UNIVERSIDADE FEDERAL DE GOIÁS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO
EM ECOLOGIA E EVOLUÇÃO

ANDRÉ ANDRIAN PADIAL

TESE DE DOUTORADO

GRUPOS SUBSTITUTOS, CORRESPONDÊNCIA DE ASSEMBLÉIAS AQUÁTICAS EM RELAÇÃO A ESQUEMAS DE CLASSIFICAÇÃO REGIONAL, E DETERMINANTES DE DIVERSIDADE BETA EM UMA PLANÍCIE DE INUNDAÇÃO NEOTROPICAL

ORIENTADOR: PROF. DR. LUIS MAURÍCIO BINI

GOIÂNIA - GO
JANEIRO - 2010

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Tese apresentada à Universidade Federal de Goiás, como parte das exigências do Programa de Pós-graduação em Ecologia e Evolução para obtenção do título de doutor.

Orientador: Prof. Dr. Luis Mauricio Bini

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Dedico esse trabalho à minha esposa Talge, aos meus pais José Carlos e Izabel e aos meus irmãos Deivys, Lucas e Milena

"Toda ciência, comparada com a realidade, é primitiva e infantil – e, no entanto, é a coisa mais preciosa que temos." Albert Eisten (1879 – 1955)

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RESUMO

Um objetivo geral em Ecologia é entender como as comunidades estão organizadas no espaço e no tempo. Um aspecto de grande interesse para conservação é avaliar as similaridades na estrutura espacial e temporal da composição de diferentes grupos biológicos que habitam um mesmo ecossistema. Utilizando a abordagem de grupos substitutos, se dois grupos biológicos apresentam estrutura espacial/temporal similar, apenas um desses grupos concordantes poderia ser avaliado em esforços de conservação ou biomonitoramento. A correspondência de comunidades a esquemas de classificação física dos ecossistemas também auxilia o entendimento das razões para a organização espacial das comunidades. Além disso, se as comunidades respondem a classificações baseadas, por exemplo, em características geológicas e ambientais dos hábitats, a seleção de prioritárias áreas amplamente distribuídas nas classes de tais esquemas de classificação pode maximizar a conservação da biodiversidade regional de um ecossistema. Finalmente, para entender os principais processos que direcionam a organização das comunidades nos ecossistemas, o papel relativo de diferentes conjuntos de variáveis preditoras na estrutura de diferentes assembléias de espécies pode ser avaliado concomitantemente. Se as assembléias são principalmente afetadas por um conjunto de variáveis ambientais, a conclusão que se chega é que os principais mecanismos que controlam as composições das espécies estão relacionados com o nicho ecológico. Por outro lado, se variáveis que representam as estruturas espaciais dos ambientes são melhores preditoras, as composições das espécies são determinadas devido a diferenças em suas capacidades de dispersão. Dessa forma, os objetivos gerais da presente tese são: (i) avaliar a concordância entre distintos grupos biológicos; (ii) avaliar a correspondência entre classificações físicas dos ecossistemas e a composição das assembléias e; (iii) avaliar o papel relativo de diferentes preditores na estrutura das assembléias em uma planície Neotropical. Para isso, utilizamos dados de seis grupos biológicos aquáticos (peixes, macroinvertebrados bentônicos, macrófitas aquáticas, zooplâncton, fitoplâncton e perifíton) coletados trimestralmente durante os anos de 2000 e 2001, em até 36 ambientes da planície de inundação do Alto rio Paraná. Padrões freqüentes de concordância entre os grupos biológicos foram encontrados. Os mecanismos mais prováveis para as concordâncias são respostas similares aos gradientes ambiental e espacial, e interações biológicas entre as espécies. Esses foram identificados após controlar o efeito das variáveis ambientais e espaciais na concordância entre dois grupos e ao avaliar a concordância somente entre as espécies

dos grupos concordantes que potencialmente são ligadas por interações biológicas. Entretanto, as magnitudes das correlações entre dois grupos quaisquer foram baixas e variaram conspicuamente ao longo do tempo. Esses resultados ressaltam que o uso de grupos substitutos é uma estratégia pouco eficaz para subsidiar esforços de conservação na planície de inundação do Alto rio Paraná. Entretanto, um esquema de classificação dessa planície considerando principalmente aspectos limnológicos e geológicos foi eficaz para representar a estrutura das diferentes grupos biológicos aquáticos. Dessa forma, ações práticas para conservação da biodiversidade ou para o biomonitoramento da flora e fauna podem se beneficiar desse esquema de classificação. Porém, a variabilidade temporal afetou a consistência das classificações, e esse é um aspecto que deve ser investigado detalhadamente em pesquisas futuras. Por outro lado, variáveis temporais foram pouco eficazes para predizer a estrutura de composição das diferentes assembléias na planície de inundação estudada. Apesar de também predizer fracamente a estrutura das assembléias, as variáveis ambientais e espaciais foram as mais importantes. Variáveis espaciais foram especialmente importantes para os organismos com menor capacidade de dispersão, como plantas aquáticas e peixes sedentários. Por outro lado, o filtro ambiental foi mais importante para explicar a estrutura de composição de pequenos organismos com alta capacidade de dispersão (como micro-algas) e de organismos com comportamento migratório de reprodução. Entretanto, todas as variáveis tiveram um baixo poder preditivo, provavelmente devido à baixa extensão dos gradientes ambiental e espacial e à não inclusão de variáveis que representam processos importantes para determinar a estrutura das assembléias aquáticas em planícies de inundação.

ABSTRACT

A general goal in community ecology is to understand how communities are organized in space and time. An aspect of great interest is to evaluate how concordant are the patterns of beta diversity depicted by different biological groups. If two taxonomic groups present a similar spatial/temporal structure, only one of these groups can be used as a surrogate group in conservation efforts or bioassessments. Also, a strong correspondence between biological groups and physical classifications of the habitat could help us to understand the reasons for spatial organization of communities. Moreover, if communities respond to *a priori* classifications based on geological and environmental features of the habitats, the selection of priority areas for conservation distributed on the classes of a classification scheme could maximize the conservation of overall biodiversity. Finally, to understand the main processes driving the organization of communities, the relative role of different set of predictor variables can be simultaneously evaluated. If species compositions are mainly predicted by environmental variables then one can conclude that species sorting mechanisms are the main drivers of community structure. On the other hand, if variables that represent spatial structure of the environments are the main predictors of variation in species composition, then neutral processes may be invoked to explain the structure of the biological group under analysis. Therefore, the main goals of this thesis are: (i) to evaluate the concordance among distinct biological groups; (ii) to evaluate the correspondence between *a priori* physical classifications of the habitat and the composition of assemblages and; (iii) to evaluate the relative role of environmental and spatial predictors on the structure of local assemblages in a Neotropical floodplain. For that, we used data sets on six biological groups (fish, benthic macroinvertebrates, aquatic macrophytes, zooplankton, phytoplankton, and periphyton) which were gathered during 2000 and 2001 in up to 36 aquatic environments of the Upper Paraná River floodplain. Patterns of assemblage concordance were frequently observed. The main mechanisms responsible for cross-taxon concordance were a similar response to environmental/spatial gradients and biological interactions between species. The mechanisms were identified after controlling for the effect of environmental/spatial variables on the cross-taxon concordance and after evaluating the level of concordance between species from each group that most likely are linked by biological interactions. However, the levels of assemblage concordance were weak and varied conspicuously with time. These results highlight that the use of surrogate groups is a flawed strategy to

support conservation efforts in the Upper Paraná River floodplain. Nevertheless, the classification scheme of the floodplain, considering mainly limnological and geological aspects, was efficient to represent the structure of different aquatic assemblages. Thus, conservation efforts and bioassessments of the aquatic flora and fauna can use this classification scheme. However, the temporal variability also affected the consistency of the correspondence and this issue should be further investigated. On the other hand, temporal variables were not effective in predicting the structure of different biological assemblages. Environmental and spatial variables were generally more important, but also with low predictive power. Spatial variables were particularly important for large organisms with low dispersal ability, such as sedentary fish and aquatic plants. On the other hand, compared to spatial predictors, environmental variables were more important to explain the structure of small-bodied organisms with high dispersal ability (such as micro-algae) and organisms with migratory behavior. Nevertheless, all variables had a low predictive power, probably due to the low extent of the environmental and spatial gradients and to the lack of variables that represent relevant processes for determining the structure of aquatic assemblages in floodplains.

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APRESENTAÇÃO

A presente tese, intitulada “Grupos substitutos, correspondência de assembléias aquáticas em relação a esquemas de classificação regional, e determinantes de diversidade beta em uma planície de inundação Neotropical” está apresentada sob a forma de capítulos, cada um contendo um manuscrito científico. Todos os dados utilizados para elaboração dessa tese foram coletados durante os anos de 2000 e 2001, por especialistas do Núcleo de pesquisas em Limnologia, Ictiologia e Aqüicultura (NUPELIA) da Universidade Estadual de Maringá (UEM) durante o projeto “Pesquisas ecológicas de longa duração - site 6”, financiado pelo Conselho Nacional de Pesquisa Científica (CNPq). Por conseguinte, uma seção intitulada “Introdução Geral” apresenta os principais referenciais teóricos e problemas ecológicos que motivaram a elaboração dessa tese, juntamente com as principais hipóteses testadas. O capítulo I, intitulado “Evidências contra o uso de grupos substitutos em uma planície Neotropical” contém um manuscrito científico que será submetido para apreciação na revista “Ecography”. O capítulo II, intitulado “Respostas de múltiplos grupos biológicos aquáticos a esquemas de classificação em duas escalas espaciais na planície de inundação do Alto rio Paraná” contém um manuscrito científico que já foi submetido para a revista “Freshwater Biology”. O capítulo III é intitulado “Determinantes das estruturas de assembléias aquáticas na planície de inundação do Alto rio Paraná”, contém um manuscrito científico que será submetido para a revista “Ecography”. Após a apresentação dos capítulos, uma seção intitulada “Conclusões Gerais” apresenta as principais conclusões da tese e as implicações para ações de conservação das comunidades e para pesquisas futuras.

INTRODUÇÃO GERAL[1]

Vários aspectos podem ser estudados com o objetivo de entender como as comunidades estão organizadas no espaço e no tempo. Entretanto, estudos em ecologia de comunidades frequentemente investigam apenas um grupo biológico ou as relações inter-específicas entre organismos de grupos biológicos (Jackson and Harvey 1993). Essa abordagem limita o espectro de interpretação à apenas uma assembléia de espécies (geralmente definida em termos taxonômicos, veja Fauth et al. 1996) e ignora o fato que taxa distintos respondem diferentemente aos mecanismos ecológicos. Nesse sentido, estudos que medem a similaridade nos padrões espaciais ou temporais da composição de diferentes assembléias de espécies são fundamentais (Jackson e Harvey 1993). Ademais, se dois grupos biológicos ordenam ou classificam as unidades de amostragem (obtidas no espaço ou no tempo) de forma similar, então um grupo poderia ser utilizada como indicador ou subtituto do outro (Heino et al. 2005, 2009, Heino 2010). O grupo indicador ou substituto ("surrogate") poderia ser utilizado em esforços de conservação, garantindo maior rapidez na elaboração de uma ação de manejo (por exemplo, a definição de áreas prioritárias para conservação). Se essa mesma ação fosse determinada somente após a investigação de todos os grupos biológicos de interesse, um tempo maior e mais recursos financeiros seriam necessários. Nesse sentido, os resultados obtidos dos estudos que focam apenas uma assembléia biológica são frequentemente utilizados para inferir sobre toda a biota (Allen et al. 1999). Implicitamente, essa ação assume que há concordância entre as distintas assembléias de espécies. No entanto, esse é um pressuposto que deve ser testado, e não assumido. Os principais mecanismos responsáveis para concordância entre duas assembélias biológicas são respostas similares aos gradientes ambientais e espaciais, e interações biológicas entre as espécies (Grenouillet et al. 2008). Em ambientes que sofrem profundas alterações temporais nas interações biológicas e nas relações comunidade-ambiente, a concordância entre grupos pode ser temporalmente variável (Paszkowski e Tonn 2000, Grenouillet et al. 2008). Entretanto, os efeitos da variabilidade temporal sobre as similaridades de diferentes assembléias ainda são pouco explorados.

Um segundo aspecto frequentemente investigado em ecologia de comunidades, e de especial interesse para a conservação, é a regionalização de

[1] Formmatado de acordo com as normas da revista "Ecography".

ambientes e sua correspondência com a estrutura das assembléias biológicas (Heino et al. 2002). Apesar de não haver dúvidas que processos ecológicos e a dispersão das espécies são mecanismos contínuos no espaço (Ricklefs 2008), unidades discretas, como biomas, são extremamente úteis, por exemplo, para definir áreas prioritárias para conservação (Myers et al. 2000). Similarmente, esquemas de classificação em diferentes escalas têm grande utilidade em ecologia aplicada. Um exemplo disso é a classificação da paisagem em classes com padrões recorrentes de características ambientais ou de composição de espécies (van Sickle e Hughes 2000, Heino et al. 2002, Heino et al. 2004). Em planícies de inundação, as seguintes unidades de análise, considerando distintas escalas espaciais, podem ser diferenciadas: bacias de drenagem, rios, lagos, e zonas litoâneas e pelágicas de lagos. Para que um esquema de classificação gerado por características físicas da paisagem seja ecologicamente relevante, a composição das assembléias também deve responder a tal categorização (Heino e Mykrä 2006). Nesse caso, os esquemas de classificação podem ser utilizados para selecionar áreas que, em conjunto, maximizem a eficácia de biomonitoramentos e a representatividade da biodiversidade regional em ações de conservação (Heino et al. 2002). De fato, a busca de ações que maximizem sua eficácia de biomonitoramentos é uma preocupação recorrente em biologia da conservação (Sheil 2001).

Finalmente, a identificação dos determinantes das espécies é um dos aspectos mais estudados para o entendimento da organização espacial e temporal das comunidades ecológicas (Holyoak 2005, Stokstad 2009). Desde antes da consolidação da ecologia como disciplina científica, naturalistas tentam entender quais os mecanismos responsáveis pela composição e abundância de espécies em ambientes naturais. Por exemplo, no início do século XIX, o naturalista alemão Alexander von Humboldt, depois de sua famosa viagem à América do Sul, mostrou que a vegetação é influenciada por diversos fatores como o clima, solo e altitude (Stokstad 2009). Tradicionalmente, interações bióticas e fatores ambientais locais são os determinantes mais investigados (Heino e Mykrä 2008). Essa visão é baseada, primordialmente, na idéia de nicho multidimensional (Hutchinson 1959). Entretanto, trabalhos com esse enfoque têm tido pouco sucesso, especialmente em ecossistemas tropicais. Concomitantemente, processos regionais não relacionados com características ambientais têm sido considerados importantes para representar a variabilidade das comunidades (Hubbell 2001). Nesse caso, se as variáveis que representam as

estruturas espaciais são boas preditoras das espécies, processos relacionados com a limitação por dispersão dos organismos são os responsáveis pela estrutura das comunidades locais (Holyoak 2005).

Portanto, há uma grande discussão em ecologia de comunidades, dentro do contexto do que agora é conhecido como metacomunidades (Leibold et al., 2004), sobre os papéis relativos de fatores ambientais e espaciais como preditores da estrutura das comunidades locais (Cottenie et al. 2003, Tuomisto et al. 2003, Cottenie 2005, Beisner et al. 2006, Van der Gucht et al. 2007, Vanschoenwinkel et al. 2007, Heino e Mykrä 2008, Vanormelingen et al. 2008, Nabout et al. 2009). Um aspecto interessante é avaliar o papel relativo desses fatores em grupos biológicos com diferentes capacidades de dispersão. Nesse caso, grupos biológicos que tenham maior capacidade de dispersão e baixa tolerância às variações ambientais, devem ser melhor preditas por fatores ambientais do que espaciais. Por outro lado, se os grupos biológicos têm uma ampla tolerância aos fatores ambientais, mas existem limitações na dispersão, fatores espaciais podem ser bons preditores da estrutura espacial das assembléias locais (Beisner et al. 2006). Em organismos aquáticos, a capacidade de dispersão é frequentemente negativamente relacionada com o tamanho corporal (Shurin et al. 2009) e depende do comportamento dos organismos (por exemplo, peixes migradores têm maior capacidade de dispersão do que peixes sedentários). Além disso, processos temporais, raramente investigados, também podem afetar a estrutura das assembléias (Anderson e Gribble 1998). A variabilidade temporal em planícies de inundação é comumente relacionada com pulsos hidrológicos periódicos que afetam, simultaneamente, características limnológicas, o grau de conectividade dos ambientes e processos fenológicos e etológicos das espécies (Junk et al. 1989, Thomaz et al. 2007).

A presente tese foi divida em três capítulos com objetivos relacionados. O primeiro objetivo foi avaliar a variabilidade temporal dos níveis de concordância entre grupos biológicos aquáticos da planície de inundação do Alto rio Paraná e a habilidade na qual a estrutura de uma determinada assembléia de espécies pode predizer a estrutura de outra. Além disso, os mecanismos responsáveis pelos padrões de concordância foram avaliados ao controlar o efeito dos fatores ambientais e espaciais sobre a concordância entre dois grupos taxonômicos (Grenouillet et al. 2008) e ao considerar expectativas sobre as interações biológicas entre os grupos biológicos. O segundo objetivo consistiu em avaliar a correspondência de diferentes

esquemas de classificação baseados em características ambientais da planície de inundação do Alto rio Paraná sobre a composição de diferentes assembléias de espécies. Ainda nesse contexto, tais esquemas de classificação foram comparados com esquemas baseados nos próprios dados biológicos com o intuito de verificar possíveis fontes espaciais e temporais de variabilidade nas assembléias. O terceiro objetivo consistiu em avaliar, simulatenamente, o papel relativo de fatores ambientais, espaciais e temporais na estrutura de diferentes assembléias de espécies na planície de inundação do Alto rio Paraná.

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CAPÍTULO I

EVIDÊNCIAS CONTRA O USO DE GRUPOS SUBSTITUTOS EM UMA PLANÍCIE NEOTROPICAL[2]

[2] Capítulo formatado de acordo com as normas da revista "Ecography".

LINES OF EVIDENCE AGAINST THE USE OF SURROGATES IN A NEOTROPICAL FLOODPLAIN

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Abstract

Assemblage concordance measures the level of relationship between the compositional patterns depicted by two groups of organisms. In this study, we evaluated the effect of temporal variability on the levels of assemblage concordance, the likely causes for assemblage concordance and the degree to which one assemblage can predict another in a set of Neotropical floodplain lakes. We used a data set collected in lakes of the Upper Paraná River floodplain (Brazil) for six biological assemblages: fish, macrophytes, benthic macroinvertebrates, zooplankton, phytoplankton and periphyton. The levels of assemblage concordance varied over time for all cross-taxon comparisons. Concordance between phytoplankton and periphyton was probably due to similar responses to environmental gradients, whereas other patterns of assemblage concordance were likely generated by interactions among groups. However, the levels of predictability were low and no particular taxonomic group significantly predicted all other groups. The low and temporally variable levels of assemblage concordance cast doubts in the use of surrogate groups in Neotropical floodplains.

Key-words: Assemblage concordance, community structure, temporal variability, predictability, Neotropical floodplain.

Introduction

Assemblage concordance measures the intensity by which distinct groups of organisms, which are generally defined in terms of taxonomic relatedness (i.e., assemblages, see Fauth et al. 1996), present similar patterns of spatial or temporal variation in species richness or in compositional similarity (Jackson and Harvey 1993). This approach reveals similarities and differences in how distinct assemblages are organized in an ecosystem (Allen et al. 1999). One mechanism responsible for assemblage concordance is a similar, but independent, response of different groups to environmental gradients (Allen et al. 1999, Paszkowski and Tonn 2000, Grenouillet et al. 2008). In this case, a high level of concordance is expected between assemblages with similar environmental requirements (Allen et al. 1999, Grenouillet et al. 2008). However, strong biological interactions can also generate concordance among different biological groups (Paine 1980), and this possibility is the most likely when the biological groups under study respond in different ways to environmental drivers (Grenouillet et al. 2008).

A high level of assemblage concordance would allow the use of surrogate groups for conservation planning and biodiversity monitoring (Heino et al. 2005, 2009, Heino 2010). For instance, if species composition of a certain taxonomic group reasonably represents the variability of the composition of another group, impacted and pristine areas could be identified by any of the concordant assemblages. This may avoid difficulties due to limitations of time and resources for comprehensive surveys of multiple biological groups (Heino et al. 2005, Moreno et al. 2007, Bini et al. 2008). Implicitly, monitoring programs and studies in community ecology frequently restrict the focus of investigation to one taxonomic group (Allen et al. 1999). However, studies evaluating assemblage concordance or the ability of a taxonomic group to predict the structure of another group are scarce (Schaffers et al. 2008). As a result, the utility of surrogates groups remains unknown for many ecosystems (Heino et al. 2005).

Several mechanisms are expected to generate concordance among aquatic assemblages. For instance, macroinvertebrates have been traditionally considered good biological indicators of environmental quality due to their sedentary behavior (Cook 1976, Resh 2008). As a consequence, recent studies have evaluated the utility of macroinvertebrates as bioindicators of overall aquatic biodiversity (Bilton et al. 2006, Aldridge et al. 2007). Significant levels of concordance may also be expected

between phytoplankton and zooplankton, as they are directly linked by trophic interactions (Søndergaard et al. 1990, Brett and Goldman 1996, Reichwaldt et al. 2004, Havens et al. 2009). On the other hand, periphyton and phytoplankton may show concordant patterns mainly because they have similar environmental requirements (see Rodrigues and Bicudo 2004, Train and Rodrigues 2004). One may also expect that aquatic macrophytes exhibit concordance with several other biological groups, given that they have a recognized structuring role in aquatic environments (Jeppesen et al. 1998, Meerhoff et al. 2003, Meerhoff et al. 2007), affecting the structure of different organisms (Meerhoff et al. 2007, Vieira et al. 2007, Pelicice et al. 2008, Thomaz et al. 2008). In addition, macrophytes are the main source of organic matter to benthic organisms (Wetzel 2001) and the main substrate for periphyton in Neotropical lakes (Leandrini et al. 2008). Finally, distinct phytoplankton species are dominant in shallow lakes depending on the architecture and abundance of aquatic macrophytes that occur in these lakes (Scheffer et al. 1993).

Temporal variability in aquatic ecosystems affects the stability of ecological patterns. Neotropical floodplains are characterized by flood pulses that temporally change limnological characteristics and habitat connectivity (Thomaz et al. 2007). As a consequence, both community-environment relationships and biological interactions, the main mechanisms responsible for cross-taxon concordance, vary over time in aquatic ecosystems (Mykrä et al. 2008, Luz-Agostinho et al. 2008). Therefore, there is a need to evaluate the effect of temporal variability on the levels of cross-taxon concordance (Grenouillet et al. 2008, Bini et al. 2007).

In this study, we used data on multiple biological organisms in a Neotropical floodplain to evaluate (i) the temporal variability in the levels of assemblage concordance, (ii) the likely causes of concordance among taxonomic groups, and (iii) the strengths of the between-assemblages relationships with the aim of validating the use of surrogates groups. We expect that interactive assemblages or assemblages with similar responses to environmental gradients would have the strongest levels of concordance (Allen et al. 1999, Paszkowski and Tonn 2000). Furthermore, we expect that aquatic macrophytes will be the most suitable assemblage to be used as a surrogate group for most other taxonomic groups. However, given that floodplains are complex and dynamic ecosystems, we hypothesize that temporal variability in connectivity patterns, as well as in physical and chemical factors, will affect assemblage concordance and the predictive ability of biological assemblages.

Study area

The Upper Paraná River and its floodplain (Figure 1) represent the last unregulated stretch of the Paraná River in the Brazilian territory (Agostinho et al. 2005). It is an important area for several migratory fish species and still supports relatively high species diversity (e.g., 50% of the fish species from the Atlantic Forest Biome have been recorded within this region; see Agostinho et al. 2005). The Upper Paraná River floodplain has a seasonal hydrological regime marked by a dry season (c. May-October) and a wet season (c. November-April) (Thomaz et al. 2004). However, due to hydrological control by recently built hydropower reservoirs, frequency, amplitude and duration of flood pulses in wet and dry season have been substantially changed (Thomaz et al. 2004).

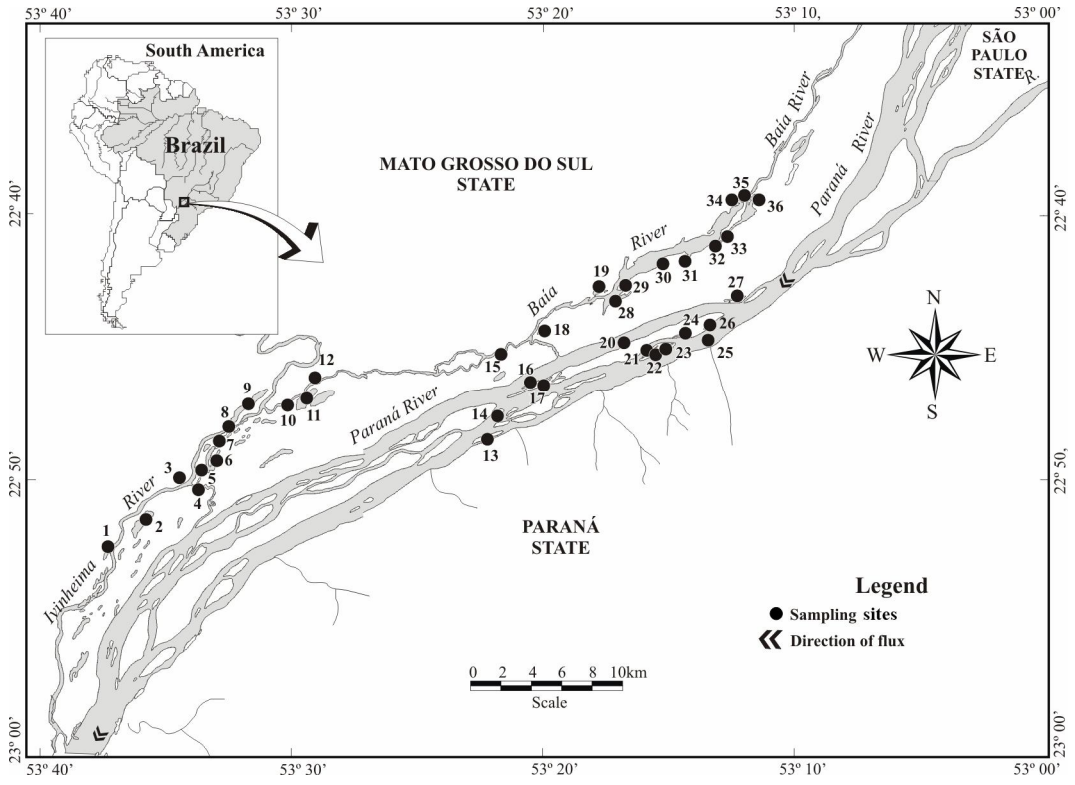

Figure 1. The Upper Paraná River floodplain and the sampling sites surveyed in this study.

