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RAMIRO DE CAMPOS

Evaluating drivers and patterns of aquatic community distribution in Neotropical floodplain systems: an approach based on beta-diversity analyses

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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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que torceram por mim e que
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“Estamos na situação de uma criancinha que entra em uma imensa biblioteca, repleta de livros em muitas línguas. A criança sabe que alguém deve ter escrito aqueles livros, mas não sabe como. Não compreende as línguas em que foram escritos. Tem uma pálida suspeita de que a disposição dos livros obedece a uma ordem misteriosa, mas não sabe qual ela é”.

(Albert Einstein)

“Nobody said it was easy
No one ever said it would be this hard”.
(Coldplay)

Avaliando os preditores e padrões da distribuição de comunidades aquáticas em sistemas de planície de inundação Neotropical: uma abordagem baseada em análises de diversidade-beta

RESUMO

Avaliar os padrões e preditores da distribuição de espécies é importante, visto que as ações antrópicas têm ameaçado a biodiversidade global. Para isso, pesquisadores têm usado medidas de diversidade-beta, definida como a variação na composição de espécies entre os locais de uma determinada área. Várias medidas de diversidade-beta têm sido produzidas, visto que através desta abordagem tem sido simples elaborar e testar hipóteses ecológicas, considerando a distribuição de espécies. O objetivo desta tese foi contribuir para o conhecimento de padrões e preditores da distribuição de comunidades aquáticas de planícies de inundação Neotropicais. Assim, foi fracionada em duas abordagens, onde foram utilizados dois métodos diferentes de medida de diversidade-beta. Na primeira abordagem, foi avaliado os fatores ambientais e espaciais que afetam as facetas da diversidade-beta (baseado nas espécies, traços e filogenia) e seus componentes (beta-total, *replacement* e *richness difference*), das comunidades de ostrácodes associados a diferentes formas de vida de macrófitas aquáticas, na planície de inundação do alto rio Paraná. Esses fatores foram comparados entre as diferentes formas de vida: emergentes, submersas e flutuantes enraizadas e submersas e flutuantes livres. Na segunda abordagem, foi utilizada a análise da contribuição local para a diversidade-beta (LCBD) para avaliar os preditores e padrões da singularidade dos locais, considerando a composição de espécies, em quatro planícies de inundação, Amazonas, Araguaia, Pantanal e Paraná. Para isso, foram analisados oito grupos biológicos aquáticos: fitoplâncton, ciliados, amebas testáceas, rotíferos, cladóceros, copépodes, ostrácodes e peixes. Em geral, os filtros ambientais foram mais importantes para explicar os padrões de distribuição das comunidades, e o mecanismo *species sorting* pode ser responsável por tais padrões, dentro e entre as planícies de inundação. Na primeira abordagem, diferentes fatores ambientais e espaciais influenciaram cada uma das facetas da diversidade-beta de ostrácodes (baseadas nas espécies, traços e filogenia). Ademais, os fatores que afetaram a diversidade-beta de ostrácodes foram diferentes entre as formas de vida das macrófitas aquáticas, evidenciando a necessidade de considerá-las em estudos ecológicos considerando as comunidades associadas. Na segunda abordagem, as planícies de inundação do Amazonas e Paraná foram as mais singulares em termos de composição de espécies, que avaliam a importância da preservação destes ecossistemas. Os padrões e preditores (variáveis ambientais) da LCBD foram diferentes entre os grupos biológicos, confirmando a importância de incluir diferentes taxa. Os resultados desta tese, baseados em análises de diversidade-beta, contribuíram para um melhor entendimento sobre os padrões e preditores da distribuição de comunidades aquáticas de planícies de inundação Neotropicais. Dessa forma, eles podem ser usados por pesquisadores como referência para planos de restauração e conservação destes ecossistemas, assim como evitar que áreas de grande valor de conservação sejam impactadas, por exemplo, pela construção de reservatórios e hidroelétricas

Palavras-chave: Fatores ambientais e espaciais. Filogenia e traços. LCBD. Escalas regionais e subcontinentais. Conservação. Amazonas.

Evaluating drivers and patterns of aquatic community distribution in Neotropical floodplain systems: an approach based on beta-diversity analyses

ABSTRACT

Evaluating patterns and predictors of species distribution is important, because anthropogenic actions have been threatening global biodiversity. Hence, researchers have used measures of beta-diversity, defined as the variation in species composition amongst sites of a given area. Several measures of beta-diversity have been created, because using this approach makes it simple to elaborate and test ecological hypotheses, considering species distribution. Here, it was aimed to contribute to the knowledge about drivers and patterns of distribution amongst aquatic communities in Neotropical riverine floodplains. For this, this thesis was fractionated into two approaches, in which was used two different methods to measure beta-diversity. In the first approach, it was assessed the environmental and spatial factors affecting the beta-diversity facets (species-, traits- and phylogeny-based), and their components (Beta-total, replacement and richness difference), of ostracod communities associated with macrophytes, in the Upper Paraná River floodplain. Furthermore, it was compared these factors amongst the different life forms: emergent, rooted floating, rooted submerged, free submerged and free floating. In the second approach, it was used the local contribution to beta-diversity approach (LCBD) to evaluate the drivers and patterns of ecological uniqueness of the sites, in terms of species composition, in four floodplain systems, Amazon, Araguaia, Pantanal and Paraná. It was gathered data on community composition for eight aquatic biological groups: phytoplankton, ciliates, testate amoebae, rotifers, cladocerans, copepods, ostracods and fish. In general, environmental filtering was more important in explaining distribution patterns of communities, and the species sorting mechanism might be responsible for them, within and amongst the floodplains. In the first approach, different environmental and spatial factors influenced each of the beta-diversity facets of ostracod communities (species-, traits- and phylogeny-based). The factors affecting ostracod beta-diversity were different amongst the macrophyte life forms, evidencing the importance of considering them in ecological surveys of associated communities. In the second approach, the Amazon and Paraná floodplains had higher uniqueness in terms of species composition, showing the importance of conservation actions in these ecosystems. Furthermore, the drivers (e.g. environmental variables) and patterns of LCBD were different amongst the different biological groups, evidencing the need to include a variety of taxa. It was considered that the results of this thesis, based on beta-diversity analyses, contributed to a better understanding of drivers and patterns of distribution amongst communities in Neotropical floodplains. This is because researchers can use them as a reference in conservation and restoration plans for these systems and to prevent the destruction of areas with high conservation value, for example, by the construction of dams and reservoirs.

***Keywords*:** Environmental and spatial factors. Phylogeny and traits. LCBD. Regional and subcontinental scales. Conservation. Amazon.

Tese elaborada e formatada conforme as normas de publicações científicas *Aquatic Sciences*[1] e *Freshwater Biology*.

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SUMMARY

1 GENERAL INTRODUCTION

One of the main goals of community ecology is to explain patterns of distribution, abundance and interaction of species (Leibold et al., 2004). These patterns are usually attributed to factors operating on a wide range of spatial scales, including local (e.g. habitat conditions) and regional factors (e.g. dispersal processes) (Göthe et al., 2017). Understanding these patterns, as well as factors driving them, is essential for conservation and restoration planning, since over the last few decades global ecosystems have undergone biodiversity losses due to factors caused by anthropogenic action (Cardinale et al., 2012). These factors include air, soil and water pollution, habitat losses, over-exploitation of species, invasive species, climate change (Singh et al., 2021), construction of dams and reservoirs, and flood regulation (Souza Filho, 2009).

Beta-diversity, defined as “the variability in species composition amongst sampling units for a given area” (Anderson et al., 2006), has been widely used for assessing diversity patterns, controlled by local and regional factors (Rickefs, 1987). Beta-diversity has been partitioned into two components: turnover (or replacement) and nestedness (Baselga, 2010). Spatial turnover is the replacement of species by others, owing to environmental filtering or spatial effects (Yang et al., 2018), whereas nestedness occurs when sites with a smaller number of species are a subset of richer sites (Baselga, 2010). However, Carvalho et al. (2012) proposed that nestedness is a particular case of species richness gradient, and beta-diversity should be analyzed through turnover and species differences (the gain or loss of species) components.

Because beta-diversity can be driven by several ecological processes, it can be easily used by researchers in developing hypotheses considering geographical patterns in diversity (Soininen et al., 2007). Consequently, several approaches related to beta-diversity measures have been proposed in the literature (Legendre, 2019), using both incidence and abundance data from communities (Beck et al., 2013). For example, studies have evaluated beta-diversity and its components (turnover and richness difference), based not only on the taxonomic identity of species, but including traits and phylogeny of species in their analyses. This is because communities can be similar in their compositional diversity, based on the taxonomic identity of species, and, at the same time, they can differ in their functional and/or phylogenetic diversity (Krasnov et al. 2019). Thus, integrating these different facets in beta-diversity analyses provides complementary and valuable information about community structuring (Alahuhta et al. 2019).

Another approach that has been used by researchers is based on the assessment of the local contribution to beta diversity (LCBD, Legendre & Cáceres, 2013). Through this index, it is possible to assess the ecological uniqueness of the sites, in terms of species composition (Archidona-Yuste, 2020). Thus, high values of LCBD can indicate that sites present a unique set of species, probably with several rare species, and that they have high conservation value, considering that the species are native (Li et al., 2020). On the other hand, sites with low LCBD values can be degraded or poor in species and considered in need of restoration (Legendre and Cáceres, 2013). High LCBD values can also indicate that the sites have unusual habitat conditions or even a set of invasive alien species (Vilmi et al., 2017).

Riverine floodplains are excellent ecosystems to study distribution patterns of a community, as they are dynamic systems, with high spatial and temporal heterogeneity (Junk et al., 1989). Furthermore, they present a wide variety of habitats, such as temporary and permanent lakes (connected or isolated), channels, backwaters, etc., which are very important for biodiversity maintenance (Thomaz et al., 2007). Studies have evaluated drivers and patterns of beta-diversity of several biological groups in riverine floodplain systems, such as phytoplankton (Nabout et al., 2007), zooplankton (Bozelli et al., 2015; Souza et al., 2021), ostracods (Conceição et al., 2017), fish (Quirino et al. 2021) and macrophytes (Pozzobom et al., 2020). However, only a few studies have integrated multiple biological groups sampled in the same set of locations (De Bie et al., 2012). Thus, evaluating changes in the patterns of community structure (such as in beta-diversity) in floodplain systems is necessary for conservation and restoration plans, as these ecosystems are amongst the most threatened by anthropogenic influence in recent decades (e.g. dam construction and habitat degradation worldwide, Tockner & Stanford., 2002).

The aim of this thesis was to contribute to the knowledge about drivers and patterns of distribution of aquatic communities in Neotropical floodplain systems. For this, it was divided into two approaches, corresponding to two independent studies, where it was performed two different beta-diversity analyses. In the first approach, it was assessed the factors affecting beta-diversity facets (species-, traits- and phylogeny-based) and their components (Beta-total, replacement and richness difference) of ostracod communities associated with macrophytes, in the Upper Paraná River floodplain. Furthermore, it was compared these factors amongst different macrophyte life forms. For this, it was used the procedures of the Biodiversity Assessment Tools (Cardoso et al., 2015), which allowed us to estimate each of the facets of beta-diversity, as well as partitioning them into the replacement and richness difference components. In the second approach, it was evaluated the drivers and patterns of ecological uniqueness of the sites, in terms of species composition, in four floodplain systems, namely the Amazon, Araguaia, Pantanal and Paraná, analyzing eight aquatic biological communities: phytoplankton, ciliates, testate amoebae, rotifers, cladocerans, copepods, ostracods and fish. For this, it was the LCBD approach (Legendre & Cáceres, 2013), which allows to assess sites with a unique set of species.

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2 MACROPHYTE LIFE FORMS INFLUENCE THE EFFECTS OF ENVIRONMENTAL AND SPATIAL FACTORS ON THE BETA-DIVERSITY OF ASSOCIATED OSTRACOD COMMUNITIES (CRUSTACEA)

ABSTRACT

Beta-diversity measures have been used to understand patterns of community distribution in natural ecosystems. Recent studies included different facets of beta-diversity analyses, e.g. trait- and phylogeny-based. Here, we used ostracod communities to evaluate the influence of environmental and spatial factors structuring different facets of beta-diversity and their components (Beta-total, replacement and richness-difference) of ostracod communities associated with different macrophyte life forms. We test the hypotheses (1) that the influence of environmental factors is higher for ostracod beta-diversity facets of communities associated with submerged plants compared to emergent and floating plants and (2) that the influence of spatial factors is higher in communities associated with rooted, compared to non-rooted plants. Ostracods were sampled from five life forms of macrophytes, including emergent, rooted floating, rooted submerged, free submerged and free floating in 25 floodplain lakes. Our results showed that the environmental factors turned out to be important for all beta-diversity facets of ostracod communities, mainly for those associated with submerged macrophytes, thus corroborating the first hypothesis. We also found that spatial factors' influence on ostracod beta-diversity was not related to whether the plant is rooted or not, thus refuting our second hypothesis. We also found differences in factors structuring each of the beta-diversity facets, showing the importance to include these three approaches (species-, traits- and phylogeny-based) in ecological surveys. Finally, we highlight the importance of considering different macrophyte life forms in biodiversity surveys for the preservation and management of the diversity of these plants and their associated communities.

Keywords: Aquatic plants, Ostracoda, microcrustaceans, tropical floodplain, local and regional factors

2.1 Introduction

Understanding the patterns of community distribution in natural ecosystems, as well as the factors (e.g. local and regional) structuring such patterns, are amongst the main goals of ecological studies (Holyoak et al. 2005). Beta-diversity, which is defined as “the variability in species composition amongst sampling units for a given area” (Anderson et al. 2006), is one of the main concepts that has been used to evaluate such patterns of community distribution (Anderson et al. 2011). Dissimilarities between communities have been attributed to two different processes, nl. species replacement or turnover (species are replaced by other species from site to site; Baselga 2010); and richness differences (the gain or loss of species from site to site; Legendre 2014).

In general, studies including beta-diversity measures are based on the taxonomic identity of species (Leibold et al. 2004). However, the communities can be similar in their compositional diversity (based on taxonomic identity of species) and, at the same time, they can differ in their functional and/or phylogenetic diversity (Krasnov et al. 2019), or vice versa (Weinstein et al. 2014). Thus, to overcome this information gap, several authors have measured other aspects of biodiversity, including trait- and phylogenetic-based analyses (Perez Rocha et al. 2018; Alahuhta et al. 2019; Cai et al. 2019; Krasnov et al. 2019). The use of traits helps to understand how species can live, the interaction amongst them, and their contribution to ecosystem functioning (Cadotte et al. 2011). On the other hand, phylogenetic beta-diversity analyses, which measure how phylogenetic relationships amongst species change across space (Graham and Fine 2008), provide information about shared phylogenetic history between two communities (Graham et al. 2009). Besides, this approach helps to identify the ability of communities to generate new evolutionary solutions in the face of environmental changes (Forest et al. 2007). Integrating these different facets in beta-diversity analyses provides complementary and valuable information about community structuring (Alahuhta et al. 2019).

Riverine floodplains are excellent ecosystems to study patterns of community distributions, owing to their wide variety of environments, such as rivers, channels and closed/open lakes, high habitat heterogeneity and high biological diversity (Junk et al. 1989). Aquatic macrophytes are abundant in South American floodplains and they play a role as food resource (Neiff and Casco 2003), in nutrient cycling (Thomaz and Cunha 2010), as a habitat for many organisms, such as fishes (Walker et al. 2013) and associated invertebrates (Rocha and Por 1998; Thomaz and Cunha 2010; Fontanarossa et al. 2013).

Macrophytes have been grouped, according to their life form, in emergent, rooted floating, rooted submerged, free submerged and free floating (Pott and Pott 2000; Souza et al. 2017). Each life form is located in different regions of the water column, mainly related to water characteristics (e.g. chemical and physical variables), leading to different habitat suitability for associated communities (Yamaki and Yamamuro 2013). This variation in environmental characteristics (environmental factors) of the water, for example in temperature, pH, dissolved oxygen and electrical conductivity, are expected to influence the occurrence and structure of associated faunal communities (Nagorskaya and Keyser 2005; Liberto et al. 2012; Mesquita-Joanes et al. 2012). In addition, the influence of spatial factors (e.g. dispersal limitation) is different between aquatic macrophytes, according to their life form (Alahuta and Heino 2013). The efficiency of dispersal might be related to the capacity of the plants to break themselves up (e.g. fixed plants) and regrow from broken dispersed fragments (Bornette and Puijalon 2011) or to detach from the littoral areas of floodplain lakes (e.g. free floating plants), drift in the main channel of rivers and reach other environments (Bulla et al. 2011).

Several studies have evaluated the relationship between the taxonomic identity or structural complexity of the macrophytes (e.g. measured by fractal dimension) and the structure of associated communities (McAbendroth et al. 2005; Matsuda et al. 2015), and it is well-known that the more complex the plant, the higher the diversity of associated animal communities (Thomaz et al. 2008). However, few studies have tested the effects of the different life forms of macrophytes on associated communities (Meerhoff et al. 2003; Cazzanelli et al. 2008; Choi et al. 2014). Thus, the aim of the present study was to evaluate factors affecting the beta-diversity facets (species-, traits- and phylogeny-based) and their components (Beta-total, replacement and richness difference) of ostracod communities associated with macrophytes and to compare these factors amongst different macrophyte life forms. From that, we also assess if the choice of the type of habitat (here: different macrophyte life forms) is an important factor to be considered in studies evaluating beta-diversity of associated animal communities.

We used ostracod (Crustacea) communities, one of the most abundant groups in freshwater ecosystems (see Thomaz et al. 2008; Bornette and Puijalon 2011; Liberto et al. 2012; Mazzini et al. 2014; Higuti and Martens 2016; Pereira et al. 2017), associated with five life forms of macrophytes, as a model group. We test two main hypotheses: (1) submerged plants (free submerged and rooted submerged) will have a more pronounced influence on the effects of environmental factors on the beta-diversity of associated ostracod communities than emergent and floating (free floating and rooted floating) plants. This is expected, because aquatic abiotic variables (e.g. water transparency, dissolved oxygen and water temperature) will have a larger impact on submerged plants, and thus also on associated (animal) communities; (2) the influence of the spatial factors (such as dispersal limitation) on ostracod beta-diversity facets will be higher for fixed (emergent, rooted floating and rooted submerged), compared to non-fixed plants in the sediment (free submerged and free floating). This is based on the expectation that fixed plants have lower dispersal capacity through the region, compared to the unrooted, floating macrophyte life forms. The distribution of ostracod communities associated with these different life forms in macrophytes will thus also be affected by this. Finally, we also test if there are mismatches in the factors (environmental and spatial) structuring each beta-diversity facet (and their components) in each macrophyte life form.

2.2 Material and Methods

2.2.1 Study site

The Upper Paraná River section is 230 km long and can reach 20 km of width, including several secondary channels and floodplain lakes (Agostinho et al. 2004). It has an extensive floodplain, approximately 60 km long, located within the Brazilian territory (Paraná and Mato Grosso do Sul states). The study area is a river-floodplain system, which encompasses three different river systems: Ivinhema, Paraná and Baía, each one with its peculiar geology, hydrology and limnology (Souza Filho 2009) (Electronic Supplementary Material, Table S1). We selected 25 permanently connected lakes along the Upper Paraná River floodplain, with eight lakes in the Ivinhema system, eight lakes in the Baía system and nine lakes in the Paraná system (Fig. 1).

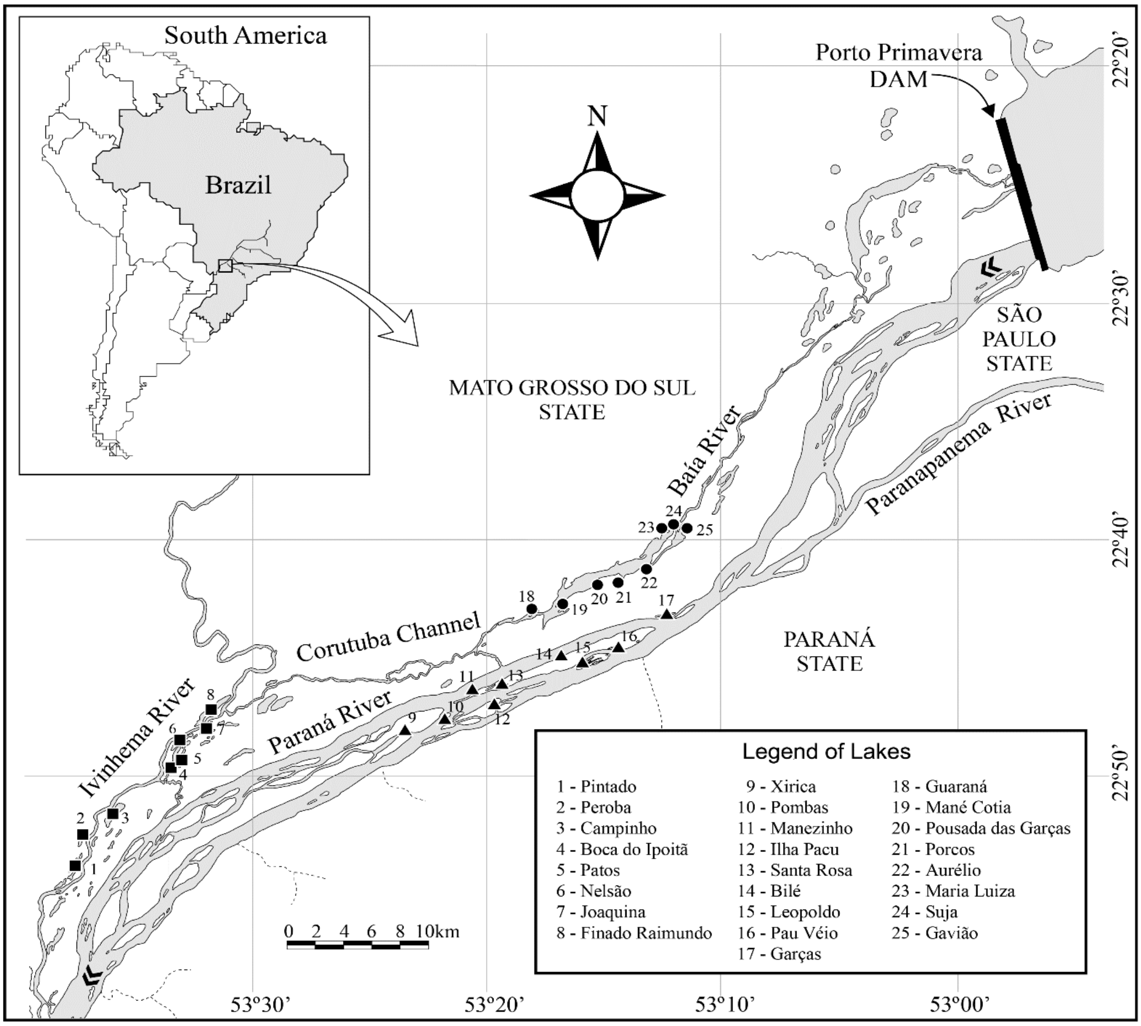

Fig. 1 Position of the twenty-five lakes in the Upper Paraná River floodplain, Brazil. Ivinhema (1-8), Paraná (9-17) and Baía (18-25) systems.

2.2.2 Sampling and laboratory analysis

Ostracod communities associated with macrophytes were sampled between March 20th and 22nd in 2018. We collected samples of five life forms of macrophytes: emergent (EM), rooted floating (RF), free floating (FF), rooted submerged (RS) and free submerged (FS). The macrophytes species belonging to each life form, are shown in the Electronic Supplementary Material (Table S2), and they were classified according to their life form following Pott and Pott (2000).

