

Do aquatic macrophytes co-occur randomly? An analysis of null models in a tropical floodplain

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Received: 10 March 2007 / Accepted: 22 January 2008
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Abstract One of the main issues in community ecology is the detection of structure and the identification of its related causes. In this study, co-occurrence null models were used to identify possible spatio-temporal patterns in the assemblage of aquatic macrophytes in the Upper Paraná River floodplain. The samples were obtained through the Long Term Ecological Research (LTER) Program at two different grains: (1) a coarser spatial grain in January and August 2001 (entire floodplain lagoons); (2) and a finer spatial grain in November 2006 (1 m² quadrats). The study was conducted in 36 lagoons, both connected and disconnected to the main river channel, located in the sub-basins of the Baía, Ivinheima and Paraná rivers. Two null models of species co-occurrence, the C-Score and Checkerboard indices, were used to test the null hypothesis of random structure of the aquatic macrophyte assemblages. The null models showed that the aquatic macrophyte assemblages were spatially structured in the distinct spatial grains. However, despite this general pattern, macrophyte assemblages are organized differently depending on the degree of connectivity, seasonal period and, at a finer grain, depth. Species co-occurrences were random in the disconnected lagoons during flood periods, in deep zones of the lagoons of the

Baía River and in the shallow littoral zone in the lagoons of the Paraná River. Analysis of the patterns of co-occurrence indicated that competition and/or habitat preferences are probably important influences on the nonrandom structure of assemblages. However, we suppose that at least three important factors (disturbances by water level fluctuation, dispersion and facilitation) counteract potential effects of competition in specific situations, leading macrophyte assemblages to assume random structure.

Keywords Habitat segregation · Competition · Flood and drought disturbances · C-Score · Checkerboard distribution

Introduction

Ecological studies of assemblages often make implicit assumptions that species have nonrandom spatio-temporal distribution patterns. Detecting assemblage structure and identifying its driving forces is one of the main issues in current community ecology. Nonrandom spatial organization of an assemblage suggests the existence of at least one structuring factor, such as a specific biological interaction and/or habitat segregation. Most papers analyze general trends in the patterns of co-occurrence in assemblages and infer that competition, for example, is an important factor influencing structure (e.g., Diamond 1975; Graves and Gotelli 1993; Oliveira et al. 2005). Other mechanisms, such as habitat requirements, biogeography and evolutionary history are also used to explain patterns of checkerboard distributions (Gotelli and McCabe 2002). On the other hand, random assemblages are usually interpreted as the result of multiple factors acting simultaneously, like environmental gradients, competition, predation, and facilitation, which

Communicated by John Silander.

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may have opposite effects that therefore prevent the formation of a spatial pattern (Gotelli and Graves 1996).

Factors explaining the structure of aquatic macrophyte associations may be nested, and their importance may vary according to the grain and extent (*sensu* Wiens 1989). At a coarse extent, geomorphometry, climate and biogeography are important, while at a catchment extent, water chemistry, flow regime, hydrology and species pool may dominate, and at a local extent, depth, wind scouring and biological interactions may play important roles in structuring assemblages (Lacoul and Freedman 2006).

The aquatic macrophyte assemblage is usually composed of species with different life forms. This has been considered very important for maintaining the integrity of aquatic ecosystems. These plants contribute to the structure of the physical space by increasing the complexity of aquatic habitats. In floodplain ecosystems, aquatic macrophyte assemblages are especially indicative of environmental variability because they respond to longitudinal as well as transverse gradients in relation to the main river (Neiff and Poi de Neiff 2003; Thomaz et al. 2004a), also including flood disturbance (Maltchik et al. 2004; Kennedy et al. 2006).

Several studies in subtropical and tropical regions suggest that some aquatic macrophyte species are associated within assemblages (e.g., Bini et al. 2001; Murphy et al. 2003; Rolon and Maltchik 2006). However, structure cannot be interpreted as real unless it is tested by specific models that analyze community structure (null/neutral/lottery models). The few investigations addressing tests of the organization of macrophytes were carried out in temperate regions (Pielou and Routledge 1976; Keddy 1983; Shipley and Keddy 1987). These works applied null models and in general they demonstrated that assemblages were organized in discrete clusters, which are driven by factors such as competition, salinity and latitude (summarized by Keddy 2000).

In this study we investigated: (1) whether the aquatic macrophyte assemblages of the Upper Paraná River floodplain lagoons are spatially structured at different extents; (2) if spatial pattern, when present, remains in different seasonal periods (high and low water levels); and (3) whether spatial pattern is affected by the degree of connectivity of the lagoons with the main river (connected and disconnected lagoons). To answer these questions, we studied a coarse spatial extent (the Upper Paraná River floodplain) at two different grains: coarser spatial grains (where lagoons were used as the unit of observation) and finer spatial grains (in which quadrats were the unit of observation). We expect that the structure of the aquatic macrophyte assemblages presents a non-random pattern at the different grains as a response to competition and/or habitat preferences, and that pattern is

affected by flood disturbance according to degree of connectivity.

Study area

The braided floodplain of the Upper Paraná River (between 22°40'S and 23°40'S latitude and between 53°10'W and 53°40'W longitude) is located inside three Conservation Units (Ilha Grande National Park, Ivinheima State Park and Environmental Protection Area of “Ilhas e Várzeas do Rio Paraná”). It is the last undammed stretch of this river in Brazil, and it is important for the conservation of several threatened aquatic and terrestrial species (Agostinho et al. 2004). Since 1999, the Upper Paraná River and its floodplain have been included in the Long-Term Ecological Research (LTER) Program. The samples were taken in lagoons associated with the Paraná River and also in lagoons associated with the Ivinheima and Baía rivers, which are important tributaries of the Paraná River.

