Temporal and spatial patterns of aquatic macrophyte diversity in the Upper Paraná River floodplain

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(With 6 figures)

Abstract

Although the importance of long-term data has been emphasized by ecologists in recent years, little is known about how communities may change over time. In this study, we describe the general patterns of aquatic macrophyte diversity in the Paraná River floodplain observed during six years of study. Temporal changes in community composition were also evaluated. Data on the presence or absence of aquatic macrophytes were collected between March 2002 and March 2008, in six lakes associated with three rivers. Different analytical strategies were used to evaluate the dynamics of aquatic macrophyte communities between the different systems in the floodplain. The composition of aquatic macrophytes differed among the rivers, mainly with respect to the different vegetation life forms (floating, submersed, emergent and rooted with floating stems). The temporal similarity of species composition during the six years and the beta-diversity index indicated that the month-to-month species turnover was, in general, lower in the connected lakes, which are directly influenced by the river. Probably the water level fluctuation is a selective force that contributes to maintaining diversity or richness. Our findings indicated the importance of abiotic characteristics and connectivity of the lakes in determining macrophyte composition and community stability over a long time frame.

Keywords: diversity, aquatic macrophytes, floodplain, long-term.

Padrões temporais e espaciais da diversidade de macrófitas aquáticas na planície de inundação do Alto Rio Paraná

Resumo

Estudos utilizando ampla escala temporal ainda são escassos na ecologia, mesmo considerando sua importância no estudo de comunidades. Esse trabalho teve como objetivo principal descrever padrões gerais sobre a diversidade de macrófitas aquáticas na planície de inundação do Alto Rio Paraná utilizando uma ampla escala temporal (seis anos de estudo). Mudanças na composição das comunidades ao longo do tempo também foram avaliadas. Dados de presença ou ausência de macrófitas foram obtidos entre Março de 2002 e Março de 2008 em seis lagoas associadas a três rios na planície de inundação. Diferentes técnicas foram utilizadas para avaliar a dinâmica das comunidades de macrófitas aquáticas entre os diferentes ambientes. De maneira geral, a composição das comunidades foi dissimilar entre os diferentes rios, principalmente considerando os diferentes grupos funcionais de macrófitas (flutuante livre, submersa, emergente e enraizada com folha flutuante). A similaridade temporal na composição de espécies e o índice de diversidade beta indicaram que a substituição de espécies ao longo dos meses foi, de maneira geral, menor nas lagoas conectadas ao rio principal. Provavelmente, a flutuação no nível da água representa uma pressão seletiva que ajuda a manter a diversidade de espécies nas lagoas diretamente influenciadas pelo rio. Os resultados desse estudo indicaram a importância das características abióticas e da conectividade das lagoas na composição e estabilidade temporal das comunidades de macrófitas aquáticas na planície de inundação do Alto Rio Paraná.

Palavras-chave: diversidade, macrófitas aquáticas, planície de inundação, longa duração.

1. Introduction

Macrophytes constitute one of the major components of freshwater environments, because they help to maintain the biodiversity (Agostinho et al., 2007a; Theel et al., 2008) and ecosystem functions (Engelhardt and Ritchie, 2001; 2002; Bouchard et al., 2007; Bianchini Jr. et al., 2008). This community is highly productive in floodplains (Junk and Piedade, 1993; Bini, 1996), and part of the macrophyte biomass can be used as food by aquatic organisms (Gaspar da Luz et al., 2002; Hahn et al., 2004; Oliveira et al., 2006; Lopes et al., 2007).

Macrophytes are affected by a variety of abiotic factors, including water and sediment nutrients, underwater light, fetch, and water-level fluctuations (e.g., Wetzel, 2001; Camargo et al., 2006; Maltchik et al., 2007). Flood pulses are especially important in river-floodplain ecosystems (Junk et al., 1989; Neiff, 1990) and they alter macrophyte biomass, productivity, composition, and richness (Bini, 1996; Camargo and Esteves, 1996; Ward and Tockner, 2001; Maltchik et al., 2007).

A number of studies have investigated the effects of limnological and hydrological features on aquatic macrophytes in the Upper Paraná River floodplain. In general, both limnological variables (Bini et al., 2001; Murphy et al., 2003) and the hydrological regime (Bini, 1996; Santos and Thomaz, 2007) are important determinants of macrophyte populations and community composition in this stretch of the Paraná. Although some of these studies have focused on large spatial scales (e.g., Bini et al., 2001; Murphy et al., 2003), little is known about the dynamics of these communities from long-term vegetation monitoring.

In this study, we describe the general patterns of aquatic macrophyte diversity in the Upper Paraná River floodplain. We first examine the species richness and life forms of aquatic macrophytes in different lakes in the floodplain. Second, we analyze the long-term changes in the vegetation composition in these environments. The effects of the degree of connectivity of lakes with the main river and water-level fluctuations are used to interpret our data. The study includes both a large spatial scale (connected and isolated lakes belonging to three rivers in the Upper Paraná River floodplain) and a long temporal scale (samples obtained over a six-year period).

2. Study Area

The Paraná River Basin covers a large area in Brazil (ca. 802,150 km^2). In its upper portion, the 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 study was undertaken in this floodplain (Figure 1), which encompasses a variety of aquatic, transitional, and terrestrial habitats (Agostinho et al., 2007b). Our study is part of the Brazilian program of "Long-Term Ecological Research" (LTER – site number 6). Several studies have suggested that habitats differ among the rivers in this floodplain, with respect to both biological and limnological features (Thomaz et al., 2004a). In general, lakes connected directly (by small canals) or indirectly (by the hyporheic corridor or major flood events) to the main river, backwaters, and channels constitute the main aquatic environments.

We selected six lakes, associated with three rivers (Paraná, Baía, and Ivinheima). For each river, two lakes were studied, one directly connected to the river, and another isolated, in direct contact with the river only during major floods, when bank overflow occurs. These lakes vary widely in area, from 0.006 ha (Osmar Lake) to 113.8 ha (Patos Lake).

