al., 2014; Troussellier et al., 2017). In addition, the first-generation sequencing technology (i.e. Sanger sequencing, Sanger, Nicklen & Coulson, 1977) is capable of sequencing only cultivable species, which limits its use for complex environmental samples (Shokralla et al., 2012). Moreover, DNA barcoding projects based on the Sanger sequencing have been extremely important for the development of enormous reference-libraries with amplicon sequences (Hajibabaei et al., 2011).

Fortunately, the advent of new methods for sequencing the environmental RNA or DNA from ribosomal small sub-unit (SSU), such as high-throughput sequencing technologies (HTS), has thrown a new era in microbial ecology (Porter & Hajibabaei, 2018). Different sequencing platforms have provided an extraordinary amount of molecular data on micro-organisms, with recent studies revealing an unexpectedly high biodiversity of protists at different environments (Grattepanche et al., 2014; de Vargas et al., 2015; Logares et al., 2015; Massana et al., 2015; Forster et al., 2016; Lentendu et al., 2018). Thus, the new potential of modern sequencing techniques overcame the limitations of traditional methods for an accurate estimation of the protist diversity, which now has a quite enhanced potential when compared with researches from 30–40 years ago.

The HTS toolkit is capable of generating hundreds of millions of amplicons, an optimal method for thorough assessment of the diversity of complex microbial communities (Mahé et al., 2015a; Lentendu et al., 2018). This novel strategy has also revealed thousands of rare species that could not be detected under microscopy or Sanger’s sequencing (Dunthorn et al., 2014; Logares et al., 2015). Therefore, HTS data is now fundamental for ecological studies on microbial organisms, especially those investigating biogeographic patterns (van der Gast, 2015). Additionally, micro-organisms may be easier to manipulate and control experimentally, providing a better alternative for testing ecological theories (Logue et al., 2011).

Recently, most HTS-based studies focused on bacterial, with little attention on protists (Pawlowski et al., 2016). Among protists, ciliates can be found almost everywhere on Earth (Foissner et al., 2008) and are considered as essential in microbial food webs because they feed on (cyano)bacteria, phytoplankton and other protists (Weisse, 2002; Meira et al., 2018), while being eaten by microcrustaceans (Adrian, 1999) and rotifers (Arndt, 1993). Moreover, particular traits of ciliates such as their high sensitivity to physical and chemical alterations and the variety of occupied niches make them good indicators of ecosystem health (Madoni & Braghiroli, 2007; Segovia et al., 2016). Therefore, many studies focusing on ciliates were recently published, as an acknowledgement of their relevance for the ecosystem functioning and stability (Stoeck et al., 2014). However, most studies investigated ciliates communities in marine (e.g. de Vargas *et al.*, 2015) and soil (e.g. Forster *et al.*, 2016) environments, whereas only a few have dived into assessing ecological aspects of the microbial eukaryotic communities in freshwater systems (Gran-Stadniczeñko et al., 2019), especially in Neotropical environments (Lentendu et al., 2019).

The river-floodplain systems stand among the most studied freshwater environments because of their high level of habitat heterogeneity and temporal dynamics (Junk et al., 1989). In these environments, the flood pulse is considered the main structuring factor of resident biological communities (Thomaz et al., 2007). The alternation between dry and flood seasons produce secondary mechanisms such as the connection and isolation of habitats, which determines community composition through a systematic tradeoff between environmental filtering and species interactions (Bozelli et al., 2015; Dias et al., 2016).

Here, we used morphological data from live organisms and molecular data from HTS to investigate the importance of spatial factors and environmental variables on structuring ciliate communities from floodplain-associated lakes. Our main goal is to verify which approach better explain the role of environmental and spatial predictors on the ciliate structuration in the four Brazil's greatest floodplains, as well as clarify their biogeography. In this way, we formulated the following hypotheses: **(i)** significant differences in species composition will be found between floodplains for both approaches; **(ii)** the dissimilarity in each floodplain will be greater for the morphological, compared to the molecular approach; **(iii)** the environment exercise greater influence in the structuration of the ciliate community based on the morphological data and, on the other hand, the community based on molecular data is more effect by broad-scale spatial processes.

4.2 Methods

4.2.1 Study area and sampling design

Our study was conducted using data on the four largest South American river-floodplain systems: Upper Paraná River (Paraná, Baía, and Ivinheima rivers), Pantanal (Miranda and Paraguai rivers), Araguaia, and Amazonia (Solimões and Amazon rivers) (Fig. 1). Sampling was conducted in 33 floodplain-associated lakes between August 2011 and May 2012 (Table S1). The four systems support their high biodiversity of organisms based on periodically flooding periods during the rainy season of the southern hemisphere (Junk et al., 1989).

The Upper Paraná River has a large anastomosed channel and a wide alluvial plain, reaching up to 20 km in width. It is extensively impounded, with more than 130 dams, which retain expressive amounts of nutrients and sediments, yielding a completely modified hydrology with oligotrophic waters in the main channel (Roberto et al., 2009). It varies in types of habitats, among them numerous secondary channels, lakes, and two main tributary rivers – Baía and Ivinheima.

The Pantanal biome is characterized by its very high biological productivity and consequently by a significant biodiversity, being one of the world’s largest wetlands (140,000 km^2 area). It is a heterogeneous ecosystem with at least 10 sub-regions with particular geomorphological and ecological aspects, which creates idiosyncrasies on the occurrence, duration, and intensity floods depending on the sub-region. The major flooding in the northernmost region coincides with the rainy season, but there is a time lapse (i.e., ~40 days) until the flood reaches the southern region through the main tributaries, streams and non-channelized flow paths (Junk et al., 2006).

Covering 377,000 km^2, the Araguaia River has one of the largest South American basins with an average flow of 6,430 m^3/s. The Middle Araguaia River is located in eastern Amazonia with a drainage area comprising 320,290 km^2 with 1,160 km in length (Lininger & Latrubesse, 2016). It is formed by a well-developed floodplain, with much of its area located in the ecoregion locally known as Cerrado (Brazilian savannah), a biodiversity hotspot (Myers et al., 2000).

The Amazon River is the world’s greatest river both in extension and water flow. Wetlands from the alluvial floodplain of the Amazon River and primary tributaries cover over 300,000 km^2 (Junk, 1997). The confluence of the Solimões and Negro rivers to form the Amazon River comprises the Brazilian Amazonia floodplain. The wetland habitats have high spatial heterogeneity, providing conditions for the establishment and development of several biological communities, which results in an enormous biodiversity. The water level can rise up to 10 m on average during floods. Usually, it begins in November and reaches its maximum level in July; the dry period starts in August when the water runs from the lakes to the rivers, with October as the driest month.

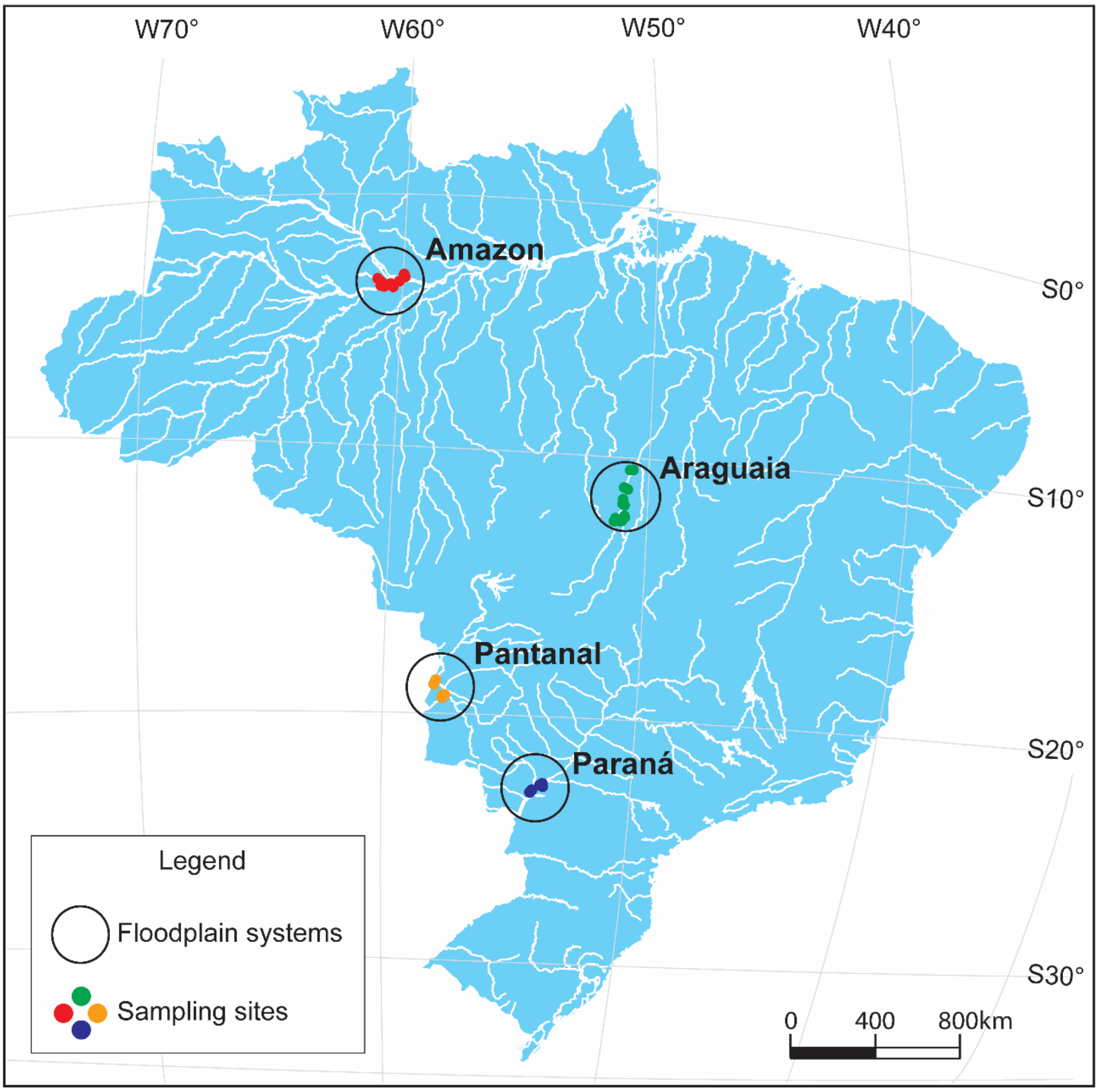

Fig. 1: Sampling sites in the four studied South American floodplains. See Table S1 for further details about lakes locations.

4.2.2 Environmental filtering

We considered key environmental variables that are known to shape the structure of ciliate communities, including both abiotic (physical and chemical) and biotic (food resources and potential predators) (Segovia et al., 2017). The following abiotic variables were measured at each lake using a handheld device (YSI 550A, Digimed DM-2) and a Secchi disk: dissolved: temperature, dissolved oxygen concentration, electrical conductivity, turbidity, pH, and transparency. Water samples were collected from the pelagic region (~ 20 cm below the water-air interface) for further quantification of nitrogen and phosphorous concentrations in the laboratory. Samples were conditioned in polyethylene flasks and stored at -20°C. Total nitrogen (μgL^{-1}) and phosphate (μgL^{-1}) concentrations were determined following Mackereth et al.

(1978). Further, nitrate (μgL^{-1}; Giné *et al.*, 1980), ammonia (μgL^{-1}; Koroleff, 1976), and total phosphorus (μgL^{-1}; Golterman, Clymno & Ohnstad, 1978) concentrations were also quantified.

Along with the abiotic variables and the ciliates samples (see next topic), we also collected water samples to quantify (cyano)bacteria, flagellates, zooplankton and phytoplankton. These groups were also included in our analyses as components of the environmental filter that shapes the community of ciliates in each environment (Weisse, 2002; Segovia et al., 2017; Meira et al., 2018). Water samples for the analyses of microbial communities (including bacteria, heterotrophic flagellates and phytoplankton) were taken at the subsurface (approximately 30 cm be- low the air-water interface) at the central, deepest region of each lake using polyethylene flasks. For zooplankton analyses, we filtered 600 L of water using a pump and a plankton net (68 μm).

Bacteria and heterotrophic flagellates were analysed from water samples treated with a fixative solution composed by alkaline Lugol's solution, borate buffered formalin and sodium thiosulfate (Sherr EB, 1993), filtered through black Nuclepore filters (0.2 and 0.8 μm, respectively) and stained with fluorochrome DAPI (4,6- diamidino-2-phenylindole; Porter & Feig, 1980). Quantification was done with an epifluorescence microscope at a magnification of ×1000 (Olympus BX51). Phytoplankton samples were preserved with acidified Lugol's solution and the analysis was performed according to Utermöhl (Utermöhl, 1958). Zooplankton community (rotifers, cladocerans and copepods were quantified and identified according to Lansac-Tôha et al. (2009), by counting at least three subsamples under an optical microscope at a magnification of×40–400 depending on the taxonomic group (Olympus CX41).

As predictor variables, we considered the density of bacteria (cels. mL^{-1}) and flagellates (cels. mL^{-1}). To summarize the multi-taxa composition of zooplankton and phytoplankton communities, we used the first two axes (PCoA1 and PCoA2) from a principal coordinates analysis (PCoA; Bray-Curtis distances) applied on each group, separately. These variables account for potential interactions among these biological groups and have been considered as fundamental for unraveling the role of environmental filters on from spatial processes (Cottenie, 2005; Brown et al., 2017). To reduce the dimensionality of the data and better visualize the variation of all abiotic and biotic predictor variables between the four floodplain systems, we performed a Principle Component Analysis (PCA), and the result is shown in Fig. S1.

4.2.3 Sampling and morphological identification of ciliates

We analyzed ciliates *in vivo* (Madoni, 1984) from a 100 mL concentrated subsample, filtered in a 10 µm net from 2L of water collected at the subsurface (~ 20 cm below the water-air interface) of the limnetic region of each lake. We analyzed ten 1-mL subsamples within 6 hours. Before taking subsamples, we homogenized samples to avoid biases in species richness and abundances. Ciliates were identified to the lowest taxonomic level (morphospecies), under optical microscopes (Olympus® CX-41) at a magnification of 100–400x, according to specialized literature (Foissner et al (Foissner et al., 1992, 1994, 1995, 1999; Foissner & Berger, 1996), Foissner et al (1993), Foissner et al (1994), Foissner et al (1995), Foissner and Berger (1996), and Foissner et al. (1999).

4.2.4 DNA extraction, and amplification

About 1.5 L of lake water were filtered through 13-mm diameter Nuclepore Polycarbonate membranes, with 0.8 µm pore size (Whatmann, Kent, UK), and stored at 20 °C. Filters were then placed in 20-mL eppendorfs, and the DNA was extracted using DNeasy Blood & Tissue kits (QIAGEN, Venlo, Netherlands). Extracted DNA was amplified with general eukaryotic primers that targeted the V3 hyper-variable region of the 18S-rRNA locus, following Nolte et al. (2010). Amplified products were then sequenced with Illumina MiSeq technology. The raw sequences were deposited at ENA's Sequence Read Archive and are publicly available under the BioProject (PRJEB26716).

4.2.5 Bioinformatics

Paired-sequences were merged using VSEARCH v2.3.2 (Rognes et al., 2016) with default parameters and converted into the 'fasta' format. Assembled paired-end sequences were filtered using Cutadapt v1.13 (Martin, 2011) and retained if they contained both primers (minimum overlap set to 2/3 of the primer length), a minimum length of 90 nucleotides, and had no ambiguous positions. Reads were replicated with VSEARCH and clustered using Swarm v2.1.9 (Mahé et al., 2015b), with parameter d = 1 and the fastidious option enabled. The most abundant amplicon in each OTU had chimeric sequences removed with VSEARCH. Taxonomic assignment followed VSEARCH's global pairwise alignments with the Protist Ribosomal Reference (PR2) database v203 (Guillou et al., 2012). Using ecoPCR v0.8.0 (Ficetola et al., 2010), the PR2 database was extracted for each specific sequence regions that were further amplified and sequenced to allow for comparisons using a global pairwise alignment. Amplicons were assigned to their best hit, or co-best hits, in which case the taxonomy was resolved using the least-common ancestor with an 80% consensus threshold

(Lentendu et al., 2019). We only considered OTUs assigned to Alveolata, a recognized successful lineage of ciliates (Foissner et al., 2008). For simplicity, the radius of each OTU was estimated by calculating the global pairwise distance between the Swarm seed amplicon and all amplicons members of that Swarm, using Sumatra v.1.0.20 (Mercier, C., Boyer, F., Bonin, A., & Coissac, 2013). Thus, the radius of each OTU was calculated from the sequence center (which is usually the most abundant amplicon) to the distance (in terms of percent similarity) of the least similar sequence.

4.2.6 Data analysis

4.2.6.1 Community composition within and across floodplains

To test for significant spatial changes in the composition of ciliates communities for both morphological and molecular data (hypothesis I), we performed a permutational multivariate analysis of variance (PERMANOVA, 9,999 permutations; Anderson et al., 2008) controlling the identity of each floodplain as a factor. Results detecting significant differences were followed by pairwise tests. PERMANOVAs were performed on Jaccard community dissimilarity data, using function "adonis" from *vegan* package (Oksanen et al., 2018), in the R Environment (R Core Team, 2019).