There are conspicuous hydrological and limnological differences among these rivers as well as among their lagoons (Thomaz et al. 2004b). In general, the Paraná River has the lowest total phosphorus ($\bar{x} = 18 \mu\text{g l}^{-1}$, $\text{SD} = 13$) and Kjeldhal nitrogen concentrations ($\bar{x} = 207 \mu\text{g l}^{-1}$, $\text{SD} = 138$), and the highest conductivity, pH and Secchi disk values ($\bar{x} = 54 \mu\text{S cm}^{-1}$, $\text{SD} = 5$; $\bar{x} = 7.3$, $\text{SD} = 0.3$; $\bar{x} = 1.6 \text{ m}$, $\text{SD} = 0.8$ respectively). The Ivinheima River is richer in total phosphorus ($\bar{x} = 50 \mu\text{g l}^{-1}$, $\text{SD} = 19$), has the lowest Secchi disk values ($\bar{x} = 0.7 \text{ m}$, $\text{SD} = 0.4$) and intermediate values for Kjeldhal nitrogen, conductivity and pH ($\bar{x} = 342 \mu\text{g l}^{-1}$, $\text{SD} = 151$; $\bar{x} = 43 \mu\text{S cm}^{-1}$, $\text{SD} = 4$; $\bar{x} = 7.0$, $\text{SD} = 0.3$, respectively). The Baía River has intermediate total phosphorus concentrations and Secchi disk ($\bar{x} = 44 \mu\text{g l}^{-1}$, $\text{SD} = 13$; $\bar{x} = 1.0$, $\text{SD} = 0.3$ respectively), the highest values of Kjeldhal nitrogen ($\bar{x} = 467 \mu\text{g l}^{-1}$, $\text{SD} = 173$) and low values of pH and conductivity ($\bar{x} = 6.8$, $\text{SD} = 0.4$; $\bar{x} = 26 \mu\text{S cm}^{-1}$, $\text{SD} = 9$ respectively). Although the floodplain is mostly affected by the water level of the Paraná River, local differences occur in response to the hydrology of each river (Souza Filho et al. 2004). In addition to these physical and chemical differences, these three rivers are in different basins: the Baía River has its sources in the Upper Paraná River floodplain, the Ivinheima River flows from the north-west (State of Mato Grosso do Sul) and has no reservoirs in its basin, whereas the Paraná River runs from the north-east and has several reservoir cascades in its basin.

Reservoirs located upstream from the floodplain are colonized by many submersed species, and these have increased in the lagoons connected to the Paraná River during the past decade (Thomaz et al. 2004a). The physical

and chemical variability, together with differences in the species pool, affect the aquatic macrophyte assemblages, whose compositions differ among the lagoons associated with each different river (Bini et al. 2001).

Materials and methods

Sampling

The first sampling period was conducted in January (a wet period with higher water levels) and in August (a dry period with lower water levels) in 2001 (Fig. 1), herein called the “high water” and “low water” periods. In both periods, ten lagoons connected to the main river channel (five connected to the Baía River, three to the Ivinheima River and two to the Paraná River) and 14 disconnected lagoons (four associated with the Baía River, six with the Ivinheima River and four with the Paraná River) were investigated to test general patterns of structure of aquatic macrophyte assemblages. The connected lagoons remain permanently linked to the river through channels of various lengths (ca. 20–200 m), while the disconnected lagoons receive water from the rivers only during high water levels, through overflow. Lagoon areas, measured during low waters, were highly variable: from 0.006 to 89 ha. The entire shoreline of each lagoon was surveyed by boat at a low and constant velocity. Rakes were used to sample the submersed vegetation. The collected material was deposited in the herbarium of the Maringá State University (HUM).

Although surveys carried out in entire lagoons could provide important information about the general patterns of species aggregation and segregation, it is difficult to evaluate mechanisms behind these patterns. For example,

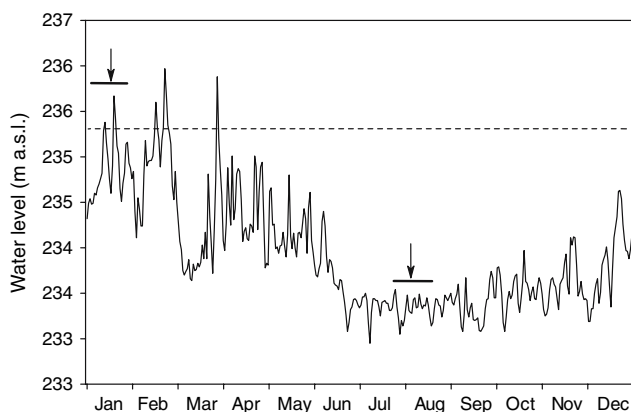


Fig. 1 Daily water level of the Upper Paraná River floodplain in 2001, at Porto São José city. Arrows indicate the sampling periods of this study. The dashed line indicates overflow level. Data supplied by the ANEEL—National Agency of Electrical Energy/Ministry of Mines and Energy of Brazil

results (based on the indices measuring the strength of species associations) departing from the null expectation could be erroneously interpreted as competition because two species could not co-occur due to different habitat preferences (e.g., submersed species occur more in the Paraná lagoons, where water transparency is higher, but not in Ivinheima lagoons, where the water is more turbid). On the other hand, facilitation could also be erroneously inferred by patterns of aggregation found in the entire lagoons, since two species could co-occur in the same lagoon more often than expected by chance, but could colonize different depths. This last statement is especially valid for macrophytes because these plants are usually arranged according to depth gradients or zonation (Sculthorpe 1967; Keddy 2000). In addition, different species could be segregated by other habitat constraints (e.g., flow regime, disturbances and wind scouring). Since biological interactions and depth are among the factors that affect aquatic macrophytes at a local scale (Lacoul and Freedman 2006), we refined our analysis by using finer spatial grains (1 m² quadrats in different depths). This refinement was carried out in a second extensive sample in November 2006 (low water period) in 20 lagoons: five associated with the Baía River, nine with the Ivinheima River and six with the Paraná River.

This period was chosen because it represents the end of the low water period. Thus, the absence of great floods in the eight months prior to this period leads the macrophyte assemblages to represent a relatively long period of time in which the different areas were not subjected to flood disturbances. This period was probably long enough to lead to organization derived from intra and interspecific interactions, different from that of the flood season, when macrophyte assemblages are expected to be disorganized (Neff 1979; Thomaz et al. 2007).

