UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

PADRÕES ESPAÇO-TEMPORAIS DE MACRÓFITAS AQUÁTICAS EM AMBIENTES AQUÁTICOS CONTINENTAIS NEOTROPICAIS

SOLANA MENEGHEL BOSCHILIA

PORTO ALEGRE, MAIO 2012

PADRÕES ESPAÇO-TEMPORAIS DE MACRÓFITAS AQUÁTICAS EM AMBIENTES AQUÁTICOS CONTINENTAIS NEOTROPICAIS

SOLANA MENEGHEL BOSCHILIA

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutor em Ciências com ênfase em Ecologia.

Orientador: Prof. Dr. Albano Schwarzbold
Co-orientador: Edson Fontes de Oliveira
Comissão Examinadora
Prof. Dr. Sidinei Magela Thomaz
Prof. Dra. Ana Silvia Rolon
Prof. Dr. Fernando Becker

PORTO ALEGRE, MAIO 2012

Viver é enfrentar desafios.
Quem nunca enfrentou desafios, apenas passou pela vida, não viveu.
Sim, todo mundo quer uma vida tranquila e estável, mas não se consegue isso sem luta, esforço
e muita coragem.
E ninguém quer uma vida medíocre, sem sal nem açúcar. Definitivamente, isso não é coisa que
engradece a alma. Mas se quiseres seguir adiante com glória, tenha ciência de que às vezes é
necessário mudar a estratégia do jogo radicalmente.
Você poderá perder muitas peças e muitas batalhas no caminho. E não importa o quanto você
sofra, o quanto você apanhe. Você precisa reunir suas forças e seguir em frente.
Mesmo que tudo pareça perdido, não esqueça: na vida, assim como num jogo de Xadrez,
enquanto você estiver de pé e lutando, nada estará perdido. Basta que você mantenha o Espírito
e siga em frente.

Augusto Branco

"Você pode medir um líder pelo tamanho dos desafios que ele assume. Ele sempre procura algo
do próprio tamanho."

John C. Maxwell

AGRADECIMENTOS

Sumário

LISTA DE FIGURAS

(PRIMEIRO CAPÍTULO)

(SEGUNDO CAPÍTULO)

Paspalum repens; caper-*Caperonia castaneifolia*; ipome- *Ipomoea* sp.; hydro-*Hydrocotyle ranunculoides*; echin-*Echinochloa* sp.; rynch-*Rhynchospora corymbosa*; tydom-*Typha domingensis*; limno- *Limnobium laevigatum* oxcub-*Oxycaryum cubense;* hyver-*Hydrilla verticillata*; bacop-*Bacopa* sp.; ponte-*Pontederia* sp.; eclip-*Eclipta* sp……………….…..**58**

(**TERCEIRO CAPÍTULO**)

LISTA DE TABELAS

LISTA DE APÊNDICES

(**PRIMEIRO CAPÍTULO**)

RESUMO

A presente tese avaliou os efeitos de dois distúrbios de larga escala sobre estrutura das assembleias de macrófitas aquáticas em distintos ecossistemas neotropicais: uma grande depleção do nível da água no reservatório de Itaipu (Brasil/Paraguai) e os pulsos de cheia e seca na planície do Alto Rio Paraná. O primeiro capítulo da tese avaliou o impacto imediato e de médio prazo da depleção no nível hidrométrico sobre os padrões de co-ocorrência das espécies e a estrutura espaço-temporal da assembleia de macrófitas aquáticas em cinco braços do reservatório de Itaipu. O segundo e terceiro capítulos analisaram os padrões de diversidade beta e a contribuição relativa dos seus diferentes componentes (substituição de espécies e aninhamento) para a estruturação das assembleias no reservatório de Itaipu e na planície de inundação do Alto Rio Paraná, respectivamente. Diferentemente do esperado, a assembleia de macrófitas do reservatório de Itaipu revelou um padrão de organização das espécies diferente do acaso no ano em que ocorreu a depleção, provavelmente devido à colonização de novas espécies na margem exposta e à morte de muitos indivíduos pertencentes a diversas espécies do grupo das submersas. Imediatamente após o distúrbio, evidenciamos um padrão tipicamente aleatório de distribuição, devido ao reestabelecimento das espécies submersas, concomitantemente à colonização de espécies emergentes que haviam se estabelecido nas margens durante o distúrbio. Tanto no reservatório de Itaipu como na planície de inundação do Alto Rio Paraná, a substituição de espécies (*turnover*) revelou-se como principal mecanismo responsável pelos padrões de diversidade beta, o que provavelmente está diretamente associado com as diferenças de dinâmica hidrológica e limnológica entre cada ambiente dentro dos ecossistemas analisados (braços do reservatório e lagoas da planície).

Palavras-chave: cheia, co-ocorrência de espécies, depleção, distúrbio, diversidade beta, seca.

ABSTRACT

The present thesis evaluated two large-scale disturbances upon the structure of aquatic macrophytes assemblages in distinct Neotropical ecosystems: an historic drawdown occurred in the Itaipu reservoir (Brazil/Paraguay) and the flood and drought pulses in the Upper Paraná River floodplain. The first chapter evaluated the immediate and long term impact of the drawdown over the co-occurrence patterns and the spatio-temporal structure of the aquatic macrophytes assemblage in five arms of the Itaipu reservoir. The second and third chapters analyzed the beta diversity patterns and the relative contribution of its different components (species turnover and nestedness) to the assemblage's structure in the Itaipu reservoir and the Upper Paraná River floodplain, respectively. Contrary to expected, the macrophytes assemblage in the Itaipu reservoir presented a non-random spatial organization pattern of the macrophyte species in the year of the drawdown probably due to the colonization of the exposed area by new species and by the death of many individuals of submersed species. Immediately after the disturbance, we evidenced a random distribution guided by the reestablishment of the submersed species concomitantly with the emergents, which occupied the shore since the disturbance. Both Itaipu reservoir and the Upper Paraná River floodplain, the species turnover revealed to be the main process reflecting high values of beta diversity, which probably is directly linked with the distinct hydrological and limnological dynamic within the environments in each analyzed environment (reservoir arms and floodplains lagoons).

Key-words: beta diversity, co-occurrence, disturbance, drawdown, drought, flood, time lag.

INTRODUÇÃO GERAL

Ao observarmos o ambiente, o fazemos numa limitada amplitude de escalas devido às limitações de nossa própria percepção ou pelas impossibilidades tecnológicas e logísticas (Levin 1992). Porém, a escala de observação tem um profundo efeito no delineamento dos padrões encontrados, e diferentes padrões podem emergir a partir de diferentes escalas (Wiens 1989). Por isso a importância de estudar ecossistemas de ampla escala, considerando amplas variabilidades espaciais. Cabe ressaltar a importância da escala temporal em análises ecológicas, a qual, quando analisada a partir de eventos relativamente curtos de tempo, não nos permite dizer se determinados eventos são raros ou ocorrem com certa frequência no tempo.

Considerando uma escala temporal pequena, de dias a poucas semanas, os padrões encontrados são em sua maioria direcionados por efeitos de amostragem ou fatores temporais que não tiveram tempo suficiente para moldar as assembleias. Numa escala de tempo intermediária, de meses a anos, os padrões de substituição de espécies já passam a ser moldados por processos ecológicos, tais como colonização e extinção e, esses processos, são comumente direcionados por variações temporais no ambiente ou padrões de dispersão através dos locais (Korhonen et al. 2010). Nesse contexto, Korhonen et al. (2010) demonstraram que estudos de longa duração são essenciais para o entendimento dos mecanismos básicos que direcionam as substituições temporais nos ecossistemas.

A presente tese tem como uma das principais metas a investigação de padrões ecológicos de ampla escala em dois ecossistemas extensos e com elevada heterogeneidade espaço-temporal: um reservatório dendrítico profundo com braços desenvolvidos e uma planície de inundação com elevada diversidade de hábitats. Reservatórios experimentam um processo de ontogenia semelhante ao observado nos ecossistemas lacustres e, portanto, em algum estágio de desenvolvimento, geralmente serão colonizados em menor ou maior grau por macrófitas aquáticas. O ritmo de colonização dependerá das características morfométricas do reservatório, de fatores físicos e químicos associados à coluna de água e ao sedimento e de processos biológicos, tais como o "pool" regional de espécies, mecanismos de dispersão e de interações interespecíficas. Por outro lado, as planícies de inundação se revelam ecossistemas megadiversos, sob influência direta dos ciclos de cheia

e seca. Esses pulsos possibilitam o desenvolvimento dos ciclos biológicos naturais de diversos grupos de organismos, os quais se mostram adaptados aos distúrbios regulares promovidos pelos períodos de águas altas e baixas. Esses ecossistemas têm sofrido amplo espectro de impactos, tais como: poluição, assoreamento, canalização e represamento. A planície do Alto Rio Paraná, por exemplo, sofre consequências indiretas da instalação de hidrelétricas e seus reservatórios a montante. A regulação do fluxo por essas represas tem modificado a estrutura e funcionamento da planície, impactando negativamente vários organismos (Agostinho et al. 2000, 2003; Rodrigues et al. 2009). Mesmo sob efeito constante do controle imposto pelo grande número de barragens, o regime hidrológico da planície do Rio Paraná ainda é o principal fator estruturador das comunidades aquáticas (Thomaz et al. 2004; Agostinho et al. 2001, 2007a).

A assembleia de macrófitas aquáticas possui um papel determinante na integridade dos ecossistemas aquáticos, contribuindo para a estrutura física do ambiente e aumentando a complexidade dos hábitats aquáticos. As macrófitas aumentam a heterogeneidade espacial e promovem hábitat para diversos organismos, como perifíton (Mormul et al. 2010), invertebrados (Thomaz e Cunha 2010) e peixes (Agostinho et al. 2007; Pelicice e Agostinho 2006). Além disso, contribuem para aumentar a estrutura e a diversidade de hábitats, interferem na ciclagem de nutrientes e participam da base das teias alimentares (Wetzel 2001). A assembleia de macrófitas aquáticas é composta por espécies que pertencem a diferentes formas de vida e que exploram de várias formas os recursos ambientais disponíveis ao longo da coluna d´água (emergentes, flutuantes, enraizadas submersas, enraizadas com folhas flutuantes, submersas livres, anfíbias e epífitas).

As macrófitas aquáticas são ótimos organismos para testar padrões espaciais e temporais em assembleias de ambientes tropicais (e.g., Bini et al. 2001; Rolon e Maltchik 2006), devido às suas características inerentes, tais como, altas taxas de crescimento (Riis et al. 2009), altas taxas de dispersão (Barrat-Segretain 1996), predomínio de reprodução assexuada e alta habilidade regenerativa (Barrat-Segretain 1996; Barrat-Segretain e Bornette 2000; Silveira et al. 2009), além de uma variação sazonal menor de sua biomassa (Camargo e Esteves 1996). Essa pouca variação é interessante para poder isolar o efeito que queremos estudar do efeito que a temperatura e foto-período provocam na biomassa (regiões tropicais possuem menores variações do que em regiões temperadas). As macrófitas aquáticas são capazes de colonizar ambientes com diferentes características

físicas e químicas por apresentarem várias adaptações morfológicas e fisiológicas que as tornam consideravelmente plásticas (Sculthorpe 1985).

Estudos ecológicos de assembleias frequentemente postulam pressupostos implícitos de que as espécies possuem padrões de distribuição espaço-temporais não aleatórios. Para que uma assembleia tenha uma organização espacial não aleatória é necessário que pelo menos um fator estruturador esteja agindo, como por exemplo, interações bióticas e/ou segregação de hábitat. A maioria dos estudos que analisam tendências gerais nos padrões de co-ocorrência nas assembleias infere que a competição, por exemplo, é um dos principais fatores que influenciam a estrutura das comunidades (e.g. Diamond 1975, Graves e Gotelli 1993). Outros mecanismos como requerimento de hábitat, biogeografia e história evolutiva também são padrões usados para explicar distribuições não aleatórias como, por exemplo, *checkboard* ("tabuleiro de xadrez", Gotelli e McCabe 2002). Por outro lado, assembleias ditas aleatórias são geralmente interpretadas como resultado de múltiplos fatores agindo simultaneamente, como gradientes ambientais, competição, predação e facilitação, os quais podem ter efeitos contrários, que então previnem a identificação e formação de um padrão espaço-temporal (Gotelli e Graves 1996).

Entender quais mecanismos determinam os padrões de diversidade está entre os principais objetivos da Ecologia (Cody e Diamond 1975, Hubbell 2001). O estudo destes mecanismos avançou consideravelmente nas últimas décadas, incluindo a integração de processos em diferentes escalas de espaço (e.g. interações ecológicas locais e a influência do conjunto regional de espécies) e de tempo (escalas ecológicas / evolutivas) (Whittaker 1972, Koleff et al. 2003, Ricklefs 2004, Legendre et al. 2005). A diversidade biológica é dividida em três componentes de acordo com a amplitude da escala: diversidade alfa (α), geralmente sendo medida através da riqueza de espécies local; diversidade beta (β), medindo a diferença na composição de espécies entre duas ou mais áreas e a diversidade gama (γ), que corresponde à diversidade total da região (Whittaker 1970, Baselga 2010, Tuomisto 2010). A diversidade beta é uma medida importante da biodiversidade regional, constituindo uma ferramenta extremamente útil para a conservação e manejo dos recursos naturais (Legendre et al. 2005, Baselga e Jiménez-Valverde 2007).

Os distúrbios são eventos de ampla magnitude com potencial para influenciar os padrões de diversidade, pois modificam a estrutura e a dinâmica dos ecossistemas, criando

heterogeneidade espacial e temporal. Além disso, possui um papel importante na formação de novos hábitats e na facilitação de espécies invasoras (Davis et al. 2000). Os distúrbios são considerados fonte de múltiplos níveis de heterogeneidade ambiental e promotores de uma base complexa de partição de recursos entre as espécies coexistentes (Denslow 1985). Resh et al. (1988) estudando ecossistemas aquáticos, conceituou distúrbio como um evento relativamente discreto no tempo, caracterizado pela frequência, intensidade e severidade incomuns à amplitude previsível, rompendo a estrutura de ecossistemas, populações e comunidades, modificando recursos ou o ambiente físico.

Distúrbios frequentes têm sido amplamente estudados (como pulsos de inundação), enquanto que aqueles distúrbios que possuem como características serem infrequentes e de grande amplitude são ainda pouco entendidos. É difícil estudar esse tipo de evento, pois eles são imprevisíveis e fatalmente não verdadeiramente replicados. Ainda, dados disponíveis antes desses distúrbios são normalmente escassos ou disponíveis apenas em pequenas regiões dentro da área afetada (Turner e Dale 1998). No presente estudo foram analisados os efeitos de dois distúrbios considerados severos para a assembleia de macrófitas aquáticas: a depleção do nível da água e a consequente exposição das margens nos braços do reservatório de Itaipu e, os pulsos de cheias e secas na planície de inundação do Alto Rio Paraná. Para avaliar esses efeitos, foram elaborados três capítulos.

O primeiro capítulo intitulado "*Immediate and long-term effects of water drawdown on macrophytes assemblage in a large subtropical reservoir (Itaipu-Brazil)*" o qual analisa os padrões de co-ocorrência da assembleia de macrófitas aquáticas em cinco braços do reservatório de Itaipu entre 1999 a 2007. Em especial, este capítulo enfatizou o efeito de uma depleção histórica de 4,6m no nível da barragem e como esse distúrbio afetou a estrutura da assembleia enquanto o nível permanecia baixo e após esse período. O reservatório de Itaipu é do tipo dendrítico e possui baixa declividade em suas margens. Espera-se que essa característica aumente o efeito que a depleção de quase cinco metros na barragem causou sobre os braços do reservatório.

O segundo capítulo intitula-se "*Partitioning beta diversity of aquatic macrophytes assemblage in a subtropical reservoir: turnover or nestedness prevalence?*" e buscou-se compreender qual o mecanismo predominante na partição de diversidade beta nos braços do reservatório de Itaipu. Segundo o conceito proposto por Baselga (2010), a diversidade

beta pode ser particionada em dois fenômenos diferentes: a substituição espacial das espécies e o aninhamento das comunidades (Harrison et al. 1992; Baselga 2007), fornecendo uma estrutura unificada para distinguir a real contribuição da substituição e do aninhamento para o padrão de diversidade beta (Baselga 2010). Como o reservatório possui grandes dimensões e um monitoramento temporal e espacial extensivo, com ampla amostragem dentro dos braços, o presente trabalho pretendeu avaliar os padrões de partição de diversidade beta em substituição de espécies e aninhamento na assembleia de macrófitas aquáticas em cinco braços de Itaipu, durante os anos de 1999 a 2007. Além disso, procurou-se identificar quais variáveis ambientais, espaciais e temporais (anos de coleta, braços, condutividade, transparência da água e fetch) contribuíram para os padrões de diversidade beta e seus componentes.

No terceiro capítulo da tese intitulado "*Swing of waters: the effect of floodpulse on aquatic macrophytes' beta diversity, species turnover and nestedness*", estudou-se o efeito que o pulso de inundação da planície de inundação do Alto Rio Paraná exerce sobre a partição de diversidade beta, substituição de espécies e aninhamento da assembleia de macrófitas aquáticas entre os anos de 2005 e 2009. Nele destacam-se as variáveis limnológicas que contribuem para a diversidade beta nos períodos de inundação e de águas baixas. Nesse trabalho também avaliamos o "time lag" necessário para que o efeito do pulso de inundação afete a assembleia de macrófitas nas lagoas conectadas e desconectadas dos três subsistemas que compõem a planície de inundação do Alto Rio Paraná.

PRIMEIRO CAPÍTULO

IMMEDIATE AND LONG-TERM EFFECTS OF WATER DRAWDOWN ON MACROPHYTES ASSEMBLAGE IN A LARGE SUBTROPICAL RESERVOIR (ITAIPU-BRAZIL) [1]

TRABALHO REALIZADO EM CONJUNTO COM: EDSON

FONTES DE OLIVEIRA E ALBANO SCHWARZBOLD

ABSTRACT

Disturbances play central role in determining the spatial and temporal dynamics of a variety of plant communities. Co-occurrence null models and spatiotemporal analyses were used to verify the patterns in aquatic macrophytes assemblage before, during and after an atypical water drawdown occurred in a subtropical reservoir (2000, Itaipu reservoir, Brazil-Paraguay border). Macrophyte samples were obtained in 150 sites, distributed in five arms of reservoir from 1999 to 2007. C-Score co-occurrence index tested the null hypothesis of random structure of the aquatic macrophyte assemblages. Detrended correspondence analysis and multi-response permutation procedure were used to verify if species composition differed before, during and after the drawdown disturbance. Differently of expected during the drawdown, the null models showed that the aquatic macrophyte assemblages were spatially structured, however the species composition was significantly different from previous year and also in the following years. Significant species co-occurrence patterns were generated by the drawdown disturbance, leading to death and new species colonization from propagules and seed bank germination. The randomness expected in 2000 occurred surprisingly in 2001 probably due to the occurrence of the most frequent life forms at the same time in the shore, since the reestablishment of water lever made possible submerged and free floating leaves colonize again the shore where emergents inhabited since drawdown. Along the years after the disturbance, biotic interactions seemed to increase and also the reestablishment of the aquatic macrophytes habitat preferences. These factors promoted an organized spatial distribution pattern and higher similarity in species composition.

KEY WORDS: co-occurrence patterns, C-Score index, MRPP, water depletion .

INTRODUCTION

Disturbances are considered the major factors modifying structure and dynamic in the ecosystems, creating temporal and spatial heterogeneity. Disturbance plays an important role forming new habitats and facilitating invasions (Burke & Grime, 1996; Davis, Grime & Thompson, 2000). Therefore, disturbances are the source of multiple levels of environmental heterogeneity, and thus potentially provide a complex basis for resource partitioning among coexisting species (Denslow, 1985). Disturbances can be defined as any relatively discrete event in time that is characterized by a frequency, intensity and severity outside a predictable range, disrupting ecosystems, population or community structure, and changing available resources or the physical environment (Resh et al. 1988). Frequent disturbances have been widely studied, while those characterized as large and infrequent are not well understood. It is difficult to study because they are unpredictable, frequently not truly replicated. Moreover, predisturbance data may be lacking or available only from small regions within the affected area (Turner & Dale, 1998).

Aquatic macrophytes are good models to test spatial and temporal patterns of tropical environments (e.g. Bini, Thomaz & Souza, 2001; Rolon & Maltchik, 2006; Boschilia, Oliveira & Thomaz, 2008), due to high growth (Pistori, Camargo & Henry-Silva, 2004; Riis, Madsen & Sennels, 2009) and dispersion rates (Barrat-Segretain, 1996; Santamaria, 2002), asexual reproduction, regenerative ability and small seasonal biomass variation (Barrat-Segretain, 1996; Barrat-Segretain & Bornette, 2000; Silveira et al. 2009). The macrophyte assemblages are usually composed of several species belonging to different life forms that explore different spatial niches in the water column (e.g. free floating, epiphyte, submersed and emergent plants; Cook, 1990). They are considered important for integrity and maintenance of the aquatic systems, contributing to the structure of the physical space and increasing the habitat complexity. Moreover, they influence the hydrology and sediment dynamics of freshwater ecosystems through their effects on water flow (shifts in current velocity; Madsen et al. 1991) and particle trapping or re-suspension (Vermaat, Santamaria & Roos, 2000). Macrophytes also provide substrate to macroinvertebrates and microbial communities' colonization, and are used by many aquatic animals as refuge sites and food resources (Lacoul & Freedman, 2006; Pelicice, Thomaz & Agostinho, 2008).

Generally ecological studies assume that assemblages are organized presenting non-random spatiotemporal distribution patterns. Such patterns are driven by, at least, one structuring factor, as dispersion ability and/or biological interactions. The factors affecting the colonization of reservoirs by macrophytes are generally related to spatial structure, in which heterogeneity can be reduced by deteriorating environments or increased by the formation of new habitats and microhabitats. This heterogeneity can be mainly due to water level variation, and eventually drawdowns, imposed or not by the reservoir, reduction of water velocity and more accentuated sedimentation process, resulting in higher light penetration and loss of nutrients in the water column (Thomaz, 2002). Reservoir morphology, its sheltered and/or open areas, shallow waters and the vegetation density, partially inundated, also contribute to the successful or unsuccessful establishment of the aquatic assemblages (Mitchell, Pieterse & Murphy, 1990). For instance, the depth of reservoir limits the growth of rooted submerged species, while the free floating ones are subject to wind and waves in open areas (Keddy, 1982; Keddy & Fraser, 2000; Lacoul & Freedman, 2006).