Data gathering

Data were collected for six biological assemblages: fish, benthic macroinvertebrates, aquatic macrophytes, periphyton, phytoplankton and zooplankton. Sampling campaigns were conducted in February (wet season) and

August (dry season) in 2000 and 2001, and up to 36 sites in the Upper Paraná River floodplain were surveyed (Figure 1). As data for some groups in some sites and periods are lacking, not all cross-taxon comparisons were carried out (see Appendix S1).

Abundance of fish (individuals×24 hours/1000m^2gillnet) were determined after experimental fishery using gillnets with different mesh sizes. Presence and absence of aquatic macrophytes were recorded in the field from a boat and with the help of a grapnel. Benthic macroinvertebrates were collected using a modified Petersen's grab. Total number of individuals of each taxon was used as abundance data. Zooplankton species densities (individuals/m^3) were estimated by pumping 600 L of water over a 70μm mesh net. Van Dorn bottles and phytoplankton nets (15μm mesh) were used to sample phytoplankton assemblage, and species densities were expressed as individual units (cells, coenobia, colonies, or filaments) per milliliter. Periphyton was sampled from petioles of *Eichhornia azurea* Kunth in the mature stage, as this macrophyte was common in most of the environments in the Upper Paraná River floodplain. Abundance was expressed in individuals/cm^2. A detailed description of sampling procedures for the different biological assemblages is available in Appendix S2.

The following environmental variables were obtained for each site: depth (m), water temperature (°C), dissolved oxygen (mg/L), water transparency (m), pH, electric conductivity (μS/cm), total alkalinity (mEq/L), turbidity (NTU), total nitrogen concentration (μg/L), total phosphorus concentration (μg/L), chlorophyll-*a* (μg/L), total suspended matter (mg/L), and dissolved organic matter (mg/L). For a detailed description of sampling procedures and laboratory analyses, see Appendix S2. All environmental variables, but pH, were log (x) transformed prior to the analyses described below.

Data analysis

Prior to all multivariate analyses described below, abundance data were log (x + 1) transformed to reduce the influence of dominant species. In addition, all analyses were done twice: using log-transformed abundance and using presence/absence data. Bray-Curtis (Faith et al. 1987) and Sørensen (Sørensen 1948) coefficients were used for abundance and presence/absence data, respectively. This can give us insights on the effect of numerical resolution on our ability to detect patterns of assemblage

concordance. However, we used presence/absence of macrophytes in all analyses, given that only this type of data is available for this group.

Firstly, we assessed the importance of each sampling period on the overall level of concordance between a given pair of assemblage by using a technique that maximizes the correspondence of two assemblages over sampling periods, the so called STATICO ("Structuration des Tableaux à Trois Indices de la Statistique" and CO-inertia; Thioulouse et al. 2004). In STATICO, two tables containing data from all sampling periods are firstly summarized by an ordination method. The two tables should have the same sites in a certain sampling period and each table should have the same number of species (columns) across sampling periods. However, not all species need to be present in all sampling periods and not all sites need to be the same across sampling periods (Thioulouse et al. 2004). To our summarize data, we used principal coordinate analysis based on the Bray-Curtis index (PCoA, Gower 1966). Then, ordination scores corresponding to a given sampling period were linked by a co-inertia analysis, generating a series of cross-tables (Thioulouse et al. 2004). Finally, partial triadic analysis (PTA, Thioulouse and Chessel 1987) was used to analyze the series of cross-tables. The aim of this method is to analyze a three-way table (i.e., a data cube; for example, species × sites × time), seen as a sequence of two-way tables. PTA comprises three steps: the "interstructure", the "compromise", and the "trajectories" (Thioulouse et al. 2004). Aiming to evaluate the temporal variability in the levels of assemblage concordance, we generated graphs representing the contribution of each sampling period to the overall level of concordance between two assemblages, corresponding to the "interstructure" step in PTA (see Thioulouse et al. 2004).

We also tested the level of assemblage concordance in each sampling period using the Procrustean Randomization test (PROTEST; Jackson 1995, Peres-Neto and Jackson 2001) and the Mantel test (Mantel 1967). A permutation procedure with 10,000 randomizations was used to assess the statistical significance of the correlation coefficient calculated based on the statistics m^2 in the PROTEST (Jackson 1995) and of the Mantel's correlation coefficient.

We also carried out Mantel tests between the Bray-Curtis matrices (or Sørensen matrices for the presence/absence data) generated by a given assemblage and the matrices containing the environmental (standardized Euclidean) distances and the geographic distances (watercourse distances; in meters) between the sampling

sites. We used this procedure given that if two concordant assemblages are simultaneously related to environmental and geographic distances, then concordance could be due to similar responses to these factors (see Grenouillet et al. 2008). For significantly concordant assemblages, which were also simultaneously affected by environmental and/or geographic distances, we used partial Mantel tests to evaluate for the existence of assemblage concordance while controlling for the effect of these factors (Smouse et al. 1986, Grenouillet et al. 2008). If the level of assemblage concordance is no longer statistically significant after controlling for the effect of environment and/or space, then the concordance between assemblages can be explained by their shared responses to environmental and/or spatial gradients.

We also tried to identify the mechanism responsible for the cross-taxon concordance by considering the traits of different taxa that comprise an assemblage. For instance, if the concordance between zooplankton and fish is significant, it could be mainly due to predator-prey relationships between zooplanktivorous fish and microcrustaceans (Pelicice and Agostinho 2006, Crippa et al. 2009). Therefore, we also tested the concordance (using Mantel tests) between several combinations of taxa considering expectations based on the biological interactions between them (Table 1). We expect high levels of concordance between interactive assemblages. The detailed information about the traits of the different groups and their possible implications for the patterns of cross-taxon concordance are described in Appendix S3.

Finally, we used predictive co-correspondence analysis (predictive CO-CA, ter Braak and Schaffers 2004) to evaluate the performance of one taxonomic group in predicting the structures of other assemblages. In many ways, CO-CA is equivalent to canonical correspondence analysis (CCA). However, it can use species composition tables in an explanatory role (ter Braak and Schaffers 2004). Predictive CO-CA is considered more appropriate for this purpose given that the exploratory or predictor matrix is comprised by several variables that show unimodal structures, such as biological data (ter Braak and Schaffers 2004). In such cases, calculating percentages of explained variation (such as in CCA) is uninformative, given that with enough explanatory variables, all variation in a dependent data set can be explained even without any actual relationship (see Schaffers et al. 2008). Therefore, in predictive CO-CA, the predictive percentage of fit is calculated implementing a “leave-one-out” cross-validation, an approach that circumvents this limitation (ter Braak and Schaffers 2004). We applied “leave-one-out” cross-validation in CO-CA using data of each

sampling period for each available comparison (see Appendix S1). Significance of cross-validatory fit was assessed after 1,000 random permutations.

We used the program "R" (R Development Core Team 2007), with the packages "vegan" (Oksanen et al. 2008) and "ecodist" (Goslee and Urban 2007) for PCoA ordinations, Mantel and Procrustean randomization tests, the package "ADE4" (Dray et al. 2007) for the STATICO analysis, and the package "cocorresp" (Simpson 2005) for the CO-CA.

Figure 2 summarizes the analytical approach used in this study.

Table 1. Cross-taxon comparisons and the combination of groups for the concordance analysis, with the main reasoning. For further details, see Appendix S3.

Cross-taxon comparison	Combination of groups	Reasoning	Key-references
Fish - Benthic Macroinvertebrates	Invertivorous fish - Benthic Macroinvertebrates	The fish predation on benthic macrioinvertebrates may be mainly due to invertivorous fish	Hahn et al. (2004), Graça and Pavanelli (2007)
Fish - Macrophytes	Detritivorous fish - Macrophytes which provide detritus	Small species of macrophytes that quickly decompose may not provide detritus for detritivorous fish	Pott and Pott (2000), Evangelista et al. (2009)
Fish - Macrophytes	Littoral fish - different life forms of macrophytes	The different life forms of macrophytes (submersed, emergent, etc.) provide different habitat structure to littoral organisms	Meerhoff et al. (2003)
Fish - Zooplankton	Zooplanktivorous fish - Microcrustaceans	Zooplankton, mainly microcrustaceans, are the food source only for fish with zooplanktivorous behavior	Hahn et al. (2004), Graça and Pavanelli (2007)
Benthic Macroinvertebrates - Macrophytes	Benthic Macroinvertebrates - Macrophytes which provide detritus	Small species of macrophytes that quickly decompose may not provide detritus for benthic macroinvertebrates	Pott and Pott (2000), Evangelista et al. (2009)
Macrophytes - Zooplankton	Littoral zooplankton - different life forms of macrophytes	The different life forms of macrophytes provide different habitat structure to littoral organisms	Meerhoff et al. (2003)
Phytoplankton - Zooplankton	Microcrustaceans/rotifers-testate amoebas - phytoplankton	Microcrustaceans and rotifers-testate amoeba have differences in their filtering ability, and, thus, phytoplankton may affect these groups differently	Burns 1968, Cyr and Curtis (1999)
Periphyton - Zooplankton	Littoral zooplankton - Periphyton	Periphyton may be an alternative food resource only for the species of zooplankton that inhabit littoral habitats	Siehoff et al. (2009)

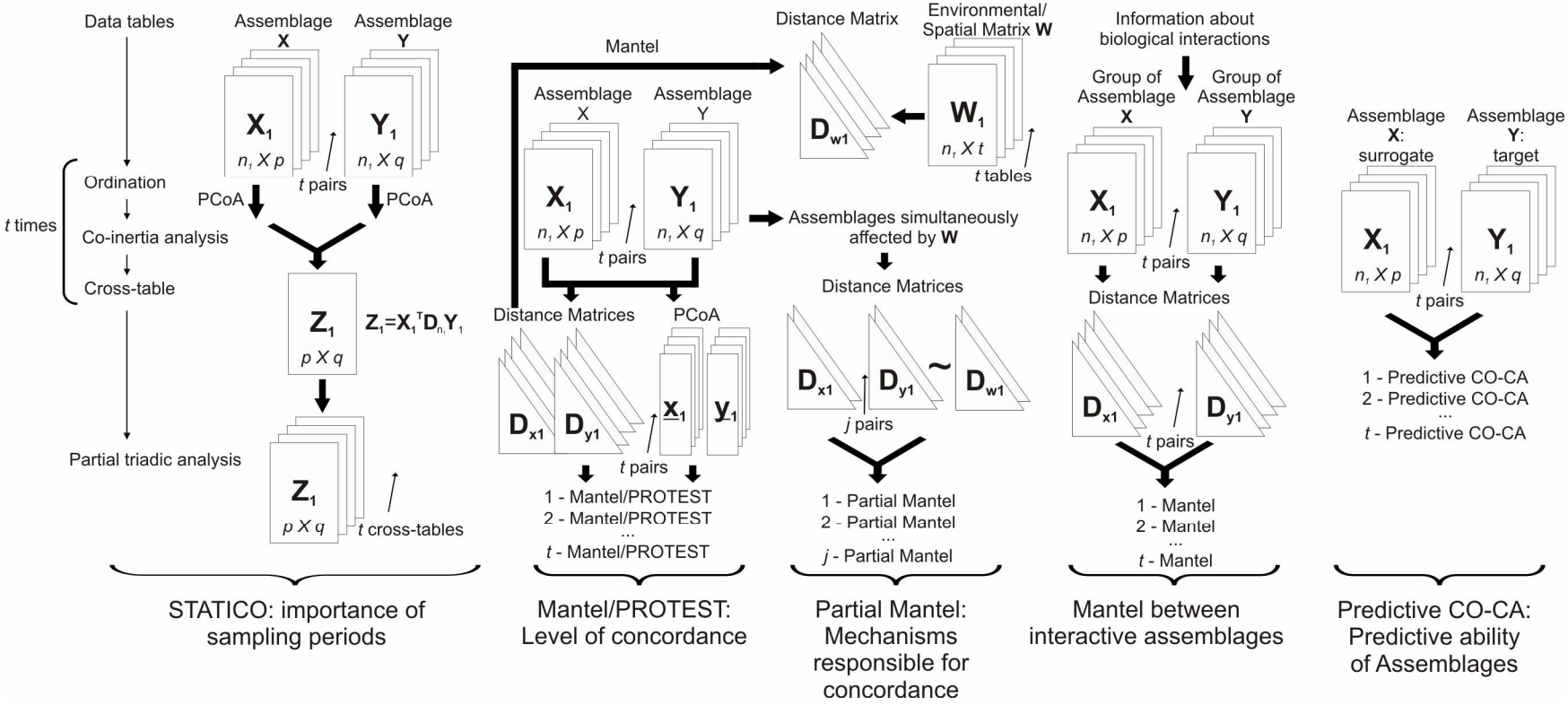

Figure 2. Summary of the analytical approach used in this study. n = number of samples; p = number of species of assemblage **X**; q = number of species of assemblage **Y**; t = number of sampling periods; j = number of sampling periods in which assemblages were simultaneously affected by environmental/spatial gradients.

Results

The levels of concordance between assemblages varied conspicuously with time, as demonstrated by changes in the relative importance of sampling periods to the common structure of two biological tables using abundance data (Figure 3). In addition the relative importance of sampling periods varied depending on the cross-taxon comparison (Figure 3; presence/absence data yielded similar results (see Appendix S4). Significant levels of assemblage concordance were identified for almost all cross-taxon comparisons, at least in the sampling periods considered most important to coherence (see Mantel correlation coefficients in Figure 3). In spite of being frequently significant, the levels of assemblage concordances were, in general, weak. Only macrophyte-phytoplankton and macrophyte-zooplankton comparisons were concordant in all sampling periods (Figure 3). Levels of concordance between benthic macroinvertebrates and periphyton were never significant (Figure 3; Mantel tests and Procrustean analyses yielded similar results; see Appendix S4).

Partial Mantel tests controlling for the effect of environmental or geographical distances were done only for pairs of assemblages exhibiting significant levels of concordance (Figure 3) and that were simultaneously associated with environmental or geographical distances (see Table 2). After controlling for the effect of environmental distances, concordance between periphyton and phytoplankton in February 2000 was no longer significant (see correlation coefficients within parenthesis in Figure 3). The other significant concordant assemblages that were simultaneously affected by environmental and/or geographical distances also presented significant partial Mantel correlation coefficients (see correlation coefficients within parenthesis in Figure 3). Presence/absence and abundance data yielded similar results (Appendix S4).

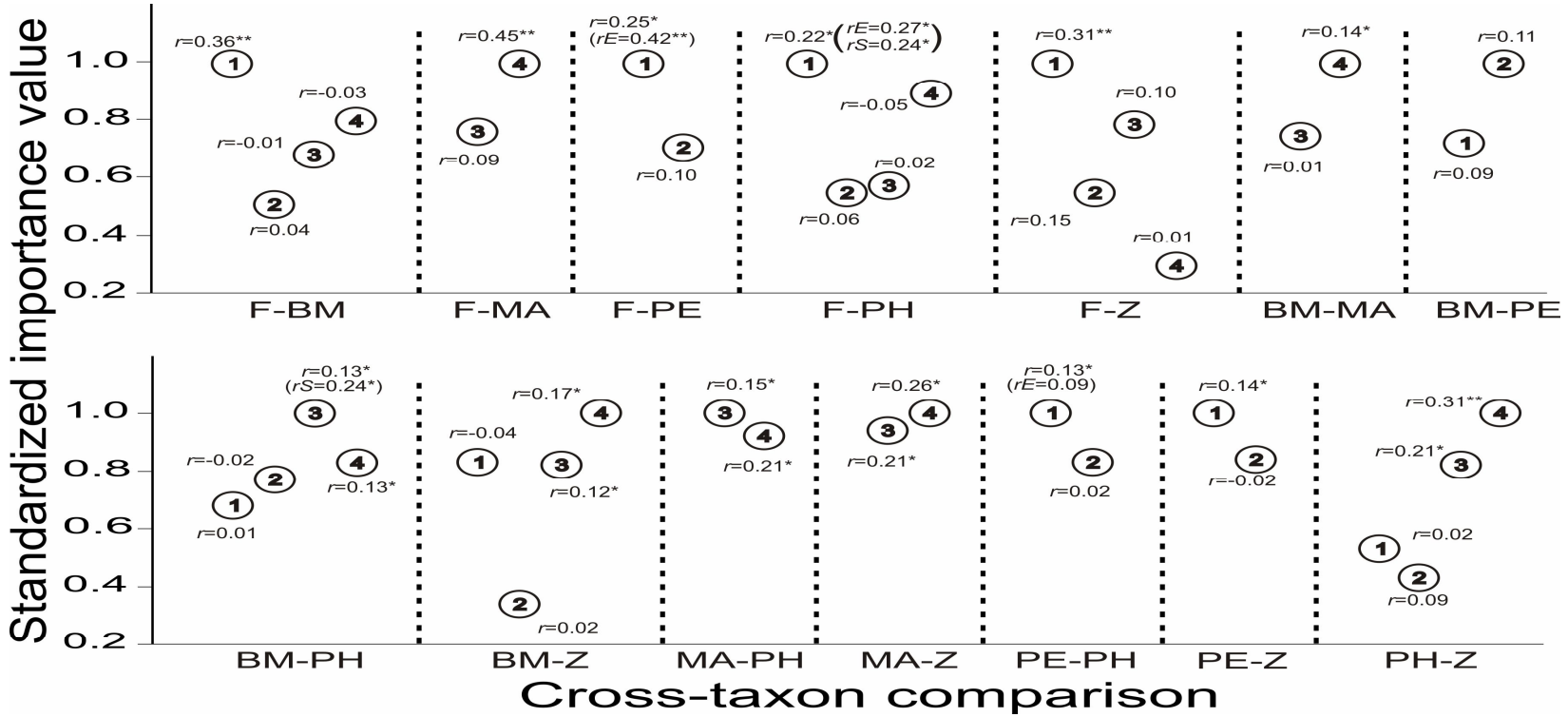

Figure 3. Importance values of samplings periods, standardized to the most important sampling period, to the common assemblage structure of cross-taxon comparisons using abundance data (except for macrophytes). F = Fish; BM = Benthic Macroinvertebrates; MA = Macrophytes; PE = Periphyton; PH = Phytoplankton; Z = Zooplankton. Circled numbers indicate sampling periods: (1) February of 2000; (2) August 2000; (3) February 2001 and; (4) August 2001. For each sampling period, the Mantel's correlations (*r*) between two dissimilarity matrices under comparsion are shown. Partial Mantel tests were done for pairs of assemblages significatively correlated to each other and that were simultaneously correlated with the environmental and geographical distances among sampling sites (see Table 2). In these cases, partial Mantel correlation coefficients controlling for the effects of environmental and/or geographical distances (*rE* and *rS*, respectively) are shown within parenthesis. Significance levels were based on 10,000 random permutations (**P* < 0.05; ***P* < 0.01).

Table 2. Mantel correlation coefficients between distance matrices derived from biological assemblages[§] and distance matrices derived from environmental variables (EV) or geographic coordinates (GD) of sampling sites for each sampling period. Bold numbers indicate significant values. Dashes indicate no data available.

Assemblage	February 2000		August 2000		February 2001		August 2001	
	EV	GD	EV	GD	EV	GD	EV	GD
Fish	**0.21**	**0.19**	0.06	**0.17**	-0.01	0.08	0.07	0.12
Macrophytes	-	-	-	-	0.06	0.09	-0.01	**0.13**
Benthic Macr.	-0.07	0.06	-0.06	**0.24**	-0.03	**0.12**	**0.32**	0.01
Zooplankton	0.13	0.01	0.09	0.03	0.09	0.01	-0.08	0.01
Phytoplankton	**0.17**	**0.19**	**0.39**	**0.20**	**0.25**	**0.32**	0.03	0.09
Periphyton	**0.24**	0.06	-0.01	0.05	-	-	-	-

[§] Abundance data except for macrophytes.

Table 3. Cross-taxon concordance for groups in which concordance is expected to be higher (see Table 1). Bold numbers indicate significant values. Dashes indicate no available cross-taxon comparison.

Combination of groups	**Mantel *r***			
	Feb00	**Aug00**	**Feb01**	**Aug01**
Detritivorous and invertivorous fish - Benthic Macr.	**0.41**	0.09	0.01	0.05
Detritivorous fish - Detritus of Macrophytes	-	-	**0.25**	0.14
Littoral fish - emergent macrophytes	-	-	0.11	**0.46**
Littoral fish - free-floating macrophytes	-	-	0.16	0.05
Littoral fish - submersed macrophytes	-	-	0.12	0.11
Littoral fish - rooted-floating macrophytes	-	-	**0.29**	**0.48**
Zooplanktivorous fish - Microcrustaceans	**0.33**	0.04	0.09	0.09
Benthic Macr. - Detritus of Macrophytes	-	-	**0.20**	**0.25**
Littoral zooplankton - emergent macrophytes	-	-	0.08	**0.33**
Littoral zooplankton - free-floating macrophytes	-	-	0.06	0.06
Littoral zooplankton - submersed macrophytes	-	-	**0.28**	0.06
Littoral zooplankton - rooted-floating macrophytes	-	-	0.05	0.06
Cladocerans-copepods - phytoplankton	0.01	0.04	0.09	**0.30**
Rotifers-testate amoebas - phytoplankton	**0.29**	**0.24**	**0.21**	**0.50**
Littoral zooplankton -periphyton	**0.20**	0.02	-	-

Patterns of concordance considering the expectations based on the traits of the groups were slightly stronger than those observed considering the entire assemblages (see

Mantel's *r* in Table 3 and Figure 3). Moreover, those patterns were more frequently observed in some cross-taxon comparisons. Invertivorous and detritivorous fish exhibited high concordance with benthic macroinvertebrates than considering the entire fish and invertebrates assemblages in February 2000 (Table 3 and Figure 3). In spite of not being significant in February 2001 considering the entire assemblages, invertivorous and detritivorous fish and macrophytes that mostly contribute to detritus exhibited significant levels of concordance in February 2001 (Table 3). Macrophytes that mostly contribute to detritus also exhibited significant concordance with benthic macroinvertebrates in all sampling periods (Table 3). Littoral fish exhibited significant concordance with a particular life-form of macrophytes depending on the sampling period: with emergent in August 2001 and with rooted-floating macrophytes in all sampling periods (Table 3). Considering littoral zooplankton, significant levels of concordance were observed with submerged macrophytes in February 2001 and with emergent macrophytes in August 2001 (Table 3). The concordance between zooplankton and phytoplankton were substantially higher considering rotifers-testate amoebas and phytoplankton than considering cladocerans-copepods and phytoplankton (Table 3). Moreover, the concordance between rotifers-testate amoebas and phytoplankton was significant in all sampling periods (Table 3). Finally, littoral zooplankton presented a higher level of concordance with periphyton than considering the entire assemblage in February 2000 (Table 3 and Figure 3).

In general, the assemblage composition of a given group had low or no ability to predict the assemblage composition of another group (Table 4). Furthermore, there was not a particular assemblage that significantly predicted all other assemblages in any sampling period (Table 4). Presence/absence of benthic macroinvertebrates, zooplankton and periphyton were not significantly predicted by any other assemblage in any sampling period (Table 4).

Table 4. Cross-validatory fit[§] of significant axes of predictive CO-CA ($P < 0.05$) between assemblages, using both abundance (Ab) and presence/absence (Pa) data. Only significant values are shown. Dashes indicate no available cross-taxon comparison.

		Feb-2000		Aug-2000		Feb-2001		Aug-2001	
Predictor	**Target**	**Ab**	**Pa**	**Ab**	**Pa**	**Ab**	**Pa**	**Ab**	**Pa**
Fish	Benthic Macroinv.								
	Macrophytes	–	–	–	–	–		–	
	Zooplankton								
	Phytoplankton	**1.1%**							
	Periphyton	**0.6%**				–	–	–	–
Macrophytes	Fish	–	–	–	–			**1.4%**	**4.7%**
	Benthic Macroinv.	–	–	–	–			**2.7%**	
	Zooplankton	–	–	–	–				
	Phytoplankton	–	–	–	–				
Benthic Macroinv.	Fish								
	Macrophytes	–	–	–	–	–		–	**12%**
	Zooplankton								
	Phytoplankton			**1.3%**	**1.3%**			**3.6%**	**1.4%**
	Periphyton					–	–	–	–
Zooplankton	Fish								
	Macrophytes	–	–	–	–	–		–	
	Benthic Macroinv.								
	Phytoplankton							**3.8%**	**1.6%**
	Periphyton					–	–	–	–
Phytoplankton	Fish		**4.1%**						
	Macrophytes	–	–	–	–	–		–	
	Benthic Macroinv.								
	Zooplankton	**0.5%**						**0.3%**	
	Periphyton					–	–	–	–
Periphyton	Fish		**7.8%**			–	–	–	–
	Benthic Macroinv.					–	–	–	–
	Zooplankton					–	–	–	–
	Phytoplankton				**0.1%**	–	–	–	–

[§] This metric can not be compared to explained variation of exploratory methods (see Data analysis). In this case, any predictive power (%) above 0 is significant (see ter Braak and Schaffers 2004).

Discussion

Studies on assemblage concordance in aquatic ecosystems are receiving increasing attention (Allen et al. 1999, Paszkowski and Tonn 2000, Paavola et al. 2003, Grenouillet et al. 2008), mainly motivated by the need of surrogate groups for conservation purposes (Heino et al. 2003, 2005, 2009, Paavola et al. 2003, Heino 2010). Here, we focused on two questions which are still overlooked in studies of assemblage concordance that can directly affect the search for surrogate groups: (i) the effect of

temporal variability on assemblage concordance and (ii) the degree to which one assemblage can predict another, using data from multiple aquatic assemblages from a Neotropical floodplain.

Moreover, the identification of the main mechanisms that drive patterns of assemblage concordance is a challenging task. Authors usually investigate whether concordant groups are affected by the same sort of environmental variables in an exploratory way (e.g. Heino et al. 2005, Soininen et al. 2009). In our study, we directly controlled for the effects of environmental and/or spatial variables on assemblage concordance when concordant groups were simultaneously correlated with these variables (see also Grenouillet et al. 2008). Finally, we also evaluated the concordance between groups which biological information suggests high levels of concordance, giving us insights of the likely causes for the cross-taxon relationships.