In order to estimate differences in dissimilarities within each floodplain (hypothesis II), we performed an analysis of homogeneity of multivariate dispersions (PERMDISP, Anderson, Ellingsen & McArdle, 2006). This test is based on the average dissimilarities from each sample to the centroid of its group, in a multivariate space built using principal coordinate analysis (PCoA; Anderson *et al.*, 2006). Thus, higher variations in community structure across sites (i.e., beta diversity) are depicted by greater dissimilarities to a group's centroid (Anderson et al., 2006). Four groups were considered, representing each individual floodplain (Amazonia, Araguaia, Pantanal, and Paraná). Ordinations were performed on dissimilarity matrices generated using the Jaccard index, calculated from site-by-species presence-absence data. Statistical significance between morphological and molecular data, and among group centroids for each floodplain, was assessed through analysis of variance (Two-Way ANOVA).

4.2.6.2 Community-environment relationships

To evaluate the role of the environment and the dispersal potential on the composition of ciliates communities (hypothesis III), we used variation partitioning with distance-based redundancy analysis (dbRDA; Legendre & Andersson, 1999) for morphological and molecular approaches, separately. As explanatory matrices, we used environmental data (E), and two different models considering different spatial extents. For the fine-scale spatial model (F), we used the method developed by Declerck et al. (2011), which is highly suitable for sampling designs where basins are disposed far from each other, as was our case. This approach is based on Moran's eigenvector maps (MEM), which are spatial analysis method derived from the Cartesian geographical coordinates of the lakes. MEMs eigenvectors were used as explanatory variables in the fine-scale spatial model. Using function 'create.MEM.model' from the R-package *adespatial* (Dray et al., 2018), we created a staggered matrix of spatial variables such that each block represented the spatial structure of lakes from the same floodplain, while lakes from other floodplains received zero. To construct the broad-scale spatial component (B), we used a dummy variable representing floodplain identity (among-floodplains), because MEMs perform poorly when there are large gaps among regions, such as those of the studied floodplains.

Variations in the composition of ciliates communities were decomposed into purely environmental (E│F+B), purely fine-scale spatial extent (F│E+B) and purely broad-scale spatial extent (B│E+F) components, as well as their shared effects. We estimated the proportion of explained variance of each component through adjusted coefficients of determination (adj. R^2; Peres-neto *et al.*, 2006). The significance of each pure component was achieved with 999 permutations (Peres-neto et al., 2006). dbRDA was built using function "capscale" and variation partitioning was run using the function "varpart" from the R-package *vegan* (Oksanen et al., 2018).

4.2.6.3 Selection of explanatory variables

To select the best set of local environmental features and fine- and broad-scale explanatory variables associated with the variations in ciliates communities, we used forward selection procedure with two stopping rules (Blanchet et al., 2008). We did this to prevent artificially inflated explanatory powers of our constrained ordination models (i.e., model overfitting). Forward selection assumes that there is evidence to suggest that all variables affect the community composition and proceeds only if the global model, which is tested at first, is significant. The first stopping rule entails the reduced model adjusted R^2 value exceeding that of the critical p value (at $\alpha = 0.05$), and the second is related to global model. The selection of explanatory variables was carried out using the function "ordiR2step" in the R-package *vegan* (Oksanen et al., 2018). Before statistical analyses, we checked the multicollinearity of environmental matrix, by computing the variance inflation factors (VIF), and removed variables which the variance of a regression coefficient is inflated in the presence of other explanatory variables (i.e. VIF > 5) (Borcard et al., 2018).

4.3 Results

4.3.1 Ciliates diversity and composition

We registered a total of 69 morphospecies and 338 OTUs of ciliates, considering the morphological and molecular approaches, respectively. For the morphological approach, Paraná (44) and Pantanal (38) showed greater species richness, compared to Amazonia (20) and Araguaia (18). The average alpha diversity was more homogeneous among floodplains, with the highest value recorded for the Pantanal (10) (Fig. 2). For the molecular approach, the difference in OTUs between the floodplains was less clear, with the highest value recorded in the Pantanal (292) and the lowest in the Amazonia (222). In terms of alpha diversity, the highest averages occurred in Araguaia (140) and Pantanal (136), while Amazonia (112) and Paraná (106) had the lowest number of lake-level OTUs (Fig. 2).

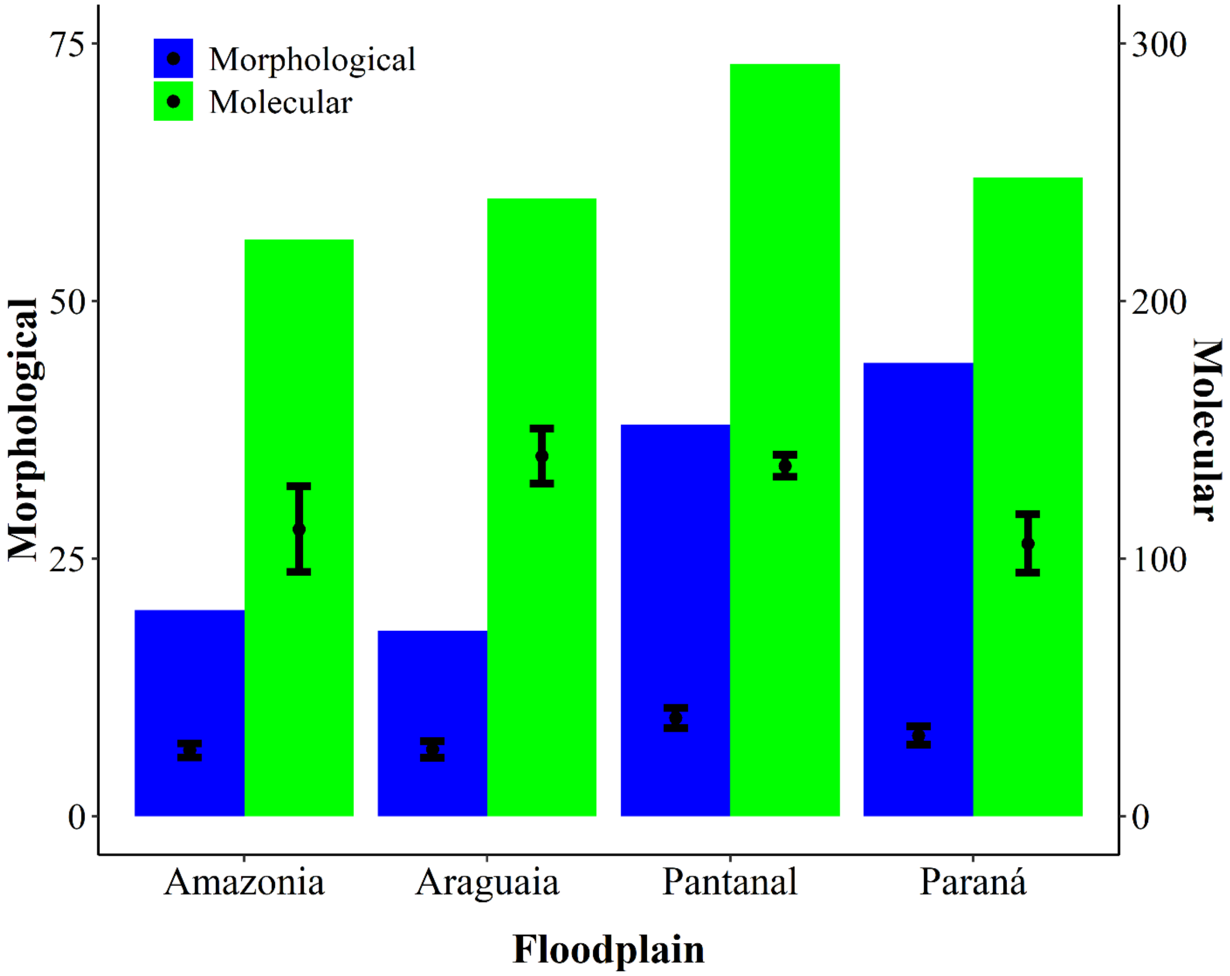

Fig. 2: Diversity of protist ciliates in each analyzed floodplain. Barplot represents total diversity in each floodplain and errorplots decipts the mean and standard error for each lake. Blue = Morphological approach; Green = molecular approach.

The PCoA ordination suggested a clear distinction of each floodplain centroid group, especially for the molecular approach (Fig. 3a,b). This pattern was evidenced by the PERMANOVAs (main and pair-wise tests), which revealed significant differences among all floodplains based on both morphological and molecular approaches (Table S2). The two-way ANOVA indicated that lakes were significantly more dissimilar under the morphological than under the molecular approach (Fig. 3c; Table S3). The ANOVA also revealed that the among-floodplain dissimilarities were significantly different only between the Paraná and Araguaia ecosystems (Fig. 3c; Table S3).

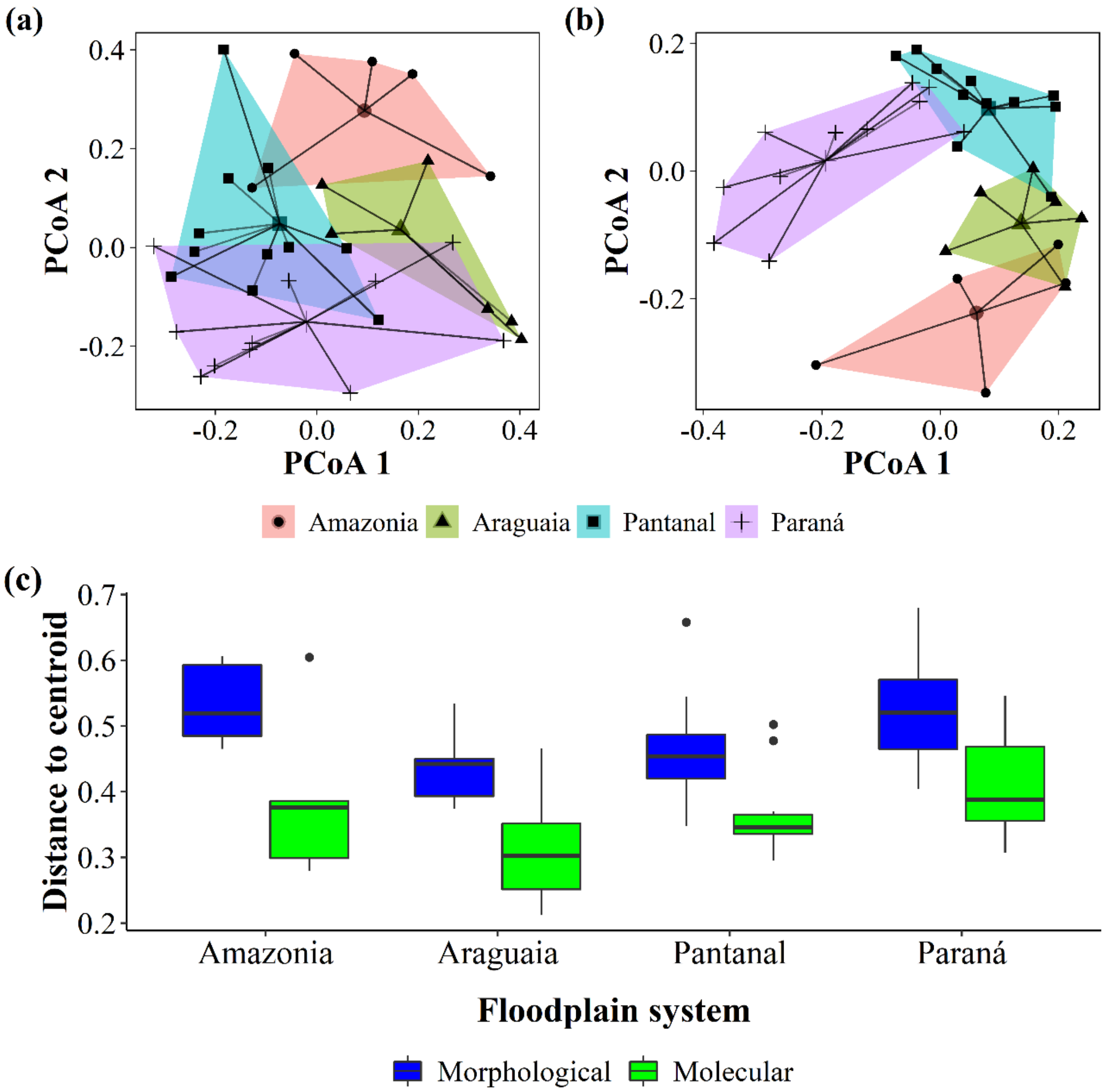

Fig. 3: Dissimilarities registered at each floodplain system. Principal coordinate plots derived from the morphological (a) and the molecular (b) data. Lines represent the distances between the sampling sites and the centroid of each group, as defined by the floodplain system. (c) Boxplots of distances to centroid group for morphological (blue) and molecular (green) approaches. The central lines denote the median value, box denotes 25th and 75th percentiles, whiskers represent respectively the smallest and largest value within 1.5 times interquartile range below and above percentiles, and dots indicate outliers.

4.3.2 Relative importance of environmental and spatial factors

Variation partitioning results revealed that the contribution of environmental and spatial factors differed in explaining community composition, whether considering morphological or molecular approaches (Fig. 4; Table 1). According to the explanatory power (adjusted R^2), the morphological-based taxonomic composition of the ciliates communities showed a stronger underlying role of the environment conditions [E] (17%) than that observed under the molecular-based approach (8%). Meanwhile, the broad-scale spatial component [B] was higher for molecular-based approach (20%) when compared to morphological-based communities (8%). In the same way, fine-scale spatial component [F] was mainly related to molecular (8%) than morphological (3%) approach. The shared components among all factors are given in Fig. 4. Besides, a great amount of variation remained unexplained for both approaches.

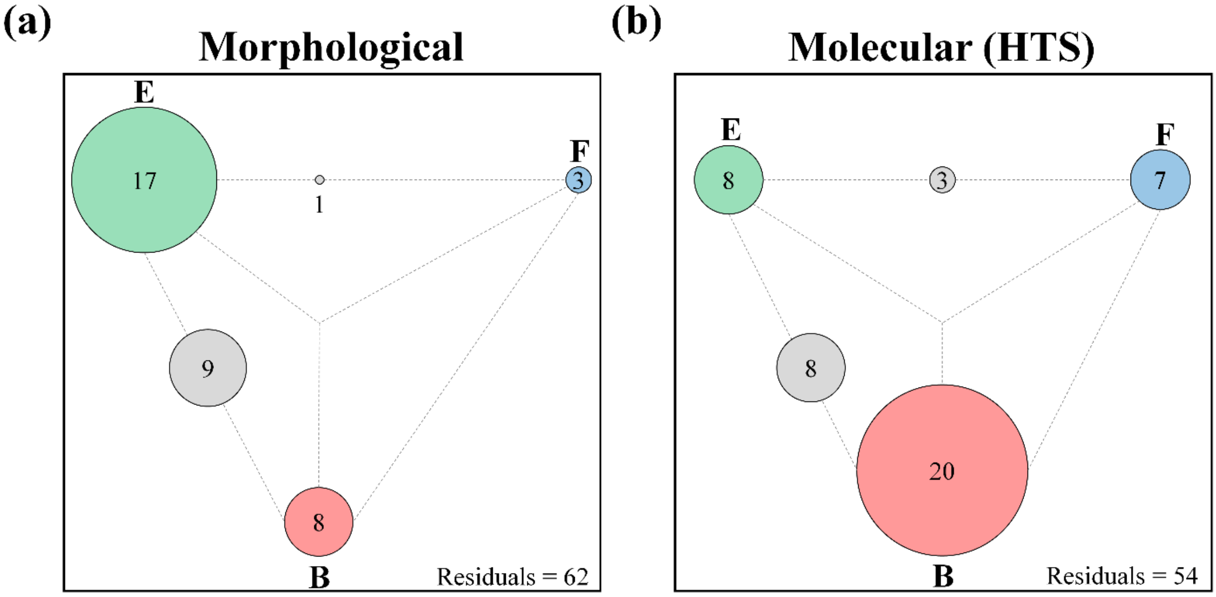

Fig. 4: Variation partitioning analysis of morphological and molecular ciliates communities explained (% adjusted R^2) by environmental component [E] (green), fine-scale spatial component [F] (blue), broad-scale spatial component [B] (red) and their shared components (grey). Circle size is proportional to the respective percentages of explained variation.

Those environmental variables selected as the best set to explain the compositional patterns of ciliates communities varied depending on the approach (Table 1). For instance, bacteria density, dissolved oxygen, PCoA1 of copepods, conductivity, water temperature, phosphate and PCoA1 of rotifers were selected for the morphological approach, while dissolved oxygen, water temperature, bacteria density, PCoA1 of copopods and pH were selected for the molecular approach. Furthermore, out of the seven derived dbMEM, the fine-scale spatial component was composed by the same eigenvectors (dbMEM.2 and db.MEM.6), for both morphological and molecular approaches.

Table 1: Total explanation of dbRDA for pure environmental [E], fine-scale spatial [F], broad-scale spatial [B] components and their relative contribution after variation partitioning analysis in explain ciliate community variation patterns for morphological and molecular approaches.