In this study we analyzed the structure of aquatic macrophyte assemblages in a tropical reservoir (Itaipu reservoir, Brazil/Paraguay border) after an atypical depletion of hydrometric levels (until 4.6m), between November 1999 and March 2000 (108 days; Figure 1) caused by a long regional drought period. The historical rainfall recorded in three cities around the Itaipu reservoir (Missal, Santa Terezinha de Itaipu and Santa Eliza) showed that the year 1999 had the lowest annual rainfall record (annual mean= 3.5mm/day (0.0mm ± 89.5mm)) compared to other years (1998-2007). As macrophytes in this reservoir colonize mainly the shallow and sheltered areas of the arms (Thomaz et al. 1999), the drawdown is expected to significantly affect macrophyte assemblages.

This study evaluated the co-occurrence patterns and the spatiotemporal structure of the aquatic macrophyte assemblages in Itaipu reservoir, before, during the drawdown and *post* disturbance. Previously to the disturbance we believe that the aquatic macrophyte assemblages were spatially organized, i.e., that species pairs were segregated, promoting a co-occurrence structured pattern. We expected to find a rupture in the co-occurrence patterns during the drawdown, with random distribution of the species pairs in the whole reservoir and in the arms studied. Considering the aquatic

macrophytes assemblage, it was expected the return of the previous co-occurrence patterns after the water depletion period.

MATERIALS AND METHODS

STUDY AREA

The Itaipu reservoir is a large (1,350km^2), deep (mean depth= 21.5m) and dendritic impoundment located in the Paraná River, along Brazilian-Paraguayan borders (Figure 2; 24°05'S and 25 ^{o}33'S; 54 ^{o}00'W and 54 ^{o}37'W). The reservoir was built in 1982 and presents a large number of shallow arms. They represent the areas flooded lower valleys of tributaries that drain adjacent sub-catchments, having spatially and seasonally varied characteristics. Five arms located along the Brazilian margin of the Paraná River were surveyed immediately before (1999; first year of sampling), during (2000) and over seven years (2001-2007) after the major drawdown in the reservoir in December 1999 (arms: São Francisco Verdadeiro –SFV, São Francisco Falso –SFF, São Vicente –SV, Ocoí –OC and Paço Cuê –PC; Figure 2).
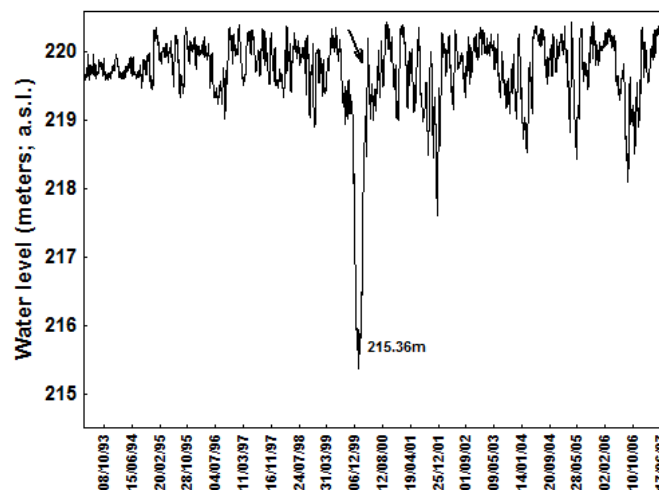
Figure 1. Water level fluctuations in the Itaipu reservoir from 1993 to 2007. Measurements were taken daily at the level of the dam. The arrow means the sampling done in 2000.

São Francisco Verdadeiro arm presented the lowest values of Secchi and was greatly colonized by algae, due in part to the high water phosphorus and nitrogen concentrations originated from urban areas upstream (eutrophic arm). São Francisco Falso was classified as mesotrophic, while São Vicente was oligotrophic and had the

highest fetch values. Ocoí and Paço Cuê arms are located in the lacustrine zone of the reservoir and presented high values of water transparency and fetch (oligo-mesotrophic arms). For more detailed information see Bini et al. (1999) and Bini & Thomaz (2005).
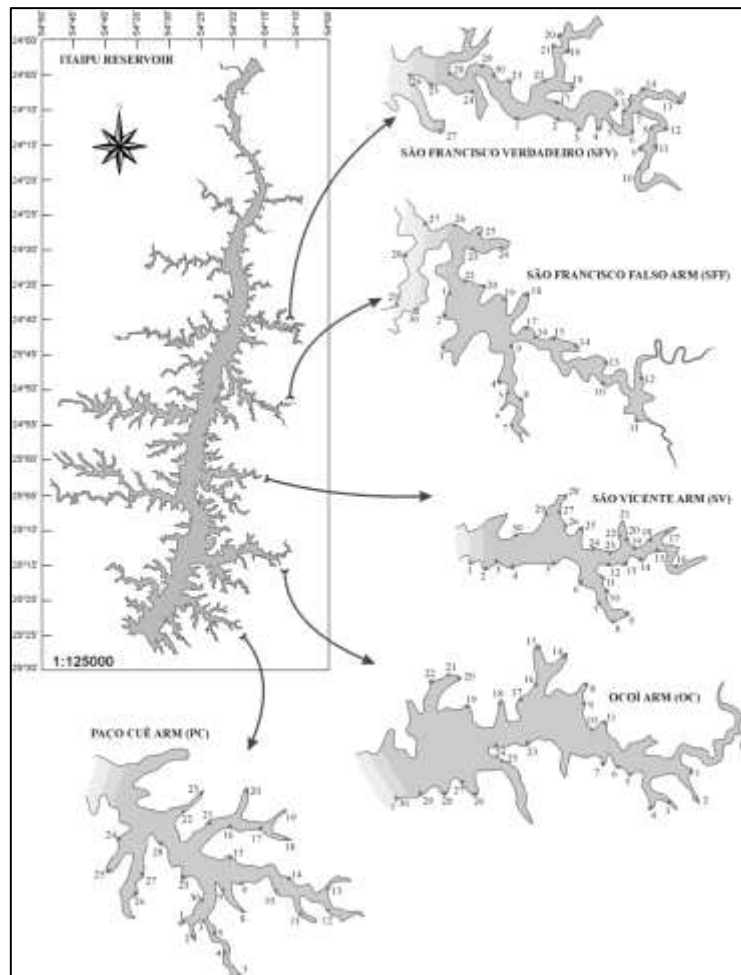
Figure 2. Location of the Itaipu reservoir and sampling sites (150). Arms codes used in the text are as follow: São Francisco Verdadeiro (SFV), São Francisco Falso (SFF), São Vicente (SV), Ocoi (OC), and Paço Cuê (PC).

SAMPLING

A total of 150 sites (30 per arm) were georeferenced. We recorded and collected aquatic macrophytes in each sampling site during 8-12 minutes (~100m), from a boat in constant velocity. A long-handled rake was used to collect submerged vegetation. The samplings occurred twice a year; except in the two first years (1999 and 2000) which had only one sampling. Samplings became sampled each six months to a better monitoring.

For this study amphibious and euhydrophytes were considered, i.e. plants that depend on the water to complete their reproductive cycle (Sculthorpe, 1967; Pott & Pott, 2000). The use of such criterion prevents problems caused by dubious ways to distinguish aquatic from non-aquatic species (see also Rørslett, 1991). We used life forms of aquatic macrophytes defined by Sculthorpe (1967) as: emergents, floating leaved, free floating, rooted submerged and free submerged.

DATA ANALYSIS

We tested the null hypothesis of randomness in the aquatic macrophyte assemblages in the arms of the reservoir with a co-occurrence null model. A presence-absence matrix was used, presenting one (1) when species is present in a given site and zero (0) when it is absent. The co-occurrence matrix was randomized following the SIM9 algorithm (Gotelli, 2000), which preserves the columns (sites) and rows (species) totals. Consequently, each species in the random matrix will be presenting the same number of sites of the observed matrix. Similarly, sites will maintain their species richness. We chose SIM9 algorithm because it is less prone to Type I error (Gotelli, 2000). Absence of biological interactions and physical environment effects were expected in the randomized matrix generated by null model (Gotelli & Graves, 1996). The C-Score index (Stone & Roberts, 1990) was chosen as a metric to quantify the pattern of co-occurrence. This index detects species pairs that do not co-occur frequently, but does not require a perfect checkerboard pattern. The index is obtained with the average of number of checkerboard units among all species pairs; therefore small changes on the data would not alter significantly the index. If communities are structured by competitive/ facilitative interactions or segregated by habitat preferences, the C-Score would be greater or lower than expected by chance, respectively (Gotelli, 2000). Random distributions could be interpreted as many contrasting factors acting simultaneously.

We removed rare species from all analyses, defined here as species that occurred until twice in the matrix observed, considering all years together in each arm of the reservoir. Rare species were not considered because it is not possible to determine if the rarity is due to a possible sampling failure and because rare species could inflate the

estimates of co-occurrence patterns (Oliveira, Minte-Vera & Goulart, 2005). Co-occurrence index was calculated using the C-score function at the bipartite package (Dormann & Gruber, 2008) and the observed matrix was randomized 30,000 times according with Lehsten & Harmand (2006) recommendations. All the analyses and the randomization procedures using the SIM 9 algorithm were performed using the R software (R development Core Team, 2008).

We used a detrended correspondence analysis (Hill & Gauch, 1980) to assess changes in aquatic macrophyte assemblage life form before, during and one year after the drawdown event (2001). A non-parametric analysis (Kruskal-Wallis) was performed to evidence differences between these periods. The DCA was performed on presence-absence matrix of the sampling sites in the studied arms. We tested for differences in macrophyte species composition in each arm among the years 1999, 2000 and 2001 by means of pair-wise multi response permutation procedure (MRPP; Biondini, Bonham & Redente, 1985), using Jaccard as a distance measure. MRPP is a multivariate nonparametric technique for testing group differences (species composition). MRPP provide a T and A statistics. The former describes the segregation among groups (more negative T, stronger the segregation). The latter (Agreement) describes within-group similarity, ranging from <0 to 1, where 1 means total similarity within-groups. Even with significant segregation of groups, A statistics values less than 0.1 are common with community data (McCune and Grace 2002). Both DCA and MRPP analysis were performed in PcOrd 5.15 (McCune & Mefford 2006).

RESULTS

We found 38 euhydrophyte taxa belonging to 24 families (Table 1). Of this total, the most frequent taxa were *Urochloa subquadripara*, Ludwigia spp., Eleocharis filiculmis, Nitella sp. *Polygonum* sp. and the less frequent were *Eclipta* sp., *Pontederia* sp., Bacopa sp. and *Hydrilla verticilata* (first time registered in 2007). The frequency of occurrence of many species drastically decreased (e.g. *Egeria densa*, *Egeria najas*, *Nymphea amazonum* and *Eleocharis filiculmis*) and disappeared during the period of water depletion (e.g. *Eleocharis minima* and *Commelina* sp.). On the other hand, some species arose (*Paspalum repens* and *Najas* sp.) and increased their occurrence (e.g.

Chara sp. and *Polygonum* spp.; Table 1).   The species *Urochloa subquadripara* presented a continuous increase during the whole study.   Furthermore, after the water level returned to its normal, some species that disappeared during the drawdown returned in 2001, followed with new species colonization (e.g. *Caperonia castaneifolia*, *Lemna valdiviana*, *Nymphoides indica*, *Rhynchospora carymbosa*, *Salvinia* spp.; Table 1).

Table 1. Species recorded during the whole study (1999-2007), their life forms, frequency of occurrence (%) in 1999 (99), 2000 (00) and 2001 (01), mean frequency between 2002 to 2007 (02-07) and the occurrence of species in each arm studied in the Itaipu Reservoir. Arms: SFV= São Francisco Verdadeiro, SFF= São Francisco Falso, SV= São Vicente, OC= Ocoí, PC= Paço Cuê. Life forms: EM= emergent; EP= epiphyte; RS= rooted submersed; FS= free submersed; FL= floating leaved; FF= free floating.

Life forms	Family	Species	Frequence (%)				Arms				
			99	00	01	02-07	SFV	SFF	SV	OC	PC
Emergents	Alismataceae	*Sagittaria montevidensis* Cham. & Schltdl.	5.91	0	2.1	6.16		X	X	X	X
	Amarantaceae	*Alternanthera philoxeroides* (Mart.) Griseb.	6.75	3.59	0.35	8.52	X	X	X	X	X
	Araliaceae	*Hydrocotyle ranunculoides* L.f.	1.66	0	0	1.47	X				X
	Asteraceae	*Eclipta* sp.	0	0	0	0.43		X	X		
	Commelinaceae	*Commelina* sp.	7.42	0	8.79	5.82	X	X	X	X	X
	Convolvulaceae	*Ipomoea* sp.	0	0	0	4.8	X	X	X	X	X
	Cyperaceae	*Rhynchospora corymbosa* (L.) Britton	0	0	0	1.94	X	X	X	X	X
		Eleocharis filiculmis Schur	57.24	26.6	25.1	21.1	X	X	X	X	X
	Euphorbiaceae	*Caperonia castaneifolia* (L.)A. St.-Hil.	0	0	1.17	4.84	X	X		X	
	Onagraceae	*Ludwigia* spp.	68.9	40.6	28.1	18.7	X	X	X	X	X
	Poaceae	*Panicum* sp.	0	0	0	54.6	X	X	X	X	X
		Paspalum repens P.J. Bergius	0	0.68	0.86	4.52	X	X	X	X	X
		Urochloa subquadripara.(Trin.) R.D. Webster	56	34.7	66.6	70.3	X	X	X	X	X
		Echinochloa sp.	1.11	0	1.17	0.76		X	X		X
	Polygonaceae	*Polygonum* spp.	16.8	27.9	25.2	33.5	X	X	X	X	X
	Pontederiaceae	*Eichhornia azurea* (Sw.) Kunth	6.78	1.14	2.89	5.1	X	X			
		Pontederia sp.	0	0	0	0.44					
	Plantaginaceae	*Bacopa* sp.	0	0	0	0.52					
	Typhaceae	*Typha domingensis* Pers.	0	0	0	1.83					

Growth form	Family	Species									
Free floating leaves	Araceae	*Pistia stratiotes* L.	0.83	0	0.41	9.8	X	X	X	X	
	Hydrocharitaceae	*Limnobium laevigatum* (Humb .& Bonpl. ex Willd.) Heine	0	0	0	1.82	X			X	
	Lemnaceae	*Lemna valdiviana* Phil.	0	0	0.46	7.45	X	X	X	X	
	Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms	15.5	12.3	18.9	13					
	Salviniaceae	*Salvinia* spp.	8.16	6.49	8.6	23.3					
Epiphyte	Cyperaceae	*Oxycaryum cubense* (Poepp. & Kunth) Palla	0	0	0	1.7	X	X	X	X	
Rooted submersed	Characeae	*Chara* spp.	12	26.7	9.32	15.7	X	X	X	X	X
		Nitella sp.	37.7	28.9	19	23.15	X		X	X	X
	Cyperaceae	*Eleocharis minima*.Kunth	3.38	0	1.7	5.7	X	X	X	X	X
	Haloragaceae	*Myriophyllum aquaticum* (Vell.) Verdc.	4.44	0	2.28	4.44		X		X	X
	Hydrocharitaceae	*Egeria densa* Planch.	12.6	0.69	1.7	22.3	X	X	X	X	X
		Egeria najas Planch.	35	6.91	6.55	34.6	X	X	X	X	X
		Hydrilla verticillata (L.f.) Royle	0	0	0	0.9		X		X	
	Najadaceae	*Najas* sp.	0	2.25	1.3	3.49		X	X	X	X
Free submersed	Lentibulariaceae	*Utricularia* sp.	2.66	1.11	0.35	3.48	X	X	X	X	X
Floating leaved	Menyanthaceae	*Nymphoides indica* (L.) Kuntze	0	0	4.28	21.58	X	X		X	X
	Nympheaceae	*Nymphea amazonum* Mart. & Zucc.	24	6.5	9.23	12.6	X	X	X	X	X

After the historic drawdown event in 1999-2000, which presented 108 days of water depletion and the hydrometric level reached the lowest values, four other depletions occurred (see Fig.1). However, analysis of variance (ANOVA) and a *post hoc* test (Tukey) revealed that the first event was significantly different from the others (Fig. 3).
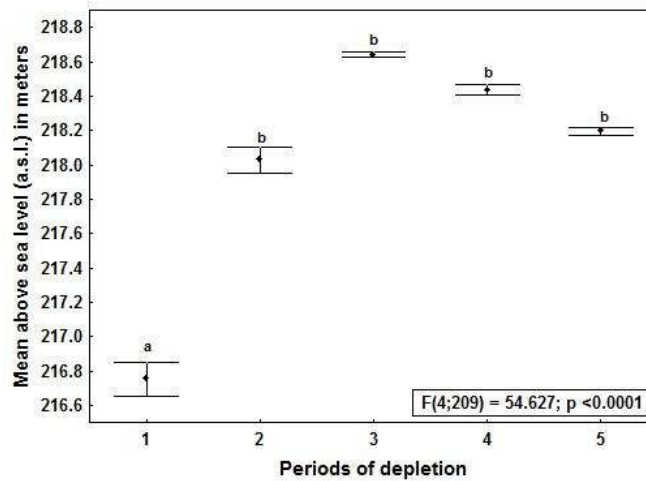
Figure 3.Analysis of variance among of five depletion periods identified in the hydrogram of water level fluctuation of reservoir (Mean and standard error- Fig.1). The period 1 correspond to the historic depletion (Nov 18th 1999 to Mar 04th 2000); period 2 (Dec 5th to Dec 25th 2001), period 3 (Feb 18th to Mar 07th 2004), period 4 (Aug 04th to Sep 03rd 2006) and period 5 (Nov 27th to Dec 31st 2007). Tukey test was performed and the symbols above the means (*a* and *b*) indicate that period 1 differs from others (*a*), but the others (periods 2-5) did not differed significantly from each other (*b*).

The periods 2, 3, 4 and 5 also differed significantly from the mean normal water variation of the reservoir ($F_{4, 3173} = 304.10$; *p*<0.001). When the entire dataset was used, i.e. considering all arms together along period, the C-Score index was higher than expected by chance, rejecting the hypothesis of absence of spatial organization (Table 2). This pattern was consistent throughout the study period, including the year of the occurrence of drawdown (2000). However the effects of this event are reflected in the second half of 2001, when species co-occurrence was random.

Our analyses of species co-occurrence patterns rejected our null hypothesis that the drawdown did cause a disruption in the co-occurrence patterns on the macrophyte assemblages in the arms of the reservoir in 2000 (Fig. 4). Most arms presented C-Score index larger than expected by chance in 1999 and 2000. In the year after the drawdown (2001), most arms had their aquatic macrophyte assemblages distributed randomly. The

recovery of previous co-occurrence patterns occurred in 2003 and the following years most arms presented C-score index higher than expected by chance (Fig. 4).

Table 2. Results of the C-Score index observed (obs.) and expected (exp.) for aquatic macrophyte assemblages, considering the whole Itaipu reservoir (five arms together). The number in parenthesis means the first (1) or second (2) semester of year sampled.

Year	S	N	Obs.	Exp.	SD	p (obs.>exp)
all	39	3428	71617.10	67188.79	72.96	<0.001
1999	21	146	220.11	212.78	1.87	<0.001
2000	16	97	113.44	108.60	1.20	<0.001
2001(1)	23	139	74.82	68.78	1.30	<0.001
2001(2)	19	131	133.11	131.05	1.61	0.11
2002(1)	25	143	168.70	163.70	1.30	<0.001
2002(2)	24	129	109.71	106.18	1.29	0.006
2003(1)	23	143	233.64	225.28	1.50	<0.001
2003(2)	23	131	172.27	164.66	1.42	<0.001
2004(1)	27	138	108.61	100.33	1.30	<0.001
2004(2)	30	142	166.22	156.61	1.32	<0.001
2005(1)	31	142	168.30	156.92	1.40	<0.001
2005(2)	27	142	126.35	118.39	1.45	<0.001
2006(1)	25	146	270.53	255.80	2.00	<0.001
2006(2)	26	149	201.72	189.65	1.43	<0.001
2007(1)	32	146	245.49	226.50	1.56	<0.001
2007(2)	32	146	228.87	217.88	1.31	<0.001

N number of sites; S species richness, SD standard deviation of the expected values

DCA also showed a disparity between species composition in 1999 and 2001 (Figure 5a), more affected by the presence of submersed and free floating, respectively (Figure 5b).
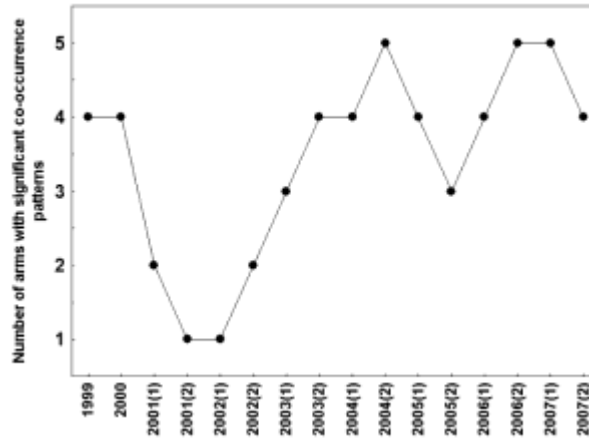
Figure 4. Number of arms of Itaipu reservoir (out of 5 possible) with the C-score larger than predicted by the null models in the years sampled (p<0.05). In 2000, the arm SV did not run the null model (matrix with only with four species).