To standardize our sampling effort, we collected one sample of each macrophyte life form in each lake (when present). The sampling sites of each lake (one for each macrophyte life form) were chosen visually, based on the largest macrophyte bed of each life form. This selection was made because the larger the patches, the higher the chance of a good representation of the ostracod community in terms of diversity (e.g. richness, density and composition). However, not all life forms of macrophytes were always found in all lakes (see Electronic Supplementary Material, Table S2). A total of 75 samples were collected in 25 lakes, with 20 RF samples, 19 FF samples, 17 EM samples, 10 FS samples and 9 RS samples.

Ostracods associated with emergent macrophytes were sampled with a rectangular hand net (28x14 cm and mesh size of 160 µm), which was moved amongst the plants. Macrophytes with RF, FF, RS and FS life forms were removed manually from the water and transferred to a plastic bucket (see Campos et al. 2017). Either the entire plants or only the roots were washed to remove the ostracods. The material retained in the bucket was washed through a hand net (mesh size of 160 µm). The sampling methods have been shown as adequate to represent associated fauna (see Higuti et al. 2009, 2010, Castillo-Escrivà et al. 2016b, Campos et al. 2017). All material was preserved in 70º ethanol buffered with sodium tetraborate. In the laboratory, ostracods were sorted using a stereoscopic microscope and were identified down to species level (see Martens and Behen 1994 and articles included therein; Rossetti and Martens 1998; Higuti and Martens 2012a, b, 2014; Higuti et al. 2013; Ferreira et al. 2020).

2.2.3 Ostracod traits and taxonomic information

Ostracods were classified according to the functional traits: locomotion mode, body size, presence/absence of spines, general body morphology and reproductive mode (Electronic Supplementary Material, Tables S3). The locomotion mode was differentiated, considering the presence/absence or the length of natatory setae on the Antenna, in two categories: swimmer (long setae) and non-swimmer (reduced setae or setae absent, Meisch 2000). The body size classification was based on the length (L) and height (H) of the ostracod carapace. These measurements were obtained mostly using scanning electron microscopy (SEM) and in some cases with a stereoscope microscope. The species were categorized as small ($L \leq 0.54$ mm and/or $H \leq 0.32$ mm), medium ($0.55 \leq L \leq 1.32$ mm and/or $0.33 \leq H \leq 0.72$ mm) and large ($L > 1.32$ mm and/or $H > 0.72$ mm) (Matsuda et al. 2015). Spines of any size were classified as present/absent, according to visual observations of the ostracod carapace in a stereoscope microscope and SEM. Amongst the species treated here, all spines (when present) were relatively large. Reproductive mode was differentiated in parthenogenic, sexual and mixed reproduction. Body morphology was distinguished in flat (laterally compressed) and rounded in dorsal or ventral view, according to Martens and Behen (1994) and articles included therein; Rossetti and Martens (1998); Meisch (2000); Higuti and Martens (2012a, b, 2014); Higuti et al. (2013) and Ferreira et al. (2020). All these traits were chosen owing to their importance in life history characteristics (e.g. body size, Matsuda el al. 2015), dispersal limitation (e.g. locomotion mode and body morphology, Matsuda et al. 2015), defence against predators (e.g. presence of spines) and population establishment (e.g. reproductive mode, Horne et al. 1998) of ostracod species. Besides, these are the traits for which we have complete information for all taxa found in our survey.

We used taxonomic distance based on the path lengths in the Linnean taxonomic trees as a proxy for phylogeny (Clarke and Warwick 1998; Winter et al. 2013). Six taxonomic levels were included in this taxonomic tree: species, genus, tribe, subfamily, family and superfamily, and we followed Meisch et al. (2019) for higher taxonomy (Electronic Supplementary Material, Table S4).

2.2.4 Environmental and spatial factors

Chemical and physical variables, such as pH and electrical conductivity (µS cm^{-1}) (YSI 63), dissolved oxygen (mg L^{-1}) and water temperature (ºC) (YSI 550A oximeter), and water transparency (black and white Secchi disk) were measured *in situ*. The perimeter (in km) of the lakes and length of the meandering channel that connect each lake to the main river (in km) were obtained through the Google Earth image program, all from images taken during the dry season. All these variables (see Electronic Supplementary Material, Table S1), were considered “environmental factors”.

We generated the “spatial factors” calculating matrices of Euclidean distances (“overland”, derived from geographical coordinates) of the sites. These matrices were submitted to the PCNM method (Principal Coordinates of Neighbour Matrices) for the construction of the eigenvectors (explanatory spatial variables, Borcard and Legendre 2002). The PCNM analysis was truncated by minimum distance that kept all sampling sites connected (minimum spanning tree procedure, Landeiro et al. 2011). In the present study, the first PCNMs generated represent larger scales of amplitude, whereas the latter ones represent smaller scales of amplitude. Campos et al. (2019) compared three methods to generate spatial effects on ostracod metacommunities, “overland”, “watercourse” (considering distances amongst the environments, following watercourse) and Asymmetric Eigenvectors Maps (AEM, considering the sampling sites connected in the watercourse, following the flow direction of the river), and showed that the results for "overland" were similar to the other methods.

2.2.5 Data analysis

We performed rarefaction curves to evaluate if the sampling effort for each macrophyte life form (20 RF samples, 19 FF samples, 17 EM samples, 10 FS samples and 9 RS samples) was sufficient to represent the associate ostracod communities in terms of richness over all 25 lakes. For that, we used Hill numbers through the function *iNEXT* (iNEXT R-package, Hsieh et al. 2016). The iNEXT R-package uses Chao 2 (for incidence data or "reference sample") to estimate the number of undetected species. We used $q = 0$ to estimate species richness and the maximum extrapolated size was up to 100% of the reference sample size. According to Heck et al. (1975), the occurrence of 50%–75% of the estimated richness might be satisfactory (considering that most of the common species were recorded). We assessed possible differences in the ostracod composition amongst the life forms of macrophytes to highlight the relevance of analyzing each life form separately. For this, we first visualized the (dis)similarity in ostracod composition amongst the macrophytes life forms using the Principal Coordinate Analysis (PCoA, Legendre and Legendre 1998), based on a presence/absence matrix and Jaccard index. For testing such (dis)similarity, we performed a Multivariate Permutational Variance Analysis (PERMANOVA, Anderson 2006), using a total of 999 permutations. After that, we used a pairwise PERMANOVA to evaluate ostracod composition (dis)similarity amongst the macrophytes life forms. Finally, we performed Multivariate Dispersion Analysis (PERMDISP, Anderson 2006) to evaluate variability of the dispersion of ostracod communities amongst the macrophytes life forms. PERMDISP was based on a presence/absence matrix and Jaccard index, and the significance amongst the groups (macrophytes life forms) was tested using a total of 999 permutations. When PERMDISP results show significant differences in the variability of dispersal between groups, it can be related to differences in the scatter of data, indicating that the comparisons between groups (e.g. in PERMANOVA results) must be interpreted with caution. PERMANOVA and PERMDISP were performed using the vegan R-package (Oksanen et al. 2017).

We used distance-based redundancy analysis (db-RDA, Legendre and Anderson 1999), as well as variation partitioning procedures (Legendre et al. 2005) to evaluate the influence of environmental and spatial factors on ostracod beta-diversity facets, amongst different life forms of macrophytes. Before the analyses, we checked the multicollinearity amongst the environmental variables (environmental factors) using the variance inflation factor (VIF). Variables with VIF> 10 should be removed (Oksanen et al. 2017).

We used the function *beta* (BAT R-package, Cardoso et al. 2015) according to Perez Rocha et al. (2018) to generated three dissimilarity matrices (with Jaccard family measures): total beta-diversity (B-tot) and its components, replacement (B-repl) and richness difference (Rich-Diff), for each beta-diversity facet. These dissimilarity matrices were based on:

(1) Species: sites x species matrices of presence-absence of ostracods;

(2) Traits: we used the Gower distance (Gower 1971) to calculate between-species distances, based on the traits data, using the function *gowdis* (FD R-package, Laliberté et al. 2014). Subsequently, this species-by-species matrix was subjected to a hierarchical clustering (UPGMA agglomeration method) procedure using the function *hclust* (STATS R-package);

(3) Phylogeny: we used ostracod taxonomic information as a proxy for phylogeny. We used the function *taxa2dist* (vegan R-package) to calculate taxonomic distance between ostracod species. Subsequently, this species-by-species matrix was also subjected to a hierarchical clustering (UPGMA agglomeration method) procedure using the function *hclust* (STATS R-package). The BAT R-package requires an *hclust* object to calculate beta-diversity metrics, thus clustering (phylogenetic tree, such as traits tree) was necessary (Perez Rocha et al. 2018).

After that, average beta-diversity (B-tot) and their components (B-repl and Rich-Diff), based on species, traits and phylogeny, were calculated using the function *beta.multi* (BAT R-package). This function returns three values (also named average values), which represent the total multi-site dissimilarity across the sites (B-tot) and its B-repl and Rich-Diff components. Finally, each of the dissimilarity matrices of each ostracod beta-diversity facet was used in the db-RDA and variation partitioning. The environmental and spatial factors, which should be included in the analyses, were selected using the function *ordiR2step* ($p < 0.05$, 999 permutations, vegan R-package). The db-RDA analyses were performed using the function *capscale* (vegan R-package). Subsequently, ostracod community variation in each of the beta-diversity measures (B-tot, B-repl and Rich-Diff) was partitioned in purely environmental (E|S) and spatial factors (S|E), and in a component explained by the intersection of these factors (E∩S). The results were adjusted R^2 values and the significance of the components was tested using the *Anova* function ($p < 0.05$, vegan R-package). We used the *sqrt.dist* correction in all db-RDA analyses, for negative eigenvalues (Legendre 2014). All the analyses described above were performed separately for ostracod communities associated with each life form of macrophytes, using R 3.4 software (R Core Team 2017).

2.3 Results

2.3.1 Abiotic factors

The mean of the chemical and physical variables was more different between the Ivinhema and Paraná systems (Electronic Supplementary Material, Table S1). The Ivinhema system had the highest mean value of water temperature, lake perimeter and length of the meandering channel, while the Paraná system had the lowest values for the same variables. On the other hand, the Paraná system had the highest mean values of electrical conductivity, pH and water transparency, while the Ivinhema system had the lowest values for these variables. Mean values of all the variables in the Baía system were intermediate amongst the three systems. Lake perimeter, length of the meandering channel, dissolved oxygen and electrical conductivity were the variables that had the highest coefficient of variation amongst the lakes of all systems (see Electronic Supplementary Material, Table S1).

According to the spatial variables, 8 PCNMs were generated for EM, 9 PCNMs for RF, 6 PCNMs for FF and FS, and 4 PCNMs for RS. In EM, PCNMs 1-4 indicate broad-scaled and 5-8 fine-scaled patterns; in RF, PCNMs 1-5 indicate broad-scaled and 6-9 fine-scaled patterns; in FF and FS, PCNMs 1-3 indicate broad-scaled and 4-6 fine-scaled patterns; and in RS, PCNMs 1-2 indicate broad-scaled and 3-4 fine-scaled patterns.

2.3.2 Ostracod communities

We recorded 38 species of ostracods associated with 13 macrophyte species. Higher ostracod richness was found in RF (35 species), followed by FF (33), EM (30), RS (27) and FS (24) (Table 1). The observed richness represents between 82.17% (FS) and 98.45% (EM) of the estimated richness and the rarefaction curves show asymptotic levelling-off (Fig S1). These results suggest that the sampling effort was adequate to represent the ostracod communities in each macrophyte life form.

Table 1 Ostracod species occurrence in different macrophyte life forms in the Upper Paraná River floodplain, indicating the number of lakes where each ostracod species was found, in each macrophyte life form. EM = emergent, RF = rooted floating, FF = free floating, RS =

rooted submerged and FS = free submerged. Values in parenthesis indicate the number of lakes in which the macrophyte life forms were sampled.

	EM (17)	**RF (20)**	**FF (19)**	**RS (9)**	**FS (10)**
Family Cyprididae (Baird 1845)					
Diaphanocypris meridana (Furtos 1936) Würdig and Pinto 1990	12	17	15	8	8
Stenocypris major (Baird 1859) Daday 1898	0	4	4	2	0
Stenocypris malayica Victor & Fernando 1981	0	3	3	3	1
Strandesia psittacea (Sars 1901) Roessler 1990	7	7	6	3	2
Strandesia colombiensis (Roessler 1990) Ferreira et al. 2020	5	6	4	1	3
Strandesia mutica (Sars 1901) G.W. Müller 1912	4	4	7	2	0
Strandesia variegata (Sars 1901) G.W. Müller 1912	3	2	6	0	2
Strandesia tolimensis Roessler 1990	1	5	8	0	1
Strandesia nakatanii Ferreira et al. 2020	6	5	0	3	2
Strandesia lansactohai Higuti and Martens 2013	5	2	0	3	0
Strandesia velhoi Higuti and Martens 2013	9	13	13	5	6
Strandesia nupelia Higuti and Martens 2013	4	4	3	0	0
Bradleytriebella trispinosa (Pinto and Purper 1965) Savatenalinton and Martens 2009	3	7	7	0	2
Bradleytriebella lineata (Victor and Fernando 1981) Savatenalinton and Martens 2009	0	0	1	0	1
Cypricercus alfredo Almeida et al. 2021	5	5	1	2	0
Chlamydotheca deformis Farkas 1958	12	15	15	7	6
Chlamydotheca iheringi (Sars 1901) Klie 1930	6	8	6	5	6
Chlamydotheca cf. *iheringi* sp. 2	7	11	7	2	2
Chlamydotheca sp. 3	3	5	3	1	0
Cypretta costata G.W. Müller 1898	0	2	0	0	1
Cypretta sp. 3 n.sp	8	11	16	2	2
Cypridopsis vidua (O.F. Müller 1776) Brady 1867	9	5	3	5	1
Cypridopsis cf. *vidua* sp. 2	3	1	0	3	1
"*Cypridopsis*" n. gen. 1 n.sp.	9	8	7	1	3
"*Cypridopsis*" n. gen. 2 n.sp.	0	1	2	0	0
Cabelodopsis hispida (Sars 1901) Higuti and Martens 2012	0	1	4	0	0
Neocypridopsis nana (Sars 1901) Klie 1940	2	12	10	3	2
Family Candonidae (Kaufmann 1900)					
Candobrasilopsis brasiliensis (Sars 1901) Higuti & Martens 2012	6	4	4	2	3
Candobrasilopsis rochai Higuti and Martens 2012	7	5	3	1	0
Candobrasilopsis elongata Higuti and Martens 2014	5	2	7	0	1
Pseudocandona agostinhoi Higuti and Martens 2014	3	5	11	1	1
Pseudocandona cillisi Higuti and Martens 2014	3	0	5	0	0
Physocypria schubarti Farkas 1958	4	1	6	1	0

Candonidae n. gen. n.sp.	3	2	0	3	0
Family Limnocytheridae (Kile 1938)					
Cytheridella ilosvayi Daday 1905	16	17	15	6	9
Family Darwinulidae (Brady and Norman 1889)					
Alicenula serricaudata (Klie 1935) Rossetti and Martens 1998	3	6	13	2	1
Vestalenula pagliolii (Pinto and Kotzian 1961) Rossetti and Martens 1998	0	2	10	1	0
Penthesilenula brasiliensis (Pinto and Kotzian, 1961) Rossetti and Martens 1998	0	0	5	0	0

The PCoA and PERMANOVA results show significant differences in ostracod composition amongst the macrophyte life forms (F= 2.02; p = 0.001, Fig. S2). The pairwise PERMANOVA results show differences in the ostracod composition between free floating plants and all other macrophyte life forms (Table S5). The PERMDISP results show no significant differences in the variability of the dispersion of ostracod communities amongst the macrophytes life forms (F = 0.64, P = 0.65). The average distance from the centroid is similar amongst the macrophytes life forms: RS = 0.54, RF and FS = 0.52, EM = 0.51 and FF = 0.49. PERMDISP results thus show that differences in PERMANOVA results are not influenced by differences in the scatter of ostracod data amongst the macrophytes life forms (e.g. difference in the number of samples amongst macrophytes life forms), thus indicating that the data of these groups are comparable.

2.3.3 Average values of total beta-diversity and its components

In this section, we compare both differences amongst macrophytes life forms and amongst beta-diversity-facets. The average values (derived from the dissimilarity matrices) of total species-based ostracod beta-diversity are higher than the traits- and phylogeny-based ones (Table 2). The total species-based beta-diversity (B-tot, average values ranging between 0.689 and 0.754) is mostly explained by B-repl in all macrophyte life forms (ranging between 55% and 67% of B-tot). Traits-based total beta-diversity (B-tot, average values ranging between 0.478 and 0.577) is more explained by B-repl in FF, EM and RS (60%, 57% and 54% of B-tot, respectively), and by Rich-Diff in FS and RF (55% and 52% of B-tot, respectively). Finally, phylogeny-based total beta-diversity (B-tot, average values ranging between 0.507 and 0.593) is more explained by B-repl in EM, RS, FF and RF (58%, 57%, 57% and 51% of B-tot, respectively), and by Rich-Diff in FS (61% of B-tot, Table 2).

2.3.4 Comparing factors affecting ostracod beta-diversity facets amongst macrophyte life forms

The influence of the environmental and spatial factors structuring ostracod beta-diversity facets are variable amongst different life forms of macrophytes (Fig. 2). The total percentage of explained variation (R^2) of the factors (sum of pure environmental, pure spatial and shared fraction) had the highest values in FS (up to 86%), followed by RF (up to 49%), FF (up to 44%), RS (up to 43%) and EM (up to 27%).

Variation partitioning shows that the environmental factors are important for ostracod beta-diversity facets in all macrophyte life forms, while higher percentages of explanation are found in submerged life forms (FS up to 68% and RS up to 32%), than in floating and emergent life forms (FF up to 19%, RF up to 13% and EM up to 19%). Spatial factors are mostly non-significant in structuring ostracod beta-diversity. However, significant percentages of explanation of these factors are found for B-repl in RF and FS (up to 30%), and for Rich-Diff in EM and FS (up to 21%). We do not observe higher percentages of explanation of spatial factors in rooted life forms (EM, RF and RS), as compared to the free-living ones (FF and FS, Fig. 2). Shared fractions between environmental and spatial factors are high (up to 21%, Fig. 2) in some life forms, mainly in FF and RS.

Table 2 Average values of total beta-diversity (B-tot, total multi-site dissimilarity across the sites derived from the dissimilarity matrices) and its components (B-repl = replacement and Rich-Diff = richness difference), obtained through the function *beta.multi* in the BAT R-package. Values in parenthesis indicate the percentage that the B-repl or Rich-diff represent of the B-tot. Environmental (E. sel. = environmental variables selected) and spatial (S. sel. = PCNMs selected) variables selected for the pRDA, and P significance of these factors (P (E) and P (S)) for each beta diversity facet, in different macrophyte life forms. EM = emergent, RF = rooted floating, FF = free floating, RS = rooted submerged and FS = free submerged. Ec = electrical conductivity, Tr = water transparency, Wt = water temperature, Do = dissolved oxygen, Per = lake perimeter and Len = length of the meandering connecting channel. Values in bold were significant at $P < 0.05$. In EM, PCNMs 1-4 indicate broad-scaled and 5-8 fine-scaled patterns. In RF, PCNMs 1-5 indicate broad-scaled and 6-9 fine-scaled patterns. In FF and FS, PCNMs 1-3 indicate broad-scaled and 4-6 fine-scaled patterns. In RS, PCNMs 1-2 indicate broad-scaled and 3-4 fine-scaled patterns.

		Species					**Traits**					**Phylogeny**				
		Average values/%	E. sel.	S. sel.	P (E)	P (S)	Average values/%	E. sel.	S. sel.	P (E)	P (S)	Average values/%	E. sel.	S. sel.	P (E)	P (S)
EM	B-total	0.728	Ec	-	**0.001**	0.429	0.479	Ec	-	**0.001**	0.446	0.507	Ec	-	**0.001**	0.083
	B-repl	0.491 (67)	Ec	-	**0.001**	0.294	0.273 (57)	Ec	PCNM 6	**0.001**	**0.049**	0.296 (58)	Ec	PCNM1	**0.001**	**0.021**
	Rich-Diff	0.237 (33)	-	PCNM3	0.399	**0.05**	0.205 (43)	-	-	0.142	0.08	0.211 (42)	-	PCNM3	0.284	**0.032**
RF	B-total	0.724	Ec, Wt	-	**0.003**	0.848	0.506	pH	-	**0.012**	0.789	0.535	pH, Wt	-	**0.002**	0.292
	B-repl	0.487 (67)	pH, Len	-	**0.002**	0.313	0.243 (48)	pH	PCNM1, PCNM3, PCNM5, PCNM6	**0.005**	**0.001**	0.268 (51)	Ec	PCNM1, PCNM2, PCNM3, PCNM5, PCNM6	**0.046**	**0.002**
	Rich-Diff	0.237 (33)	-	-	0.125	0.523	0.263 (52)	Wt	-	**0.049**	0.21	0.266 (49)	Wt	-	**0.031**	0.408
FF	B-total	0.689	Ec, Do, Tr	-	**0.001**	0.376	0.478	Ec, Do, pH	-	**0.005**	0.184	0.512	Ec, Do, pH	PCNM2, PCNM5	**0.005**	**0.044**
	B-repl	0.459 (67)	Ec, Do, Tr	-	**0.005**	0.657	0.289 (60)	Ec, Do, Tr	PCNM1, PCNM2, PCNM5	**0.001**	**0.002**	0.292 (57)	Ec, Do	-	**0.001**	0.116
	Rich-Diff	0.23 (33)	-	-	0.244	0.211	0.189 (40)	-	-	0.336	0.14	0.219 (43)	-	-	0.312	0.416
RS	B-total	0.754	-	-	0.891	0.899	0.577	Ec, Do	-	**0.05**	0.358	0.593	-	-	0.09	0.11
	B-repl	0.477 (63)	-	-	0.237	0.786	0.31 (54)	Ec, Do	-	**0.012**	0.606	0.339 (57)	pH, Wt	-	**0.028**	0.162
	Rich-Diff	0.276 (37)	-	-	0.814	0.672	0.266 (46)	-	-	0.336	0.325	0.254 (43)	-	-	0.079	0.908
FS	B-total	0.733	Ec, pH	-	**0.002**	0.234	0.519	Ec, pH	-	**0.002**	0.039	0.524	Ec	PCNM1	**0.042**	**0.049**
	B-repl	0.406 (55)	Ec, pH, Tr	PCNM5	**0.001**	**0.026**	0.231 (45)	Ec, pH	-	**0.001**	0.456	0.203 (39)	Ec	PCNM5	**0.002**	**0.026**
	Rich-Diff	0.327 (45)	-	PCNM1	0.538	**0.001**	0.288 (55)	-	PCNM1	0.485	**0.021**	0.32 (61)	-	PCNM1	0.498	**0.039**

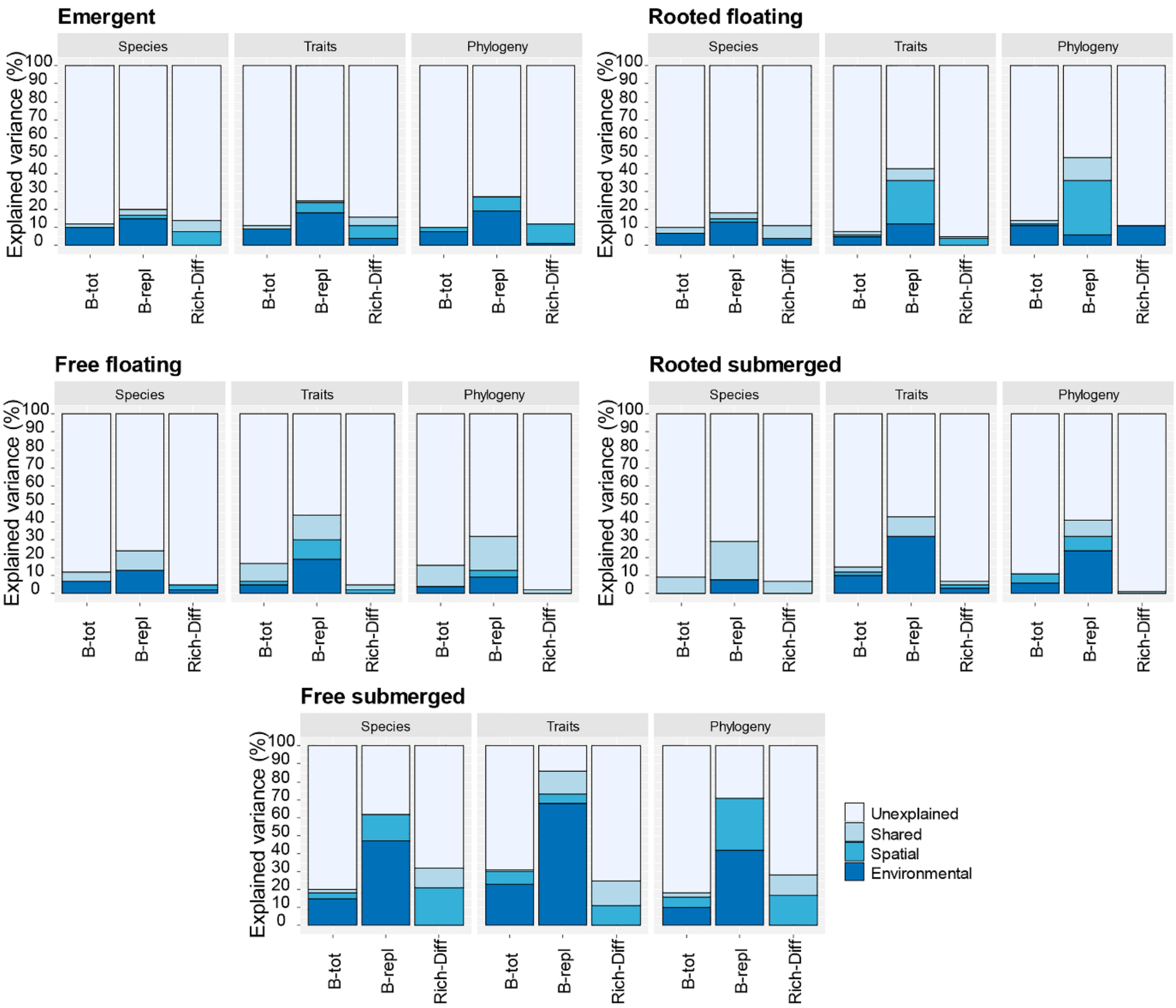

Fig. 2 Results of variation partitioning analyses showing the relative contributions (% of explanation) of the environmental, spatial, shared fraction between environmental and spatial factors and the unexplained fraction for each beta diversity measure (B-tot = beta total, B-repl = replacement and Rich-Diff = richness difference), amongst the facets of ostracod beta diversity, in different macrophyte life forms.