In each lagoon, we collected between two and eight transects, according to their area. In each transect, we recorded all species of macrophytes within an area of 1 m² in two sites: one located as close as possible to the margin and the other located in a more distal (opposite) position, i.e., in the limit of the stand with the limnetic region. Where necessary, rakes were used to verify the presence of submersed macrophytes. The mean depth of quadrats positioned close to the margin ($\bar{x} = 0.79$ m; SE = 0.05) was significantly lower than the depth of quadrats positioned farther from the lagoon margins ($\bar{x} = 1.69$; SE = 0.05) (ANOVA; $F = 141.7$; $df = 1$, error $df = 183$; $P < 0.001$). Herein they will be described as “shallow” and “deep” quadrats. A total of 93 transects (186 quadrats) were surveyed. Thus, patterns identified by this procedure were generated by species co-occurring in the same microhabitat (1 m²) and might be more affected by species interactions or habitat preferences.

Data analysis

We used two null models of species co-occurrence to test the null hypothesis of random structure of aquatic macrophyte assemblages. A presence–absence matrix was used which contains one when a species is present in a given sampling unit and zero when it is absent. The co-occurrence matrix was randomized to maintain constant totals for lines (species) and columns (sites), using the SIM9 algorithm (Gotelli 2000). Consequently, the species in a randomized matrix are found in the same number of sites, and each site keeps the same number of species as in the observed co-occurrence matrix. The matrix was randomized to produce random patterns that would be expected in the absence of biological interactions and in the absence of effects of the physical environment (Gotelli and Graves 1996). The SIM9 algorithm was chosen because it shows a smaller probability of type I error (Gotelli 2000). This algorithm retains the ecological characteristics associated with the assemblage and incorporates them into the null model.

We used two co-occurrence indices: the Checkerboard Score of a matrix (hereafter the C-Score, Stone and Roberts 1990) and the Checkerboard index (hereafter Checker, Diamond 1975). The C-Score measures species segregation (i.e., this index detects species pairs that do not occur together frequently) but does not require a perfect checkerboard distribution (Gotelli 2000). On the other hand, the Checker index computes the number of species pairs forming a perfect checkerboard distribution, which is the total number of species pairs that do not co-occur in different sites. The rows of the matrix are scanned for species pairs forming checkerboards. We did not prefer one index over the other because they capture different aspects of a co-occurrence pattern and may not always give similar results (Gotelli 2000). If communities are structured by competition and/or habitat segregation among species, then the C-Score and Checker indices should be higher than expected by chance. However, when their values are lower than expected by chance, facilitation or environmental affinities among species might be important. Random distributions could be interpreted as the action of many contrasting factors simultaneously, or just by chance.

Using the first sampling (2001), the null models were firstly performed for the whole data set, including all species with more than two occurrences. It is recommended to exclude rare species from the analyses because it is not possible to determine if rarity is a sampling artifact or not, and because rare species could inflate the estimates of the co-occurrence patterns (Oliveira et al. 2005). The analysis for the whole floodplain was also repeated considering seasonality effects (low and high water periods), the degree

of connectivity (connected and disconnected lagoons) and the relative importance of the isolated factors (i.e., connected at high and low water levels, and disconnected at high and low water levels). We also used the first sampling data set to determine the proportion of pairs of species that co-occurred more considering the degrees of connectivity (disconnected and connected lagoons) and seasonal periods (low water and high water periods). We carried out this analysis to investigate if the percentage of pairs of co-occurring species varied according to degree of connection and season.

Using the second sampling period (2006), we first applied the null models to the entire data set and then to groups of lagoons belonging to each river in order to check if patterns detected by the entire lagoons were repeated when only the quadrats were analyzed (i.e., if patterns generated by samples in the coarser grain would be repeated in the finer grain). Then, a refinement was made by analyzing shallow quadrats separate from deeper quadrats. In this case, C-Score or Checker scores that were significantly higher than expected by chance in the total data set and in the shallow or deep quadrats were considered to be indicative of competition and/or habitat preferences (e.g., sediment or water chemistry). On the other hand, indices significantly higher than expected by chance in the total data set but random in the shallow and deep quadrats would indicate that some species occur only in shallow or deep areas (i.e., habitat preference).

Analyses were performed using EcoSim software v.7.2 (Gotelli and Entsminger 2001) with presence–absence matrices of species in sampling units. For each analysis, the observed matrix was randomized 20,000 times.

Results

Samplings in entire lagoons

We found 50 species of aquatic macrophytes, belonging to 23 families, in the 24 lagoons in the first samplings (Table 1). Of these, eight were excluded from the analysis for being rare or occasional. The most frequently observed species were *Eichhornia azurea* and *Ludwigia suffruticosa* (90% of samplings), *Eichhornia crassipes* (83%), *Polygonum ferrugineum* (81%), *Oxycaryum cubense* (75%), *Salvinia auriculata* and *Nymphaea amazonum* (71%), *Polygonum stelligerum* (69%) and *Salvinia herzogii* (56%).