A non-parametric analysis of variance (Kruskal-Wallis) showed significant differences between 1999 to 2000 and 2001 (H=39.99 *p*<0.001) in relation to axis 1. However, the year of the disturbance (2000) did not present differences to 2001. This could be attributed to the emergents, which arrived in the new open areas and colonized after the drawdown.
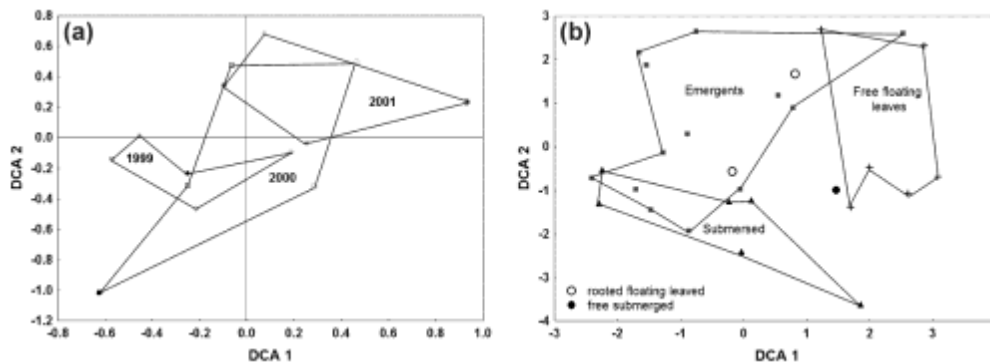
Figure 5. Diagram of DCA (axis 1 eigenvalue: 0.503; axis 2 eigenvalue: 0.419) for presence/absence data of the aquatic macrophytes assemblages in the Itaipu reservoir in the years 1999, 2000 and 2001, equivalent to before, during and after the water drawdown periods (a) and aquatic macrophytes life forms during the same period (b).

The MRPP indicated that the composition of macrophyte species were significantly different from one another (*p*<0.04; Table 3), considering all arms and the

periods before (1999), during (2000) and after (2001) the drawdown. The greatest differences were found comparing the periods "before" and "after" in all arms, for example in SV (T= -13.605), SFF (T= -12.383) and PC arms (T= -11.623). It is possible to infer that species composition was more strongly segregated between these periods. To all arms and in all comparing periods, we observed that the within-group similarity values (*A*) were really low, indicating a high species heterogeneity within arms.

Table 3. Results of multi-response permutation procedure tests (MRPP) among before (1999), during (2000) and after the drawdown period (2001) in the Itaipu reservoir. SFV= São Francisco Verdadeiro arm, SFF= São Francisco Falso arm=SFV, SV= São Vicente arm, OC= Ocoí arm, PC= Paço Cuê arm.

Arm	Period pair wise comparison	T-statistic	*A*-value	*p* value
	before x during	-2.832	0.01	0.01
SFV	before x after	-8.172	0.04	<0.001
	during x after	-3.494	0.02	0.007
	before x during	-8.908	0.05	<0.001
SFF	before x after	-12.383	0.04	<0.001
	during x after	-6.885	0.03	<0.001
	before x during	-3.36	0.04	0.006
SV	before x after	-13.605	0.06	<0.001
	during x after	-2.662	0.02	0.02
	before x during	-5.121	0.03	<0.001
OC	before x after	-8.86	0.03	<0.001
	during x after	-1.99	0.04	0.04
	before x during	-6.596	0.05	<0.001
PC	before x after	-11.623	0.05	<0.001
	during x after	-8.537	0.05	<0.001

T describes the segregation among groups (more negative T, stronger the segregation) and A describes within-group similarity (value 1 means total similarity within-groups)

An indicative of assemblage structure recovery after the water depletion was observed in pairwise years' comparisons. It was possible to note that in some arms, specifically SFF and SFV, the species composition after 2003 was more similar than the previous years (Table 4). This was also observed by Carvalho et al (submitted). This revealed higher temporal similarity in species composition. In other words, after the

reestablishment of water level, the promoted stability generated less stress and consequently, the strengthening of biotic interactions that had been weakened by the disturbance. These interactions, like competition and facilitation, together with other factors, promoted the spatial co-occurrence patterns seen in this reservoir.

Table 4. Results of *A*- algorithm (Agreement- within group similarity) of multi-response permutation procedure tests (MRPP) presenting the pairwise semesters which had no significant results and therefore, similarity in species composition. The parenthesis after the years means which semester the arm was sampled: 1-first semester; 2- second semester. SFV= São Francisco Verdadeiro arm, SFF= São Francisco Falso arm=SFV, SV= São Vicente arm, OC= Ocoí arm, PC= Paço Cuê arm.

SFV	SFF	SV	OC	PC
2002(1) = 2006(1)	2001(1) = 2001(2)	2000 = 2001(1)	2000 = 2001(2)	2002(1) = 2002(2)
2003(1) = 2003(2)	2002(2) = 2003(1)	2003(2) = 2004(2)	2001(2) = 2004(1)	2002(2) = 2003(1)
2003(2) = 2004(1)	2003(1) = 2003(2)	2004(1) = 2004(2)	2002(2) = 2003(1)	2002(2) = 2003(2)
2003(2) = 2005(1)	2003(1) = 2006(1)	2006(1) = 2006(2)	2002(2) = 2004(1)	2002(2) = 2004(1)
2003(2) = 2005(2)	2003(2) = 2004(1)		2004(1) = 2005(1)	2002(2) = 2004(2)
2003(2) = 2006(1)	2003(2) = 2004(2)		2004(2) = 2005(1)	2003(2) = 2004(1)
2004(1) = 2005(1)	2003(2) = 2005(2)		2005(1) = 2006(1)	2003(2) = 2004(2)
2004(1) = 2005(2)	2003(2) = 2006(1)		2005(1) = 2006(2)	2004(1) = 2004(2)
2004(1) = 2006(1)	2003(2) = 2006(2)		2006(1) = 2006(2)	2004(1) = 2005(2)
2004(1) = 2006(2)	2004(1) = 2005(2)			
2004(2) = 2005(1)	2004(1) = 2006(2)			
2004(2) = 2005(2)	2004(2) = 2005(1)			
2004(2) = 2006(1)	2004(2) = 2005(2)			
2004(2) = 2006(2)	2004(2) = 2006(1)			
2004(2) = 2007(2)	2004(2) = 2006(2)			
2005(1) = 2005(2)	2005(2) = 2006(1)			
2005(1) = 2006(1)	2005(2) = 2006(2)			
2005(1) = 2006(2)	2006(1) = 2006(2)			
2005(2) = 2006(1)				
2005(2) = 2006(2)				
2006(1) = 2006(2)				

DISCUSSION

Disturbance effects over ecosystems have been intensively discussed (Allison, 2004; Jiang & Patel, 2008), nevertheless the effect of intense and unpredictable events are still not totally understood due to the absence of long-term ecological studies (Turner & Dale, 1998). The atypical drawdown contemplated in this study was conspicuously different from other water depletions occurring along the years in Itaipu reservoir, allowing us to consider it as a unique event.

After damming, some rivers may experience relative stability of water levels, which helps to form habitats suitable for growth and development of macrophytes. This stability is also important for the colonization of certain life forms of macrophytes, especially free floating species (Riis & Biggs, 2003; Lacoul & Freedman, 2006), which had high regular presence in the arms of lacustrine zone of Itaipu reservoir.

As expected before the drawdown event, the species co-occurrences were less frequent than expected by chance, i.e., aquatic macrophytes assemblage were spatially organized in relation to the entire reservoir as well as most arms. Until 1999, the reservoir had long term environmental stability in relation to water level (usually fluctuates less than 1 m year^{-1}; Thomaz et al. 2006), which provided suitable environmental conditions for macrophytes development. According to Townsend (1989), this type of environment is called "niche controlled", and it has low temporal heterogeneity, and the factors controlling populations consist in competition and the coexistence of populations in the same habitat. Also important as competition, it is worth to consider that macrophytes have an important aquatic-terrestrial transition zone, segregating naturally different life forms according to their requirements. As this reservoir had long time water stability, the aquatic macrophyte assemblages had time to segregate. This could be promoted by competition and/or also by habitat preference (Boschilia et al. 2008). Beyond these factors, the dispersion of seeds, propagules and stems should be considered. Most aquatic plants have hydrochory dispersion, which can promote higher similarity between sites; even with this capability, some factors could be limiting the species dispersion along the arms of the reservoir.

Contrary to what we supposed, during the drawdown event (2000), our results showed that species co-occurrence differed from expected by chance (i.e., the macrophyte assemblages were spatially organized), considering the whole Itaipu reservoir and each arm separately. The species composition presented statistical differences among the year 2000 and the previous and the posterior years. Thus, the co-occurrence pattern can be attributed to significant shift of species composition (see Fig.5), the death of many species belonging to the submerged life form (*Egeria densa*, p. ex.), the colonization of new emergent species (e.g. *Paspalum repens*) and the increase in frequency of occurrence in tolerant species (*Chara* sp., *Polygonum* sp.).

Drawdown disturbances affect the species composition, relative abundance, distribution and successional dynamics of aquatic macrophytes (Keddy, 2000). They directly affect aquatic macrophytes by exposing them to aerial conditions and indirectly through the modification of substrate properties (Bornette & Puijalon, 2011). Submerged species also colonized shallow areas and with the dewatering, for being drought intolerant, they suffered from desiccation and died. Indeed, DCA analysis showed that the most representative group in 1999 was the submerged species. Beyond the death of submerged life form, the drying up thus favored regeneration of the bank of seeds (Keddy & Reznicek, 1982, 1986; Brock & Rogers, 1998), unspecialized fragments (Combroux & Bornette, 2004) and propagules (Riis & Biggs, 2003). It has been shown that rare drawdowns favor ruderal species with abundant seed banks, such as Charophytes, to the detriment of vascular species (Havens et al. 2004), due to long lasting viability of their oospores (Wade, 1990). Indeed, the frequency of *Chara* sp. increased together with some emergents (*Alternanthera philoxeroides* and *Polygonum* spp.) and free floating leaves (*E. crassipes* and *Salvinia auriculata*). The last group mentioned above was primarily responsible for the ordination after the water depletion, in 2001.

The water level returned to normal in March 2000. Surprisingly, assemblage disruption expected during the water depletion in 2000 actually occurred in 2001, which showed no significant co-occurrence patterns in most arms and also considering the whole reservoir. Studies suggest that new species could colonize the open niche from buried seeds (Keddy & Fraser, 2000), and vegetative propagation after a disturbance (Barrat-Segretain & Amoros, 1996; Barrat-Segretain, Bornette & Hering-Vilas-Bôas, 1998). The absence of patterns found in 2001 could be attributed to the shore occupancy by the three life forms at the same time. Species, in special emergents, colonized the shores during the water depletion, co-occurred with the reestablishment of the submerged and free floating species. *Urochloa* sp. almost doubled its frequency of occurrence, showing its spread in the shores before occupied by submerged species.

The lowest *T*-values of the MRPP analyses were obtained when comparing the periods before and after the drawdown. This can be attributed to the establishment of new species colonizing firstly the open area in the shores and also to the death of many submerged species, which promoted an increase of species heterogeneity. A reservoir

drawdown disturbance can lead to loss of biomass and death of drought-intolerant aquatic macrophyte species, as well as replacement by species emerging from propagules, seed banks or buried seeds (e.g. Brock & Rogers, 1988; Combroux & Bornette, 2004). Therefore, drying periods affect specific life forms of macrophytes, reducing competition with other species and allowing a higher species diversity. Some species that may become extinct by water depletion disturbance can return in a few months after the water level has reestablished (e.g. submerged species; Thomaz et al. 2006) and recolonize the open area from seed bank and living propagules in the sediment (Rørslett, 1989; Richardson, Hanson & Locke, 2002).

The aquatic macrophyte assemblages in the whole reservoir and most of arms presented spatial organization patterns from 2002 to 2007. During the years *post* drawdown, biotic interactions and habitat preferences may have become stronger and promoted the exclusion or inclusion of species (e.g. *Hydrilla verticilata*; exotic firstly found in 2007). Besides the ecological interactions we must consider that life forms of the aquatic macrophytes have a conspicuous spatial segregation along the shore. This segregation promoted spatial co-occurrence patterns in the years following drawdown. This is consistent to pioneer interactions models, which predict that the importance of biotic interactions and in particular, competition, increase with reduction of disturbance (MacArthur & Wilson, 1967; Tilman, 1982). The underlying logic of competition theory is that productivity will increase until one or more resources become limited; and only the higher competitors will remain, eliminating the less able competitor from the assemblage (Tilman, 1982; Keddy, 2001). However, according to Keddy & Fraser (2000), generally, many kinds of natural disturbances promote a high biological diversity of macrophytes and then the margins are able to support many types of species, in particular, the emergents. Much of this co-occurrence in life forms reflects shared habitat preferences (Gotelli, Buckley & Wiens, 1997).

After 2003 it was possible to verify that species composition in macrophyte assemblages appeared to be more similar in relation to anterior years. According to Menge & Sutherland (1987), when physical and physiological disturbances decrease, species abundance tend to increase and, when the space is fully occupied, species compete. After competition and the exclusion of the less tolerant species, the species remained coexist. It has not occurred any disturbance like the drawdown occurred in

2000 (until 2007) and then we can assume that the similarity found in species composition in some arms of the reservoir can be attributed to the coexistence of many species occupying different places along the shore, as also was evidenced by the null model.

In summary, our study presented trends of co-occurrence patterns in aquatic macrophytes assemblage after a historic water depletion in a large subtropical reservoir. Distinctly of our expectations, in the drawdown year a pattern in co-occurrence distribution occurred. Colonization of the new open area by new species and death of many by desiccation promoted segregation of the life forms. Randomness was found one year later, where species were coexisting in areas supposed to be exclusive to some life forms. The aquatic macrophytes assemblage was spatially segregated in most arms of the reservoir, presenting also, higher similarity in species composition in posterior years after the return of normal level of the reservoir.

REFERENCES

Allison G. (2004) The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs*, 74, 117-134.

Barrat-Segretain M.H. (1996) Strategies of reproduction, dispersion and competition in river plants: a review. *Vegetatio,* 123, 13-37.

Barrat-Segretain M.H. & Amoros C. (1996) Recovery of riverine vegetation after experimental disturbance: a field test of the Path Dynamics Concept. *Hydrobiologia,* 321, 53-68.

Barrat-Segretain M.H., Bornette G. & Hering-Vilas-Bôas A. (1998) Comparative abilities of vegetative regeneration among aquatic plants growing in disturbed habitats. *Aquatic Botany*, 60, 201-211.

Barrat-Segretain M.H. & Bornette G. (2000) Regeneration and colonization abilities of aquatic plant fragments: effect of disturbance seasonality. *Hydrobiologia*, 421, 31-39.

Bini L.M., Thomaz S.M., Murphy K.J. & Camargo A.F.M. (1999) Aquatic macrophytes distribution in relation to water and sediment conditions in the Itaipu Reservoir, Brazil. *Hydrobiologia*, 415, 147-154.

Bini L.M., Thomaz S.M. & Souza D.C. (2001) Species richness and β-diversity of aquatic macrophytes in the Upper Paraná River floodplain. *Archiv für Hydrobiologie*, 151, 511-525.

Bini L.M. & Thomaz S.M. (2005) Prediction of *Egeria najas* and *Egeria densa* occurrence in a large subtropical reservoir (Itaipu Reservoir, Brazil-Paraguay). *Aquatic Botany*, 83, 227-238.

Biondini M.E., Bonham C.D. & Redente E.F. (1985) Secondary successional patterns in a sagebrush (*Artemisia tridentata*) community as they relate to soil disturbance and soil biological activity. *Plant Ecology*, 60, 25-36.

Bornette G. & Puijalon S. (2011) Response of aquatic plants to abiotic factors: a review. *Aquatic Sciences*, 73, 1-14.

Boschilia S.M., Oliveira, E.F. & Thomaz S.M. (2008) Do aquatic macrophytes co-occur randomly? An analysis of null models in a tropical floodplain. *Oecologia,* 156, 203-214.

Brock M.A. & Rogers K.H. (1998) The regeneration potential of the seed bank of an ephemeral floodplain in South Africa. *Aquatic Botany*, 61, 123-135.

Burke M.J.W. & Grime J.P. (1996) An experimental study of community invisibility. *Ecology*, 77, 776-790.

Combroux I.C.S. & Bornette G. (2004) Propagule banks and regenerative strategies of aquatic plants. *Journal of Vegetation Science*, 15, 13-20.

Cook C.D.K. (1990) *Aquatic plant book*. SPB, Leiden, NL

Davis M.A., Grime J.P. & Thompson K. (2000) Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology*, 88, 528–536.

Denslow J.S. (1985) Disturbance mediated coexistence of species. In: *The ecology of natural disturbance and patch dynamics*. (Eds S.T.A. Pickett & P.S. White), pp. 307-323. Academic Press, New York, USA:

Dormann C.F. & Gruber B. (2008) The bipartite package. http://cran.r-project.org/web/packages/bipartite/bipartite.pdf [Accessed in: July 2009].

Gotelli N.J., Buckley N.J. & Wiens J.A. (1997) Co-occurrence of Australian land birds: Diamond´s assembly rules revisited. *Oikos*, 80, 311-324.

Gotelli N.J. (2000) Null models analysis of species co-occurrence patterns. *Ecology*, 81, 2606-2621.

Gotelli N.J. & Graves G.R. (1996) *Null models in ecology*. Smithsonian Institution, Washington.

Havens K.E., Sharfstein B., Brady M.A., East T.L., Harwell M.C., Maki R.P. & Rodusky A.J. (2004) Recovery of submerged plants from highwater stress in a large subtropical lake in Florida, USA. *Aquatic Botany*, 78, 67-82.

Jiang L. & Patel S.N. (2008) Community assembly in the presence of disturbance: A microcosm experiment. *Ecology*, 89, 1931-1940.

Keddy P.A. (1982) Quantifying within-lake gradients of wave energy- interrelationships of wave energy, substrate particle-size and shoreline plants in Axe lake, Ontario. *Aquatic Botany*, 14, 41-58.

Keddy P.A. & Fraser L.H. (2000) Four general principle for the management and conservation of wetlands in large lakes: the role of water levels, nutrients competitive hierarchies and centrifugal organization. *Lakes and Reservoirs: Research and Management*, 5, 177-185.

Keddy P.A. & Reznicek A.A. (1982) The role of seed banks in the persistence of Ontario Coastal-plain flora. *American Journal of Botany*, 69, 13-22.

Keddy P.A & Reznicek A.A. (1986) Great-Lakes vegetation dynamics- the role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research*, 12, 25-36.

Lacoul P. & Freedman B. (2006) Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews*, 14, 89-136.

Lehsten V. & Harmand P. (2006) Null models for species co-occurrence patterns: assessing bias and minimum iteration number for the sequential swap. *Ecography*, 29, 786-792.

MacArthur R.H. & Wilson E.O. (1967) *The theory of island bio-geography.* Princeton University Press, Princeton.

Madsen J.D., Sutherland J.W., Bloomfield J.A., Eichler L.W. & Boylen C.W. (1991) The decline of native vegetation under dense Eurasian water milfoil canopies. *Journal of Aquatic Plant Management*, 29, 94-99.

McCune B. & Grace J.B. (2002) *Analysis of Ecological Communities*. MjM Software Design, Glenedon Beach, OR.

McCune B. & Mefford M.J. (2006) *PC-ORD. Multivariate Analysis of Ecological Data.* Version 5.15.

Menge B.A. & Sutherland J.P. (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist*, 130, 730-757.

Mitchell D.S., Pieterse A.H. & Murphy K.J. (1990) Aquatic plant problems and management in Africa. In: *Aquatic Weeds* (Eds A.H. Pieterse & K.J. Murphy, pp. 341–354. Oxford University Press, Oxford.

Oliveira E.F., Minte-Vera C.V. & Goulart E. (2005). Structure of fish assemblages along spatial gradients in a deep subtropical reservoir (Itaipu Reservoir, Brazil-Paraguay border). *Environmental Biology of Fishes*, 72, 283-304.

Pelicice F.M., Thomaz S.M. & Agostinho A.A. (2008). Simple relationships to predict attributes of fish assemblages in patches of submerged macrophytes. *Neotropical Ichthyology*, 6, 543-550.

Pistori R.E.T., Camargo A.F.M. & Henry-Silva G.G. (2004) Relative growth rate and doubling time of the submerged aquatic macrophyte *Egeria densa* Planch. *Acta Limnologica Brasliensia*, 16, 77-84.

Pott V.J. & Pott A. (2000) *Plantas aquáticas do Pantanal*. EMBRAPA, Brasília.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society.*, 4, 433-455.

Richardson S.M., Hanson J.M. & Locke A. (2002) Effects of impoundment and water level fluctuations on macrophyte and macroinvertebrate communities of dammed tidal river. *Aquatic Ecology*, 36, 493-510.

Riis T., Madsen T.V. & Sennels R.S.H. (2009) Regeneration, colonization and growth rates of allofragments in four common stream plants. *Aquatic Botany*, 90, 209-212.

Riis T. & Biggs B.J.F. (2003) Hydrologic and hydraulic control of macrophyte establishment and performance in streams. *Limnology and Oceanography*, 48, 1488-1497.

Rolon A.S. & Maltchik L. (2006) Environmental factors as predictors of aquatic macrophyte richness and composition in wetlands of southern Brazil. *Hydrobiologia,* 556, 221-231.

Rørslett B. (1991) Principal determinants of aquatic macrophyte richness in northern European lakes. *Aquatic Botany*, 39, 173-193.

Santamaria L. (2002) Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica*, 23, 137-154.

Sculthorpe C.D. (1967) *The biology of aquatic vascular plants*. Edward and Arnold Publ., London.

Silveira M.J., Thomaz S.M., Mormul R.P. & Camacho F.P. (2009) Effects of desiccation and sediment type on early regeneration of plant fragments of three species of aquatic macrophytes. *International Review of Hydrobiology*, 94, 169-178.

Stone L. & Roberts A. (1990) The checkerboard score and species distributions. *Oecologia,* 85, 74-79.

Tilman D. (1982) *Resource competition and community structure*. Princeton University Press, Princeton.

Thomaz S.M., Bini L.M., Souza M.C., Kita K.K. & Camargo A.F.M. (1999) Aquatic macrophytes of Itaipu Reservoir, Brazil: Survey of species and ecological considerations. *Brazilian Archives of Biology and Technology*, 42, 15-22.

Thomaz S.M. (2002) Fatores ecológicos associados à colonização e ao desenvolvimento de macrófitas aquáticas e desafios de manejo. *Planta Daninha*, 20, 21-33.

Thomaz S.M., Pagioro T.A., Bini L.M. & Murphy K.J. (2006) Effects of reservoir drawdown on biomass of three species of aquatic macrophytes in a large sub-tropical reservoir (Itaipu, Brazil). *Hydrobiologia,* 570, 53-59.

Townsend C.R. (1989) The patch dynamic concept of stream community ecology. *Journal of North American Benthological Society*, 8, 36-50.

Turner M.G. & Dale V.H. (1998) Comparing large, infrequent disturbances: What have we learned? *Ecosystems*, 1, 493-496.