3. Methods

Aquatic macrophytes were surveyed approximately every three months, between March 2002 and March 2008 (totaling 23 sample series). In each lake, data on macrophyte species were recorded from a boat moving at a constant slow speed along the entire shoreline. Submersed plants were sampled from the boat with a rake, for 10 minutes. Taxonomic identification followed the specialized literature (Cook, 1990; Velasquez, 1994; Pott and Pott, 2000; Lorenzi, 2000).

Different analytical strategies were used to compare the structure of aquatic macrophyte communities among the different habitats in the floodplain (lakes directly connected or not to the main river, and associated with three different rivers), during these six years of study. First, the number of taxa (herein "number of species" or "richness") per lake was plotted for each month, to look for temporal patterns of this attribute and for possible effects from two exceptional floods that occurred in January 2005 and 2007. The effect of lake area on richness was tested by correlation analysis. Second, species-accumulation curves were used to compare species richness among lakes. The species-accumulation curve is the graph of the expected number of species detected as a function of the number of surveys (our sampling effort). Plotting this curve provides a useful method for both quantifying species richness and standardize the sampling effort (Gotelli and Colwell, 2001). Third, macrophytes were grouped according to their life forms (Esteves, 1998), and the lakes were compared in regard to this aspect. Finally, species composition of communities was assessed with a detrended correspondence analysis (DCA), which was applied to ordinate the macrophyte community and to visualize general patterns (Hill and Gauch, 1980).

We also estimated, for each lake, a matrix of community similarity between months, using the Jaccard index:

$$J(AB) = \frac{j}{(a + b + j)} \quad (1)$$

in which a is the number of taxa in community A (community of a lake in one sampling period), b is the number of taxa in community B (community of the same lake in another sampling period), and j is the number of taxa in both communities. This index indicated the degree of temporal stability regarding community composition.

Species turnover over time in each lake was used to measure which group of lakes (connected versus isolated) was more temporally stable. Turnover was assessed by an index of beta diversity provided by Harrison et al. (1992):

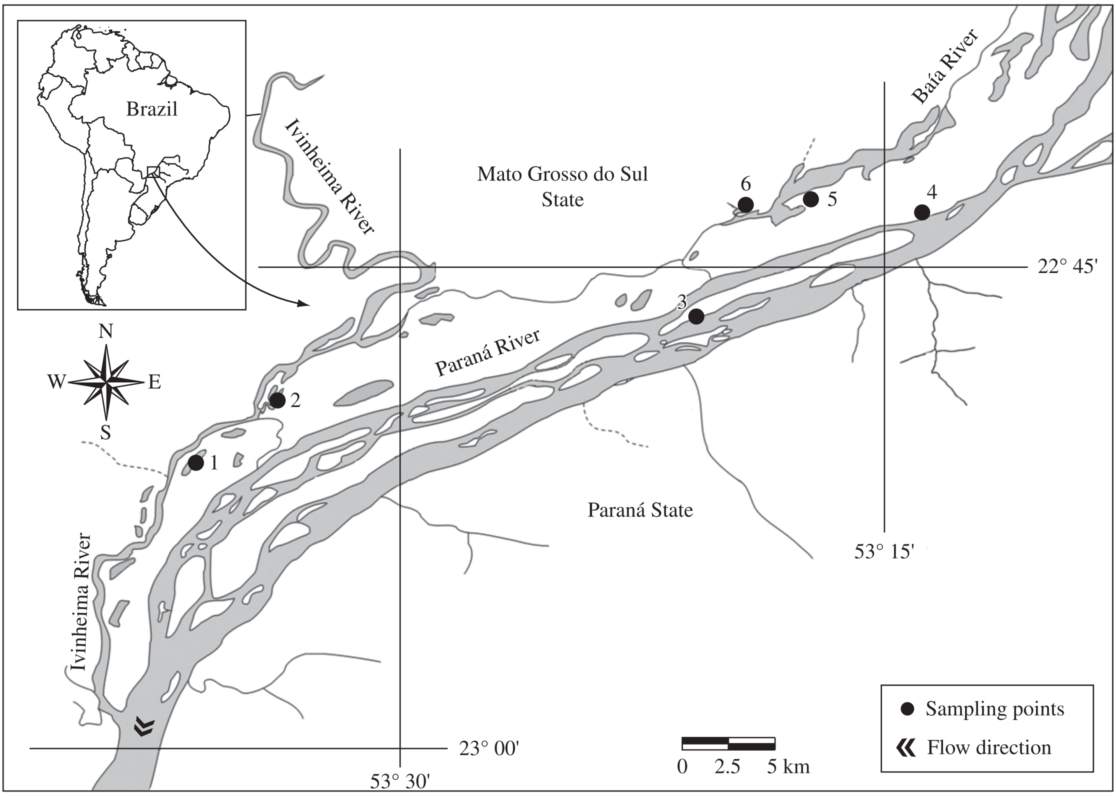

Figure 1. Study sites. 1 = Ventura Lake; 2 = Patos Lake; 3 = Osmar Lake; 4 = Garças Lake; 5 = Fechada Lake; 6 = Guaraná Lake. Lakes 1 and 2 are associated with the Ivinheima River, lakes 3 and 4 with the Paraná River, and lakes 5 and 6 with the Baía River. Lakes 1, 3 and 5 are isolated, and the others are directly connected to the river main channel.

$$\beta - 1 = [(S/\alpha_{mean}) - 1]/(N - 1) \quad (2)$$

where S = total number of species in each lake; α_{mean} = mean alpha diversity (mean S in each lake between March 2002 and March 2008); N = number of months (23).

Differences in species richness, community similarity, and community composition (represented by the first scores of the DCA) between connected and isolated lakes during all the months studied were tested using the paired-sample *t*-test.

