Does distance between aquatic plant assemblages matter in defining similarity between them during high water-level periods?

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Abstract

Aquatic environments are subject to natural water-level fluctuations. These fluctuations, in turn, are responsible for causing changes in biota in the aquatic environment, particularly those that colonize floodplains. The flood pulse concept predicts that water-level fluctuations are responsible for the formation of mosaics in biota at a small scale. During high water-level periods, however, there is evidence that the similarity among biological assemblages increases. Within this theoretical context, the present study focuses on determining whether or not the spatial distance between assemblages is a relevant factor for the similarity among them during high water-level periods and, if not, what environmental variables are associated with them? Accordingly, the present study evaluated the association between aquatic plant assemblages and some environmental variables, with emphasis on the spatial distance among assemblages. The study results indicated no association between the similarity of the assemblages and the spatial distances between them. The environmental variables most associated with the assemblages were the total phosphorus and nitrate concentrations. It was concluded that, during high water-level periods, the spatial distance between aquatic plant assemblages was not a relevant factor for greater similarity among them. Rather, the total phosphorus and nitrate concentrations were the environmental factors most associated with the assemblages.

Key words

community ecology, flood pulse concept, macrophytes, reservoirs.

INTRODUCTION

The flood pulse concept (Junk *et al.* 1989) proposed that the water-level elevation is the main factor controlling biota in floodplains. Based on that concept, these plains are periodically flooded by the lateral expansion of rivers or lakes, or the accumulation of rainwater or groundwater (Junk *et al.* 1989). Although the pulse was originally conceptualized with emphasis on high water levels, the effects of lower water levels were considered later (Junk & Wantzen 2004) and have now been expanded to consider the lacustrine environment (Wantzen *et al.* 2008a).

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The flood pulse concept refers to the effects of water-level fluctuations (hereafter referred to as WLF) on the biota in freshwater environments. The term WLF lacks a definitive concept (Wantzen *et al.* 2008b), since it has large temporal and spatial scales (Hofmann *et al.* 2008; Wantzen *et al.* 2008a). The impacts on the biota of the WLF, however, is a topic whose importance has been highlighted, since climate change has altered the natural WLFs in many freshwater environments (Wantzen *et al.* 2008b). The literature contains examples of impacts on the biota of the WLF, with emphasis on plants, changes in the spatial distribution of species in floodplains (Leyer 2005), changes in the biomass between species (Richardson *et al.* 2002), changes in diversity (Riis & Hawes 2002),

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richness (Van Geest *et al.* 2005b) and succession of species (Van Geest *et al.* 2005a).

An interesting environment for investigating the influences of WLF on biota is reservoirs (Tundisi 2007). They are constructed to address situation where the natural water supply is not sufficient to support human activities, being generally used for flood control, water supply, irrigation and power generation (Thornton 1990). In spite of being classified as a type of lake (Hutchinson 1957), reservoirs have particular characteristics as well, including large tributary inflows and watersheds as they are constructed to capture as much water as possible (Miranda & Hunt 2011), and the partial control of WLFs, which is addressed by the operation of a dam. It is normal; therefore, those reservoirs exhibit irregular WLFs, compared with natural lakes.

Aquatic macrophytes are a group of organisms widely used to assess the effects of WLFs on biota, particularly in lacustrine environments (Leira & Cantonati 2008). They comprise vascular aquatic plants, normally colonizing the interfaces of aquatic environments (Sculthorpe 1967). WLFs cause changes in the relationships between species, noting they favour those best adapted to the new conditions. Furthermore, the aquatic plants display increased colonization of the environment during high water levels (O'Farrell *et al.* 2011).

According to the flood pulse concept, WLFs result in losses of aquatic organisms in a floodplain (Junk *et al.* 1989), which recover because of quick growth characteristics, early maturity and high reproduction rates. Such characteristics are typical of organisms exhibiting an *r* reproduction strategy (Pianka 1970). Associated with favouring organisms with an *r* reproduction strategy, WLFs cause the development of biotic 'mosaics' in different stages of succession at the same time and on a small spatial scale (Junk & Wantzen 2004). There also are indications that the increased water level acts as a process reducing the environmental variability which, in turn, leads to increased similarity among biological characteristics of aquatic environments during high water-level periods (Thomaz *et al.* 2007). Thus, flooding may be associated with increased distance decay of similarity between biological assemblages because of the homogenization of environmental characteristics (Nekola & White 1999).