When the entire data set was used, both the C-Score and Checker indices were higher than expected by chance (Table 2). In an additional analysis which used the data set of low and high water periods separately, similar results were obtained, indicating that macrophyte assemblages

Table 1 Families and species recorded during two extensive samplings in 24 lagoons of the Upper Paraná River floodplain

Family	Species	LF	A	B
Amaranthaceae	<i>Althernanthera philoxeroides</i> (Mart.) Griseb.	EM	×	×
Alismataceae	<i>Echinodorus grandiflorus</i> (Cham. & Schltld.) Micheli	EM	×	×
Apiaceae	<i>Hydrocotyle ranunculoides</i> L.f.	EM	×	×
Araceae	<i>Pistia stratiotes</i> L.	FF	×	
Azollaceae	<i>Azolla microphylla</i> Kaulf.	FF	×	
Begoniaceae	<i>Begonia cucullata</i> Willd.	EM	×	
Cabombaceae	<i>Cabomba furcata</i> Schult. & Schult.f.	RS		×
	<i>Cabomba caroliniana</i> A. Gray	RS	×	
Commelinaceae	<i>Commelina diffusa</i> Burm.f.	EM	×	
Cyperaceae	<i>Cyperus ferax</i> Rich.	EM	×	
	<i>Cyperus giganteus</i> Vahl	EM	×	
	<i>Eleocharis filiculmis</i> Kunth	EM	×	×
	<i>Fimbristylis cf. autumnalis</i> (L.) Roem. & Schult.	EM	×	
	<i>Oxycaryum cubense</i> (Poepp. & Kunth) Lye	EP	×	×
	<i>Rhynchospora corymbosa</i> (L.) Britt.	EM	×	
Euphorbiaceae	<i>Caperonia castaneifolia</i> (L.) A. St.-Hil.	EM	×	
Haloragaceae	<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	RS	×	
Lemnaceae	<i>Lemna</i> sp.	FF		×
	<i>Wolffiella</i> sp.	FF	×	
Lentibulariaceae	<i>Utricularia foliosa</i> L.	FS	×	×
	<i>Utricularia breviscapa</i> Wright ex Griseb.	FS		×
	<i>Utricularia gibba</i> L.	FS	×	×
Hydrocharitaceae	<i>Limnobium laevigatum</i> (Humb. & Bonpl. ex Willd.) Heine	FF	×	×
	<i>Egeria densa</i> Planch.	RS		×
	<i>Egeria najas</i> Planch.	RS		×
	<i>Hydrilla verticillata</i> (L.f.) Royle	RS		×
Marantaceae	<i>Thalia geniculata</i> L.	EM	×	
Najadaceae	<i>Najas conferta</i> A. Braun	RS	×	
	<i>Najas microcarpa</i> K. Schum.	RS		×
Nymphaeaceae	<i>Nymphaea amazonum</i> Mart. & Zucc.	RF	×	×
Onagraceae	<i>Ludwigia octovalvis</i> Jacq.	EM	×	
	<i>Ludwigia peruviana</i> (L.) H. Hara	EM		×
	<i>Ludwigia peploides</i> (Kunth) P.H.Raven	RS	×	
	<i>Ludwigia leptocarpa</i> (Nutt.) Hara	EM	×	
Orchidaceae	<i>Habenaria repens</i> Nutt.	EP	×	
Poaceae	<i>Paspalum repens</i> Berg.	EM	×	×
Polygonaceae	<i>Polygonum acuminatum</i> H.B.K.	EM	×	×
	<i>Polygonum ferrugineum</i> Wedd.	EM	×	×
	<i>Polygonum hydropiperoides</i> Michx.	EM	×	×
	<i>Polygonum meissnerianum</i> Cham. & Schltld.	EM	×	×
	<i>Polygonum punctatum</i> Elliott	EM	×	×
	<i>Polygonum stelligerum</i> Cham.	EM	×	×
Pontederiaceae	<i>Eichhornia azurea</i> (Sw.) Kunth	EM	×	×
	<i>Eichhornia crassipes</i> (Mart.) Solms	FF	×	×
	<i>Heteranthera</i> sp.	RS	×	
	<i>Pontederia cordata</i> L.	EM	×	×
Ricciaceae	<i>Ricciocarpus natans</i> (L.) Corda	FF	×	×
Salviniaceae	<i>Salvinia auriculata</i> Aubl.	FF	×	×
	<i>Salvinia herzogii de la Sota</i>	FF	×	×
	<i>Salvinia minima</i> Baker	FF	×	×
Scrophulariaceae	<i>Bacopa</i> sp.	EM		×

Their life forms (LF) are also shown: *EM* emergent, *EP* epiphyte, *FL* floating leaved, *FF* free-floating, *RS* rooted submersed and *FS* free submersed; *A* are species recorded in the first sampling (lagoons as unit) and *B* are species recorded in the second sampling (1 m² quadrats as units)

Table 2 Results of the C-Score and Checkerboard indices observed (obs.) and expected (exp.) for aquatic macrophyte assemblages in the lagoons of the Upper Paraná River floodplain

Level	N	S	C-Score				Checker			
			Obs.	Exp.	SD	p (obs. > exp.)	Obs.	Exp.	SD	p (obs. > exp.)
Whole data set	48	42	53.84	51.81	0.24	<0.001	59.00	32.86	6.32	<0.001
Seasonal effect										
High water period	24	42	14.52	13.05	0.08	<0.001	85.00	53.32	9.07	<0.001
Low water period	24	40	12.76	12.30	0.09	<0.001	162.0	129.8	8.84	<0.001
Degree of connectivity effect										
Connected lagoons	10	40	2.29	2.08	0.02	<0.001	89.00	51.96	7.83	<0.001
Disconnected lagoons	14	42	4.85	4.73	0.03	0.007	121.0	114.21	5.78	0.242
Season × connectivity										
High water and connected	10	38	2.27	2.07	0.01	<0.001	55.00	34.05	7.28	0.008
High water and disconnected	14	38	5.25	5.13	0.04	0.01	95.00	81.44	8.82	0.089
Low water and connected	10	36	2.40	2.26	0.03	0.002	178.0	136.5	8.72	<0.001
Low water and disconnected	14	38	4.15	3.95	0.04	<0.001	199.0	180.7	8.50	0.008

Results are separated for the total data set, seasonal periods and degree of connectivity of the lagoons

N number of lagoons, S species richness, SD standard deviation of the expected results

remain segregated in different seasonal periods. These last results suggest that the co-occurrence structure within lagoons is maintained in different periods.