	Morphological		**Molecular (HTS)**	
	adj. R^2 (%)	*P*	adj. R^2 (%)	*P*
Environmental **[E]**	25.4[a]	**0.001**	15.8[b]	**0.001**
Fine-scale **[F]**	3.40[c]	**0.032**	10.6[c]	**0.001**
Broad-scale **[B]**	17.1[d]	**0.001**	27.4[d]	**0.001**
Variation partitioning				
E|(F + B)	16.6	**0.001**	8.2	**0.025**
F|(E + B)	2.7	0.089	7.4	**0.009**
B|(E + F)	8.3	**0.013**	19.8	**0.001**

[a] [E] model constructed with the environmental variables bacteria density, dissolved oxygen, copepod PCoA1, conductivity, water temperature, phosphate, rotifer PCoA1

[b] [E] model constructed with the environmental variables dissolved oxygen, water temperature, bacteria density, copepod PCoA1, pH

[c] [F] model constructed with MEM variables dbMEM.2, dbMEM.6

[d] [B] dummy variable differentiating the floodplains

4.4 Discussion

We found striking evidences about the underlying mechanisms of community assembly, whether considering morphological or molecular approaches to inventory the diversity of ciliates from floodplain-associated lakes. Using a continent-wide sampling design, we studied four different biomes: Amazonian rainforest, Cerrado (a Savannah-like environment), Pantanal, and Atlantic forest. Each one of ecosystems has particular habitats and environmental heterogeneities, providing optimal conditions for the establishment of several different biological communities that increase the regional biodiversity. Among these biological groups, ciliates provide an ideal response-group for assessing to what extent the community-level results is affected by either morphological or molecular approaches. Unlike many other microbial eukaryotes, ciliates have elaborate morphologies that allow for comparisons between morphospecies and molecular approximations to different OTUs (Stoeck et al., 2014).

Our results showed that the diversity of OTUs was much higher than that of morphospecies but values were not consistent across floodplains. Indeed, genetic variations are usually higher than morphology-based estimators, especially because the correspondence between morphotypes and phylotypes is not always evident (Santoferrara et al., 2014). The differences between morphological- and molecular-based approaches may result, in part, from high polymorphism in SSU-rDNA among species (Dunthorn et al., 2014). For instance, cryptic species (i.e., genetic species that converge into very close morphological resemblances) are widespread among eukaryotes and have been found in several freshwater ciliates (Sáez & Lozano, 2005). Thus, for many protists, the morphology-based taxonomic description is quite restricted in terms of number of species (Boscaro et al., 2017).

Another major aspect to consider is the core definition of OTUs. In most cases, OTUs are defined based on a similarity threshold, so that all sequences that are more similar than a given threshold are grouped into the same OTU (Logares et al., 2015). Our OTUs were defined at a 98% similarity level, as this has been suitable for species-level distinctions of most protist groups (Mahé et al., 2015a). However, many OTUs matched reference sequences from the same species. For instance, we had *Tintinidium balechi* and *Vorticella aquadulcis* assigned to 27 and 15 different OTUs, respectively, while the morphological approach considered both as unique species. Thus, we identified a delicate tradeoff between morphological and taxonomic approaches, with the number of OTUs probability inflating the estimation of the true species diversity.

Despite the method of identification, we found a consistent spatial assembly pattern of ciliates communities across the four floodplains systems. This is in agreement with the growing body of evidence that protists may show biogeography patterns that resemble those of macro-organisms, which are based on dispersal constraints (Martiny et al., 2006b; Fontaneto & Hortal, 2013; de Vargas et al., 2015; Filker et al., 2016). However, one commonly used approach to assess the role of the dispersal limitation in shaping biological communities is through the distance-decay relationship (Astorga et al., 2012). Within this scope, the geographic proximity makes communities more similar, overwhelming the effect of environmental variation on space (Soininen et al., 2011). Biogeographical processes that may influence the current distribution of organisms include dispersal, past/contemporary environmental filtering, and ecological drift, which may result in compositional variations among communities related to morphology of molecular features (Heino et al., 2017).

A potential method of inferring about the relative importance of niche- and dispersal-based dynamics at different communities is to apply variation partitioning in constrained ordination analysis (Leibold et al., 2010; Heino et al., 2015; Brown et al., 2017), as we did.

When we controlled for the effects of environmental factors, as well as fine- and broad-scale dispersal proxies, we evidenced substantial differences between morphological- and molecular-based approaches, which directly interfere with the interpretation of the main community assembly mechanism. We showed that the effects of environmental structuring factors under the morphology-based identification approach were much higher than the broad-scale distancing effect, comparatively. This matches the assumption that high reproduction rates sustain large population sizes, which would increase the propagule pressure and, consequently, the dispersal potential of many micro-organisms (Van der Gucht et al., 2007).

The traditional identification and description of microbial eukaryotes has been microscopy-based, which led some researchers to the conclusion that the global protist diversity could be relatively low (Fenchel & Finlay, 2004b). Furthermore, the evolutionary process underlying this assertion led to the notion of a cosmopolitan distribution of most protists (Finlay, 2002). Based on our morphological results, we only partially support this assumption. However, the molecular-based results make us comfortable to speculate that the fact that ciliate communities are strongly spatially structured seems defensible. This suggests that biogeographic factors and the distance among sites limit the dispersal of ciliates, at least in large-scales, resulting in significantly different species compositions in each of the floodplain-associated lakes analyzed. Even though studies providing strong evidence for spatial structures in entire protist communities are still scarce (Porter & Hajibabaei, 2018), our findings support recent molecular-based studies on eukaryotes diversity and distribution patterns (e.g. Santoferrara *et al.*, 2016), suggesting that ecologists should account for biogeographical patterns instead of assuming a ubiquitous dispersal for protists (van der Gast, 2015).

One of the main advantages of using the molecular approach is the record of many rare OTUs, which are often overlooked in studies based only on morphology (Dunthorn et al., 2014; Logares et al., 2015). Once HTS-based studies capture a large proportion of the rare biosphere, the assumption that high population densities would increase the potential for dispersal is no longer entirely true. The rare biosphere could, therefore, present spatio-temporal distribution patterns more similar to that of macro-organisms, that could derive from dispersal limitation (Dunthorn et al., 2014). In fact, recent studies indicate that the rare biosphere has biogeography, which, in turn, may contribute to spatial distribution of the entire community (Weisse, 2014; Lynch & Neufeld, 2015). It is noteworthy that although morphological studies fail to register a large part of rare species within a regional species pool, it has been shown that even in studies based only on microscope identification, large-scale spatial structuring of rare species of ciliate it can be much clearer than for common species (Segovia et al., 2017).

In terms of ecosystem functioning, the differences between the accuracy of morphology- and molecular-based approaches also has important implications. We found that environmental filters had a greater influence on the morphological than on the molecular site-by-site dissimilarities. We believe that some factors may have contributed to these findings. First, from the biomonitoring perspective, the main challenge is to maintain the ecological relevance of OTUs without over-interpreting genetic polymorphism (Pawlowski et al., 2016). For example, species differ in the use of resources and their distributions depend on their functional traits (i.e., dispersal modes, resistance forms), which directly affects the species-level fitness of the organisms (Violle et al., 2007). Therefore, in situations with little or no information about how functional traits of ciliates might overlap among OTUs, it is indicative that biomonitoring protocols should consider DNA barcoding in the routine of ecological diagnosis (Pawlowski et al., 2016). However, cryptic species still share similar functional traits that yield low niche differentiation between them, which may be determined actually by the same environmental filters (Stoks et al., 2005). Thus, although unraveling community composition into a high number of OTUs may strengthen the signal of spatial processes in community assembly, it is also important to account for molecular heterogeneities produced by polymorphism, which may result in empirical patters with low contributions of the environment.

Alternatively, the morphological identification of ciliates requires not only *in vivo* processing of samples, but an accurate identification at lowest taxonomic level requires the use of impregnation techniques that allow for the observation of infraciliature and nuclear apparatus (Foissner et al., 1999). Therefore, we acknowledge that our morphological identification based only on living organisms is biased and some potentially different species may have been grouped into only one species, likely those rare ones. For instance, the morphospecies identified as *Paramecium aurelia*, an easily recognizable and cosmopolitan ciliate, was first recorded in bromeliad tanks located near the banks of the Paraná River, but later impregnation techniques and molecular analyzes identified it as *Paramecium multimicronucleatum* (Buosi et al., 2014). However, the use of these methods in biomonitoring is limited by overpricing and the lack of skilled people (Stoeck et al., 2014). For this reason, several studies evaluating the sufficiency of different taxonomic approaches would serve as an additional parameter to promote the inclusion of ciliates in biomonitoring, especially because the results generally point out that genus-level data outperforms other resolutions in detecting the effects of the environmental gradients (Xu et al., 2011; Cabral et al., 2017). Indeed, species from the same genus tend to share similar functional traits (Vandewalle et al., 2010) and, in opposite to molecular approaches, coarser and simplistic morphological identification may bias the species-environment relationships.

Unfortunately, the fact that the environmental DNA comprises both intra- and extra-cellular DNA is a major issue. The presence of extra-cellular DNA can be very useful for biomonitoring and is widely used for the early detection of invasive and endangered species (Pawlowski et al., 2016). However, for bioassessment, the distinction between living, deceased or inactive cells is necessary to predict the impacts of environmental changes on community composition (Ramírez et al., 2018). In this case, the presence of extra-cellular DNA retained in the sediment, associated with the transportation of extra-cellular DNA in flowing waters, creates an undesired noise that may confound the empirical patterns at some instance (Aylagas et al., 2016).

Finally, the metacommunity theory may also provide grounding to explain the weak environmental filtering when molecular approach was considered. According this theory, high dispersal rates may overcome the possible effects of local environmental conditions, such that poor adapted species are able to persist in unfavorable environments due to dispersal surplus (Leibold et al., 2004). There are fundamental differences in our findings between morphological- and molecular-based approaches that allow us to infer that the dispersal surplus may be catch in greater magnitude by the last. For example, when spatial factors are significant, it is an indicative that community variation is influenced by dispersal limitation or dispersal surplus (Ng et al., 2009). Following the premise that dispersal surplus potentially increases in importance with decreasing distance between sites (Heino et al., 2015), fine-scale spatial variables is more likely to pertain to this mechanism, also known as "mass effects" (Brown et al., 2017). As the spatial Moran's eigenvector maps, related to within-floodplain extent, was significantly only for molecular approach, this is an indicative of dispersal surplus in such method. This inference is reinforced with the PERMDISP results, that showed that lakes were significantly more similar under the molecular than under the morphological approach, i.e., homogenizing effects are greater-reaching in the molecular approach through increased gene flow.

There are a few caveats in our study. From an ecological viewpoint, we recognize that dispersal among sites may involve a number of mechanisms and different propagule dispersal (e.g., animal and physical vectors), that are impossible for us to control in this study. In addition, from a methodological and statistical viewpoint, we sampled only few lakes in each floodplain, which could weaken the relation between ciliates community and the predictor variables in the variance partitioning analysis (Gilbert & Bennett, 2010). Although part of the variation remained uncertain for both morphological- and molecular-based approaches, a significant amount could be explained by environmental conditions and/or fine- and broad-scale spatial variables. We used in this study a combination of predictors variables, including physicochemical variables, nutrition resources (bacteria, flagellates and phytoplankton) and potential predators (rotifer, cladocerans and copepods), all recognized for exercising a strong influence on ciliates community. Thus it is unlikely that this would be the consequence of few samplings, and instead it could be reflecting the importance of stochastic processes during community assembly (Nabout et al., 2009). Despite this, we emphasize that the explanation of the predictor variables was much higher than most studies developed with micro-organisms.

Combining HTS approach with morphological data (by parallel microscope examination), we showed that assessing microbial diversity requires accounting for both the limits of the approaches. Our results showed that site-by-site dissimilarity vary greatly across floodplain systems, independently of the approach utilized. Furthermore, the mechanisms shaping the composition of the ciliates communities, as expected, showed striking differences between morphological- and molecular-based approaches. In general, morphological-based composition of the ciliates communities was stronger influenced by local environment conditions (i.e., species sorting), while molecular-based composition were mainly influenced by broad-scale spatial processes (i.e., dispersal limitation). In addition, dispersal surplus seems to be more pronounced in the morphological-based composition. This finding suggests that ecological researches and biomonitoring activities needs to find a counter-balance, as each approach provides unique insights. On one hand, molecular OTUs detected by HTS include hidden diversity that can be fundamental for detecting biogeographical patterns. At the same time, morphological-based approach may be useful bioindicators for monitoring water quality, since they accurately reflect the environmental gradient.

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5 FINAL CONSIDERATIONS

In this thesis, composed of three papers, we evaluate the patterns of dissimilarity and its applicability in complementary ways. As resources for biodiversity surveys and conservation planning are limited, an intensively debated issue in ecology is whether variability in the patterns of diversity of different groups of organisms is congruent in space and time, a phenomenon referred to as cross-taxon congruence. Thus, in the first paper, to try fill these knowledge gaps, we examined the multi-faceted (i.e. taxonomic and functional beta diversity) cross-taxon congruence of freshwater communities across the four major floodplains. We showed how cross-taxon congruence is highly dependent on the spatial and temporal context. and the choice of the better surrogate group for biomonitoring depends on the question and aims of the project. For instance, at broad scales, where differences in distribution patterns of macro- and micro-organisms are usually maximized, the results suggest that taking into account the functional distance between biological groups is essential. More interestingly, we found that functional congruence is weaker than taxonomic congruence in many cases. This finding leads us to conclude that different organismal groups may be governed by different environmental factors and ecological processes.

In the second paper, we apply the concepts of beta diversity to verify how damming-induced changes affect beta diversity components downstream of the reservoir. To do that, we used the biological groups with the greatest functional dissimilarity found in the first paper (i.e, fish and phytoplankton), to describe in practice, what are the mechanisms behind the differences in the beta diversity patterns found between these two biological groups. Our results based on beta diversity partitioning approach, ratifies the idea that even within the same study area, biodiversity patterns exhibited by single biological groups do not necessarily match those of other groups that show wide variation in biological features, such as body size and dispersal mode. In addition, by demonstrating the conditions under which tributaries reduce the cumulative impacts of multiple dams on river-floodplain systems, our findings have improved understanding of tributary-induced heterogeneity and highlight the importance of dam-free stretches of rivers for preserving the integrity of dammed river basins.

Finally, in the last paper, we aim to assess how the patterns of dissimilarity can vary within the same biological group, but with different taxonomic accuracy. We use a currently debated issue, which involves the extent to which micro-organisms can exhibit clear biogeographic patterns. We showed that combining HTS approach with morphological data, morphological-based composition of the ciliates communities was stronger influenced by local environment conditions (i.e., species sorting), while molecular-based composition were mainly influenced by broad-scale spatial processes (i.e., dispersal limitation). This finding suggests that ecological researches and biomonitoring activities needs to find a counter-balance, as each approach provides unique insights. While OTUs detected by HTS include hidden diversity that can be fundamental for detecting biogeographical patterns, morphological-based approach may be useful bioindicators for monitoring water quality, since they accurately reflect the environmental gradient.

In conclusion, considering that both protection and sustainable use of biodiversity requires planning, the efforts must focus on establishing strategies that maximize the use of existing species distribution databases. In such circumstances, we demonstrated that beta diversity has large potential to be a useful tool of biodiversity research, improving our understanding of the causes (through the processes of community assembly) and consequences (for ecosystem functioning) of biodiversity change.

APPENDIX A - Laboratory analysis used for each biological group

Phytoplankton (Diatoms, Cyanobacteria, Chlorophytes (chlorophyceans and zygnemaphyceans), Xanthophyceans and Phytoflagellates (cryptomonads, dinoflagellates, chrysophyceans, euglenoids and raphidophyceans)

Data type: abundance (ind.mL^{-1})

Sample collection: Quantitative phytoplankton samples were taken on the subsurface (depth 20 cm) of the limnetic region of each environment. Samples were directly collected with bottles. These samples were preserved *in situ* with acidified Lugol’s solution (Bicudo & Menezes 2006).

Sample analyses: We performed the counting randomly per field, using an inverted microscope, according to Utermöhl (1958) and Lund *et al.* (1958), estimating the phytoplankton density. The alpha diversity of phytoplankton is defined as the species richness of an environment and for this we also used the qualitative samples collected with a micro-plankton net (15 µm). For numerical analyses we used only the quantitative samples.

Identification: Komárek *et al.* (1983); Komárek & Anagnostidis (1986); Tell & Conforti (1986), Anagnostidis & Komárek (1988); Komárek & Anagnostidis (1989); Bicudo & Menezes (2006).

Ciliate communities

Data type: abundance (cels.L^{-1})

Sample collection: Five liters of water were taken on the subsurface of the limnetic region (depth 10-20 cm) from each environment, using polyethylene flasks. The samples were stored in a cooler, and then transported to the laboratory, where they were concentrated into 100 mL via a micro-plankton net (5 µm).

Sample analyses: Ciliates were counted and identified *in vivo* within a maximum period of 4h after sampling. using an optical microscope (Olympus CX-41). According to the live counting technique described by Madoni (1984), 10 replicates of 100 µl drops were counted per site.

Identification: Foissner *et al.* (1992); Foissner *et al.* (1994); Foissner *et al.* (1995); Foissner & Berger (1996); Berger (1999); Foissner *et al.* (1999); Foissner *et al.* (2002).

Zooplankton (planktonic testate amoebae, Copepoda, Cladocera and Rotifera)

Data type: abundance (ind. m^{-3})

Sample collection: Zooplankton was sampled in the limnetic region, using a motorised pump with the boat moving at a constant velocity (to take a composite samples from each environment), and plankton net (68 μm) to filter 600L of water per sample (Lansac-Tôha *et al.* 2009). The samples were preserved in formaldehyde (4%) buffered with calcium carbonate.