4. Results

We recorded a total of 50 taxa of macrophytes during these six years. The richness per lake ranged between 5 (Osmar Lake in March 2006 and 2007) and 24 (Guaraná Lake in December 2004) (Figure 2). The mean number of species was lowest in Osmar Lake (8.4) and highest in Guaraná Lake (17.0). The species-accumulation curves (Figure 3) show that the highest richness was found in the lakes associated with the Baía River (Guaraná Lake), while the lowest number of species was recorded in Osmar Lake, an isolated lake located on an island of the Paraná River. The number of species was not affected by lake area ($r = -0.337$; $p = 0.514$), but it was affected by the degree of connectivity: lower mean richness was found in the isolated lakes (10.6 ± 2.28) than in the connected lakes (13.9 ± 2.25) ($t = 8.352$, $df = 22$, $p < 0.001$).

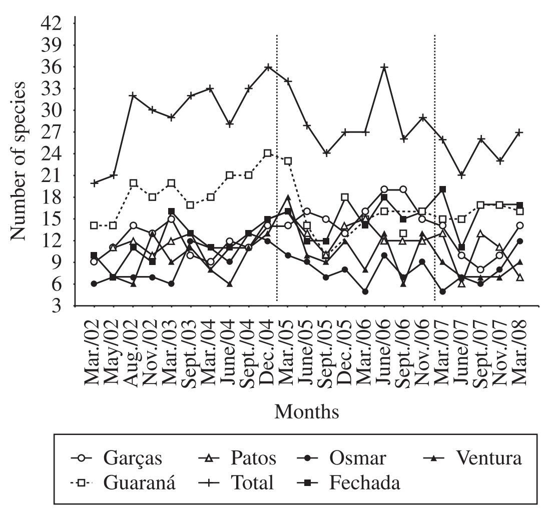

Figure 2. Temporal trends in species richness in six lakes of the Paraná River floodplain.

Despite these differences, there was no clear temporal trend in species richness per lake (Figure 2). Although the exceptional floods in 2005 and 2007 apparently decreased macrophyte richness, it is difficult to associate both variables because of the wide and irregular fluctuations in richness, which also decreased in several months that did not experience major floods (Figure 2).

The most frequent species recorded in the lakes associated with the Paraná River were *Eichhornia azurea* Kunth. (100%), *Nymphaea amazonum* Mart. and Zucc., *Polygonum ferrugineum* Wedd. (95.6%), *Polygonum stelligerum* Cham., and *Salvinia auriculata* Aubl. (86.9%), in Garças Lake; and *P. ferrugineum* and *N. amazonum* (86.9%) in Osmar Lake. In the lakes associated with the Baía River, the most frequent species were *Paspalum repens* Berg. (100%), *P. ferrugineum*, *Hydrocotyle ranunculoides* L.f., *E. azurea*, and *Eichhornia crassipes* (Mart.) Solms (95.6%) in Guaraná Lake; and *Pistia stratiotes* L. (100%), *P. stelligerum* (95.6%), and *E. crassipes* (91.3%) in Fechada Lake. In the lakes associated with the Ivinheima River, *E. azurea* (95.6%) and *E. crassipes* (91.3%) were the most frequent species in Patos Lake; while *E. crassipes* (95.6%), *P. stelligerum* (91.3%) and *E. azurea* (82.6%) were frequent in Ventura Lake.

Although they were recorded in low frequencies in the lakes, two exotic species were also found: the emergent Poaceae *Urochloa subquadripara* (Trin.) R.D. Webster (syn. *Brachiaria subquadripara*) and the rooted submersed *Hydrilla verticillata* L.f. Royle. The latter species was also recorded only twice in Garças Lake, connected to the Paraná River main channel. Although it is rare in lakes, *H. verticillata* develops very rapidly and attains high biomass in the Paraná River main channel and its lateral channels (W. T. Souza, unpublished), where it was first recorded in June 2005. Other submersed native species found in our surveys were *Egeria najas* Planch., *Cabomba furcata* Schult. and Schult.f., *Najas microcarpa* K. Schum., *Nitella furcata*, and *Chara guairensis* R.Bicudo.

The frequency of macrophyte life forms also differed among lakes. The frequency of emergent species was similar among lakes, but free-floating species (represented mainly by *Salvinia* spp.) and rooted species with floating stems (represented mainly by *Eichhornia azurea*) were more frequent in the Baía River lakes (Figure 4). Rooted submersed species were most frequent in Garças Lake (Figure 4).

Ordination clearly separated lakes associated with the three rivers. The first axis separated the Paraná lakes (positioned on the left side) from the Baía and Ivinheima lakes (positioned on the right side). Axis 2 separated the lakes from the other two rivers (Figure 5a). In general, the lakes connected to the Paraná River were characterized by the presence of rooted submersed species (e.g., *E. najas*, *H. verticillata*, *Nitella furcata* (Roxburgh ex Bruzelius) C. Agardh emend. R.D. Wood and *C. furcata*). The difference between macrophyte communities in the lakes connected to the Ivinheima and Baía rivers was mainly caused by the presence of *Thalia* sp. and *Cyperus giganteus* Vahl in the former, and *Ricciocarpus natans* (L.) Corda, *Polygonum meisnerianum* Schan. et Schl., and *Utricularia foliosa* L. in the latter.

The temporal fluctuations of the first axis was quite erratic, and there was no indication that even the exceptionally large floods of 2005 and 2007 affected community structure (Figure 5b). However, the composition of connected and isolated lakes was significantly different in lakes of the Paraná ($t = 5.22$; $p < 0.001$) and Ivinheima rivers ($t = 3.2$; $p = 0.004$). Composition of the connected and isolated lakes did not differ in the Baía River ($t = -1.55$; $p = 0.13$).