Because of the occurrence of WLFs in rivers, lakes and reservoirs, similarities in ecological responses of the biota of the floodplains of these environments may exist (Junk *et al.* 1989). If the WLFs lead to formation of biotic mosaics (Junk & Wantzen 2004), while the degree of similarity between these mosaics also is related to the phase of the WLF, which is predominant in the floodplain (Thomaz *et al.* 2007), during the period of high water level, a resulting question is whether or not the spatial distance between assemblages is a relevant factor for the similarity among them? If that is not the case, which environmental variables are associated? To attempt to address these questions, the present study evaluates the structure of ten assemblages of aquatic plants in a reservoir floodplain.

MATERIALS AND METHODS

Study area

The reservoirs located in the semiarid region of Brazil normally capture a large volume of water during the rainy season, which is irregular in intensity and duration in this area because of a complex climatic pattern (Liu & Juárez 2001). The terrain topography in the region containing the Araras Reservoir (Fig. 1b) presents slight undulations, with the prevailing climate being semiarid

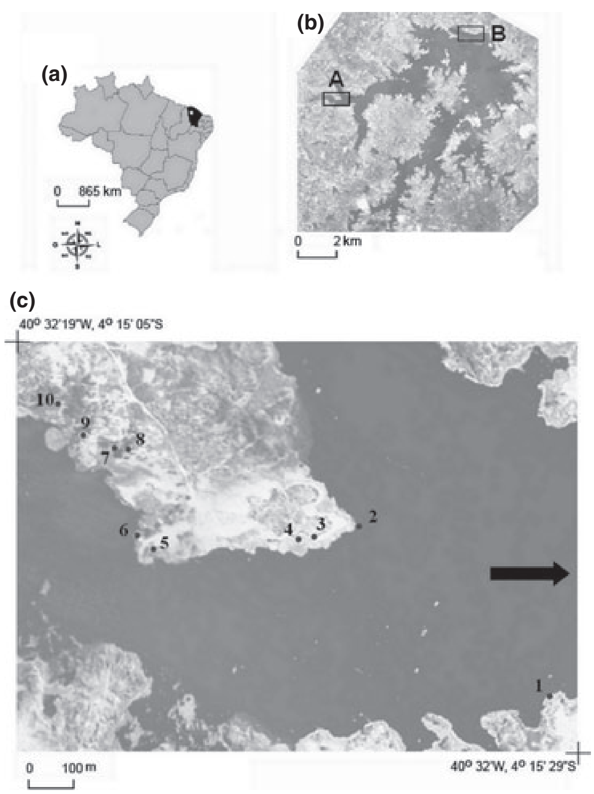

Fig. 1. Location of Araras Reservoir and sampling sites (solid dots indicate sites 1 to 10; map source: COGERH (mod.) 2009, 1:80.000) (a) Ceará State, Northeastern Brazil; (b) Araras Reservoir squares A and B represent study area locations and dam, respectively); (c) Detailed study area, with sampling points (1–10; black arrow indicates direction of dam).

(i.e. BSh in the Köppen Geiger climatic classification). The average annual rainfall is approximately 804 mm, concentrated between January and July (Figueirêdo *et al.* 2007). The WLFs in Araras Reservoir, for which data were taken at the dam from November 2010 to November 2011, are illustrated in Figure 2.

The Araras Reservoir dam is located near the town of Varjota in the state of Ceará, Brazil. It dam was completed in 1958, with the reservoir to be used for supplying water to neighbouring cities and for irrigation of agricultural production areas. The flooded area is approximately 70.26 km², with a stored water volume of 891 million m³ (Figueirêdo *et al.* 2007). The area containing the aquatic plants assemblages sampling in the present study (Fig. 1c) exhibited a history of colonization during the high water level of the reservoir. There are no tributary inflows that could cause deleterious effects on aquatic plant assemblages in this area, which has an estimated size of 779,960 m² (Fig. 1c).