Sample analyses: Zooplankton abundance was determined using a Sedgewick-Rafter counting chamber under an optical microscope. At least 80 individuals were counted (Bottrell *et al.* 1976) in each of three sequential samples, obtained with a Hensen-Stempell pipette (2.5mL).

Identification: Koste (1978); Reid (1985); Matsumura-Tundisi (1986); Segers (1995); Velho & Lansac-Tôha (1996); Velho *et al.* (1996); Elmoor-Loureiro (1997); Lansac-Tôha *et al.* (2002).

Phytophilous Ostracoda

Data type: abundance (ind.g^{-1} dry weight of macrophytes)

Sample collection: Ostracods associated with aquatic macrophytes were collected by washing the submerged parts of these plants (either root systems or the whole plant) in a plastic bucket. The ostracods in the bucket were washed and filtered through a 160 μm mesh hand net and preserved in 70% alcohol (Higuti *et al.* 2010; Campos *et al.* 2017).

Sample analyses: After removing the ostracods, these submerged parts of the aquatic macrophytes were stored in previously labeled plastic bags. Subsequently, they were oven-dried, and then weighed to calculate densities. Subsamples of the ostracods samples were taken with a Folsom fractioner, and ¼ of samples was counted. Ostracods were sorted under a stereomicroscope and species richness was always estimated from the total sample, i.e. all specimens in the sample were identified. Valves and appendages were examined using scanning electron microscopy and optical microscope, respectively.

Identification: Martens & Behen (1994); Higuti & Martens (2012a); Higuti & Martens (2012b); Higuti & Martens (2014); Higuti *et al.* (2013); Rossetti & Martens (1998); Pinto *et al.* (2003); Pinto *et al.* (2004).

Aquatic macrophytes

Data type: presence / absence

Sample collection: In all sampling sites we recorded aquatic macrophytes presence by boat at a slow speed along the entire lake shoreline. Submerged species were recorded with a grapple, treble hooks and a rake attached to an aluminium stick, which were dragged along the lake. Species that could not be identified in the field were collected for later identification in the laboratory and kept in the Herbarium of the University of Maringá (HUEM).

Identification: Cook (1990); Kissman (1997); Kissman & Groth (1999); Kissman & Groth (2000); Lorenzi (2000); Pott & Pott (2000).

Fish

Data type: abundance (CPUE)

Sample collection: For fish capture were used 20m trawls (20m x 1.5m) and seine nets (0.54 cm mesh size) with standardized effort of 3 drag per environment, according Malabarba & Reis (1987). The fish were anesthetized with benzocaine diluted.

Sample analyses: Fish were identified at the species level and their biometric data were obtained in the laboratory (total weight – TW, total length – TL, and standard length – SL). Voucher specimens of all species have been deposited in the ichthyological collection of the Research Centre in Ichthyology Limnology and Aquaculture (Nupélia), State University of Maringá (UEM).

Identification: Graça & C.S. 2007; Ota *et al.* 2018.

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APPENDIX B - Strength of congruence of all pairs of combinations between biological groups based on data presence-absence and abundance data for the dry and rainy periods

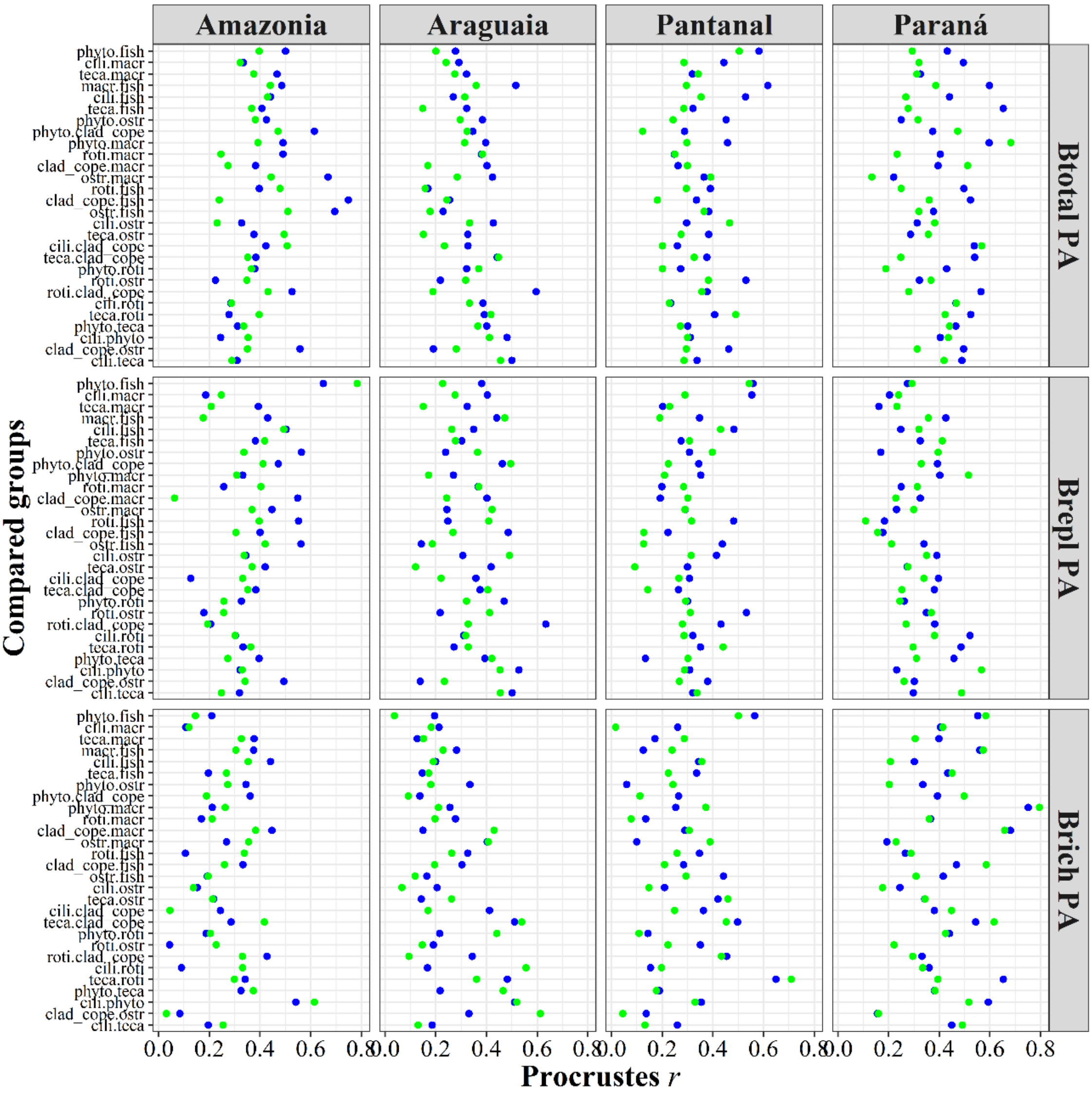

Fig. S1: Strength of congruence of all pairs of combinations between biological groups based on data presence-absence data for the dry period. Blue = Taxonomic approach. Green = Functional approach.

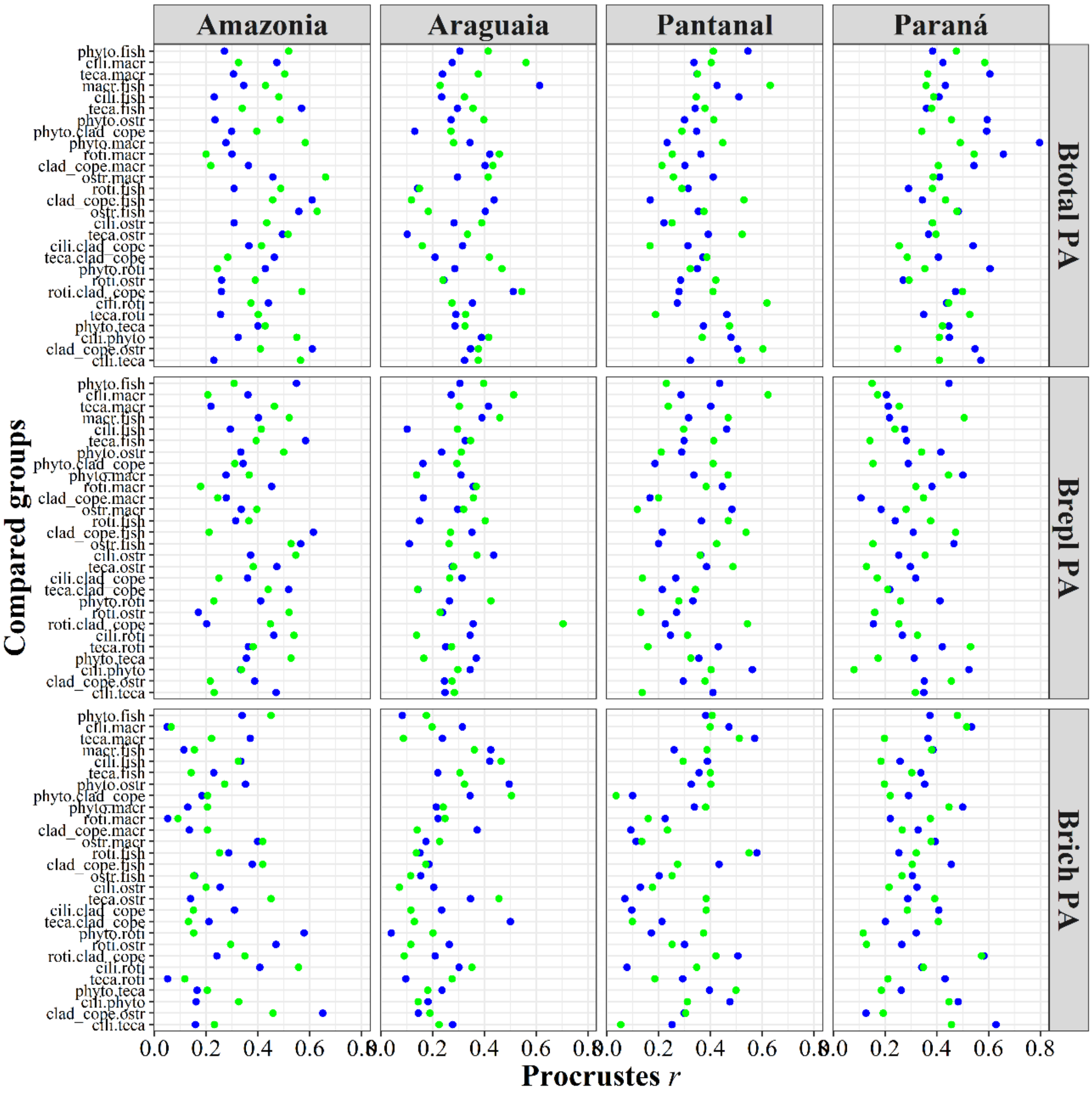

Fig. S2: Strength of congruence of all pairs of combinations between biological groups based on data presence-absence data for the flood period. Blue = Taxonomic approach. Green = Functional approach.

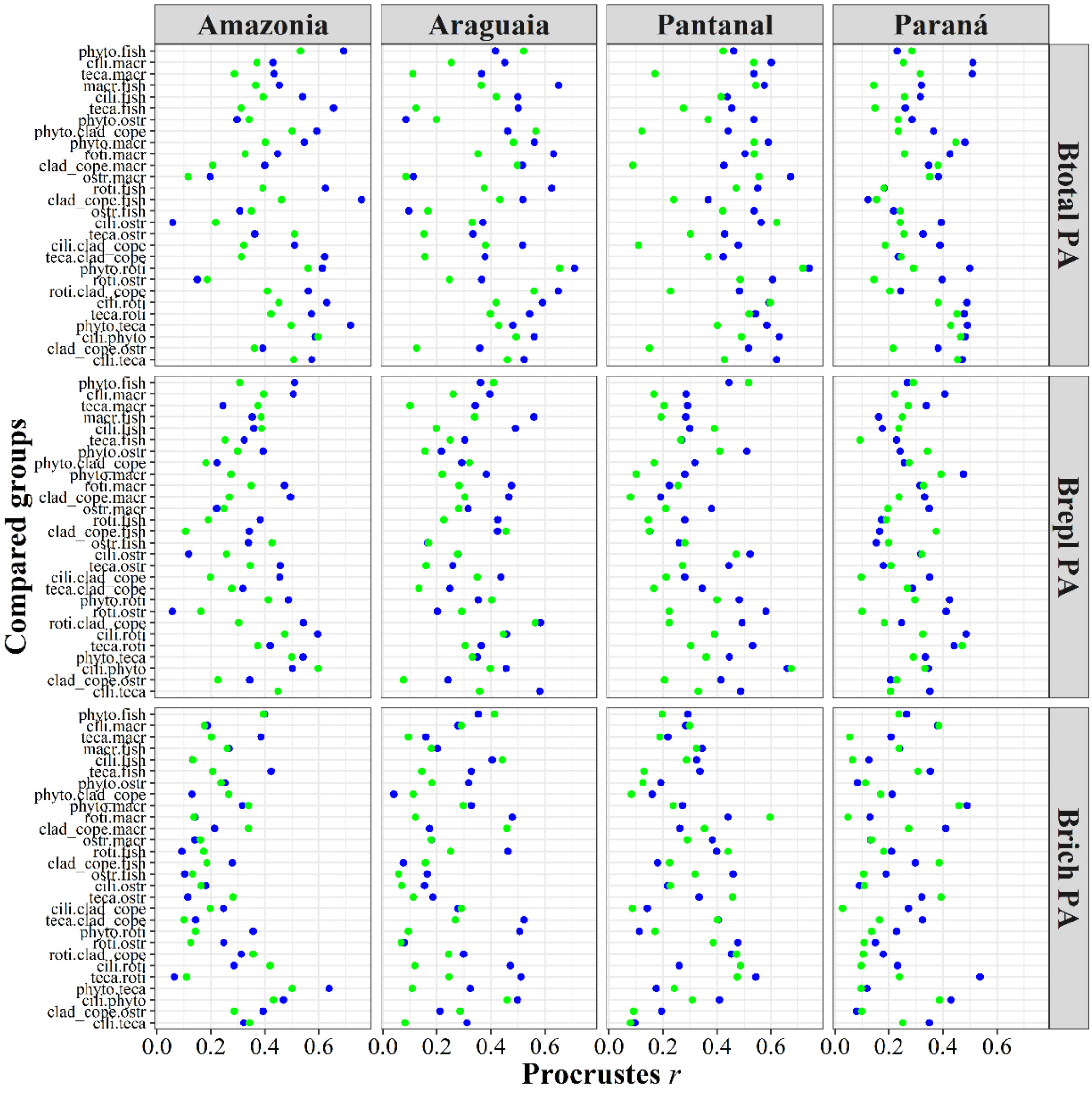

Fig. S3: Strength of congruence of all pairs of combinations between biological groups based on data presence-absence data for dry and flood periods together. Blue = Taxonomic approach. Green = Functional approach.

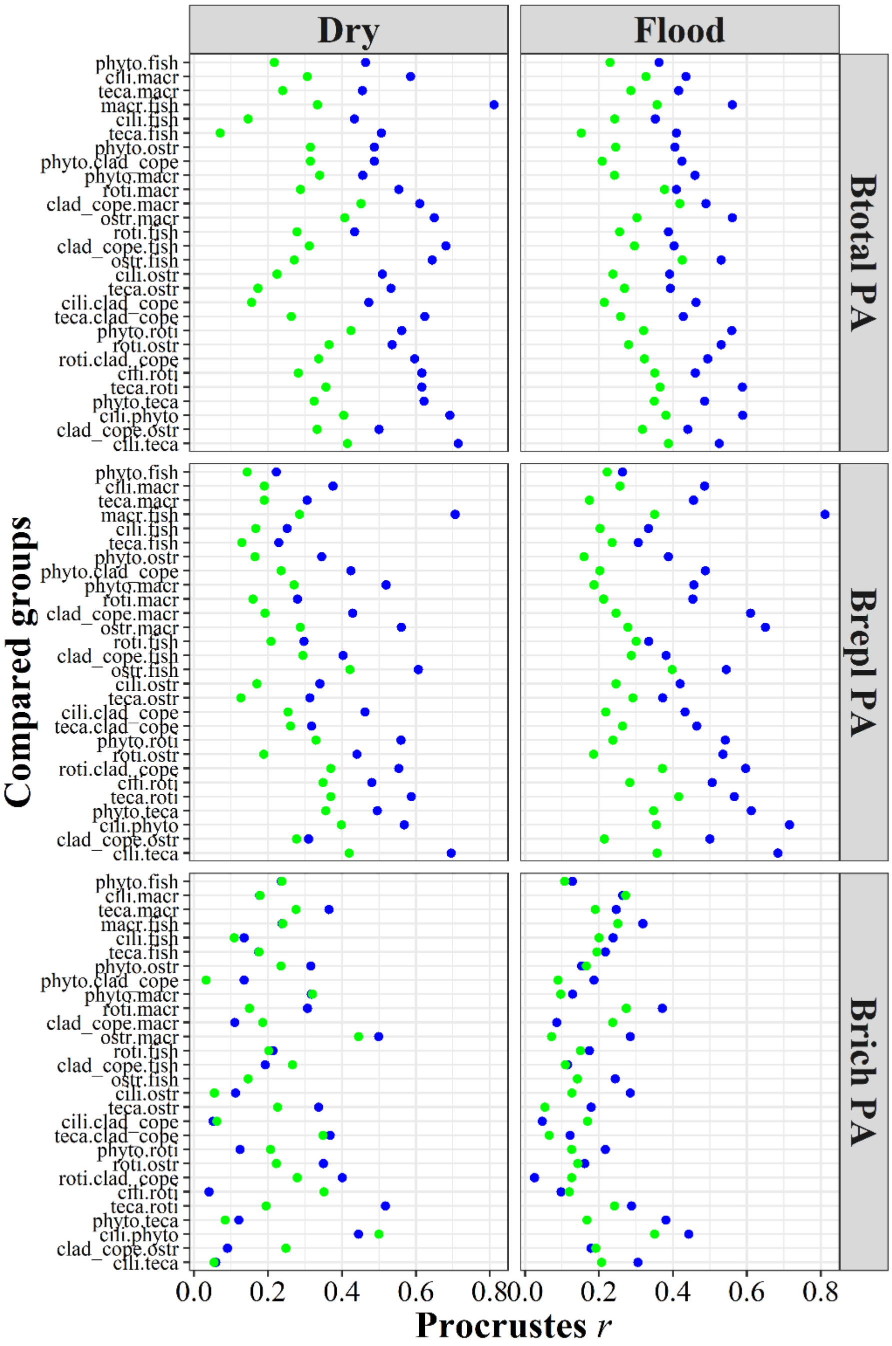

Fig. S4: Strength of congruence of all pairs of combinations between biological groups based on data presence-absence data for continental scale. Blue = Taxonomic approach. Green = Functional approach.