Patterns of concordance and their likely causes

After controlling the effect of environmental distances, concordance between phytoplankton and periphyton was no longer significant and a similar response to environmental gradient is likely the best explanation for the observed cross-taxa concordance. As both assemblages are mostly comprised of micro-algae, they may share the same overall environmental requirements and rates of responses to environmental gradients (see Rodrigues and Bicudo 2004, Train and Rodrigues 2004). None of the other significant comparisons could be explained by a common response to the environmental or geographic gradients. We reached this conclusion based on the fact that assemblages exhibiting significant concordance were not simultaneously affected by environmental and/or geographic distances (see correlation coefficients in Table 2), or still presented significant concordance after controlling for these effects. Therefore, most concordance patterns observed by us are probably generated by biological interactions, contradicting previous researches that stress that similar responses to environmental/spatial gradients are the most likely causes for cross-taxon congruence in aquatic habitats (Paszkowski and Tonn 2000, Paavola et al. 2006, but see Grenouillet et al. 2008).

Significant concordance between zooplankton and phytoplankton may be related to trophic interactions, given that zooplankton mainly feeds on micro-algae (Søndergaard

et al. 1990, Brett and Goldman 1996, Reichwaldt et al. 2004). This was evident considering rotifers and testate amoebas. Rotifers and testate amoebas are smaller than microcrustaceans and, probably feed on mainly smaller phytoplankton (Burns 1968, Cyr and Curtis 1999). Thus, these zooplanktonic groups are more dependent on the assemblage structure of phytoplankton, which probably generated assemblage concordance. Cladocerans-copepods, on the other hand, are able to feed on a variety of phytoplankton species with different sizes, and thus may be less dependent on the assemblage structure of phytoplankton (Burns 1968, Cyr and Curtis 1999).

We detected a significant level of concordance between zooplankton and periphyton only during one sampling period, suggesting that these assemblages are weakly linked. Indeed, periphyton has been considered only an alternative food source for zooplankton (Siehoff et al. 2009). This may be particular important for littoral zooplankton, which had a higher concordance with periphyton than considering the entire zooplankton assemblage.

Aquatic macrophytes have an important structuring role on aquatic habitats, affecting the structure of other aquatic assemblages (Meerhoff et al. 2003, Meerhoff et al. 2007, Pelicice et al. 2008, Thomaz et al. 2008). Indeed, we observed significant concordance between aquatic macrophytes and nearly all other aquatic assemblages due to reasons other than similar responses to environmental/spatial gradients. Firstly, assemblage structure of phytoplankton may be related to macrophyte assemblage as result of alternative stable states (Scheffer et al. 1993, Scheffer 2004). For instance, certain phytoplankton species and submerged macrophytes develop only in clear waters. In contrast, turbid waters are dominated by free-floating and emergent species and other phytoplankton species (e.g., cyanobacteria). Secondly, macrophytes provide shelter for fish and zooplankton. Indeed, previous studies have shown that the structure of fish assemblages changed along stands of macrophytes (Agostinho et al. 2007). Moreover, certain zooplankton species are known to prefer aquatic macrophytes with specific spatial complexity as refuge against predators (Meerhoff et al. 2007). Here, patterns of concordance were found between littoral fishes and emergent or rooted-floating macrophytes. Similartly, littoral zooplankton was mainly associated with emergent or submersed macrophytes. The effects of submerged macrophytes on zooplankton have

been frequently reported in the literature (Jeppesen et al. 1998, Meerhoff et al. 2007). Finally, macrophyte detritus is the main source of organic matter to the sediment (Wetzel 2001). Lakes colonized by different species of macrophytes provide detritus of different nutritional quality, a feature that affect species composition of benthic macroinvertebrates (Bogut et al. 2007). Indeed, the concordance between macrophytes that mostly contribute to the detritus and benthic macroinvertebrates was evident in our study.

Significant assemblage concordance was also observed for organisms with different environmental requirements such as fish and zooplankton, fish and phytoplankton and fish and periphyton. In these cases, trophic interactions may be important processes driving concordance (Grenouillet et al. 2008). For instance, higher concordance was observed between zooplanktivorous fish and microcrustaceans than between all species of fish and zooplankton. Moreover, previous studies that have shown that planktivorous fish reduce the abundance of zooplankton grazers, mainly microcrustaceans, which in turn can affect autotrophic assemblages (Brett and Goldman 1996, Meerhoff et al. 2007, Havens et al. 2009). This could be the explanation for the concordance between fish and assemblages comprised by micro-algae.

Particular interesting is the lack of concordance between benthic macroinvertebrates and the other biological groups. In spite of being considered a good bioindicator of organic pollution (Cook 1976) and aquatic biodiversity (Bilton et al. 2006, Aldridge et al. 2007), benthic macroinvertebrates do not seem to be reliable surrogates of other aquatic assemblages. Nevertheless, our results at least offer evidence for predator-prey interaction between invertivorous fish and benthic macroinvertebrates, and for the role of macrophytes as the main source of detritus to invertebrates living in the sediment.

Temporal variability and use of surrogate communities

Temporal variation in community composition, environmental variables, community-environment relationships and biological interactions have been often documented in aquatic ecosystems (Thomaz et al. 2007, Bovo-Scomparin and Train 2008, Mykrä et al. 2008, Luz-Agostinho et al. 2008, Leigh and Sheldon 2009, Ilg et al. 2009). Thus, temporal variation in the level of assemblage concordance can be anticipated, especially in ecosystems that experience strong seasonality (e.g., Bini et al.

2007), such as floodplains. Our data indeed show that assemblage concordance is variable in time in floodplains, but the patterns did not exhibit seasonality. Upstream reservoirs in the Paraná River can be pointed out as the likely explanation for the lack of seasonality in assemblage concordance. Community dynamics and even persistence of populations have been changed due to flood control in the Upper Paraná River floodplain (Gubiani et al. 2007). Indeed, there were no seasonal flood events during 2000 and 2001 (Agostinho et al. 2004).

The use of surrogate groups in aquatic ecosystems can help managers in conservations efforts (e.g., Paszkowski and Tonn 2000, Paavola et al. 2003, Heino et al. 2005). Monitoring programs would avoid practical limitations of time and money if only one or few biological groups are enough to infer about the overall biota of aquatic ecosystems. However, only nearly persistent (i.e., temporally invariable) or temporally predictable patterns of assemblage concordance would allows the reliable use of surrogate groups (Heino et al. 2005). We observed high temporal variability in assemblage concordance, and the sampling period that contributed most to assemblage concordance varied depending on the cross-taxon comparison. Therefore, the use of surrogate groups may be unreliable, especially in a dynamic ecosystem, such as the Upper Paraná River floodplain.

Furthermore, concordance between assemblages has to be strong in order to allow for the use of surrogates (Paavola et al. 2003). We found low levels of assemblage concordance, probably due to the fine spatial scale of our study (e.g., Paavola et al. 2006, Bini et al. 2008). Previous studies have also found low levels assemblage concordance both in terms of assemblage structure (Bini et al. 2007, Davis et al. 2007) and richness (Heino et al. 2005, Declerck et al. 2005, Oertli et al. 2005), indicating that distinct organisms perceive environment in different ways (Allen et al. 1999), particularly in fine spatial scales (Paavola et al. 2003, Heino et al. 2003, Infante et al. 2009, but see Grenouillet et al. 2008).

The predictive powers of all biological assemblages were also low and, in general, not statistically significant. The method we used to evaluate the predictive power of the assemblages, the co-correspondence analysis (ter Braak and Schaffers 2004), is also useful to compare the relative predictive ability of different predictors (e.g., Schaffers et

al. 2008). This method may reveal a particular assemblage that best predict all others. If this assemblage is found, it could be used as a surrogate for the other assemblages. However, we did not find any particular group that significantly predicted all other groups in any sampling period. This result highlights that the use of surrogate taxa, at least in the ecosystem and at the spatial scale investigated by us, is not reliable (see also Heino et al. 2003, 2009, Heino 2010).

Concluding remarks

Patterns of concordance between aquatic assemblages were recurrent. In these cases, the evaluation of shared responses to environmental/spatial gradients and the information on natural history of biological groups were helpful to identify the likely causes for cross-taxa concordance. In addition, our results have important implications for conservation and biomonitoring planning, given the potential usefulness of surrogate groups. Taken as a whole, our results cast doubt on the validity of the use of surrogate taxa in Neotropical, temporally-variable, aquatic ecosystems. Although significant assemblage concordances were commonly observed (i.e., in several cross-taxon comparisons and in several sampling periods), this general conclusion was achieved by the weak and temporal variable concordance patterns (see Figure 3). Moreover, the ability of the different taxa to predict the species composition of another biological group was low or not significant, and there is no sole assemblage that can consistently predict all the others. Therefore, considering the need of reliable data in systematic conservation planning and biomonitoring, our results indicate that there are no alternatives to systematic surveys of different assemblages (see also Heino et al. 2009, Heino 2010) and other shortcut strategies should be considered to improve the efficiency of biological surveys. Among the promising strategies in floodplains, two should be further investigated: (i) the environmental classification of the habitat to define conservation areas that maximize variability of biota (Heino and Mykrä 2006, Padial et al. 2009), and (ii) the use of coarser taxonomic (i.e., genus instead of species) or numeric (i.e., presence/absence instead of abundance) resolutions (Carneiro et al. 2009).

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CAPÍTULO II

RESPOSTAS DE MÚLTIPLOS GRUPOS BIOLÓGICOS AQUÁTICOS A ESQUEMAS DE CLASSIFICAÇÃO EM DUAS ESCALAS ESPACIAIS NA PLANÍCIE DE INUNDAÇÃO DO ALTO RIO PARANÁ[3]

[3] Capítulo formatado de acordo com as normas da revista "Freshwater Biology".

RESPONSES OF MULTIPLE AQUATIC BIOLOGIAL GROUPS TO CLASSIFICATION SCHEMES AT TWO SPATIAL SCALES IN A NEOTROPICAL FLOODPLAIN

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Abbreviated title: Effectiveness of classification schemes in a Neotropical floodplain

Key-words: Assemblage structure, classification strength, regionalization, temporal variability, Neotropical floodplain.

SUMMARY

1. The correspondence between physical classification schemes and the structure of biological assemblages has been intensively investigated in recent years for the implementation of bioassessment, biomonitoring and conservation programs.

2. We evaluated the effect of temporal variability on the classification strengths of geographically and limnologically delimited regions and types of environments (i.e., isolated and connected lakes) for biological assemblages in a Neotropical floodplain.

3. We sampled data for several aquatic assemblages from lakes in the Upper Paraná River floodplain over two seasons. Two classification criteria were used, considering (i) lakes associated with three sub-systems (at a regional scale) and (ii) lakes with and without watercourse connections to the river main channel (at a local scale). We directly evaluated the effects of sampling period, sub-systems and connectivity using Permutational Multivariate Analysis of Variance. For the significant factors, we calculated the extent to which the mean within-class similarity exceeded the mean between-class similarity (a measure of classification strength). Finally, we generated classes based on the biological data to evaluate whether they overlapped with the classifications we proposed.

4. The correspondence between the classification criteria and the structures of the assemblages depended on the taxonomic group analyzed. Regionalization based on sub-systems was important to account for the variability in the structures of different biological assemblages. Classification at a finer scale was important only for macrophytes and zooplankton. However, temporal variability is an important component affecting responses of biological assemblages to physical divisions at different spatial scales. In addition, strengths of classifications were generally weak. The *a posteriori* classifications presented higher strengths of classifications, also indicating that sub-systems, environment types and sampling periods are important factors contributing to the variability of different biological assemblages.

5. Further investigations in Neotropical floodplains should also take into account other local factors (e.g., aquatic macrophyte cover) to increase the predictive power of regionalization schemes.

Introduction

Ecosystem classification is an effective way to infer patterns in ecological datasets. Thus, it is not surprising that studies on classification schemes are becoming more common in the ecological literature (Hawkins *et al.*, 2000; Heino *et al.*, 2002; Sánches-Montoya *et al.*, 2007; Growns & West, 2008; Snelder *et al.*, 2009), though existing studies have used different terminology (e.g., classification schemes, classification division, regionalization). The general premise is that biological communities respond to physiographic variables used to delineate ecoregions or ecological units (Heino & Mykrä, 2006). Ideally, a classification scheme should identify geographically distinct ecological units (Sánches-Montoya *et al.*, 2007), represent the variability of biodiversity of the regional pool, and be simple enough (i.e., with relatively few classes) to facilitate interpretation (Karr & Chu, 1999). A successful classification scheme (i.e., one that is a strong predictor of beta diversity patterns) could be useful for conservation planning and for the implementation of effective biomonitoring programs (Harding *et al.*, 1997; Hawkins *et al.*, 2000; Heino *et al.*, 2002). Accordingly, biological assessments frequently rely on the classification of ecosystems (Oliver *et al.*, 2004). Physical classifications can also act as a predictive tool for indicating likely changes in the ecosystem as a result of management practices (Harding & Winterbourn, 1997).

Most studies in the freshwater realm rely on broad-scale classifications in order to validate the utility of using ecoregions or drainage basins to represent the variability of biological assemblages (e.g., van Sickle & Hughes, 2000; Heino *et al.*, 2002). However, the explanatory powers of different classification schemes (e.g., based on physiographic variables) for predicting biodiversity patterns or community structure are, in general, rather low (Hawkins & Vinson, 2000; Hawkins *et al.*, 2000; Sandin & Johnson, 2000; Mykrä *et al.*, 2004; Heino & Mykrä, 2006; Heino *et al.*, 2008). Environmental variation in smaller units nested within an ecoregion (e.g., catchments within a drainage basin) may override the effects of regional variables (Heino *et al.*, 2004). In these cases, classifications at a finer spatial scale may be useful (Hawkins *et al.*, 2000).

Studies on ecosystem classifications as physical surrogates for conservation of multiple biological assemblages in Neotropical floodplains are scarce. These ecosystems are especially challenging because they are composed of a myriad of local habitats, such

as connected lakes, isolated lakes, rivers and channels (Thomaz *et al.*, 2004). Moreover, floodplains are usually composed of geological and limnological sub-systems at a regional scale (Thomaz *et al.*, 2004; Tockner *et al.*, 2006). Finally, floodplains have a temporally variable hydrological regime affecting limnological features and habitat connectivity (Junk *et al.*, 1989). In fact, temporal variability is an important, albeit neglected, feature affecting classifications of biological assemblages (Mykrä *et al.*, 2008). Therefore, classifications of biological data should take temporal variability into account and consider schemes that represent the nested nature of Neotropical floodplains. In this study, we aimed to assess the utility of ecosystem classification schemes in predicting patterns of aquatic assemblages in a Neotropical floodplain. We used data from assemblages of five different taxonomic groups and defined *a priori* landscape classifications based on distinct physical features at regional and local scales. As a consequence, we were able to determine which spatial scale accounts for the greatest part of the variation in the structures of the assemblages. In addition, we classified environments based on biological data (an *a posteriori* approach to ecosystem classification, see Heino & Mykrä, 2006) to evaluate whether this classification system overlapped with the *a priori* classifications we proposed. In addition, we visualized possible spatial and/or temporal sources of variation in biological data that could be considered in conservation efforts. We tested for the strengths of the *a priori* and *a posteriori* classifications and evaluated their stability over time.

Methods

Study area and a priori *classification criteria*

The study area is the Upper Paraná River floodplain (22°40’ to 23°00’ S; 53°00’ to 53°40’ W, Figure 1) in the La Plata River Basin (South America). This floodplain represents the last dam-free stretch (ca. 230 km) of the Paraná River in the Brazilian territory (Pelicice & Agostinho, 2005).

Since 2000, a long-term ecological project (PELD) has been conducted in the Upper Paraná River floodplain. In its first two years (2000 and 2001), several environments (including connected and isolated lakes) were studied, and data on different abiotic variables and biological assemblages (i.e., fish, aquatic macrophytes, benthic

macroinvertebrates, zooplankton and phytoplankton) were gathered. The Upper Paraná River floodplain is clearly divided into three sub-systems according to geological, hydrological and limnological variables (see Appendix S5): (i) the Paraná River sub-system; (ii) the Baía River sub-system; and (iii) the Ivinheima River sub-system (Figure 1). Therefore, we first tested the correspondence of floodplain assemblages to this classification system at a regional scale (i.e., the three regions of the Upper Paraná River). A higher compositional similarity within regions than between regions would indicate a significant effect of regional characteristics (e.g., geological, hydrological and limnological) on assemblages.

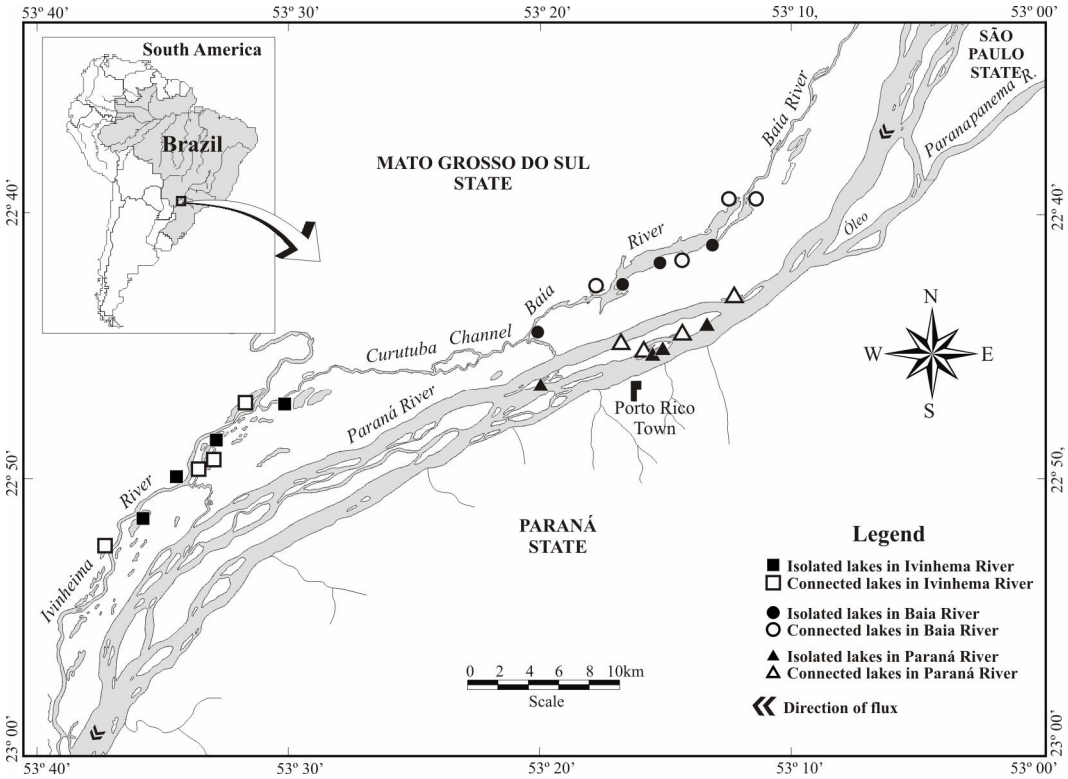

Figure 1. Sampling sites in the Upper Paraná River floodplain. Symbols differentiate sampling sites associated with the three sub-systems and the environment types in each sub-system, thus illustrating the two classification criteria (see Methods).

The second classification model considers the hydrological connectivity of the lakes to the main channel of the river, dividing the sample into connected and isolated lakes. This classification criterion at a local scale is supported by a physical characteristic

of each environment type that directly affects the dispersal of organisms. Connected lakes have permanent connections to the river's main channel, allowing continuous organismal dispersal. On the other hand, isolated lakes have only an intermittent connection to the main river, sporadically allowing dispersal by water course. Dispersal limitation has been considered as an important factor structuring metacommunities, mainly of macro-organisms (Shurin *et al.*, 2009). Accordingly, previous studies in the Upper Paraná River floodplain have demonstrated that connectivity favors the dispersal of organisms and affects the spatial configuration of aquatic assemblages (Agostinho & Zalewski, 1995; Aoyagui & Bonecker, 2004; Santos & Thomaz, 2007).

Field sampling

We used data on the abundance and the presence/absence of fish, benthic macroinvertebrates, zooplankton and phytoplankton sampled from up to 24 different connected and isolated lakes in the Upper Paraná River floodplain during the wet (February) and dry (August) seasons of 2000 and 2001. In addition, presence/absence data on macrophytes were also obtained for the wet and dry seasons of 2001 (Table 1).

Data on fish abundance (individuals.24hours.1000m^{-2} gillnet) were determined by experimental fishery using gillnets of several mesh sizes. Presence/absence data of aquatic macrophytes were recorded in the field from a boat moving at constant velocity. Benthic macroinvertebrates were collected using a Petersen grab modified for benthic samples. Density (individuals.m^{-3}) of zooplankton samples was obtained by pumping 600 L of water over a 70-µm mesh net. Van Dorn samplers and phytoplankton nets (15-µm mesh) were used for phytoplankton, and data were expressed as individual units (cells, coenobia, colonies, or filaments) per milliliter. A detailed description of the sampling procedures used for each biological assemblage is available in the Appendix S2.

Table 1. Available data for each biological assemblage. For fish, samplings were carried out in connected lakes only. Thus, we only tested for the effects of sub-system and sampling period (see the section titled "Study area and *a priori* divisions").

Assemblage	Sub-systems	Environment types	Sampling periods	Classification schemes tested
Fish	Four lakes in each sub-system	12 connected lakes	February and August of 2000 and 2001	Sub-systems in four sampling periods
Macrophytes	Eight lakes in each sub-system	12 connected and 12 isolated lakes	February and August of 2001	Sub-systems and environment types in two sampling periods
Benthic Macroinvertebrates	Eight lakes in each sub-system	12 connected and 12 isolated lakes	February and August of 2000 and 2001	Sub-systems and environment types in four sampling periods
Zooplankton	Eight lakes in each sub-system	12 connected and 12 isolated lakes	February and August of 2000 and 2001	Sub-systems and environment types in four sampling periods
Phytoplankton	Six Lakes in each sub-system	Nine connected and nine isolated lakes	February and August of 2000 and February of 2001	Sub-systems and environment types in three sampling periods

Data analysis

We used the Permutational Multivariate Analysis of Variance procedure (PERMANOVA; Anderson, 2001) to directly evaluate the effects of the two classification criteria (i.e., sub-system: Paraná, Baia, and Ivinheima; and environment type: connected and isolated lakes) and sampling periods on biological data. This is a multi-factorial ANOVA suitable for analyzing multivariate data that are based on any distance measure. Permutation methods are used to measure the significance level of the statistical criterion (see Anderson, 2001). In our case, each classification scheme represented one factor with different levels (i.e., three sub-systems, two environment types and up to four sampling periods). Therefore, the method is analogous to a three-way ANOVA. Given that fish assemblage data were available only for connected lakes, PERMANOVA was done, in this case, using only two factors: sub-systems and sampling

periods. We applied PERMANOVA to each assemblage separately. PERMANOVA software (Anderson, 2005) and a Monte Carlo method with 10,000 random permutations were used to assess significance levels.

We then calculated the Classification Strength (CS) of each classification criterion (van Sickle & Hughes, 2000). This analysis measures the strength of the correspondence between a classification scheme and the biological data by calculating the difference between the average within-group similarity (W) and the average between-group similarity (B) of the biological data (CS = W - B; see van Sickle & Hughes, 2000). A large CS value indicates high within-group and low between-group similarity. CS was calculated only to test for the classification strengths of significant factors, as detected in PERMANOVA. For instance, if the interaction between sub-system and environment type was significant, we calculated CS by considering sub-system as the classification factor for each environment type separately and *vice versa*. Bray-Curtis (for abundance data) and Jaccard (for presence/absence data) similarity coefficients were used for all analyses. Significance levels of CS values were also assessed by the Monte Carlo method using 10,000 permutations. Non-linear Multidimensional Scaling (NMDS) was used to ordinate sites in a bivariate scatter-plot. Dimensionality was determined by evaluating the standardized residual sum of squares (STRESS; Mather, 1976). STRESS values lower than 20 indicate a stable solution (McCune & Grace, 2002). One NMDS ordination per biological assemblage was done, incorporating data from all sub-systems, environment types and sampling periods. However, scores of sites were used to generate different figures illustrating how well a significant classification scheme accounted for the variation in assemblage structure among sites when significant CS values were detected. NMDS analyses were carried out using PC-ORD software (McCune & Mefford, 2006).

Finally, we used the *k*-means method to generate groups by using the biological data (i.e., the *a posteriori* classification). This algorithm assigns k centers to represent the clustering of n points ($k < n$). The points are iteratively adjusted so that each of the n points is assigned to one of the k clusters, and each of the k clusters is the mean of its assigned points (Bishop, 1995). This technique serves as an exploratory technique that suggests how best to divide the landscape into meaningful groups, in terms of both the number of classes and their definitions. We used the first two axes of the NMDS to

generate classes for each biological group using abundance data, except for aquatic macrophytes (as abundance is not available for this assemblage). As a stopping rule for the number of groups, we use used the following statistics (see also Hartigan, 1975):

$$R = \left(\frac{tr(\mathbf{W})(k)}{tr(\mathbf{W})(k+1)} - 1 \right)(n-k-1)$$

where $tr(\mathbf{W})$ is the trace of the dispersion matrix within groups, n is the number of samples, and k is the number of groups. Thus, this statistic was calculated for different k and the resultant values were compared with an F distribution (d.f. = p (the number of variables, which in our case is always equal to 2) and n-k-1).

We calculated the CS for the groups generated by the k-means method and visualized them in maps of the floodplain to compare the *a priori* and *a posteriori* classifications.

Results

Correspondence between the classification criteria and spatial patterns in biological assemblages depended on the taxonomic group analyzed (Table 2). CS values were generally low (always < 0.2). Given that CS results using abundance and presence/absence data were roughly similar, NMDS ordination plots were generated using only abundance data, except for aquatic macrophytes.

Independent of the sampling period, the structure of fish assemblages differed significantly among sub-systems (Table 2). In addition, the structure of fish assemblages did not vary significantly over time (Table 2). The strength of the correspondence between the sub-system delineation and the fish observed was significant, albeit low, for both abundance and presence/absence data (Table 3). The NMDS ordination plot showed that, to some extent, the abundance of fish assemblages differed among sub-systems (Figure 2).

Table 2. PERMANOVA results for each biological assemblage; *d.f.* = degrees of freedom; *P* = significance based on 10,000 randomizations. Bold letters indicate significant P-values.