Data collection

An expedition was made to Araras Reservoir in 2010, with data on the flora of aquatic plants being collected. The samples were subjected to herborization techniques, in accordance with the procedure of Haynes (1984) and Bridson and Forman (1998), and deposited in the Herbarium Prisco Bezerra (EAC). The taxonomic identification of families was based on the work of Cook (1996), with a specialized bibliography being used for the species (Forno 1983; Renvoize 1984; Cook 1996; Pott & Pott 2000; Souza & Giulietti 2009). The database of The International Plant Names Index (IPNI 2011) was utilized for nomenclatural terminology and abbreviations of author's

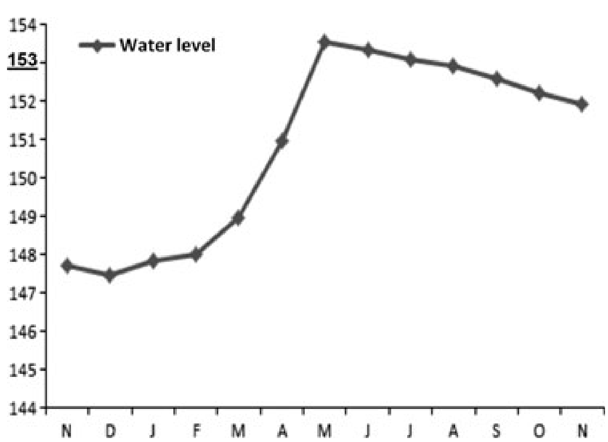

Fig. 2. Water-level fluctuations in Araras Reservoir from November 2010 to November 2011, taken from the dam (highlighted value is maximum height of reservoir (m)).

names. The life forms were classified in accordance with the procedure of Sculthorpe (1967).

Aquatic vegetation sampling was conducted in May 2011, a period when Araras Reservoir reached its maximum quota. Ten sampling sites were selected for the presence of a full coverage of aquatic plants, which were not influenced by any urban areas or agricultural activities adjoining the shores of the reservoir. The sampling sites were georeferenced by Garmin 12 GPS, with the site numbers corresponding to the sequence shown in Figure 1c.

The GPS data were used to calculate the distance between each aquatic plant assemblage, as well as the distance between each assemblage and the dam. At each sampling site, ten transects perpendicular to the banks of the reservoir were marked, each 2 m apart, using canoes, measuring tape, stakes, ropes and buoys. Each transect was 10 m in length. Six equidistant points were arranged 1.66 m apart at each transect, totalling 60 points at each of the sampling sites assessed. After obtaining the biological data, the depth was measured on each of the 60 points.

Aquatic vegetation was surveyed using the point sample method (Yarranton 1966), with an isolated vertical needle. This method was selected on the basis of its accuracy, speed and low disturbance to vegetation during sampling (Mantovani & Martins 1990). The data were obtained with an apparatus similar to that used by Tabosa *et al.* (2012), in which the apparatus was coupled to a bubble level to calibrate the needle at a right angle to the plane formed by the aquatic vegetation.

Water samples were taken in the reservoir after the vegetation sampling. Three water samples of 1 L volume were collected at two, seven and 12 m distance from the shore at each sampling site, in the space between the central transects. The water samples were analysed for nitrogen and total phosphorus, nitrate, phosphate and chlorophyll-*a*, according to the methodology of the American Public Health Association (2005).

Data analysis

The absolute frequency was the only parameter used of the point sample method (Eqn 1). This parameter indicates the probability of finding an individual in the set of sampled points (Mantovani & Martins 1990). The absolute frequency values were transformed using the arcsine square root of the absolute frequency (McCune & Grace 2002). The non-metric multidimensional scaling (NMDS) analysis was used in the ordination of aquatic plant assemblages, with the transformed values of absolute frequency of species. In implementing the NMDS, the

Euclidean distance was used, and the minimum span tree option was enabled. A significant correlogram with Moran's I index (Legendre & Fortin 1989) with scores shaft was executed to detect the possible influence of spatial autocorrelation in the NMDS outcome. The correlogram was run with four distance classes and 999 randomizations. The sequential Bonferroni correction was used in the evaluation of the ρ value obtained for each distance class (Fortin & Dale 2005). The Mantel test was performed, using the transformed data of absolute frequency of species in the biological matrix and the data in the array of latitude and longitude of the sampling sites in the environmental matrix, in decimal degrees. The Monte Carlo test was run with 1000 randomizations for a significance level of $\rho < 0.05$ (Urban *et al.* 2002).