Vermaat J.E., Santamaria L. & Roos P.J. (2000) Water flow across and sediment trapping in submerged macrophyte beds of contrasting growth form. *Archiv für Hydrobiologie*, 148, 549-562.

Wade P.M. (1990) The colonisation of disturbed freshwater habitats by Characeae. *Folia Geobotanica*, 25, 275-278.

Partitioning beta diversity of aquatic macrophyte assemblages in a subtropical reservoir: turnover or nestedness prevalence?[2]

Trabalho realizado em conjunto com: Edson

Fontes de Oliveira e Albano Schwarzbold

---

[2] O trabalho será submetido a revista Oikos. A formatação está conforme as normas da revista, exceto pela posição das figuras no texto, pelo espaçamento e pelo alinhamento do texto.

ABSTRACT

Identification of factors promoting biodiversity and, more specifically, the causes that contribute to beta diversity is a central and growing issue in ecology. In this study, long term data were used to assess the beta diversity partitioning of aquatic macrophyte assemblages in five arms of Itaipu reservoir, Brazil-Paraguay border. We partitioned beta diversity (β_{sor}) in two components: nestedness (β_{nes}) and species turnover (β_{sim}). To verify if some environmental variables (electrical conductivity, water transparency and fetch) affected the components of beta diversity, we used a permutational multivariate analysis of variance. For the study period (1999-2007) we observed high values of beta diversity and a prevalence of spatial turnover of species occurred. They were affected by all environmental factors studied, which demonstrated significant interaction. Dendritic form of arms, high shore development, water physical and chemical local conditions and biotic interactions could be factors determining prevalence of spatial turnover of aquatic macrophyte assemblages. Although macrophytes are considered highly dispersive, most species in the reservoir presented low frequency of occurrence during the whole study. This indicates that species colonizing the arms had some specific environmental requirements that prevented them from colonizing the whole reservoir.

INTRODUCTION

The identification of factors promoting biodiversity and, more specifically, the causes that contribute to beta diversity is a central and growing issue in ecology. Diversity in nature was first conceptualized by Whittaker (1960, 1972), which used the term beta-diversity (β-diversity) as the difference in composition between habitats. The last two decades had an increase of interest in studies about β-diversity (e.g. Whittaker 1972; Koleff et al 2003; Baselga 2010), which is considered crucial for the identification of long-term processes and local factors that determine regional biodiversity patterns (Ricklefs, 2004).

Beta diversity can be partitioned in two different processes: the spatial turnover of species and the community nestedness (Baselga 2007). The study of β diversity components, Baselga (2010) presented a unified structure that distinguishes the real contribution of the turnover and nestedness for beta diversity pattern. Spatial turnover is implied in the replacement of some species by others (Harrison et al 1992; Baselga 2007; Baselga 2010), while nestedness consists in species-poor sites being subsets of species-rich sites (Patterson and Atmar 1986; Ulrich and Gotelli 2007).

The species turnover should be the outcome of environmental sorting and/or spatial and historical constraints (Nekola and White 1999; Qian et al 2005), including geographical isolation due to dispersal barriers (Gaston et al 2007). On the other hand, nestedness reflects a non-random process of regional species loss as consequence of local factors that promote constraints of assemblage development, such as: selective colonization, differential extinction, environmental pressure on rare species, nestedness of habitats and interspecific ecological variation in tolerance to environmental conditions.

Attributing the different beta diversity patterns to their respective physical and/or ecological phenomena is essential to analyze the causality of the processes underlying biodiversity. Local and regional processes that influence beta diversity interact on a continuum of space and time, which creates a regional effect on diversity (Ricklefs, 2004). Therefore, spatial variation in species assemblage structure is one important aspect of beta diversity, because it predicts broad-scale environmental changes (Nekola and White 1999; Tuomisto et al 2003; Soininen et al 2007a,b). On the other hand,

because of the dispersal of individuals through populations, the interactions among species coexisting occur over large, environmentally heterogeneous regions rather than within local communities in relatively uniform habitats (Hubbell 2001; Cottenie 2005).

Large reservoirs became important water bodies in Brazil, especially after the 1970s, mainly for hydroelectric power generation, and secondarily for fisheries, navigation, tourism and water supply (Agostinho et al. 1995). These ecosystems exhibit similar ecological succession to that observed in lakes, although in shorter timescale (Thornton 1990; Thomaz and Bini 1998). At some stage of their aging, usually since filling with water, aquatic plants colonize reservoirs (Agostinho et al 1995; Thomaz and Bini 1998). Although macrophytes are generally deemed as "weeds", they are important for the integrity and functioning of the aquatic ecosystem. Aquatic macrophytes typically increase the complexity of environmental structure (Thomaz et al 2008), provide habitats for a range of organisms such as phytoplankton, zooplankton and fish (Biggs 1996; Pelicice and Agostinho 2006; Padial et al 2009; Mormul et al 2010). They also influence the hydrology and sediments dynamics of the system, shifting the water flow (Madsen et al 1991) and trapping, resuspending particles (Vermaat et al 2000).

Studies conducted with large-term data provide us the understanding of phenomena that arise over time. The opportunity emerged when occurred a historic water depletion (ca. 5m) at the dam level (between November 1999 and March 2000; 108 days) in one of the largest reservoirs in the world, Itaipu, allowing us to evaluate the change in the aquatic macrophyte assemblages structure, before, during and after this event. The water depletion that occurred in this reservoir was characterized as spatially and temporally intense. Great disturbances like this one can promote death of large amounts of vegetal biomass and also local species extinctions, mainly because the reservoir is very dendritic and the shores were largely exposed during this period. These factors increase the dissimilarity between sites, which increase *per se*, the beta diversity. As the disturbance affects differently the depth gradient along the arms of the reservoir, the turnover of species should be higher than nestedness.

Using this particular circumstance, we aimed to analyze the β-diversity spatial-temporal patterns of aquatic macrophyte assemblages in the Itaipu reservoir, over eight years. Therefore, considering five arms sampled along eight years (1999-2007) in the

Itaipu reservoir, we: (i) analyzed general patterns of beta diversity and its components (nestedness and turnover); (ii) tested whether environmental variables (electrical conductivity, Secchi and fetch) had relation with the patterns aforementioned and (iii) verified if the drawdown promoted shift in the beta diversity, mainly in the turnover and nestedness patterns of the macrophyte assemblages, comparing with the year before and after the event.

It is worth mentioning that Thomaz et al (2003) studied beta diversity patterns of the aquatic plants assemblage in this reservoir in eight arms in 1999. The indexes used were β_1 and β_2 from Harrison et al (1992). According to the indexes, species turnover was slightly higher among arms than among stands of a same arm and the sum of the coefficients of variation of environmental variables on species turnover was significant.

Due to inherent differences of each arm (e.g. nutrients, shoreline length, and physic-chemical characteristics; Bini et al 1999; Thomaz et al 2003) we expect high values of beta diversity, with turnover demonstrating importance among arms, while nestedness would be the prominent process within arms. Indeed, due to these differences and because each species has its particular ecological and physiological tolerances, we also expect an interaction between beta diversity with the environmental factors. In 2000, during the water depletion, we expect extinction of many species, especially submersed ones, increasing species composition dissimilarity and spatial turnover between arms, while within arms we expect also species turnover instead of nestedness (due to e.g. species extinction and colonization from new ones). The following year is expected to have predominance of high beta diversity and also spatial turnover between arms and within them due to physiologic constraints and biotic interactions (e.g. competition).

STUDY AREA

The study was conducted in the Itaipu Reservoir, a dendritic impoundment, located along Brazil-Paraguay border (24^o05'S and $25\ ^o33$'S; $54\ ^o00$'W and $54\ ^o37$'W), in the Paraná River (Fig.1). It is characterized by being large (1,350 km²) and deep (mean depth = 21.5m). The mean residence time is 40 days, but it reaches 29 days in the

main water body (Thomaz et al 2003), being longer in the arms of the reservoir (which are the drowned valleys of influent streams). Five arms in this reservoir were analyzed, which are located in the Brazilian margin and surveyed from 1999 to 2007. These arms were: São Francisco Verdadeiro (SFV), São Francisco Falso (SFF), São Vicente (SV), Ocoí (OC) and Passo Cuê (PC). São Francisco Verdadeiro arm presented the lowest values of Secchi and was greatly colonized by algae, due in part to the high water phosphorus and nitrogen concentrations originate from agricultural areas, mainly cattle raising, upstream (eutrophic arm).
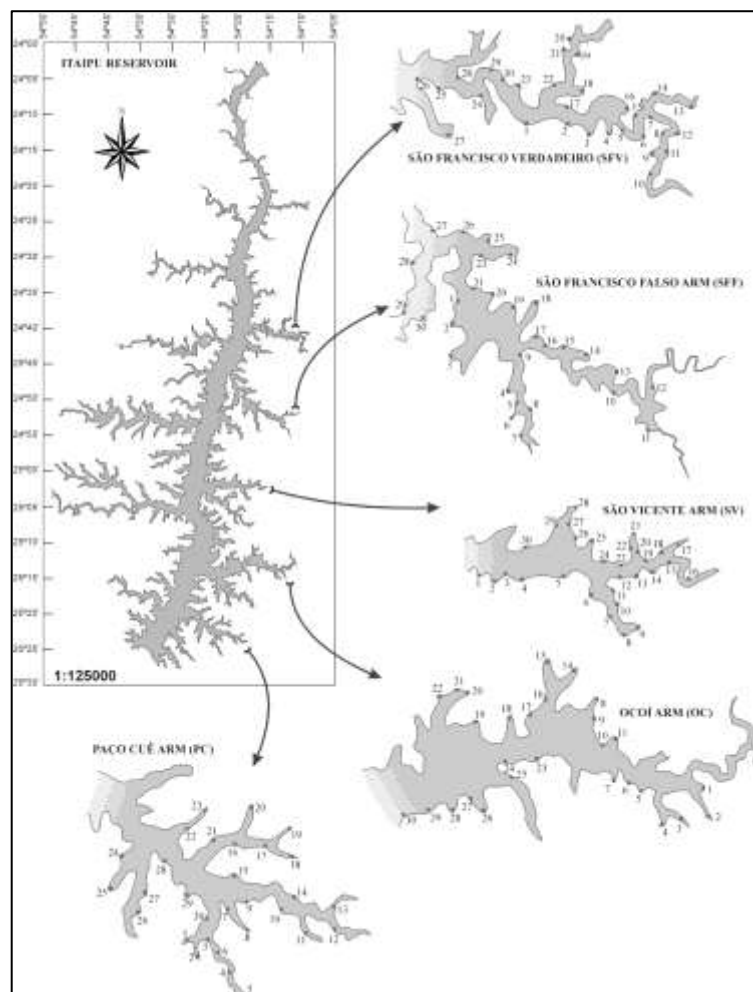

Figure 1. Location of the Itaipu reservoir and sampling sites (150). Arms codes used in the text are as follow: São Francisco Verdadeiro (SFV), São Francisco Falso (SFF), São Vicente (SV), Ocoi (OC), and Paço Cuê (PC).

São Francisco Falso was classified as mesotrophic, while São Vicente was oligotrophic and had the highest fetch values. Ocoí and Paço Cuê arms are located in the lacustrine zone of the reservoir and presented high values of water transparency and

fetch (oligo-mesotrophic arms). For more detailed information see Bini et al. (1999), Thomaz et al. (1999).and Bini and Thomaz (2005).

MATERIAL AND METHODS

SAMPLING

A total of 150 sites (30 per arm) were georeferenced. From a boat in constant velocity, during 8-12 minutes (~100m), we recorded and collected aquatic macrophytes in each sampling site. In the Itaipu Reservoir, the maximum depth colonized by aquatic macrophytes is approximately 4m, exceptionally reaching 8m (Thomaz et al. 1998). Three meter long rake, with curved prongs were also used to collect submerged vegetation. This method minimizes underestimating the submerged species richness. Only euhydrophytes were included in this study, because they present body parts with functional photosynthetic structures and/or rooting structures on the surface of the hydrosoil or water column overlying the hydrosoil, for at least 50% of the time (Bini et al 2001). Using this criterion circumvents problems caused by dubious ways to distinguish aquatic from non-aquatic species (see more in Rørslett 1991).

Beyond aquatic macrophytes sampling, some limnological data were also collected. Electrical conductivity values were obtained by a digital potentiometer Digimed®, while water column transparency was measured with a Secchi disc (in meters). Fetch, the variable that indicates the free water surface for wind action, revealing also its intensity (Azza et al 2007; Håkanson and Jansson 1983) was calculated for each sampling site. For each site, a vertical line was projected in the direction of the center of the arm (90°), while the distances (X_i, in km) from the sampling site to land or an island were measured for every deviation angle (λ_i), where $\lambda_i = \pm10^{o}, \pm20^{o},\dots \pm80^{o}$, totaling 160°. The effective fetch (not corrected by wind direction), L_f, was calculated from the formula (Håkanson and Jansson 1983): $L_f = [(\Sigma X_i.\cos_i)/(\Sigma \cos_i)].s$, where s is constant referent to the scale of the map. Fetch can be considered as a surrogate variable indicating the wave disturbance by the wind, as demonstrated by Thomaz et al (2003).

Beta diversity was estimated for aquatic macrophytes in all sites in the five arms in the Itaipu reservoir. Sørensen dissimilarity index (β_{sor}) formula is $\beta_{sor} = (b+c)/(2a+b+c)$, in which a is the number of species that occur in both sites; b is the number of species that appears only in the first site and c is the number of species occurring only in the second site. β_{sor} is one of the most used measures due to its dependence on the proportion of species shared between two communities and this measure is well known to incorporate the true spatial turnover and differences in richness along gradient (Koleff et al 2003).

Using the additive partitioning framework proposed by Baselga (2010), we also provided the decomposition of the pairwise dissimilarity index (β_{sor}) in two additive components: spatial turnover (β_{sim}) and nestedness (β_{nes}). Therefore $\beta_{sor}= \beta_{sim}+\beta_{nes}$. The formula used for β_{sim} and β_{nes} are as follows: $\beta_{sim}= \min(b,c)/[a+\min(b,c)]$; $\beta_{nes}= \{[\max(b,c)-\min(b,c)]/[2a+\min(b,c)+ \max(b,c)]\} \times \{a/[a+\min(b,c)]\}$, in which, variables a, b and c were as described above.

It is important to highlight that dissimilarity due to nestedness (β_{nes}) is related to, but different from, nestedness *per se* (Baselga 2010). Many authors suggest that the species turnover or decay of similarity is caused by at least two, not mutually excluding, processes: the environmental filtering hypothesis (Keddy 1992) and the dispersal limitation hypothesis (Hubble 2001). In an attempt to visualize better the components of Sørensen dissimilarity index, β_{sim} and β_{nes} results values were standardized ($\beta_{nes\ stardardized}=\beta_{nes}/\beta_{sor}$ and $\beta_{sim\ standardized}= \beta_{sim}/\beta_{sor}$), ranging from 0 to 1 and their sum equals value one (1). The standardized values of β_{sim} and β_{nes} in all text, figures and tables are named as β_{sim} and β_{nes}.

To test whether the aquatic macrophytes beta diversity pattern, turnover and nestedness dataset were affected by year, arms sampled, limnological variables (fetch, Secchi and electrical conductivity) and their interactions we used a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001; McArdle and Anderson 2001). Our data did not reach the assumptions of parametric statistical analysis (normality Shapiro-Wilk test, $p<0.001$ and homogeneity of variance Levene test $p<0.001$), so this analysis is well appropriate. PERMANOVA tests the simultaneous

response of one or more variables to one or more factors in an ANOVA experimental design on the basis of any distance measure, using permutation methods. PERMANOVA is different from traditional ANOVA because it calculates the P-values using permutations, rather than relying on tabled p-values which assume normality. More details about PERMANOVA are found in Anderson (2001). We analyzed untransformed, unstandardized data, using the Bray-Curtis measure of dissimilarity, with 999 permutations per test.

Due to sampling issues, we could not measure electrical conductivity and Secchi in 2000. When this year was not included in the analysis, Secchi and electrical conductivity and fetch (beyond another years and arms) were included in the PERMANOVA test. When 2000 ran with all years, only arms and years were considered as predictive variables.

To assess if the drawdown of 2000 was capable to shift beta diversity, turnover or nestedness, we ran PERMANOVA precisely in the years 1999, 2000 and 2001 and used those years and arms as predictive variables. To evaluate if there were any significant differences among arms and years in relation to beta diversity and its components, we ran Kruskal-Wallis *post hoc* comparisons. This test was carried out in STATISTICA 7.0 (StatsoftInc, USA). The analyses (beta diversity partitioning and PERMANOVA) were carried out through the statistical program R, version 2.14.0 (R development Core Team, 2011), using the "beta.pairwise" function provided by Baselga (2010) and function "adonis", both from the vegan package (Oksanen et al 2012).

RESULTS

We found 37 euhydrophyte taxa belonging to 23 families (Table 1). Of this total, the most frequent taxa were *Urochloa subquadripara*, *Panicum* sp., *Egeria najas* and *Polygonum* sp. and the less frequent were *Typha domingensis*, *Pontederia* sp and *Bacopa* sp. (Fig.2).

Table 1. Families and species recorded during the whole study (1999-2007) in the Itaipu reservoir. Life forms: EM= emergent; EP= epiphyte; RS= rooted submerged; FS= free submerged; FL= floating leaved; FF=free floating.

| Family	Species	LF
Alismataceae	*Sagittaria montevidensis* Cham. & Schltdl.	EM
Amarantaceae	*Alternanthera philoxeroides (Mart.) Griseb.*	EM
Araceae	*Pistia stratiotes* L.	FLU
Araliaceae	*Hydrocotyle ranunculoides* L.f.	EM
Characeae	*Chara* spp. L. Emend C.Agardh emend R. Braun	SE
	Nitella sp. C. Agardh emend R. Braun emend Leonhard	SE
Commelinaceae	*Commelina* sp. L.	EM
Convolvulaceae	*Ipomoea* sp.L.	EM
Cyperaceae	*Eleocharis minima.* Kunth	EM
	Eleocharis filiculmis Schur	EM
	Oxycaryum cubense (Poepp. & Kunth) Palla	EP
	Rhynchospora corymbosa (L.) Britton	EM
Euphorbiaceae	*Caperonia castaneifolia* (L.) A. St.-Hil.	EM
Haloragaceae	*Myriophyllum aquaticum* (Vell.) Verdc.	SE
Hydrocharitaceae	*Egeria densa* Planch.	SE
	Egeria najas Planch.	SE
	Hydrilla verticillata (L.f.) Royle	SE
	Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine	FLU
Lemnaceae	*Lemna valdiviana* Phil.	FLU
Lentibulariaceae	*Utricularia* sp. L.	SL
Menyanthaceae	*Nymphoides indica* (L.) Kuntze	FF
Najadaceae	*Najas* sp. L.	SE
Nympheaceae	*Nymphea amazonum* Mart. & Zucc.	FF
Onagraceae	*Ludwigia* spp. L.	EM
Poaceae	*Panicum* sp. L.	EM
	Paspalum repens P.J. Bergius	EM
	Urochloa sp. P. Beauv.	EM
	Echinochloa sp. P. Beauv.	EM
Polygonaceae	*Polygonum* spp. L.	EM
Pontederiaceae	*Eichhornia azurea* (Sw.) Kunth	EM
	Eichhornia crassipes (Mart.) Solms	FLU
	Pontederia sp. L.	EM
Salviniaceae	*Salvinia auriculata* Aubl.	FLU
	Salvinia herzogii de la Sota	FLU
	Salvinia minima Baker	FLU
Plantaginaceae	*Bacopa* sp. Aubl.	EM
Typhaceae	*Typha domingensis* Pers.	EM
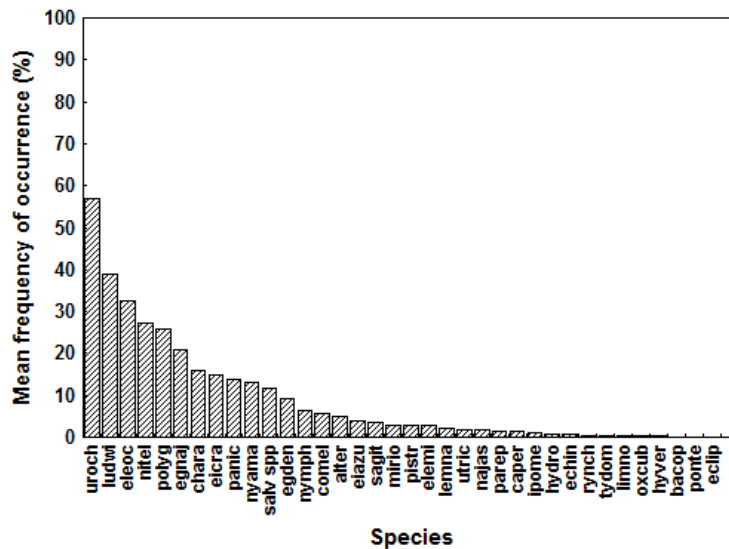
Figure.2. Mean frequency of occurrence of aquatic macrophyte species, considering all years (1999-2007) and reservoir arms. Species code: uroch-*Urochloa subquadripara*; ludwi-*Ludwigia* spp.; eleoc-*Eleocharis filiculmis*; nitel-*Nitella* sp.; polyg-*Polygonum* spp.; egnaj-*Egeria najas*; chara-*Chara* spp.; eicra-*Eichhornia crassipes*; panic-*Panicum* sp.; nyama-*Nymphea amazonum*; salv spp- *Salvinia* spp.; egden-*Egeria densa*; nymph-*Nymphoides indica*; comel-*Commelina* sp.; alter-*Alternanthera philoxeroides*; eiazu-*Eichhornia azurea*; sagit-*Sagittaria montevidensis*; mirio-*Myriophyllum aquaticum*; pistr-*Pistia stratiotes*; elemi-*Eleocharis minima*; lemna-*Lemna valdiviana*; utric-*Utricularia* sp.; najas-*Najas* sp.; parep-*Paspalum repens*; caper-*Caperonia castaneifolia*; ipome- *Ipomoea* sp.; hydro-*Hydrocotyle ranunculoides*; echin-*Echinochloa* sp.; rynch-*Rhynchospora corymbosa*; tydom-*Typha domingensis*; limno- *Limnobium laevigatum* oxcub-*Oxycaryum cubense;* hyver-*Hydrilla verticillata*; bacop-*Bacopa* sp.; ponte-*Pontederia* sp.; eclip-*Eclipta* sp.