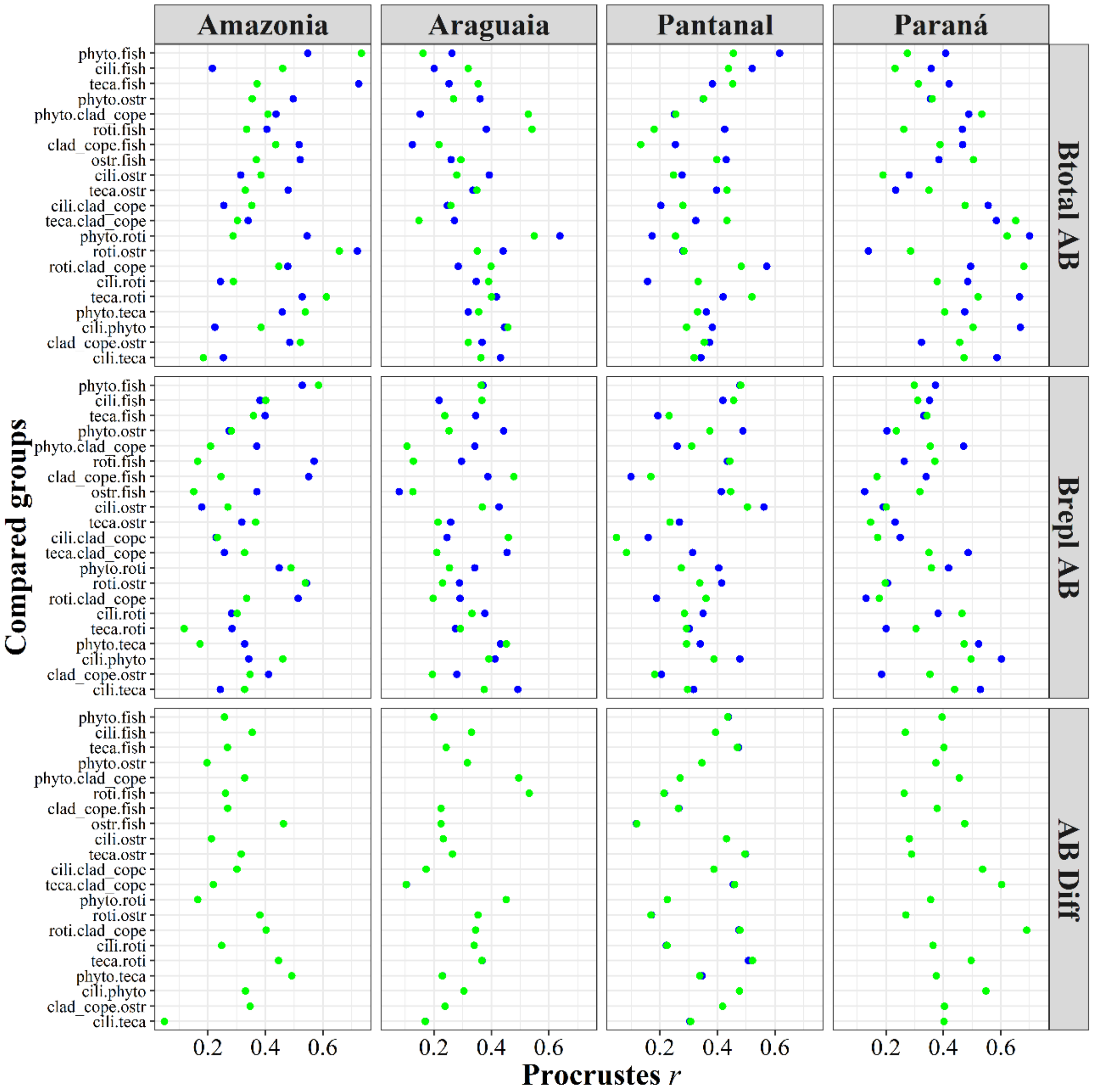

Fig. S5: Strength of congruence of all pairs of combinations between biological groups based on data abundance data for the dry period. Blue = Taxonomic approach. Green = Functional approach. Circles only in green depicts the same congruence between approaches.

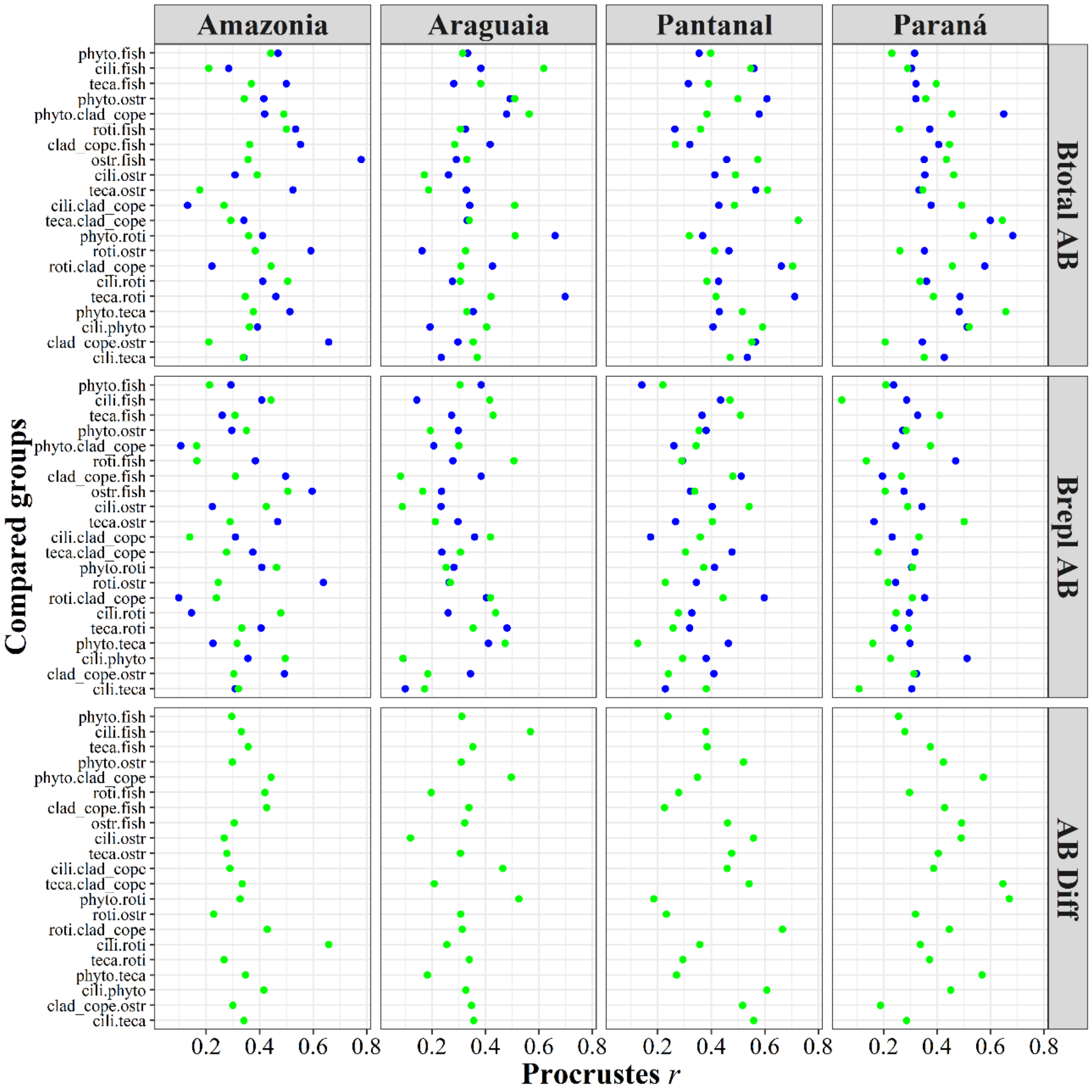

Fig. S6: Strength of congruence of all pairs of combinations between biological groups based on data abundance data for the flood period. Blue = Taxonomic approach. Green = Functional approach. Circles only in green depicts the same congruence between approaches.

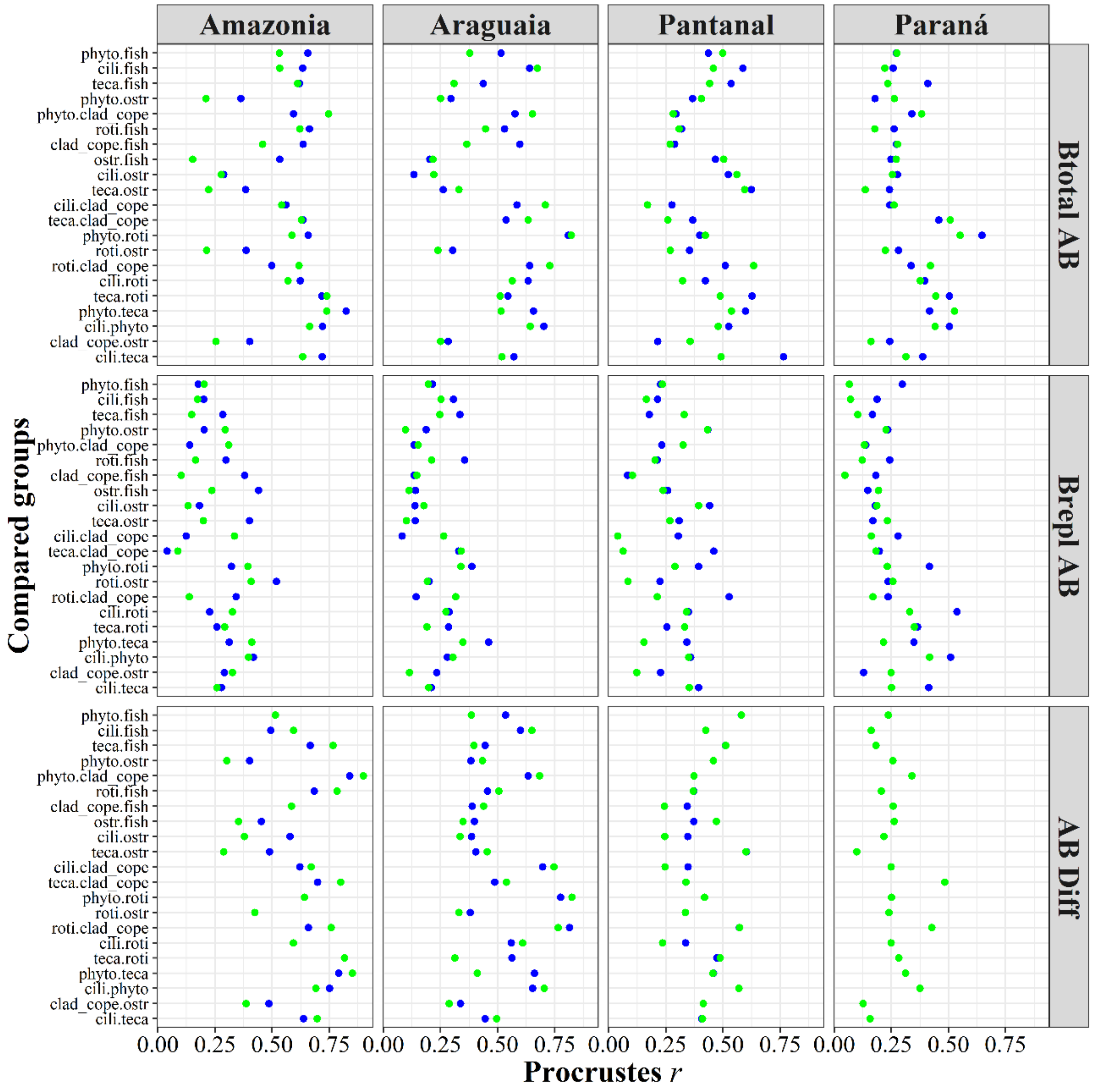

Fig. S7: Strength of congruence of all pairs of combinations between biological groups based on data abundance data for dry and flood periods together. Blue = Taxonomic approach. Green = Functional approach. Circles only in green depicts the same congruence between approaches.

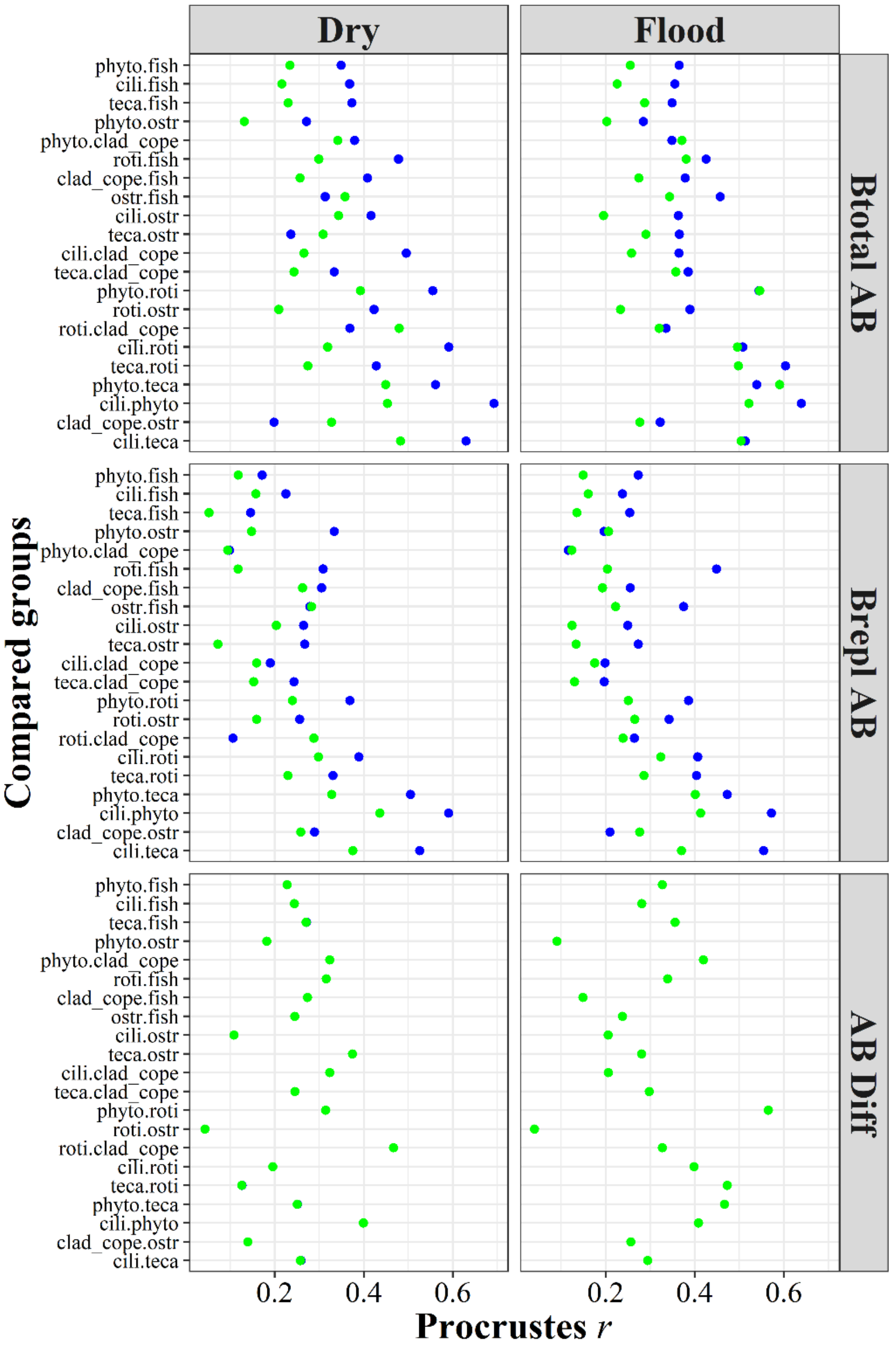

Fig. S8: Strength of congruence of all pairs of combinations between biological groups based on data abundance data for continental scale. Blue = Taxonomic approach. Green = Functional approach. Circles only in green depicts the same congruence between approaches.