2.3.5 Factors affecting each facet of ostracod beta-diversity

In general, the influence of the environmental factors is high for B-repl (up to 68%) and low for B-tot (<24%) and Rich-Diff (<12%) for all beta-diversity facets. However, this influence is variable amongst the beta-diversity facets. Frequently, the percentages of explanation of environmental factors are higher for B-tot (ranging between 5 and 23%) and B-repl (ranging between 12 and 68%) for traits-based beta-diversity, than for those of species- (B-tot ranging between 0 and 15%, B-repl ranging between 8 and 47%) and phylogeny-based beta-diversity (B-tot ranging between 4 and 11%, B-repl ranging between 6 and 42%). As environmental factors were always less explanatory for Rich-Diff, we do not see differences in their influence amongst the beta-diversity facets. The percentages of explanation of spatial factors are always low (<31%) for all beta-diversity facets. Higher values for such effects of spatial factors are observed for B-repl (up to 30%) as compared to Rich-Diff (up to 21%) and B-tot (up to 7%). The influence of spatial factors is higher for phylogeny-based beta-diversity (up to 30%) than for species- (up to 21%) and traits-based beta-diversity (up to 24%, Fig. 2).

2.3.6 Selected environmental and spatial factors

In this section, we compare selected environmental and spatial variables in the db-RDA models, both amongst macrophyte life forms and amongst ostracod beta-diversity-facets. Considering the environmental factors, the selected variables are quite similar amongst the beta-diversity facets but quite different amongst the macrophytes life forms (Table 2). Furthermore, the environmental variables are frequently significant for B-tot and for B-repl components, but are rarely significant for the Rich-Diff component, for all beta-diversity facets in all macrophytes life forms. The most frequently selected environmental variables are electrical conductivity (e.g. for B-repl of all beta-diversity facets in almost all macrophytes life forms), pH (e.g. for B-repl of species- and traits-based beta-diversity in FS and FF; and for B-tot of trait- and phylogeny-based beta-diversity in RF, FF and FS), dissolved oxygen (e.g. for B-tot and B-repl of all beta-diversity facets in FF), and water temperature (e.g. for B-tot of species- and phylogeny-based beta-diversity in RF, Table 2). Considering the spatial factors, the generated PCNMs are rarely selected for species-based beta-diversity in all macrophyte life forms (Table 2). For traits-based beta diversity, the selected PCNMs are variable amongst macrophytes life, representing fine-scaled (e.g. PCNM6 for B-repl in EM) broad-scaled (e.g. PCNM1 for Rich-Diff in FS), and both fine- and broad-scaled spatial patterns (e.g. PCNM1, PCNM3, PCNM5 and PCNM6 for B-repl in RF). Similarly, for phylogeny-based beta-diversity, the selected PCNMs represent fine-scaled (e.g. PCNM5 for B-repl in FS), broad-scaled and both fine- (e.g. PCNM1 for Rich-Diff and PCNM3 for B-tot in EM) and broad-scaled spatial patterns (e.g. PCNM1, PCNM2, PCNM3, PCNM5 and PCNM6 for B-repl in RF, Table 2).

2.4 Discussion

2.4.1 Environmental and spatial effects amongst different macrophyte life forms

Environmental factors significantly structure ostracod beta-diversity facets and their percentages of explanation were higher for submerged macrophytes life forms, compared to the floating and emergent ones, supporting the first hypothesis of the present study. This pattern of percentage of explanation of the environmental factors may reflect the presence and repartition of the life forms in the water column, which are important factors in determining habitat structure (Choi et al. 2014). Such occupancy creates a higher variation in chemical and physical characteristics of the water around the roots (or even around the entire plant). For example, submerged macrophytes can live in a great variety of depths, compared to floating macrophytes, because they are adapted to regions where transparency is higher (Meerhoff et al. 2003), apart from the fact that they themselves also have the capacity to increase the water clarity by reducing nutrients (Scheffer et al. 1993). On the other hand, floating macrophytes (FF or RF) penetrate less in the vertical dimension as compared to the EM ones, and might furthermore reduce the light penetration in the water column owing to the floating leaves that form patches on the water surface (Cattaneo et al. 1998; Cremona et al. 2008). Floating macrophytes can still supply oxygen to the water around the roots, as they can transport oxygen from the atmosphere to these structures (Rehman et al. 2017). Consequently, ostracod species (or sets of traits and phylogenetic lineages of ostracods) may have been sorted, mainly in submerged life forms, owing to their physiological tolerances to certain environmental conditions. For example, some ostracod species are very sensitive to low concentrations of dissolved oxygen, as shown by Ruiz et al. (2013), and we observe lower concentrations of this variable around submerged macrophytes (see also below in “Selected environmental and spatial factors”).

In addition, we find that environmental factors had a higher influence on ostracod beta-diversity facets in FS macrophytes than in other life forms. The FS life form was represented by *Utricularia foliosa*, which is known as a “carnivorous plant”. This plant genus is adapted to life in aquatic regions that are poor in nutrients, and they remove these directly from the water or from their prey (Adamec 2008). Guisande et al. (2000) showed that there is a relationship between the decrease of zooplankton abundance and the increase in the number of bladders (for prey) per leaf in *U. foliosa*, as an adaptation to improve its carnivory and input of nutrient. These authors also showed that higher electrical conductivity had a negative influence on the bladder production of *U. foliosa*. Although we did not measure bladder productivity of *U. foliosa* in the present study, we infer that electrical conductivity may have indirectly influenced ostracod communities by increasing (or decreasing) the quantity of these plant structures. For example, some species of ostracods may have been more easily trapped by plants with higher numbers of bladders, which have led to such higher environmental influence on beta-diversity facets in our survey.

Spatial factors have some importance in structuring ostracod beta-diversity facets and we did not find higher values of spatial effects on ostracods associated with fixed macrophyte life forms, indicating that ostracods might present some dispersal limitation, regardless of the plant dispersal capacity, thus refuting our second hypothesis. Despite the fact that ostracods in general are good passive dispersers, especially the species of the family Cyprididae (Meisch 2000; Brochet et al. 2010; Pereira et al. 2017), several studies have also found spatial effects on ostracod communities, related to dispersal limitation (Castillo-Escrivà et al. 2016a; Castillo-Escrivà et al. 2017; Campos et al. 2019).

We highlight that the environmental and spatial factors discussed here explain at most 25% of the variability in ostracod beta-diversity in some macrophyte life forms (e.g. EM) in the Upper Paraná River floodplain. A high shared fraction of environmental and spatial factors in some cases (e.g. 21% in species-based beta-diversity in RS), suggests that part of the environmental gradient was spatially structured, which may, for example, have led to a decrease in the effect of environmental or spatial factors.

2.4.2 Differences amongst the beta-diversity facets and their components

Our results show that there were mismatches in the factors structuring each of the ostracod beta-diversity facets in each of the macrophyte life forms. This is so, because communities consist not only of different taxonomic assemblages but also of species with different traits (Alahuhta et al. 2019). Thus, using different data (either species-, traits- or phylogeny-based) on beta-diversity metrics can show species responding differently to the environmental gradient (e.g. variation in habitat formed by the different macrophyte life forms), thus generating a mismatch in the factors affecting each beta-diversity facet (Devictor et al. 2010). Similarly, Cai et al. (2019) found that the effect of the factors structuring the beta-diversity of freshwater molluscs, such as geography, energy and environment, were different amongst the three facets. However, such pattern of mismatches in the factors affecting the beta-diversity facets depends on the biological group under study. For example, Perez Rocha et al. (2018) found that local environment and space were factors that affected all the facets of macroinvertebrates beta-diversity in streams of western Finland in a similar way.

Considering the total beta-diversity, our results indicate that high species-based beta-diversity does not necessarily indicate high traits- and phylogeny-based beta-diversity. This might be related to the redundancy in the set of traits of ostracod species amongst the lakes, or even to the lack of information about other (unknown) ostracod traits (such as feeding preferences, behavioral responses to light or predators, parasites and burrowing abilities), which might have led to a lower traits-based diversity. Braghin et al. (2018), analysing zooplankton communities in the lakes of the Paraná River, also found lower functional beta-diversity, because species that were replaced amongst the environments probably had functional redundancy. Likewise, the set of ostracod species amongst the environments may have closely related taxonomic levels (same genus, same subfamily, …), which led to a lower phylogeny-based beta-diversity. According to Graham and Fine (2008), if lineages have conserved phylogenetic niches, species might be expected to be sorted by habitat, whereas if their phylogenetic niche is variable, closely related species are predicted to exist in different habitats. Our results indicated that (phylogenetically) closely related ostracod species might present conserved phylogenetic niches.

The fact that the replacement component was the main driver of the ostracod beta-diversity facets, in almost all macrophyte life forms, confirms that the variation in the environmental conditions replaces species (or traits and lineages of ostracod) from one lake to another. This might be associated with the difference in ecological conditions throughout the systems of the Paraná River floodplain (such as electrical conductivity which was the most variable amongst the systems). For example, the Paraná system can present lower environmental heterogeneity than the Ivinhema and Baía systems (Higuti et al. 2009), because of the effects resulting from dam regulation (Braghin et al. 2018), which evens-out or even eliminates small water level changes that are still present in the other two rivers.

2.4.3 Selected environmental and spatial factors

Most studies evaluating the influence of environmental factors on ostracod community structure are species-based, and this information is less applicable using the other facets of ostracod beta-diversity. Only one previous study (Marmonier et al. 1994) showed that environmental variables (such as variation of habitat characteristics) had an effect on traits-based diversity of ostracods, and the distribution of the set of traits of this community was found to be related to the habitat type. The selected variables in the present study, such as dissolved oxygen, electrical conductivity, pH and water temperature, are known to be important for the structure of ostracod communities in species-based studies. For example, such studies have found a correlation between ostracod community attributes and dissolved oxygen (Nagorskaya and Keyser 2005; Higuti et al. 2017) and electrical conductivity (Liberto et al. 2012). pH was relatively acidic in some lakes of the Upper Paraná River (Table S1), and this parameter was probably selected because low values of pH might affect freshwater ostracod valve calcification. Most ostracod species prefer alkaline or only slightly acidic waters (Ruiz et al. 2013; Mesquita-Joanes et al. 2012 and references therein). Finally, water temperature can affect the (length of the) life history and resulting body size of the adult organisms, i.e. the development rate of species might accelerate with increasing temperature (Aguilar-Alberola and Mesquita-Joanes 2014; Castillo-Escrivà et al. 2016a).

The spatial factors selected here indicate that dispersal limitation might have influenced some ostracod beta-diversity facets (and their components), from narrow (e.g. within systems of the Paraná River floodplain) to broad (e.g. amongst systems) scales of variation, differently in the different macrophyte life forms.

2.5 Conclusion

Environmental factors are significantly structuring ostracod beta-diversity facets, mainly for submerged macrophytes. This is probably related to the variation in water chemical and physical characteristics around the roots (or entire body) of these life forms, which replaces species (or ostracod traits and lineages), according to their ecological niche, thus affecting beta-diversity patterns. Furthermore, environmental and spatial factors have different influence on each of the beta-diversity facets, thus highlighting the importance to include these three approaches (species-, traits- and phylogeny-based) in ecological surveys. Therefore, biological communities associated with different macrophyte life forms should be considered in local as well as regional biodiversity surveys, owing to the variation in the factors affecting these communities associated with each macrophyte life form. In addition, we stress the importance of preservation and management of the different macrophyte life forms in river-floodplain ecosystems, as they provide higher diversity of available habitat for associated biological communities. Besides, we predict that if more dams are constructed (e.g. in Paraná River and its adjacent tributaries) and the diversity of macrophyte life forms is negatively affected, direct effects might change the structure of associated communities such as invertebrates and small fish.

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APPENDIX A - Electronic Supplementary Material

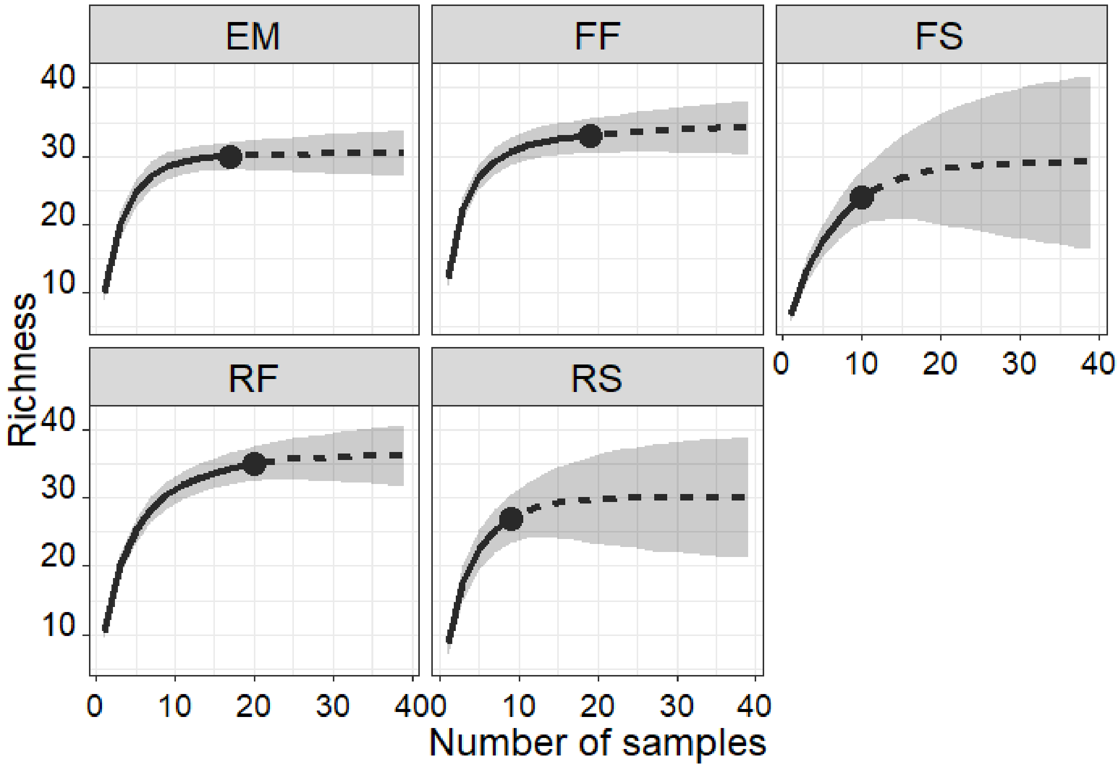

Fig. S1 Sample-size-based rarefaction (solid line) and extrapolation (dashed lines) for Hill numbers (q = 0, species richness) from ostracod species associated with different macrophyte life forms. EM = Emergent, FF = Free floating, FS = Free submerged, RF = Rooted floating and RS = Rooted submerged. The 95% confidence intervals (grey zone) were obtained by a bootstrap method.

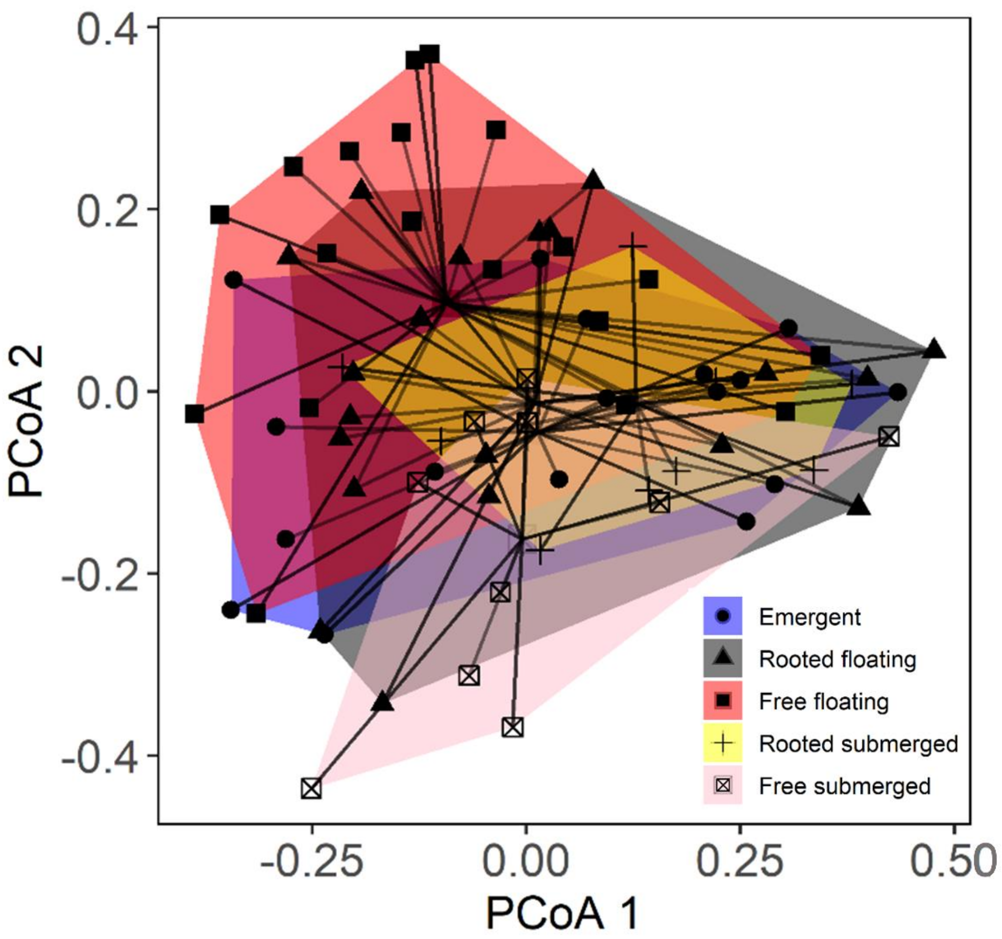

Fig. S2 Principal Coordinate Analysis (PCoA) ordination diagram derived from associated ostracod communities to the different macrophyte life forms.

Table S1 - Mean values and standard deviation of the environmental variables in different macrophyte life forms and in the different systems of the Upper Paraná River floodplain. Values in parenthesis represent the coefficient of variation (mean/standard deviation) of the environmental variables.

	Dissolved oxygen	Electrical conductivity	Water temperature	pH	Water transparency	Lakes Perimeter	Length of the meandering channel
Emergent	2.59±1.45(0.56)	39.82±18.21(0.46)	30.82±1.82(0.06)	5.81±0.5(0.08)	0.61±0.23(0.37)	3.99±4.73(1.18)	0.21±0.41(1.95)
Rooted floating	2.6±1.65(0.63)	37±18.01(0.49)	30.64±1.57(0.05)	5.64±0.59(0.1)	0.72±0.26(0.36)	3.48±4.5(1.29)	0.13±0.32(2.46)
Free floating	2.09±1.2(0.57)	32.7±17.24(0.53)	31.14±1.48(0.05)	5.63±0.51(0.09)	0.82±0.28(0.34)	3.45±4.53(1.31)	0.18±0.38(2.11)
Rooted submerged	1.97±0.96(0.49)	44.78±20.6(0.46)	30.12±1.87(0.06)	5.81±0.41(0.07)	0.79±0.31(0.39)	1.97±2.54(1.29)	0.06±0.19(3.17)
Free submerged	1.92±1.03(0.53)	30.9±14.62(0.47)	31.36±1.6(0.05)	5.67±0.45(0.08)	0.79±0.23(0.29)	3.7±5.79(1.56)	0.26±0.51(1.96)
Ivinhema	1.76±1.29(0.73)	33.73±17.5(0.52)	31.81±1.12(0.03)	5.38±0.49(0.09)	0.73±0.26(0.35)	6.21±6.62(1.06)	0.34±0.48(1.41)
Paraná	2.47±1.13(0.46)	40.13±18.86(0.47)	29.31±1.04(0.03)	6.14±0.28(0.04)	0.76±0.26(0.34)	1.87±1.36(0.72)	0.02±0.04(2)
Baía	2.65±1.42(0.53)	37±16.11(0.43)	31.29±1.53(0.07)	5.59±0.38(0.07)	0.73±0.27(0.36)	2.13±0.96(0.45)	0.14±0.34(2.42)

Table S2 - Occurrence of the different species of macrophytes which compose each life form in the lakes of the Upper Paraná River floodplain. "X" indicates presence and empty spaces indicate absence.