Beta diversity (β_{sor}) presented high values (up to 0.7) along the eight years of the study (Fig. 3b) and also in all arms of the reservoir (Fig. 3d). The nestedness pattern expected within arms was not met. The predominant process within the arms and also between arms was spatial turnover (Fig.3h). This also occurred temporally, all years presented high spatial turnover (Fig. 3f). In the arms of Itaipu reservoir it was possible to observe that in all years of the study, including before (1999), during (2000) and just after (2001) the water depletion, the process responsible for the beta diversity was spatial turnover of species.

In an attempt to assess if there are abiotic differences between the arms, the Kruskal-Wallis showed no significant statistical differences in relation to fetch (H=2.98; *p*=0.55). However, electrical conductivity (H=69.96; *p*<0.001) and Secchi (H=95.64; *p*<0.001) had significant differences. When considering electrical conductivity, the last arm, PC, was different from the others. Analyzing the multiple comparisons (*post hoc* test), we noticed one gradient from upstream to downstream: in relation to Secchi, the

first two arms (SFF, SFV) did not differ from each other and are different from the other three (SV, OC and PC), which are downstream.

Both Sørensen dissimilarity index (β_{sor}) and species turnover (β_{sim}) were affected by the interaction with all variables (fetch, Secchi, electrical conductivity, arm and year) considered in the analysis (F=1.125; p=0.02 and F=1.613; p=0.002 respectively). Nestedness pattern was affected by the interaction of year, arm and fetch, which presented significant results (F=2.93; p=0.001).

Considering the first three years of the study and focusing on the possible consequences caused by water depletion in 2000, the year before the event presented significant increase in beta diversity in 2000 and 2001 ($H_{(2,\ 375)}$=57.95; p<0.001; Fig. 3a), while they did not differ from each other. Indeed, all arms also differed significantly ($H_{(4,375)}$= 30.42; p<0.001; Fig. 3c).

We had a significant difference for species turnover and consequently nestedness in 2000 ($H_{(2,375)}$ =18.95; p<0.001; Fig.3e), comparing with 1999. Species turnover values kept higher than nestedness values. The five arms in the reservoir (SFV, SFF, SV, OC and PC) had predominance of spatial turnover before, during and after the water depletion (Fig.3g). After the drawdown in 2000, the following years were characterized by high values of beta diversity (β_{sor}; Fig. 3b) and by species turnover (β_{sim}; Fig. 3f). This phenomenon prevailed in all years, inclusively in all arms (Fig 3f and 3h).
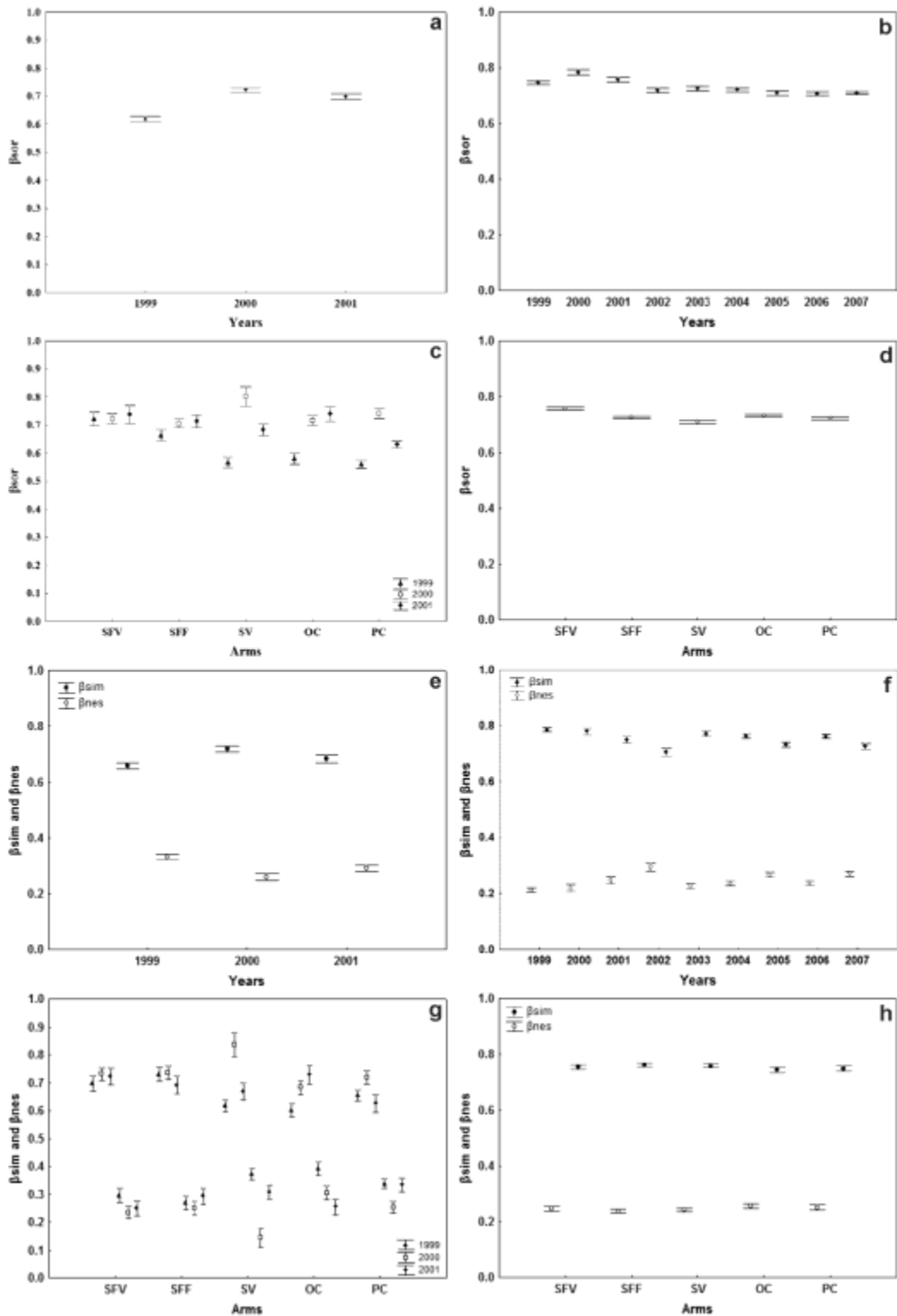
Figure 3. Mean and standard error for the first three years (before, during and after the drawdown) for (a) β_{sor} and (e) β_{sim}, β_{nes} values. Along the whole study (b) Sørensen dissimilarity index (β_{sor}) and (f) species turnover (β_{sim}) and nestedness (β_{nes}).When comparing arms in the three first years, (c) β_{sor} and (g) β_{sim} and β_{nes}. Comparing the arms along the study years (d) β_{sor} and (h) β_{sim} and β_{nes}. Arms code: SFV- São Francisco Verdadeiro; SFF- São Francisco Falso; SV- São Vicente; OC- Ocoí and PC- Paço Cuê. Values of β_{sim} and β_{nes} are standardized.

Relating the arms separately, we noticed that the two first arms in the reservoir, SFV and SFF, did not differ in any year (1999-2001) for beta diversity and its components β_{sim} and β_{nes} (Fig 3c and 3g; Table 2). The other three arms (SV, OC, PC), located downstream, presented significant differences, generally presenting increase in in 2000 for β_{sor} and β_{sim} values (Fig 3c and 3g; Table 2).

Table 2. Nonparametric Kruskal-Wallis test. Differences in relation to β_{sor}, and β_{sim} in the five arms of the reservoir considering only the three first years of sampling. Values of β_{sim} were standardized.

		β_{sor}			β_{sim}		
	F	p	Differed years	F	p	Differed years
SFV	0.05	0.97		0.19	0.90	
SFF	3.18	0.20		1.18	0.55	
SV	21.89	<0.001	99≠00 and 99≠01	10.09	0.006	99≠00
OC	24.49	<0.001	99≠00 and 99≠01	11.05	0.004	99≠01
PC	34.08	<0.001	all years differed	3.38	0.18	

DISCUSSION

Beta diversity may be caused by environmental factors acting in the present time (niche-difference model) and by spatial factors and historical events (model of temporal and spatial constraint) as suggested by Nekola and White (1999). The former case of decay of similarity results from a simple decrease in environmental similarity with distance. The underlying reason is competitive sorting of species with different physiological tolerances. The latter refers to temporal and spatial structures and their influences on species across landscapes.

In Itaipu reservoir both processes could cause high beta diversity and species turnover. Our analyses showed that beta diversity and species turnover prevailed in all arms, during the whole study (1999-2007). For the aquatic macrophyte assemblages in Itaipu reservoir, geographical and limnological diversification along longitudinal gradient and their temporal variation demonstrated that these factors can explain the spatial turnover within and between arms.

The studied arms are dendritic and present large shoreline length (Thomaz et al 2006). This is a favorable area for aquatic macrophytes colonization and development (Rørslett 1991). Thomaz et al (2003) found a significant relationship between shore

lengths predicting species richness in Itaipu reservoir. According to authors, the upper portion of the Itaipu reservoir is richer and presented an increase of 0.16 species *per* km. This could be due to higher nutrient concentrations (SFF and SFV present the highest values for phosphorus and nitrogen, Bini et al 1999), shallower sites, with low exposure to wind, and constant input of propagules upstream. These characteristics were found in other dendritic tropical reservoirs (Esteves and Barbieri 1983; Bini et al 2005). The high diversity found in the studied reservoir may be due spatial heterogeneity and this may have promoted high beta diversity values. With the water depletion event, some life forms, which inhabit the shores, were affected and could cause turnover predominance instead nestedness. Previous study about the limnological characterization of the Itaipu reservoir presented a longitudinal difference: the upper arms showed high conductivity, an indication of high nutrient concentrations and suspension solid material that comes from upstream stretches of reservoir. The same occurred with water transparency, which presented higher values in arms located closer to the dam due to the sediment trapping (Pagioro and Thomaz 2002). It was expected that limnological factors should have interactions between them. It is known that in sites with low steep margins and shallow waters, fetch can cause sediment resuspension and promote low water transparency. This reduction in transparency is due to suspended materials in water, increasing ions concentration and consequently, electrical conductivity. Some studies have assessed this effect on aquatic plants (Rea et al 1998; Van der Berg et al 2003; Istvánovics et al 2008).

These environmental gradients tend to segregate some species according to their physiological tolerances. Beta diversity is more a function of their niche breadths combined with the temporal and spatial structures of the landscape. Thomaz et al (2003) studied the Itaipu reservoir arms and detected, in 1999, that the sum of the coefficients of variation of environmental variables (electrical conductivity, secchi disc, turbidity, k and fetch) on species turnover was significant, i.e., such results may be accounted for by peculiarities of the limnological and morphometric features of each arm. In a study with macrophytes in Ireland, Heegaard (2004) concluded that the most important factors determining the species turnover were the combined influence of chemical gradients and the distance between lakes. For example, we observed in Itaipu more free floating leaves species occupying the superior arms (riverine zone) while submerged ones

generally occur in the inferior arms (lacustrine zone), which had more transparent waters (Bini et al 1999). Heegaard et al (2001) showed that macrophyte species in lakes were affected by conductivity gradient and suggests the presence of two species pools, species preferring either high or low ionic concentrations. We observed a gradient of ionic concentrations in the arms of the reservoir. Besides these factors, fetch is an important environmental variable for macrophyte species distribution (Azza et al 2007) and species richness (Thomaz et al (2003). Although our measurement of this variable made it constant over time, its wide range within arms (from 0 to 30), can promote different suitable habitats (sites with low values of fetch) for many macrophyte species (Azza et al 2007; Boschilia et al submitted).

We expected a nestedness pattern within arms due to high dispersion rates (Barrat-Segretain and Bornette 2000) and prevalence of asexual reproduction (Heegaard et al 2001) in aquatic macrophytes (Barrat-Segretain 1996). Even with this ability, the spatial species turnover were very high, providing us evidences that there are important factors capable of limiting the species distribution. It has been hypothesized that environmental conditions may filter species: species arriving from regional species pool only colonize in local habitats if functional physiological, morphological, and/or life-history traits are compatible with habitat characteristics (Keddy 1992). Beyond environmental features, biotic interactions, (such as competition for more stable habitats), and varying conditions of attenuation of solar radiation, are also important in determining species distribution and composition (e.g., Barrat-Segretain 1996; Van der Berg et al. 2003). As a result, quantifying the links between a habitat´s conditions and the functional traits of its species represents a first, necessary step in determining the processes governing species distributions.

A species considered specialized is confined to a relatively narrow limit of environmental conditions. As we observed in our data, most species found in the arms of the reservoir had less than 20% of frequency of occurrence, and these species can be considered specialized to certain environments and this may account for their relative rarity. Other reasons can be considered, for example, competitive exclusion, limited dispersal ability or lack of a suitable substrate to anchorage within the arm. Species that are strongly restricted to specific habitat conditions, therefore, automatically will be rare in a dataset that covers a wide range of environmental characteristics.

As the first two upper arms of the reservoir (SFF and SFV) did not differ in the first three years for β_{sor}, β_{sim} and β_{nes} values, these arms could be influenced by the constant input of propagules from upstream (from the Upper Paraná River floodplain). Indeed, these arms are characterized by low water transparency and consequently low frequency of submersed species inhabiting the water column. When drawdown occurred, the death of these species promoted less impact in these arms than the other three located more downstream (SV, OC and PC) which have more transparent water and more submersed species. This panorama revealed higher values of β_{sor} and β_{sim} in 2000 for these arms. The differences occurring in 2000 also continued in 2001, showing that the effect of the water depletion upon the macrophyte assemblage in the Itaipu reservoir was still driving changes in species composition in the downstream arms.

The drawdown promoted an enormous quantity of dead macrophyte biomass, specifically the submerged species that colonized preferentially the shallow margins of the arms. Consequently, large open areas were available for colonization of ruderal species and of bank seed germination (Bonis and Grillas 2002; Havens et al. 2004). New species have colonized in this area while several species had become extinct. The following years remained with high values of beta diversity and species turnover. This pattern remained until the end of studied period, characterizing the aquatic macrophytes of Itaipu reservoir as an assemblage with high beta diversity and predominance of species turnover above nestedness during the whole study, between and within the arms.

In sum, the Itaipu reservoir has some features that contributed to the prevalence of species spatial turnover in all arms, in great spatio-temporal dimensions. Arms morphology, limnological conditions of each arm and biotic interactions could be factors determining the spatial turnover of macrophyte assemblages. Although macrophytes are considered highly dispersive, most species in the reservoir presented low frequency of occurrence during the whole study. This is indicative of many environmental filters guiding the distribution of the aquatic macrophytes species in the arms of the reservoir preventing them to inhabit the whole reservoir. It should encourage future studies about how many other factors, not evaluated in this study, contribute to the spatial turnover of macrophyte assemblages in large reservoirs.

ACKNOWLEDGEMENTS

REFERENCES

Agostinho, A. A. et al. 1995. The High Paraná River Paraná basin: limnological and ichthyological aspects. – In: Tundisi, J. G., Bicudo, C. E. M., Matsumura-Tundisi T. (eds), Limnology in Brazil. Brazilian Academy of Science/Brazilian Society of Limnology, Rio de Janeiro, pp 59–104.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. – *Austral Ecol.* **26**: 32–46

Azza, N. et al. 2007. Shoreline vegetation distribution in relation to wave exposure and bay characteristics in a tropical great lake, Lake Victoria. – J. Trop. Ecol. 23: 353-360.

Barrat-Segretain, M. H. 1996. Strategies of reproduction, dispersion and competition in river plants: a review. – J. Veg. Sci. 123: 13-37.

Barrat-Segretain, M. H. and Bornette, G. 2000. Regeneration and colonization abilities of aquatic plant fragments: effect of disturbance seasonality. – Hydrobiologia 421:31-39.

Baselga, A. 2007. Disentangling distance decay of similarity from richness. – Ecography 30:838-841.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. – Glob. Ecol. Biogeogr. 19: 134–143.

Biggs, B. J. F. 1996. Hydraulic habitat of plants in streams. – Regul.River. 12: 131-144.

Bini, L. M. et al. 1999. Aquatic macrophytes distribution in relation to water and sediment conditions in the Itaipu Reservoir, Brazil. – Hydrobiologia 415: 147-154.

Bini, L. M. et al. 2001. Species rich-ness and β -diversity of aquatic macrophytes in the Upper Paraná River floodplain. – Arch. Hydrobiol. 151: 511–525.

Bini, L. M. and Thomaz, S. M. 2005. Prediction of Egeria najas and Egeria densa occurrence in a large subtropical reservoir (Itaipu Reservoir, Brazil-Paraguay). – Aquat. Bot. 83: 227-238.

Bini, L. M. et al. 2005. Patterns of the aquatic macrophytes cover in Cachoeira Dourada reservoir (GO-MG). – Braz. J. Biol. 65: 19-25.

Bonis, A. and Grillas, P. 2002. Deposition, germination and spatio-temporal patterns of charophyte propagule banks: a review. – Aquat. Bot. 72: 235-248.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecol. Lett. 8: 1175-1182.

Esteves, F. A. and Barbieri, R. 1983. Dry weight and chemical change during decomposition of tropical macrophytes in Lobo reservoir –São Paulo, Brazil. – Aquat. Bot. 16: 285-295.

Gaston, K. J. et al. 2007. Spatial turnover in the global avifauna. – Proc. R. Soc. B. 274: 1567–1574.

Harrison, S. et al. 1992. Beta-diversity on geographic gradients in Britain. – J. Anim. Ecol. 61: 151 – 158.

Havens, K. E. et al. 2004. Recovery of submerged plants from highwater stress in a large subtropical lake in Florida, USA. – Aquat. Bot. 78: 67–82.

Heegaard, E. et al. 2001. Species-environmental relationships of aquatic macrophytes in Northern Ireland. – Aquat. Bot. 70: 175-223.

Heegaard, E. 2004. Trends in aquatic macrophyte species turnover in Northern Ireland – which factors determine spatial distribution of local species turnover? – Global Ecol. Biogeogr. 13: 397-408.

Hubbell, S. P. 2001. The unified neutral theory of biodi-versity and biogeography. – Princeton Univ. Press.

Håkanson, L. and Jansson, M. 1983. Principles of lake sedimentology. – Springer-Verlag, Berlin.

Istvánovics, V. et al. 2008. Distribution of submerged macrophytes along environmental gradients in large, shallow Lake Balaton (Hungary). – Aquat. Bot. 88: 317-330.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. – J. Veg. Sci 3: 157-164.

Koleff, P. et al. 2003. Measuring beta diversity for presence-absence data. – J. Anim. Ecol. 72: 367–382.

McArdle, B. H. and Anderson, M. J. 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. – *Ecology* **82**: 290–297.

Madsen, J. D. et al. 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. – J. Aquat. Plant Manage. 29: 94-99.

Mormul, R. P. et al. 2010. Epiphyton or macrophyte: Which primary producer attracts the snail *Hebetancylus moricandi*? – Am. Malacol. Bull. 28, 127-133.

Nekola, J. C. and White, P. S. 1999. The distance decay of similarity in biogeography and ecology. – J. Biogeogr. 26: 867-878.

Oksanen, J. et al. 2012. Vegan: Community ecology package.R package version 2.14.0., http://CRAN.R-project.org/package=vegan

Padial, A. A. et al. 2009. .Effects of structural heterogeneity provided by floating macrophyte *Eichhornia azurea* on the predation efficiency and habitat use of the small Neotropical fish *Moenkhausia sanctaefilomenae*. – Hydrobiologia 624: 161-170.

Pagioro, T.A. and Thomaz, S.M. 2002. Longitudinal patterns of sedimentation in a deep, monomictic subtropical reservoir (Itaipu, Brazil-Paraguay). – Archiv für Hydrobiol. 154: 515–528.

Patterson, B. D. and Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. – Biol. J. Linn .Soc. 28: 65–82.

Pelicice, F. M. and Agostinho, A. A. 2006. Feeding ecology of fishes associated with *Egeria* spp. patches in a tropical reservoir, Brazil. – Ecol. Freshw. Fish 15: 10-19.

Qian, H. et al. 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. – Ecol. Lett. 8: 15–22.

R Development Core Team, 2011. R: Language and Environmental for Statistical Computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, http://www.R-project.org.

Rea, T. E. et al. 1998 The relative effects of water depth, fetch and other physical factors on the development of macrophytes in a small southeastern US pond. – Aquat. Bot. 61: 289-299.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. – Ecol. Lett. 7: 1-15.

Rørslett, B. 1991. Principal determinants of aquatic macrophytes richness in Northern European lakes. – Aquat. Bot. 39: 173–193.

Soininen, J. et al. 2007a. The distance decay of similarity in ecological communities. – Ecography 30: 3-12.

Soininen, J. et al. 2007b. A multivariate analysis of beta diversity across organisms and environments. – Ecology 88: 2830-2838.

StatSoft, Inc. 2004. STATISTICA (data analysis software system), version 7.0 www.statsoft.com.

Thomaz, S. M. and Bini, L. M. 1998. Ecologia e manejo de macrófitas aquáticas em reservatórios. – ActaLimnol.Bras. 10: 103-116.

Thomaz, S. M. et al. 1998. Biomass and maximum colonization depth of *Egeria najas* Planchon (Hydrocharitaceae) at Itaipu Reservoir, Brazil. – In: Monteiro, A., Vasconcelos, T. and Catarino, L. (eds), Management and Ecology of Aquatic Plants. Proceedings of the 10th EWRS International Symposium on Aquatic Weeds. EWRS/APRH, Lisbon, pp. 223–226.

Thomaz, S. M. et al. 1999. Aquatic macrophytes of Itaipu Reservoir, Brazil: Survey of species and ecological considerations. – Braz. Arch. Biol. Technol. 42: 15–22.

Thomaz, S. M. et al. 2003. Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir, Brazil): the influence of limnology and morphometry. – Hydrobiologia 505: 119-128.

Thomaz, S. M. et al. 2006. Effect of reservoir drawdown on biomass of three species of aquatic macrophytes in a large sub-tropical reservoir (Itaipu, Brazil). – Hydrobiologia 570: 53-59.

Thomaz, S. M. et al. 2008. Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. – Freshw. Biol. 53: 358-367.

Thornton, K. W. 1990. Sedimentary processes. – In: Thornton, K. W., Kimmel, B. L. and Payne, F. E. (eds), Reservoir Limnology: Ecological Perspectives. John Wiley & Sons, New York, pp. 43–69.