The averages ($n = 3$) of limnological parameters were subjected to logarithmic transformation (Eqn 2), including the distance to the dam and the averages ($n = 60$) of depth (Eqn 3). After logarithmic transformations, environmental data were subjected to Pearson correlation to detect possible associations between variables. The biological matrix used in NMDS, together with the transformed data of environmental variables, was used in the execution of a canonical correspondence analysis (CCA). The CCA was performed with scaling type 2, which emphasizes the species (Legendre & Legendre 1998). The CCA axes were subjected to the Monte Carlo test with 999 randomizations. The NMDS, Mantel test, CCA and their graphics were done with the PAST 2.17b software (Hammer *et al.* 2001), while the correlogram was done with SAM 4.0 software (Rangel *et al.* 2010).

RESULTS

The inventory of aquatic flora identified 12 families, 14 genera and 14 species. The highest richness was for the family Plantaginaceae, with three species, while the remaining families were represented by one species each. The predominant life forms were found both to be attached to the substrate and free-floating (Table 1). The species of the families Cleomaceae, Plantaginaceae and Menyanthaceae were not observed in the sampling performed with the point sample method. The values of the absolute frequency of species at each sampling site are summarized in Table 2. *Salvinia auriculata* exhibited the highest absolute frequency at nine sites. *N. oleracea* exhibited the highest absolute frequency at sampling site nine. *Salvinia auriculata*, *N. oleracea*, *E. crassipes*, *P. stratiotes* and *L. helminthorrhiza* were the only species present at all sites.

The NMDS resulted in a one-dimensional solution for axis 1 (Fig. 3), whose stress was 0.1369 and R^2 was 0.8568. NMDS orderings can be interpreted only when stress values are below 0.2, and ideally below 0.1 (Quinn & Keough 2002). The NMDS organized the aquatic plant assemblages in biological gradient of space occupation by species, whose assemblages in the extremes of significant axis were dominated by *S. auriculata* and *N. oleracea*. The presence of spatial autocorrelation was not detected in the NMDS scores as all ρ values for all distance classes were greater than 0.05 (Fig. 4). The spatial autocorrelation is related to the lack of independence between observations (Legendre & Fortin 1989). The result of the Mantel test did not indicate significant correlations between the spatial proximity of the aquatic plant assemblages and the biological similarity between them (rM = 0.152127, $P > 0.05$).

Table 3 summarizes the dam distance, average depth ($n = 60$) and limnological parameters ($n = 3$) for each

Table 1. Aquatic plants species in Araras Reservoir (A – Hydrophytes attached to the substrate: 1 – emergents; 2.2 – floating-leaved; B – Free-floating hydrophytes; life form classification based on Sculthorpe 1967)

Family Species	Life form	Acronomy
ARACEAE		
Pistia stratiotes L.	B	Pisstr
CERATOPHYLLACEAE		
Ceratophyllum demersum L.	B	Cerdem
CLEOMACEAE		
Cleome spinosa Jacq.	A1	Clespi
CYPERACEAE		
Oxycaryum cubense (Poepp. & Kunth) Palla	A1	Oxycub
FABACEAE		
Neptunia oleracea Lour.	B	Nepole
MENYANTHACEAE		
Nymphoides indica (L.) Kuntze	A2.2	Nymind
ONAGRACEAE		
Ludwigia helminthorrhiza (Mart.) H.Hara	B	Ludhel
PLANTAGINACEAE		
Angelonia biflora Benth	A1	Angbif
Scoparia dulcis L.	A1	Scodul
Stemodia marítima L.	A1	Stemar
POACEAE		
Echinochloa polystachya (Kunth) Hitchc.	A1	Echpol
POLYGONACEAE		
Polygonum ferrugineum Wedd.	A1	Polfer
PONTEDERIACEAE		
Eichhornia crassipes (Mart.) Solms	B	Echcra
SALVINIACEAE		
Salvinia auriculata Aubl.	B	Salaur