		Abundance		Presence/Absence	
Biological assemblages and factors	***d.f.***	**F**	***P***	**F**	***P***
Fish					
(1) Sub-systems	2	6.10	**<0.001**	3.02	**<0.001**
(2) Sampling periods	3	0.05	0.997	1.25	0.108
Interaction (1) X (2)	6	1.76	0.056	1.33	0.071
Aquatic macrophytes					
(1) Sub-systems	2			11.69	**<0.001**
(2) Environment types	1			5.38	**<0.001**
(3) Sampling periods	1			3.73	0.006
Interaction (1) X (2)	2	Not available data		3.03	**0.002**
Interaction (1) X (3)	2			1.00	0.451
Interaction (2) X (3)	1			0.15	0.943
Interaction (1) X (2) X (3)	2			0.76	0.645
Benthic Macroinvertebrates					
(1) Sub-systems	2	10.33	**<0.001**	6.18	**<0.001**
(2) Environment types	1	3.58	**0.023**	0.69	0.699
(3) Sampling periods	3	5.41	**<0.001**	3.59	**<0.001**
Interaction (1) X (2)	2	1.09	0.865	1.36	0.153
Interaction (1) X (3)	6	0.77	**0.004**	1.75	**0.003**
Interaction (2) X (3)	3	1.62	0.701	1.05	0.391
Interaction (1) X (2) X (3)	6	1.72	0.984	0.69	0.933
Zooplankton					
(1) Sub-systems	2	6.72	**<0.001**	2.26	**<0.001**
(2) Environment types	1	7.42	**<0.001**	1.48	**0.029**
(3) Sampling periods	3	16.75	**<0.001**	5.34	**<0.001**
Interaction (1) X (2)	2	5.73	**<0.001**	1.21	0.090
Interaction (1) X (3)	6	1.75	**0.005**	1.34	**<0.001**
Interaction (2) X (3)	3	3.12	**0.004**	1.22	**0.041**
Interaction (1) X (2) X (3)	6	0.36	0.982	0.97	0.571
Phytoplankton					
(1) Sub-systems	2	4.98	**<0.001**	3.03	**<0.001**
(2) Environment types	1	3.13	**0.021**	1.42	0.069
(3) Sampling periods	2	5.06	**<0.001**	2.20	**<0.001**
Interaction (1) X (2)	2	1.67	0.121	1.13	0.148
Interaction (1) X (3)	4	2.05	**0.002**	1.25	**0.007**
Interaction (2) X (3)	2	0.74	0.701	0.93	0.685
Interaction (1) X (2) X (3)	4	0.63	0.842	0.82	0.982

Table 3. Classification strength results for each assemblage and significant factor according to PERMANOVA analysis (see Table 2). CS = classification strengths; *P* = significance based on 10,000 random permutations. NSF = Not significant factor according to PERMANOVA. Bold letters indicate significant P-values.

	Abundance		**Presence/Absence**	
Biological assemblage and classification scheme	**CS**	***P***	**CS**	***P***
Fish				
Sub-systems in all sampling periods	0.046	**<0.001**	0.043	**<0.001**
Aquatic Macrophytes				
Sub-systems in connected lakes			0.140	**<0.001**
Sub-systems in isolated lakes			0.098	**0.002**
Environment types in Baía sub-system	Not available data		0.104	**0.005**
Environment types in Ivinheima sub-system			0.061	**0.005**
Environment types in Paraná sub-system			0.037	0.088
Benthic Macroinvertebrates				
Sub-system in February 2000	0.043	**0.040**	0.075	**<0.001**
Sub-systems in August 2000	0.027	0.098	0.066	**<0.001**
Sub-systems in February 2001	0.097	**<0.001**	0.043	**0.015**
Sub-systems in August 2001	0.149	**<0.001**	0.079	**<0.001**
Environment types in all sub-systems and sampling periods	0.003	0.230	NSF	
Zooplankton				
Sub-system in connected lakes	0.018	**0.035**		
Sub-system in isolated lakes	0.038	**<0.001**		
Environment types in Baía sub-system	0.000	0.426	NSF	
Environment types in Ivinheima sub-system	0.002	0.373		
Environment types in Paraná sub-system	0.092	**<0.001**		
Sub-systems in February 2000	0.014	0.201	0.019	0.055
Sub-systems in August 2000	0.033	**0.002**	0.021	**0.017**
Sub-systems in February 2001	0.008	0.276	0.018	0.067
Sub-systems in August 2001	0.039	**0.043**	0.034	**0.007**
Environments in February 2000	0.065	**0.008**	0.022	**0.034**
Environments in August 2000	0.019	0.109	0.000	0.763
Environments in February 2001	0.022	0.085	0.005	0.251
Environments in August 2001	0.001	0.392	0.001	0.365
Phytoplankton				
Sub-systems in February 2000	0.023	0.156	-0.015	0.908
Sub-systems in August 2000	0.052	**0.033**	0.008	0.185
Sub-systems in February 2001	0.079	**0.007**	0.024	**0.028**
Environment types in all sub-systems and sampling periods	0.008	0.129	NSF	

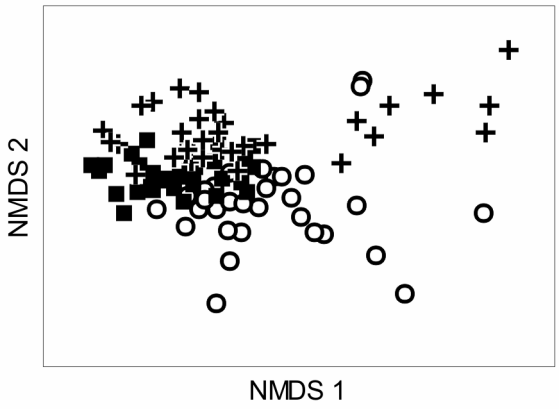

Figure 2. Plot of NMDS ordination scores for abundance (STRESS = 19.33) of fish assemblage showing sub-systems in all sampling periods. ○ = Baía River sub-system; ■ = Ivinheima River sub-system; + = Paraná River sub-system.

Aquatic macrophyte assemblage structures varied significantly over time, but the interactions between sampling period and sub-system and between sampling period and environment type were not significant (Table 2). A significant interaction between sub-system and type of environment was detected (Table 2). CS values for sub-system delineation were significant considering both environment types, but notably higher for connected lakes than for isolated lakes (Table 3), as also indicated by the low overlap among sub-systems in the ordination plot (Figure 3A-B). Comparisons between environmental types indicated the highest and significant classification strengths in the Baia River and Ivinheima River sub-systems, but not in the Paraná River sub-system (Table 3). The low overlap between the scores of isolated and connected lakes in the ordination plots for the first two sub-systems highlights the importance of this criterion for accounting for the variation in structure of aquatic macrophyte assemblages (Figure 3C-D).

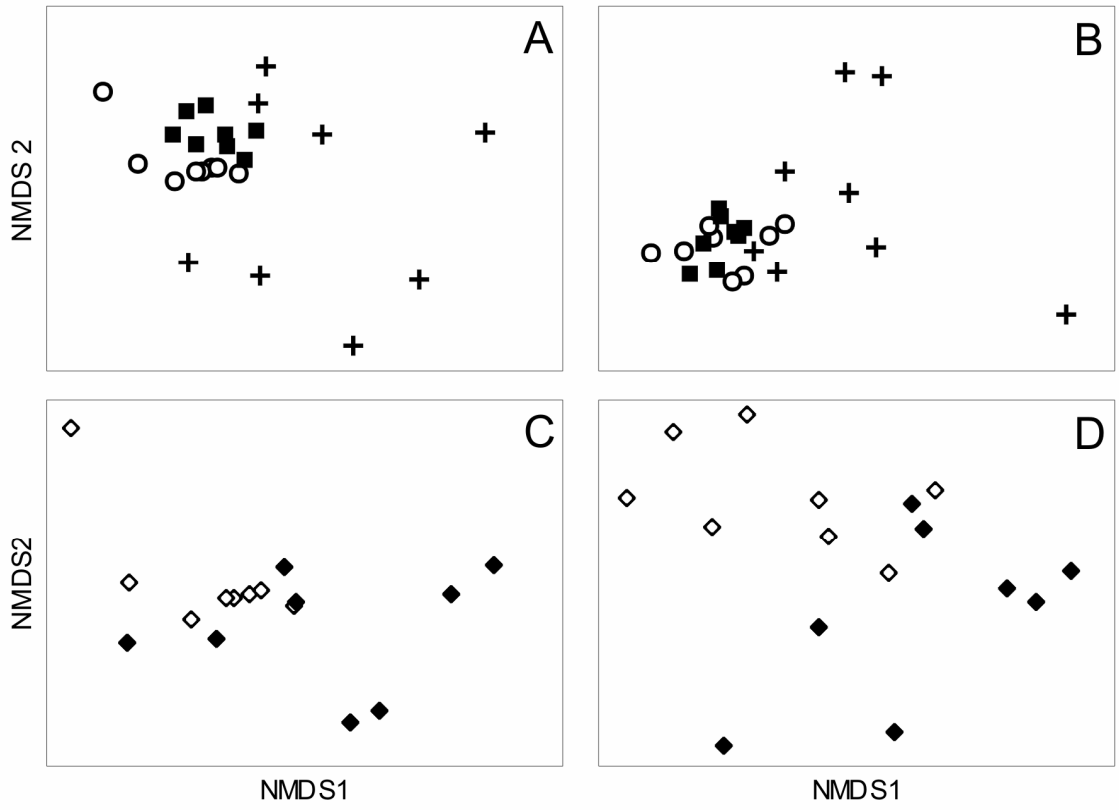

Figure 3. Plots of NMDS ordination scores for presence/absence data of aquatic macrophyte assemblages (STRESS = 19.85) showing: (A) sub-systems in connected lakes; (B) sub-systems in isolated lakes; (C) environment types in the Baía sub-system; (D) environment types in the Ivinheima sub-system. ○ = Baía River sub-system; ■ = Ivinheima River sub-system; + = Paraná River sub-system; ◇ = Connected lake; ◆ = Isolated lake.

The effect of sub-system on benthic macroinvertebrates depended on the sampling period (Table 2). Classification strengths of sub-systems for the abundance of benthic macroinvertebrate assemblages were significant for the February 2000, February 2001 and August 2001 datasets (Table 3). In general, these results are mainly attributable to the differences between the assemblages of lakes associated with the Ivinheima and Paraná sub-systems (Figure 4). Considering presence/absence, CS values were significant for all sampling periods (Table 3). Results from PERMANOVA and CS analysis applied to benthic assemblages were contradictory because the former indicated a significant effect of environment type on the abundance of benthic macroinvertebrates (Table 2) and the latter indicated a CS that could be expected by chance alone (Table 3). Considering

presence/absence data, the effect of environment type was not significant in PERMANOVA (Table 2).

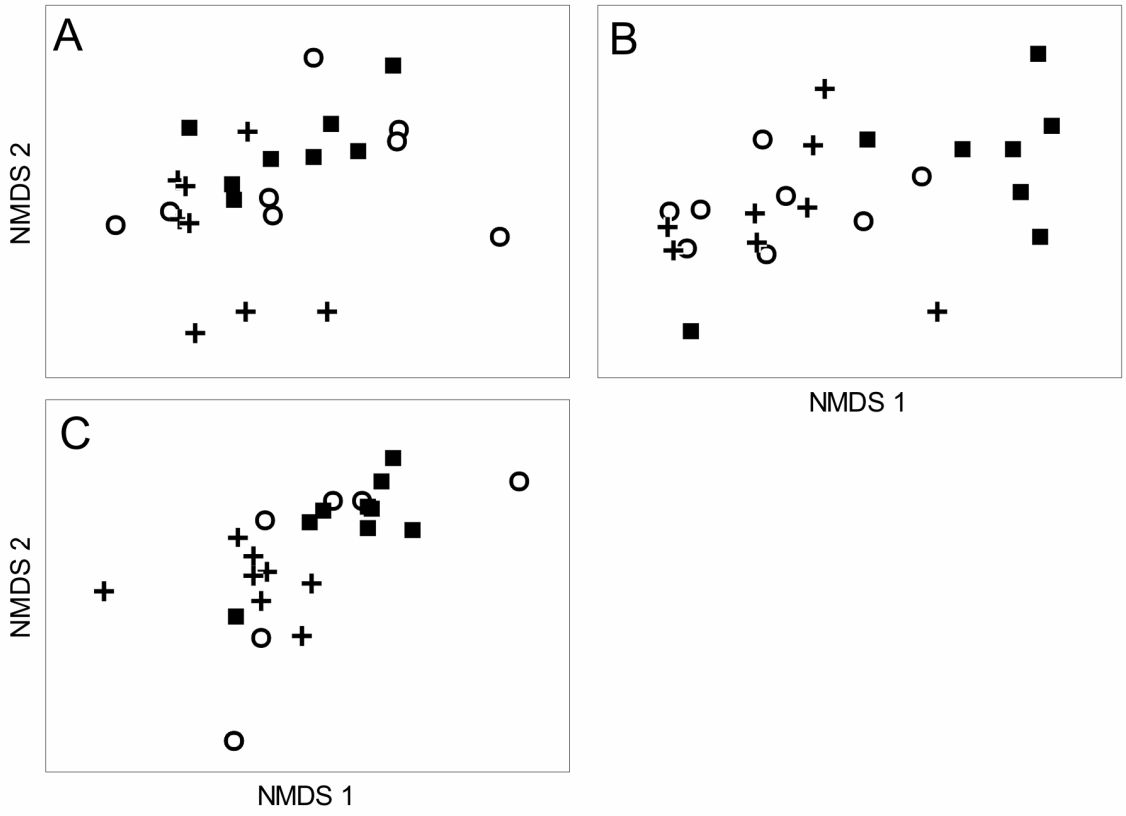

Figure 4. Plots of NMDS ordination scores for abundance of benthic macroinvertebrate assemblages (STRESS= 13.84) showing: (A) sub-systems in February 2000; (B) sub-systems in February 2001; (C) sub-systems in August 2001. ○ = Baía River sub-system; ■ = Ivinheima River sub-system; + = Paraná River sub-system.

Effects of sub-systems and environment types on the structure of zooplankton assemblages varied over time (Table 2). In addition, there was a significant interaction between sub-system and environment type on zooplankton abundance (Table 2). Nevertheless, classification strengths of sub-systems were significant for both connected and isolated lakes (Table 3). However, due to the significance of different interactions, the interpretation of the patterns is more complex. For instance, the differences in zooplankton abundance among sub-systems (in both types of environments; Figure 5A-B) were less conspicuous than the differences between environment types within the

Paraná River sub-system (Table 3, Figure 5C). CS of sub-systems were valid only for dry seasons (Table 3, Figure 5D-E), and CS of environment types were significant only for the wet season of 2000 (Table 3, Figure 5F) for both abundance and presence/absence data.

The interaction between sub-system and sampling period was significant for phytoplankton assemblages (Table 2). However, sub-systems affected phytoplankton assemblages independently of environment type (Table 2). CS of sub-systems was significant during the dry season of 2000 and the wet season of 2001 considering phytoplankton abundance (Table 3; Figure 6A-B). However, sub-system classification was significant only for the wet season of 2001 considering presence/absence of phytoplankton (Table 3). Despite the significant effect detected in PERMANOVA (Table 2), CS of environment type for abundance of phytoplankton was not significant (Table 3). Considering presence/absence of phytoplankton, the effect of environment type was not significant in PERMANOVA (Table 2).

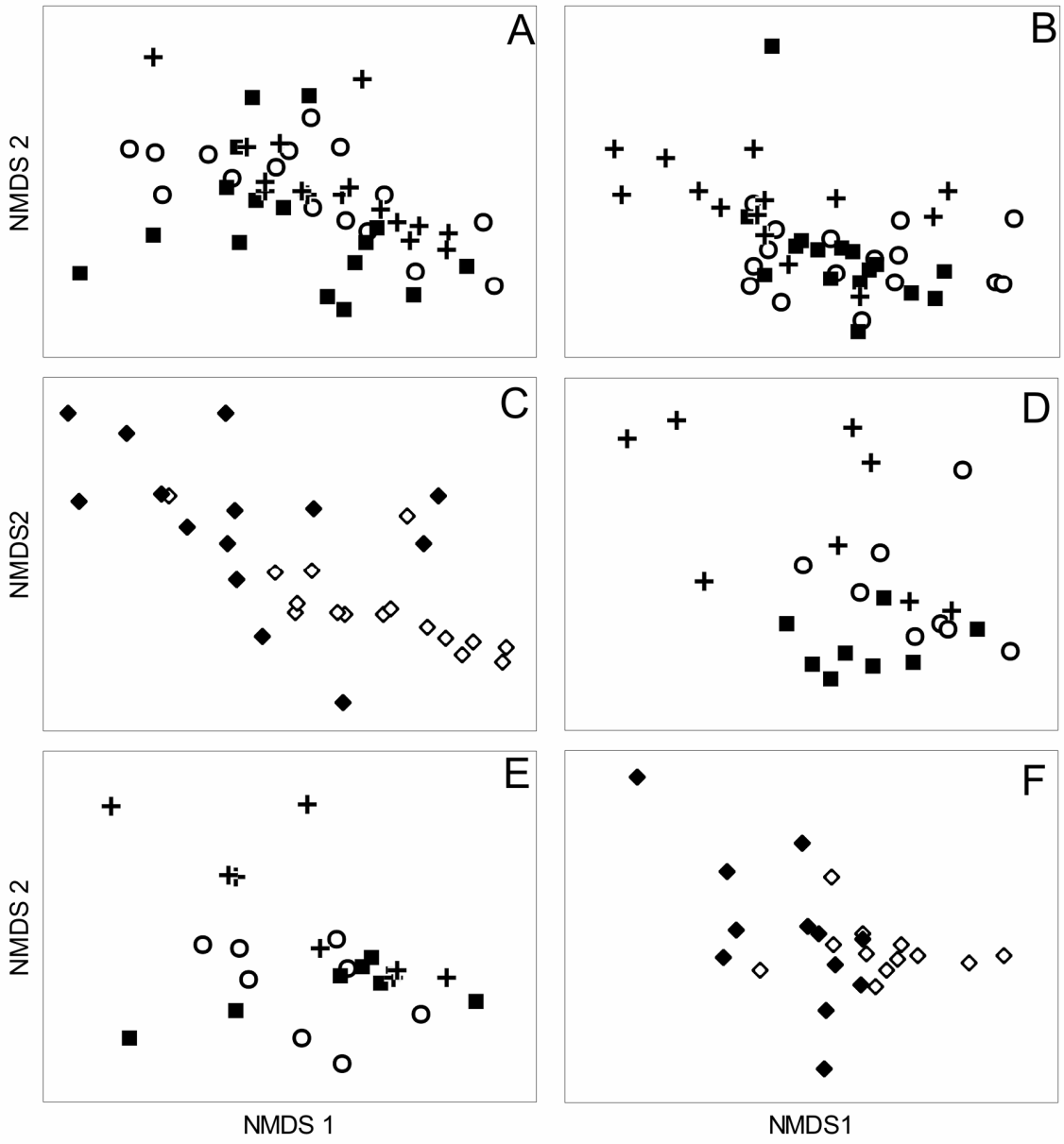

Figure 5. Plots of NMDS ordination scores for abundance of zooplankton assemblages (STRESS = 14.58) showing: (A) sub-systems in connected lakes; (B) sub-systems in isolated lakes; (C) environment types in Paraná River sub-system; (D) sub-systems in August 2000; (E) sub-systems in August 2001; (F) environment types in February 2000. ○ = Baía River sub-system; ■ = Ivinheima River sub-system; + = Paraná River sub-system; ◇ = Connected lake; ◆ = Isolated lake.

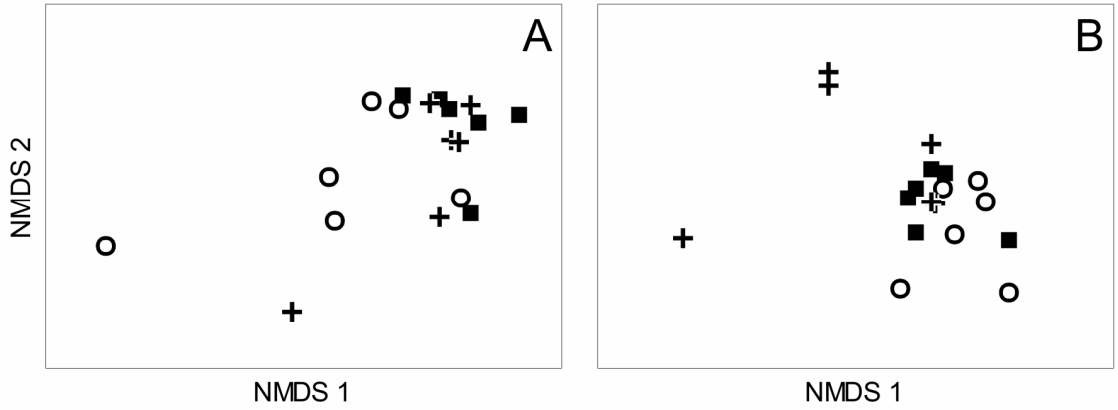

Figure 6. Plots of NMDS ordination scores for abundance of phytoplankton assemblages (STRESS = 16.30) showing: (A) sub-systems in August 2000; (B) sub-systems in February 2001. ○ = Baía River sub-system; ■ = Ivinheima River sub-system; + = Paraná River sub-system.

The number of classes generated using the *k*-means method varied from 7 to 10, depending on the taxonomic group (Table 4). The CS values of the *a posteriori* classifications were higher than those calculated for the *a priori* classification schemes, except for fish assemblages (see Tables 3 and 4). To a certain extent, the *a posteriori* classifications grouped lakes located near one other (usually within the same sub-system) and sampled at roughly the same sampling period or sampling season (Figure 7). This can be observed by the high frequency of similar letters (that represent the *a posteriori* classes) in each sub-system sampling period or sampling season (February or August) (Figure 7). On the other hand, connected and isolated lakes were poorly differentiated according to the *a posteriori* classification (Figure 7). It is important to note, however, that the variation in biological data was not fully structured spatially or temporally for any biological assemblage (Figure 7).

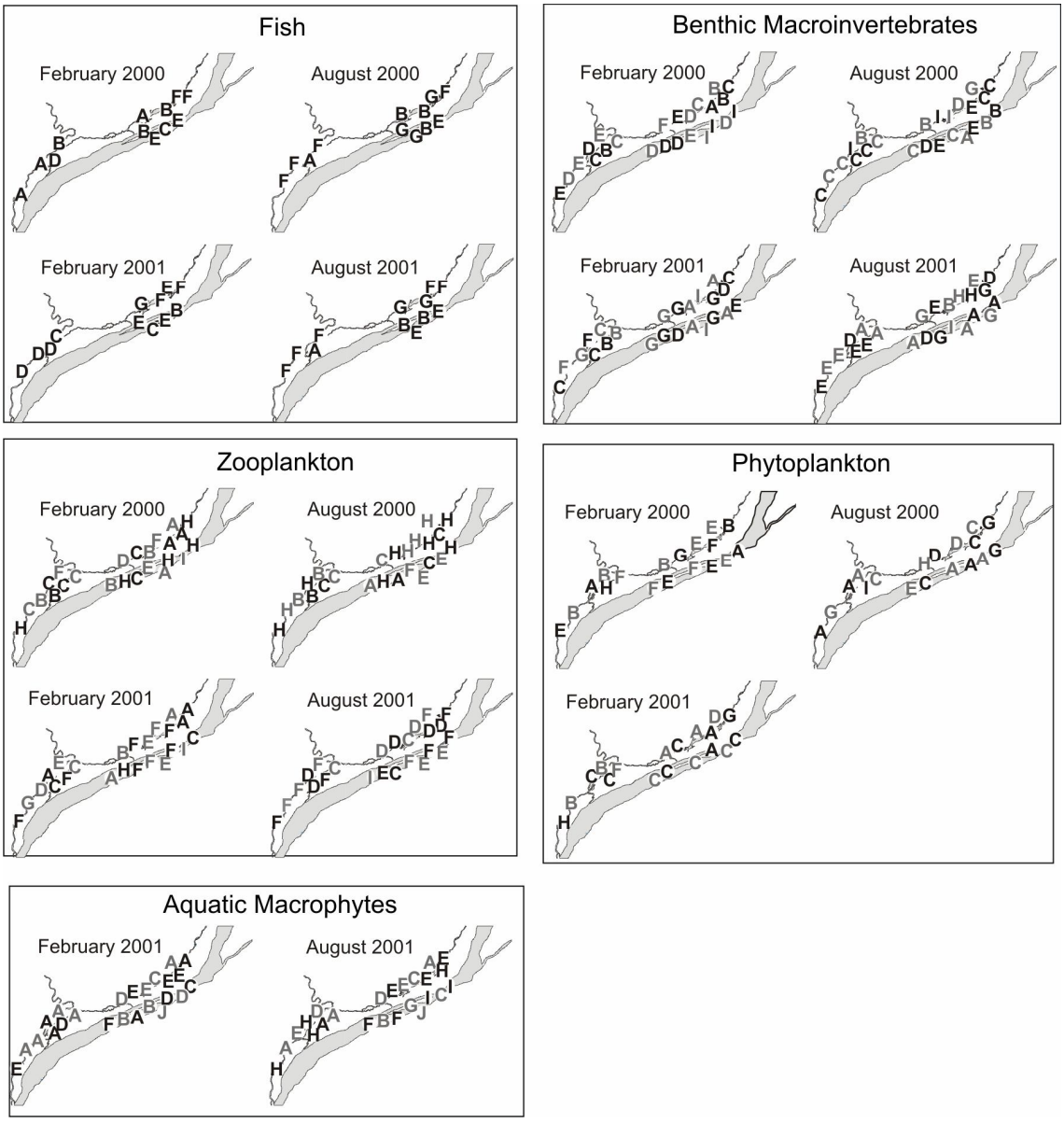

Figure 7. Maps of the floodplain (see a detailed map in Figure 1) with lakes grouped according to the *a posteriori* classifications for each biological assemblage. Up to 10 classes were generated using biological data and each letter represents a different class (A-J). Grey letters indicate isolated lakes, and black letters indicate connected lakes. For fish assemblages, only connected lakes were sampled (see Methods).

Discussion

Physical classifications should ideally incorporate information relevant to the biological assemblage under study (Orians, 1993; Angermeier & Schlosser, 1995). A typical feature of Neotropical floodplains is the presence of sub-systems composed of the main river channel and lateral water bodies (Junk *et al.*, 1989; Thomaz *et al.*, 2004).

Differences in the compositions of biological assemblages among these sub-systems have generally been related to the physical and chemical aspects of water bodies, the level of connectivity between habitats, as well as seasonal floods (Junk *et al.*, 1989; Aoyagui & Bonecker, 2004; Bonecker *et al.*, 2005; Dos Santos & Thomaz, 2007; Leigh & Sheldon, 2008).