However, when the degree of connectivity (connected and disconnected lagoons) was considered, contrasting results were obtained. Species co-occurrences were random in the disconnected lagoons during the high water period, as measured using the Checker index but not the C-Score. Since these indices capture different features of a co-occurrence pattern, our results indicate that the spatial distribution structure of the macrophytes species within the assemblages can be considered to be nonrandom, but this depends on the connectivity of the lagoons. When factors (degree of connectivity and flood regime) were isolated, the structure of aquatic macrophyte assemblages was generally nonrandom. Species were randomly distributed only in the disconnected lagoons during the high water period, as shown by the Checker index (Table 2).

Of all possible species pairs in disconnected lagoons, about 70% occurred in less than 10% of lagoons during low water, and no species pairs occurred in more than 80% of lagoons. During high water in connected lagoons, only 14% of the pairs occurred in less than 10% of sites and 13% of pairs occurred in >60% of lagoons (Fig. 2). The pairs of species that co-occurred most frequently, independent of seasonality and connectivity degree of the lagoon, were: *E. azurea* × *E. crassipes*, *E. crassipes* × *L. suffruticosa*, *O. cubense* × *E. azurea*, *O. cubense* × *E. crassipes*, *E. azurea* × *S. auriculata* and *E. azurea* × *P. stelligerum*.

Sampling using quadrats

A total of 41 species of macrophytes, belonging to 17 families, were recorded in the 186 quadrats (Table 1). Of these, nine were excluded from the analysis for being rare or occasional. The most frequent species were *E. azurea* (59%), *S. auriculata* (40%), *S. minima* (26%), *O. cubense* and *E. crassipes* (24%). The least frequent species were *Bacopa* sp., *Najas microcarpa*, *Pontederia cordata* and *Echinodorus grandiflorus* (2%) and *Althernanthera philoxiroides*, *Egeria densa* and *Polygonum meissnerianum* (1.6%).

When we used the quadrats of all groups of lagoons (all rivers), both the C-Score and Checker indices were higher than expected by chance (Table 3). Similarly, the results of both indices indicated species segregation in the lagoons connected to the Baía and Ivinheima rivers (Table 3). The Checker index indicated that species were segregated in Paraná River lagoons as well, although the C-Score indicated that species were arranged randomly.

In order to assess the patterns of co-occurrence isolating the effects of depth, we analyzed shallow and deep quadrats separately. The assemblages of shallow quadrats in lagoons connected to the Baía (Fig. 3) and Ivinheima (Fig. 4) rivers presented values of both indices that indicated nonrandom patterns. On the other hand, for shallow quadrats of the Paraná lagoons, both C-Score and Checker values were within the distribution obtained at random (Fig. 5). Considering deep quadrats, in the lagoons of the Baía River, only the C-Score results were higher than expected by chance (Fig. 3). Both C-Score and Checker indices were

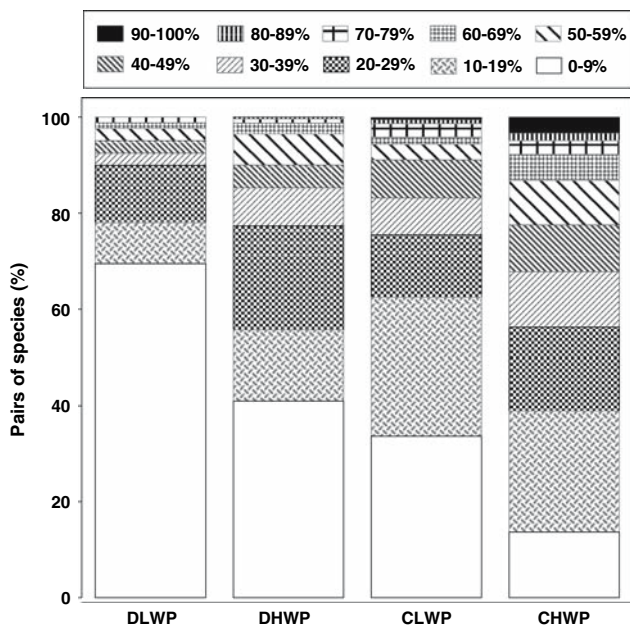


Fig. 2 Proportion of pairs of species in the frequency classes of co-occurrence considering the degrees of connectivity (disconnected and connected lagoons, *D* and *C*, respectively) and seasonal periods (low water and high water periods, *LWP* and *HWP*, respectively) in lagoons of the Upper Paraná River floodplain in 2001

higher than expected by chance in the lagoons connected to the Ivinheima (Fig. 4) and Paraná (Fig. 5) rivers.

Discussion

Sampling in entire lagoons

The nature of communities and the effect of disturbance upon their structure are central issues in community ecology. Two contrasting visions dominate the plant ecology literature, namely the individualistic (Gleason) versus superorganismic (Clements). Most investigations testing these hypotheses have been based on the analysis of plant

distribution along spatial gradients, which has largely supported the individualistic vision (e.g., Keddy 2000 and several ecology textbooks). The interesting issue here is that, contrary to what has been found in forests, spatial boundaries do exist in herbaceous zonation (Pielou and Routledge 1976; Keddy 1983; Shipley and Keddy 1987). Our null model approach contributes to the above discussion because we used results of macrophyte co-occurrence within a tropical floodplain to test if the spatial pattern of this assemblage was different from the assemblages originated at random (i.e., to determine if the assemblage was spatially structured).

Our results showed that species co-occurrences were less frequent than expected by chance (i.e., assemblages are spatially organized) in the large data set, when entire lagoons were used as units (our coarser grain analysis), but it approaches a random distribution in disconnected lagoons during the flood period. There were no cases in which a pattern of aggregation (i.e., C-Score or Checker lower than expected by chance) was found. These results suggest that: (1) in general, there are important factors behind the structure of macrophytes community at a coarse extent (as suggested by whole data set analysis) and they remain important regardless of the period (high and low water); and (2) these factors share their importances with other, opposite effects during high water period in the disconnected lagoons.