Table 2. Absolute frequencies of aquatic plants species at sampling sites in Araras reservoir

Species (acronomy; see Table 1)	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10
Salaur	90.00	96.67	86.67	91.67	90.00	78.33	83.33	91.67	51.67	88.33
Nepole	3.33	41.67	33.33	18.33	35.00	3.33	38.33	30.00	63.33	31.67
Echcra	1.67	16.67	15.00	1.67	16.67	1.67	16.67	10.00	11.67	13.33
Pisstr	6.67	10.00	15.00	10.00	11.67	5.00	10.00	6.67	3.33	11.67
Ludhel	5.00	6.67	18.33	10.00	10.00	3.33	5.00	5.00	6.67	6.67
Cerdem	1.67	0.00	6.67	8.33	5.00	10.00	5.00	0.00	0.00	0.00
Echpol	1.67	3.33	5.00	1.67	0.00	1.67	0.00	1.67	3.33	0.00
Polfer	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00	0.00
Oxycub	0.00	1.67	1.67	1.67	0.00	0.00	0.00	0.00	0.00	0.00

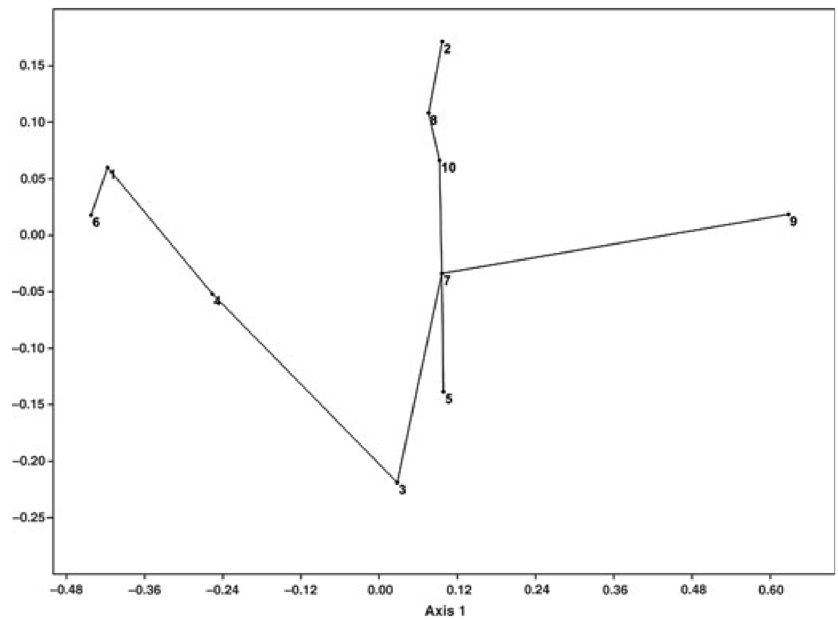

Fig. 3. Non-metric multidimensional scaling ordination of 10 aquatic plants assemblages in Araras Reservoir.

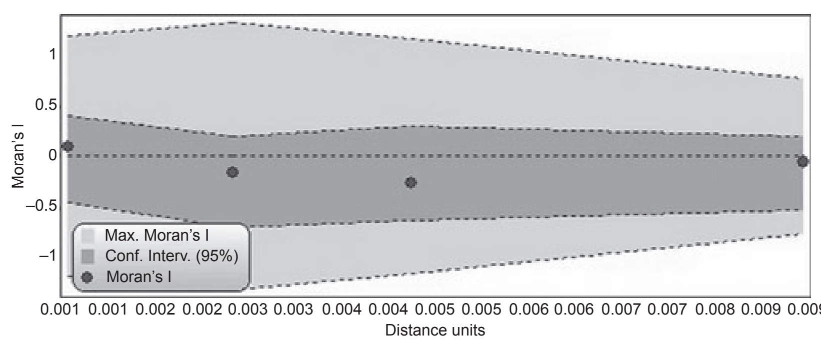

Fig. 4. Moran's I correlogram of NMDS scores.

sampling site. Significant correlations were detected (ρ<0.05) between total nitrogen and chlorophyll-*a* (r = 0.81507), and total phosphorus and phosphate (r = 0.8809). Total nitrogen and phosphate was not used in the CCA as the chlorophyll-a concentration (expressed hereafter as chlorophyll-*a*) is an estimator of phytoplankton (Esteves 1998), while total phosphorus is an estimator of the aquatic environment trophic status (Wetzel 2001). Furthermore, the nitrate represents a major source of nitrogen for primary producers in aquatic environments (Esteves 1998), exhibiting no significant correlation with the other variables in this case.