Classification at a regional scale involved sub-systems of water bodies characterized by different physical and chemical properties (Thomaz *et al.*, 2004). On the other hand, classification at a local scale considered lakes with different levels of connectivity to the river main channel. Combining regional and local factors in ecosystem classification is considered a suitable approach to improve bioassessment programs (Sandin & Johnson, 2000; Heino *et al.*, 2002; Heino *et al.*, 2004; Mykrä *et al.*, 2004; Soininen *et al.*, 2004), mainly when several biological assemblages are focused (Pan *et al.*, 2000). Moreover, we took water level variability into account by using data gathered during different hydrological seasons. Temporal variability has also been demonstrated as an important factor for ecosystem classification (Mykrä *et al.*, 2008). Overall, we found that the classification strength of sub-systems was significant for all biological assemblages. On the other hand, only macrophytes and zooplankton showed a significant correspondence to environment type. Finally, the importance of these criteria varied over time for planktonic and benthic assemblages.

A posteriori classifications are naturally the best approach to classifying biological groups, given that they use the biological data to generate the classes and, thus, better represent variation in biological data (Gordon, 1987). However, their utility for practical purposes should be evaluated, since *a posteriori* classes do not always have a useful spatial or temporal structure for conservation purposes. Generally, the *a posteriori* classifications showed that sub-systems and time in particular contribute to the variation in biological data (see Figure 7), highlighting the usefulness of this classification for conservation purposes as also demonstrated by the *a priori* classification. However, *a posteriori* classes also showed that there are other sources of variability in assemblage structure not related to the *a priori* classification schemes. This result suggests that variability of biological assemblages is continuous and also determined by idiosyncratic processes (Heino & Mykrä, 2006).

Classification at a regional scale: sub-systems

Classifications at larger scales of river networks have been demonstrated as important for fish assemblage in New Zealand (Snelder *et al.*, 2009). Accordingly, we found that the level of correspondence between classifications at a regional scale and fish assemblages was significant in the Upper Paraná River floodplain. Furthermore, the regionalization was invariant over time, and the effect of time on fish assemblages was not significant. This is surprising given that the structure of fish assemblages is expected to vary seasonally in floodplains (Hoeinghaus *et al.*, 2003), mainly due to migration and reproduction (Agostinho *et al.*, 2004). However, it is also known that migratory fish require considerable changes in the flood regime to disperse and colonize new environments (Agostinho & Zalewski, 1995). Due to flood regime control in the Upper Paraná River floodplain, the amplitude of floods has decreased, affecting the dispersal and persistence of fish populations (Gubiani *et al.*, 2007). This may have caused the lack of temporal variability in fish assemblages and the consequent stability of physical classifications on a regional scale.

Temporal variability in floodplains usually has a substantial effect on the species composition and/or richness of aquatic macrophyte assemblages (Tockner *et al.*, 2000; Maltchik *et al.*, 2007; Padial *et al.*, 2009). However, the high resilience of macrophyte assemblages can explain the robustness of this regionalization criterion (Padial *et al.*, 2009). Only zonation along depth gradients seems to be substantially affected by floods, and correspondence between sub-system regionalization and macrophyte assemblage is invariant over temporal changes in water level (Padial *et al.*, 2009). Moreover, considering sub-system as the classification criterion, CS was higher for connected lakes than for isolated lakes (see Table 3). Isolated lakes are probably under the influence of local (e.g., biotic interactions) and idiosyncratic processes, and therefore, within-class compositional similarity (i.e., similarity within a given sub-system) tends to be lower than between-group similarity. On the other hand, connected lakes within a sub-system share the same pool of colonizers, and dispersal rates are also higher in connected than in isolated lakes. These factors and the higher limnological similarity within than between

sub-systems (Thomaz *et al.*, 2007) likely contributed to the high correspondence between sub-system classification and aquatic macrophyte assemblages in connected lakes.

Sub-systems significantly accounted for variation in benthic macroinvertebrate and planktonic assemblages. Large-scale classification schemes have also been demonstrated as important to explain variability in the assemblage structure of stream macroinvertebrates (Heino *et al.*, 2002) and spring metaphyton (Keleher & Rader, 2008). In our study, however, these communities were not significantly classified by sub-systems in all sampling periods. As a result, the use of sub-systems to delineate discrete biological assemblage types in floodplains for the purposes of conservation planning and bioassessment may be a flawed strategy due to temporal variability (see also Mykrä *et al.*, 2008).

Differences among sub-systems considering benthic macroinvertebrates and zooplankton, when significant, were found mainly between the Ivinheima and Paraná River sub-systems (see Figures 4-5). This is probably due to the degree of spatial relatedness between the three sub-systems. The sampling sites of the Ivinheima and Paraná River sub-systems are the most distant from each other (see Figure 1). On the other hand, lakes located in the Baía River sub-system can easily receive organisms dispersing from both the Paraná River and Invinheima River through lateral channels (Figure 1). Dispersal limitation has been considered important to explain variation in the community composition of benthic algae (Keleher & Rader, 2008). However, the phytoplankton assemblage did not reflect this environmental variation (see Figure 6). This may be due to the high dispersal ability of phytoplankton (Padisák, 2004), which are able to reach new habitats from even very distant locations.

It is also noticeable that the structure of zooplankton assemblages was not significantly predicted by sub-systems during periods characterized by high water levels (see Table 3). Indeed, floods may homogenize different environmental and biotic characteristics of floodplains at large spatial scales (Thomaz *et al.*, 2007). On the other hand, no clear temporal pattern could be observed for benthic macroinvertebrates or phytoplankton regarding temporal variation. There may be several non-mutually exclusive reasons for the temporal variability in these assemblages, such as temporal variations in environmental variables (Mykrä *et al.*, 2008), priority effects (De Meester *et*

al., 2002), mass effects (Hasegawa *et al.*, 2008) and/or stochastic events (Webster & Harris, 2004). Therefore, the response of plankton and benthos to regionalization over time is still a matter of debate.

Classification at a local scale

The predictive capability of environment type based on connectivity level varied among the biological assemblages analyzed. The significant effect of local classification on macrophytes over time is probably related to dispersal limitations, given that these organisms disperse mostly by vegetative propagules via watercourse (van Geest *et al.*, 2005). Therefore, isolated lakes receive propagules only accidentally or sporadically during large flood events, whereas connected lagoons receive continuous inputs. However, environment type did not account for the variation in the structure of aquatic macrophyte assemblages in the Paraná River sub-system (see Table 3). The reason for that probably depends on the fact that lakes of the Paraná River sub-system have frequent low-magnitude floods (Thomaz *et al.*, 2004). This represents a stress for the biota, diminishing species richness per lake (Padial *et al.*, 2009) and probably maintaining only resilient and similar species in different environment types.

High overland dispersal ability (by wind and/or other vectors) can also be the reason for the finding that environment type was not a good classification scheme for planktonic assemblages (Padisák, 2004; see also Vanormelingen *et al.*, 2008; Vanschoenwinkel *et al.*, 2008). Environment type was also not important to predict the patterns of similarities generated by benthic macroinvertebrates, indicating that overland dispersal over short distances is not limiting for this assemblage. Classification schemes at a finer spatial scale (habitats within a wetland) also did not contribute to variation in benthic algae in North American desert springs (Keleher & Rader, 2008). However, classification schemes considering even finer scales, such as riffles within the same stream, supported the presence of substantially different macroinvertebrate assemblages (Heino *et al.*, 2004). Previous studies have also shown that the importance of local habitat features to the structure of biological assemblages increases with decreasing spatial scale (Mykrä *et al.*, 2007; Ilmonen *et al.*, 2009). Considering even finer scale analyses in floodplains, a potential classification scheme to be tested in further studies may be related

to the presence or absence of aquatic macrophytes. Indeed, aquatic macrophytes play a central role in determining the structures of other aquatic assemblages (e.g., Søndergaard & Moss, 1998; Scheffer, 1998), even when the vegetation cover is low (Gasith & Hoyer, 1998).

Concluding remarks

Evaluating the effectiveness of environmental surrogates is particularly interesting when multiple taxonomic groups that potentially respond uniquely to environmental features are considered (Johnson & Hering, 2009). Overall, our results confirmed that the Upper Paraná River floodplain can be divided into three environmental units (i.e., Baía, Ivinheima and Paraná River sub-systems), which support different biological assemblages (see also Bini *et al.,* 2001; Padial *et al.,* 2009). Thus, this classification criterion may be useful for future biological assessments and conservation efforts. However, the ability of this criterion to predict the structure of planktonic and benthic assemblages was temporally variable. To a certain extent, the *a posteriori* classifications have also shown the importance of sampling period and sub-system in accounting for the variability of different biological assemblages. However, the *a posteriori* classification clearly showed that the variability of biological data cannot be fully attributed to spatial or temporal patterns, suggesting that idiosyncratic events may flaw general ecosystem classifications. Even when significant, the classification strengths were generally weak. This pattern has been observed in previous studies of ecosystem classification (Hawkins *et al.,* 2000; Sandin & Johnson, 2000; Heino & Mykrä, 2006; Mykrä *et al.,* 2008). Nevertheless, even a classification with low predictive power can be a starting point for more detailed approaches aiming to predict assemblage structures based on a physical division or a base for further landscape classifications (Heino & Mykrä, 2006). Accordingly, previous studies have found that large-scale classifications (i.e., ecoregions) do not sufficiently partition variance in assemblage structure, and a nested approach including more local habitat characteristics would improve ecoregion classifications (Hawkins *et al.,* 2000; Sandin & Johnson, 2000; Heino *et al.,* 2002; Heino *et al.,* 2004; Mykrä *et al.,* 2004; Shears *et al.,* 2008). Indeed, identifying the scales of variability in assemblages is not trivial (Heino *et al.,* 2004), especially if the study involves multiple

biological assemblages that perceive the environment at different spatial scales (Pan *et al.*, 2000). Nevertheless, we found that division by environment type (at a local scale) is only important to explain variability of macrophytes and zooplankton. Classifications at even finer spatial scales (see Heino *et al.*, 2004) and transformation of local variables to reflect possible non-linear relationships between physical features and biological data (see Snelder *et al.*, 2009) may improve the predictive power of classifications for Neotropical lakes. For instance, lakes with a clear littoral zone dominated by macrophytes may have a horizontal structure of fish and/or plankton assemblages (Agostinho *et al.*, 2007; Meerhoff *et al.*, 2007), which could be used as a classification criterion. Therefore, further investigations should include other features in classifications and a multi-scale approach to identify the scales of variability in aquatic assemblages. Finally, we conclude that temporal variability is an important component affecting most biological assemblages of Neotropical floodplains and their responses to physical divisions.

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CAPÍTULO III

PAPEL RELATIVO DE FATORES AMBIENTAIS, ESPACIAIS E TEMPORAIS NA COMPOSIÇÃO DE ASSEMBLÉIAS AQUÁTICAS EM UMA PLANÍCIE DE INUNDAÇÃO NEOTROPICAL[4]

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Palavras-chave: Estrutura de comunidades, metacomunidades, preditores ambientais, preditores espaciais, preditores temporais, planície de inundação do Alto rio Paraná.

Key-words: Community structure, metacommunity, environmental filter, spatial predictors, temporal predictors, Upper Paraná River floodplain.

Resumo

A avaliação do papel relativo de processos relacionados ao nicho e processos neutros na estruturação das assembléias é um dos principais objetivos em Ecologia de Comunidades. Essa discussão é especialmente relevante quando organismos com diferentes requerimentos ambientais e diferentes capacidades de dispersão são simultaneamente investigados em um ecossistema. Entretanto, processos temporais têm sido pouco investigados, e esses podem ser importantes em ecossistemas aquáticos que apresentam variação temporal nas variáveis ambientais e no grau de conectividade dos ambientes. O objetivo do presente trabalho foi avaliar o papel relativo de variáveis ambientais, espaciais e temporais na estrutura de diferentes assembléias aquáticas (que apresentam diferentes capacidades de dispersão) da planície de inundação do Alto rio Paraná. Utilizamos dados de peixes, macroinvertebrados bentônicos, macrófitas aquáticas, zooplâncton, fitoplâncton e perifíton coletados em até 36 ambientes durantes os anos de 2000 e 2001. Utilizamos uma técnica de partição da variância para avaliar o papel relativo de matrizes compostas por: (i) variáveis ambientais relacionadas com a limnologia dos ambientes; (ii) variáveis que representam diferentes estruturas espaciais utilizadas como substitutas de vias de dispersão dos organismos e; (iii) variáveis que representam diferentes dinâmicas temporais que potencialmente afetam os organismos. A importância dos fatores variou de acordo com o grupo biológico considerado. Entretanto, as variáveis temporais apresentaram baixa capacidade de predição para praticamente todos os grupos biológicos. Para organismos com limitação na capacidade de dispersão, como peixes sedentários e plantas aquáticas, as variáveis espaciais foram mais importantes. Nesses casos, a dinâmica neutra pode ser mais importante que processos baseados no nicho para estruturar as assembléias locais. Por outro lado, variáveis ambientais apresentaram maior poder de explicação para organismos com alta capacidade de dispersão, como micro-algas e peixes migradores. Isso indica maior efeito de processos relacionados com o nicho das espécies. Entretanto, os poderes de explicação das variáveis preditores foram, em geral, baixos. A inclusão de outras variáveis relevantes para cada grupo biológico, e uma investigação em um período de tempo maior pode aumentar o poder de explicação da variabilidade das estruturas dessas assembléias.

Abstract

The identification of the relative importance of processes related to the niche and neutral processes is a major goal in community ecology. This is particularly relevant if organisms with different ecological requirements and dispersal abilities are simultaneously investigated in an ecosystem. However, temporal processes are rarely investigated, but they may be important in ecosystems with high temporal variability in the environmental features and in the level of connectivity among habitats. The goal of this study was to evaluate the relative role of environmental, spatial and temporal variables on the structure of different aquatic assemblages (with different dispersal abilities) in the Upper Paraná River floodplain. We used data on fish, benthic macroinvertebrates, aquatic macrophytes, zooplankton, phytoplankton, and periphyton collected in up to 36 habitats during the years 2000 and 2001. We used a variation partitioning technique to evaluate the relative role of matrices comprised by: (i) environmental characteristics; (ii) spatial variables that represent different spatial structures and are used as a proxy of dispersion routes; (iii) temporal variables that represent different temporal dynamics that potentially affect the organisms. The importance of the predictors varied among the biological groups. However, temporal variables were not important for almost all biological groups. Spatial variables were particularly important for organisms with dispersal limitation, such as sedentary fish and aquatic macrophytes. In this case, neutral processes are probably more important than niche-based processes for the structure of the local assemblages. On the other hand, environmental variables were particularly important for organisms with high dispersal ability, such as micro-algae and migratory fish. This indicates a higher effect of niche-based processes. However, the predictive powers were, in general, low. The inclusion of other variables relevant for each biological group can increase the predictive power of the variability of the assemblage strucutures.

Introdução

Fatores que operam em diferentes escalas (por exemplo, fatores ambientais locais e fatores regionais) afetam simultaneamente a composição das comunidades biológicas (Ricklefs 1987). Isso é explicito no conceito de metacomunidades, que pode ser definido como o conjunto de comunidades locais ligadas por dispersão de espécies que potencialmente interagem entre si (Leibold 2004, Chase 2005). Nesse sentido, o esclarecimento do papel relativo de interações biológicas, variação aleatória, limitação por dispersão e determinismo ambiental na manutenção da diversidade beta é central em ecologia de comunidades (Tuomisto et al. 2003). Tradicionalmente, fatores locais como características ambientais têm sido considerados importantes determinantes das comunidades locais (Heino e Mykrä 2008, Vanormelingen et al. 2008). Essa abordagem é baseada, principalmente, na teoria de nicho multidimensional (Hutchinson 1959). Uma visão alternativa, entretanto, tem enfatizado que as comunidades locais podem ser estruturadas por fatores espaciais que refletem as capacidades de dispersão das espécies (Hubbell 2001). Desde então, vários trabalhos têm buscado avaliar o papel relativo dos fatores ambientais e espaciais na estrutura das metacomunidades (Cottenie et al. 2003, Tuomisto et al. 2003, Chase 2005, Beisner et al. 2006, Vanschoenwinkel et al. 2007, Heino e Mykrä 2008, Vanormelingen et al. 2008, Nabout et al. 2009, Heino et al. 2010).

Investigações com esse propósito frequentemente utilizam somente uma comunidade biológica geralmente definida em termos taxonômicos (ou seja, assembléia, veja Fauth et al. 1996) como objeto de estudo (Cottenie et al. 2003, Heino e Mykrä 2008, Nabout et al. 2009). Poucos estudos focaram diferentes grupos com diferentes capacidades de dispersão em um mesmo ecossistema (Beisner et al. 2006, Vanschoenwinkel et al. 2007). Isso é fundamental para entender como a dinâmica de diferentes organismos em uma mesma região é afetada por fatores locais e espaciais. Por exemplo, organismos com maior capacidade de dispersão devem ser menos afetados por características espaciais devido simplesmente ao fato de que há maior chance desses organismos colonizarem todos os ambientes de uma região (Martiny et al. 2006). Nesse caso, os gradientes ambientais devem servir como um "filtro" para determinar a estrutura das comunidades locais (Beisner et al. 2006, Vanschoenwinkel et al. 2007, Sommaruga e Casamayor 2009). Em ambientes aquáticos, isso é frequentemente observado para

organismos com menores tamanhos de corpo, como bactérias e micro-algas (Langenheder e Ragnarsson 2007, Sommaruga e Casamayor 2009, Shurin et al. 2009), até mesmo em amplas escalas espaciais (Van der Gucht et al. 2007).

Processos temporais também podem afetar a estrutura das comunidades (Bengtsson 1994). De fato, é amplamente reconhecido que a variação temporal é uma propriedade inerente das comunidades ecológicas (Bengtsson et al. 1997). Entretanto, estudos focando, concomitantemente, o papel relativo de fatores ambientais, espaciais e temporais na estrutura de comunidades locais são raros (Anderson e Gribble 1998). O tempo pode ser especialmente importante em ecossistemas nos quais comportamentos temporalmente estruturados são observados nas espécies (por exemplo, a migração de peixes, ou a floração de plantas aquáticas). A variabilidade temporal em planícies de inundação é frequentemente relacionada com pulsos hidrológicos periódicos que afetam características limnológicas e alteram o grau de conectividade dos ambientes (Junk et al. 1989, Thomaz et al. 2007). Isso afeta processos fenológicos e etológicos das espécies, como crescimento de plantas e migração em peixes (Junk et al. 1989).

Nesse estudo, nós avaliamos o papel relativo de fatores ambientais, espaciais e temporais na estrutura de diferentes assembléias aquáticas na planície de inundação do Alto rio Paraná, Brasil. Nós testamos a hipótese de que assembléias com maior capacidade de dispersão, como pequenos organismos que dispersam passivamente pela água ou pelo ar ou organismos que tenham comportamento de migração, são pouco afetados por fatores espaciais. Nesse caso, as assembléias locais devem ser determinadas primiordialmente por fatores ambientais e temporais. Ademais, o tempo deve afetar todas as assembléias, refletindo variações ambientais e espaciais temporalmente estruturadas relevantes para os grupos biológicos, como pulsos hidrológicos que alteram as características limnológicas e a conectividade dos hábitats.

Métodos

Área de estudo

A planície de inundação do Alto rio Paraná (Figura 1) é o último trecho desse rio livre de barragens em território brasileiro (Agostinho et al. 2005). Essa é uma importante área para a conservação de vários peixes migradores e contém uma elevada diversidade

biológica (por exemplo, 50% das espécies de peixe do bioma Floresta Atlântica foram registrados nessa região; Agostinho et al. 2005). Historicamente, a planície de inundação do Alto rio Paraná tem um regime hidrológico marcado por períodos de seca (aproximadamente de maio a outubro) e cheia (aproximadamente de novembro a abril) (Thomaz et al. 2004). Entretanto, devido ao controle hidrológico de reservatórios de usinas hidroelétricas localizados a montante, a freqüência, amplitude e duração de períodos de seca e cheia foram substancialmente alteradas (Agostinho et al. 2004).

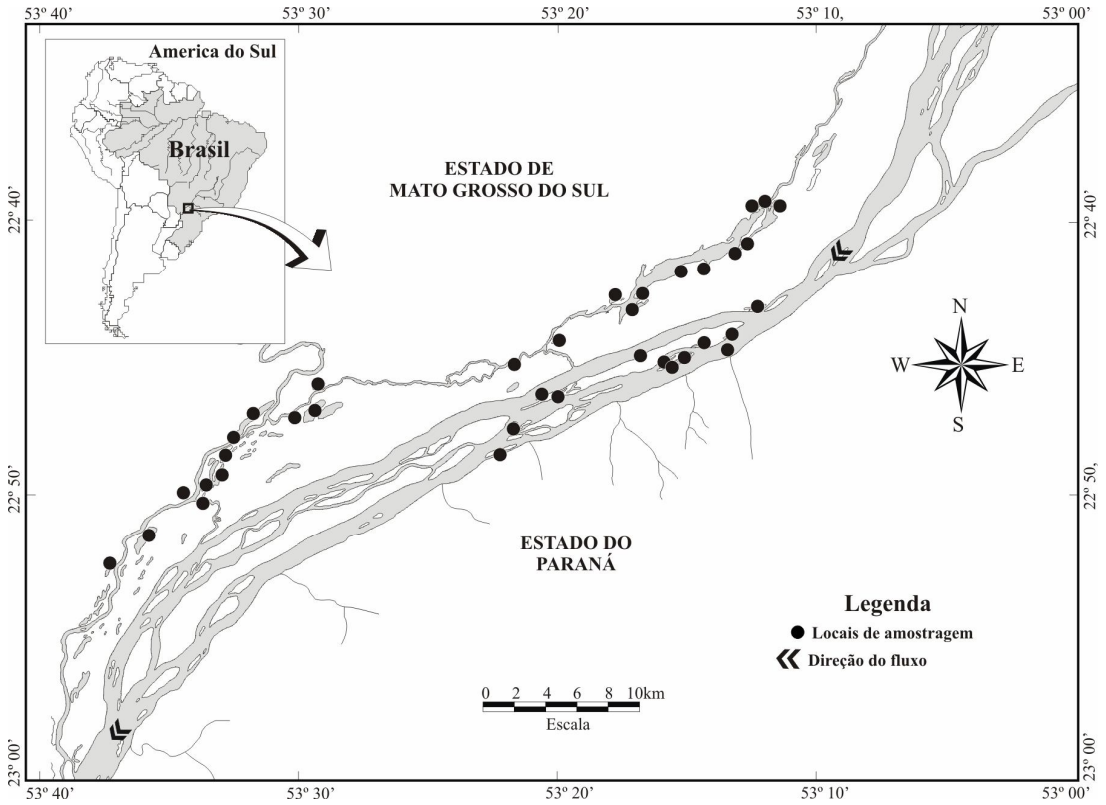

Figure 1. Mapa da área investigada na planície de inundação do Alto rio Paraná mostrando também a posição dos locais de amostragem.

Coleta dos dados

Foram coletados dados de seis assembléias biológicas: peixes, macroinvertebrados bentônicos, macrófitas aquáticas, perifíton, fitoplâncton e zooplâncton. As amostragens foram realizadas em fevereiro, maio, agosto e novembro de 2000 e 2001 e em até 36 locais (Figura 1). Como os dados de alguns grupos em alguns

períodos de amostragem não estão disponíveis, as análises foram realizadas com diferentes conjuntos de dados, dependendo do grupo (veja Anexo S6).

A abundância de peixes (indivíduos×24 horas/1000m^2 malha) foi determinada por pesca experimental utilizando redes de espera com diferentes aberturas de malha. Dados de ocorrência (presença/ausência) de espécies de macrófitas aquáticas foram registrados percorrendo as margens dos ambientes. Macroinvertebrados bentônicos foram coletados com auxílio de uma draga tipo Petersen modificada para amostras de sedimento. O número total de indivíduos de cada táxon de macroinvertebrado foi utilizado como dados de abundância. A densidade (indivíduos/m^3) de zooplâncton foi obtida ao filtrar 600 L de água em uma rede de plâncton com abertura de malha de 70µm. Garrafas de Van Dorn e redes de fitoplâncton (15µm abertura de malha) foram utilizadas para a coleta do fitoplâncton, e os dados foram expressos em unidades individuais (células, cenóbios colônias ou filamentos) por mililitro. A assembléia de perifíton foi amostrada em pecíolos de *Eichhornia azurea* Kunth em estado maduro, visto que essa macrófita aquática foi encontrada na maioria dos locais de amostragem. Abundância foi expressa em indivíduos/cm^2. Uma descrição detalhada dos procedimentos de amostragem para as diferentes assembléias biológicas está disponível como Material Suplementar (veja Anexo S2).

Análise de dados

Utilizamos uma técnica de partição da variância para avaliar a contribuição relativa das variáveis ambientais, espaciais e temporais na estrutura dos dados biológicos. Para isso, a porcentagem total de variação explicada por uma análise de redundância (RDA, Lambert et al. 1988) é dividida em contribuições partilhadas e únicas do conjunto de preditores ambientais, espaciais e temporais (Bocard et al. 1992). Essa análise pode ser entendida como uma regressão múltipla, mas com múltiplas variáveis respostas (espécies de uma determinada assembléia). Como matrizes respostas, utilizamos os dados de abundância para todas as assembléias biológicas, exceto macrófitas aquáticas. Os dados de peixes foram divididos em matrizes de peixes migradores e sedentários (Graça e Pavanelli 2007), para testar a hipótese que organismos com maior capacidade de dispersão apresentam menor efeito das variáveis espaciais.

A matriz de dados ambientais foi composta pelas seguintes variáveis: temperatura da água (°C); oxigênio dissolvido ($mg.L^{-1}$); transparência da água (m); pH; condutividade elétrica ($\mu S.cm^{-1}$); turbidez (NTU); concentração de nitrogênio total ($\mu g.L^{-1}$); concentração de fósforo total ($\mu g.L^{-1}$); clorofila-*a* ($\mu g.L^{-1}$), matéria em suspensão total ($mg.L^{-1}$), e matéria orgânica dissolvida ($mg.L^{-1}$). Clorofila-*a* não foi utilizada como variável explanatória das assembléias de fitoplâncton e perifíton visto que essas variáveis são claramente dependentes. Procedimentos detalhados da amostragem dos fatores ambientais estão descrito no material suplementar (veja Anexo S2). Uma matriz de correlação entre as variáveis ambientais foi utilizada para detectar multicolinearidade entre as variáveis explanatórias. No caso de altos valores de correlação (*r* Pearson > 0.5), somente uma variável foi utilizada para compor a matriz exploratória. As variáveis ambientais foram log-transformadas (exceto o pH) e padronizadas.