	1. Pintado	**2. Peroba**	**3. Campinho**	**4. Boca do Ipoitã**	**5. Patos**	**6. Nelsão**	**7. Joaninha**	**8. Finado Raimundo**	**9. Xirica**	**10. Pombas**	**11. Manezinho**	**12. Ilha Pacu**	**13. Santa Rosa**	**14. Bilé**	**15. Leopoldo**	**16. Pau Véio**	**17. Garças**	**18. Guaraná**	**19. Mané Cotia**	**20. P. das Garças**	**21. Porcos**	**22. Aurélio**	**23. Maria Luiza**	**24. Suja**	**25. Gavião**
Emergent																									
Polygonum acuminatum H. B. K.										X									X						
Polygonum stelligerum Cham.																				X					
Polygonum ferrugineum Wedd.																								X	
Polygonum sp.	X		X		X		X	X	X		X			X	X	X	X	X					X		
Rooted floating																									
Eichhornia azurea (Sw.) Kunth	X	X	X	X	X		X	X	X	X			X	X	X	X	X	X				X	X		
Paspalum repens Berg.																			X		X				X
Free floating																									
Eichhornia crassipes (Mart.) Solms	X	X		X	X	X	X					X									X	X	X	X	X
Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine																		X							
Salvinia auriculata Aubl.								X		X							X		X						
Salvinia herzogii de la Sota.			X										X												
Rooted submerged																									
Cabomba furcata Schult & Schult.f.	X			X							X			X								X			X
Egeria najas Planch.										X			X			X									
Free submerged																									
Utricularia foliosa L.				X	X	X	X							X				X	X		X	X		X	

Table S3 - Ostracod species and their respective set of biological traits.

Species/Taxa	Locomotion mode	Body size	Spine	Body morphology	Reproduction mode
Diaphanocypris meridana	swimmer	medium	absence	flat	parthenogenesis
Stenocypris major	swimmer	large	absence	flat	parthenogenesis
Stenocypris malayica	swimmer	medium	absence	flat	parthenogenesis
Strandesia psittacea	swimmer	large	presence	rounded	parthenogenesis
Strandesia colombiensis	swimmer	large	presence	rounded	parthenogenesis
Strandesia mutica	swimmer	large	absence	rounded	parthenogenesis
Strandesia variegata	swimmer	large	absence	rounded	parthenogenesis
Strandesia tolimensis	swimmer	medium	absence	rounded	parthenogenesis
Strandesia nakatanii	swimmer	medium	absence	rounded	parthenogenesis
Strandesia lansactohai	swimmer	medium	absence	rounded	parthenogenesis
Strandesia velhoi	swimmer	medium	absence	rounded	parthenogenesis
Strandesia nupelia	swimmer	medium	absence	rounded	parthenogenesis
Bradleytriebella trispinosa	swimmer	medium	presence	rounded	parthenogenesis
Bradleytriebella lineata	swimmer	medium	absence	rounded	parthenogenesis
Cypricercus alfredo	swimmer	medium	presence	rounded	mixed
Chlamydotheca deformis	swimmer	large	absence	rounded	parthenogenesis
Chlamydotheca iheringi	swimmer	large	presence	rounded	mixed
Chlamydotheca cf. *iheringi* sp. 2	swimmer	large	presence	rounded	parthenogenesis
Chlamydotheca sp. 3	swimmer	large	absence	rounded	parthenogenesis
Cypretta costata	swimmer	small	absence	rounded	parthenogenesis
Cypretta sp. 3 n.sp	swimmer	small	absence	rounded	parthenogenesis
Cypridopsis vidua	swimmer	small	absence	rounded	parthenogenesis
Cypridopsis cf. *vidua* sp. 2	swimmer	small	absence	rounded	parthenogenesis

Species/Taxa	**Locomotion mode**	**Body size**	**Spine**	**Body morphology**	**Reproduction mode**
“*Cypridopsis*” n. gen. 1 n.sp.	swimmer	small	absence	rounded	mixed
“*Cypridopsis*” n. gen. 2 n.sp.	non-swimmer	small	absence	flat	parthenogenesis
Cabelodopsis hispida	swimmer	medium	absence	rounded	parthenogenesis
Neocypridopsis nana	non-swimmer	small	absence	rounded	parthenogenesis
Candobrasilopsis brasiliensis	non-swimmer	medium	absence	flat	sexual
Candobrasilopsis rochai	non-swimmer	medium	absence	flat	sexual
Candobrasilopsis elongata	non-swimmer	medium	absence	flat	sexual
Pseudocandona agostinhoi	non-swimmer	medium	absence	flat	sexual
Pseudocandona cillisi	non-swimmer	medium	absence	flat	sexual
Physocypria schubarti	swimmer	medium	absence	flat	sexual
Candonidae n. gen. n.sp.	swimmer	large	absence	rounded	sexual
Cytheridella ilosvayi	non-swimmer	medium	absence	rounded	sexual
Alicenula serricaudata	non-swimmer	small	absence	flat	parthenogenesis
Vestalenula pagliolii	non-swimmer	small	absence	flat	parthenogenesis
Penthesilenula brasiliensis	non-swimmer	small	absence	flat	parthenogenesis

Table S4 - Ostracod species and their respective taxonomic classification, according Meisch et al. (2019). Empty spaces indicate that there is no information about that taxonomic level in the literature.

Species/Taxa	**Genus**	**Tribe**	**Subfamily**	**Family**	**Superfamily**
Diaphanocypris meridana	*Diaphanocypris*	Nealecypridini	Cypricercinae	Cyprididae	Cypridoidea
Stenocypris major	*Stenocypris*	Stenocypridini	Herpetocypridinae	Cyprididae	Cypridoidea
Stenocypris malayica	*Stenocypris*	Stenocypridini	Herpetocypridinae	Cyprididae	Cypridoidea
Strandesia psittacea	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Strandesia colombiensis	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Strandesia mutica	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Strandesia variegata	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Strandesia tolimensis	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Strandesia nakatanii	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Strandesia lansactohai	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Strandesia velhoi	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Strandesia nupelia	*Strandesia*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Bradleytriebella trispinosa	*Bradleytriebella*	Bradleystrandesiini	Cypricercinae	Cyprididae	Cypridoidea
Bradleytriebella lineata	*Bradleytriebella*	Bradleystrandesiini	Cypricercinae	Cyprididae	Cypridoidea
Cypricercus alfredo	*Cypricercus*	Cypricercini	Cypricercinae	Cyprididae	Cypridoidea
Chlamydotheca deformis	*Chlamydotheca*	-	Cypridinae	Cyprididae	Cypridoidea
Chlamydotheca iheringi	*Chlamydotheca*	-	Cypridinae	Cyprididae	Cypridoidea
Chlamydotheca cf. *iheringi* sp. 2	*Chlamydotheca*	-	Cypridinae	Cyprididae	Cypridoidea
Chlamydotheca sp. 3	*Chlamydotheca*	-	Cypridinae	Cyprididae	Cypridoidea

Species/Taxa	**Genus**	**Tribe**	**Subfamily**	**Family**	**Superfamily**
Cypretta costata	*Cypretta*	-	Cyprettinae	Cyprididae	Cypridoidea
Cypretta sp. 3 n.sp	*Cypretta*	-	Cyprettinae	Cyprididae	Cypridoidea
Cypridopsis vidua	*Cypridopsis*	Cypridopsini	Cypridopsinae	Cyprididae	Cypridoidea
Cypridopsis cf. *vidua* sp. 2	*Cypridopsis*	Cypridopsini	Cypridopsinae	Cyprididae	Cypridoidea
"*Cypridopsis*" n. gen. 1 n.sp.	n. gen. 1	Cypridopsini	Cypridopsinae	Cyprididae	Cypridoidea
"*Cypridopsis*" n. gen. 2 n.sp.	n. gen. 2	Cypridopsini	Cypridopsinae	Cyprididae	Cypridoidea
Cabelodopsis hispida	*Cabelodopsis*	Zonocypridini	Cypridopsinae	Cyprididae	Cypridoidea
Neocypridopsis nana	*Neocypridopsis*	Cypridopsini	Cypridopsinae	Cyprididae	Cypridoidea
Candobrasilopsis brasiliensis	*Candobrasilopsis*	Candonopsini	Candoninae	Candonidae	Cypridoidea
Candobrasilopsis rochai	*Candobrasilopsis*	Candonopsini	Candoninae	Candonidae	Cypridoidea
Candobrasilopsis elongata	*Candobrasilopsis*	Candonopsini	Candoninae	Candonidae	Cypridoidea
Pseudocandona agostinhoi	*Pseudocandona*	Candonini	Candoninae	Candonidae	Cypridoidea
Pseudocandona cillisi	*Pseudocandona*	Candonini	Candoninae	Candonidae	Cypridoidea
Physocypria schubarti	*Physocypria*	-	Cyclocypridinae	Candonidae	Cypridoidea
Candonidae n. gen. n.sp.	n. gen. 3	-	-	Candonidae	Cypridoidea
Cytheridella ilosvayi	*Cytheridella*	-	Timiriaseviinae	Limnocytheridae	Cytheroidea
Alicenula serricaudata	*Alicenula*	-	-	Darwinulidae	Darwinuloidea
Vestalenula pagliolii	*Vestalenula*	-	-	Darwinulidae	Darwinuloidea
Penthesilenula brasiliensis	*Penthesilenula*	-	-	Darwinulidae	Darwinuloidea

Table S5 - Pairwise PERMANOVA of the ostracod species composition amongst the different macrophyte life forms

	p- values	**F. model**
Emergent x Rooted floating	0.212	1.386
Emergent x Free floating	**0.006**	4.449
Emergent x Rooted submerged	0.207	1.397
Emergent x Free submerged	0.055	2.063
Rooted floating x Free floating	**0.046**	2.159
Rooted floating x Rooted submerged	0.135	1.609
Rooted floating x Free submerged	0.110	1.752
Free floating x Rooted submerged	**0.001**	4.183
Free floating x Free submerged	**0.000**	4.486
Rooted submerged x Free submerged	0.242	1.380

APPENDIX B - First page of the published article, derived from the thesis

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Aquatic Sciences

RESEARCH ARTICLE

Macrophyte life forms influence the effects of environmental and spatial factors on the beta-diversity of associated ostracod communities (Crustacea)

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Abstract

Beta-diversity measures have been used to understand patterns of community distribution in natural ecosystems. Recent studies included different facets of beta-diversity analyses, e.g. trait- and phylogeny-based. Here, we used ostracod communities to evaluate the influence of environmental and spatial factors structuring different facets of beta-diversity and their components (Beta-total, replacement and richness-difference) of ostracod communities associated with different macrophyte life forms. We test the hypotheses (1) that the influence of environmental factors is higher for ostracod beta-diversity facets of communities associated with submerged plants compared to emergent and floating plants and (2) that the influence of spatial factors is higher in communities associated with rooted, compared to non-rooted plants. Ostracods were sampled from five life forms of macrophytes, including emergent, rooted floating, rooted submerged, free submerged and free floating in 25 floodplain lakes. Our results showed that the environmental factors turned out to be important for all beta-diversity facets of ostracod communities, mainly for those associated with submerged macrophytes, thus corroborating the first hypothesis. We also found that spatial factors' influence on ostracod beta-diversity was not related to whether the plant is rooted or not, thus refuting our second hypothesis. We also found differences in factors structuring each of the beta-diversity facets, showing the importance to include these three approaches (species-, traits- and phylogeny-based) in ecological surveys. Finally, we highlight the importance of considering different macrophyte life forms in biodiversity surveys for the preservation and management of the diversity of these plants and their associated communities.

Keywords Aquatic plants · Ostracoda · Microcrustaceans · Tropical floodplain · Local and regional factors

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3 PATTERNS AND DRIVERS OF LOCAL CONTRIBUTIONS TO BETA DIVERSITY OF AQUATIC COMMUNITIES IN NEOTROPICAL FLOODPLAIN SYSTEMS

ABSTRACT

1. Understanding the patterns of species distribution along environmental or spatial gradients is one of the main goals in ecology and conservation biology. The local contribution to the total beta-diversity (LCBD) is a tool to assess sites with high LCBD values are considered unique in terms of species composition. Here, we used the LCBD approach to evaluate the drivers and patterns of ecological uniqueness of the 64 lakes from four Neotropical floodplain systems: Amazon, Araguaia, Pantanal and Paraná. For this, we analysed data of eight aquatic biological communities: phytoplankton, ciliates, testate amoebae, rotifers, cladocerans, copepods, ostracods and fish.

2. We calculated LCBD values at two scales, regional, considering each floodplain separated, and subcontinental, considering all floodplains together. We analysed LCBD patterns throughout two groups of predictor variables (1) biological metrics (richness, mean abundance and mean occupancy) and (2) environmental, spatial and local contribution to the environmental heterogeneity (LCEH). We used random forests procedures to evaluate which of the predictors were more important in explaining LCBD variation. Using random forests results, we performed the variation partitioning to evaluate the contribution (R^2) of each of the predictor variables of the second group of predictors.

3. Our results showed that the subcontinental scale was more effective than the regional scale to evaluate LCBD patterns, showing that broad scale studies are more representative for assessing the ecological uniqueness. The Amazon and Paraná were the most unique floodplains in terms of species composition, showing the importance of conservation actions in these ecosystems. We found that the mean occupancy was the biological metric most negatively correlated with the LCBD variation, showing that this metric and species rarity should be considered in studies evaluating LCBD patterns. Furthermore, the environmental and LCEH had important contribution to LCBD values, and the variability in environmental heterogeneity sorted species amongst the sites, affecting LCBD patterns. Finally, LCBD patterns and predictors were different amongst the biological groups, showing the importance of considering taxa with differences in biological traits (e.g. different dispersal mode and ability) for a better evaluation and understanding of LCBD.

Keywords: Biological groups, ecological uniqueness, environmental predictors, environmental heterogeneity, regional scale, subcontinental scale

3.1 Introduction

Understanding the pattern of species distribution along environmental, spatial or temporal gradients is one of the main goals in ecology (da Silva et al., 2018) and conservation biology, mainly because of the current scenario of globally declining biodiversity. In this context, the study of beta-diversity, defined as the amount of change in species composition from one location to another (Anderson et al., 2011), has been considered important to link processes operating at local (e.g. affecting alpha diversity) and regional scales (e.g. affecting gamma diversity), providing conservation-relevant insights for the protection of biodiversity (Socolar et al., 2016; Ellingsen et al., 2020).

Over the last years, several approaches to measure beta-diversity have been proposed (Legendre et al., 2005; Baselga 2010, 2017; Tuomisto, 2010; Anderson et al., 2011). One of them, proposed by Legendre & De Cáceres (2013), has allowed researchers to partition beta-diversity into local contribution to the total beta-diversity (LCBD) for every single site. This approach can be used to illustrate how the ecological uniqueness, in terms of species composition, changes across environmental gradients (Archidona-Yuste et al., 2020). Therefore, sites with higher LCBD values (as compared to the mean LCBD of the other sites) are unusual in terms of species composition (e.g. presence of rare species), indicating that they have high conservation value, considering if the species are native (Li et al., 2020). On the other hand, if the same sites with unusual species composition (and high LCBD values) have a combination of several alien invasive species, this might be warning for the need of restoration programs (Legendre & De Cáceres, 2013; Gavioli et al., 2019).

Studies have used several predictor variables to understand which factors are responsible for LCBD variation and, consequently, which mechanisms are responsible for compositional uniqueness patterns in the region (Leibold & Chase, 2018). Usually, such predictors include ecological variables (e.g. environmental features) and spatial effects (e.g. spatial configuration of the sites, da Silva et al., 2018). Furthermore, the correlation between LCBD values and community metrics (e.g. richness and abundance) has also been assessed (da Silva et al., 2018). However, most of the studies evaluating LCBD predictors, mainly in freshwater ecosystems, are based on a single biological group, for example, algae (Vilmi et al., 2017), macroinvertebrates (Sor et al., 2018; Bo et al., 2020; Li et al., 2020), macrophytes (Pozzobom et al., 2020) and fish (López-Delgato et al., 2019; Dai et al., 2020, Leão et al., 2020). Thus, different conclusions about the local contribution to the beta-diversity do not consider that the spatial and environmental factors influence differently each biological group, because of their differences in biological characteristics and traits (e.g. body size and dispersal ability of the organisms, De Bie et al., 2012; Yang et al., 2018; Pelaez & Pavanelli, 2019).

Riverine floodplains are amongst the most biologically productive and most diverse freshwater ecosystems of the world (Tockner & Stanford, 2002), as result of their wide variety of habitats, such as rivers, channels and lakes, as well as because of their high temporal variation in water level and habitat heterogeneity (Junk et al., 1989). However, floodplains have been seriously threatened by anthropogenic activities, such as dam construction and flood regulation (Souza Filho, 2009), over-exploration (Harrison et al., 2010), introduction of alien invasive species (Mölder & Schneider, 2011), and pollution (Hein et al., 2016). All of these activities have threatened and reduced their biodiversity. In the current scenario of increasing global threats to biodiversity (Dudgeon et al., 2006), the need to evaluate patterns and understand the factors responsible for the processes shaping species distribution, abundance and composition, both at local and regional scales, is urgent (Holyoak et al., 2005). Such results are required to allow scientifically underpinned conservation and management plans of ecosystems (Ferrier, 2002), also in riverine floodplains

Here, we evaluated drivers and patterns of ecological uniqueness of the sites, in terms of species composition, in four Neotropical riverine floodplain systems, using the LCBD approach (Legendre & De Cáceres, 2013). For this, we analysed data of eight aquatic communities: phytoplankton, ciliates, testate amoebae, rotifers, cladocerans, copepods, ostracods and fish. We tested four hypotheses:

(1) Sites of the Amazon system will show the most important contribution to the total beta-diversity of aquatic organisms amongst the floodplains, because its well-known high biodiversity levels.

(2) Mean occupancy will be more (negatively) correlated to LCBD values than the other biological metrics (species richness and mean abundance), mostly because of the influence of species rarity. Thus, sites with rare species will be more unique in species composition than the others. Furthermore, based on previous studies using the LCBD approach, we expect that species richness will be negatively correlated with LCBD values (Heino et al., 2017; Landeiro et al., 2018, da Silva et al., 2018) and mean abundance will be weakly correlated with LCBD values (Heino & Grönroos, 2017, da Silva et al., 2018).

(3) Environmental predictors and local contributuin to the environmental heterogeneity (LCEH) will be the most important drivers of LCBD variation. This is so because niche-based processes related to environmental filtering (Leibold et al., 2004;

HilleRisLambers et al., 2012) have been the main drivers of aquatic community distributions, and consequently they will affect LCBD patters.

(4) The influence of the predictors will be related to the traits of the biological groups. Thus, groups with larger species which are also more active dispersers (e.g. fish), will be more affected by spatial drivers (e.g. dispersal limitation), whereas smaller and passive dispersers (e.g. phytoplankton), will be more affected by environmental predictors (environmental and LCEH predictors), as shown by De Bie et al. (2012), consequently affecting LCBD patters more.

3.2 Methods

3.2.1 Study area and sampling periods

This study was conducted in connected (open) and closed lakes of four Neotropical floodplain systems: Amazon, Araguaia, Pantanal and Paraná. These floodplain systems are located in Brazil and together comprise wide latitudinal gradients (3° to 23°S) at a subcontinental scale of approximately 2,300 km (Figure 1). The present study was part of the National Program for Research in Biodiversity (SISBIOTA Brazil), which studied several biological groups simultaneously.

The Amazon basin is considered to be the largest drainage basin in the world, and is (mostly) located in the northern region of Brazil (Figure 1). We sampled the Amazon floodplain in the sub-region of Amazonas-Solimões and Amazonas rivers (03°14'34.2"S, 59°58'23.2"W), which covers an area of approximately 400,000 km². The annual average fluctuation in the water level ranges around 10 meters, and high-water periods start in November with its maximum in July, whereas the lowest water period is in October (Yamamoto et al., 2004).

The Araguaia floodplain is located in central Brazil (Figure 1) and comprises a drainage area of around 377,000 km². This drainage area includes a phytogeographical transition zone between the Amazonia rainforest in the north and the Cerrado in the south. We sampled in the centre of the Araguaia sub-region between Britânia and São Miguel do Araguaia municipalities (13°21'33.1"S, 50°36'42.9"W). In this floodplain, the high-water period occurs between November and April, whereas the dry water period is from May to October (Latrubesse & Stevaux, 2002).

The Pantanal floodplain, located in central western Brazil, is considered one of the largest wetlands in the world, and flooding occupies about 80% of the whole Pantanal during the wet period. The sampling area comprises the sub-regions of Paraguay and Miranda rivers (19°02'03.7"S, 57°28'13.9"W) (Figure 1). The two high-water periods in the Pantanal floodplain region occur between January and April, and between June and September (Assine & Silva, 2009).

The Paraná floodplain, located in southern Brazil, is strongly influenced by an upstream cascade of man-made reservoirs, which significantly reduces the amplitude of the flood pulses (Souza Filho, 2009). The study area is located in the Upper Paraná River (13°13'34.2"S, 50°34'39.8"W), between the Porto Primavera Dam and the Itaipu Reservoir (Figure 1). It encompasses three different river systems: Ivinhema, Paraná and Baía, each one with its peculiar geology, hydrology and limnology (Souza Filho, 2009). In this floodplain, the high water period occurs between November and March and the low water period between May and October (Agostinho et al., 2004).

Samples were performed from August 2011 to May 2012, in the wet period of each floodplain: Pantanal = August 2011, Paraná = February 2012, Araguaia = March 2012 and Amazon = May 2012. We sampled 64 lakes connected to the main river or tributaries in these four floodplains: Pantanal = 15 lakes, Paraná = 18 lakes, Araguaia = 17 lakes and Amazon = 14 lakes (See more details about the names and coordinates of the lakes in Table S1).

3.2.2 Biological communities

We sampled eight biological communities in all floodplain lakes: phytoplankton, ciliates, testate amoebae, rotifers, cladocerans, copepods, ostracods and fish. Sampling was standardized for all environments and identification and counting of species of each biological group were performed by the same teams of specialists. The sampling methods and laboratory processing techniques for each biotic community are summarized in Table 1. More details can be found in Appendix A (adapted from Lansac-Tôha et al., 2021). 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**.** Data type = abundance.

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

3.2.3 Predictor variables

We used three biological metrics as predictor variables: richness (number of species for sampled site), mean abundance (mean of each species abundance for sampled site), and mean occupancy. For calculating mean occupancy, firstly the matrix of species abundance was transformed in a presence and absence matrix. After that, the occupancy of each species was calculated as the sum of sites occupied by each species. Finally, the mean occupancy was calculated, dividing the sum of occupancy of all species (present in each sampled site) by the total number of species of each sampled site.

Physical and chemical variables were considered environmental predictors. These variables were measured with simultaneous communities sampling in all four floodplains, as follows: water temperature (^{o}C; thermometer coupled to the oximeter), air temperature (^{o}C; thermometer), pH (Digimed portable potentiometer), electrical conductivity (µS.cm^{-1}; Digimed portable potentiometer), dissolved and saturated oxygen (mg. L^{-1}; YSI portable oximeter), turbidity (NTU, LaMotte2008© portable turbidimeter) and water transparency (m; Secchi disk). Water depth (m) and euphotic zone were obtained in each lake with a portable depth sounder. Water samples were collected for laboratory analysis, of total phosphorus (µg. L^{-1}) and total nitrogen (µg. L^{-1}) (Golterman et al., 1978; Mackereth, 1978). All these variables were log transformed, except for pH. Geographical coordinates (latitude and longitude) of the sampled sites were considered spatial predictors (see more details of environmental and spatial predictors in Table S2).

We calculated the local contribution of the sites to the environmental heterogeneity (here called LCEH), using the environmental predictors. Thus, it was possible to assess the uniqueness of the sites in terms of abiotic variables variability, where high values of LCEH indicate that the site exhibits particularized environmental conditions (Castro et al., 2019). LCEH was calculated using the *LCBD.comp* function from the *adespatial* R package (Dray et al., 2018), based on the standardized Euclidean distance of the environmental predictors.

3.2.4 Data analysis

We calculated the LCBD values according to the method described by Legendre & De Cáceres (2013). We first used Hellinger-transformation for abundance data, and subsequently calculated the LCBD values using the function *beta.div*, from the *adespatial* R package (Dray et al. 2018). LCBD values were calculated in two ways, considering two scales: subcontinental and regional, to evaluate which form is more appropriate for our data base. At the subcontinental scale, the analyses were carried out considering the abundance data of all floodplains together. Thus, it was possible to evaluate which floodplain was more unique in terms of species composition and contributed the most to the total beta-diversity considering a broad spatial scale. At the regional scale, the analyses were carried out separately for abundance data of each floodplain, mainly to illustrate in detail which sites contributed the most to the total beta diversity within the systems. All the analyses, considering both regional and subcontinental scales, were made separately for each biological group.