Tuomisto, H. et al. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. – Science 299: 241-244.

Ulrich, W. and Gotelli, N. J. 2007. Null models analysis of species nestedness patterns. – Ecology 88: 1824-1831.

Van der Berg, M. S. et al. 2003. A statistical model predicting the occurrence and dynamics of submerged macrophytes in shallow lakes in the Netherlands. – Hydrobiologia 506-509: 611-623.

Vermaat, J. E. et al. 2000. Water flow across and sediment trapping in submerged macrophyte beds of contrasting growth form. – Arch. Hydrobiol. 148: 549–562.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30: 279–338.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. – Taxon 21: 213–25.

Swing of Waters: The Effect of Floodplain Pulses on Aquatic Macrophytes Beta Diversity, Species Turnover and Nestedness[3]

Trabalho realizado em conjunto com: Edson

Fontes de Oliveira e Albano Schwarzbold

---

[3] O trabalho será submetido à revista *Diversity and Distribution*. A formatação está conforme as normas da revista, exceto pela posição das figuras no texto, pelo espaçamento e pelo alinhamento do texto.

ABSTRACT

River-floodplain systems are disturbance-dominated environments characterized by high levels of habitat diversity and biota adapted to exploit the spatio-temporal heterogeneity promoted by flood and drought pulses. Our aim was to verify if beta diversity and its components (species turnover and nestedness) are affected by hydrological regime (flood-drought cycles), spatial structure of floodplain (sub-systems), connectivity degree between lagoons and main channel and sampling period. Samples were collected quarterly (March 2005 to December 2009) in six lakes of the Upper Paraná River floodplain with different degrees of connectivity (connected and disconnected to the main river). In each lake, we analyzed macrophyte composition and limnological variables. Sørensen dissimilarity index presented significantly higher values for disconnected lakes and also for Paraná River sub-systems. Species turnover and nestedness showed non-significant results within all periods analyzed. When comparing whole periods, species turnover revealed to be the main process of beta diversity in the systems of the Upper Paraná River floodplain. Flood time lag period presented higher values and then significant differences with flood period for Sørensen index and species turnover, confirming the flood homogenization hypothesis, which postulates a decrease in beta diversity during flooding period.

INTRODUCTION

River-floodplain systems are disturbance-dominated environments characterized by high levels of habitat diversity and biota adapted to exploit the spatio-temporal heterogeneity (Junk et al., 1989; Neiff, 1990; Agostinho et al., 2004; Thomaz et al., 2007; Lansac-Tôha et al., 2009). The flood and drought pulses are considered by many authors the most important environmental parameter in floodplain aquatic ecosystems. Rivers and their surrounding floodplain channels and lakes can be considered integrated components of a single dynamic system, linked by strong interactions between hydrological and ecological processes (Junk et al., 1989; Neiff, 1990; Santos & Thomaz, 2007; Boschilia et al., 2008; Lansac-Tôha et al., 2009; Souza et al., 2011).

Despite their ecological importance, more than 50% of the wetlands in the world were already lost in the last century due to human activities (MEA, 2005). The regulation of flow by upstream dams has modified the structure and function of the Upper Paraná River floodplain and negatively impacted many organisms (Agostinho et al., 1995, 2004; Bonecker et al., 2009; Souza et al., 2011). As a consequence, the natural fluctuations in water level changed and the areas naturally flooded by rivers decreased. Dam operation can generally cause a flattening of the floodplain pulses, which reduces the connectivity between the main river channel and the floodplain habitats (e.g. isolate lakes) (Agostinho et al., 2000). The degree of connectivity of floodplain lakes to the main river has also gained attention as an important controlling factor in structuring aquatic communities in floodplains systems (Ward et al., 1999; Bini et al., 2003; Agostinho et al., 2004; Thomaz et al., 2007; Bonecker et al., 2009). Despite the control imposed by the large number of upstream dams, the flood regime of the Paraná River is still the main determinant of the structure of aquatic communities (Gomes & Agostinho, 1997; Agostinho et al., 2001; Thomaz et al., 2007).

Water level fluctuation has a great influence on the environmental characteristics of lotic and lentic ecosystems. It is one of a few environmental factors controlling the wetlands (Keddy, 2000). Flooding and drought affect species composition, relative abundance, distribution and succession dynamics of the aquatic macrophyte assemblages (Van der Valk, 1987; Keddy, 2000; Boschilia et al., 2008; Thomaz et al., 2007, Santos & Thomaz, 2007). Whether the water level keeps relatively constant, the

assemblages of aquatic plants in the littoral zone tend to stabilize and present lower species richness (Keddy & Reznicek, 1986; Van der Valk et al., 1994) than environments with water levels that naturally fluctuate during rainy and dry seasons. This occurs because great and frequent variations of water level make the littoral zone unsuitable for species that are highly competitive under stable conditions, favoring flood-drought pulse tolerant species (Keddy 2000, Keddy & Reznicek, 1986). Floods, even of short duration, influence the dominance of aquatic macrophytes in shallow wetland systems (Maltchik et al., 2005). This type of environment has natural oscillation of water level and is generally dominated by amphibious and ruderal helophytes (emergents) on the shore (Casanova & Brock, 2000; Lacoul & Freedman, 2006; Ferreira et al., 2011).

In floodplains such as the Upper Paraná River floodplain, we observe a different pattern of flood pulses than in large systems like the Amazon region. In the latter, a pattern of long duration unimodal predictable flood pulses is observed. Contrary to large systems, smaller floodplains, usually present a polynomial pattern (Agostinho et al., 2000, Thomaz et al., 2004; Fernandes et al., 2009). The Upper Paraná River floodplain is composed of multiple aquatic habitats, such as connected and disconnected (permanent or temporary) lakes, channels and backwaters. This habitat heterogeneity plus the flood pulse variation promote high species diversity (Bornette et al., 1998; Ward & Tockner, 2001; Agostinho et al., 2004; Santos & Thomaz, 2007; Ferreira et al., 2011).

Understanding the patterns and processes related to beta diversity is a central issue to applied and theoretical ecology (Gaston et al., 2007; Anderson et al., 2011). Beta diversity may reflect two different components: spatial turnover of species and assemblage nestedness (Baselga, 2010). The former implies the substitution of some species over others as a consequence of environmental gradient or geographical and historical constraints (Qian et al., 2005); while the latter occurs when species composition from depauperate samples are largely proper subsets of those from progressively species richer regional samples.

Thomaz et al. (2007) proposed the flood homogenization hypothesis, when flood events promote the increase of similarity in ecological processes and biological

communities in different habitats within the river-floodplain system. It is also expected a time lag until the effects of the homogenization become apparent. Assuming the wide range of habitats in the floodplain, its high species richness and the flood-drought cycles, we assumed that this system should present high beta diversity. We evaluated the spatial and temporal patterns of beta diversity and its components (turnover and nestedness) in the Upper Paraná River floodplain within its sub-systems and lakes (connected and disconnected) along five years of study. Specifically, we aimed to verify if the beta diversity and its components are affected by hydrological regime (flood-drought cycles), spatial structure of floodplain (sub-systems), connectivity degree between lakes and main channel and sampling period. We expect: a well-defined beta diversity pattern (Sørensen dissimilarity index) due to the high environmental heterogeneity promoted by the flood-drought cycles; higher values of species turnover as the main processes driving changing species composition in the Upper Paraná River floodplain; and we expect high species nestedness within lakes, especially disconnected lakes, because of their isolation with the main river is higher than connected lakes.

STUDY AREA

The Paraná River Basin covers a large area in Brazil (ca. 802,150 km²). It is the tenth longest river in the world (4,695 km), with a watershed area of 2.8 x 10^6 km² that includes most of south-central South America from the Andes to the Serra do Mar, near the Atlantic Ocean. In its upper portion, the Upper Paraná River is associated with a wide floodplain (the Upper Paraná River floodplain, 5-20 km width), the last undammed stretch of this river in Brazil. The braided floodplain is located between 22° $40´$S and 23° $40´$S latitude and between 53° $10´$W and 53° $40´$W longitude (Fig.1), in which are inserted three Conservation Units: Ilha Grande National Park, Ivinheima State Park and Environmental Protection Area of "Ilhas e Várzeas do Rio Paraná". For being the only stretch not dammed in this river, it is important for the conservation of several threatened aquatic and terrestrial species (Agostinho et al., 2004).
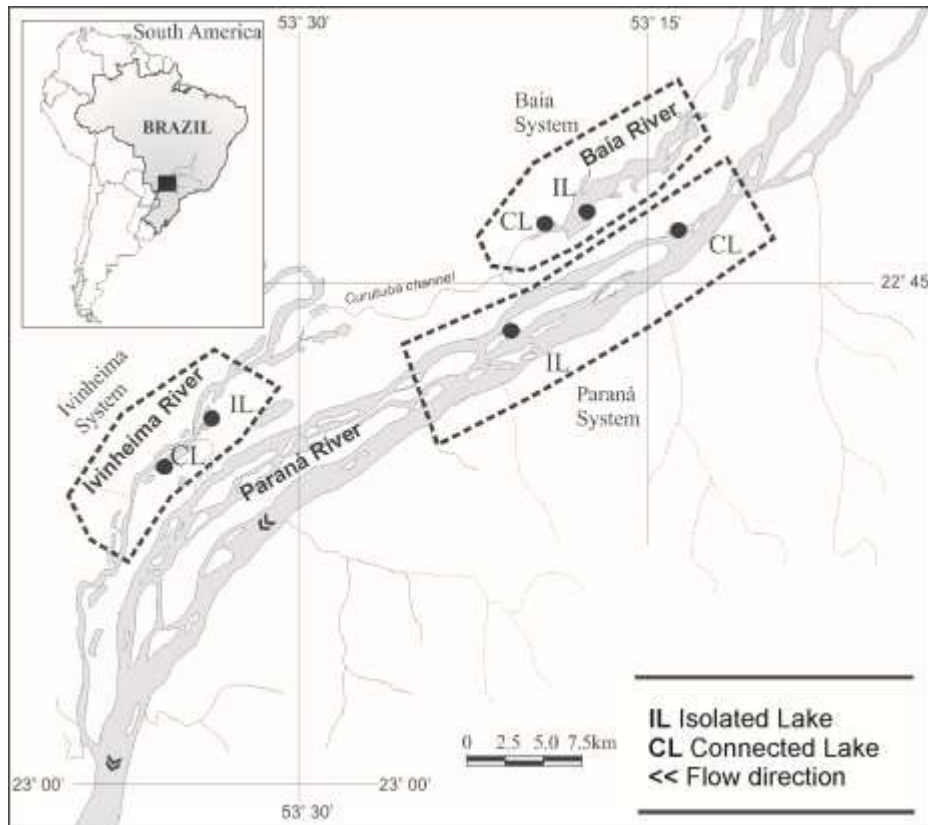
Figure 1. Study area and sampling stations in the Upper Paraná River floodplain.

This present study was undertaken in this floodplain (Fig.1), which encompasses a variety of aquatic, transitional and terrestrial habitats (Agostinho et al., 2007). The samples were taken in six lakes associated with Paraná River and with two of its main tributaries (Ivinheima and Baía Rivers; Fig. 1). For each river, two lakes were studied, one directly connected to the river (CL) and another disconnected, in direct contact with the river only during the major floods (IL), when occurs bank overflow (above 450mm water level; Fig.2).
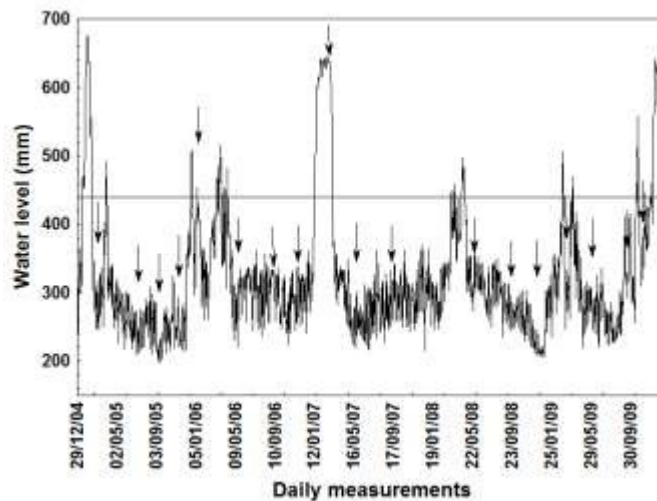
Figure 2. Daily water level of the Upper Paraná River floodplain from 2005 to 2009, at Porto São José city. Arrows indicate the sampling periods considered in this study.

MATERIAL AND METHODS

SAMPLING

Aquatic macrophytes were surveyed quarterly, from March 2005 to December 2009 (totaling 18 sample series). In each lake, data on macrophyte species were recorded from a boat moving at a constant slow speed along of the shoreline. Submerged species plants were sampled from the boat with a rake, for 10 minutes. Taxonomic identification followed the specialized literature (Hoehne, 1948; Cook, 1996; Pott & Pott, 2000; Lorenzi, 2000; Amaral et al., 2008). The list of taxa contains families and genera according to the "Angiosperm Phylogeny Group-APG II" (2003) for Magnoliophyta (Angiospermae), Willis (1973) for Pteridophyta and Crandall-Stotler (1980) for Hepatophyta.

In each sampling, water was collected with a Van Dorn bottle from the sub-surface layer in one point situated in the pelagic zone of all lakes. The water was immediately analyzed for pH, conductivity (Digimed portable meters) and total alkalinity (Gran titration: Carmouze, 1994). Water transparency was measured with Secchi disk and the water temperature and dissolved oxygen with an YSI meter. Water was also frozen (-20 ºC) for further nutrient analyses. Total-N was analyzed according to Bergamin et al., (1978) methods and Total-P to Golterman et al., (1978). For more analytical details see Roberto et al., (2009).

76

Daily measurements of water level of Paraná River (at São José station) were used to select periods of flood and drought in the Upper Paraná River floodplain (Fig.2). We established river level of 450cm as the reference intensity (threshold) level that characterizes flooding (when water overflows and invade disconnected lakes; Fernandes et al., 2009). Exceptional floods occur when water levels are above 600cm (Fernandes et al., 2009) and all the systems are connected (islands become immersed). The selection criterion for the sampled periods for the beta diversity and posterior analyses were: (i) flood, (ii) flood time lag, (iii) drought, (iv) drought time lag (Table 1). As our sampling was made every three months, the time lag considered in this study has a length of three months after the flood and drought periods.

Table 1. Criteria used to characterize the periods considered in this study. SP=number of sampling periods. Coincidentally one sampling, June 2007, was considered two times, once in drought period and another in flood time lag period.

Period	Definitions	SP
Flood	Sampling period occurred exactly in the period of flood, i.e., when water level is above 450cm (Fernandes et al., 2009).	2
Flood time lag (Flood TL)	Sampling period occurred immediately after a flood period.	7
Drawdown	Sampling period occurred in the lowest water levels in the year.	5
Drawdown time lag (Drawdown TL)	Sampling period occurred immediately after the sampling of the drawdown.	5

BETA DIVERSITY ANALYSIS

Beta diversity was estimated for aquatic macrophytes in all habitats of the Upper Paraná River floodplain, i.e., connected and disconnected lakes in the three sub-systems (Ivinheima, Baía and Paraná rivers) from 2005 to 2009. Thomaz et al. (2007) suggested a time lag to evaluate the effects of the homogenization effect until it becomes apparent. We agree with these authors that the increase of environmental dissimilarity after isolation is not immediate, mainly for aquatic macrophyte assemblages. We evaluate beta diversity, turnover and nestedness of the aquatic macrophyte assemblages in four

periods (Flood, Flood TL, Drought and Drought TL) during the five years of the study described in the Table 1.

Sørensen dissimilarity index (β_{sor}) formula is $\beta_{sor} = (b+c)/(2a+b+c)$, in which a is the number of species that occur in both sites; b is the number of species that appears only in the first site and c is the number of species occurring only in the second site. β_{sor} is one of the most used measures due to its dependence on the proportion of species shared between two communities and this measure is well known to incorporate the true spatial turnover and differences in richness along a gradient (Koleff et al., 2003). Using the additive partitioning framework proposed by Baselga (2010), we also provided the decomposition of the pairwise dissimilarity index (β_{sor}) in two additive components: spatial turnover (β_{sim}) and nestedness (β_{nes}). Therefore, $\beta_{sor}= (\beta_{sim}+\beta_{nes})$. The formula used for β_{sim} and β_{nes} are as follows: $\beta_{sim}= \min(b,c)/[a+\min(b,c)]$; $\beta_{nes}= \{[\max(b,c)-\min(b,c)]/[2a+\min(b,c) + \max(b,c)]\} \times \{a/[a+\min(b,c)]\}$, in which, variables a, b and c were already described above. It is important to highlight that dissimilarity due to nestedness is related to, but different, from nestedness *per se* (Baselga 2010). Nestedness proposed by Baselga (2010) reflects the increasing dissimilarity between nested communities produced by the increasing differences in the number of species. Many authors suggest that the species turnover or decay of similarity is caused by at least two, not mutually exclusive, processes: the environmental filtering hypothesis (Keddy, 1992) and the dispersal limitation hypothesis (Hubble, 2001). In an attempt to visualize better the components of Sørensen dissimilarity index, β_{sim} and β_{nes} results values were standardized ($\beta_{nes\ stardardized}=\beta_{nes}/\beta_{sor}$ and $\beta_{sim\ standardized}= \beta_{sim}/\beta_{sor}$), ranging from 0 to 1 and their sum equals value one (1). The standardized values of β_{sim} and β_{nes} along this paper are named as β_{sim} and β_{nes}.

STATISTICAL ANALYSIS

We used analyses of variance (ANOVA) to verify if the values of $\beta_{sør}$, β_{sim} and β_{nes} were statistically different in different sub-systems (Paraná, Ivinheima and Baía lakes), degree of connectivity (connected and disconnected lakes) and the sampled years (2005-2009) during the periods Flood, Flood TL, Drought and Drought TL. Non-

parametric analyses of variance (Kruskal-Wallis) were performed when the variables did not reach assumptions of normality and homoscedasticity.

In order to reduce the dimensionality of physical and chemical data (pH, electrical conductivity, alkalinity, Secchi, water temperature and dissolved oxygen, Total nitrogen and phosphorus), we used a Principal Components Analysis (PCA) in the four periods analyzed (Flood and Flood TL, Drought and Drought TL). The scores were selected according to Broken-stick criterion (Jackson 1993). With the aim of verify if the PCA scores of environmental data influence the patterns of Sørensen dissimilarity index, species turnover and nestedness in the periods analyzed, we used a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; McArdle & Anderson, 2001). PERMANOVA tests the simultaneous response of one or more variables to one or more factors in an ANOVA experimental design on the basis of any distance measure, using permutation methods. PERMANOVA is different from traditional ANOVA because it calculates the *P*-values using permutations, rather than relying on tabled *P*-values which assume normality. More details about PERMANOVA are found in Anderson (2001). We analyzed untransformed, unstandardized data, using the Bray-Curtis measure of dissimilarity, with 999 permutations per test.

The analyses of variance (both parametric and non-parametric data) were carried out in STATISTICA 7.0 (Statsoft Inc, USA). The Principal Component Analysis (PCA) was performed in PC-ORD v. 5.15 (McCune & Mefford, 2006). The analyses beta diversity partitioning and PERMANOVA were carried out through the statistical program R, version 2.14.0 (R development Core Team, 2011), using the "beta.pair" function provided by Baselga (2010) and function "adonis" respectively, from betapart and vegan packages (Oksanen et al., 2012).

RESULTS

Eighty three species belonging to 37 families were found in the whole floodplain considering all years of sampling (Appendix 1). The most specious families were Cyperaceae (10 species), Poaceae (9 species) and Polygonaceae (6 species). The most frequent species were *Polygonum stelligerum* (87.9%), *Oxycaryum cubense* (79.63%),

Eichhornia azurea (70.4%), *Eichhornia crassipes* (68.5%), *Polygonum ferrugineum* (65.7%) and *Paspalum repens* (63.8%). The less frequent species with 0.93% were *Cyperus* cf. *sesquiflorus*, *Panicum hylaeicum*, *Setaria pauciflora*, cf. *Rhynchanthera* and *Hyptis* sp., while *Chara guairensis*, *Nitella furcata*, *Azolla microphylla*, *Oxypetalum* sp., *Eupatorium squalidum* and *Rhabdanenia pohlii* had 1.95% of relative frequency of occurrence.

Considering the whole Upper Paraná River floodplain in five years of sampling, beta Sørensen mean value was 0.54 (SD= 0.08) and higher values were found for species turnover (mean= 0.75; SD=0.10) than to nestedness (mean=0.24; SD=0.10). Only Sørensen dissimilarity index presented significant effects of connectivity and sub-systems (Table 2). The ANOVA presented significant differences in $\beta_{sør}$ within all periods for lakes connectivity and sub-systems in the floodplain; except for sub-systems in the Flood period (Table 2). Disconnected lakes and Paraná sub-system presented higher values of $\beta_{sør}$, confirming our hypothesis. Non-significant results were obtained for the years of the study, i.e., the years studied presented similar values of $\beta_{sør}$ in each period analyzed. Species turnover and nestedness did not differ statistically in relation to connectivity, sub-systems and the years of the study in the Upper Paraná River floodplain.

Table 2. Results of analysis of variance for differences of beta diversity ($\beta_{sør}$) in relation to periods and levels. No period presented significant differences within of levels considered for species turnover (β_{sim}) and nestedness (β_{nes}).

		βs		
Periods	Levels	F	p	
	sub-systems	2.46	0.14	
Flood	connectivity	8.12	0.017	Disc.>Connec.
	years	0.31	0.58	
	sub-systems	3.61	0.03	PR>BA
Flood TL	connectivity	23.02	<0.001	Disc.>Connec.
	years	1.57	0.18	
	sub-systems	4.24	0.025	PR >BA and IVI
Drawdown	connectivity	12.67	0.001	Disc.>Connec.
	years	1.57	0.127	
	sub-systems	6.62	0.004	PR>BA and IVI
Drawdown TL	connectivity	9.46	0.004	Disc.>Connec.
	years	2.09	0.11	

No period present significant differences within of levels considered for species turnover (β_{sim}) and nestedness (β_{nes}).