Utilizamos diferentes estratégias para gerar preditores espaciais. Primeiramente, estimamos variáveis substitutas da dispersão "overland" (ou seja, sem seguir o curso d'água) ao utilizar uma matriz (**D**) composta por distâncias Euclidianas entre os ambientes. Após isso, calculamos as distâncias "watercourse" (via curso d'água) (**W**) entre os ambientes. Nesse caso, quatro diferentes rotas de dispersão foram consideradas em relação o fluxo e os canais laterais da planície de inundação do Alto rio Paraná (veja Anexo S7). Acreditamos que essas rotas representam possíveis vias de dispersão "watercourse" de organismos entre lagoas, devido ao fluxo unidirecional dos rios principais e do fluxo bidirecional dos canais laterais. Dessa forma, quatro matrizes de distância "watercourse" e uma matriz de distância "overland" foram construídas para gerar os preditores espaciais.

As variáveis espaciais (também conhecidas como filtros espaciais), baseadas nas matrizes de distância descritas acima, foram criadas utilizando auto-análises (Borcard e Legendre 2002, Diniz-Filho e Bini 2005, Dray et al. 2006, Griffith e Peres-Neto 2006). Nesse caso, os autovetores extraídos das matrizes de distâncias são utilizados como variáveis espaciais. Dessa forma, as variáveis espaciais representam diferentes proposições de como as unidades amostrais estão relacionadas espacialmente. Baixos autovalores (em módulo) indicam baixa autocorrelação espacial, e baixo poder de definir estruturas espaciais (Griffith e Peres-Neto 2006, Dray et al. 2006). Portanto, nós

selecionamos somente os autovetores com coeficientes *I* de Moran maiores que 0.1 supondo que os autovetores selecionados dessa forma corresponderiam às estruturas espaciais que potencialmente podem ser utilizadas como variáveis substitutas da dispersão (veja também Nabout et al. 2009). As análises espaciais foram realizadas no programa gratuito "Spatial Analysis in Macroecology v. 3.0" (SAM, Rangel et al. 2006).

A matriz temporal foi composta por três variáveis indicando diferentes aspectos da dinâmica temporal que potencialmente afetam os organismos. A primeira variável expressa a variação entre os períodos de amostragem, utilizando a data Juliana (expressa em número total de dias desde 1 de Janeiro de 1900). Nesse caso, representaríamos, por exemplo, uma alteração contínua da comunidade como resultado de sucessão ecológica. A segunda variável representou a periodicidade diária, utilizando o tempo total desde o início do nascer do sol até o fim do por do sol de cada dia de amostragem. Essa variável também é relacionada com a sazonalidade dos períodos de amostragem (períodos na mesma estação têm durações do dia parecidas). A terceira variável foi relacionada com a variação hidrológica, e utilizamos o número de dias desde o último evento de cheia como variável. As variáveis temporais foram padronizadas subtraindo cada valor pela média e dividindo pelo desvio padrão.

Ao utilizar três matrizes exploratórias (ambiental, espacial e temporal), oito componentes foram gerados (Anderson e Gribble 1998):

(1) Ambiental puro, E: Variação ambiental que não é espacialmente e temporalmente estruturada. Essa é a fração da variação que pode ser explicada por descritores ambientais independentemente de qualquer estrutura espacial ou temporal.

(2) Espacial puro, S: variação explicada pelas variáveis espaciais que é independente de qualquer variável ambiental ou temporal incluída na análise.

(3) Temporal puro, T: variação explicada pelas variáveis temporais que independe de qualquer variável ambiental ou espacial incluída na análise.

(4) Componente ambiental espacialmente estruturado, SE: Como descrito em Borcard et al. (1992), esse componente é a sobreposição não temporal da variação explicada pelas variáveis espaciais e ambientais. Isso pode ser considerado como o componente do ambiente espacialmente estruturado e/ou o componente do espaço ligado a uma ou mais variáveis ambientais.

(5) Componente ambiental temporalmente estruturado, TE: Similarmente ao componente (4), esse componente é a fração não espacial da variação explicada por variáveis ambientais temporalmente estruturadas.

(6) Componente combinado espaço/tempo, ST: A fração da variação nos dados de espécies que não é relacionada com as variáveis ambientais, mas que pode ser atribuída puramente a padrões espaços-temporais.

(7) Componente combinado espaço/tempo do ambiente, STE: A fração da variação que pode ser explicada pela ação combinada das variáveis espaciais, temporais e ambientais.

(8) Não explicada, U: Esse componente é o resíduo da análise. É a fração que não pode ser atribuída aos efeitos exclusivos das variáveis espaciais, temporais ou ambientais e tão pouco às interações entre essas variáveis.

As variações explicadas por cada componente descrito acima foram baseadas nas frações ajustadas. Frações ajustadas são melhores estimadores, pois levam em consideração o número total de preditores e o tamanho da amostra (Peres-Neto et al. 2006). A significância de cada fração foi testada utilizando testes de permutação com 999 aleatorizações (Peres-Neto et al. 2006). Nesse caso, somente os componentes (1), (2) e (3) são testáveis (Peres-Neto et al. 2006). Ademais, as diferenças entre esses componentes também foram testadas (Peres-Neto et al. 2006).

Antes das análises apresentadas acima, os dados de abundância foram log (x + 1) transformados para reduzir a influência de dados discrepantes. Transformações de Hellinger também foram utilizadas para os dados de abundância para proporcionar uma estimativa não tendenciosa da partição da variância baseada na RDA (Legendre e Gallagher 2001, Peres-Neto et al. 2006). Os resultados foram similares após a exclusão de espécies raras (aquelas que ocorreram apenas em uma unidade amostral). Portanto, as análises foram feitas somente com o conjunto total de dados. Utilizamos o programa VarCan v.1 para Matlab (Peres-Neto et al. 2006) para a partição de variância.

Resultados

As matrizes espaciais construídas a partir de distâncias seguindo os cursos de água que potencialmente representam diferentes rotas de dispersão apresentaram

resultados similares. Portanto, somente os resultados de uma das matrizes de distâncias via curso d'água estão mostrados e os resultados das outras matrizes de distâncias estão apresentados na forma de material suplementar (veja Anexo S7). As partições de variância utilizando dados de presença/ausência foram similares àquelas obtidas utilizando dados de abundância. Dessa forma, apenas os resultados para os dados de abundância estão apresentados, com exceção de macrófitas aquáticas (somente dados de presença/ausência estão disponíveis para esse grupo biológico). Os resultados considerando dados de presença/ausência dos demais grupos biológicos também estão apresentados na forma de material suplementar (veja Anexo S7).

A contribuição relativa dos fatores ambientais, espaciais e temporais variou de acordo com grupo biológico considerado (Figuras 2-6). Entretanto, o poder de predição das matrizes explanatórias foi sempre baixo e, em alguns casos, não significativo (Figuras 2-6). Isso foi especialmente observado para as variáveis temporais, que sempre explicaram uma baixa porção da variabilidade dos dados biológicos (Figuras 2-6). Além disso, os componentes partilhados foram, geralmente, pouco evidentes (Figuras 2-6).

Os efeitos das características ambientais e espaciais na composição de peixes migradores foram similares considerando as distâncias puras entre os locais de amostragem ("overland") (Figura 2). Entretanto, variáveis espaciais explicaram melhor a variabilidade dos dados de peixes migradores considerando as distâncias via curso de água (Figura 2). A estrutura das assembléias de peixes sedentários foi sempre mais bem predita por variáveis espaciais, especialmente considerando distâncias seguindo os cursos de água entre as unidades amostrais (Figura 2).

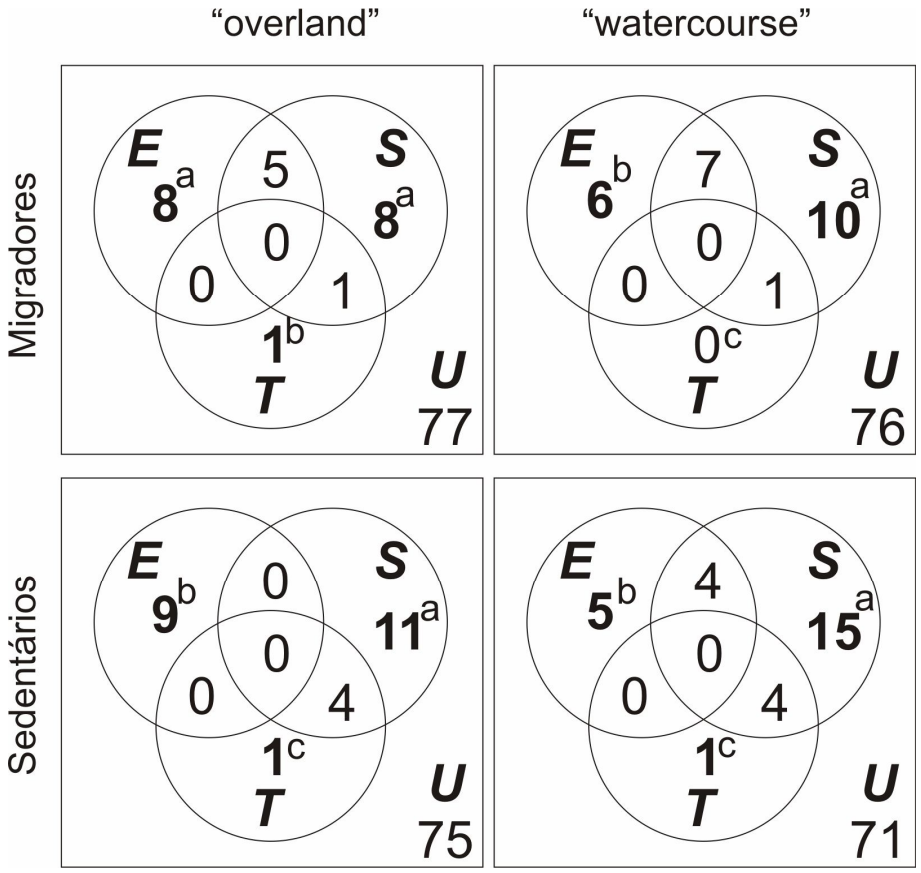

Figura 2. Contribuição relativa (% de explicação) das variáveis ambientais (E), espaciais (S), temporais (T) e dos componentes partilhados para explicar a variabilidade da distribuição da abundância de peixes migradores e sedentários, utilizando matrizes espaciais como substitutas de potenciais rotas de movimentação seguindo os cursos de água ou distâncias puras entre os pontos de amostragem ("watercourse" e "overland", respectivamente). U = componente não explicado. Zeros indicam valores menores que 0.5%. Os componentes puros (E, S e T) são testáveis e, nesse caso, valores em negrito indicam valores significativos e letras compartilhadas indicam valores estatisticamente similares.

A contribuição das características ambientais foi maior para explicar a variabilidade dos dados de macroinvertebrados bentônicos quando as distâncias puras ("overland") foram utilizadas como variáveis espaciais (Figura 3). Por outro lado, o poder de explicação das variáveis espaciais aumentou quando distâncias via curso de água foram consideradas (Figura 3). Nesse caso, as variáveis ambientais e espaciais apresentaram poder de explicação similar (Figura 3). A despeito dos conjuntos de variáveis espaciais e ambientais apresentarem poder de explicação significativa, esses pouco explicaram da variabilidade da abundância desse grupo biológico (Figura 3).

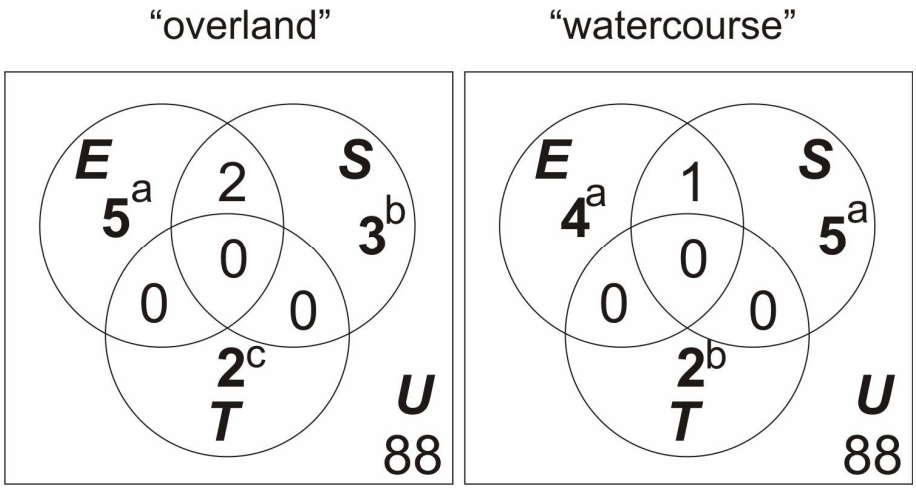

Figura 3. Contribuição relativa (% de explicação) das variáveis ambientais (E), espaciais (S) e temporais (T), e os componentes partilhados para explicar a variabilidade da distribuição da abundância de macroinvertebrados bentônicos, utilizando matrizes espaciais como substitutas de potenciais rotas de movimentação seguindo os cursos de água ou distâncias puras entre os pontos de amostragem ("watercourse" e "overland", respectivamente). U = componente não explicado. Zeros indicam valores menores que 0.5%. Os componentes puros (E, S e T) são testáveis e, nesse caso, valores em negrito indicam valores significativos e letras compartilhadas indicam valores estatisticamente similares.

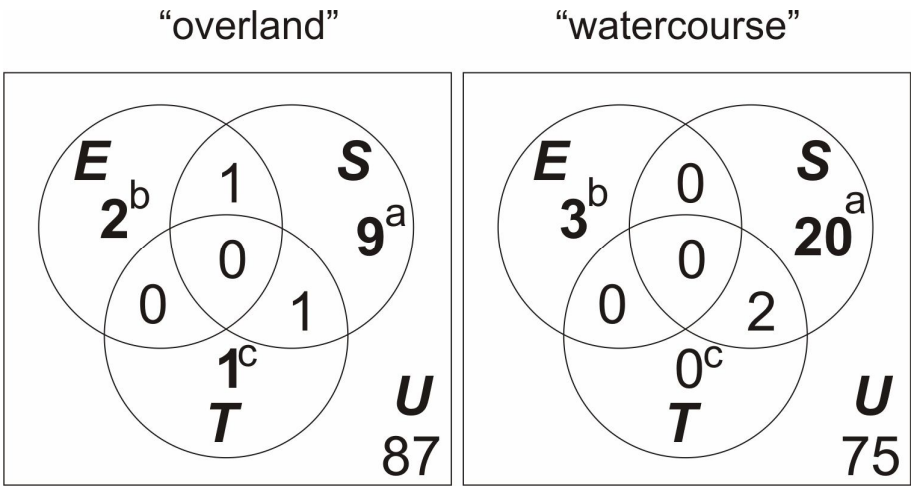

Figura 4. Contribuição relativa (% de explicação) das variáveis ambientais (E), espaciais (S) e temporais (T), e os componentes partilhados para explicar a variabilidade da composição de macrófitas aquáticas, utilizando matrizes espaciais como substitutas de potenciais rotas de movimentação seguindo os cursos de água ou distâncias puras entre os pontos de amostragem ("watercourse" e "overland", respectivamente). U = componente não explicado. Zeros indicam valores menores que 0.5%. Os componentes puros (E, S e T) são testáveis e, nesse caso, valores em negrito indicam valores significativos e letras compartilhadas indicam valores estatisticamente similares.

As variáveis espaciais foram as mais importantes para explicar a variabilidade da estrutura de composição de macrófitas aquáticas, principalmente quando as distâncias seguindo os cursos de água foram consideradas (Figura 4). Nesse caso, 20% da variabilidade dos dados biológicos foram explicadas somente pelas variáveis espaciais. Apesar de significativo, o poder de explicação das variáveis ambientais foi sempre baixo (Figura 4).

A contribuição relativa das variáveis ambientais e espaciais para explicar a variabilidade da abundância da assembléia zooplanctônica foi similar quando as distâncias "overland" foram consideradas (Figura 5). Porém, o poder de explicação das variáveis ambientais diminuiu quando as distâncias seguindo os cursos de água foram consideradas (Figura 5). Em ambos os casos, a abundância da assembléia zooplanctônica foi pouco, apesar de significativamente, explicada pelos conjuntos de variáveis ambientais e espaciais (Figura 5).

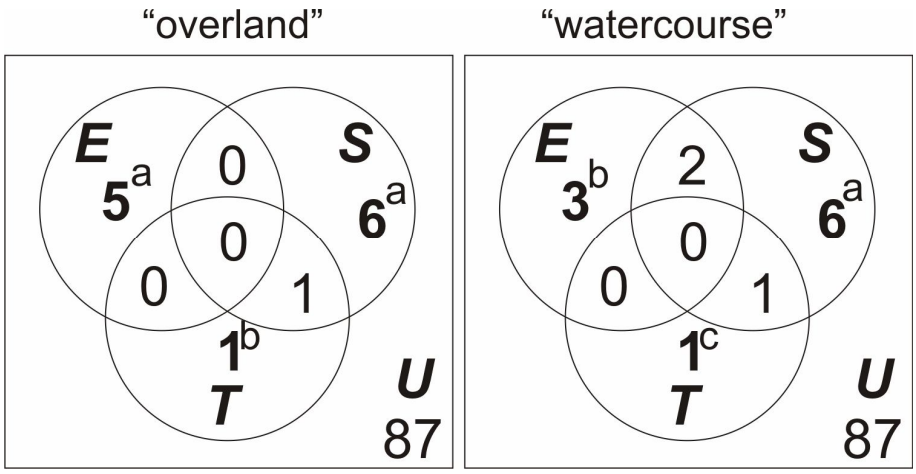

Figura 5. Contribuição relativa (% de explicação) das variáveis ambientais (E), espaciais (S) e temporais (T), e os componentes partilhados para explicar a variabilidade da distribuição da abundância de zooplâncton, utilizando matrizes espaciais como substitutas de potenciais rotas de movimentação seguindo os cursos de água ou distâncias puras entre os pontos de amostragem ("watercourse" e "overland", respectivamente). U = componente não explicado. Zeros indicam valores menores que 0.5%. Os componentes puros (E, S e T) são testáveis e, nesse caso, valores em negrito indicam valores significativos e letras compartilhadas indicam valores estatisticamente similares.

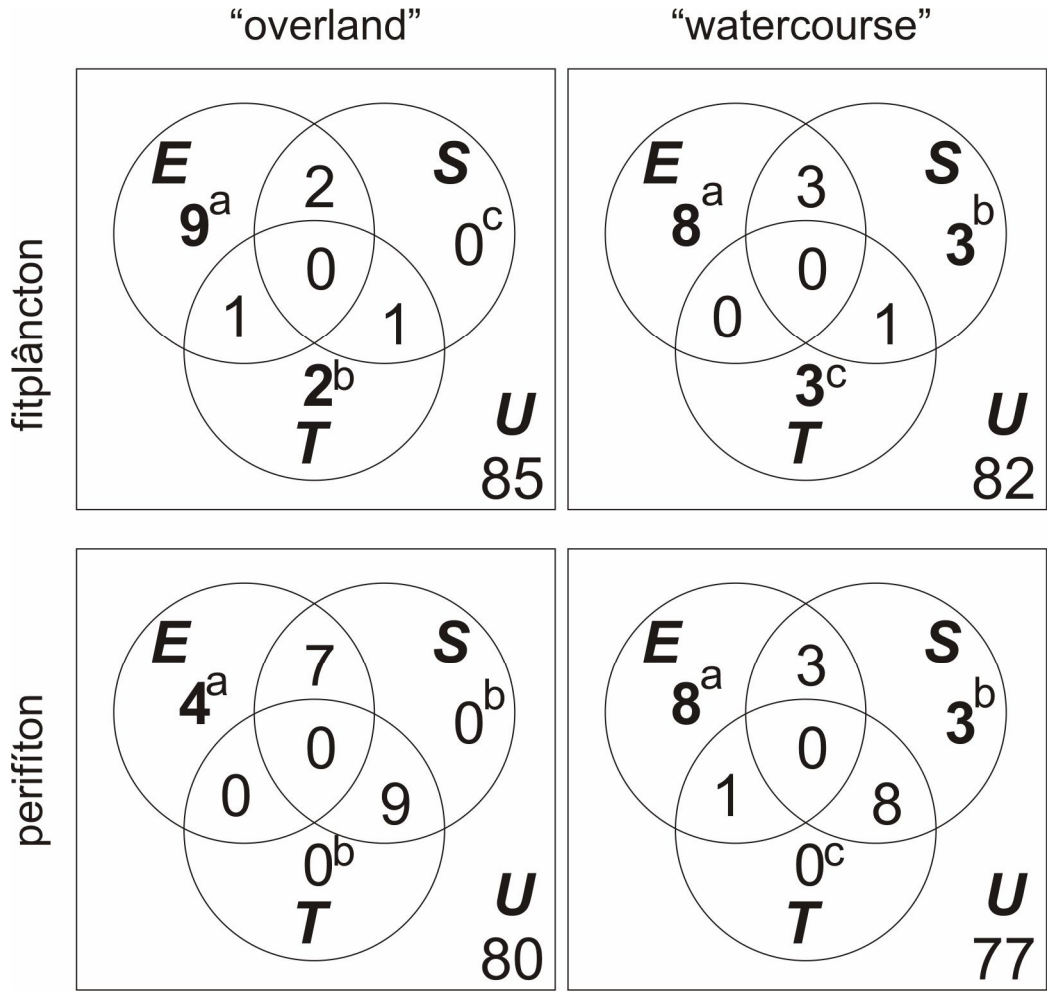

Figura 6. Contribuição relativa (% de explicação) das variáveis ambientais (E), espaciais (S) e temporais (T), e os componentes partilhados para explicar a variabilidade da distribuição da abundância de fitoplâncton e perifíton, utilizando matrizes espaciais como substitutas de potenciais rotas de movimentação seguindo os cursos de água ou distâncias puras entre os pontos de amostragem ("watercourse" e "overland", respectivamente). U = componente não explicado. Zeros indicam valores menores que 0.5%. Os componentes puros (E, S e T) são testáveis e, nesse caso, valores em negrito indicam valores significativos e letras compartilhadas indicam valores estatisticamente similares.

Os fatores ambientais foram sempre os mais importantes para explicar a variabilidade da abundância dos grupos biológicos compostos por micro-algas (fitoplâncton e perifíton) (Figuras 6). Variáveis espaciais tiveram um poder de explicação significativo, apesar de baixo, somente quando as distâncias seguindo os cursos de água foram consideradas (Figuras 6). O componente espacial temporalmente estruturado

apresentou um poder de explicação considerável para a abundância da assembléia perifítica (Figura 6).

Discussão

Determinantes da composição das comunidades são freqüentemente divididos em variáveis ambientais que refletem processos locais, e variáveis espaciais que refletem processos regionais (Ricklefs, 1987; Holyoak et al., 2005). A partir dos resultados da partição de variância dos dados biológicos, diferentes perspectivas (determinismo ambiental-"species sorting"-, modelo neutro-"neutral model"-, efeito de massa-"mass effect"-, e dinâmica de locais-"patch dynamics") são sugeridas como representações da dinâmica das metacomunidades (Cottenie 2005). Essas perspectivas são baseadas, principalmente, na importância da dispersão, do nicho e das interações biológicas na estrutura das comunidades locais (Cottenie 2005). Dessa forma, informações detalhadas sobre as habilidades competitivas e de dispersão das espécies, além dos resultados da partição da variância dos dados biológicos, são necessárias para definir qual perspectiva é mais adequada para descrever uma determinada metacomunidade (Cottenie 2005). Por exemplo, espécies especialistas tendem a ser mais determinadas por fatores locais, enquanto que espécies generalistas são afetadas principalmente por variáveis espaciais (McCauley 2007, Pandit et al. 2009). Além disso, os processos que regulam comunidades locais podem atuar simultaneamente ou apenas efemeramente, dificultando conclusões gerais sobre a validade das perspectivas das metacomunidades (Driscoll e Lindenmayer 2009). De fato, efeitos puros do ambiente e do espaço foram observados em praticamente todos os grupos biológicos. Todavia, investigações sobre organismos com diferentes capacidades de dispersão, como nesse estudo, podem auxiliar o entendimento de qual é o processo mais adequado para explicar a dinâmica de diferentes grupos (Driscoll e Lindenmayer 2009).

Em estudos com múltiplos grupos biológicos, uma expectativa clara é que organismos maiores, com menor capacidade de dispersão, serão mais afetados pela estrutura espacial dos ambientes (Beisner et al. 2006, Shurin et al. 2009). Por exemplo, locais ambientalmente similares podem apresentar distintas composições simplesmente porque não estão próximos geograficamente. Essa expectativa foi corroborada em nosso

estudo. Ademais, as variáveis espaciais geradas a partir das distâncias seguindo os cursos de água (ver Beisner et al. 2006), foram especialmente relevantes para organismos que, de fato, dispersam primordialmente via curso d'água, como peixes e plantas aquáticas (Barrat-Segretain 1996, Schmutz e Jungwirth 1999, Beisner et al. 2006, Heino et al. 2010). Isso ressalta a importância da conectividade em ambientes de planícies de inundação (Ward et al. 1999, Santos e Thomaz 2007, Fernandes et al. 2009, Thomaz et al. 2009). Por outro lado, organismos pequenos com alta capacidade de dispersão (micro-algas) foram preditos primordialmente por características ambientais e as variáveis espaciais apresentaram menor importância. Além disso, o poder preditivo das variáveis espaciais não diferiu considerando dispersão seguindo ou não o curso d'água para organismos que dispersam simultaneamente pelo curso d'água e por outros vetores (vento ou vertebrados), como zooplâncton e micro-algas (Finlay 2002, Padisák 2004, Vanschoenwinkel et al. 2008).