APPENDIX C - Functional traits of the eight biological groups

Table S1: Functional traits of the eight biological groups including types of traits, categories and their ecological importance.

Biological Groups	Traits	Type	Categories	Trait importance	Biological group references
Phytoplankton	Body size	Continuous	Average length (µm)	Body length is a trait which directly influence on dispersal ability. Also, this trait is related with the secondary productivity and energetic transference, reflecting the quantity of energy.	Litchman & Klausmeier, 2008; Padisák, Soróczki-Pintér, & Rezner, 2003
	Cell organization	Categorical	Coenobium Colony Chains Filament Unicellular	Resource acquisition and predator avoidance	Litchman & Klausmeier, 2008; Padisák, Soróczki-Pintér, & Rezner, 2003
	Pigment	Categorical	Green Brown Green	Resource acquisition	Litchman & Klausmeier, 2008; Padisák, Soróczki-Pintér, & Rezner, 2003
	Capacity for mixotrophy	Categorical	Mixotrophic Non-mixotrophic	Resource acquisition	Litchman & Klausmeier, 2008; Padisák, Soróczki-Pintér, & Rezner, 2003
	Cell motility	Categorical	Abscence Aerotopes Flagellated	Resource acquisition and predator avoidance	Litchman & Klausmeier, 2008; Padisák, Soróczki-Pintér, & Rezner, 2003
	Presence of silica	Binary	Presence Abscence	Predator avoidance	Litchman & Klausmeier, 2008; Padisák, Soróczki-Pintér, & Rezner, 2003
Ciliates	Body size	Continuous	Average length (µm)	Body length is a trait which directly influence on dispersal ability. Also, this trait is related with the secondary productivity and energetic transference, reflecting the quantity of energy.	Foissner & Berger, 1996
	Feeding type	Categorical	Nano/Micro-interceptors Nano-filterers Pico/Nano-filterers	Trait related to the foraging strategy, influencing the way of detecting and capturing prey and affecting predator-prey interactions.	Mironova, 2013

			Pico-filterers		
	Mode of life	Categorical	Benthic Planktonic Periphitic Epibiont	Trait related to the organisms habitat use, and involves different compartments of the aquatic environment. Species with different mode of life contribute differently to nutrients cycle and ecosystem functions.	Foissner & Berger, 1996
	Encystment capacity	Binary	Presence Abscence	Resilience	Foissner & Berger, 1996
Testate amoebae	Body size	Continuous	Average length (µm)	Body length is a trait which directly influence on dispersal ability. Also, this trait is related with the secondary productivity and energetic transference, reflecting the quantity of energy.	Lampert & Sommer, 1997; Velho *et al.*, 2003
	Gas vacuole	Binary	Presence Abscence	Testate amoebae that present gas vacuoles are able to dislocate from the bottom to the surface by floating.	Ogden, 1991; Arrieira *et al.*, 2015
	Shell compression	Binary	Presence Abscence	Characteristic that minimizes resistance to water and floatation.	Lampert & Sommer, 1997; Velho *et al.*, 2003
	Shell constituition	Categorical	Agglutinated Protein Siliceous	Differences in shell constitution may represent adaptations regarding changes in the environment, influencing the occurrence of each species.	Fournier *et al.*, 2012; Arrieira *et al.*, 2015
Rotifers	Body size	Continuous	Average length (µm)	Body length is a trait which directly influence on dispersal ability. Also, this trait is related with the secondary productivity and energetic transference, reflecting the quantity of energy.	Koste, 1978; Braghin *et al.*, 2018
	Mode of life	Categorical	Littoral Pelagic	Trait related to the organisms habitat use, and involves different compartments of the aquatic environment. Species with different mode of life contribute differently to nutrients cycle and ecosystem functions.	Koste,1978; Braghin *et al.*, 2018
	Feeding type	Categorical	Filtration Sugador Predator	Trait related to the foraging strategy, influencing the way of detecting and capturing prey and affecting predator-prey interactions.	Fryer, G. 1996 Braghin *et al.*, 2018
	Lorica	Binary	Presence Abscence	Predator defense	Koste (1978)

Microcrustaceans	Body size	Continuous	Average length (µm)	Body length is a trait which directly influence on dispersal ability. Also, this trait is related with the secondary productivity and energetic transference, reflecting the quantity of energy allocated and excreted nutrients.	Litchman, Ohman & Kiørbe, 2013; Hébert, Beisner & Maranger, 2016; Braghin *et al.*, 2018
	Mode of life	Categorical	Littoral Pelagic	Trait related to the organisms habitat use, and involves different compartments of the aquatic environment. Species with different mode of life contribute differently to nutrients cycle and ecosystem functions.	Barnett, A. J., Finlay, K. & Beisner, B. E., 2013. Lynch, M., 1980
	Feeding type	Categorical	Daph-filterers Sidi-filterers Cop-filterers Scraper Raptorial	Trait related to the foraging strategy, influencing the way of detecting and capturing prey and affecting predator-prey interactions.	Andersen & Hessen, 1991 Dodson, S. I. & Brooks, J. L., 1965 Elmoor-Loureiro, L. M, 1997
	Trophic group	Categorical	Herbivorous Herb-Detritivorous Omnivorous	This trait is recognized as an important tool to group organisms that use the same resources. Therefore, it is directly related to the aquatic food webs and how species differ in their nutrient requirements.	Winder & Jassby, 2011
	Predatory escape response	Categorical	Low Medium Big Maximum	Ability of species to repel a predatory investment. Several characteristics may influence the escape, such as swimming agility, body shape and size, and visibility of a predator.	Brooks & Dodson, 1965; Allan, 1976
Ostracods	Body size	Categorical	Small (≤ 0.54 mm) Medium (≥0.55 mm; ≤1.32 mm) Large (> 1.32 mm)	Body length is a trait which directly influence on dispersal ability. Also, this trait is related with the secondary productivity and energetic transference, reflecting the quantity of energy allocated and excreted nutrients.	Campos *et al.*, 2018
	Locomotion	Categorical	Swimmers Non-swimmers	Although all ostracods species are passive dispersers, some species have a swimming ability to find more suitable habitats in a given location.	Campos *et al.*, 2018
	Reproduction mode	Categorical	Parthenogenesis Sexual Mix	Trait directly related to the potential for dispersion and colonization of new habitats. Also, it influences the genetic diversity of a population.	Campos *et al.*, 2018

	Spine	Binary	Presence Abscence	Trait related to the organism potential defense against predators.	Campos *et al.*, 2018
	Body morphology	Categorical	Flat Rounded	This trait may be a consequence of mode of life, dispersal ability and predatory escape response, influencing the ecologycal occupancy within a given ecosystem.	Campos *et al.*, 2018
Fish	Body size	Continuous	Average length (mm)	Body length is a trait which directly influence on dispersal ability. Also, this trait is related with the secondary productivity and energetic transference, reflecting the quantity of energy.	Giam & Olden 2018 Dos Santos *et al.*, 2017
	Mode of life	Categorical	Benthopelagic Pelagic Demersal	Trait related to the organisms habitat use, and involves different compartments of the aquatic environment. Species with different mode of life contribute differently to nutrients.	Dos Santos *et al.*, 2017
	Trophic group	Categorical	Benthivorous Omnivorous Piscivorous Invertivorous Planktivorous Detritivorous Herbivorous	This trait is recognized as an important tool to group organisms that use the same resources. Therefore, it is directly related to the aquatic food webs and how species differ in their nutrient requirements.	Hahn *et al.*, 2004 Dos Santos *et al.*, 2017
	Trophic level	Continuous	Numeric variable	Position of each species in the aquatic food web. Trophic position calculations have the potential to provide energetically based representations of trophic relationships.	Vander Zanden & Rasmussen, 1996
	Migration	Binary	Presence Abscence	Species potential to perform long reproductive migrations (over 100 km). Migratory species usually are less dispersal limitated.	Agostinho *et al.*, 2004; De Bie *et al.*, 2012
	Parental Care	Binary	Presence Abscence	Although involving higher energetic demand for adults, species that have parental care generally present more reproductive success.	Gebhardt, 1987 Agostinho *et al.*, 2004;
Macrophytes	Body size	Continuous	Average length (cm)	Body length is a trait which directly influence on dispersal ability. Also, this trait is related with the secondary productivity and energetic transference, reflecting the quantity of energy.	Kissman & Groth (2000); Lorenzi (2000); Pott & Pott (2000)

Mode of life	Categorical	Emergent Free-floating Rooted submerged Free submerged Submerged fixed Submerged fixed/emergent	Trait related to the organism's habitat use, and involves different compartments of the aquatic environment. Species with different mode of life contribute differently to nutrients and structural complexity, supporting different range of taxa.	Kissman & Groth (2000); Lorenzi (2000); Pott & Pott (2000)
Propagule unit	Categorical	Artículo Ep Fragment Fragment/Ep Fragment/Ep/Bulbe Nuculas Seed Seed/Seedling Seed/Fragment Seed/Ep Seed/Rhizome Spore Spore/Ep Stolon Stolon/Seedling Stolon/Ep Spikes Spikes/Nuculas Rhizome	Propagule type is an importanct factor that may influence the establishment success, growth and spread of submerged plant populations.	Kissman & Groth (2000); Lorenzi (2000); Pott & Pott (2000)
Dispersion mode	Categorical	Autochory Autochory/Hydrochory Autochory/Zoochory Autochory/Hydrochory/Zoochory Hydrochory	This trait is related to the transport of propagules to areas far from their production site, where they will develop. Then, dispersion mode may also influence the success of aquatic plants to colonize new areas.	Kissman & Groth (2000); Lorenzi (2000); Pott & Pott (2000)

		Hydrochory/Zoochory Zoochory		
Seasonality	Categorical	Annual Annual/Perennial Perennial	The growth of aquatic macrophytes presents seasonal dynamics that determine the period of persistence of plants in the environment.	Kissman & Groth (2000); Lorenzi (2000); Pott & Pott (2000)

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APPENDIX D - Upper Paraná River water level

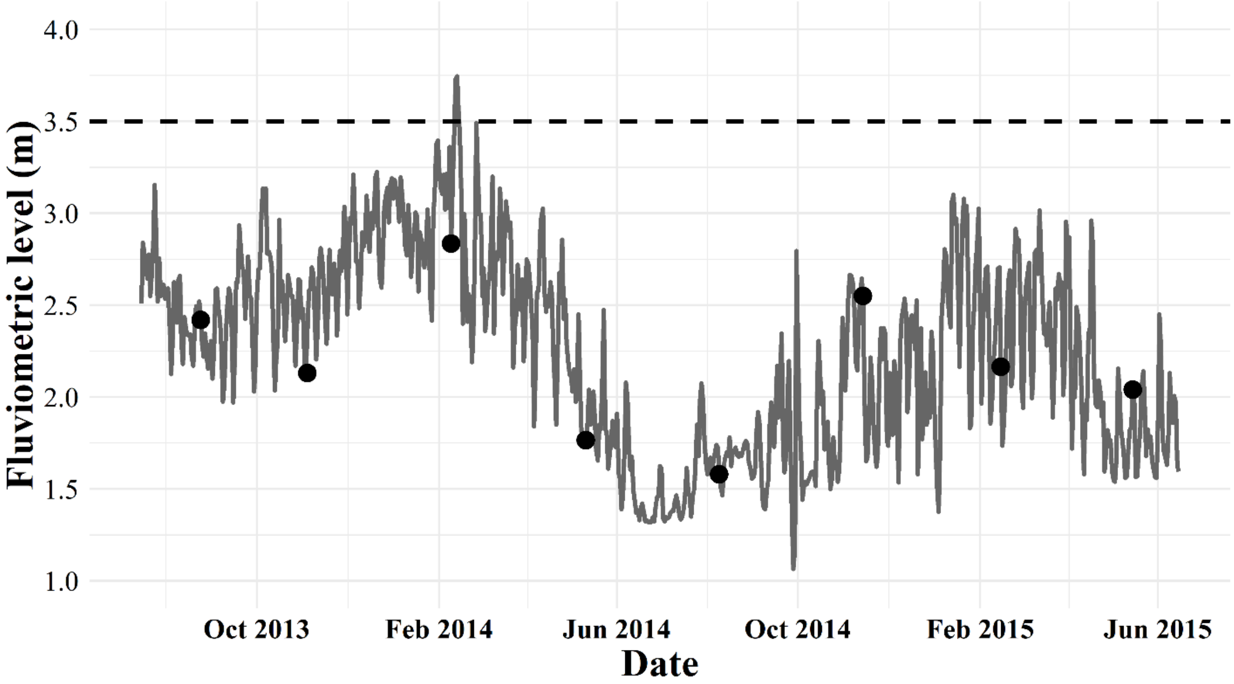

Fig. S1. Upper Paraná River water level recorded between July 2013 and June 2015. The circles represent the sampling times. The dashed lines correspond to the reference level that provide the overflow in the Upper Paraná River floodplain (above 3.5 m).

APPENDIX E - Spatial AEMs selected by forward selection

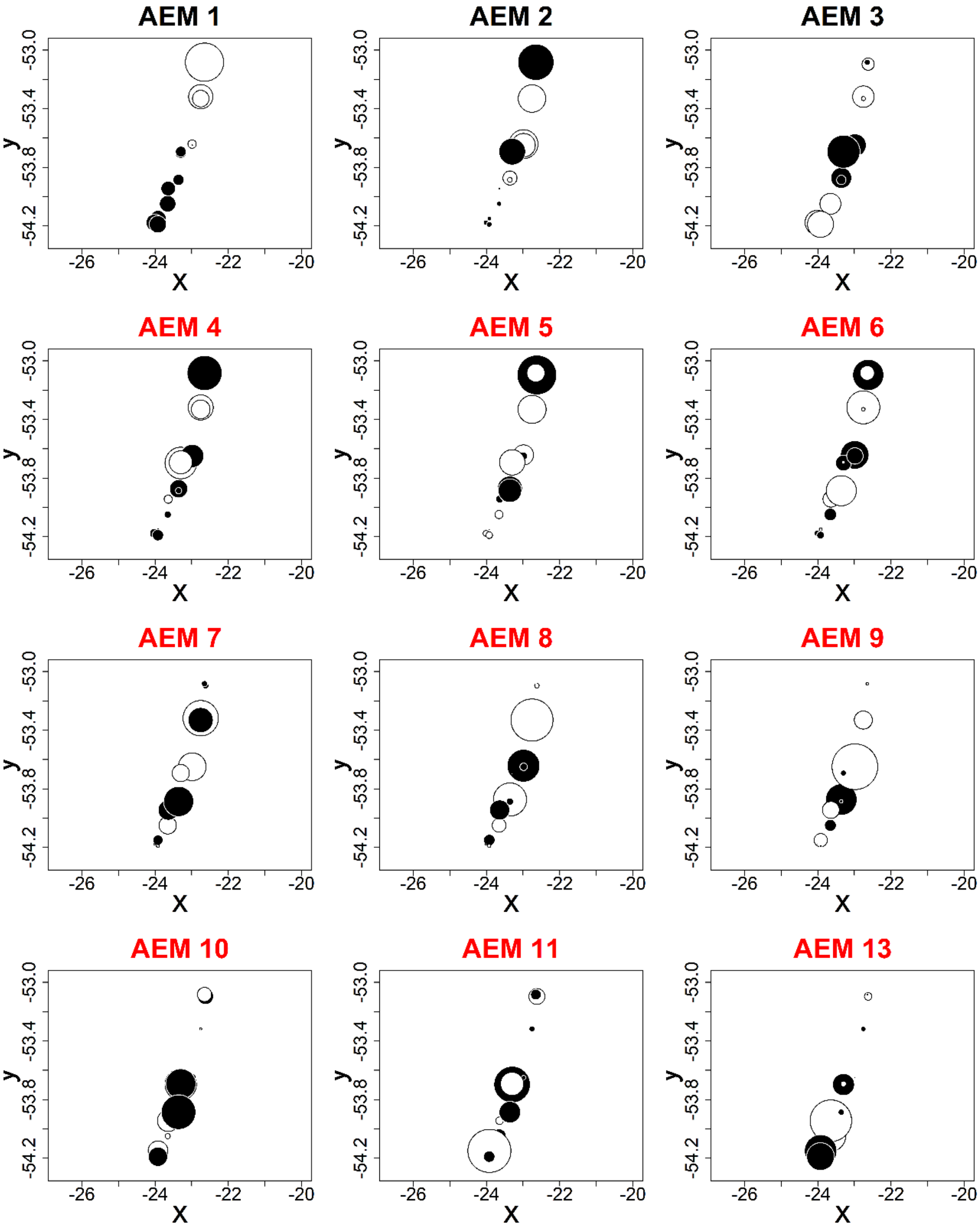

Fig. S2. The 12 spatial AEMs selected by forward selection ($p < 0.05$). For AEM 1, 2 and 3 which model positive spatial correlation based on Moran's I, titles are plotted in black, while for AEM 4, 5, 6, 7, 8, 9, 11 and 13 which correspond to negative spatial correlation based on Moran's I, titles are plotted in red. The circle bubble size is proportional to the value associated to it, whereas the color reflects the signs of the number (black represents positive values; white represents negative values).