Furthermore, we tested if the values of $\beta_{sør}$, β_{sim} and β_{nes} were different when comparing the periods of Flood, Flood TL, Drought and Drought TL. When evaluating the Sørensen dissimilarity index, the Flood period presented lower values and differed from the others ($F_{(3,110)}$=5.56; p=0.001; Fig.3a). The species turnover and nestedness also presented significant differences in relation to periods. Flood also differed from the Flood TL, but not from the others (Fig. 3b).
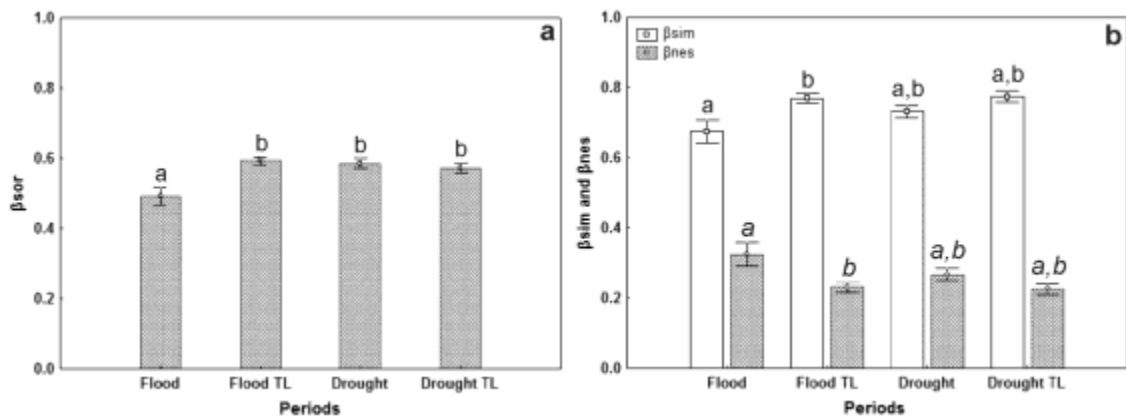
Figure 3. Mean and standard error for (a) Sørensen dissimilarity index ($\beta_{sør}$), (b) species turnover (β_{sim}) and nestedness (β_{nes}) in the periods studied. The letters above the spreads are differences according to Tukey (a) and multi comparisons Kruskal-Wallis tests (b).

β_{sim} was significantly different from β_{nes} and the former prevailed in all periods analyzed, confirming our hypothesis (Fig.4). We did not find any significant difference between β_{sim} values within each period, considering connectivity and sub-systems. The same occurred to β_{nes}, what means that comparing β_{sim} with β_{nes} we found differences in all periods but, within lakes, the β_{sim} or β_{nes} values were not statistically different.
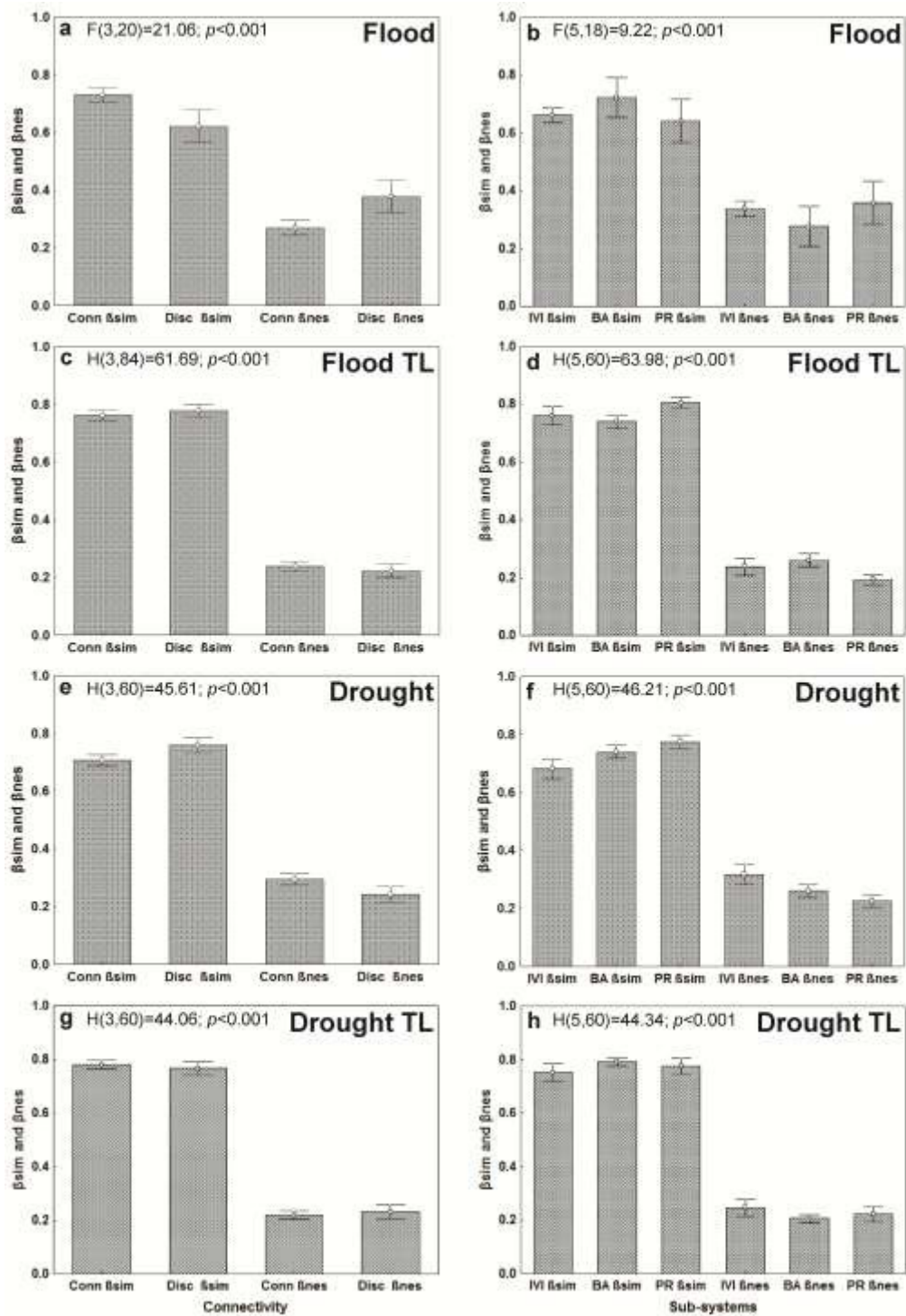
Figure 4. Mean and stardard error values and analyses of variance (ANOVA and Kruskal-Wallis) comparing values of β_{sim} and β_{nes} in different periods (Flood, Flood TL, Drought and Drought TL) in relation to connectivity (a, c, e and g) and sub-system (b, d, f and h).

Principal Component Analyses summarized the abiotic variables that most influenced the four periods analyzed (Table 3). PCA revealed the formation of significant axes according to the broken stick model, which were selected for interpretation. Flood and Flood TL periods present three significant axes (total variance

explained 85% and 81.39%, respectively), while Drought period present only a significant axis (36.45% of explained variance) and Drought TL period revealed two significant axes (66.85% of explication).

Table 3. Principal Component Analysis (PCA) of the abiotic variables sampled in the periods of Flood, Flood TL, Drought and Drought TL. Between parentheses are the eigenvalues of the variables selected for each axis. PERMANOVA analyzed which axis affected beta diversity in each period. Asterisks show which axis had significant results this analysis. Cond.= Electrical conductivity, TP= Total phosphorus, Alc.= Alkalinity, OD= Dissolved oxygen, TN= total nitrogen, Temp.= water temperature, Secchi= water transparency.

Periods	Axis1	Axis 2	Axis 3
Flood	Secchi (0.88) * Cond. (0.83) * TP (-0.88) *	pH (-0.94) Alc. (-0.73)	OD (0.64) TN (-0.62)
Flood TL	Secchi (0.73) * Alc. (0.69) * TN (-0.62) * TP (-0.71) *	OD (0.71) * Temp. (-0.81) *	pH (-0.63) *
Drawdown	Alc. (0.83) Secchi (0.70) Cond. (0.68) TN (-0.62) TP (-0.73)		
Drawdown TL	Alc. (0.83) * Cond. (0.71) * TN (-0.72) * TP (-0.8*)	Temp. (-0.6) OD (-0.75)	

PERMANOVA tested which axis contributed significantly for beta diversity ($\beta_{sør}$) in all periods analyzed. Species turnover and nestedness were not evaluated because there is no significance in analyses of variance within the periods, connectivity and years analyzed. The Flood period had only the first axis significant (F=3.78; R²= 0.33; p=0.04). The variables contributing to this first axis were Secchi and electrical conductivity (positive eigenvalues) and phosphorus (negative eigenvalues; Table 3). When evaluating the Flood TL period, the three axes were significant by the PERMANOVA (axis 1 - F=2.56; R²=0.05; p=0.01; axis 2 - F=5.84; R²=0.11; p=0.001; and axis 3 - F=3.40; R²=0.06; p=0.003). The Drought period did not have any significant axis for the analysis. Finally, Drought TL had only its first axis significant

(F=2.37; R²=0.07; *p*=0.03). The variables most contributing to this first axis were alkalinity and electrical conductivity (positive eigenvalues) and nitrogen and phosphorus (negative eigenvalues; Table 3).

DISCUSSION

In this study, the null hypothesis of absence of effect of spatial structure of floodplain (connectivity degree of lakes and sub-systems) on beta diversity patterns was rejected. This implies that connection dynamic of lakes with the main river, as well as the spatial distribution of different sub-systems formed from of tributaries of Paraná River, are good predictors of the beta diversity patterns in the floodplain. Severe disturbances usually cause drastic effects on biotic communities. However, when natural disturbances are recurrent, such as flood and drought pulses in floodplains, an increase of environmental heterogeneity and biological diversity can be promoted. Alternation of flooding and drought periods affect plant establishment from seed bank and propagules by stimulating or inhibiting germination. Therefore, the water level determines the oxygen availability in the soil and subsequent concentrations of nutrients and toxic substances, by desiccating aquatic plants in drought or inundating terrestrial plants in flood, changing the water transparency with depth changes (Casanova & Brock, 2000). Here we will discuss each period separately.

FLOOD

During the flood, while amphibious species can propagate vegetatively under water, emergent species will die out under deeper water conditions (Keddy & Reznicek, 1986). In the Upper Paraná River floodplain disconnected lakes present water depth stability (Santos & Thomaz, 2007), independent of the water level fluctuations of the main river due to water seepage. Therefore, when the flood connected all lakes with the main river, species that inhabit disconnected lakes are less habituated to water level oscillation (more emergent than amphibious species; mean 27.5 and 9.75 respectively), leading to loss of local diversity in this period.

Lake-edge species tolerant to water level oscillations are typically amphibious, ruderal helophytes, whose seeds require low water levels and oxygenated conditions to

germinate and grow in low-competition habitats (Hutchinson, 1975). Also longer-lived species with broader environmental tolerances may have phenotypically plastic responses to the water variation and associated environmental conditions (Sand-Jensen & Frost-Christensen, 1999). This dynamic was reflected in Sørensen dissimilarity index, showing higher values for disconnected lakes than in the connected ones. When comparing periods, flood period presented the lowest values of $\beta_{sør}$ and species turnover (β_{sim}). This could be due to the increase of similarity between the rivers, channels and lakes of floodplain with the homogenization effect (Bini et al., 2001; Thomaz et al., 2007). According to these authors, this similarity is first found in the limnological parameters of the floodplain, and consequently promoted an increase of similarity in aquatic macrophytes composition leading to a reduction of beta diversity and species turnover values.

During the Flood period it was possible to detect high values of water transparency and low values of total phosphorus in this floodplain (Thomaz et al., 2007; Roberto et al., 2009) and high values of electrical conductivity probably due to biomass decomposition and the release of dissolved ions on the water (Junk et al., 1989). The dilution effect in the floodplain waters promoted a decrease of beta diversity values for the aquatic macrophytes assemblage and also the reduction of species turnover in the habitats within the Paraná River floodplain.

FLOOD TIME LAG

The same trend occurred in flood time lag period in relation to connectivity, when the flood pulse had already occurred and the isolation of disconnected lakes was reestablished. After the return of the water level each environment (connected and disconnected lakes) initiates their own succession, which depends upon the propagules input and seed bank success in colonization and establishment. Beyond propagule production, there are more important traits for recolonization success, such as germination and survival rates and dispersal ability, establishment, rooting and growth rate when established (Grime, 1979). In this period is expected change in species composition due to high seasonal losses for most euhydrophytes during high waters and the recovery by quick growth, early maturity, high reproduction rates from *r*-strategists and fast dispersal species (Junk et al., 1989).

The increase of spatial heterogeneity in this period (comparing with the previous period) eases the species coexistence and avoids the dominant species establishment (Maltchik et al., 2005). This difference in Sørensen dissimilarity index during Flood TL period may be due to the constant propagules input, seed bank germination, reestablishment of species that were washed way during flooding. In this period, the sub-systems began to return to their peculiar abiotic characteristics. These initial differences provide also an increase of beta diversity and higher values of species turnover. Differences in $\beta_{sør}$ between Paraná and Baía lakes may be due to species composition and inherent limnological differences. Paraná sub-system has the highest values of Secchi, electrical conductivity and alkalinity and Baía has lowest, but highest values in total nitrogen (Roberto et al., 2009). Indeed, as suggested by Thomaz et al. (2009), these limnological differences promote distinct species composition and therefore, highest $\beta_{sør}$ in Paraná lakes due to the species turnover process. An example could be the dominance of submersed species inhabiting Paraná River lakes, while Baía are habitat preferable for free floating leaves.

Many limnological variables were responsible, in part, to this pattern. Nutrients as nitrogen and phosphorus reestablish their usual concentrations in connected and disconnected lakes, increasing even more the differences between sub-systems. Correlated with nutrients were water transparency and alkalinity. In this period, while nutrients were not so diluted anymore, water transparency decreased because lakes depth diminished leading to an increase in alkalinity values (e.g. ions release from sediment; Carvalho et al., 2001). The reduction of pH can be attributed to decomposition of organic matter and high inputs of humic compound from surroundings areas (Thomaz et al., 1992).

DROUGHT

Drought strongly affects aquatic macrophytes composition because it is a prerequisite for successful germination and survival of many species (Bonis & Grillas, 2002). The floodplain aquatic habitats are isolated from each other and subject to local driving forces during low water periods (Carvalho et al., 2001; Thomaz et al., 2007). We observed higher $\beta_{sør}$ values for disconnected lakes than connected ones. According to the study of Santos and Thomaz (2007) in this floodplain, differences in species

composition and consequently in beta diversity should be due to connectivity, i.e., the permanent connection with the main river makes connected lakes allow constant input of propagules and insertion of new species in this habitat. During the drought occurs a habitat contraction, where the aquatic habitat becomes exposed, promoting new area for colonization of emergent, amphibious and exotic terrestrial species (Casanova & Brock, 2000; Santos & Thomaz, 2007). Due to drought features, some species will change their growth form to adapt to drier conditions, but some species intolerant will die and be replaced by species from buried seeds or propagules that came with the last flooding (Keddy & Reznicek, 1986).

The disconnected lakes had more stable conditions in relation to water level than the previous period and some species were locally extinct from flooding period, allowing coexistence of many other species with similar habitat requirements (Junk et al., 1989). That may be a factor contributing to higher $\beta_{sør}$ and β_{sim} values for disconnected lakes. Paraná River lakes had higher $\beta_{sør}$ than other sub-systems during the drought probably due to limnological differences. Roberto et al., (2009) concluded that, due to upstream reservoirs, the Paraná River suffered an enormous increase of water transparency and decrease of total phosphorus (reservoirs trap sediments; Thornton, 1990). These factors are not shared with Baía and Ivinheima sub-systems during drought, when they have a high load of nutrients and low water transparency. The limnological peculiarities could drive the successional trajectory of each lake promoting high values of species turnover in this period.

DROUGHT TIME LAG

This period was characterized by long term of dry period (more than 6 months after the last flood). This time is expected to be enough to promote biotic interactions between organisms (Boschilia et al., 2008) since the disturbance of flooding leaded to isolation from the main river (for disconnected lakes) and lower variation of water (connected lakes). Roberto et al. (2009) suggested that habitats become more dissimilar in this period due to limnological features. This pattern was also discussed elsewhere (Tockner & Ward, 1999; Amoros & Bornette, 2002; Thomaz et al., 2007). Long periods of drought may lead to maximization of competitive exclusion by space, luminosity and nutrients, consequently, promoting local extinctions (Thomaz et al., 2007).

Long dry phases give opportunity for terrestrial species to establish in the exposed area. This dynamic of drought eliminate intolerant species and allow the establishment of ruderal species (pioneers), generating a pattern of species substitution in the lakes of the Upper Paraná River floodplain. As cited before, the Paraná lakes possess limnological features which differ from the others sub-systems generating higher values of beta diversity (β_{sor}) evidencing the species turnover (β_{sim}) as the main process driving the beta diversity. The inherent ecological succession of each lake may also generate high values of species turnover in this period. These differences were in part due to higher values of nutrients (total nitrogen and phosphorus) and lower values of Secchi and conductivity in the disconnected lakes. Three main forces could also be inducing heterogeneity and, therefore, beta diversity and species turnover pointed out from Thomaz et al., (2007): water inputs from lateral tributaries and water seepage, wind, fetch and animal disturbance inducing sediment re-suspension and differences in local ecological succession.

GENERAL COMMENTS

Lakes are important functional environments in floodplain landscapes. They differ in origin, hydrology, connectivity, morphology, limnology and biotic features. Due to this high heterogeneity of environments within floodplains, it is expected that all habitats have high values of beta diversity (Ward et al., 1999). High beta diversity contributes in part, to high biodiversity of floodplain ecosystems (Agostinho et al., 2000). Species turnover among lakes in the Upper Paraná River floodplain was the major process driving beta diversity. The establishment and death of macrophytes species, propagules transportation, biotic interactions, limnological features guided by the flood and drought pulses are some factors promoting high species turnover in the sub-systems within Upper Paraná River floodplain.

During the Flood period we confirmed the hypothesis of floodplain homogenization proposed by Thomaz et al., (2007), when we observed higher limnological and biotic similarities and lower beta diversity values among all environments within the floodplain. This was also observed when comparing the periods studied, because the lowest values of β_{sor} and β_{sim} were found during the floods. Limnological variables become more similar and consequently, biotic responses were

also expected as shift in species composition, spatial patterns and beta diversity (Santos & Thomaz, 2007; Boschilia et al., 2008; Padial et al., 2009). When the connection between isolated systems is reestablished, the homogenization caused the death of submersed species, transported propagules, and promoted, depending of the flood degree, a "reset" in the aquatic vegetation. The beginning of a new succession of the aquatic macrophytes assemblage in each lake of the Paraná floodplain during the drought periods may promote environmental heterogeneity and thus species turnover among the lakes.

In this study we observed real differences related to time lag, especially after the flood pulse. As aquatic macrophytes have the peculiarity of high rates of reproduction and propagation, this time lag considered in this study maybe could be shorter. We encourage future studies in determining the precise time lag for aquatic macrophyte assemblages in relation to the effects of flood and drought pulses on beta diversity patterns in floodplains.

REFERENCES

Agostinho, A.A, Vazzoler, A.E.A.M., Thomaz, S.M. (1995) The high River Paraná Basin: Limnological and ichtyological aspects. *Limnology in Brazil* (ed. by J.G. Tundisi, C.E.M. Bicudo and T. Matsumura-Tundisi), pp. 59–103. ABC/ SBL, Rio de Janeiro.

Agostinho, A.A., Thomaz, S.M., Minte-Vera, CV & Winemiller, K.O. (2000) Biodiversity in the high Paraná River floodplain. *Biodiversity in Wetlands: Assessment, Function and Conservation* (ed. by B. Gopal, W.J. Junk and J.A. Davis), pp. 89–118. Backhuys, Leiden.

Agostinho, A.A., Gomes, L.C., Zalewski, M. (2001) The importance of floodplains for the dynamics of fish communities of the upper river Paraná. *Ecohydrology and Hydrobiology*, 1, 209-217.

Agostinho, A.A., Gomes, L.C., Veríssimo, S. & Okada, E.K. (2004) Flood regime, dam regulation and fish in the Upper Paraná River: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, 14, 11–19.

Agostinho, A.A., Thomaz, S.M., Gomes, L.C. & Baltar, S.L.S.M.A. (2007) Influence of the macrophyte *Eichhornia azurea* on fish assemblage of the Upper Paraná River floodplain (Brazil). *Aquatic Ecology*, 41, 611-619.

Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos,* 117, 1227-1239.

Amaral, M.C., Bittrich, V., Faria, A.F., Anderson, L.A. & Aona, L.Y.S. (2008) *Guia de campo para plantas aquáticas e palustres do Estado de São Paulo*. Holos, Ribeirão Preto, São Paulo.

Amoros, C. & Bornette, G. (2002) Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, 47, 761-776.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32-46.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. (2011). Navigating the multiple meanings of b-diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14, 19–28.

APG II (2003) An update of the Angiosperm Phylogeny Group classification for orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society*, 141, 399-436.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143.

Bergamin, H., Reis, B.F.& Zaggato, E.A.G. (1978) A new device for improving sensitivity and stabilization in flow injection analysis. *Analytica Chimica Acta,* 97, 427-431.

Bini, L.M., Thomaz, S.M. & Souza, D.C. (2001) Species richness and β-diversity of aquatic macrophytes in the Upper Paraná River floodplain. *Archiv für Hydrobiologie*, 151, 511-525.

Bini, L.M., Velho, L.F.M. & Lansac-Tôha, F.A. (2003) The effect of connectivity on the relationship between local and regional species richness of testate amoebae (Protozoa, Rhizopoda) in floodplain lagoons of the Upper Paraná River, Brazil. *Acta Oecologica (Montrouge)*, 24, 145-151.

Bonecker, C.C., Aoyagui, A.S.M. & Santos, R.M. (2009) The impact of impoundment on the rotifer communities in two tropical floodplain environments: interannual pulse variations. *Brazilian Journal of Biology*, 69, 529-537.

Bornette, G., Amoros, C. & Lamouroux, N. (1998) Aquatic plant diversity in riverine wetlands: the role of connectivity. *Freshwater Biology*, 39, 267–283.

Boschilia, S.M., Oliveira, E.F. & Thomaz, S.M. (2008) Do aquatic macrophytes co-occur randomly? an analysis of null models in a tropical floodplain. *Oecologia*, 156, 203-214.