As the LCBD values did not fulfil the assumptions of homoscedasticity and normality in our previous analyses, we performed a non-parametric analysis of variance (Kruskal-Wallis) to test for significances of differences in LCBD amongst the four floodplains, considering the mean LCBD of all biological groups. In case of significance, a post-hoc test (Wilcoxon) was performed. Furthermore, we tested for significances of differences between LCBD values amongst the floodplains for each biological group separated. Because the LCBD values always range between 0 and 1, proportionally to number of samples sites, it was possible to compare the systems only considering the subcontinental scale, since each floodplain (regional scale) had a different number of sampling sites. However, at the regional scale, we calculated the coefficient of variation of the LCBD values, to evaluate in which floodplain they were more variable. For this, we divided the standard deviation by the mean of LCBD values.

We checked for possible correlations between LCBD values and the biological metrics (richness, mean occupancy and mean abundance) using Spearman's correlations, for both subcontinental and regional scales. Also, we used Spearman's correlations to check for possible correlations between LCBD values and biological metrics for each biological group, at the subcontinental scale.

We performed random forest (RF) analyses to evaluate which factors were responsible for LCBD variation using the *randomForest* function of the RandomForest R package (Breiman, 2001, Liaw & Wiener, 2002), at both subcontinental and regional scales. We created two different models: (1) considering the biological metrics (richness, mean abundance and mean occupancy) and (2) considering the environmental, spatial and LCEH predictors. RF is a machine-learning algorithm that uses a combination of multiple regression trees (a "forest") to make a single consensus for the most important predictors, based on bootstrapped data ("bagging"). This approach uses a random subset of predictors for each tree to assess predictor importance in the presence of multi-collinearity (Breiman, 2001). We recorded the percent variance explained and importance of specific variables using mean decrease accuracy (%IncMSE) for each model. Before the analyses, we checked the multicollinearity amongst the environmental predictors, using the variance inflation factor (VIF), where variables with VIF > 10 were removed. We used variation partitioning procedures (Peres-Neto et al., 2006) based on the results of RF of the second model. LCBD variation was partitioned in purely environmental (E|S|LCEH), in purely spatial (S|E|LCEH), in purely explained by LCEH (LCEH|S|E), in a component explained by the intersection of environmental and spatial ($E \cap S$), environmental and LCEH ($E \cap LCEH$), spatial and LCEH ($S \cap LCEH$) and all predictors together ($E \cap S \cap LCEH$). The results were adjusted R^2 values.

We constructedour figures using the ggplot2 R package (Wickham et al., 2016). The construction of the maps was done with QGis 3.4.5 software (QGIS Development Team, 2019). All statistical analyses were performed in R 4.0.5 software (R Core Team, 2021).

3.3 Results

3.3.1 LCBD patterns

At the subcontinental scale, the largest local contributions to the total beta-diversity were found mostly in sites of the Amazon floodplain (Figure 1), with a higher number of sites with significant LCBD values ($p < 0.05$, Table S1), than the other floodplains.

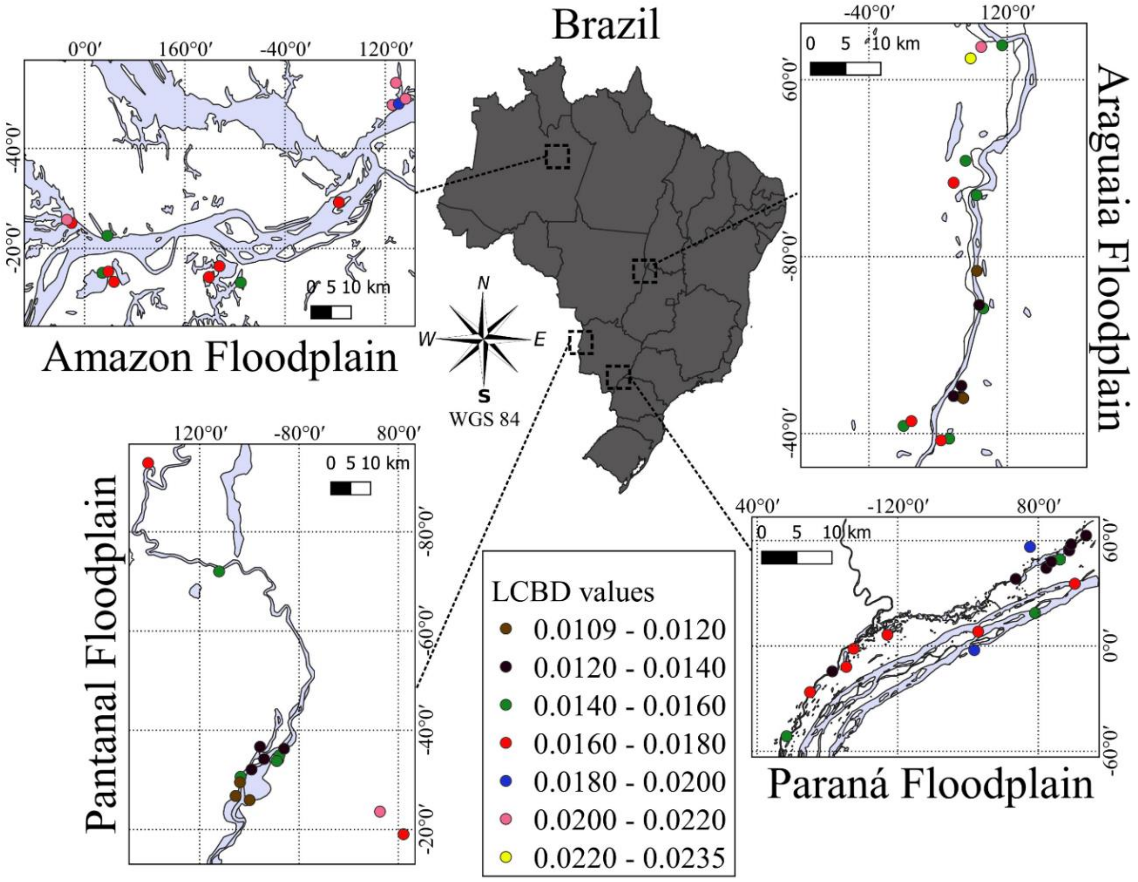

Figure 1 Location of the 64 sampled connected (open) and closed lakes from Brazilian floodplains. LCBD values amongst Amazon, Araguaia, Pantanal and Paraná floodplains at the subcontinental scale. Different colours of the circles represent the variation in LCBD values

The LCBD values (considering the means of all biological groups for each site) ranged between 0.0109 and 0.023, with the highest median value found in Amazon (0.0174), followed by Paraná (0.0149), Araguaia (0.0147) and Pantanal (0.0139, Figure 2). We found significant differences in the LCBD values amongst the floodplains ($H = 13.238$, $p = 0.004$), where the Amazon differed from all others ($p < 0.05$). The highest LCBD values, considering each group separated, were also found in Amazon for ciliates, testate amoebae, copepods and ostracods (Figures S2, S3, S5 and S7); in Paraná for phytoplankton and rotifers (Figures S1 and S4); and in Araguaia for cladocerans and fish (Figures 2, S6 and S8). Significant differences in LCBD values amongst the floodplains were found for all biological groups ($p < 0.05$).

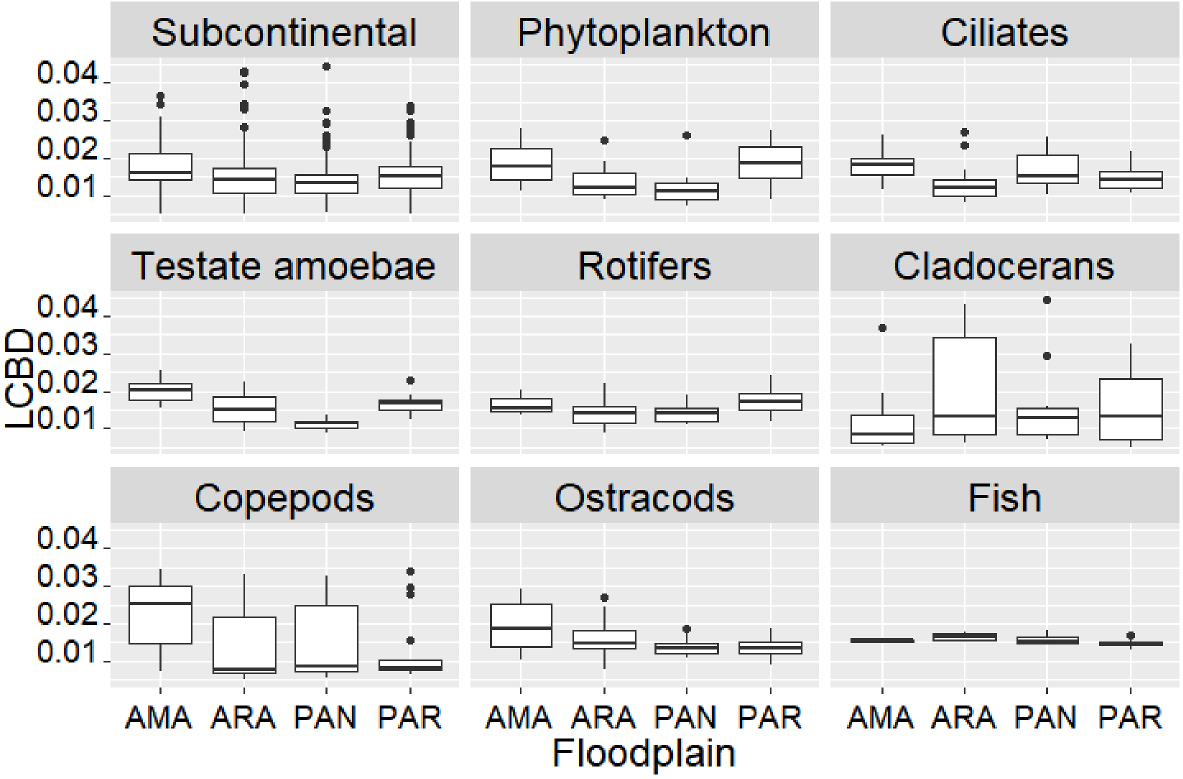

Figure 2 Boxplots illustrating the range of variation of local contributions to the total beta-diversity values (LCBD) amongst the four Brazilian floodplains and amongst the biological groups at the subcontinental scale. AMA = Amazon, ARA = Araguaia, PAN = Pantanal and PAR = Paraná.

At the regional scale, the LCBD values (considering the mean of all biological groups for each site) ranged between 0.055 and 0.095 in Amazon; 0.039 and 0.095 in Araguaia; 0.037 and 0.104 in Pantanal; and 0.029 and 0.089 in Paraná. The LCBD values were frequently significant ($p < 0.05$) in Paraná (18 times), followed by Araguaia (17 times), Pantanal (16 times) and Amazon (15 times, Table S1). The coefficient of variation showed that the LCBD values were more variable in Paraná (31%), followed by Pantanal (27%), Araguaia (23.09%) and Amazon floodplains (16.28%). The variation of LCBD values are shown in Figure 3. As we aimed to compare only LCBD patterns at subcontinental and regional scales, in a general way, we did not compare LCBD values amongst the biological groups at the regional scale in the present study.

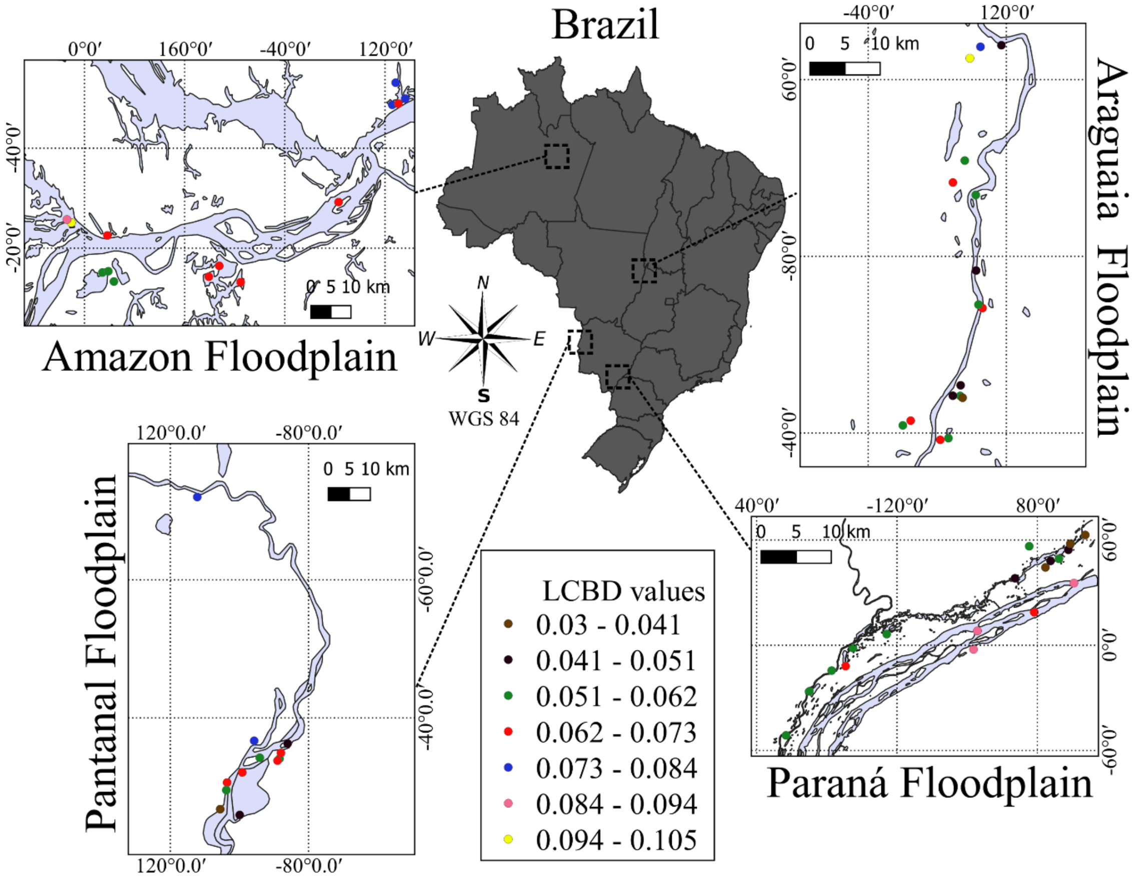

Figure 3 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains at the regional scale. Different colours of the circles represent the variation in LCBD values.

3.3.2 LCBD vs biological metrics

The results of Spearman's correlation between LCBD values and biological metrics showed significant negative correlations to mean occupancy (r = -0.3, p < 0.0001) and to richness (r = -0.13, p = 0.0045) at the subcontinental scale, indicating decreasing values of these metrics with increasing LCBD values (Figure 4). Analysing each biological group separately, Spearman's correlations also showed significant and negative correlations for most of the groups to mean occupancy (except for ciliates, testate amoebae and cladocerans), richness (except for phytoplankton, cladocerans, ostracods and fish), and mean abundance (except for phytoplankton, cladocerans and ostracods, Figure S9). At the regional scale, Spearman's correlations showed significant and negative correlation only to mean occupancy for Araguaia (r = -0.29, p < 0.0001) and for Paraná floodplains (r = -0.23, p = 0.0052, Figure 4).

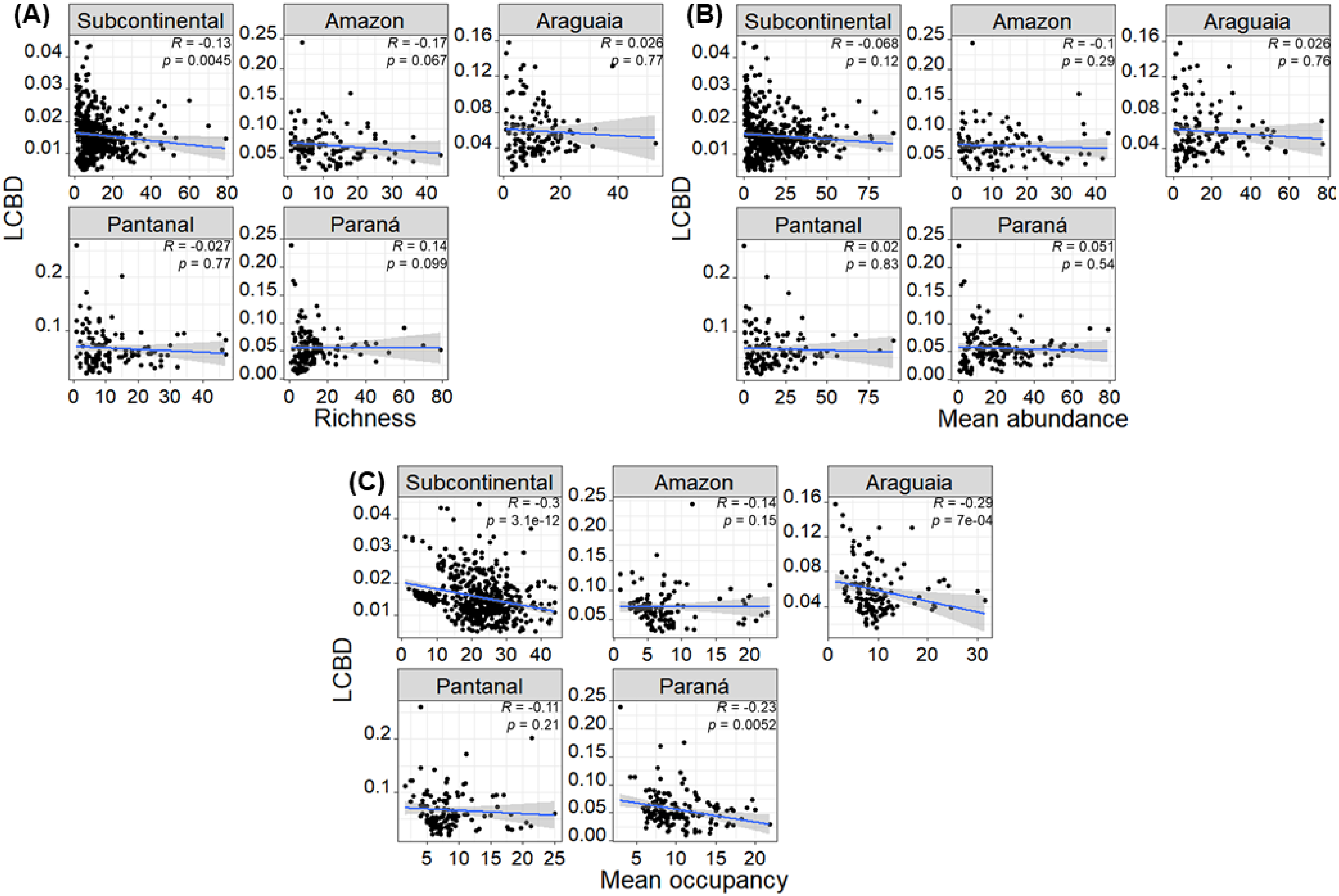
(A)
Subcontinental
R = -0.13
p = 0.0045
Amazon
R = -0.17
p = 0.067
Araguaia
R = 0.026
p = 0.77
Pantanal
R = -0.027
p = 0.77
Paraná
R = 0.14
p = 0.099
LCBD
Richness
(B)
Subcontinental
R = -0.068
p = 0.12
Amazon
R = -0.1
p = 0.29
Araguaia
R = 0.026
p = 0.76
Pantanal
R = 0.02
p = 0.83
Paraná
R = 0.051
p = 0.54
LCBD
Mean abundance
(C)
Subcontinental
R = -0.3
p = 3.1e-12
Amazon
R = -0.14
p = 0.15
Araguaia
R = -0.29
p = 7e-04
Pantanal
R = -0.11
p = 0.21
Paraná
R = -0.23
p = 0.0052
LCBD
Mean occupancy

Figure 4 - Spearman’s correlations between LCBD values and biological metrics, richness (A), mean abundance (B) and mean occupancy (C), considering all biological groups together, at the subcontinental and regional scales.

Random forest (RF) algorithms showed that the mean occupancy was the strongest predictor for LCBD values, amongst the biological metrics (median %IncMSE = 23), at the subcontinental scale. Considering the regional scales, RF algorithms also showed that the mean occupancy was the main biological predictor of LCBD values (median %IncMSE Amazon = 4, Araguaia = 10 and Pantanal and Paraná = 5, Figure 5).

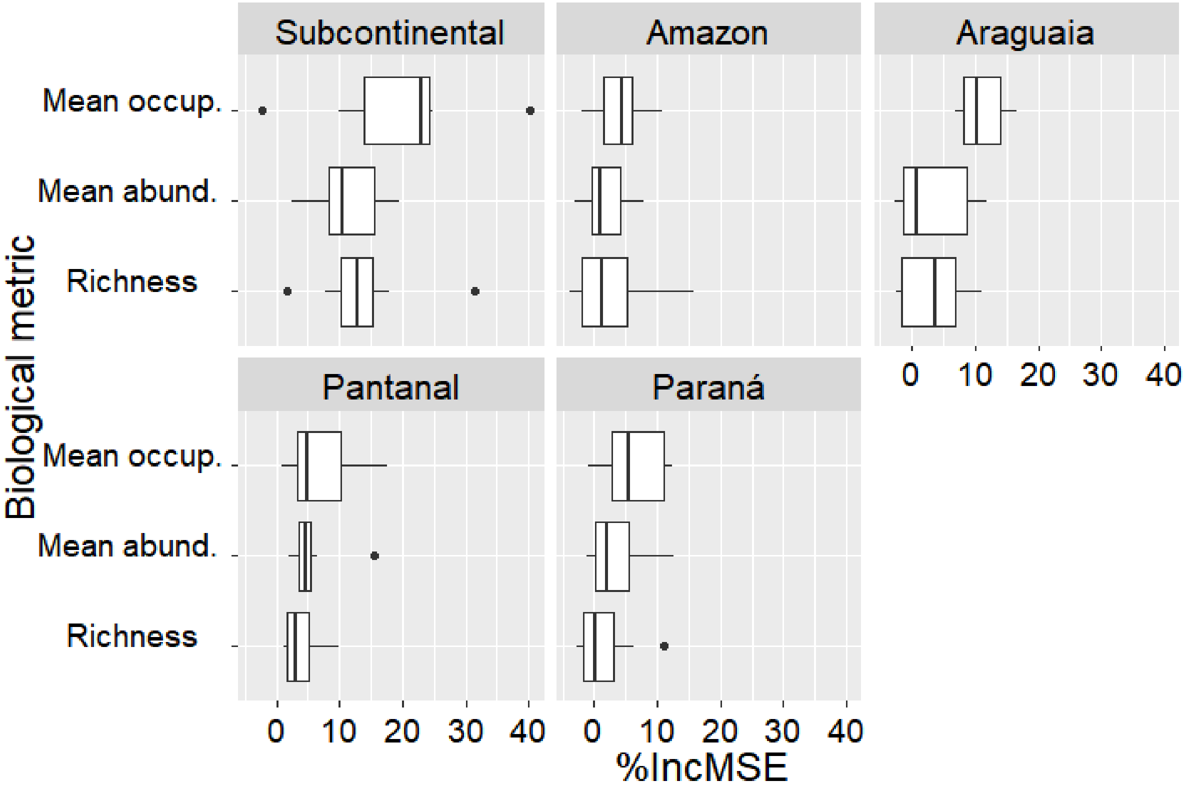

Figure 5 Median percentage of increase in mean square error (%IncMSE) of all biological groups together, for each biological metric (Mean occup. = mean occupancy, Mean abund. = mean abundance and richness), at subcontinental and regional scales.