Competition and environmental affinities have been widely inferred as a plausible mechanism to explain species segregation within assemblages such as we found for our whole data set. Competition has often been emphasized as an important biological interaction among macrophytes in river-floodplain systems (Bornette et al. 1998; dos Santos and Thomaz 2007). Competitive interactions may occur between species belonging to the same life form, such as between free-floating (Agami and Reddy 1990; Henry-Silva and Camargo 2005; dos Santos and Thomaz 2007), submersed (Barrat-Segretain 2004; see also review in McCreary 1991) and emergent species (Grace and

Table 3 Results of the C-Score and Checkerboard indices observed (obs.) and expected (exp.) for aquatic macrophyte assemblages in the quadrats of the lagoons connected to the Baía, Ivinheima and Paraná rivers

Level	<i>N</i>	<i>S</i>	C-Score				Checker			
			Obs.	Exp.	SD	<i>p</i> (obs. > exp.)	Obs.	Exp.	SD	<i>p</i> (obs. > exp.)
All rivers	186	32	214.30	208.47	1.52	<0.001	279.00	202.60	8.15	<0.001
By rivers										
Baía	50	21	44.52	39.79	0.49	<0.001	94.00	60.09	5.51	<0.001
Ivinheima	80	14	134.07	127.08	1.3	<0.001	22.00	12.75	2.64	0.001
Paraná	56	17	37.33	37.44	0.53	0.56	85.00	62.43	3.65	<0.001

Results are separated for the total data set and by rivers

N number of lagoons, *S* species richness, *SD* standard deviation of the expected results

Fig. 3 Histograms of the observed and expected values of the C-Score and Checkerboard indices for shallow and deep zones recorded at finer grain (1 m² quadrats) in the connected lagoons of the Baía River

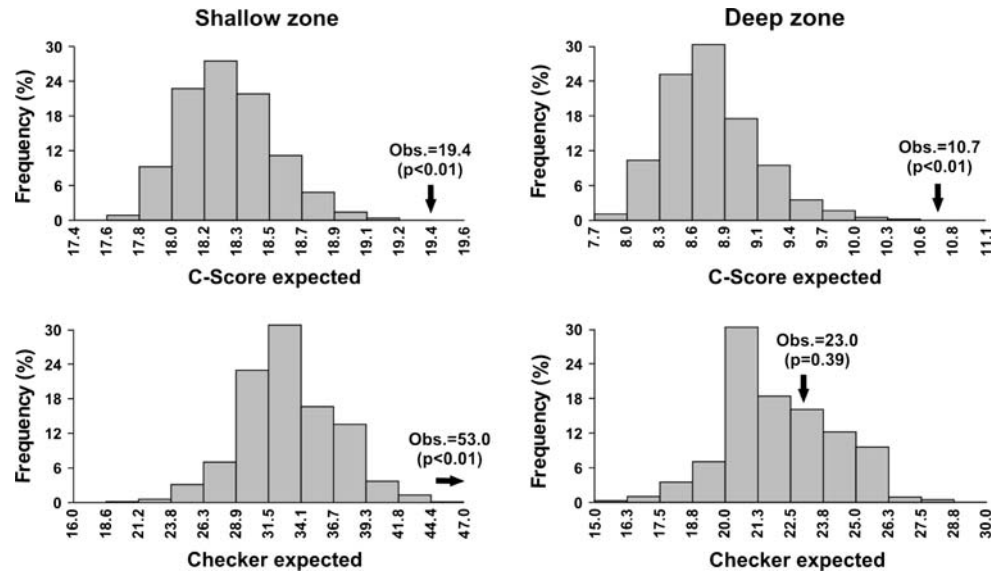
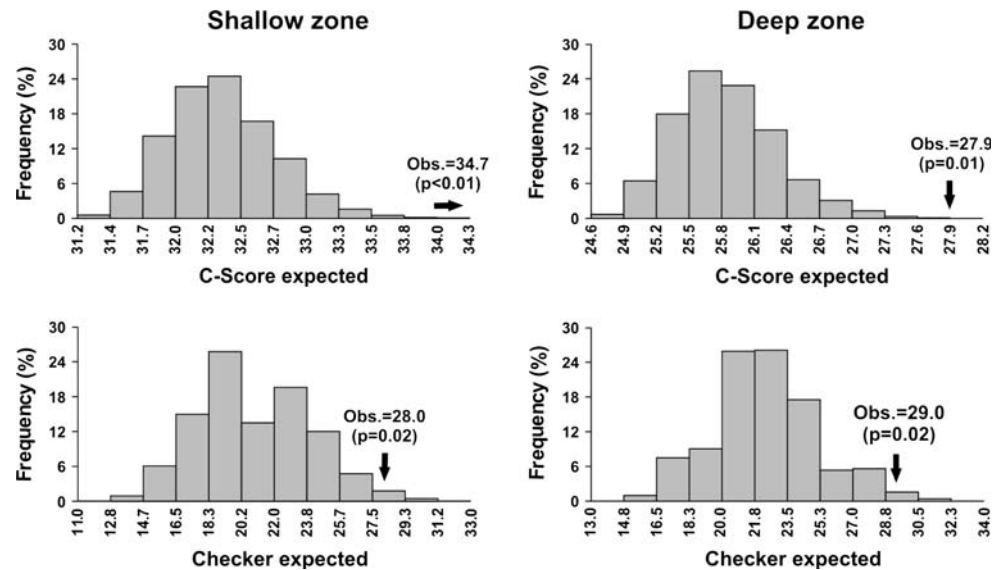


Fig. 4 Histograms of the observed and expected values of the C-Score and Checkerboard indices for shallow and deep zones recorded at finer grain (1 m² quadrats) in the connected lagoons of the Ivinheima River