Table 3. Distance from dam (Dam), mean depth (n = 60) and means (n = 3) of total nitrogen (NT), total phosphorus (PT), nitrate (NO_3), phosphate (PO_4) and chlorophyll-*a* (Cl.a) concentrations at the 10 sampling sites in Araras Reservoir (sampling site locations in Figure 1)

Variable	1	2	3	4	5	6	7	8	9	10
Dam (km)	9.94	10.11	10.22	10.25	10.56	10.58	10.53	10.50	10.58	10.60
Depth (m)	1.42	1.55	1.73	2.10	1.87	4.18	1.65	2.18	2.34	2.58
NT (mg L^{-1})	0.979	1.103	1.048	1.225	1.106	1.058	0.803	0.760	0.834	0.949
NO_3 (mg L^{-1})	0.202	0.201	0.202	0.199	0.196	0.195	0.196	0.205	0.198	0.202
PT (mg L^{-1})	0.194	0.164	0.192	0.201	0.279	0.199	0.196	0.176	0.178	0.197
PO_4 (mg L^{-1})	0.017	0.017	0.015	0.017	0.042	0.012	0.011	0.010	0.012	0.013
Cl. a (μg L^{-1})	29.88	32.24	38.00	35.15	32.64	29.14	26.70	26.94	26.23	28.68

The CCA (Fig. 5) was formed by two axes, which together accounted for 85.43% of the variance in the data. Only axis one (56.73%), however, was significant in a Monte Carlo test (P = 0.006). The axis one eigenvalue was 0.074543, exhibiting positive correlations with total phosphorus (0.96958), distance from the dam (0.34647), chlorophyll-*a* (0.12383) and depth (0.0055831). The only opposing variable was nitrate (−0.50767). These results indicate the total phosphorus and nitrate concentrations were the environmental variables most associated with the aquatic plants assemblages in Araras Reservoir. The reservoir depth was the environmental variable exhibiting the lower association with the aquatic plant assemblages.

DISCUSSION

Araras Reservoir exhibited lower numbers of species in the present study than observed for other Brazilian reservoirs. The number of species in the inventories of the latter ranging between 15 and 62, and with the families Poaceae, Cyperaceae and Pontederiaceae were the ones containing the most aquatic plant species (Thomaz *et al.* 1999; Carvalho *et al.* 2003, 2005; Bini *et al.* 2005; Cavenaghi *et al.* 2005; Pitelli *et al.* 2008). Bini *et al.* (2005) suggested attributes such as the sampling effort and the reservoir surface area should be considered when comparing species inventories of different reservoirs. Hydrological regimes whose environments are normally regulated, however, exhibit plant assemblages containing less diverse, but more exotic species (Hill *et al.* 1998), with the species of aquatic plants in Araras Reservoir consistent with this observation.

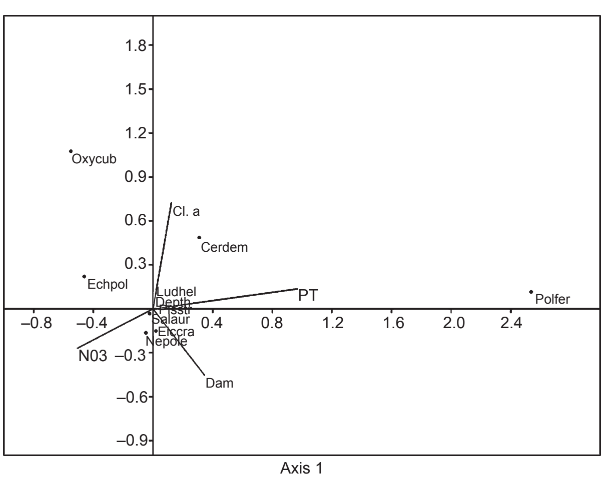

Fig. 5. Canonical correspondence analysis of species and environmental variables at ten sampling sites in Araras Reservoir.