3.3.3 LCBD vs environmental, spatial and LCEH predictors

The capacity of the predictor variables in explaining LCBD variation was higher when analysing the data at subcontinental than regional scales. At the subcontinental scale, the total percentage of explained variation (R^2) of all predictor variables ranged from 10%

(ciliates) to 36% (testate amoebae) amongst the biological communities. At the regional scale, the predictor variables were most explanative in the Amazon floodplain, mostly for phytoplankton (43%) and ostracods (32%). In the other floodplains, the predictor variables were not explanative for most of the communities, excepted for copepods in Araguaia and Pantanal (30 and 54%, respectively) and for cladocerans in Paraná (33%, Figure 6).

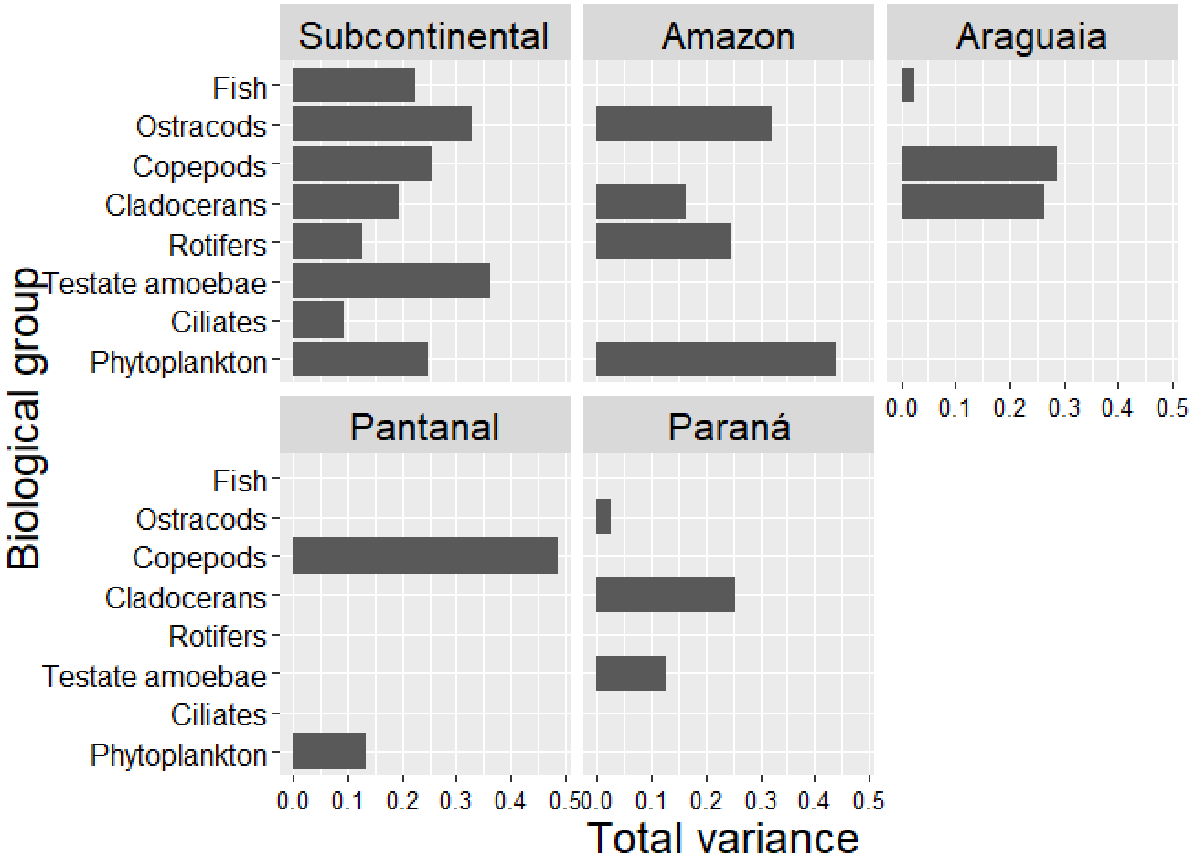

Figure 6 Results of variation partitioning showing the total contribution (total explained variance, %) of the predictor variables amongst the different biological groups, at subcontinental and regional scales.

Variation partitioning showed that the pure environmental and shared fractions between environmental and spatial predictors were the most important in explaining LCBD variation, with median percentages of explanation of 9 and 10%, respectively, at the subcontinental scale (Figure 7A). Considering each biological group separately, we found an important variation in the percentages of explanation of the predictor variables amongst the groups. The shared fraction between environmental and spatial predictors was important for LCBD variation of most of the groups, mainly for testate amoebae (36%), ostracods (18%)

and cladocerans (16%, Figure 7B). The pure fraction of explanation of the environmental predictors was important for copepods (17%), ostracods (16%), fish (13%) and phytoplankton (11%). We also found some explanation of the spatial predictors in the LCBD variation for phytoplankton and fish (both 4%) and rotifers (3%), and of the LCEH for ciliates (9%). The shared fraction between environmental and LCEH for copepods (10%) and ostracods (7%, Figure 7B). The explanation power of the predictor variables was not significant when analysing the data at the regional scale (Figure 7A). We only found some percentage of explanation of the shared fractions between environmental and spatial predictors, in explaining LCBD variation, in the Amazon floodplain, with a median of 3%.

RF algorithms showed that water temperature and latitude were the strongest predictors of LCBD values at the subcontinental scale (median %IncMSE = 9 and 7%, respectively, Figure S10). Analysing each biological group separately, RF showed that the predictors of LCBD values were different amongst the groups. Water temperature and total nitrogen were important for phytoplankton (%IncMSE = 9 and 12, respectively), LCEH for ciliates (%IncMSE = 9), water temperature for testate amoebae (%IncMSE = 16), latitude for rotifers and ostracods (both %IncMSE = 12), Secchi and turbidity for cladocerans (%IncMSE = 10 and 9, respectively), electrical conductivity for copepods (%IncMSE = 10) and water temperature for fish (%IncMSE = 9, Figure S11). At the regional scale, dissolved oxygen was the most important predictor of LCBD values in the Amazon and Pantanal (median %IncMSE = 4 and 2, respectively), latitude in the Araguaia (median %IncMSE = 2) and electrical conductivity in the Paraná floodplain (median %IncMSE = 4, Figure S10).

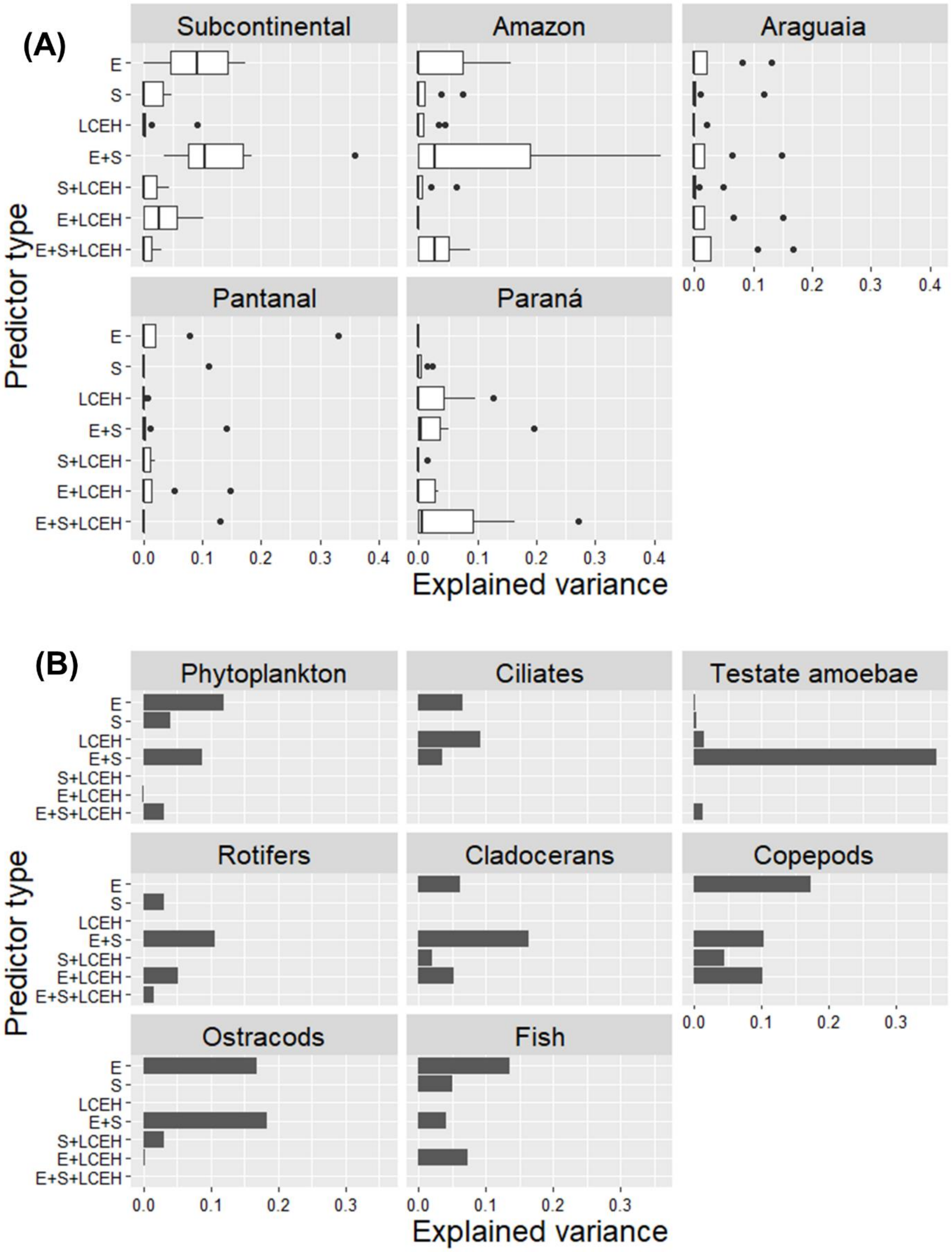

Figure 7 Results of variation partitioning showing the pure and shared percentage of contribution of the predictor variables. (A) Median values at subcontinental and regional scales, considering all biological groups together, and (B) values for each biological group at the subcontinental scale. E = environmental, S = spatial and LCEH = local contribution to the environmental heterogeneity.

3.4 Discussion

3.4.1 Patterns of local contribution to beta-diversity

The Amazon floodplain showed a greater uniqueness in terms of species composition, as compared to the other floodplains, indicating that sites of this system contributed most to the total beta-diversity of aquatic organisms at a subcontinental scale. The most distinct set of species found in this floodplain may reflect the fact that the Amazon basin is the largest river basin on Earth (Jézéquel et al., 2020), in addition to the Amazon region being one of most important hotspots of biodiversity in the world, housing more than one-third of the Earth's known species (Heckenberger et al., 2007). We also found important contribution of sites of the Paraná River floodplain to the total beta-diversity, with high uniqueness in species composition, when analysing the data at a regional scale. This is because the sites of this floodplain are located in an important preserved area of the Paraná River, the largest stretch without dams, which plays an important role in the regional maintenance of the biodiversity of aquatic organisms (Agostinho et al., 2004).

The Amazon and Paraná basins have been suffering from several anthropogenic threats (Agostinho et al., 2004; Castello & Macedo, 2016). For example, the Paraná River has undergone extensive dam constructions and at least 130 reservoirs were constructed in its basin up to now (Agostinho et al., 2004). Thus, we show the importance of conservation actions in the areas of the present survey. For example, as some countries (e.g. Brazil) have decision-making processes to ensure that new hydroelectric dams are at the same time economically viable and minimize environmental impacts (Castello & Macedo, 2016), they should consider that new dam constructions in the areas of the present study should be avoided, owing to its high uniqueness in species composition. Such a strategy would prevent sites that contribute greatly to the total beta-diversity of the region from being lost. Another important action is the establishment of protected areas (PAs), because they provide protection to freshwater environments by controlling riparian deforestation, pollution and over-exploration of natural resources, and consequently protecting its biodiversity (Jézéquel et al., 2020). Such conservation actions must be considered, especially in the current Brazilian situation of changes in national legislation on protected areas, which threaten biodiversity (Begotti & Peres 2019; Golden Kroner et al., 2019).

When we analysed the data at a regional scale, the Amazon had lower number of significant LCBD values, in addition to the lowest coefficient of variation of these values, compared to the other floodplains. However, these results do not mean that the Amazon floodplain sites have a low conservation value, but show that this floodplain presents higher numbers of unique sites, in terms of species composition, which contributed almost equally to the total beta-diversity. For example, although Paraná had more sites with significant LCBD values, in addition to the highest coefficient of variation of these values, it also comprises several sites that contribute weakly to the total beta-diversity. Consequently, the entire Paraná floodplain was not necessarily the most important, with the highest conservation value, when analysing the data at a regional scale. Because of the bias of these analyses, we think that analysing the data at a subcontinental scale was more informative when assessing ecological uniqueness of the sites in our survey (see also below).

3.4.2 Biological metrics and local contribution to beta-diversity

The fact that species mean occupancy was strongly related to the high LCBD values indicates that the rarity of the species was an important factor that contributed to the degree of uniqueness, in terms of species composition, in some sites of our study area. We can infer that these sites were also unique in their environmental characteristics (e.g. high environmental heterogeneity) capable of harbouring these rare species. This is because rare species generally have small populations, narrow ecological niches and, consequently, are restricted to small geographical ranges (Gaston, 1994). Therefore, they are more vulnerable than common species to disturbance, environmental change, and competitive exclusion (Gaston et al., 1994).

Another reason why we found sites with greater uniqueness in the Amazon system, when analysing at a subcontinental scale, other than the one discussed above, is probably related to latitude. The importance of this variable was already shown in other studies, considering wide spatial scales of distribution and it was confirmed that many taxonomic groups have a latitudinal gradient of diversity (Scott et al., 2011; Murphy et al., 2020). The most common pattern found shows that the lower the latitude, the greater the diversity, which thus increases toward the equator (Willig et al., 2003). These latitudinal diversity gradients have been attributed to several factors, such as temperature, productivity and habitat heterogeneity (Hillebrand & Azovsky, 2001). Latitude also affects the geographical range-size of the species. For example, according to Rapoport’s rule, “species that occur at higher latitudes tend to have wider distributional ranges than species having ranges limited to latitudes closer to the equator’ (Stevens, 1989). Therefore, we infer that the high rates of rare (or endemic) species, and consequently the high uniqueness of sites in the Amazon system, might also be owing to the relationship between geographical range-size and latitude amongst the floodplains.

The relationship between species' mean occupancy and uniqueness in our survey reinforces the importance of conserving unique sites (here in the Amazon and Paraná systems, for example). This is because rare (and endemic) species are critical components of the community structure and their loss can lead to homogenization and simplification of communities, reducing their uniqueness (Burlakova et al., 2011). Our results agree with Dubois et al. (2020), who also found positive relationships between the uniqueness of the sites and the proportion of rare species of riparian wetland plant communities, and highlighted the importance of protecting unique species assemblages, because they are considered of great conservation value.

The weak negative relationship between species richness and LCBD values partially supported the idea that unique sites will probably be poor in number of species, as shown by studies that have found negative associations between taxonomic richness and ecological uniqueness (da Silva & Hernández, 2014; Heino et al., 2017; Heino & Grönroos, 2017; Brito et al., 2020). However, there is no consensus on the causality of this relationship, which also differs between the groups of organisms and the ecosystems under study (Szabó et al., 2019). Furthermore, the fact that there was no relationship between mean abundance of species and LCBD values (i.e. at the subcontinental scale), shows that the idea that species with high total abundance, generally present greater abundance variation amongst the sites and, therefore, present high contributions to beta-diversity (Heino & Grönroos, 2017) was not supported by the aquatic communities of riverine floodplains studied here. These results indicate that floodplain systems, with unique species composition, are at risk of being neglected in conservation plans that focus only on species richness or abundance.

3.4.3 Correlates of local contribution to beta-diversity

Assessing factors that predict de variation in LCBD has been difficult, mainly in freshwater ecosystems, as this metric is relatively new (Leão et al., 2020). However, studies have found significant explanation of environmental variables for LCBD variation (Sor et al., 2018; López-Delgado et al., 2019; Brito et al., 2020; Li et al., 2020). We also found some contribution of the environmental variables to the LCBD variation. This is because the variability in the local environmental variables (environmental heterogeneity) creates high availability of different habitats, providing the establishment of a different set of species amongst the sites, such as explained by Leão et al. (2020), who analysed LCBD of fish in Amazonian streams. Therefore, species are sorted amongst the regions owing to their fundamental niche or physiological tolerances to certain environmental conditions. Thus, the more unique the sites in their environmental characteristics, the higher the chances of having unique species occurring in these sites (Pajunen et al., 2017).

The predictors variables (mainly environmental variables) were more explanative to the total variance of LCBD when we analysed all floodplains together (the subcontinental scale), than when analysing each floodplain separately (fine scale). This is so because habitat availability and environmental heterogeneity increases with the spatial scale of the study (Heino et al., 2015). It was also confirmed by the shared fraction between environmental and spatial predictors, found in our results, indicating that environmental variables were spatially structured. Consequently, species sorting also increasing with increasing environmental gradient (Jackson et al., 2001; Grönroos et al., 2013). Thus, we consider that analysing all floodplains together was more effective to the LCBD approach, and such results show the importance of considering broad scales in ecological studies. That is so because broad-scale studies allow the identification of robust patterns and lead to broad generalizations about metacommunity organization, in addition to the factors responsible for such organization (Heino et al., 2015). We also found that water temperature and latitude (see also below) were the most important variables in explaining LCBD variation at the subcontinental scale. Water temperature influence might be related to niche control, where sites with high LCBD values, for example, were housing only few species, adapted to wide water temperature fluctuations.

3.4.4 Local contribution to beta-diversity amongst biological groups

Our findings show that the drivers and patterns of LCBD values were variable amongst the biological groups. These results might be related to the niche characteristics, species biological traits, such as feeding mode, body size and dispersal capacity, which can affect species’ contributions (of each biological group) to beta-diversity, (Heino & Grönroos, 2017), and consequently to LCBD variation. Several studies have shown the importance of considering biological traits when analysing the influence of environmental and spatial predictors. For example, De Bie et al. (2012) showed that body size and dispersal mode were important traits affecting metacommunity structure. Thus, the larger the organisms, the more they were affected by spatial drivers (e.g. dispersal limitation). The same pattern was found for organisms that have the capacity of passive dispersal, compared to active dispersers (De Bie et al., 2012). Furthermore, Padial et al. (2014) showed that environmental predictors were more explanative to organisms with high dispersal capacity (e.g. microalgae). Despite the importance of considering these traits of organisms, we did not find direct influence of the relationship between dispersal mode and body size and spatial predictors on LCBD patters, thus refusing our fourth hypothesis.

The selected variables are known to be important for some biological groups, which consequently affected LCBD patterns. For example, nitrogen is generally considered a primary nutrient, limiting the growth of phytoplankton in lakes (Elser et al., 1990). Furthermore, dissolved oxygen and conductivity have been found as variables responsible for spatial variability of zooplankton communities (such as cladocerans and copepods, Picapedra et al., 2019). Because of the possible influence of biological traits on species' distribution, in addition to the difference in predictors affecting each group, we also stress the importance of considering different taxonomic groups in studies assessing LCBD patterns, because studies based on a single biological group are at risk of misrepresenting the uniqueness of the sites in terms of species composition of the entire community.

3.5 Conclusions

The Amazon and Paraná floodplains had the most unique sites in terms of species composition, showing the importance of the conservation of these ecosystems, owing to their great contribution to global biodiversity. We highlight that the other floodplains should also be conserved (or remain conserved), as they also present unique characteristics, as well as unique species. We found that mean occupancy of species was the most important biological metric associated with LCBD values. These results highlight the importance of considering species rarity in studies evaluating the uniqueness of ecological environments. We found that environmental factors had important contribution to the site's uniqueness, indicating that species can be sorted amongst the environments owing to their ecological requirements. Furthermore, spatial components, especially latitude, influence de uniqueness of the sites (for example, in the Amazon system). Finally, we found that the LCBD drivers and patterns are different amongst the biological groups, probably related to their biological traits, such body size and dispersal mode, which influence, for example, their dispersion potential. The present survey contributes to the understanding of broad-scale pattern distributions of a variety of taxa. Such studies are needed and are becoming urgent, because ecosystems, such as riverine floodplains, are increasingly being transformed and threatened by anthropogenic actions.

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APPENDIX A - Electronic Supplementary Material - Laboratory analysis used for each biological group (Adapted from Lansac-Toha et al., 2021)

Phytoplankton

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).

Ciliates

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).

Testate amoebae, Copepods, Cladocerans and Rotifers

Sample collection: These communities were 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: The 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).

Ostracods

Sample collection: It was collected ostracods associated with aquatic macrophytes. Aquatic macrophytes were collected manually and the submerged parts of these plants were washed (either root systems or the whole plant) in a plastic bucket, to remove the ostracods associated with these macrphytes. 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 from the macrophytes, the submerged parts of these plants were stored in previously labeled plastic bags. Subsequently, they were oven-dried, and then weighed to calculate densities. Samples were divided with the Folsom fractioner, and ¼ of samples were 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); Ferreira et al. (2019); Ferreira et al. (2020); Almeida et al. (2021)

Fish

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 & Pavanelli (2007), Ota et al. (2018).

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Table S1 - Significance of LCBD values for each sampled site at each floodplain system. Asterisks show the sites where LCBD was significant ($p < 0.05$), based on analyses at the subcontinental and regional scales. Phy = phytoplankton, Cil = ciliates, Tes = testate amoebae, Rot = rotifers, Cla = cladocerans, Cop = Copepods, Ost = ostracods and Fis = Fish.