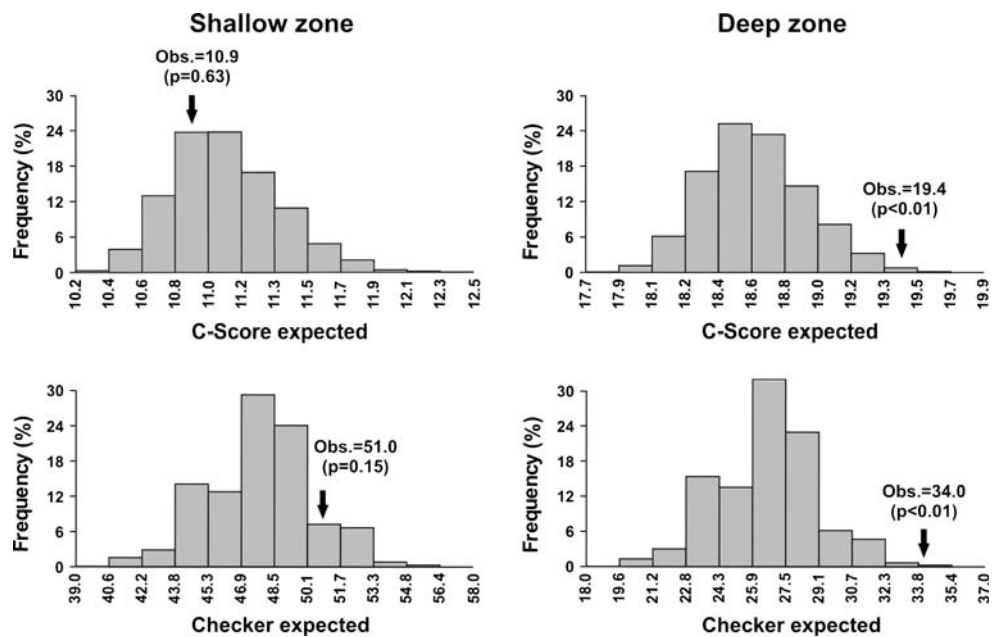
Wetzel 1981; Gopal and Goel 1993) or between species belonging to different life forms, such as submersed and free-floating forms (Scheffer et al. 2003).

Environmental affinities may be considered an alternative explanation for spatial segregation, since macrophytes are sensitive to the physical and chemical characteristics of water and sediment (Grace and Wetzel 1981; Milne et al. 2006; dos Santos and Thomaz 2007). In the Paraná floodplain, lagoons connected to different rivers differ significantly in their chemical aspects, such as phosphorus, nitrogen and turbidity (Thomaz et al. 2004b). Differences in depth and water chemistry are also found between connected versus disconnected lagoons (dos Santos and Thomaz 2007). In conjunction, differences in water and sediment have been used to explain differences in plant assemblages between lagoons of this floodplain system

(Bini et al. 2001) and they could also account for the segregation observed in our work.

Nonrandom spatial patterning seems to be especially important in the disconnected lagoons during low water periods, when they presented the highest percentage of species pairs that rarely co-occurred and when there were no pairs of species that co-occurred in more than 80% of the sites. In the year of this study the flood intensity was low (Souza-Filho et al. 2004) due to upstream reservoirs that regulate the flood regime. Some studies in floodplains investigating how the floods are regulated by hydroelectric dams have shown that the flow, the inundated area and the duration of the flood are reduced, altering the connectivity patterns between the main channel and the marginal environments as well as the depths of these environments (Bornette et al. 1998; Souza-Filho et al. 2004). During this

Fig. 5 Histograms of the observed and expected values of the C-Score and Checkerboard indices for shallow and deep zones recorded at finer grain (1 m² quadrats) in the connected lagoons of the Paraná River



period, lagoons are not subjected to disturbances from floods, and species interactions (especially competition) assume an important role in structuring macrophytes and other communities in lagoons (Neiff 1979; Bornette et al. 1998; Oliveira et al. 2001; Okada et al. 2003; Agostinho et al. 2004; Thomaz et al. 2007). In addition, the expansion of amphibious macrophyte species is common in the dry period (Riis and Sand-Jensen 2001) and during this period these highly competitive species, like emergent aquatic macrophytes (e.g., species of *Polygonum* in our sites), may dominate the assemblages because of their higher stress tolerance (caused by drought) (Coops et al. 2003).

The disorganization of macrophyte assemblages during high waters indicates that different (and antagonistic) factors affect these assemblages in the disconnected lagoons during this period. We propose that at least three important factors counteract potential effects of competition and/or habitat preferences, giving rise to random assemblages in this period: physical disruption of community (caused by floods), dispersal (a source of propagules carried by floods) and facilitation. We will address each of these three factors in the following paragraphs.

Macrophyte composition in floodplain lakes is largely determined by the water level regime (Neiff 2001; Neiff and Poi de Neiff 2003; Thomaz et al. 2004a; Maltchik et al. 2005; Van Geest et al. 2005). Physical disruption caused by floods seems the most parsimonious explanation for assemblage disruption (and for the loss of structure) detected during high waters in disconnected lagoons. During the sampling period, there were overbank floods (see Fig. 1) and even before overbank floods, the water levels of Paraná River were high and allowed connectivity

though groundwater (“flow pulses”, sensu Tockner et al. 2000). This increased the depth of lagoons, representing a disturbance. The inundation prevents the re-establishment and growth of some aquatic macrophyte species, and the interval of the pulses of inundation is an important determinant of macrophyte succession in the floodplain lagoons (Maltchik et al. 2004) and interferes directly in the spatial organization of the assemblages. The absence of spatial structure in the aquatic macrophyte assemblage in the disconnected lagoons in the flood periods can be explained by the “flood homogenization hypothesis” (sensu Thomaz et al. 2007), which predicts an increased connectivity (a regional driving force) and a decreased environmental heterogeneity during high waters. The lagoons that remain connected to the main river are more similar to each other since the exchange of propagules is maintained even during low waters.

In addition to being dependent on propagules in sediments (dos Santos and Thomaz 2007), hydrophytes are dependent upon water fluxes for dispersal and thus their presence in disconnected lagoons may depend on overflow. The transport of propagules by water flow is considered an important determinant of the structure of backwaters and cut-off assemblages (Bornette et al. 1998; Bornette et al. 2001). It has also been shown that recolonization of floodplain habitats following disturbances is partially stochastic, corresponding to the replacement of equivalent species through lottery establishment (Barrat-Segretain 1996). In lagoons of the Upper Paraná River floodplain, floods can transfer small free-floating species between lagoons and thus, since a new succession begins after new species recruitment, it is less probable that competition

would be an important factor organizing such assemblages in this period. However, floods could explain part of the random distribution (as predicted by lottery establishment) detected in these lagoons during high waters. On the other hand, competition during the low water period would be important, since there would be enough time for interspecific interactions to occur.