Salvinia auriculata and *N. oleracea* were considered the major species in the aquatic plant assemblages, based on their absolute frequencies observed at the reservoir sampling sites, which resulted in the polarization observed in the NMDS. *Salvinia auriculata* is an herbaceous, free-floating plant pioneer involved in the succession of disturbed sites, or in new water bodies after a drought period (Pott & Pott 2000). This species may colonize large areas in a short time because of rapid reproduction characteristics, which can result from spores or vegetative forms, and which are associated with the persistence of *S. auriculata* in the environment (Coelho *et al.* 2005). *N. oleracea* is a leguminous plant, exhibiting the ability to float because of the presence of aerenchyma (Sculthorpe 1967). The reproduction of this species can be via seeds or vegetative forms, and it typically colonizes the littoral of aquatic environments (Pott & Pott 2000).

Salvinia auriculata colonized the water surface without the formation of vertical strata, being observed under the coverage of other species capable of forming vertical stratification. The ability to occupy the space under the cover of other species certainly contributed to the high absolute frequency of *S. auriculata*, relative to other species observed in the reservoir. *Salvinia auriculata* has fragile branches (Forno 1983), with this fragility being an important feature for its asexual reproduction. Species with spaced ramets and capable of infiltrating into the surrounding vegetation, can adopt a clonal growth strategy, with an occupation of space, called 'guerrilla' (Doust 1981). The guerrilla strategy is very common in the early stages of succession as it allows for a rapid occupation of the environment (Ye *et al.* 2006). Performance evaluation of guerrilla demonstrated the effectiveness of this strategy in the colonization of new areas becoming available because of the better resource exploitation (Humphrey & Pyke 1998).

The NMDS of aquatic vegetation indicated that sampling sites one, four, six and nine exhibited some dispersion regarding the other sites, which occupied the central space of ordination. This suggests that structures showed similarities with one another during the period of high water level in some assemblages. The sequence of sampling sites, however, demonstrates that assemblages located spatially nearby may not be so similar. This is expected in a biota mosaic, based on the flood pulse concept (Junk & Wantzen 2004). In fact, the Mantel test indicated no relationship between spatial proximity and the similarity of biological assemblages. Similar results were observed for aquatic plant assemblages in the Pantanal region in South America (Pivari *et al.* 2008).

The CCA result indicated the variables most associated with aquatic plant assemblages were the concentrations of total phosphorus and its antagonist, nitrate. The total phosphorus concentration represents the sum of all forms of phosphorus in the water body (Esteves 1998) and is used as a variable to calculate indices for classifying the trophic status of specific aquatic environments (Wetzel 2001). For most of the observations, nitrate is the main nitrogen source for aquatic plants (Esteves 1998). These results are not surprising, because the last assessment of vulnerability to eutrophication indicated that the Araras Reservoir was highly vulnerable (Figueirêdo *et al.* 2007). The reservoir depth exhibited the lower association with the aquatic plant assemblages, due possibly to the fact that most of the observed species had the ability to float on water. Similar results were obtained by Casanova and Brock (2000) in segregating plant assemblages in arid environments.

Despite the limitations in then dataset in the present study (e.g. samples taken in only one region, limited number of samples, and uncontrolled conditions), the study results are consistent with those of other studies cited in this report. This observation allows one to conclude that (i) the spatial distance between aquatic plant assemblages is not a relevant factor for a larger similarity among them during the period of high water level in the reservoir; and (ii) total phosphorus and nitrate concentrations were the variables most associated with assemblages among the environmental variables assessed, while water depth exhibited a lower association.

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REFERENCES

American Public Health Association (2005) Standard Methods for the Examination of Water and Waste Water. APHA, Washington, DC

Bini L. M., Oliveira L. G., Souza D. C., Carvalho P. & Pinto M. P. (2005) Patterns of the aquatic macrophyte cover in Cachoeira Dourada Reservoir (GO-MG). *Brazilian J. Biol.* **65**, 19–24.