Floodplain	Lake name	Coordinates	Subcontinental								Regional							
			Phy	Cil	Tes	Rot	Cla	Cop	Ost	Fis	Phy	Cil	Tes	Rot	Cla	Cop	Ost	Fis
Amazon	1. Comprido	S 03° 14' 34.2" W 059° 58' 23.2"							*									
	2. Calado	S 03° 18' 29.5" W 060° 34' 16.9"																
	3. Piranha	S 03° 16' 59.5" W 060° 39' 51.5"		*	*							*					*	*
	4. Monte Cristo	S 03° 16' 37.3" W 060° 40' 32.7"			*		*	*					*		*			
	5. Grande	S 03° 22' 51.3" W 060° 35' 03.0"			*													
	6. Poço Curuça	S 03° 22' 42.4" W 060° 34' 07.5"																
	7. Cadete	S 03° 23' 54.9" W 060° 33' 15.7"			*													
	8. Grande II Janauca	S 03° 22' 04.7" W 060° 16' 54.5"	*		*			*								*		
	9. Tutaí	S 03° 23' 20.8" W 060° 18' 31.7"	*		*						*							
	10. Castanho	S 03° 24' 00.0" W 060° 13' 35.9"	*															
	11. Poraquequara I	S 03° 03' 07.5" W 059° 50' 03.6"			*	*		*	*					*			*	
	12. Poraquequara II	S 03° 00' 31,2" W 059° 49'32.0"	*					*	*					*				
	13. Poraquequara III	S 03° 02' 59.1" W 059° 49' 06.0"							*								*	
	14. Poraquequara IV	S 03° 02' 23.9" W 059° 48' 02.9"			*			*	*		*					*		
Araguaia	15. Crixas I	S 13° 21' 33.1″ W 050°36' 42.9″		*						*		*						
	16. Crixas II	S 13° 21' 42.8″ W 050° 36' 26.9″								*								
	17. Crixas III	S 13° 21' 32.2″ W 050° 37' 32.5″																
	18. Crixas IV	S 13° 20' 37.5″ W 050° 36' 40.0″								*								*
	19. Japones I	S 13° 25' 15.0″ W 050° 38' 02.4″					*								*			
	20. Japones II	S 13° 25' 23.6″ W 050° 38' 57.4″							*								*	
	21. Montaria I	S 13° 24' 07.9″ W 050° 43' 10.2″					*						*				*	
	22. Montaria II	S 13° 23' 43.1″ W 050° 42' 17.3″					*											

Floodplain	Lake name	Coordinates	Subcontinental								Regional							
			Phy	Cil	Tes	Rot	Cla	Cop	Ost	Fis	Phy	Cil	Tes	Rot	Cla	Cop	Ost	Fis
	23. Piranha	S 13° 02' 53.5″ W 050° 37' 32.2″				*												
	24. Varal	S 13° 00' 58.4″ W 050° 36' 12.0″							*									
	25. Piratinga	S 13° 03' 58.9″ W 050° 34' 57.6″			*	*								*				
	26. Brito	S 13° 10' 35.2″ W 050° 34' 55.4″																
	27. Comprido I	S 12° 52' 02.3″ W 050° 35' 37.9″		*			*	*		*		*	*		*	*		
	28. Comprido II	S 12° 51' 02.2″ W 050° 34' 26.1″					*	*							*	*		
	29. Goiaba	S 12° 50' 54.1″ W 050° 32' 04.7″																
	30. Luis Alves I	S 13° 13' 52.1″ W 050° 34' 12.3″	*		*					*	*		*					*
	31. Luis Alves II	S 13° 13' 34.2″ W 050° 34' 39.8″							*								*	
Pantanal	32. Arrozal	S 19° 02' 03.7" W 057° 28' 13.9"	*	*							*	*						
	33. Tuiuiu	S 18° 48' 30.2" W 057° 39' 20.4"					*			*			*					*
	34. Odila I	S 19° 27' 47.6" W 057° 24' 52.6"						*										
	35. Odila II	S 19° 28' 28.5" W 057° 24' 57.7"																*
	36. Baía Ponte	S 19° 30' 11.7" W 057° 25' 39.1"																
	37. Baía Bugre	S 19° 30' 43.3" W 057° 23' 27.3"											*					
	38. Miranda I	S 19° 25' 38.2" W 057° 18' 58.4"																
	39. Miranda II	S 19° 25' 07.7" W 057° 18' 49.0"						*								*		
	40. Miranda IV	S 19° 25' 49.0" W 057° 19' 12.0"																
	41. Mirandinha	S 19° 24' 16.6" W 057° 18' 03.5"																
	42. Figueira	S 19° 24' 24.0" W 057° 18' 49.3"																
	43. Albuquerque	S 19° 24' 01.5" W 057° 21' 49.6"											*	*				*
	44. Piuva	S 19° 26' 52.7" W 057° 23' 09.9"		*										*				
	45. Rebojão	S 19° 35' 00.4" W056° 59' 22.1"		*								*					*	*
	46. Corixão	S 19° 32' 09.7" W 057° 03' 03.3"					*	*							*			*
Paraná	47. Patos	S 22° 49' 33.6" W 53° 33' 9.9"				*	*							*	*			
	48. Ventura	S 22° 51' 23.7" W 53° 36' 1.02"	*		*								*					

Floodplain	Lake name	Coordinates	Subcontinental								Regional							
			Phy	Cil	Tes	Rot	Cla	Cop	Ost	Fis	Phy	Cil	Tes	Rot	Cla	Cop	Ost	Fis
	49. Sumida	S 22° 46' 54.78" W 53° 29' 22.2"					*								*			
	50. Finado Raimundo	S 22° 47' 57.6" W 53° 32'29.16"	*				*											
	51. Peroba	S 22° 54' 30.3" W 53° 38' 24.3"										*					*	
	52. Boca do Ipoitã	S 22° 50' 7.92" W 53° 33' 55.38"	*															
	53. Guaraná	S 22° 43' 16.68" W 53° 18' 9.24"																
	54. Fechada	S 22° 42' 37.92" W 53° 16' 33.06"	*			*	*							*				
	55. Onça	S 22° 39' 48.42" W 53° 12' 1.62"																
	56. Gavião	S 22° 40' 47.94" W 53° 13' 53.46"																
	57. Aurélio	S 22° 41' 34.68" W 53° 13' 50.58"																
	58. Pousada das Garças	S 22° 42' 1.14" W 53° 15' 23.52"																
	59. Maria Luiza	S 22° 40' 30.18" W 53° 13' 11.16"																
	60. Porcos	S 22° 42' 4.44" W 53° 14' 40.08"	*															
	61. Garças	S 22° 43' 27.18" W 53° 13' 4.56"				*		*								*	*	*
	62. Manezinho	S 22° 46' 44.7" W 53° 20' 56.76"											*	*		*		
	63. Pombas	S 22°47' 55.92" W 53° 21' 32.58"						*				*	*			*		*
	64 Leopoldo	S 22° 45' 24" W 53° 16' 7.98"	*			*					*							

Table S2 - Mean and standard deviation values of environmental variables at each floodplain system.

	Floodplain			
	Amazonas	**Araguaia**	**Pantanal**	**Paraná**
Air temperature (°C)	31.36±2.37	30.82±1.85	21.31±4.84	29.48±1.53
Depth (m)	13.73±1.71	6.01±0.96	4.02±1.27	3.66±0.74
Euphotic zone (m)	3.85±0.7	4.46±1.97	5.83±1.59	2.99±1.3
Secchi (m)	2.05±0.26	2.28±0.73	2.79±0.59	1.73±0.48
Turbidity (NTU)	8.36±4.38	9.87±6.79	5.84±5.23	22.46±18
Water temperature (°C)	32.94±0.54	30.04±0.89	21.93±1.47	29.21±0.67
Saturated oxygen (%)	27.04±15.76	34.64±16.13	37.46±18.39	73.56±14.86
Dissolved oxygen (mg. L^{-1})	2.9±1.15	3.63±1.31	4.26±1.65	6.66±1.12
Electrical conductivity (µS.cm^{-1})	55.32±9.54	39.86±5.8	87.94±39.45	37.18±12.88
Total nitrogen (µg. L^{-1})	698.35±40.66	732.12±688.47	1079.91±725.77	917.86±400.23
Total phosphorus (µg. L^{-1})	23.21±9.73	22.82±7.44	61.39±65.82	64.72±25.2
pH	7.33±1.29	6.45±0.28	7.54±0.32	6.22±0.44

APPENDIX B - Electronic Supplementary Material

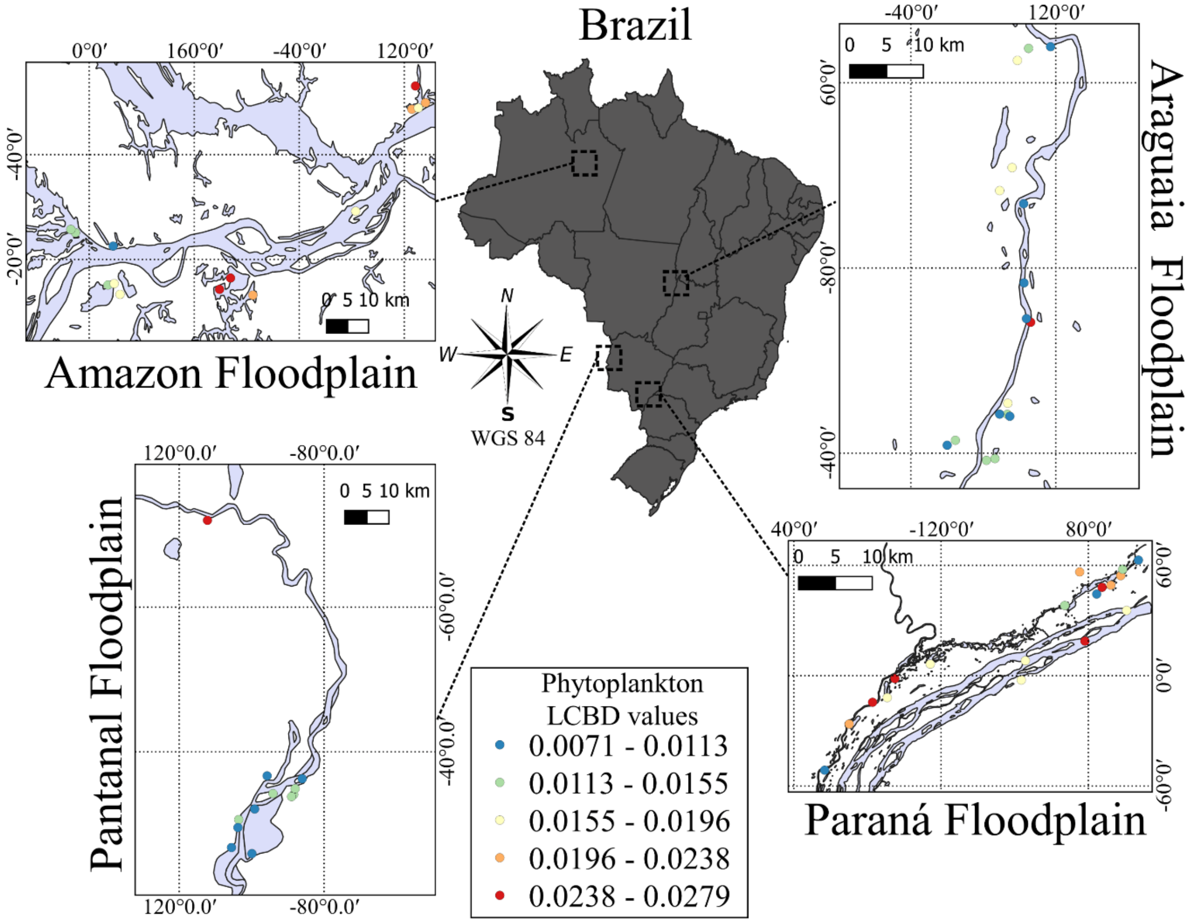

Figure S1 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on phytoplankton communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

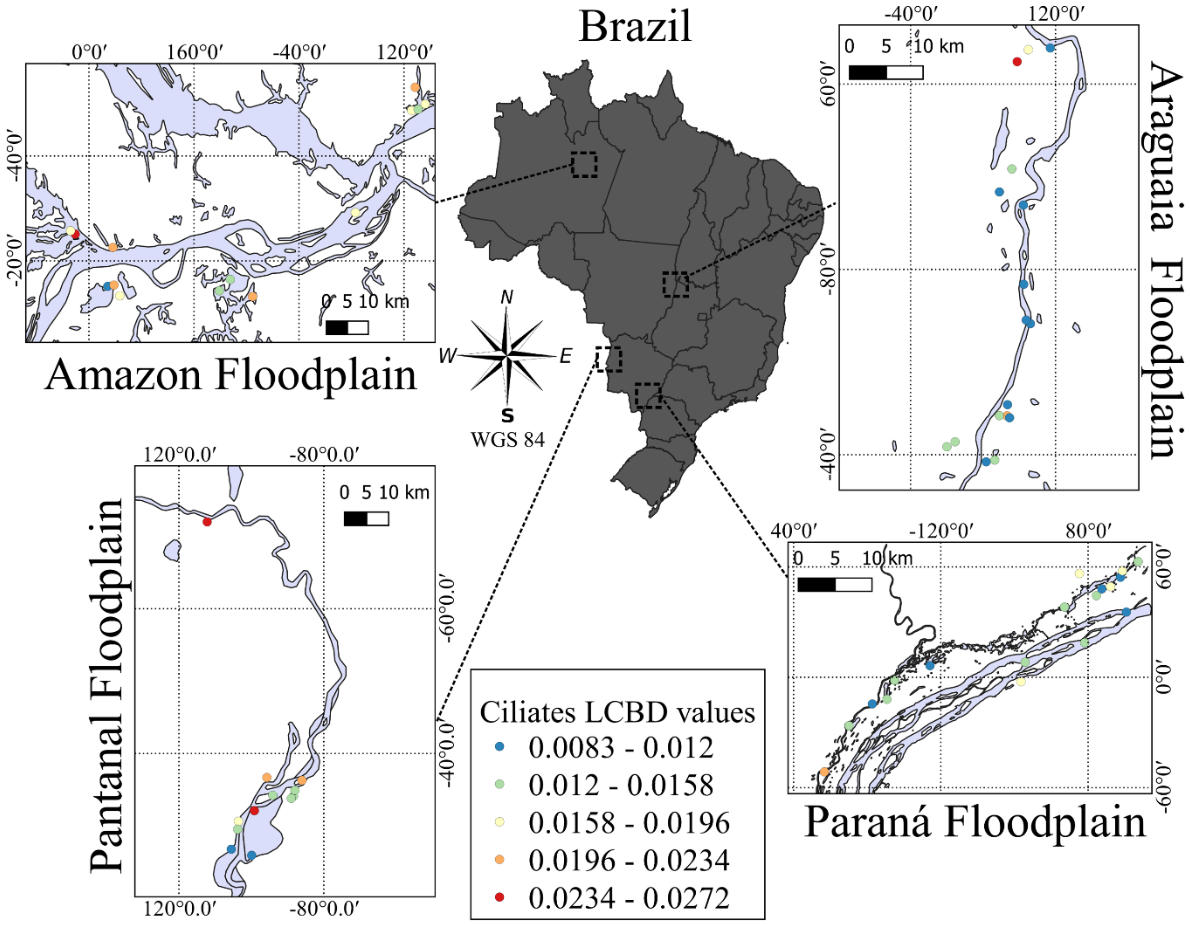

Figure S2 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on ciliate communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

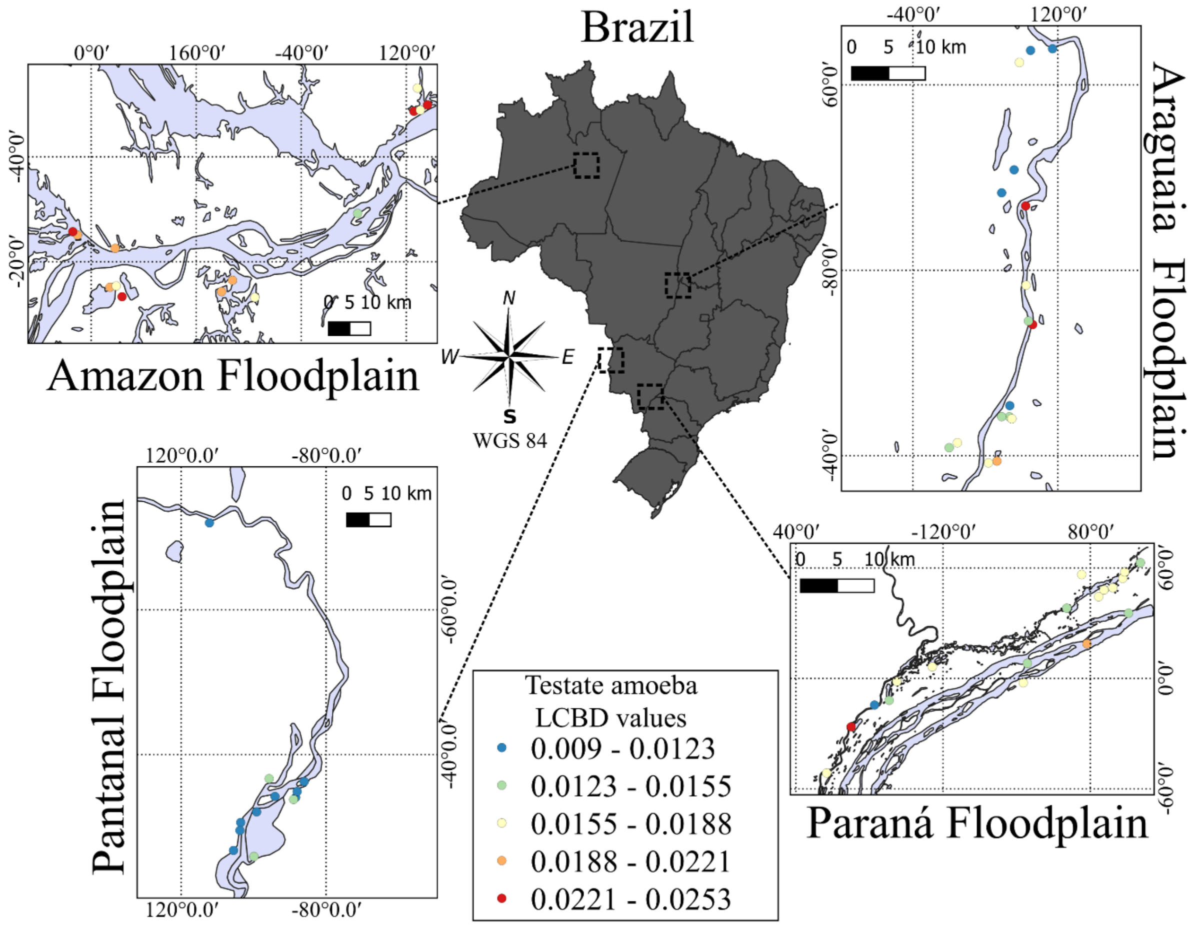

Figure S3 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on testate amoeba communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

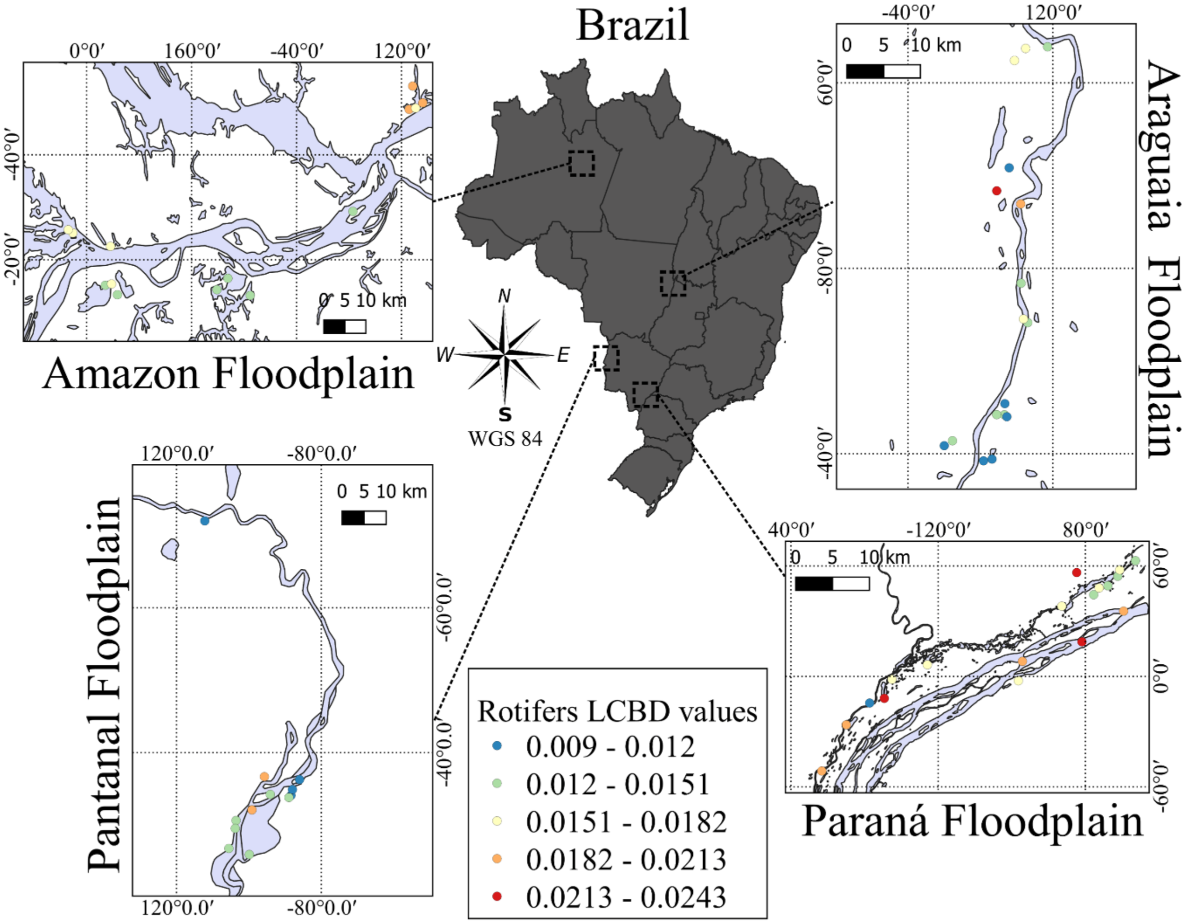

Figure S4 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on rotifer communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

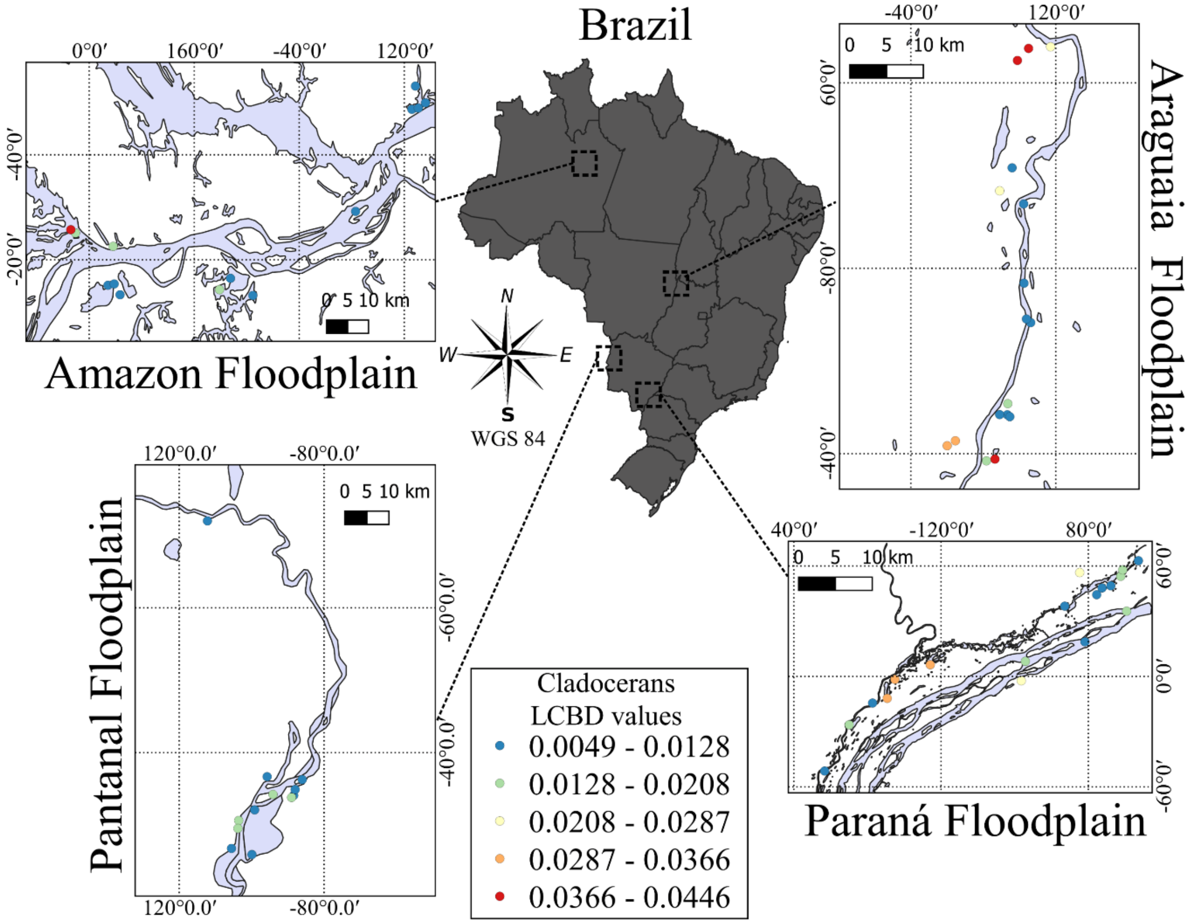

Figure S5 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on cladoceran communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