Entretanto, é importante salientar que o poder preditivo das matrizes explanatórias foi, em geral, baixo. Baixas frações explicadas são freqüentemente encontradas em estudos com esse propósito (Beisner et al. 2006, Heino e Mykrä 2008, Nabout et al. 2009, Heino et al., 2010). Uma das razões para tal observação pode ser relacionada com a pequena escala espacial da área de estudo. Em pequenas escalas, como apenas uma planície de inundação, os gradientes ambientais podem ser pouco evidentes (Nabout et al. 2009). Limitações de dispersão também devem contribuir para influenciar a estrutura das assembléias locais. Entretanto, mesmo em estudos em grandes escalas espaciais, a contribuição relativa de diferentes conjuntos de variáveis explanatórias tende a ser baixa (Driscoll e Lindenmayer 2009, Heino et al. 2010). Nesses casos, a principal razão para a baixa porcentagem de explicação é, em geral, atribuída a não inclusão de variáveis relevantes para a estruturação das comunidades (Beisner et al. 2006, Soininen et al., 2007). Entre essas, destacam-se outras variáveis que compõe o gradiente ambiental, como variáveis hidrológicas (Gruberts et al. 2007), variáveis que representam processos como interações biológicas em teias tróficas (Declerck et al. 2005), variáveis espaciais relacionadas com processos direcionais característicos dos sistemas hídricos (Blanchet et al. 2008), e variáveis que indicam a dinâmica temporal dos organismos (Anderson e Gribble 1998), como crescimento sazonal de plantas e migração anual de peixes.

Nesse estudo, utilizamos uma matriz explanatória composta por variáveis temporais que potencialmente indicariam as dinâmicas temporais das espécies. Na planície de inundação do Alto rio Paraná, o efeito do tempo nas dinâmicas das assembléias é dependente de características ambientais e espaciais que variam de acordo com pulsos de inundação temporalmente estruturados (Junk et al. 1989, Thomaz et al. 2007, Fernandes et al. 2009). Nesse caso, os componentes partilhados deveriam ser evidentes. Entretanto, ao contrário do esperado, os componentes temporais puros e partilhados não apresentaram um elevado poder preditivo. Um efeito substancial do componente temporal espacialmente estruturado foi observado somente para a comunidade perifítica, indicando que o tempo, possivelmente afetando a capacidade de dispersão dos organismos, é potencialmente importante para esse grupo biológico. De fato, pulsos de inundação alteram a conectividade do ambiente, e por conseqüência, a capacidade de dispersão das assembléias locais (Junk et al. 1989, Thomaz et al. 2007). Efeitos fracos de variáveis temporais também foram detectados anteriormente (Anderson e Gribble 1998). Todavia, é importante ressaltar que um pequeno intervalo de tempo foi investigado em nosso estudo e grandes eventos de inundação não foram observados durante o período estudado (Agostinho et al. 2004). Paralelamente, distúrbios são considerados importantes determinantes de metacomunidades (Urban 2004).

É amplamente conhecido que o comportamento reprodutivo afeta diretamente a estrutura espacial de composição de espécies de peixes (Agostinho et al. 2004). Isso é claro em planícies de inundação, devido à migração reprodutiva sazonal (Agostinho et al. 2004). Nós observamos que o comportamento migratório também interfere no papel relativo das variáveis ambientais e espaciais sobre a composição das assembléias. Efeitos de variáveis espaciais, que potencialmente indicam limitação por dispersão, foram mais importantes para explicar a variação da abundância de espécies sedentárias. Para os peixes migradores, características ambientais devem ser mais importantes. A inclusão de outras variáveis ambientais relevantes, como a abundância de plantas aquáticas ou outras que indicam complexidade do habitat (Agostinho et al. 2007) pode aumentar o poder preditivo de variáveis ambientais.

O baixo poder de explicação das variáveis ambientais, considerando a composição da comunidade de macroinvertebrados bentônicos, pode ser devido ao fato de que

utilizamos somente variáveis limnológicas para compor a matriz de dados ambientais. No entanto, as espécies desse grupo provavelmente são mais afetadas por características do sedimento (Gayraud e Philippe 2003) e, portanto, a inclusão dessas variáveis poderia aumentar o poder de predição das variáveis ambientais (Heino et al., 2003). Além disso, alguns grupos de macroinvertebrados são identificados somente a altos níveis de resolução taxonômica, como classe ou mesmo filo (Takeda e Fujita 2004). Investigações utilizando maior resolução taxonômica poderiam evidenciar correlações mais fortes entre os dados biológicos e os gradientes ambientais (Cushman e McGarigal, 2004). As variáveis espaciais também não foram importantes para explicar a variabilidade da assembléia de macroinvertebrados bentônicos. Isso pode ser explicado pela grande variedade funcional, em termos de capacidade de dispersão, das espécies desse grupo biológico (Shurin et al. 2009). Devido à baixa resolução taxonômica de alguns grupos de macroinvertebrados, não foi possível diferenciar corretamente grupos com diferentes capacidades de dispersão. Uma investigação detalhada utilizando as informações sobre as estratégias de dispersão dos diferentes grupos taxonômicos pode esclarecer os efeitos das variáveis espaciais na estrutura da assembléia de macroinvertebrados bentônicos (Heino et al. 2003, Van de Meutter et al. 2006, McCauley 2007). De qualquer forma, o fraco poder de explicação das variáveis espaciais pode estar relacionado com o fato de que parte da assembléia de macroinvertebrados é composta por larvas de insetos que têm alta capacidade de dispersão durante a fase adulta (Van de Meutter et al. 2006). De fato, as diferenças nas capacidades de dispersão parecem ser mais importantes do que características de conexão entre os ambientes para macroinvertebrados aquáticos (Van de Meutter et al. 2006).

A estratégia de dispersão por propágulos vegetativos de macrófitas aquáticas deve explicar porque as variáveis espaciais foram substancialmente mais importantes que as variáveis ambientais para explicar a variação da composição de espécies desse grupo. Devido a configuração anastomosada de planícies de inundação (Barrat-Segretain 1996, Thomaz et al. 2004), dispersores passivos que utilizam exclusivamente o curso d'água tem pouca probabilidade de alcançar ambientes distantes. Isso potencialmente representa uma limitação na dispersão das macrófitas nesses ecossitemas. Ainda, propágulos que alcançam ambientes longínquos provavelmente encontram locais já colonizados, e efeitos

“monopolizadores” e de “prioridade” podem contribuir para a diferença espacial das comunidades (De Meester et al. 2002, Vanschoenwinkel et al. 2007). Por exemplo, é conhecido que certas espécies de plantas aquáticas e anfíbias, quando estabelecidas e dominantes, dificultam a colonização de propágulos viáveis provenientes de outras localidades (van Geest et al. 2005, Michelan et al. 2010). Isso é especialmente observado em planícies de inundação nos quais distúrbios que promovem a diversidade local, como pulsos de inundação, são controlados (van Geest et al. 2005). Visto que há controle hidrológico na planície de inundação do Alto rio Paraná, poucos efeitos de homogeneização promovidos pelos pulsos de inundação (Thomaz et al. 2007) contribuem para redução da estrutura espacial das assembléias de macrófitas aquáticas (Padial et al. 2009, Thomaz et al. 2009).

Variáveis espaciais foram consideradas importantes para organismos zooplanctônicos em lagos do Canadá (Beisner et al. 2006). Em nosso estudo, o baixo poder de explicação das matrizes espaciais é possivelmente devido à pequena extensão da área de estudo e a alta conectividade dos ambientes. De fato, diferentes vetores são responsáveis pela dispersão de organismos zooplanctônicos (Michels et al. 2001, Cohen e Shurin 2003, Havel e Shurin 2004, Vanschoenwinkel et al. 2008) e, conseqüentemente, variáveis espaciais podem ser pouco importantes para explicar a variabilidade dos dados biológicos em ambientes altamente conectados (Forbes e Chase 2002, Cohen e Shurin 2003, Cottenie et al. 2003, Havel e Shurin 2004). Nesses ambientes, as variáveis ambientais seriam mais importantes (Jenkins 1995, Jenkins e Underwood 1998, Cohen e Shurin 2003, Cottenie et al. 2003). Porém, o baixo poder preditivo das variáveis ambientais em nosso estudo também deve ser devido à baixa heterogeneidade ambiental. Além disso, variáveis relacionadas com interações biológicas, como a abundância de peixes zooplanctívoros e algas palatáveis, ou a disponibilidade de refúgios contra predadores, podem aumentar o poder preditivo de processos locais na estruturação desse grupo biológico (Cottenie e De Meester 2004).

Estudos anteriores explicaram fracamente, ou mesmo não conseguiram explicar, a variabilidade dos dados de fitoplâncton a partir de variáveis ambientais (Beisner et al. 2006, Nabout et al. 2009). Além da baixa extensão dos gradientes ambientais, outros fatores também podem ser responsáveis para tal conclusão, como variáveis não

mensuradas relacionadas a outros processos importantes que controlam as assembléias de micro-algas (Beisner et al. 2006, Nabout et al. 2009). Por exemplo, a porcentagem de cobertura de espécies de plantas aquáticas e a densidade de *Daphnia* foram consideradas variáveis importantes para explicar a composição fitoplanctônica em um estudo realizado em lagos altamente conectados na Bélgica (Vanormelingen et al. 2008). Além disso, variações importantes nos fatores ambientais, como distúrbios, não são necessariamente detectadas no momento da coleta dos dados biológicos (Beisner et al. 2006, Nabout et al. 2009). Assim como variáveis ambientais, o baixo poder preditivo das variáveis espaciais é um padrão freqüentemente encontrado em estudos que envolvem as assembléias de fitoplâncton (Nabout et al. 2009, Beisner et al., 2006). Para esses pequenos organismos a limitação por dispersão tem sido considerada como virtualmente inexistente (Finlay 2002, Shurin et al. 2009).

De maneira geral, não encontramos variáveis explanatórias com elevado poder de predição. Contrariamente a nossa expectativa inicial, as variáveis utilizadas para representar a dinâmica temporal pouco explicaram da variação dos dados biológicos. Entretanto, nossos resultados suportam as expectativas que organismos com menor capacidade de dispersão (peixes sedentários e plantas aquáticas) são mais correlacionados com variáveis espaciais e que assembléias compostas por táxons com elevada capacidade de dispersão (micro-algas) devem ser determinadas primordialmente por filtros ambientais (Beisner et al. 2006). Isso foi evidenciado tanto utilizando dados de abundância como de presença/ausência, indicando que as respostas das comunidades aos gradientes ambientais e espaciais não são dependentes da resolução numérica (Heino et al. 2010). Entretanto, investigações futuras incluindo outras variáveis que supostamente são importantes para diferentes organismos (como cobertura vegetal para peixes, zooplâncton e micro-algas; e características do sedimento para macroinvertebrados) devem melhor elucidar os efeito de processos locais e regionais na dinâmica das comunidades locais em ecossistemas dinâmicos como planícies de inundação.

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CONCLUSÕES GERAIS[5]

A biodiversidade total é desconhecida na maioria dos ecossistemas (Whittaker et al. 2005), particularmente nos trópicos (Ferrier 2002). Dessa forma, esforços de conservação e programas de biomonitoramentos buscam estratégias para maximizar a representatividade da biodiversidade do grupo alvo, mesmo sem o completo conhecimento acerca de sua composição total de espécies (Sheil 2001). Entre as estratégias mais investigadas estão a busca de grupos substitutos, que representariam padrões de variação da riqueza de espécies e da diversidade beta de grupos não investigados (Allen et al. 1999) e a classificação dos ecossistemas em unidades discretas que são utilizadas para selecionar áreas prioritárias de biomonitoramento e/ou conservação (Heino et al. 2002). Nesse sentido, importantes implicações para a conservação de planícies de inundação foram alcançadas nessa tese. Ao encontrar padrões de concordância entre assembléias fracos e temporalmente variáveis, o uso de grupos substitutos em planícies de inundação pode ser considerado uma estratégia pouco confiável para subsidiar esforços de conservação. Portanto, grupos alvos devem ser focados individualmente em biomonitoramentos ou em esforços de conservação, sem o objetivo extrapolar os resultados para os outros grupos biológicos.

Por outro lado, a regionalização da planície de inundação do Alto rio Paraná em subsistemas distintos é uma estratégia promissora para representar a variabilidade das assembléias aquáticas. Nesse caso, biomonitoramentos, como os já realizados nessa planície de inundação (veja Thomaz et al. 2004), devem considerar a variabilidade física de ambientes associados a diferentes subsistemas lóticos com o objetivo de maximizar a representação da biota. Entretanto, diferentes grupos biológicos apresentam fontes de variabilidade idiossincráticas em escalas espaciais particulares (Heino et al. 2004), e a definição das principais escalas de variação de cada grupo biológico na planície de inundação do Alto rio Paraná merece ser devidamente investigada em futuros estudos.

De fato, encontramos diferentes respostas dos grupos biológicos aos gradientes ambientais. Por outro lado, as variáveis temporais pouco explicaram dos padrões de diversidade beta das diferentes assembléias aquáticas, provavelmente devido à ausência, durante o período estudado, de grandes eventos de inundação, que são considerados

[5] Formatado de acordo com as normas da revista “Ecography”.

primordiais em sistemas alagáveis (Junk et al. 1989). O controle hidrológico pelos reservatórios na bacia do rio Paraná foi o principal responsável para falta de eventos de inundação no período estudado (Agostinho et al. 2004). Apesar de também encontrarmos fracos poderes de explicação das variáveis ambientais e espaciais, informações acerca da capacidade de dispersão dos organismos foram essenciais para entender o papel relativo de fatores ambientais, espaciais e temporais na estrutura das comunidades locais (veja também Beisner et al. 2006, Driscoll e Lindenmayer 2009). De modo geral, nossos resultados ressaltam a importância da conectividade e de processos neutros para determinar a estrutura de assembléias de espécies que dispersam primordialmente via curso d'água, como peixes e plantas aquáticas. Para organismos com alta capacidade de dispersão, mecanismos relacionados com o nicho das espécies são provavelmente os mais importantes para determinar estruturar as assembléias locais. A inclusão de outras variáveis particularmente relevantes para cada grupo biológico, e uma investigação em escalas espaciais mais amplas, pode revelar mais fortes correlações entre a estrutura das assembléias e os gradientes ambientais.

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ANEXOS[6]

Appendix S1 (Anexo S1). Available cross-taxa comparisons:

Table 1. List of available cross-taxa comparisons which were for concordance analyses.

Cross-taxon Comparison	Year		Sampling sites
	2000	2001	
Fish - Macrophytes		✓	20
Fish - Benthic Macroinvertebrates	✓	✓	20
Fish - Zooplankton	✓	✓	20
Fish - Phytoplankton	✓	✓	19
Fish - Periphyton	✓		19
Macrophytes - Benthic Macroinvertebrates		✓	36
Macrophytes - Zooplankton		✓	36
Macrophytes - Phytoplankton		✓	30
Benthic Macroinvertebrates - Zooplankton	✓	✓	36
Benthic Macroinvertebrates - Phytoplankton	✓	✓	30
Benthic Macroinvertebrates - Periphyton	✓		32
Zooplankton - Phytoplankton	✓	✓	30
Zooplankton - Periphyton	✓		32
Phytoplankton - Periphyton	✓		32

[6] Formatado de acordo com as normas da revista “Ecography”.

Appendix S2 (Anexo S2). Detailed description of sampling data:

Fish community

Fish were sampled through experimental fishery using gillnets with 11 different mesh sizes (2.4; 3; 4; 5; 6; 7; 8; 10; 12; 14 and 16 cm mesh) exposed for 24 h with samplings at 08:00 am, 04:00 pm and 10:00 pm. Abundance was expressed in CPUE (individuals×24 hours/1000m^2gillnet). Specimens were counted and taxonomically identified in the field. When identification was not possible, they were labeled and preserved in formaldehyde solution 4% for further identification.

Aquatic macrophyte community

In each lake, aquatic macrophytes species were recorded from a boat moving at low and constant velocity along the whole margin. Submersed plants were sampled from the boat with a grapnel during 10 minutes. Only presence/absence data are available for this community. Taxonomic identification followed the specialized literature (Cook 1990, Velasquez 1994, Pott and Pott 2000, Lorenzi 2000).

Benthic macroinvertebrate community

In each sampling lake, nine sediments samples (three in each margin and three in the middle of each lake) were collected to sample benthic macroinvertebrates. For that, we used a Petersen's grab modified for benthic samples. Sediments were washed in nets of different mesh size (2.0 mm, 1 mm, and 0.2 mm mesh). Organisms retained in the nets were immediately transferred to plastic bottles with formaldehyde solution 4% for further identification to the lowest taxonomic level possible. Total number of individuals of each taxon was used as abundance data.

Zooplankton community

Zooplankton samples were obtained by pumping 600 L of water over a 70µm mesh net. Sampled material was transferred to labeled polyethylene bottles with formaldehyde 4% cold solution and calcium carbonate buffer for further identification. Abundance was calculated by counting the individuals in a Sedgwick-Rafter in three sub-sampling taken

with a Stempell pipette. Final densities were expressed as individuals/m^3. Taxonomic identification followed the specialized literature (Deflandre 1928, 1929, Gauthier-Lièvre and Thomas 1958, Koste 1972, 1978, Paggi 1973 a,b, 1979, 1995, Vucetich 1973, Smirnov 1974, 1992, Ogden and Hedley 1980, Korinek 1981, Sendacz and Kubo 1982, Dussart and Frutos 1985, Reid 1985, Matsumura-Tundisi 1986, Korovinsky 1992, Segers 1995, Velho and Lansac-Tôha 1996, Velho et al. 1996).

Phytoplankton community

Phytoplankton samples were taken both in littoral and limnetic zones. In limnetic zones, samples were taken at in surface, at the central region of the lake, whereas in littoral zone, samples were taken near macrophyte stands. Van Dorn samplers were used, and samples were transferred to amber bottles with acetic Lugol solution 5% for further identification. In order to facilitate taxonomic classification, concentrated samplings with phytoplankton nets (15µm mesh) were also carried and preserved in Transeau solution (Bicudo and Bicudo 1970). Taxa were identified using the following literature: Komarék and Fott (1983); Tell and Conforti (1986); and Krammer and Lange-Bertalot (1986, 1988, 1991). Fitoplankton abundance was estimated in inverted microscope Carl Zeiss (Axiovert 135), after sedimentation in Utermöhl chambers (Utermöhl 1958), following APHA methods (APHA 1985). Results were expressed in individuals (cells, cenobians, colonies or filaments) per milliliter.

Periphyton community

Periphyton community were sampled from petioles of *Eichhornia azurea* Kunth in the mature stage, as this macrophyte was best represented in most environments on the Upper Paraná River floodplain. For that, we sampled three petioles of *E. azurea* per lake, each one from a different macrophyte stand randomly chosen along the lake. The periphyton removed from the substratum was fixed and preserved in 0.5% acetic Lugol. Organisms were quantified using a Carl Zeiss (Axiovert 135) inverted microscope, after sedimentation in Utermöhl chambers (Utermöhl 1958), following APHA methods (APHA 1985). Abundance was expressed in individuals/cm^2. Taxonomic identification

followed specialized literature (Bourrelly 1975, 1981, Prescott 1982, Komárek and Fott 1983)

Environmental variables

The following limnological variables were obtained from each lake: depth (m); water temperature (°C, using a thermometer attached to a termistor); dissolved oxygen (mg/L), using a YSI portable digital oxymeter; water transparency (m), using a Secchi disk of 0.30 m diameter; pH and electric conductivity (μS/cm), through portable digital potentiometers; total alkalinity (mEq/L) estimated through the "Gran" method (Carmouze 1994), using 0.01N H_2SO_4; turbidity (NTU), measured using a LaMote-2008© portable digital turbidimeter; total nitrogen concentration (μg/L) following Zagatto et al. (1982); total phosphorus concentration (μg/L) following Mackereth et al. (1978); chlorophyll-a (μg/L), using an aliquot of water filtered over Whatman GF/C filters (Golterman et al. 1978); total suspended matter (mg/L), using another aliquot of water filtered in filters previously combusted in muffle furnace at 550°C for 4 h and; dissolved organic matter (mg/L), estimated on filtered water in a Shimadzu© TOC 5000 Carbon Analyzer.

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Appendix S3 (Anexo S3). Traits of taxa and expectations about cross-taxon concordance:

Considering the behavior and biological interactions of biota in floodplain lakes, different concordance patterns are expected between groups of each assemblage. For that, we used information on textbooks and regional articles about the biology of groups and species of the assemblages used here. We evaluated the concordance level only using Mantel test, and in each sampling period separately. The cross-taxon comparison considered the traits were:

(i) Invertivorous fish with benthic macroinvertebrates, because benthic macroinvertebrates compose the diet of these fish (Hahn et al. 2004, Graça and Pavanelli 2007).

(ii) Zooplanktivorous fish with microcrustaceans (cladocerans and copepods), because microcrustaceans are the main prey species for zooplanktivorous fish (Hahn et al. 2004, Graça e Pavanelli 2007). There is only one truly zooplanktivorous fish species in the Upper Paraná River floodplain, the *Hypophtalmus edentatus* (Hahn et al. 2004). However, other fish species can use planktonic organisms as an accessory food resource and/or microcrustaceans that are usually found associated with macrophytes. We included these fish species as zooplanktivorous for the analysis.

(iii) Detritivorous fish with macrophytes that mostly contribute to the detritus. Macrophytes are surely the main source of detritus in floodplains (Wetzel 2001). We exclude macrophyte species in which individuals are very small, with high label content and that decompose in few days (such as *Azzolla* sp. and *Utricularia gibba*), because they poorly contribute to the detritus and, thus probably poorly contribute to detritivorous fish diet. We used information about each macrophyte species to exclude small macrophytes that quickly decompose (Pott e Pott 2000, Evangelista et al. 2009).

(iv) Benthic macroinvertebrates with macrophytes that mostly contribute to the detritus. Idem (iii).

(v) Fish species that inhabit littoral habitats with different life forms of macrophytes. The rationale behind is that different life forms of macrophytes can differently affect assemblage structure of organisms (e.g. Meerhoff et al. 2003) We used

four life forms of macrophytes (see Pott e Pott 2000): Emergent macrophytes (rooted in the sediment and with above-water leaves); free-floating macrophytes (most of the plant is at or near the surface of the water, and roots, if present, hang free in the water and are not anchored to the bottom); submersed macrophytes (entire plant is below the surface of the water); rooted-floating (macrophytes rooted in the sediment with floating leaves).

(vi) Zooplankton species that inhabit littoral habitats with different life forms of macrophytes. Idem (v).

(vii) Zooplankton of different body sizes with phytoplankton of different body size. Small species of zooplankton (e.g., rotifers and testate amoeba) are not able to feed on large species of phytoplankton (Burns 1968, Cyr e Curtis 1999), and thus may more dependent on the assemblage structure of phytoplankton. Thus, small zooplankton and phytoplankton may present higher levels of concordance. Large zooplankton species (cladocerans and copepods) are probably opportunistic, and can access a broader size spectrum of phytoplankton (Burns 1968, Cyr e Curtis 1999).

(viii) Zooplankton species that inhabit littoral habitats and periphyton. These zooplankton species may use periphyton as an alternative food resource (Siehoff et al. 2009).

Appendix S4 (Anexo S4). Results of cross-taxon concordance considering different statistical approaches and presence/absence data:

Table 1. Mantel correlation coefficients for comparisons between distance matrices of community data (presence/absence) and distance matrices of environmental variables (EV) or geographical positions (GD) of sampling sites for each sampling periods. Bold numbers indicate significant values. Dashes indicate no data available.

Community	February 2000		August 2000		February 2001		August 2001	
	EV	GD	EV	GD	EV	GD	EV	GD
Fish	**0.21**	**0.17**	0.06	**0.17**	0.02	-0.02	0.01	0.09
Macrophytes	–	–	–	–	0.06	0.09	-0.01	**0.13**
Benthic Macr.	-0.11	**0.10**	-0.02	**0.24**	-0.05	0.07	**0.29**	0.02
Zooplankton	0.12	-0.01	0.05	0.04	0.02	0.02	-0.10	0.01
Phytoplankton	**0.18**	**0.20**	**0.42**	**0.2**	**0.27**	**0.31**	0.09	0.10
Periphyton	**0.22**	0.04	-0.05	0.02	–	–	–	–

Table 2. Correlation coefficients derived from PROTEST* (*rP*) and Mantel (*rM*) analyses Mantel for each sampling period and cross-taxon comparison (Ab = Abundance data; Pa = Presence/absence data). Bold numbers indicate significant values. Dashes indicate no available cross-taxon comparison.

Cross-taxon comparison		February 2000		August 2000		February 2001		August 2001	
		rM	*rP*	*rM*	*rP*	*rM*	*rP*	*rM*	*rP*
Fish-B. Macroinvertebrates	Ab	**0.36**	**0.45**	0.04	0.20	-0.01	0.29	-0.03	0.23
	Pa	0.04	0.32	-0.11	0.23	0.03	0.25	-0.18	0.21
Fish-Macrophytes	Ab	-	-	-	-	0.09	0.15	**0.45**	**0.56**
	Pa	-	-	-	-	-0.01	0.39	**0.41**	**0.47**
Fish-Periphyton	Ab	**0.25**	**0.37**	0.10	0.22	-	-	-	-
	Pa	**0.40**	**0.45**	-0.08	0.40	-	-	-	-
Fish-Phytoplankton	Ab	**0.22**	**0.58**	0.06	0.28	0.02	0.22	-0.05	0.22
	Pa	**0.23**	**0.44**	-0.01	0.30	0.13	0.21	**0.28**	**0.44**
Fish-Zooplankton	Ab	**0.31**	**0.49**	0.15	0.35	0.10	0.18	0.01	0.34
	Pa	**0.27**	**0.43**	**0.27**	**0.52**	-0.01	0.19	0.08	0.21
B. Macroinvertebrates-Macrophytes	Ab	-	-	-	-	0.01	0.15	**0.14**	**0.37**
	Pa	-	-	-	-	0.01	0.15	**0.14**	**0.42**
B. Macroinvertebrates-Periphyton	Ab	0.09	0.25	0.11	0.29	-	-	-	-
	Pa	0.01	0.26	0.06	0.33	-	-	-	-
B. Macroinvertebrates-Phytoplankton	Ab	0.01	0.19	-0.02	0.30	**0.13**	**0.50**	**0.13**	**0.40**
	Pa	0.07	0.17	0.07	0.2	**0.22**	**0.41**	0.01	0.16
B. Macroinvertebrates-Zooplankton	Ab	-0.04	0.11	0.02	0.20	**0.12**	**0.39**	**0.17**	**0.36**
	Pa	0.08	0.25	-0.06	0.20	**0.13**	**0.31**	-0.10	0.07
Macrophytes-Phytoplankton	Ab	-	-	-	-	**0.15**	**0.44**	**0.21**	**0.32**
	Pa	-	-	-	-	**0.13**	**0.46**	**0.33**	**0.36**
Macrophytes-Zooplankton	Ab	-	-	-	-	**0.21**	**0.35**	**0.26**	**0.30**
	Pa	-	-	-	-	**0.14**	**0.30**	**0.28**	**0.39**
Periphyton-Phytoplankton	Ab	**0.13**	**0.36**	0.02	0.30	-	-	-	-
	Pa	**0.17**	**0.36**	0.07	0.32	-	-	-	-
Periphyton-Zooplankton	Ab	**0.14**	**0.38**	-0.02	0.12	-	-	-	-
	Pa	-0.13	0.31	-0.02	0.13	-	-	-	-
Phytoplankton-Zooplankton	Ab	0.02	0.18	0.09	0.13	**0.21**	**0.33**	**0.31**	**0.37**
	Pa	**0.14**	**0.36**	0.01	0.29	**0.26**	**0.36**	**0.38**	**0.49**

***** In PROTEST, the ordination scores derived from the PCoA which was applied to each assemblage, were scaled and rotated in order to find an optimal superimposition that maximizes their fit (see Peres-Neto and Jackson 2001).