APPENDIX F - Temporal AEMs selected by forward selection

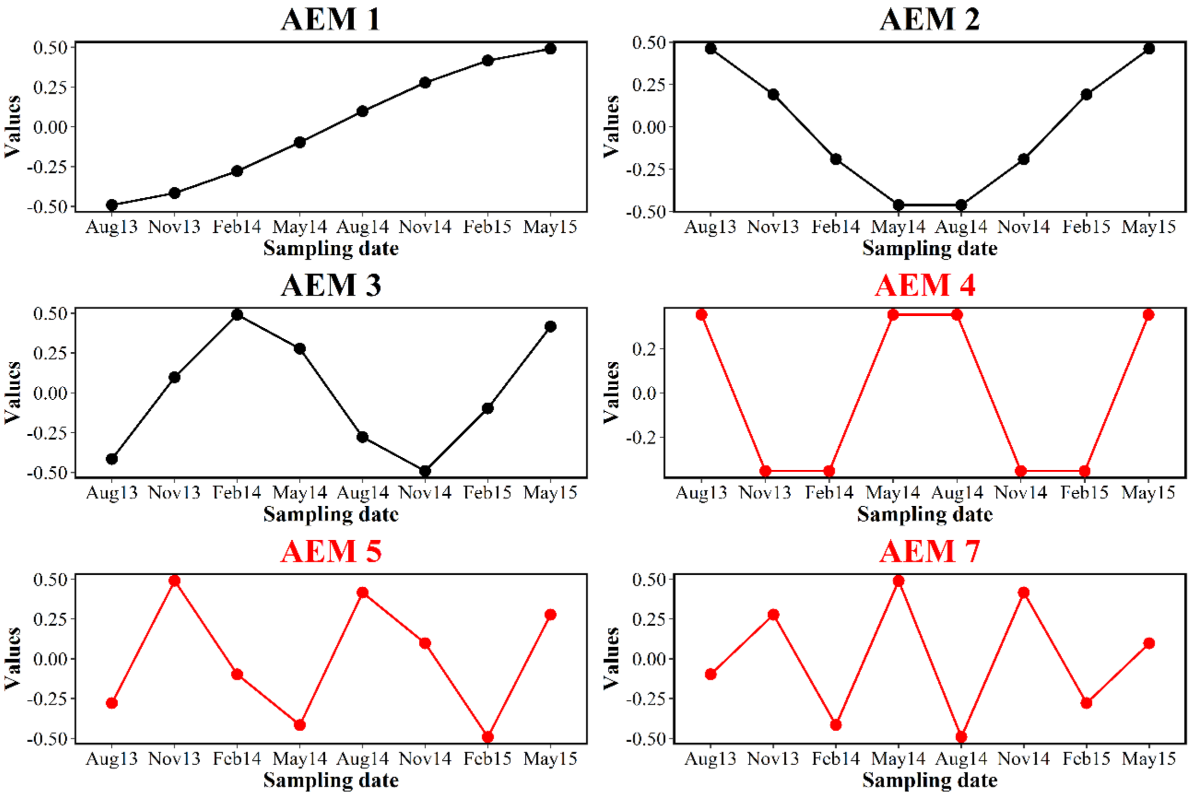

Fig. S3. The 6 temporal AEMs selected by forward selection ($p < 0.05$). AEM 1, 2, and 3 which model positive temporal correlation, are plotted in black, while AEM 4, 5 and 7 which correspond to negative temporal correlation, are plotted in red. The sampling dates are shown along the x-axis.

APPENDIX G - Environmental RGB colour maps based on principal component analysis

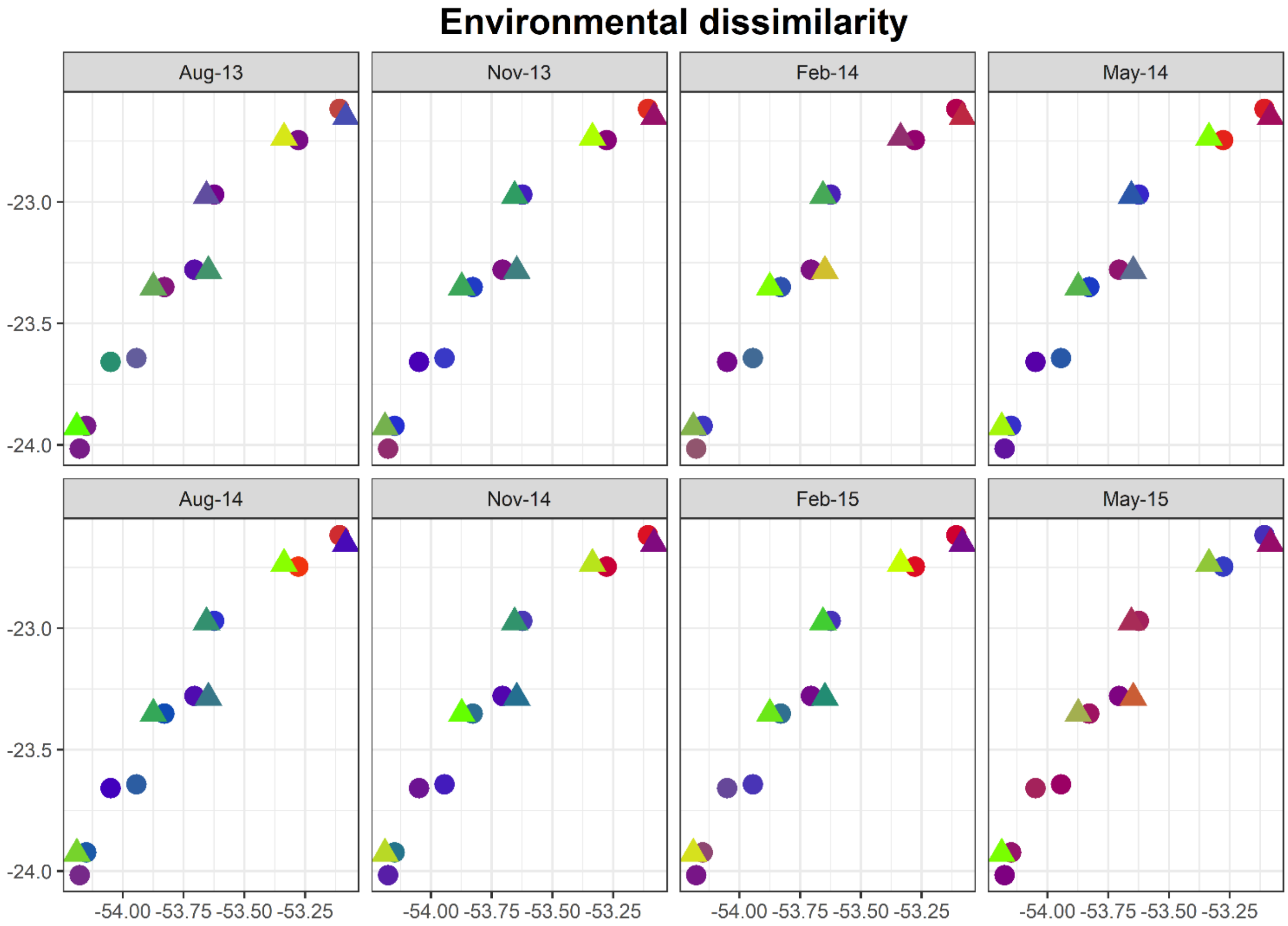

Fig. S4. RGB colour maps based on principal component analysis for a matrix of Euclidean distances on the standardized environmental variables along the longitudinal gradient of the last non-dammed stretch of the Paraná River at each sampling time. Similar colours represent low dissimilarity among sites. Triangle = tributaries; circles = Paraná River.

APPENDIX H - Fish RGB colour maps based on non-metric multidimensional scaling

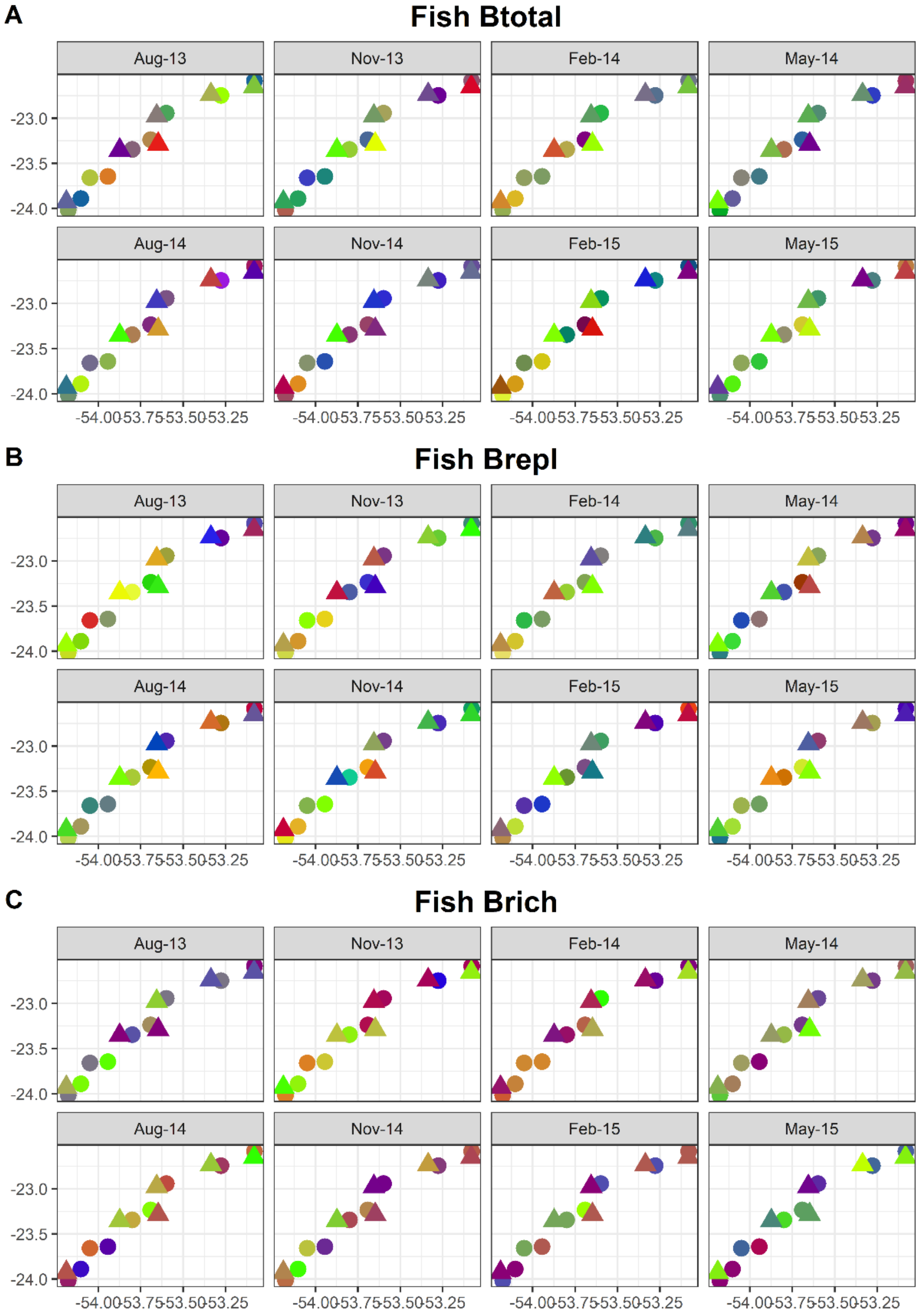

Fig. S5. RGB colour maps based on non-metric multidimensional scaling for Btotal (A), Brepl (B) and Brich (C) components along the longitudinal gradient of the last non-dammed stretch of the Paraná River at each sampling time for fish. Similar colours represent low dissimilarity among sites.

APPENDIX I - Phytoplankton RGB colour maps based on non-metric multidimensional scaling

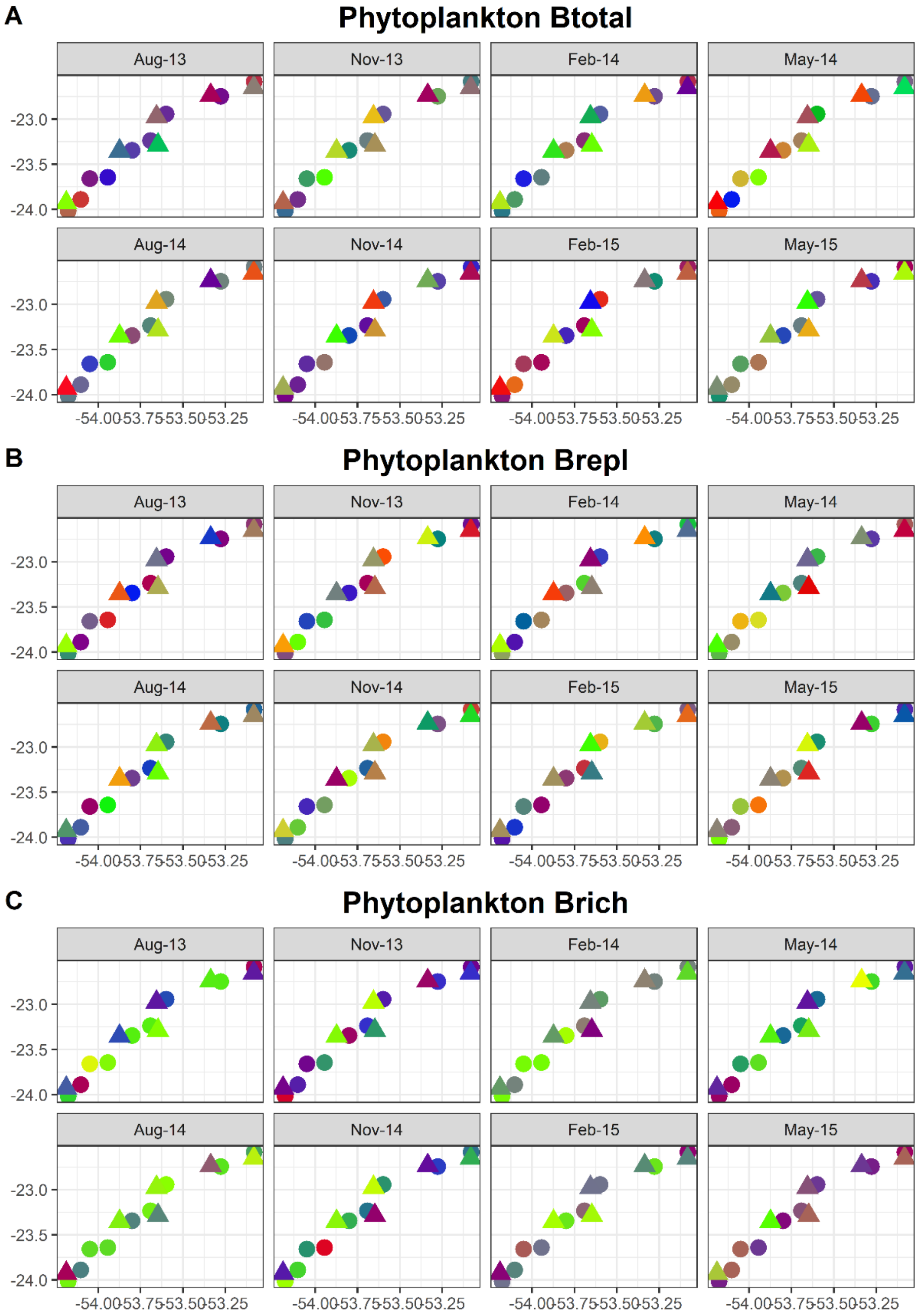

Fig. S6. RGB colour maps based on non-metric multidimensional scaling for Btotal (A), Brepl (B) and Brich (C) components along the longitudinal gradient of the last non-dammed stretch of the Paraná River at each sampling time for phytoplankton. Similar colours represent low dissimilarity among sites.

APPENDIX J - Alpha diversity and environmental variables used in the db-RDAs analysis

Table S1. Mean and standard deviation values of alpha diversity and environmental variables used in the db-RDAs before checking for multicollinearity based on variance inflation factors (VIF). PRpanema = Paranapanema, SR = species richness, OSM = organic suspension material, ISM = inorganic suspension material.