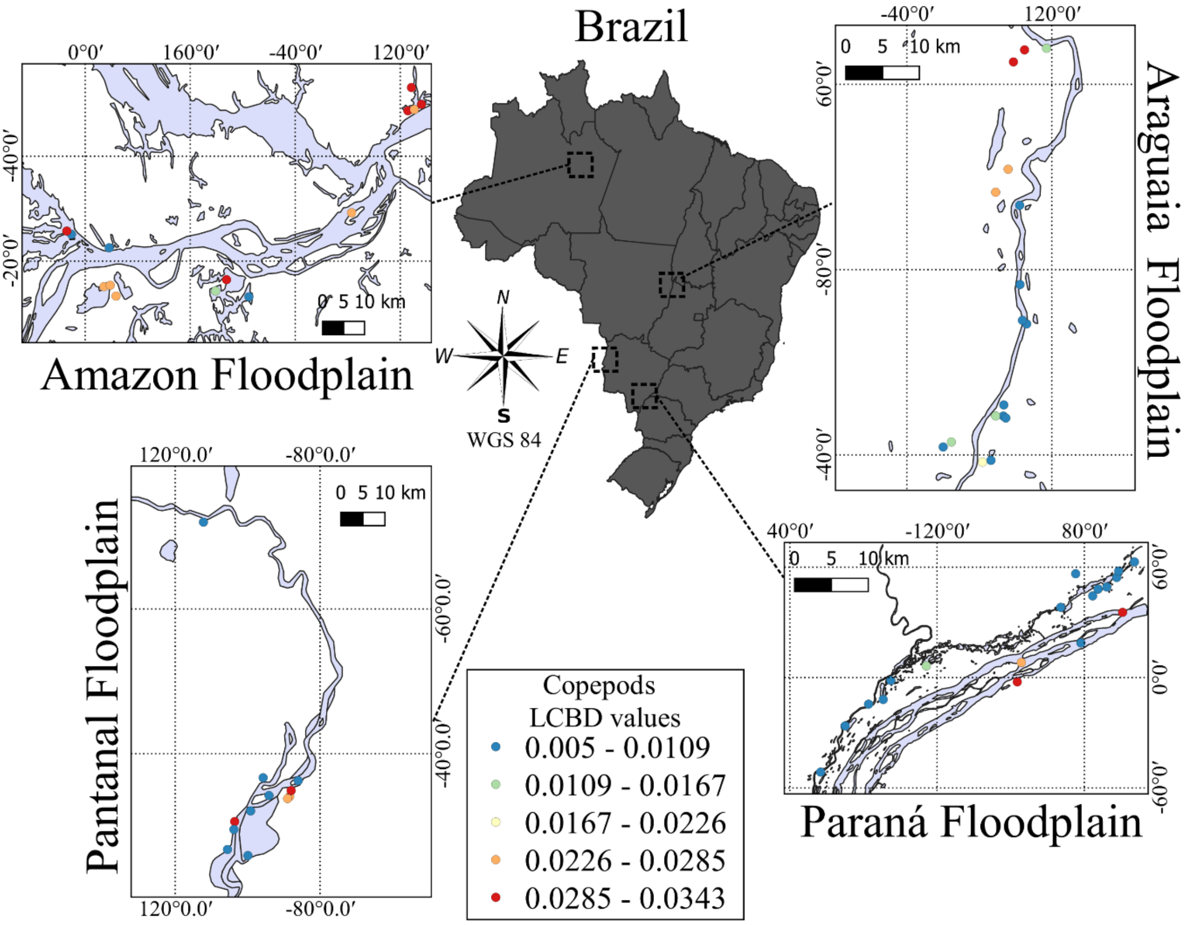

Figure S6 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on copepod communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

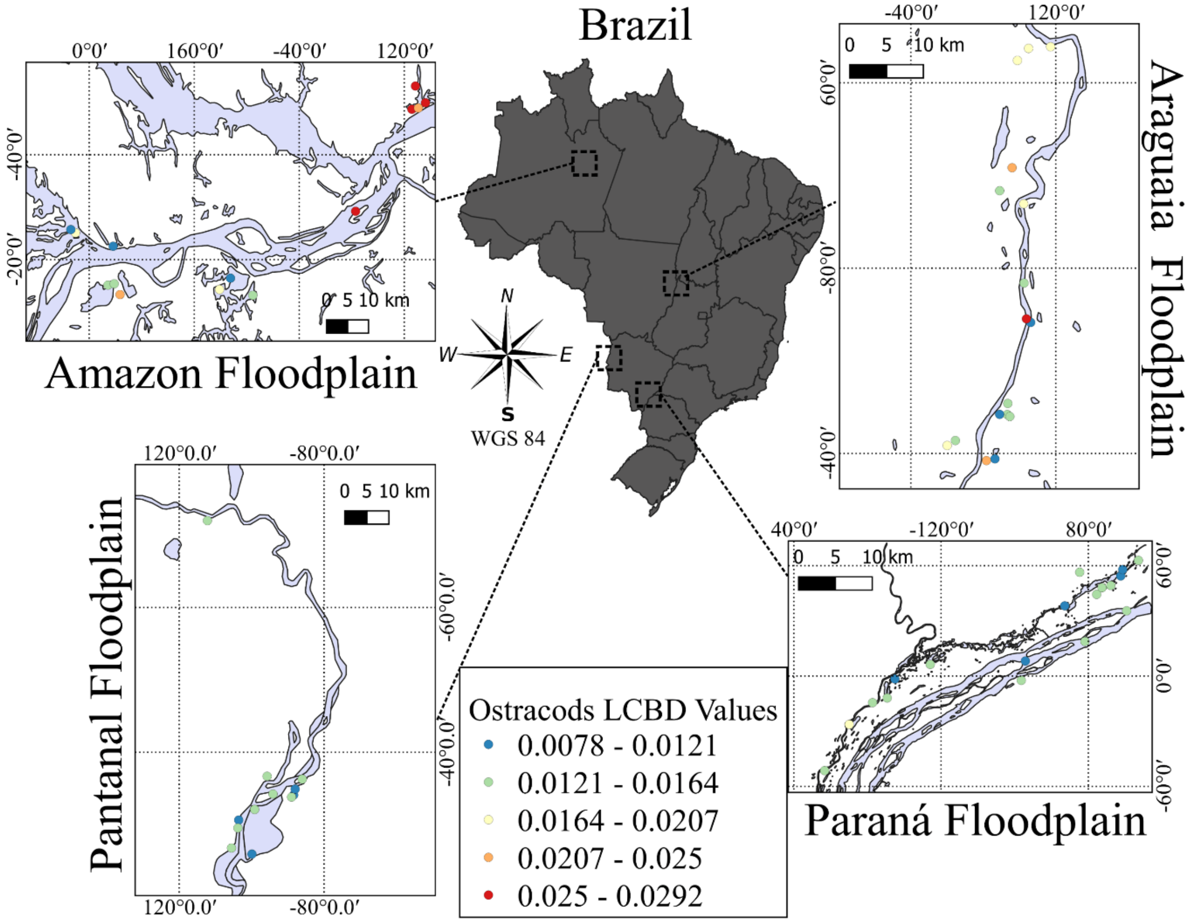

Figure S7 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on ostracod communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

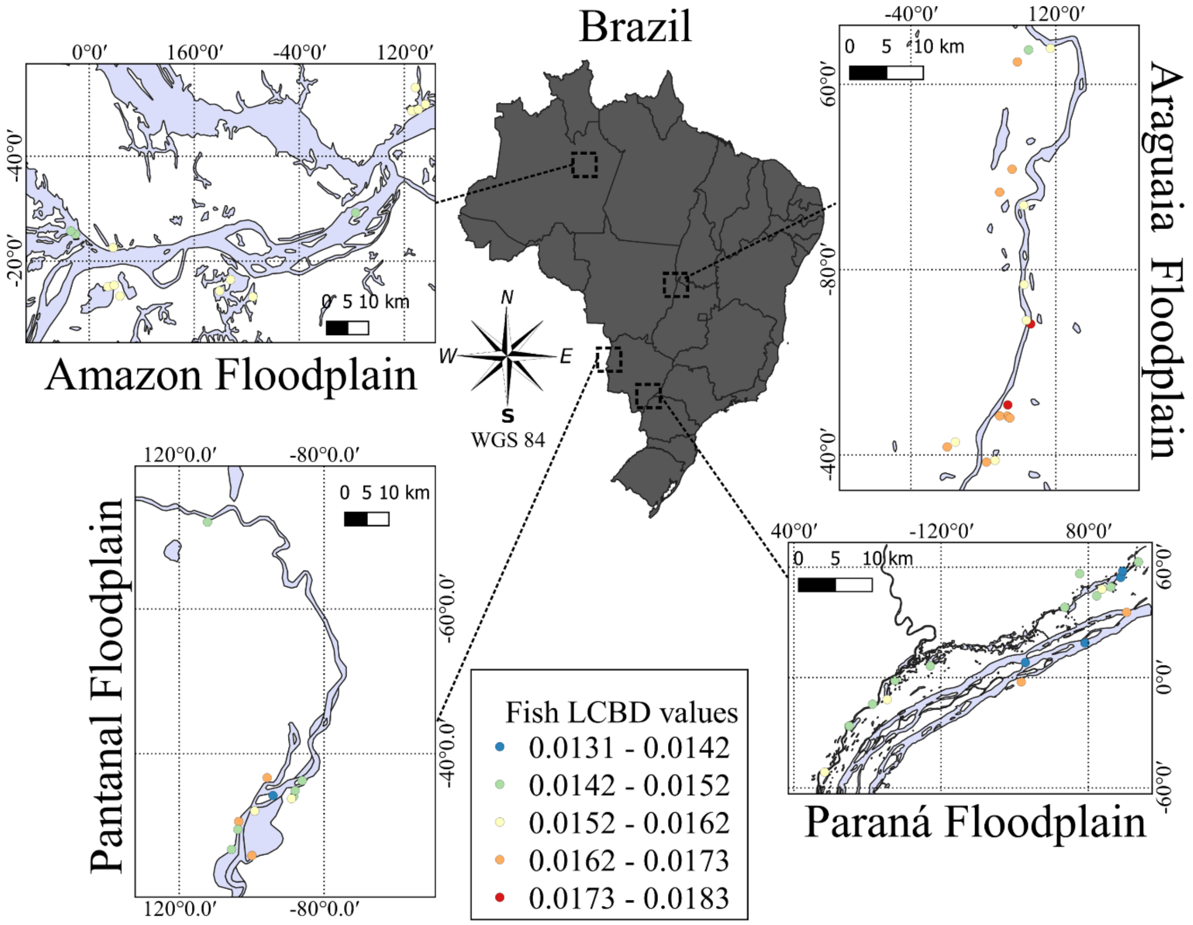

Figure S8 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on fish communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

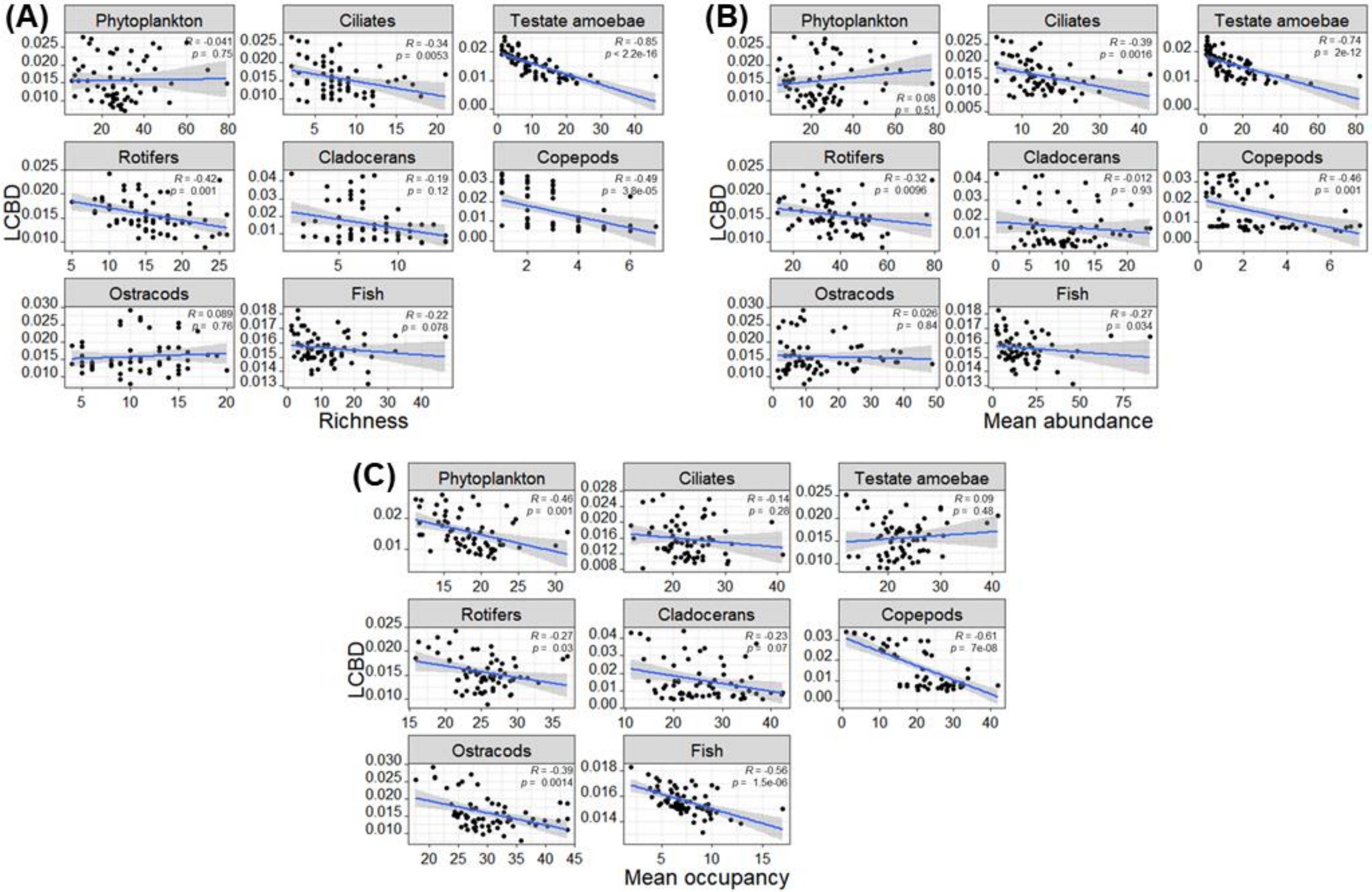

Figure S9 Spearman's correlations between LCBD values and biological metrics, richness (A), mean abundance (B) and mean occupancy (C), for each biological group, at the subcontinental scale.

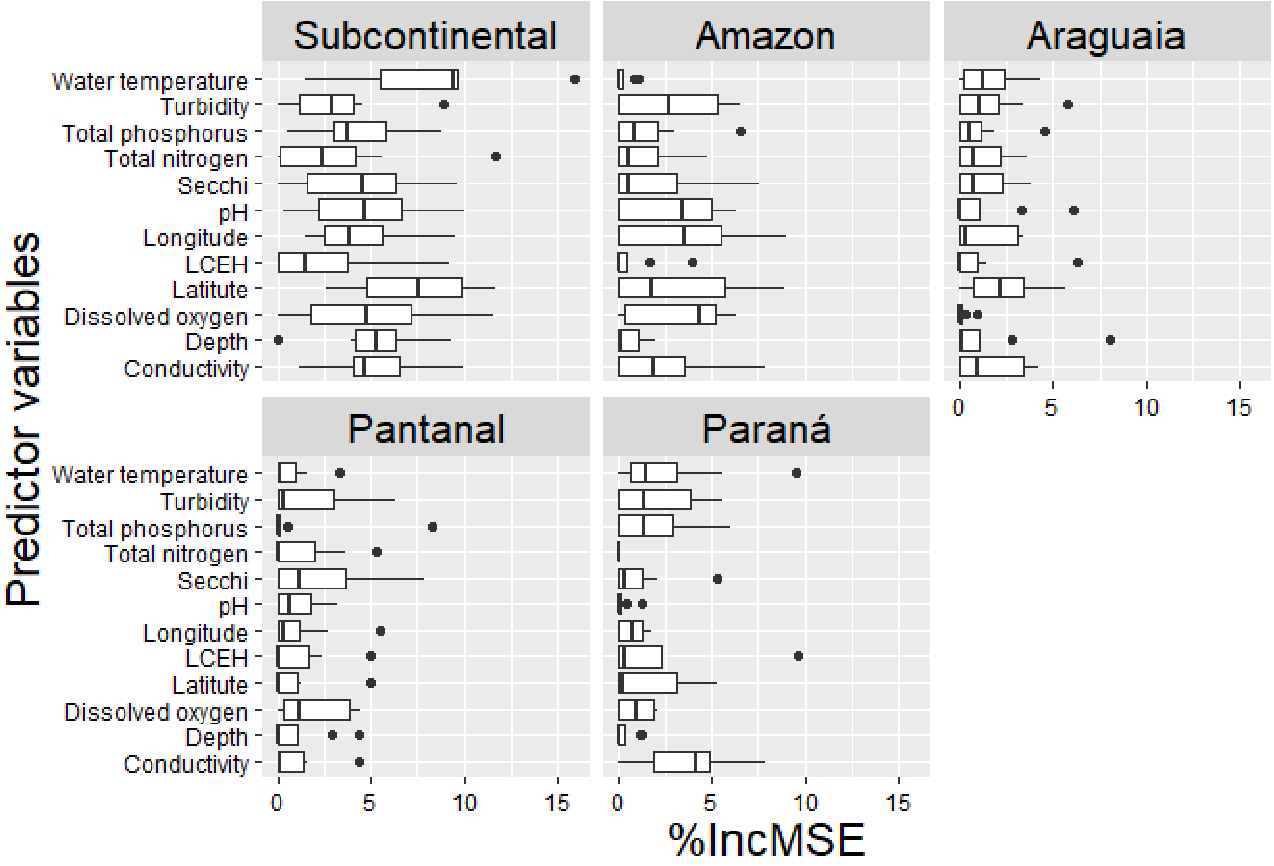

Figure S10 Median percentage of increase in mean square error (%IncMSE), considering all biological groups together, for each LCBD predictor, considering the subcontinental and regional scales.

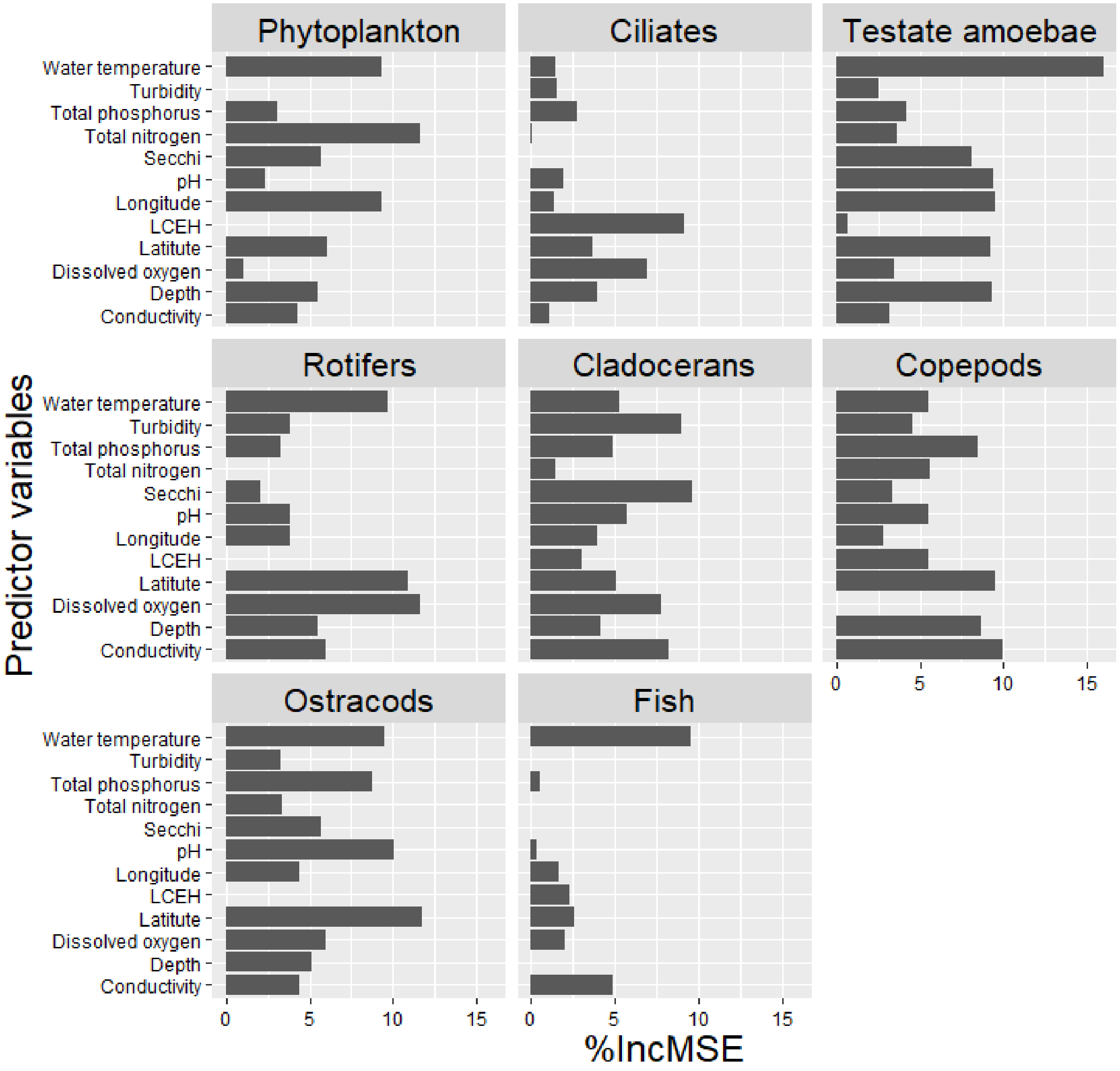

Figure S11 Figure S8 LCBD values in the Amazon, Araguaia, Pantanal and Paraná floodplains, based on fish communities, at the subcontinental scale. Different colours of the circles represent the variation in LCBD values.

4 FINAL CONCLUSIONS

In general, it was concluded that environmental filtering was more important in explaining communities' distribution patterns. Thus, the species sorting mechanism might be responsible for such patterns, within and amongst Neotropical floodplain systems, probably related to ecological requirements of the species. The first approach of this thesis showed that ecological drivers (e.g. spatial and environmental predictors) have different influences on each of the beta-diversity facets of ostracod communities, thus showing that including species-, traits- and phylogeny-based approaches can be complementary in ecological surveys. Therefore, biological communities associated with different macrophyte life forms should be considered in local and regional biodiversity surveys, owing to the variation in the factors affecting these communities associated with each macrophyte life form. In the approach, LCBD analysis showed that the Amazon and Paraná floodplains had the most unique sites in terms of species composition, showing the importance of the conservation of these ecosystems, owing to their great contribution to global biodiversity. Drivers and patterns (e.g. environmental variables) of LCBD were also different amongst the biological groups, probably related to their biological traits, evidencing the importance of understanding broad-scale distribution patterns of a variety of taxa.

Finally, it was concluded that this survey, based on beta-diversity analyses, contributed to a better understanding of distribution drivers and patterns amongst communities (e.g. unique set of species are located in sites of the Amazon floodplain) in Neotropical floodplain systems. Thus, the results could be used by researchers and environmental managers as a reference in conservation and restoration plans (e.g. establishment of protected areas) and in preventing areas with high conservation value from being destroyed, for example, by the construction of dams and reservoirs.