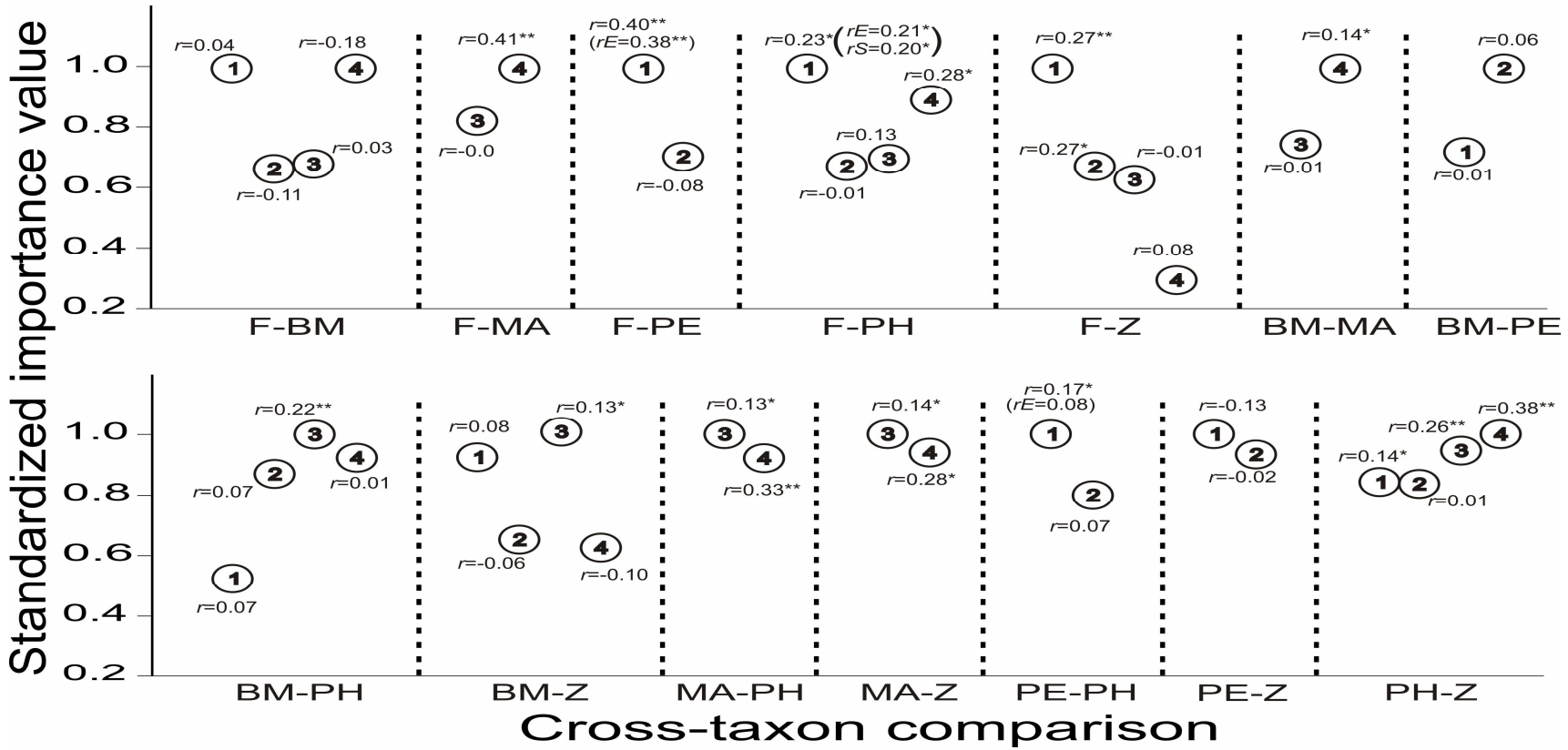

Figure 2. Importance values of samplings periods, standardized to the most important sampling period, to the common assemblage structure of cross-taxon comparisons using presence/absence data. F = Fish; BM = Benthic Macroinvertebrates; MA = Macrophytes; PE = Periphyton; PH = Phytoplankton; Z = Zooplankton. Circled numbers indicate sampling periods: (1) February of 2000; (2) August 2000; (3) February 2001 and; (4) August 2001. For each sampling period, the Mantel's correlations (*r*) between two dissimilarity matrices under comparsion are shown. Partial Mantel tests were done for pairs of assemblages significatively correlated to each other and that were simultaneously correlated with the environmental and geographical distances among sampling sites (see Table 2). In these cases, partial Mantel correlation coefficients controlling for the effects of environmental and/or geographical distances (*rE* and *rS*, respectively) are shown within parenthesis. Significance levels were based on 10,000 random permutations (**P* < 0.05; ***P* < 0.01).

Appendix S5 (Anexo S5). Abiotic differences among sub-systems:

According to Thomaz et al. (2004), the Upper Paraná River floodplain is clearly divided into three different sub-systems: (i) the Paraná River sub-system; (ii) the Baía River sub-system; and (iii) the Ivinheima River sub-system. Long-term data have shown that the Paraná River sub-system has high water transparency, high water flow, low nutrient inputs and frequent flood pulses of low magnitude (Thomaz et al. 2004). On the other hand, the Baía River sub-system has relatively low water flow, high nitrate concentrations, low pH values and high dissolved carbon concentrations due to the presence of humic compounds (Thomaz et al. 2004). Finally, the Ivinheima River sub-system has intermediate water flow, high water turbidity and high phosphorus concentrations (Thomaz et al. 2004). Mean values of environmental variables during February and August of 2000 and 2001 also showed these trends (Table 1).

To illustrate the differences among sub-systems and sampling periods, we used a cluster analysis (Mardia et al. 1979) with Euclidean distances using standardized means of 12 environmental variables sampled in each period. We used the following environmental variables: water temperature (°C), using a thermometer attached to a thermistor; dissolved oxygen ($mg.L^{-1}$), using a YSI portable digital oxymeter; water transparency (m), using a Secchi disk of 0.30 m diameter; pH and electric conductivity ($\mu S.cm^{-1}$), through portable digital potentiometers; total alkalinity ($mEq.L^{-1}$), estimated through the "Gran" method (Carmouze 1994) using 0.01 N H_2SO_4; turbidity (NTU), measured using a LaMote-2008© portable digital turbidimeter; total nitrogen concentration ($\mu g.L^{-1}$) following Zagatto et al. (1982); total phosphorus concentration ($\mu g.L^{-1}$) following Mackereth et al. (1978); chlorophyll-a ($\mu g.L^{-1}$), using an aliquot of water filtered over Whatman GF/C filters (Golterman et al. 1978); total suspended matter ($mg.L^{-1}$), using another aliquot of water filtered in filters previously combusted in a muffle furnace at 550°C for 4 h; and dissolved organic matter ($mg.L^{-1}$), estimated on filtered water in a Shimadzu© TOC 5000 Carbon Analyzer. The differences among sub-systems and sampling periods were clear during 2000 and 2001 (Figure 1). It is also interesting to note that the environmental variables showed seasonality; i.e., a given sub-system over time is more similar in the same month (Figure 1).

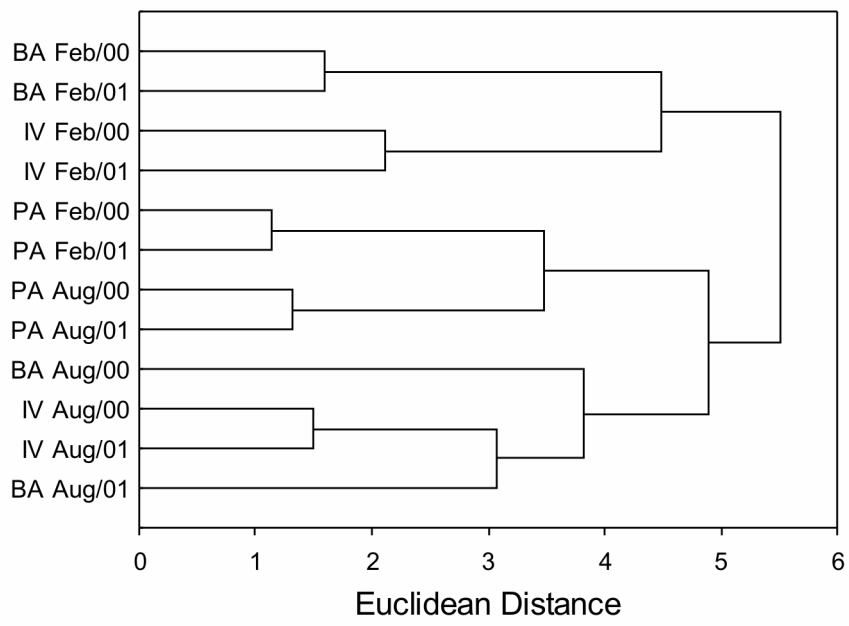

Figure 1. Classification patterns (by UPGMA clustering) of the sub-systems and sampling periods. Twelve environmental variables (means from sites within sub-systems - see Supplementary Table 1) were used to estimate the distance matrix (standardized Euclidean distance). Shown are the sub-systems and sampling periods. BA = Baía River sub-system; IV = Ivinheima River sub-system; PA = Paraná River sub-system. Feb/00 = February of 2000; Aug/00 = August of 2000; Feb/01 = February of 2001; Aug/01 = August of 2001.

Table 1. Mean values (and their standard errors in parentheses) of the 12 environmental variables sampled in lakes associated with the three different sub-systems of the Upper Paraná River floodplain, given separately for each sampling period. BA = Baía River sub-system; IV = Ivinheima River sub-system; PA = Paraná River sub-system.

	February 2000			**August 2000**			**February 2001**			**August 2001**		
	BA	IV	PA	BA	IV	PA	BA	IV	PA	BA	IV	PA
Temperature	27.5 (0.5)	26 (0.3)	29.0 (0.5)	18.8 (0.2)	18.0 (0.2)	20.4 (0.2)	26.8 (0.3)	26.1 (0.2)	29.1 (0.4)	19.6 (0.5)	18.3 (0.3)	20.9 (0.3)
Secchi	0.7 (0.1)	0.4 (0.1)	1.0 (0.1)	1.4 (0.1)	0.8 (0.2)	1.3 (0.2)	0.6 (0.1)	0.4 (0.1)	0.7 (0.1)	0.5 (0.1)	0.8 (0.2)	1.1 (0.1)
pH	6.2 (0.1)	6.6 (0.2)	6.7 (0.1)	6.5 (0.2)	6.8 (0.1)	6.8 (0.1)	6.1 (0.1)	6.5 (0.2)	6.7 (0.1)	6.4 (0.2)	6.6 (0.1)	6.7 (0.1)
Conductivity	31.0 (0.1)	35.4 (2.3)	60.7 (3.5)	32.9 (3.2)	41.1 (2.6)	62.0 (4.8)	31.4 (2.5)	35.0 (2.3)	59.8 (3.4)	32.5 (3.7)	40 (3.0)	62.0 (4.7)
Alkalinity	461 (64)	350 (66)	619 (75)	193 (30)	223 (31)	453 (43)	491 (83)	494 (120)	680 (94)	192 (29)	232 (29)	455 (43)
Turbidity	17.6 (5.2)	56 (11.1)	14.2 (2.1)	6.82 (2.2)	40.7 (17.8)	10.7 (3.9)	19.3 (5.3)	59 (11.3)	14.4 (2.3)	9.1 (2.8)	45 (20.8)	9.6 (3.7)
Oxygen	4.2 (0.6)	6.4 (0.3)	6.1 (0.8)	6.5 (0.6)	7.8 (0.2)	6.9 (0.5)	4.1 (0.6)	6.1 (0.3)	5.7 (0.7)	6.0 (0.7)	6.8 (0.4)	6.0 (0.5)
Chlorophyll-a	6.5 (1.9)	6.2 (2.7)	12.2 (4.3)	11.2 (7.1)	19.7 (11.6)	8.2 (3.1)	4.4 (1.4)	8.3 (3.2)	14.3 (5.4)	22.9 (8.7)	18.7 (9.9)	10.9 (2.5)
Nitrogen	419 (47)	409 (47)	411 (70)	461 (65)	368 (51)	305 (24)	473 (63)	399 (46)	409 (69)	416 (54)	372 (49)	316 (31)
Phosphorus	77.9 (20.3)	160 (93)	49.5 (13.2)	26.9 (7.1)	42.7 (11.7)	21.6 (5.7)	90 (21.7)	90 (22.4)	51 (13.6)	36.3 (8.2)	48 (10.4)	27.4 (7.3)
Susp. Mat.	12.5 (2.6)	25.5 (4.1)	9.3 (2.3)	5.8 (1.6)	10.3 (1.8)	8.2 (2.7)	18.0 (4.5)	27.2 (4.1)	10.8 (2.9)	11.8 (2.3)	13.4 (2.1)	10.5 (3.1)
Dis.Org. Mat.	7.1 (5.3)	5.2 (0.7)	3.8 (0.7)	6.5 (1.0)	6.2 (1.4)	3.0 (0.5)	7.7 (1.0)	5.4 (0.7)	3.9 (0.8)	6.6 (1.0)	6.9 (1.5)	3.1 (0.5)

Additional references not found in the text

Carmouze, J. P. 1994. O metabolismo dos ecossistemas aquáticos: fundamentos teóricos, métodos de estudo e análises químicas. Edgar Blucher, FAPESP, São Paulo, 253 p.

Golterman, H. L., et al. 1978. Methods for physical and chemical analysis of freshwaters. IBP Handbook no. 8. Blackwell Scientific, Oxford, 214p.

Mardia, K. V. et al. 1979. Multivariate analysis. Academic Press, San Diego.

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Anexo S6. Conjuntos de dados disponíveis para partição da variância dos diferentes grupos biológicos:

Tabela 1. Lista dos conjuntos de dados disponíveis para as análises de partição de variância de cada grupo biológico.

Grupo biológico	2000				2001				Locais
	Fev	Mai	Ago	Nov	Fev	Mai	Ago	Nov	
Peixes	✓	✓	✓	✓	✓	✓	✓	✓	20
Macroinvertebrados bentônicos	✓	✓	✓	✓	✓	✓	✓		36
Macrófitas aquáticas					✓		✓		36
Zooplâncton	✓	✓	✓	✓	✓	✓	✓	✓	35
Fitoplâncton	✓		✓		✓		✓		33
Perifíton	✓		✓						30

Anexo S7. Diferentes rotas de disperão via curso d'água e resultados da partição de variância com diferentes rotas via curso d'água e com dados de presença/ausência:

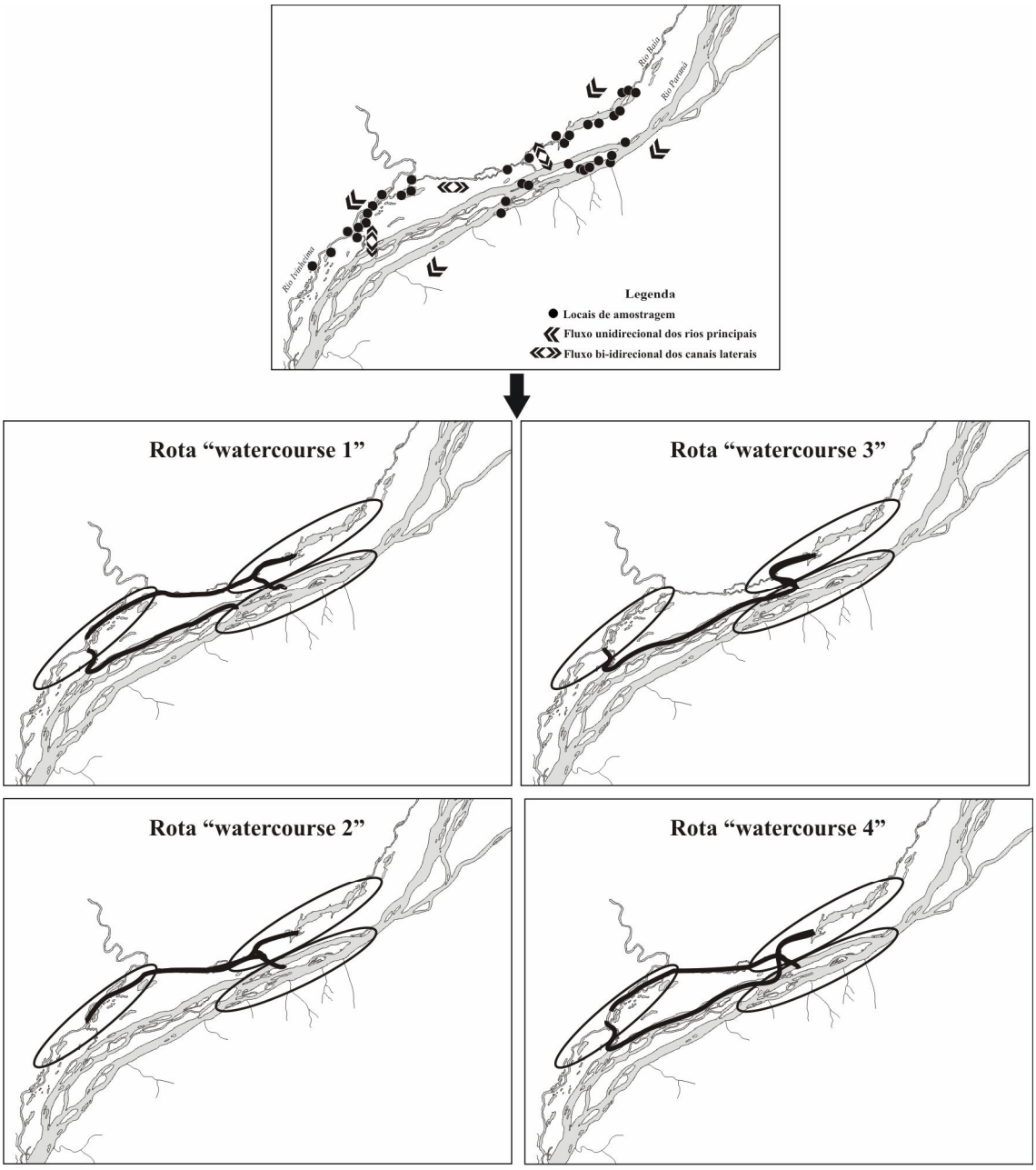

Figura 1. Quatro possíveis rotas de dispersão via curso d'água entre os locais de amostragem na planície de inundação do Alto rio Paraná. Nesse caso, os locais de amostragem foram agrupados para melhor visualização das possíveis rotas de dispersão.

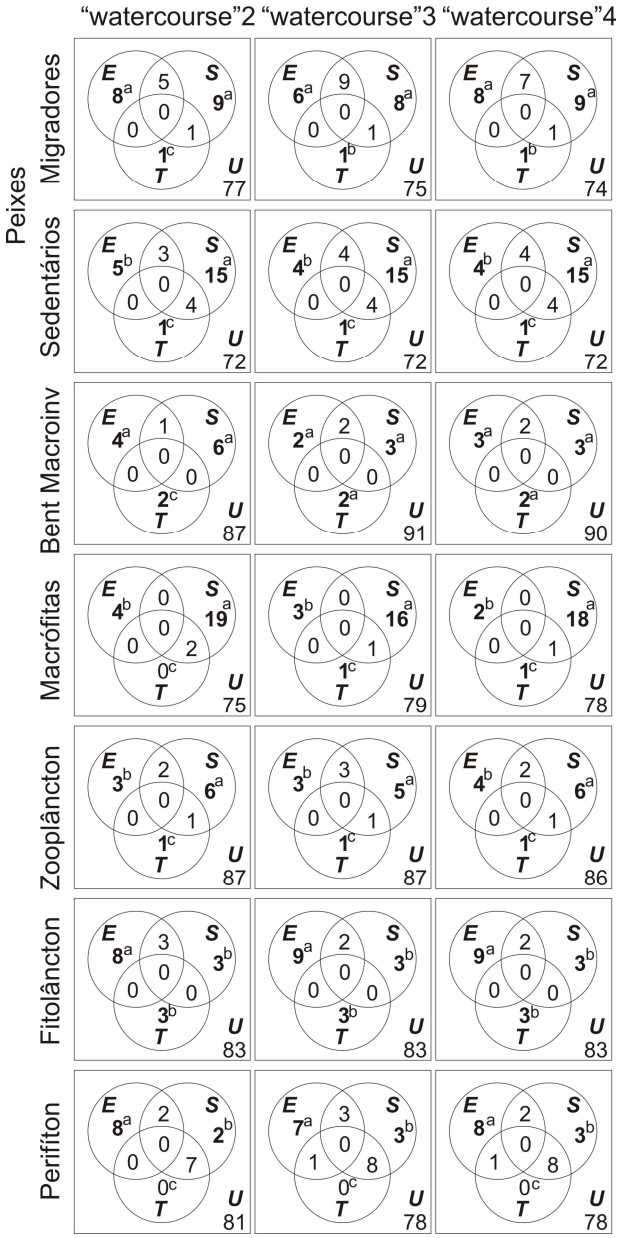

Figura 2. Contribuição relativa (% de explicação) das variáveis ambientais (E), espaciais (S) e temporais (T), e os componentes partilhados para explicar a variabilidade da abundânacia das assembléias aquáticas e da composição de macrófitas aquáticas, utilizando diferentes matrizes espaciais como substitutas de potenciais rotas de movimentação seguindo os cursos de água entre os pontos de amostragem. U = componente não explicado. Zeros indicam valores menores que 0.5%. Os componentes puros (E, S e T) são testáveis e, nesse caso, valores em negrito indicam valores significativos e letras compartilhadas indicam valores estatisticamente similares.

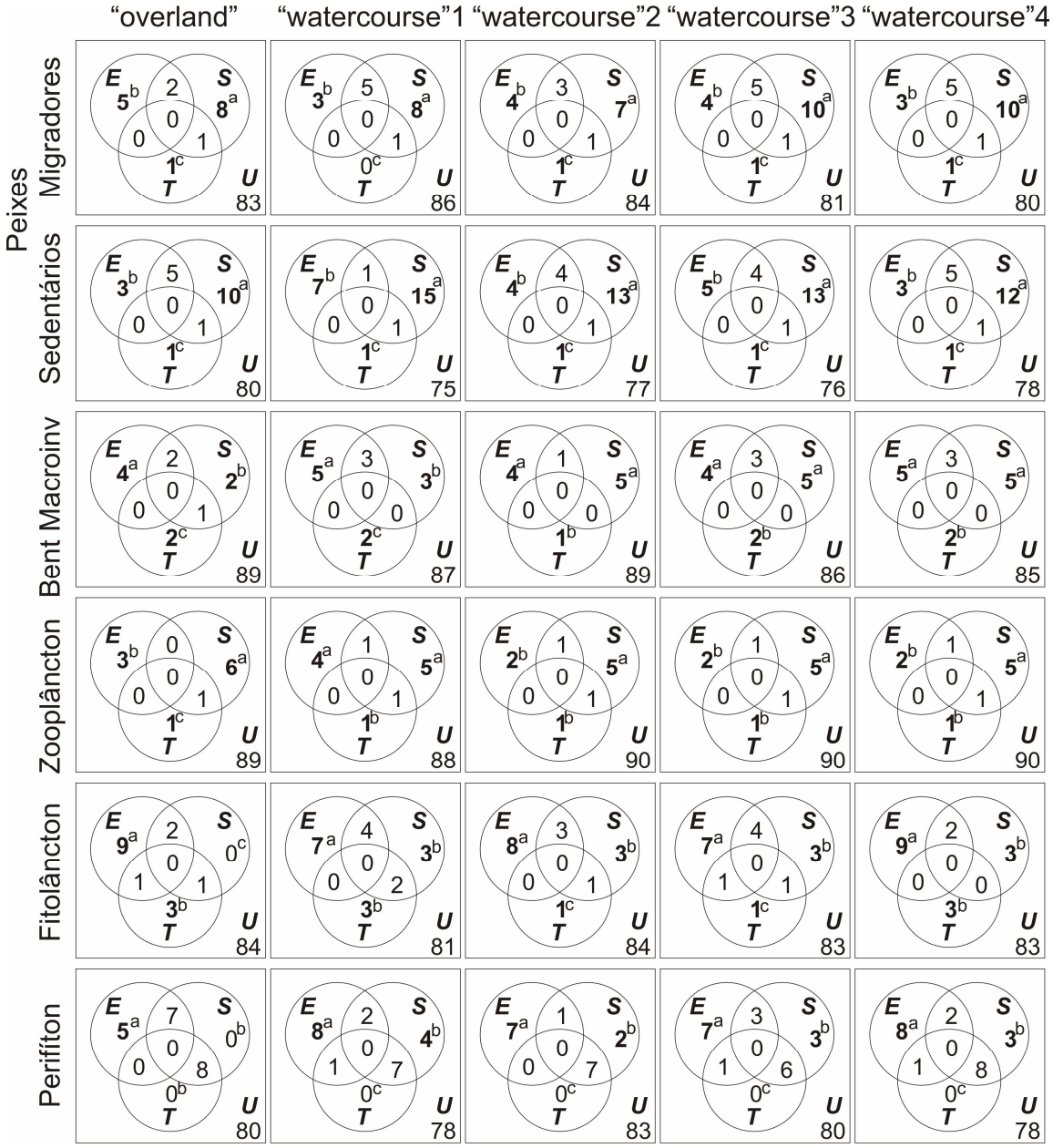

Figura 3. Contribuição relativa (% de explicação) das variáveis ambientais (E), espaciais (S) e temporais (T), e os componentes partilhados para explicar a variabilidade da composição das assembléias aquáticas (exceto macrófitas aquáticas), utilizando diferentes matrizes espaciais como substitutas de potenciais rotas de movimentação seguindo os cursos de água ou distâncias puras entre os pontos de amostragem ("watercourse" e "overland", respectivamente). U = componente não explicado. Zeros indicam valores menores que 0.5%. Os componentes puros (E, S e T) são testáveis e, nesse caso, valores em negrito indicam valores significativos e letras compartilhadas indicam valores estatisticamente similares.