Alpha diversity/ Variables	**Main channel (Paraná River)**			**Tributaries**					
	Upstream	Middle	Downstream	PRpanema	Baia	Ivinheima	Ivaí	Amambai	Iguatemi
Fish SR	10.12±3.47	8.15±3.74	9.87±4.88	5.63±2.32	7.12±3.56	11.75±4.50	6.51±1.69	6.12±2.85	8.13±4.67
Phytoplankton SR	9.42±2.52	9.84±3.83	7.56±2.22	8.87±3.23	11.0±4.59	10.38±7.42	14.25±6.09	11.88±7.47	7.25±3.96
Width (m)	1105±676	947.9±573.3	867±681	493±0	25±0	130±0	269±0	55±0	50±0
Water temperature (°C)	25.45±3.14	25.26±3.47	25.63±3.70	24.47±3.83	25.08±5.20	24.58±4.26	25.11±4.27	24.25±3.56	24.55±3.83
Depth (m)	4.21±1.64	3.72±1.28	3.08±0.37	3.88±0.84	1.74±0.41	4.74±0.46	5.83±0.36	3.46±0.52	2.58±0.35
Secchi (m)	2.04±1.16	1.18±0.64	1.64±0.89	2.04±1.21	1.33±0.77	0.69±0.37	0.52±0.24	0.37±0.20	2.26±5.15
Turbidity (NTU)	4.48±3.06	12.09±6.17	12.19±4.38	6.58±3.53	4.90±1.66	19.04±5.46	26.08±15.14	40.68±25.17	31.80±24.28
Dissolved oxygen (mg.L^{-1})	7.68±0.54	7.47±0.69	7.52±0.71	7.69±0.66	6.24±1.28	6.82±0.93	7.84±0.68	6.72±0.82	7.43±0.84
pH	7.51±0.27	7.09±0.37	6.95±0.47	7.36±0.20	6.39±0.38	6.86±0.22	7.09±0.68	6.61±0.30	6.29±0.63
Conductivity (µS.cm^{-1})	63.69±5.07	56.03±6.41	50.81±2.96	68.19±5.45	28.61±11.10	42.06±2.10	62.95±4.57	32.39±2.00	18.96±1.44
Alcalinity (mEq.L^{-1})	566.9±159.5	495.8±177.3	496.5±174.1	688.8±215.4	219.9±86.8	477.8±147.5	584.4±188.1	305.2±89.47	170.2±108.9
Nitrate (µg.L^{-1})	167.0±40.2	268.1±113.3	201.1±57.3	458.9±117.1	28.7±48.9	166.5±128.2	568.7±179.8	242.5±74.1	168.8±77.3
Ammonium (µg.L^{-1})	7.85±3.19	9.96±13.14	10.52±7.79	5.91±4.93	17.58±12.36	5.45±4.77	10.99±15.41	28.20±14.41	4.92±3.15
Total nitrogen (µg.L^{-1})	706.1±204.1	768.1±254.8	728.8±236.3	1114.2±390.9	806.7±144.1	854.2±256.2	1267.9±309.1	865.4±148.8	670.9±67.9
Phosphate (µg.L^{-1})	9.79±6.14	12.92±7.62	10.96±4.44	9.81±4.50	14.26±5.61	20.78±6.72	21.89±7.25	18.90±13.92	6.10±2.79
Total phosphorus (µg.L^{-1})	19.76±20.09	25.56±11.52	19.44±5.71	17.95±4.01	31.25±12.50	41.33±15.40	40.76±9.18	35.80±12.89	18.99±10.04
OSM (mg.L^{-1})	1.25±0.79	1.12±0.63	0.9±0.74	0.95±1.16	0.51±0.21	0.87±0.39	0.66±0.38	0.85±0.52	0.70±0.48
ISM (mg.L^{-1})	4.14±4.15	4.86±3.35	3.70±3.21	1.20±1.33	0.87±0.66	2.99±1.20	3.31±1.78	4.11±2.60	3.71±2.70

APPENDIX K - Fish-based db-RDA variable selection

Table S2. Fish-based db-RDA variable selection and cumulative adj. R^2 values obtained through forward selection. Abbreviations: ISM = inorganic suspension material, Btotal = total beta diversity, Brepl= replacement, Brich= richness-difference, X =spatial variables, T=temporal variables.

Btotal	Environment	Spatial (AEM)	Temporal (AEM)	Type of river
	Turbidity	X1	T1	Dummy variable
	Secchi	X2	T5	
	Total nitrogen	X10		
	Width	X8		
	Conductivity	X13		
	Depth	X4		
	Nitrate	X5		
		X6		
		X3		
		X9		
		X7		
		X11		
Adj. R^2	0.06	0.11	0.01	0.04

Brepl	Environment	Spatial (AEM)	Temporal (AEM)	Type of river
	Conductivity	X1	T2	Dummy variable
	Secchi	X10	T1	
	Turbidity	X2	T5	
	Total nitrogen	X4	T4	
	Depth	X13	T7	
	Width	X5		
	Dissolved oxygen	X6		
	Phosphate	X3		
		X7		
		X8		
		X11		
		X9		
Adj. R^2	0.09	0.16	0.01	0.03

Brich	Environment	Spatial (AEM)	Temporal (AEM)	Type of river
	ISM	X2	T1	Dummy variable
	Turbidity	X8	T4	
	Width	X4		
Adj. R^2	0.04	0.08	0.01	0.02

APPENDIX L - Phytoplankton-based db-RDA variable selection

Table S3. Phytoplankton-based db-RDA variable selection and cumulative adj. R^2 values obtained through forward selection. Abbreviations: ISM = inorganic suspension material, Btotal = total beta diversity, Brepl= replacement, Brich= richness-difference, X =spatial variables, T=temporal variables.

Btotal	Environment	Spatial (AEM)	Temporal (AEM)	Type of river
	Total phosphorus	X10	T2	Dummy variable
	Nitrate	X3	T1	
	Conductivity	X2	T5	
	Total nitrogen	X6	T4	
	Turbidity	X1	T3	
	Alkalinity	X4	T7	
	Ammonium	X8		
	ISM	X9		
Adj. R^2	0.04	0.04	0.03	0.02

Brepl	Environment	Spatial (AEM)	Temporal (AEM)	Type of river
	Total phosphorus	X10	T2	Dummy variable
	pH	X2	T1	
	Total nitrogen	X1	T5	
	Nitrate	X3	T4	
	Alkalinity	X8	T7	
	Ammonium	X9		
Adj. R^2	0.05	0.04	0.03	0.02

Brich	Environment	Spatial (AEM)	Temporal (AEM)	Type of river
	Turbidity	X4	T1	Dummy variable
	Nitrate	X10	T4	
		X6		
		X3		
Adj. R^2	0.07	0.07	0.03	0.01

APPENDIX M - Principal components analysis (PCA) performed with environmental variables

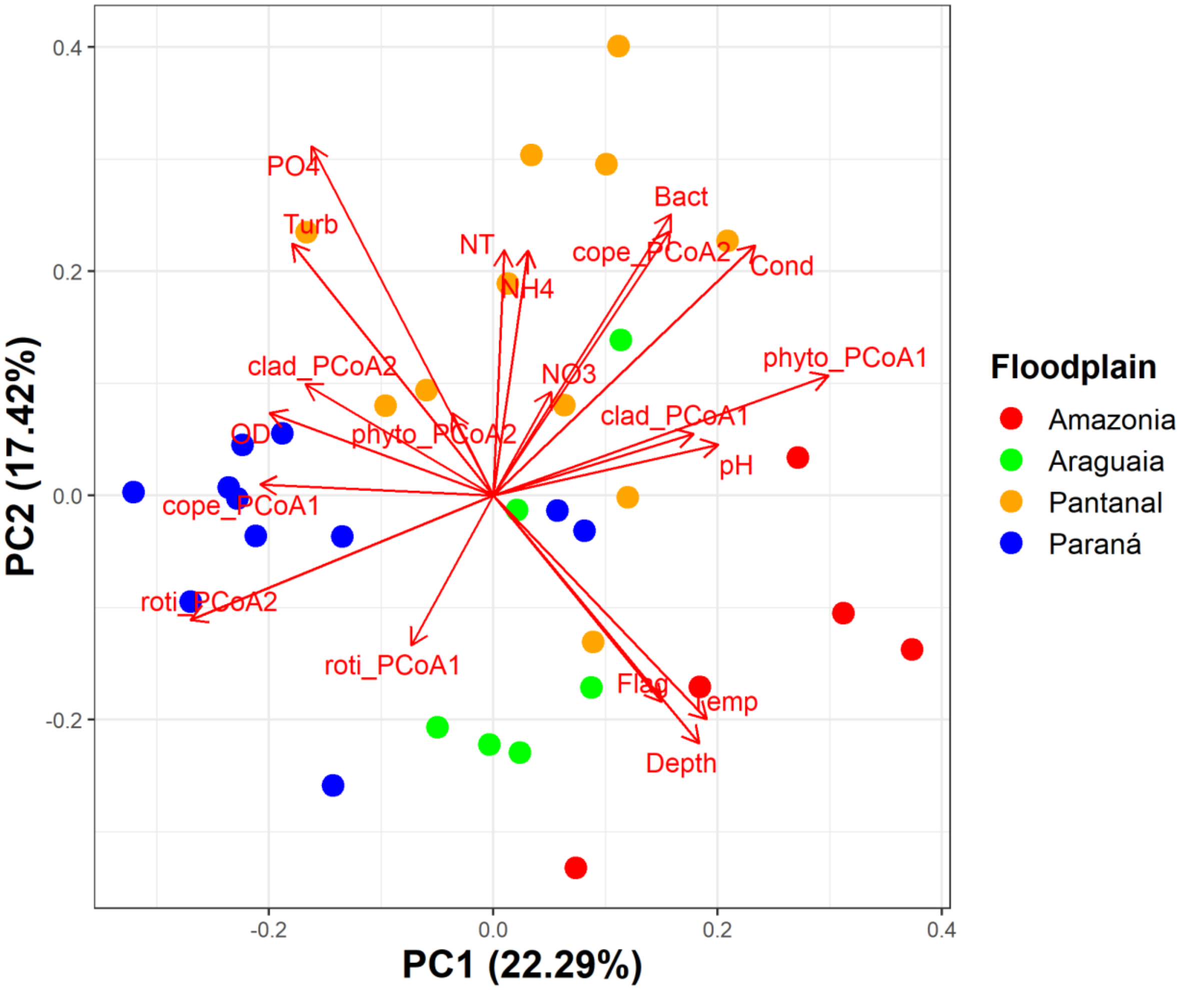

Fig. S1: Principal components analysis (PCA) performed with environmental variables used in variation partitioning analysis to describe the relationship with morphological- and molecular-based approaches. Temp = water temperature, Flag = flagellates, Bact = bacteria, Turb = turbidity, Cond = conductivity, OD = dissolved oxygen, NT = total nitrogen, PO4 = phosphate, NH4 = ammonia, phyto_PCoA1 = first axis of phytoplankton-based PCoA, phyto_PCoA2 = second axis of phytoplankton-based PCoA, roti_PCoA1 = first axis of rotifer-based PCoA, roti_PCoA2 = second axis of rotifer-based PCoA, clad_PCoA1 = first axis of cladocerans-based PCoA, clad_PCoA2 = second axis of cladocerans-based PCoA, cope_PCoA1 = first axis of copepods-based PCoA, cope_PCoA2 = second axis of copepods-based PCoA.

APPENDIX N - Geographic coordinates of each sampled lake

Table S1: Geographic coordinates (degree decimal) of each sampled lake and the respective floodplain to which they are located

Floodplain	**Lake**	**latitude**	**longitude**
Amazonia	MonteCristo	-3.277	-60.67
Amazonia	Calado	-3.3082	-60.5713
Amazonia	Castanho	-3.4	-60.2266
Amazonia	Poraquequara	-3.0087	-59.8255
Amazonia	Comprido	-3.2428	-59.9731
Araguaia	Brito	-13.1764	-50.5821
Araguaia	MontariaII	-13.3953	-50.7048
Araguaia	CrixasIV	-13.3438	-50.6111
Araguaia	JaponesII	-13.4232	-50.6493
Araguaia	MontariaI	-13.4022	-50.7195
Araguaia	MontariaIII	-13.3798	-50.6714
Pantanal	Figueira	-19.4066	-57.3136
Pantanal	MirandaII	-19.4188	-57.3136
Pantanal	IlhaGrande	-19.4259	-57.3532
Pantanal	Rebojão	-19.5834	-56.9894
Pantanal	BaiaPonte	-19.5032	-57.4275
Pantanal	MirandaI	-19.4272	-57.3161
Pantanal	BaíaBugre	-19.512	-57.3909
Pantanal	Mirandinha	-19.4046	-57.3009
Pantanal	BaíaCaceres	-18.9784	-57.7286
Pantanal	Tuiuiu	-18.8083	-57.655
Pantanal	Albuquerque	-19.4004	-57.3637
Paraná	Pombas	-22.7989	-53.3591
Paraná	Manezinho	-22.7791	-53.3491
Paraná	Patos	-22.826	-53.5528
Paraná	Onça	-22.6635	-53.2005
Paraná	Guaraná	-22.7213	-53.3026
Paraná	BocadoIpoitã	-22.8355	-53.5654
Paraná	Sumida	-22.7819	-53.4895
Paraná	Fechada	-22.7105	-53.2759
Paraná	Peroba	-22.9084	-53.6401
Paraná	Aurélio	-22.693	-53.2307
Paraná	FinadoRaimundo	-22.7993	-53.5414

APPENDIX O - Results of permutational multivariate analysis of variance

Table S2: Results of permutational multivariate analysis of variance (PERMANOVA) main and pair-wise tests, applied to morphological and molecular dissimilarities (Jaccard index) of the ciliates communities, considering the four major South American floodplain systems. Bold p-values indicate significance at $p<0.05$, df = degrees of freedom, SS = sum of squares, MS = mean square.

PERMANOVA	**df**	**SS**	**MS**	**F value**	**R^2**	**Pr(>F)**
Morphological						
Floodplain	3	2.1908	0.73026	2.6055	0.21231	**0.0001**
Molecular (HTS)						
Floodplain	3	1.6217	0.54057	3.223	0.25005	**0.0001**

Post-hoc PERMANOVA	**df**	**R^2**	**Pr(>F)**
Morphological			
Paraná x Pantanal	1	0.10407	**0.001**
Paraná x Araguaia	1	0.14065	**0.007**
Paraná x Amazonia	1	0.15713	**0.001**
Pantanal x Araguaia	1	0.14971	**0.005**
Pantanal x Amazonia	1	0.13957	**0.001**
Araguaia x Amazonia	1	0.20733	**0.002**
Molecular (HTS)			
Paraná x Pantanal	1	0.10763	**0.001**
Paraná x Araguaia	1	0.12826	**0.001**
Paraná x Amazonia	1	0.12655	**0.002**
Pantanal x Araguaia	1	0.12001	**0.002**
Pantanal x Amazonia	1	0.12414	**0.001**
Araguaia x Amazonia	1	0.16442	**0.003**

APPENDIX P - Two-way analysis of variance testing for differences in distance to centroid between morphological and molecular approaches

Table S3: Two-way analysis of variance (Two-Way ANOVA) testing for differences in distance to centroid between morphological and molecular approaches and all floodplains. Bold p-values indicate significance at a = 0.05, df = degrees of freedom, SS = sum of squares, MS = mean square.

Two-way ANOVA	**df**	**SS**	**MS**	**F value**	**Pr(>F)**
Taxonomy	1	0.2175	0.21745	33.402	**0.0000**
Floodplain	3	0.0812	0.02707	4.157	**0.0096**
Tukey HSD	**df**	***P* adj.**			
Araguaia-Amazonia	1	0.07378			
Pantanal-Amazonia	1	0.46121			
Paraná-Amazonia	1	0.995705			
Pantanal-Araguaia	1	0.509069			
Paraná-Araguaia	1	**0.00945**			
Paraná-Pantanal	1	0.149015			

ANNEX A - Research papers accepted or published during the doctoral development period that contributed to the execution of this thesis

1. **LANSAC-TÔHA, F. M.**; BINI, L. M.; HEINO, J.; MEIRA, B. R.; SEGOVIA, B. T.; PAVANELLI, C. S.; BONECKER, C. C.; DEUS, C. P.; BENEDITO, E; ALVES, G. M.; MANETTA, G. I.; DIAS, J. D.; VIEIRA, L. C. G.; RODRIGUES, L. C.; ROBERTO, M. C.; BRUGLER, M. R.; LEMKE, M. J.; TESSLER, M.; DESALLE, R.; MORMUL, R. P.; AMADIO, S.; LOLIS, S. F.; JATI, S.; SIQUEIRA, T.; SILVA, W. M.; HIGUTI, J.; LANSAC-TÔHA, F. A.; MARTENS, K.; VELHO, L. F. M. Scale-dependent patterns of metacommunity structuring in aquatic organisms across floodplain systems. JOURNAL OF BIOGEOGRAPHY, *in press*.

2. QUIRINO, B. A., **LANSAC-TÔHA, F. M.**, THOMAZ, S. M., HEINO, J.; FUGI, R. Macrophyte stand complexity explains the functional α and β diversity of fish in a tropical river-floodplain. AQUATIC SCIENCES, *in press*.

3. GOLEC-FIALEK, C.; **LANSAC-TÔHA, F. M.**; BONECKER, C. C. Response of the zooplankton community to extreme hydrological variations in a temporary lake in a neotropical floodplain system. LIMNOLOGICA, *in press*.

4. BAUMGARTNER, M. T., & **LANSAC-TÔHA, F. M.** Assessing the relative contributions of healthcare protocols for epidemic control: an example with network transmission model for COVID-19. medRxiv., 2020. doi: https://doi.org/10.1101/2020.07.20.20158576

5. BAUMGARTNER, M. T., **LANSAC-TÔHA, F. M.**, COELHO, M. T. P., DOBROVOLSKI, R.; DINIZ-FILHO, J. A. F. Social distancing and movement constraint as the most likely factors for COVID-19 outbreak control in Brazil. MEDRXIV, 2020. doi: https://doi.org/10.1101/2020.05.02.20088013.

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9. MENDES, P. M. SACHERTT; **LANSAC-TÔHA, F. M.**; MEIRA, B. R.; OLIVEIRA, F. R.; VELHO, L. F. M.; LANSAC-TÔHA, F. A. Heterotrophic flagellates (Amorpha and Diaphoretiches) in phytotelmata bromeliad (Bromeliaceae). BRAZILIAN JOURNAL OF BIOLOGY, v. 1, p. 1-13, 2019.

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