Facilitation has emerged in ecology as an important process behind community organization (Bruno et al. 2003). One of the main arguments is that facilitation can also reduce the effects of niche-shrinking factors, enabling species to exploit a greater portion of the available resources (e.g., light, nutrients and space). Although competition has been largely emphasized as an important interaction among macrophytes, few investigations suggest that facilitation between different species may occur (Agami and Reddy 1991; Espinar et al. 2002; Thomaz et al. 2005). Although we did not test it experimentally, there is evidence that *E. azurea* (one of the most frequent species recorded in our samplings) with its long floating stems reduces current and wind wave disturbance, providing a favorable microhabitat for small floating plants, such as *Salvinia* spp., *Azolla* sp. and *Ricciocarpus natans* (Thomaz et al. 2005). Another example of facilitation occurs with *Oxycaryum cubense*, an aquatic epiphyte that grows over other plants such as *E. azurea* and *S. auriculata* (Pott and Pott 2000).

Sampling using quadrats

Results obtained when lagoons were used as units indicated that, in general, competition and/or habitat preferences are important mechanisms behind assemblage structure. However, macrophytes differ according to their life forms (e.g., submersed rooted, free-submersed, free-floating, emergent and floating-leaved) that occupy different regions along a depth gradient (Sculthorpe 1967; Keddy 2000). Spatially heterogeneous competitive environments are those in which the competitive rankings of species are altered (Amarasekare 2003). Thus, depth differences found in littoral regions indicate that macrophytes live in a spatially heterogeneous competitive environment; habitat depth alters competitive performances by, for example, enabling emergent species to grow at shallower sites and rooted submersed species at deeper sites (Sculthorpe 1967). In addition to competition, habitat constraints may lead to nonrandom patterns (Peres-Neto et al. 2001; Gotelli and Ellison 2002). Thus, species segregation (or nonrandom patterns) found for macrophytes by null models at the coarse extent (whole data set—case 1) may be attributed to different responses to depth and other habitat characteristics. We tested this hypothesis using the results of our second data set, using quadrats as units.

The general pattern of nonrandomness was maintained for this second data set (i.e., quadrats as units). In most cases, both the observed C-Score and Checker indices were higher than expected by chance. It suggests that competition is probably an important structuring force of the macrophytes assemblages, although spatial segregation cannot be discounted. Since these results were recorded in finer grain sizes (1 m² quadrats), they reflect the patterns of species co-occurrences tested within microhabitats.

However, the deep quadrats of Baía, where the Checker index was not different from the simulated distribution, and the shallow quadrats of the Paraná lagoons, where both indices were within the values obtained at random, were exceptions. These results indicate that macrophyte assemblages are affected by contrasting forces in the deep zone of the Baía lagoons and in the shallow zone of the Paraná lagoons. Different mechanisms are probably affecting these two cases. In the deep zone of the Baía lagoons, facilitation probably counteracts potential effects of competition largely through the interaction between *Utricularia foliosa* and *Nymphaea amazonum*, which co-occurred in more than 50% of the quadrats (data not shown). Since the former species is free-submersed, it depends on a substrate, found in the long stems of *N. amazonum*, for attachment.

On the other hand, the most probable mechanism disrupting the assemblages in the shallow zone of the Paraná River lagoons is their water regime. Due to water regulation by reservoirs located upstream (Souza Filho et al. 2004), the discharge and water level of this river suffers large daily fluctuations (up to 1.0 m). Since these lagoons are directly connected to the main channel of the Paraná River, which distinguishes them from the Baía and Ivinheima lagoons, they are the first to be affected by such fluctuations, and thus their littoral zones are exposed and re-flooded daily. Intermediate disturbances caused by floods may limit competitive exclusion of littoral vegetation (Bornette et al. 2001; Van Geest et al. 2005), but the high frequency of disturbances experienced by shallow sites in lagoons may promote the colonization of some emergent and amphibious species (e.g., *Polygonum* spp.). Thus, in these shallow sites competition probably becomes less important in view of the high frequency of disturbances represented by exposure and emersion.

In summary, our results show that the macrophyte assemblages of a tropical floodplain are spatially segregated and probably structured by competition and/or habitat preferences. The recorded pattern of organization repeats when analyses are carried at different scales (coarser: lagoons of floodplain; finer: quadrats as units). Despite this general pattern, it seems that macrophyte assemblages are organized differently depending on the degree of connectivity, the period of the year and, at a finer grain, depth. Species were distributed randomly in only a

few areas. Thus, other biological (e.g., facilitation and dispersion) and physical (e.g., disturbance by water level fluctuation) driving forces may also be important in explaining the pattern of organization of aquatic assemblages in tropical floodplains.

Acknowledgments We acknowledge with appreciation the help of Dr. Débora Cristina de Souza (CEFET—Campo Mourão), Dr. Anderson Medeiros dos Santos (State University of Montes Claros) and Dr. Thomaz Aurélio Pagioro (CEFET—Curitiba) for sampling macrophytes in 2001. We are especially thankful to Dr. Luis Mauricio Bini (Federal University of Goiás), who made constructive comments on the manuscript. The suggestions of three anonymous reviewers were also important for improving our manuscript. This research was funded by CNPq, through the Long-Term Ecological Research (LTER) Program. Solana M. Boschilia is grateful to CNPq for a scholarship. E. F. Oliveira acknowledges FUNPESQ/Faculdade de Apucarana for funding. Sidinei M. Thomaz thanks CNPq for funding his research through a Productivity Research grant. The samplings comply with the current laws of Brazil concerning studies in conservation units.

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