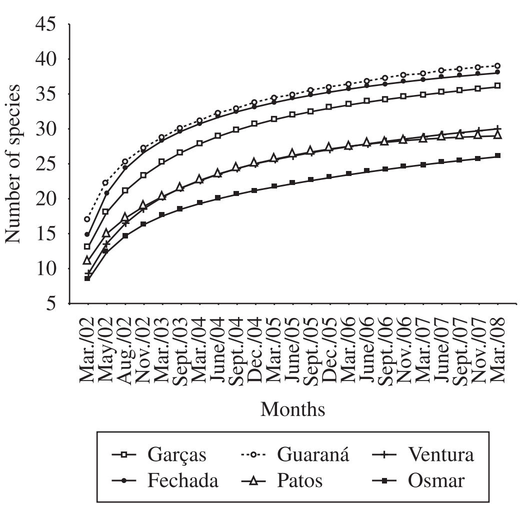

Figure 3. Species accumulation curve of aquatic macrophytes in six lakes of the Paraná River floodplain.

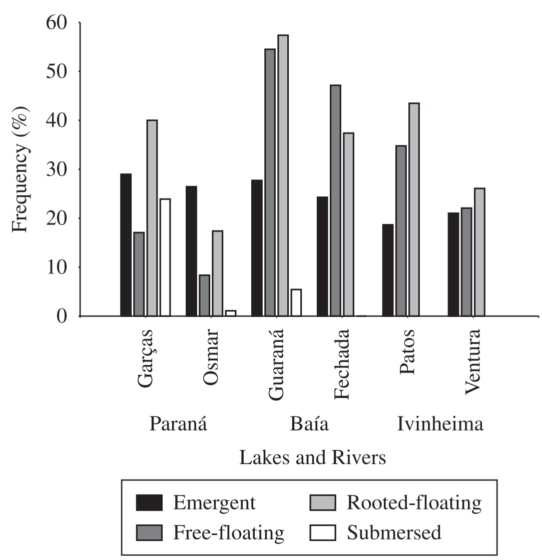

Figure 4. Frequency of macrophyte life forms in lakes of the Paraná River floodplain, between March 2002 and March 2008.

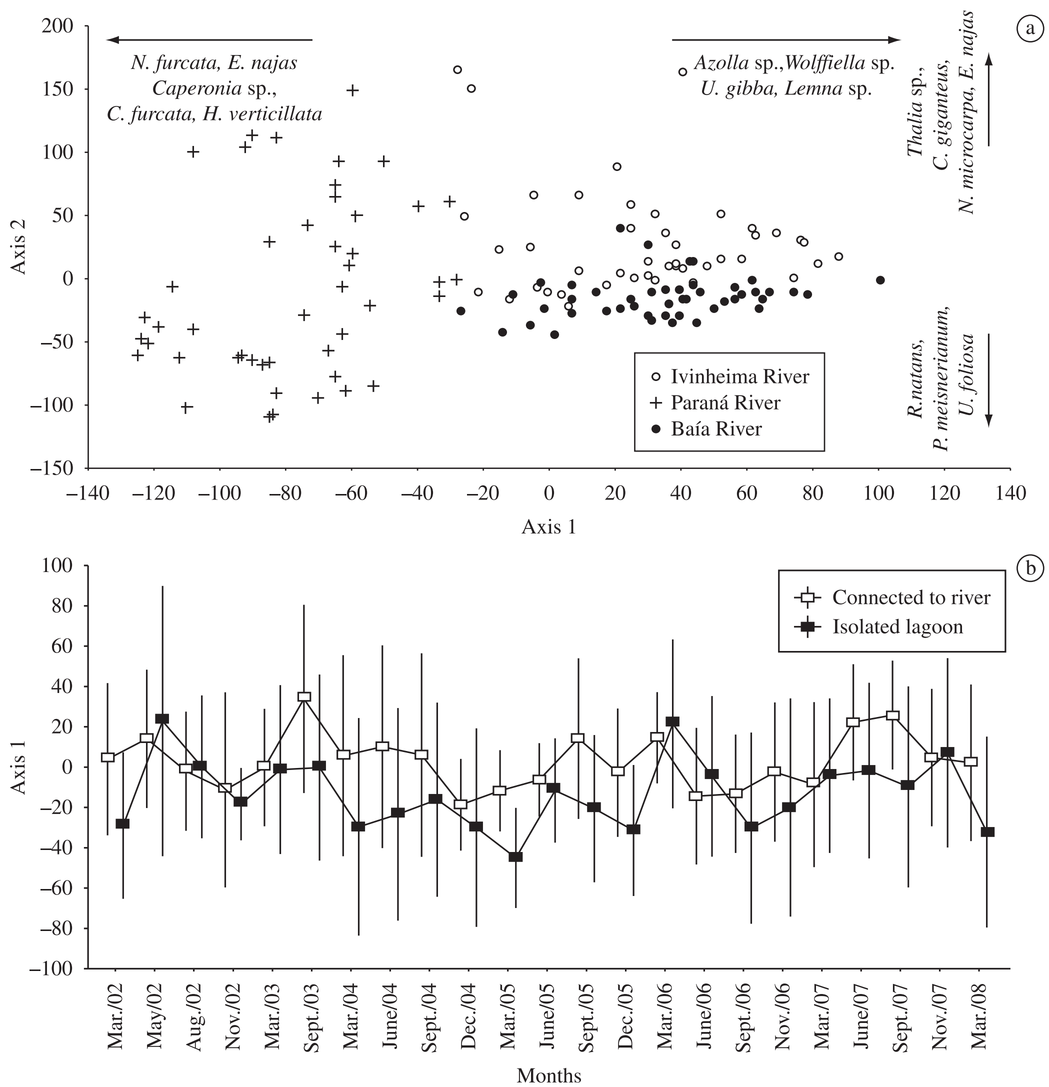

Figure 5. a) Detrended correspondence analysis (DCA) ordination of aquatic macrophyte communities surveyed between March 2002 and March 2008 in lakes associated with the Paraná River, Baía River, and Ivinheima River; and b) Scores of the first DCA axis (±SD) of isolated lakes and lakes connected to their respective rivers.