Carmouze, J.P. (1994) *O metabolismo dos ecossistemas aquáticos: fundamentos teóricos, métodos de estudo e análises químicas*, Edgard Blücher, São Paulo.

Carvalho, P., Bini, L.M., Thomaz, S.M., Oliveira, L.G., Robertson, B., Tavechio, W.L.G. & Darwisch, A.J. (2001) Comparative limnology of South American floodplain lakes and lagoons. *Acta Scientiarum*, 23, 265-273.

Casanova, M.T. & Brock, M.A. (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology*, 147, 237-250.

Cook, C.D.K. (1996) *Aquatic plant book*. SPB Academic Publishing Amsterdam.

Crandall-Stotler, B. (1980) Morphogenetic designs and theory of bryophyte origins and divergence. *BioScience*, 30, 580-585.

Diserud, O.H. & Ødegaard, F. (2007) A multiple-site similarity measure. *Biology Letters*, 3, 20-22.

Fernandes, R., Agostinho, A.A., Ferreira, E.A., Pavanelli, C.S., Suzuki, H.I., Lima, D.P. & Gomes, L.C. (2009) Effects of the hydrological regime on the ichthyofauna of riverine environments of the Upper Paraná River floodplain. *Brazilian Journal of Biology*, 69, 669-680.

Ferreira, F.A., Mormul, R.P., Thomaz, S.M., Pott, A. & Pott, V.J. (2011) Macrophytes in the upper Paraná river floodplain: checklist and comparison with other large South American wetlands. *Revista de Biología Tropical*, 59, 541-556.

Gaston, K.J., Davies, R.G., Orme, C.D.L., Olson, V.A., Thomas, G.H., Ding, T.S., Rasmussen, P.C., Lennon, J.L., Bennet, P.M., Owens, I.P.F. & Blackburn, T.M. (2007). Spatial turnover in the global avifauna. *Proceedings of the Royal Society B-Biological Science*, 274, 1567–1574.

Golterman, H.L., Clymo, R.S. & Ohmstad, M.A.M. (1978) *Methods for physical and chemical analysis of freshwater*, Blackwell Scientific, Oxford.

Gomes, L.C. & Agostinho, A.A. (1997) Influence of the flooding regime on the nutritional state and juvenile recruitment of the curimba, *Prochilodus scrofa*, Steindachner, in the Upper Paraná River, Brazil. *Fisheries Management Ecology*, 4, 263-274.

Grime, J.P. (1979). *Plant strategies and vegetation processes*. Wiley & Sons, Chichester.

Hoehne, F.C. (1948) *Plantas aquáticas*. São Paulo, Instituto de Botânica, São Paulo.

Hutchinson, G.E. (1975) *A treatise on Limnology II: Limnological botany.* Wiley & Sons, Inc. New York.

Jackson, D.A. (1993). Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology*, 74, 2204-2214.

Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian special publication of fisheries and aquatic sciences*, 106, 110–127.

Keddy, P.A. (2000) *Wetland ecology: principles and conservation*, 2nd edn. Cambridge Univ. Press, Cambridge.

Keddy, P.A. & Reznicek, A.A. (1986) Great-Lakes vegetation dynamics- the role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research*, 12, 25-36.

Koleff, P., Gaston, K.J. & Lennon, J.J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72, 367–382.

Lacoul, P. & Freedman, B. (2006) Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews*, 14, 89-136.

Lansac-Tôha, F.A., Bonecker, C.C., Velho, L.F.M., Simões, N.R., Dias, J.D., Alves, G.M. & Takahashi, E.M. (2009) Biodiversity of zooplankton communities in the Upper Paraná River floodplain: interannual variation from long-term studies. *Brazilian Journal of Biology*, 69, 539-549.

Lorenzi, H. (2000) *Plantas daninhas do Brasil: terrestres, aquáticas, parasitas e tóxicas*, 3rd edn. Nova Odessa: Instituto Plantarum de Estudos da Flora.

Maltchik, L., Oliveira, G.R., Rolon, A.S. & Stenert, C. (2005) Diversity and stability of aquatic macrophyte community in three shallow lakes associated to a floodplain system in the south of Brazil. *Interciencia*, 30,166–170.

McArdle, B.H. & Anderson, M.J. (2001) Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology*, 82, 290–297.

McCune, B. & Mefford, M.J. (2006) PC-ORD. *Multivariate Analysis of Ecological Data*. Version 5.15. MjM Software, Gleneden Beach, Oregon, U.S.A.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: Wetlands and water synthesis*. World Resources Institute, Washington, DC.

Neiff, J.J. (1990) Ideas para la interpretación ecológica del Paraná. *Interciencia*, 15, 424-441.

Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Michin, P.R., OʹHara, R.B., Simpson, G.L., Solymos, P., Stevens, H.H. & Wagner, H. (2012). *Vegan: Community ecology package.* R package version 2.14.0., http://CRAN.R-project.org/package=vegan

Pott, V.J. & Pott, A. (2000) *Plantas aquáticas do Pantanal*, Embrapa, Brasília.

Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, 8, 15–22.

Roberto, M.C., Santana, N.F. & Thomaz, S.M. (2009) Limnology in the Upper Paraná River floodplain: large-scale and temporal patterns, and the influence of reservoirs. *Brazilian Journal of Biology*, 69, 717-725.

Sand-Jensen, K. & Frost-Christensen, H. (1999) Plant growth and photosynthesis in the transition zone between land and stream. *Aquatic Botany*, 63, 23-35.

Santos, A.M. & Thomaz, S.M. (2007) Aquatic macrophytes diversity in lagoons of a tropical floodplain: The role of connectivity and water level. *Austral Ecology*, 32, 177-190.

Souza, W.T.Z., Thomaz, S.M. & Murphy, K.J. (2011) Drivers of aquatic macrophyte community structure in a Neotropical riverine lake. *Acta Oecologica*, 37, 462-475.

Tockner, K. & Ward, J.V. (1999) Biodiversity along riparian corridors. *Large Rivers*, 11, 293-310.

Thomaz, S.M., Lansac-Tôha, F.A., Roberto, M.C., Esteves, F.A. & Lima, A.F. (1992) Seasonal variation of some limnological factors of Lagoa do Guaraná, a Várzea lake of the High Rio Paraná, State of Mato Grosso do Sul, Brazil. *Revue d'hydrobiologie tropicale*, 25, 269-276

Thomaz, S.M., Bini, L.M., Pagioro, T.A., Murphy, K.J., Santos, A.M. & Souza, D.C. (2004). Aquatic macrophytes: diversity, biomass and decomposition. The Upper Parana´ River and its floodplain: Physical aspects, ecology and conservation (ed. by S.M. Thomaz, A.A. Agostinho & N.S. Hahn), pp. 331–352. Backhuys Publishers, Leiden.

Thomaz, S.M., Bini, L.M. & Bozelli, R.L. (2007) Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, 579, 1-13

Thomaz, S.M., Carvalho, P., Padial, A.A. & Kobayashi, J.T. (2009) Temporal and spatial patterns of aquatic macrophyte diversity in the Upper Paraná River floodplain. *Brazilian Journal of Biology*, 69, 617-625.

Van der Valk, A.G. (1987) Vegetation dynamics of freshwater wetlands: a selective review of the literature. *Archiv für Hydrobiologie, Beihefte Ergebnisse der Limnologie*, 27, 27–39.

Van der Valk, A.G. (1994) Effects of prolonged flooding on the distribution and biomass of emergent species along a freshwater wetland coenocline. *Journal of Vegetation Science*, 110, 185–196.

Ward, J.V., Tockner, K. & Schiemer, F. (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management*, 15, 125-139.

Ward, J.V. & Tockner, K. (2001) Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology*, 46, 807–819.

APPENDIX 1

List of taxa recorded in the Paraná River floodplain and their frequency of occurrence (FO%) between the years 2004 to 2009. Life forms (LF): EM= emergent; AM= amphibious; EP= epiphyte; RS= rooted submerged; FS= free submerged; FL= floating leaved; FF= free floating.

Taxa	FO%	LF
Characeae – Charophyta		
Chara guairensis R. Bicudo	1.85	RS
Nitella furcata (Roxb. ex Bruz.) Ag. emend. R.D. Wood	1.85	RS
Ricciaceae - Hepatophyta (Bryophyta)		
Ricciocarpus natans L. (Corda)	2.78	FF
Azollaceae - Pteridophyta		
Azolla microphylla Kaulf.	1.85	FF
Pteridaceae – Pteridophyta		
Pityrogramma calomelanos (L.) Link var. *calomelanus*	2.78	EM
Salviniaceae – Pteridophyta		
Salvinia auriculata Aubl.	56.4	FF
Salvinia biloba Raddi emend de la Sota	23.1	FF
Salvinia minima Baker	52.7	FF
Thelypteridaceae - Pteridophyta		
Thelypteris interrupta (Willd.) K. Iwats.	4.63	EM
Nymphaeaceae – Basal Angiospermae		
Nymphaea amazonum Mart. ex Zucc. subsp. *amazonum*	57.4	FL
Cabomba furcata Schult. & Schult. f.	13.0	RS
Alismatales - Monocots		
Araceae		
Lemna valdiviana Phil.	17.6	FF
Pistia stratiotes L.	46.3	FF
Wolffiella lingulata (Hegelm.) Hegelm	11.1	FF
Wolffiella oblonga (Phil.) Hegelm.	14.8	FF
Hydrocharitaceae		
Egeria densa Planch.	4.63	RS
Egeria najas Planch.	12.0	RS
Hydrilla verticillata (L.f.) Royle	4.63	RS
Limnobium laevigatum (Humb. & Blonpl. ex Willd.) Heine	29.6	FF
Alismataceae		
Echinodorus grandiflorus (Cham. & Schltdl) Micheli	9.25	EM
Asparagales		
Orchidaceae		
Habenaria repens Nutt.	4.62	EP
Poales		
Cyperaceae		
Cyperus cf. *sesquiflorus* (Torr.) Mattf. & Kük.	0.92	EM
Cyperus luzulae (L.) Retz	2.77	EM
Cyperus giganteus Vahl	10.2	EM
Cyperus sp.	17.6	EM
Eleocharis filiculmis Kunth	25.0	EM
Eleocharis geniculata (L.) Roem. & Schult	3.70	EM
Fuirena Rottb.	1.90	EM
Oxycaryum cubense (Poepp. & Kunth) Palla	79.6	EP
Rhynchospora corymbosa (L.) Britton	21.3	AM
Scleria melaleuca Rchb. ex Schltr. & Cham.	4.63	AM
Poaceae		
Echinochloa polystachya (Kunth) Hitchc	4.63	AM
Hymenachne amplexicaulis (Rudge) Nees	10.2	EM
Panicum hylaeicum Mez	0.92	EM
Panicum pernambuncense (Spreng.) Mez ex Pilg.	12.9	EM
Panicum prionitis Nees	3.70	AM
Panicum sp.	6.48	EM
Paspalum repens P.J. Bergius	63.9	EM
Setaria pauciflora Linden ex Herrm	0.93	AM
Urochloa subquadripara (Trin) R.D.Webster	2.77	EM
Comme inales		
Commelinaceae		

Commelina diffusa Burm. f.	38.9	AM
Pontederiaceae		
Eichhornia azurea (Sw.) Kunth	70.4	EM
Eichhornia crassipes (Mart.) Solms	68.5	FF
Pontederia cordata L.	27.8	EM
Zingiberales		
Maranthaceae		
Thalia geniculata L.	5.55	EM
Caryophyllales - Core Eudicotyledoneae		
Polygonaceae		
Polygonum acuminatum Kunth	57.4	EM
Polygonum ferrugineum Wedd.	65.7	EM
Polygonum hydropiperoides Michx.	19.4	EM
Polygonum meisnerianum Cham. & Schltdl.	10.2	EM
Polygonum punctatum Elliot	20.4	EM
Polygonum stelligerum Cham.	87.9	EM
Amaranthaceae		
Alternanthera philoxeroides (Mart.) Griseb.	23.1	AM
Pfaffia glomerata (Spreng.) Pedersen	5.56	AM
Haloragaceae		
Myriophyllum aquaticum (Vell.) Verdc.	3.70	RS
Vitales		
Vitaceae		
Cissus erosa Rich.	8.33	EM
Myrtales – Rosidea		
Onagraceae		
Ludwigia helminthorrhiza (Mart.) H. Hara	15.7	FF
Ludwigia lagunae (Morong) H. Hara	13.0	EM
Ludwigia leptocarpa (Nutt.) H. Hara	19.4	EM
Ludwigia peruviana (L.) H. Hara	50.9	EM
Lythraceae		
Cuphea melvilla Lindl.	5.55	EM
Cuphea sessiliflora A. St.-Hil.	4.63	AM
Melastomataceae		
Rhynchanthera cf. DC.	0.92	EM
Urticales		
Urticaceae		
Boehmeria sp.	3.70	EM
Malpighiales – Eurosideae I		
Euphorbiaceae		
Caperonia castaneifolia (L.) A. St.-Hil.	15.7	EM
Fabales		
Fabaceae		
Aeschynomene montevidensis Vogel	22.2	EM
Vigna sp.	12.0	EM
Cucurbitales		
Cucurbitaceae		
Cyclanthera hystrix (Gillies) Arn.	13.0	AM
Malvales - Eurosideae II		
Malvaceae		
Hibiscus sororius L.	11.1	EM
Melochia arenosa Benth.	13.9	AM
Gentianales - Euasterideae I		
Rubiaceae		
Diodia brasiliensis Spreng.	5.55	AM
Diodia sp.	7.41	AM
Apocynaceae		
Oxypetalum sp.	1.85	AM
Rhabdanenia pohlii Mull. Arg.	1.85	EM
Lamiales		
Plantaginaceae		
Bacopa sp.	7.41	EM
Acanthaceae		
Hygrophila costata Nees	3.70	EM
Lentibulariaceae		
Utricularia foliosa L.	29.6	FS

Utricularia gibba L.	18.5	FS
Lamiaceae		
Hyptis sp.	0.93	EM
Solanales		
Solanaceae		
Solanum glaucophyllum Desf.	5.55	AM
Apiales - Euasterideae II		
Apiaceae		
Hydrocotyle ranunculoides L.f.	54.6	FF
Asterales		
Asteraceae		
Eclipta prostata (L.) L. (= *alba*) (L.) Hassk.	5.56	AM
Eupatorium squalidum DC.	1.85	EM
Mikania cordifolia (L. f.) Willd.	3.70	AM

CONSIDERAÇÕES FINAIS

As assembleias de macrófitas aquáticas do reservatório de Itaipu e da planície de inundação do Alto Rio Paraná apresentaram respostas similares frente a distúrbios de elevada magnitude. A depleção do reservatório de Itaipu e os ciclos de cheia e seca da planície do Alto Rio Paraná promoveram, em maior ou menor grau, a morte de muitas espécies de macrófitas aquáticas, em especial das espécies submersas. Com a abertura de uma nova área para colonização, novas espécies se estabeleceram ou mesmo espécies que já ocupavam as margens do ambiente se dispersaram, ampliando sua distribuição. A mudança de composição de espécies, tanto após a depleção na barragem de Itaipu, quanto ao longo dos pulsos de cheia e seca, se refletiu diretamente nos padrões de co-ocorrência encontrados durante o distúrbio no reservatório. Da mesma forma, a mudança na composição específica implicou na predominância do processo de substituição de espécies em detrimento do aninhamento para a diversidade beta no próprio reservatório de Itaipu, bem como na planície de inundação do Alto Rio Paraná.

O reservatório de Itaipu demonstrou uma recuperação rápida da estrutura da assembleia de macrófitas após o maior distúrbio, com evidência de ocorrência de um "time lag" até o momento em que o ecossistema foi recomposto e voltou à sua flutuação normal de nível. Na planície de inundação, o distúrbio promovido pelos ciclos de cheia e seca selecionaram as espécies a processos adaptativos que permitem as suas recomposições após cada período. Como esses períodos tendem a ser regulares, a despeito da cadeia de reservatórios a montante, as assembleias da planície revelam um "time lag" mais consistente, em resposta à intensidade dos pulsos.

Quanto ao ambiente natural, a planície de inundação, mesmo com uma cascata de reservatórios a montante, mantém um pulso de inundação que influencia toda a dinâmica dos organismos desse sistema. O predomínio de substituição de espécies como o principal fator que promove a diversidade beta reflete numa alta diversidade na planície durante todos os períodos do ciclo hidrológico dos rios e lagoas que compõem o sistema da planície de inundação do Alto Rio Paraná. Ainda assim, a conservação efetiva da planície e de sua diversidade biológica dependerá de um manejo efetivo e imediato das áreas de conservação nela inseridas, e manutenção do regime hidrológico do rio Paraná o mais próximo possível do regime antes dos barramentos a montante.

REFERÊNCIAS (INTRODUÇÃO GERAL)

Agostinho AA, Thomaz SM, Minte-Vera CV and Winemiller KO (2000) Biodiversity in the high Parana´ River floodplain. In: Gopal B, Junk WJ and Davis JA (eds.), Biodiversity in Wetlands: Assessment, Function and Conservation. The Netherlands Backhuys Publishers, Leiden, pp. 89–118

Agostinho AA, Gomes LC, Suzuki HI and Júlio HF (2003) Migratory fish from the upper Paraná River basin, Brazil. In : Carolsfeld J, Harvey B, Ross C, Baer A. and Ross C (eds.), Migratory Fishes of South America: Biology, Social Importance and Conservation Status. World Fisheries Trust, the World Bank and the International Development Research Centre, Victoria, pp. 19–99

Agostinho AA, Pelicice FM, Petry AC, Gomes LC, Júlio Jr HF (2007a) Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. Aquatic Ecosystem Health & Management 10: 174–186

Agostinho AA, Thomaz SM, Gomes LC, Baltar SLSMA (2007b) Influence of the macrophyte *Eichhornia azurea* on fish assemblage of the Upper Paraná River floodplain (Brazil). Aquat. Ecol. 41: 611-619

Barrat-Segretain MH (1996) Strategies of reproduction, dispersion and competition in River plants: a review. J. Veg. Sci. 123: 13–37

Barrat-Segretain MH, Bornette G (2000) Regeneration and colonization abilities of aquatic plant fragments: effect of disturbance seasonality. Hydrobiologia 421: 31-39

Baselga A, Jiménez-Valverde A (2007) Environmental and geographical determinants of beta diversity of leaf beetles (Coleoptera: Chrysomelidae) in the Iberian peninsula, Ecological Entomology 32: 312-318

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19: 134–143

Bini LM, Thomaz SM, Souza DC (2001) Species richness and β-diversity of aquatic macrophytes in the Upper Paraná River floodplain. Arch. Hydrobiol. 151: 511-525

Camargo AFM, Esteves FA (1996) Influence of water variation on biomass and chemical composition of the aquatic macrophyte *Eichhornia azurea* (KUNTH) in a oxbow lake of the Rio Mogi Guaçu (São Paulo-Brazil). Arch. Hydrobiol. 135: 423-432.

Cody ML, Diamond JM (1975) Ecology and Evolution of Communities, Harvard University Press, Cambridge.

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invisibility. J. Ecol. 88: 528–536

Denslow JS (1985) Disturbance mediated coexistence of species. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, USA: 307-323

Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, MA, pp 342–444

Gotelli NJ, Graves GR (1996) Null models in ecology. Smithsonian Institution, Washington, DC

Gotelli NJ, McCabe DJ (2002) Species co-occurrence: a meta-analysis of J. M. Diamond´s assembly rules model. Ecology 83:2091–2096

Graves GR, Gotelli NJ (1993) Assembly of avian mixed-species flocks in Amazonia. Proc Natl Acad Sci USA 90:1388–1391

Hubbell SP (2001) The unified neutral theory of Biodiversity and Biogeography, Princeton University Press, Princeton and Oxford, 375 pp

Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. J. Anim. Ecol. 72: 367-382

Korhonen JJ, Soininen J, Hillebrand H (2010) A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. Ecology 91: 508-517

Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data, Ecological Monographs 74: 435-450

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943-1967

Mormul RP, Thomaz SM, Silveira MJ, Rodrigues L (2010) Epiphyton or macrophyte: Which primary producer attracts the snail *Hebetancylus moricandi*? Am. Malacol. Bull. 28: 127-133

Pelicice FM, Agostinho AA (2006) Feeding ecology of fishes associated with *Egeria* spp. patches in a tropical reservoir, Brazil. Ecol. Fresh. Fish. 15:10-19

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC (1988) The role of disturbance in stream ecology. J. North Am. Benthol. Soc. 4: 433-455

Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. Ecology Letters 7:1-15

Riis T, Madsen TV, Sennels RSH (2009). Regeneration, colonization and growth rates of allofragments in four common stream plants. Aquat. Bot. 90: 209-212

Rodrigues LC, Train S, Bovo-Scomparin VM, Jati S, Borsalli CCJ, and Marengoni E (2009) Interannual variability of phytoplankton in the main Rivers of upper Paraná River floodplain, Brazil: influence of upstream reservoirs. Brazilian Journal of Biology 69:501-516

Rolon AS, Maltchik L (2006) Environmental factors as predictors of aquatic macrophyte richness and composition in wetlands of southern Brazil. Hydrobiologia 556: 221-231

Sculthorpe CD (1985) The biology of vascular plants. Edward Arnold, London.

Silveira MJ, Thomaz SM, Mormul RP, Camacho FP(2009) Effects of desiccation and sediment type on early regeneration of plant fragments of three species of aquatic macrophytes. Int. Rev. Hydrobiol. 94: 169-178

Thomaz SM, Pagioro TA, Bini LM, Roberto MC, Rocha RRA (2004) Limnology of the Upper Paraná Floodplain habitats: patterns of spatio-temporal variations and influence of the water levels. In: Agostinho AA, Rodrigues L, Gomes LC, Thomaz SM and

Miranda LE (Eds) Structure and functioning of the Paraná River and its floodplain. Maringá: Eduem. p. 37-42

Thomaz SM, Cunha ER (2010) The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages´ composition and biodiversity. Acta Limn. Bras. 22: 218-236

Tuomisto H (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity, Ecography 33: 2-22

Turner MG, Dale VH (1998) Comparing large, infrequent disturbances: What have we learned? Ecosystems 1: 493-496

Wetzel R G (2001) Limnology: Lakes and river ecosystems. Academic Press, San Diego.

Whittaker RH (1970) Communities and Ecosystems, Macmillan, London.

Whittaker RH (1972) Evolution and measurement of species diversity, Taxon 21: 213-251

Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 3: 385-397