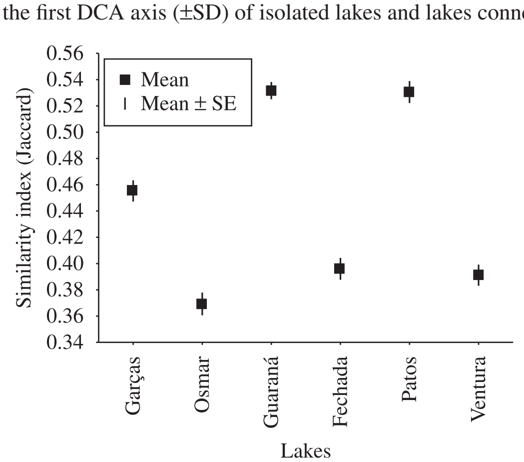

Figure 6. Similarity (Jaccard index) of aquatic macrophyte composition in six lakes of the Paraná River floodplain, during six years of study.

The temporal similarity of species composition, measured by the Jaccard index during the six-year period, was higher in the connected lakes (Baía River: $t = 14.38$; $p < 0.001$; Paraná River: $t = 8.39$; $p < 0.001$; Ivinheima River: $t = 12.57$; $p < 0.001$; Figure 6).

Species turnover during the months (beta diversity) was, in general, lower in the connected lakes (β-1: Garças = 0.079; Guaraná = 0.058; Patos = 0.071) than in the isolated lakes (β-1: Ventura: 0.101; Osmar: 0.095; Fechada: 0.076) ($t = 4.88$; $p = 0.03$), corroborating the results of the Jaccard similarity.

5. Discussion

We concentrated our efforts on only six lakes during six years of surveys. Therefore, our results represent a sub-set of the macrophyte community within the floodplain. For the lakes surveyed, it is quite probable that species richness of euhydrophytes (macrophytes that truly depend on the water table to reproduce and survive) recorded in this study represent reasonably well the real local species richness (alpha diversity). This is suggested by the species-accumulation curves, in which asymptotes were reached in all lakes (Figure 3). On the other hand, the total number of species recorded in the lakes is certainly an underestimate of the real species richness of the floodplain (gamma diversity). Underestimation is caused, in part, by the restricted sampling in a specific type of habitat (only lakes directly or indirectly connected to rivers). In fact, surveys carried out between 1992 and 2000 in several different types of habitats (including rivers, backwaters, and secondary channels) found 62 species (Thomaz et al., 2004a). Even this previous survey underestimated species richness, because several individuals could not be identified to species level, and only euhydrophytes were considered. A more recent survey with an increased diversity of habitats, including also amphibious plants and with improved taxonomic resolution, resulted in 118 species of macrophytes recorded in the Upper Paraná River floodplain (Thomaz et al., 2008).

The accumulation curves also showed that lakes (directly or indirectly) connected to the Baía River contain more species, whereas the lake located close to the Paraná River but unconnected to this river has the fewest species. Possible reasons leading to these differences are the intense disturbances from drying (in the lake unconnected to the Paraná), and intermediate water-level fluctuations in Baía River habitats (which do not undergo the diel or short-term oscillations in water level that are typical of the Paraná and Ivinheima lakes). Area could also account for these differences, as shown in other wetlands (Rolon and Maltchik, 2006), but this variable was not significant in our group of lakes.

The differences in both species richness and composition among lakes associated with the three rivers that were found from 2002 to 2008, were also recorded in surveys carried out in the 1990s (Bini et al., 2001). This information indicates that this pattern is consistent over medium time scales (ca. 10-12 years), and suggests the existence of physical factors acting over wide spatial scales on the floodplain. Also, the three rivers differ in respect to some limnological features (Thomaz et al., 2004b), which might account for the differences observed in their macrophyte communities. For example, the Paraná lakes have higher Secchi disk values and lower nutrient contents, which facilitate the development of rooted submersed species. In contrast, the Ivinheima River carries high solids and phosphorus, which favors the growth of free-floating, rather than rooted submersed species. In addition, habitats associated with the same river may have a spatial auto-correlation regarding both biotic and abiotic features. In this case, even lakes indirectly associated with the same river may have a higher connectivity with respect to individual exchanges, than lakes associated with different rivers. In fact, connectivity has been considered an important aspect to explain similarities of different groups of organisms in floodplain aquatic habitats (Thomaz et al., 2007; Ward and Tockner, 2001). This could also explain the similar species composition and richness among habitats of the same river.

The most frequent species recorded in the lakes surveyed are also very common in the Pantanal Mato-grossense wetland (Pott et al., 1989; Pott and Pott, 2000). The proximity of these floodplains and their similarities in water-level fluctuation are probable reasons for this similarity. However, it seems that lakes of the Pantanal contain more species than do lakes of the Paraná floodplain. Pott et al. (1989), for example, recorded 37 species in a single lake located in the Nhecolândia region, much higher than found in lakes of the Upper Paraná River floodplain (5 to 24 species).

Of all the species recorded, two exotics with high invasive potential deserve special attention: *Urochloa subquadripara* and *Hydrilla verticillata*. The former species is native to Africa, and has been shown to decrease significantly macrophyte diversity at small scales (quadrats with 1m^2) in the Upper Paraná floodplain (Michelan et al., 2008). The latter species is native to Australia, the Pacific Islands, Asia, and probably Africa (Madeira et al., 2007). Although still rare in lakes of the Upper Paraná River floodplain, *H. verticillata* became widespread in the Paraná main channel after 2005 (W. T. Souza, unpublished). There is a lack of information about the invasiveness of *H. verticillata* in Neotropical waterbodies. Data from other ecosystems indicate that it may outcompete native species such as *Egeria densa* (Mony et al., 2007), and it affects different aspects of its associated communities, such as invertebrate composition (Theel et al., 2008) and fish foraging behavior (Theel and Dibble, 2008).

With regard to the temporal variation of community attributes, species richness per lake and species composition (represented by the scores of the first DCA axis) oscillated erratically during the six years, making it difficult to assess the effects of two atypical floods recorded in January 2005 and 2007. Despite a reduction in species number following these floods, confounding responses due to high temporal fluctuations indicate that species richness per se and species composition are not suitable attributes to detect the effect of high flood pulses such as those recorded in the Upper Paraná floodplain in these two years. This confounding response is expected, because richness does not account for dominance or equitability, i.e., macrophytes are not usually eliminated by major floods, although their density may be strongly reduced. The species composition as measured by DCA is also not sensitive, because it was estimated only with a presence-absence matrix in our study. Although we did not measure the effects of floods on plant densities in this study, they are widely recognized in floodplain lakes (Junk and Piedade, 1993; Bini, 1996; Camargo and Esteves, 1996). In addition, rapid recovery of macrophytes from flood disturbances and/or the limitation of our analysis to a few locations may also have prevented clear perception of responses of richness and composition to major floods.

Despite the lack of a clear temporal trend in species richness, some long-term trends of individual species are apparent in the Upper Paraná floodplain. For instance, available data indicate an increase in the occurrence of submersed species after 1998 (Thomaz et al., 2004a; S. M. Thomaz, personal observation), although surveys of macrophytes in the Upper Paraná floodplain were rare before 1995 (Souza et al., 1997). The increase of rooted submersed species (including the exotic *H. verticillata*) is a direct result of the increase in water transparency of the Paraná River (Padial and Thomaz, 2008), and from the large input of propagules from the reservoirs located upstream, which are extensively colonized by submersed plants (Tanaka, 2000; Martins et al., 2008). As a result, the highest frequency of submersed species was found in Garças Lake, the only lake directly connected to the Paraná River main channel.

Besides increasing the species richness and density of submersed species, reservoirs probably contributed to reduce the occurrence of free-floating plants in the habitats connected to the Paraná River, because they drastically reduced phosphorus concentrations downstream (Barbosa et al., 1999). *E. crassipes*, for example, a free-floating macrophyte that is very common in aquatic habitats all over South America, is rare in lakes associated with this river. An experiment employing mesocosms to explore the reason for this scarcity found that phosphorus limits its growth in the Upper Paraná River (Kobayashi et al., 2008), while nitrogen is its main limiting nutrient in downstream habitats of this river (Carignan and Neiff, 1992). Thus, reservoir operation probably has an important role in structuring macrophyte assemblages in lakes of the Upper Paraná River floodplain.

Despite the effects of reservoir operation (which presumably affects almost all the lakes simultaneously), directly connected and isolated lakes differ according to species richness, composition, and degree of stability. Higher species richness in directly connected lakes may be accounted for by the constant and direct input of propagules brought by rivers into these habitats. Ward and Tockner (2001) proposed that the alpha diversity of several groups reaches a peak in habitats with an intermediate degree of connectivity. However, because our data only deal with connected versus isolated lakes, it is difficult to infer if our connected lakes really represent intermediate degrees of connectivity.

The higher temporal similarity found in the connected lakes (indicated by both Jaccard and β-1 indices) suggests that these habitats are more stable over time, compared to isolated lakes. The connected lakes are usually shallower and experience greater water-level fluctuations because of their direct connection with the river main channel (Santos and Thomaz, 2007). The variation in water level probably represents a selective force favoring certain species, which will dominate over time, and, together with the constant entrance of propagules carried in by river water, may explain the greater stability of these habitats. In fact, intermediate-level disturbances (such as floods in wetland systems) may cause selective mortality, which would contribute to maintaining diversity or species richness (Connell, 1978; Petraitis et al., 1989; Bhattacharjee et al., 2007), in agreement with our results showing higher species richness in directly connected lakes. On the other hand, isolated lakes usually follow a succession independent of each other (leading to different communities over time), and some of them may occasionally dry completely. Thus, wider temporal variations in species richness (temporal beta diversity) and composition are expected in these habitats, which is consistent with the greater dissimilarity observed over time.

In summary, our results indicated that the degree of connectivity of the lakes with the main river is an important determinant of macrophyte richness and composition. We also found that, together with species richness, species composition varies more between lakes associated with different rivers, than between lakes associated with the same river. Therefore, the degree of connectivity and regional differences increase the gamma (large-scale) diversity of macrophytes in the Upper Paraná River floodplain. Long-term trends of macrophyte species richness were not noted, but an increase in the richness and abundance of submersed species was recorded in the last ten years, as a response to increased water transparency. An understanding of the changes in community composition through time has important implications for applied ecology, especially for the application of predictive models (Milner et al., 2006). Our results improved understanding of the importance of abiotic factors on aquatic macrophyte assemblages over a long time span.

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References

AGOSTINHO, AA., PELICICE, FM., PETRY, AC., GOMES, LC. and JÚLIO Jr., HF., 2007a. Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. *Aquatic Ecosystem Health & Management*, vol. 10, no. 2, p. 174-186.

AGOSTINHO, AA., THOMAZ, SM., GOMES, LC. and BALTAR, SLSMA., 2007b. Influence of the macrophyte *Eichhornia azurea* on fish assemblage of the Upper Paraná River floodplain (Brazil). *Aquatic Ecology*, vol. 41, no. 4, p. 611-619.

BARBOSA, FAR., PADISÁK, J., ESPÍNDOLA, ELG., BORICS, G. and ROCHA, O., 1999. The cascading reservoir continuum concept (CRCC) and its application to the river Tietê-basin, São Paulo State, Brazil. In Tundisi, JG. and Straškraba, M. *Theoretical reservoir ecology and its applications*. Leiden: International Institute of Ecology, Brazilian Academy of Sciences; Backhuys Publishers. p. 425-438.

BHATTACHARJEE, J., HAUKOS, D. and NEAVILLE, J., 2007. Vegetation response to disturbance in a coastal marsh in Texas. *Community Ecology*, vol. 8, no. 1, p. 15-24.

BIANCHINI Jr., I., CUNHA-SANTINO, MB. and PERET, AM., 2008. Oxygen demand during mineralization of aquatic macrophytes from an oxbow lake. *Revista Brasileira de Biologia = Brazilian Journal of Biology*, vol. 68, no. 1, p. 61-67.

BINI, LM., 1996. Influência do pulso de inundação nos valores de fitomassa de três espécies de macrófitas aquáticas na planície de inundação do alto rio Paraná. *Arquivos de Biologia e Tecnologia*, vol. 39, no. 3, p. 715-721.

BINI, LM., THOMAZ, SM. and SOUZA, DC., 2001. Species richness and beta-diversity of aquatic macrophytes in the Upper Paraná River floodplain. *Archiv für Hydrobiologie*, vol. 151, no. 3, p. 511-525.

BOUCHARD, V., FREY, SD., GILBERT, JM. and REED, SE., 2007. Effects of macrophyte functional groups richness on emergent freshwater wetland functions. *Ecology*, vol. 88, no. 11, p. 2903-2914.

CAMARGO, AFM. and ESTEVES, FA., 1996. Influence of water level variation on biomass and chemical composition of the aquatic macrophyte *Eichhornia azurea* (Kunth) in an oxbow lake of the Rio Mogi-Guaçu (São Paulo, Brazil). *Archiv für Hydrobiologie*, vol. 135, no. 3, p. 423-432.

CAMARGO, AFM., PEZZATO, MM., HENRY-SILVA, GG. and ASSUMPÇÃO, AM., 2006. Primary production of *Utricularia foliosa* L., *Egeria densa* Planchon and *Cabomba furcata* Schult & Schult from rivers of the coastal plain of the State of São Paulo, Brazil. *Hydrobiologia*, vol. 570, p. 35-39.

CARIGNAN, R. and NEIFF, JJ., 1992. Nutrient dynamics in the floodplain ponds of the Paraná River (Argentina) dominated by the water hyacinth *Eichhornia crassipes*. *Biogeochemistry*, vol. 17, no. 2, p. 85-121.

CONNELL, JH., 1978. Diversity in tropical rain forests and coral reefs. *Science*, vol. 199, p. 1302-1310.

COOK, CDK., 1990. Origin, autecology, and spread of some of the world´s most troublesome aquatic weeds. In PIETERSE, AH. and MURPHY KJ. (Eds.). *Aquatic weeds*: the ecology and management of nuisance aquatic vegetation. Oxford: Oxford Science Publications. p. 31-38.

ENGELHARDT, KAM. and RITCHIE, ME., 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature*, vol. 411, p. 687-689.

______, 2002. The effects of aquatic plant species richness on wetland ecosystem processes. *Ecology*, vol. 83, no. 10, p. 2911-2924.

ESTEVES, FA., 1998. *Fundamentos de limnologia*. Rio de Janeiro: Interciência; FINEP. 602p.

GASPAR Da LUZ, KD., FUGI, R., ABUJANRA, F. and AGOSTINHO, AA., 2002. Alterations in the *Pterodoras granulosus* (Valenciennes, 1833) (Osteichthyes, Doradidae) diet due to the abundance variation of a bivalve invader species in the Itaipu Reservoir, Brazil. *Acta Scientiarum*, vol. 24, no. 2, p. 427-432.

GOTELLI, N. and COWELL, RK., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, vol. 4, p. 379-391.

HAHN, NS., FUGI, R. and ANDRIAN, IF., 2004. Trophic ecology of the fish assemblages. In THOMAZ, SM., AGOSTINHO, AA. and HAHN, NS. *The upper Paraná River and its floodplain*: physical aspects, ecology and conservation. Leiden: Backhuys. p. 247-269.

HARRISON, S., ROSS, SJ. and LAWTON, JH., 1992. Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology*, vol. 61, no. 1, p. 141-148.

HILL, MO. and GAUCH, HG., 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, vol. 42, no. 1-3, p. 47–58.

JUNK, WJ. and PIEDADE, MTF., 1993. Biomass and primary-production of herbaceous plant communities in the Amazon floodplain. *Hydrobiologia*, vol. 263, p. 155-162.

JUNK, WJ., BAYLEY, PB. and SPARKS, RE., 1989. The flood pulse concept in river- floodplain systems. *Canadian Special Publications in Fisheries and Aquatic Sciences*, vol. 106, p. 110-127.

KOBAYASHI, JT., THOMAZ, SM. and PELICICE, FM., 2008. Phosphorus as a limiting factor for *Eichhornia crassipes* growth in the Upper Paraná River floodplain. *Wetlands*, vol. 28, no. 4, p. 905-913.

LOPES, CA., BENEDITO-CECILIO, E. and MARTINELLI, LA., 2007. Variability in the carbon isotope signature of *Prochilodus lineatus* (Prochilodontidae, Characiformes) a bottom-feeding fish of the Neotropical region. *Journal of Fish Biology*, vol. 70, no. 6, p. 1649-1659.

LORENZI, H., 2000. *Plantas daninhas do Brasil*: terrestres, aquáticas, parasitas e tóxicas. 3 ed. Nova Odessa: Instituto Plantarum de Estudos da Flora. 608p.

MADEIRA, PT., COETZEE, JA., CENTER, TD., WHITE, EE. and tipping, pw., 2007. The origin of *Hydrilla verticillata* recently discovered at a South African dam. *Aquatic Botany*, vol. 87, no. 2, p. 176-180.

MALTCHIK, L., ROLON, AS. and SCHOTT, P., 2007. Effects of hydrological variation on the aquatic plant community in a floodplain palustrine wetland of southern Brazil. *Limnology*, vol. 8, no. 1, p. 23-28.

MARTINS, D., COSTA, NV., TERRA, MA. and MARCHI, SR., 2008. Caracterização da comunidade de plantas aquáticas de dezoito reservatórios pertencentes a cinco bacias hidrográficas do estado de São Paulo. *Planta Daninha*, vol. 26, no. 1, p. 17-32.

MICHELAN, TS., THOMAZ, SM. and MORMUL, RP., 2008. Efeito de *Brachiaria subquadripara* sobre a riqueza e composição de macrófitas aquáticas em uma lagoa do alto rio Paraná. In *Anais do III Workshop Site 6 – A planície alagável do rio Paraná: estrutura e processos ambientais.* Maringá: UEM; Nupélia. p. 16. Conservação e Biodiversidade. Abstracts.

MILNER, AM., CONN, SC. and BROWN, LE., 2006. Persistence and stability of macroinvertebrate communities in streams of Denali National Park, Alaska: implications for biological monitoring. *Freshwater Biology*, vol. 51, no. 2, p. 373-387.

MONY, C., KOSCHNICK, TJ., HALLER, WT. and MULLER, S., 2007. Competition between two invasive Hydrocharitaceae (*Hydrilla verticillata* (L. f.) (Royle) and *Egeria densa* (Planch) as influenced by sediment fertility and season. *Aquatic Botany*, vol. 86, no. 3, p. 236-242.

MURPHY, KJ., DICKINSON, G., THOMAZ, SM., BINI, LM., DICK, K., GREAVES, K., KENNEDY, MP., LIVINGSTONE, S., McFERRAN, H., MILNE, JM., OLDROYD, J. and WINGFIELD, RA., 2003. Aquatic plant communities and predictors of diversity in a sub-tropical river floodplain: the Upper Rio Paraná, Brazil. *Aquatic Botany*, vol. 77, p. 257-276.

NEIFF, JJ., 1990. Ideas para la interpretación ecológica del Paraná. *Interciencia*, vol. 15, no. 4, p. 424-441.

OLIVEIRA, ACB., SOARES, MGM. and MOREIRA, MZ., 2006. Carbon sources of fish in an Amazonian floodplain lake. *Aquatic Sciences*, vol. 68, no. 2, p. 229-238.

PADIAL, AA. and THOMAZ, SM., 2008. Prediction of the light attenuation coefficient through the Secchi disk depth: empirical modeling in two large Neotropical ecosystems. *Limnology*, vol. 9, no. 2, p. 143-151.

PETRAITIS, PS., LATHAM, RE. and NIESENBAUM, RA., 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology*, vol. 64, no. 4, p. 393-418.

POTT, VJ. and POTT, A., 2000. *Plantas aquáticas do Pantanal*. Brasília: Embrapa. 404p.

POTT, VJ., BUENO, NC., PEREIRA, RAC., De SALIS, SM. and VIEIRA, NL., 1989. Distribuição de macrófitas aquáticas numa lagoa na Fazenda Nhumirim, Nhecolândia, Pantanal, MS. *Acta Botanica Brasilica*, vol. 3, no. 2, p. 153-168.

ROLON, AS. and MALTCHIK, L., 2006. Environmental factors as predictors of aquatic macrophytes richness and composition in wetlands of southern Brazil. *Hydrobiologia*, v. 556, p. 221-231.

SANTOS, AM. and THOMAZ, SM., 2007. Aquatic macrophytes diversity in lagoons of a tropical floodplain: the role of connectivity and water level. *Austral Ecology*, vol. 32, no. 2, p. 177-190.

SOUZA, MC., CILINSKI, J. and ROMAGNOLO, MB., 1997. Levantamento florístico. In VAZZOLER, AEA., AGOSTINHO, AA. and HAHN, NS. *A Planície de inundação do Alto Rio Paraná*: aspectos físicos, biológicos e sócio-econômicos. Maringá: EDUEM. p. 343-368.

TANAKA, RH., 2000. *Levantamento da ocorrência de plantas aquáticas nos reservatórios da CESP*. São Paulo: CESP Report. 25p.

THEEL, HJ. and DIBBLE, ED., 2008. An experimental simulation of an exotic aquatic macrophyte invasion and its influence on foraging behavior of bluegill. *Journal of Freshwater Ecology*, vol. 23, no. 1, p. 79-89.

THEEL, HJ., DIBBLE, ED. and MADSEN, JD., 2008. Differential influence of a monotypic and diverse native aquatic plant bed on a macroinvertebrate assemblage: an experimental implication of exotic plant induced habitat. *Hydrobiologia*, vol. 600, p. 77-87.

THOMAZ, SM., BINI, LM. and BOZELLI, RL., 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, vol. 579, p. 1-13.

THOMAZ, SM., BINI, LM., PAGIORO, TA., MURPHY, KJ., SANTOS, AM. and SOUZA, DC., 2004a. Aquatic macrophytes: diversity, biomass and decomposition. In THOMAZ, SM., AGOSTINHO, AA. and HAHN, NS. *The upper Paraná River and its floodplain*: physical aspects, ecology and conservation. Leiden: Backhuys. p. 331-352.

THOMAZ, SM., CARVALHO, P., KOBAYASHI, JT., PADIAL, AA., MORMUL, RP., SILVEIRA, MJ., SOUSA, WT., MICHELAN, TS., EVANGELISTA, HB. and FERREIRA, FA., 2008. Macrófitas aquáticas da planície de inundação do alto rio Paraná. In *Anais do III Workshop. Site 6 – A planície alagável do rio Paraná: estrutura e processos ambientais*. Maringá: UEM; Nupélia. p. 14-15. Abstracts. Conservação e Biodiversidade.

THOMAZ, SM., PAGIORO, TA., BINI, LM., ROBERTO, MC. and ROCHA, RRA., 2004b. Limnological characterization of the aquatic environments and the influence of hydrometric levels. In THOMAZ, SM., AGOSTINHO, AA. and HAHN, NS. *The upper Paraná River and its floodplain*: physical aspects, ecology and conservation. Leiden: Backhuys. p. 75-102.

VELASQUEZ, J., 1994. *Plantas acuaticas vasculares de Venezuela*. Caracas: Universidade Central de Venezuela, Consejo de Desarrollo Cientifico y Humanistico. 992p.

WARD, JV. and TOCKNER, K., 2001. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology*, vol. 46, no. 6, p. 807-819.

WETZEL, RG., 2001. *Limnology*: lake and river ecosystems. San Diego: Academic Press. 1006p.