Bridson D. & Forman L. (1998) The Herbarium Handbook. Kew Publishing, Brough.

Carvalho F. T., Galo M. L. B. T., Velini E. D. & Martins D. (2003) Plantas aquáticas e nível de infestação das espécies presentes no reservatório de Barra Bonita, no rio Tietê. *Planta Dan.* **21**, 15–9.

Carvalho F. T., Velini E. D. & Martins D. (2005) Plantas aquáticas e nível de infestação das espécies presentes no reservatório de Bariri, no rio Tietê. *Planta Dan.* **23**, 371–4.

Casanova M. T. & Brock M. A. (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecol.* **147**, 237–50.

Cavenaghi A. L., Velini E. D., Negrisoli E. *et al.* (2005) Monitoramento de problemas com plantas aquáticas e caracterização da qualidade de água e sedimento na UHE de Mogi-Guaçu. *Planta Dan.* **23**, 225–31.

Coelho F. F., Lopes F. S. & Sperber C. F. (2005) Persistence strategy of *Salvinia auriculata* Aublet in temporary ponds of Southern Pantanal, Brazil. *Aquat. Bot.* **81**, 343–52.

Cook C. D. K. (1996) Aquatic Plant Book. SBP Academic Publishing, Amsterdam.

Doust L. L. (1981) Population dynamics and local specialization in a clonal perennial (Ranunculus Repens): the dynamics of ramets in contrasting habitats. *J. Ecol.* **69**, 743–55.

Esteves F. A. (1998) Fundamentos de Limnologia. Interciência, Rio de Janeiro.

Figueirêdo M. C. B., Teixeira A. S., Araújo L. F. P. *et al.* (2007) Avaliação da vulnerabilidade ambiental de reservatórios à eutrofização. *Eng. Sanit. Amb.* **12**, 399–409.

Forno I. W. (1983) Native distribution of *Salvinia auriculata* complex and keys to species identification. *Aquat. Bot.* **17**, 71–83.

Fortin M. J. & Dale M. R. T. (2005) Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge.

Hammer Ø., Harper D. A. T. & Ryan P. D. (2001) PAST: Paleontological Statistics Software Package for education and data analysis. *Palaeontol. Electron.* **4**, 1–9.

Haynes R. R. (1984) Techniques for collecting aquatic and marsh plants. *Ann. Mo. Bot. Gard.* **71**, 229–31.

Hill B. M., Keddy P. A. & Wisheu I. C. (1998) A hydrological model for predicting the effects of dams on the shoreline vegetation of lakes and reservoirs. *Environ. Manage.* **22**, 723–36.

Hofmann H., Lorke A. & Peeters F. (2008) Temporal scales of water-level fluctuations in lakes and their ecological implications. *Hydrobiologia* **613**, 85–96.

Humphrey L. D. & Pyke D. A. (1998) Demographic and growth responses of a guerrilla and a phalanx perennial grass in competitive mixtures. *J. Ecol.* **86**, 854–65.

Hutchinson G. E. (1957) A Treatise on Limnology. John Wiley and Sons, New York.

Junk W. J. & Wantzen K. M. (2004) The Flood Pulse Concept: New Aspects, Approaches, and Applications—An update. In: Proceedings, of Second International Symposium on the Management of Large Rivers for Fisheries (eds R. Welcomme & T. Petr) pp. 117–49. FAO, Phnom Penh, Cambodia.

Junk W. J., Bayley P. B. & Sparks R. E. (1989) The flood pulse concept in river-floodplain systems. *Can. J. Fish. Aquat. Sci.* **106**, 110–27.

Legendre P. & Fortin M. J. (1989) Spatial pattern and ecological analysis. *Vegetatio* **80**, 107–38.

Legendre P. & Legendre L. (1998) Numerical Ecology. Elsevier Scientific Publishing Company, Amsterdam.

Leira M. & Cantonati M. (2008) Effects of water-level fluctuations on lakes: an annotated bibliography. *Hydrobiologia* **613**, 171–84.

Leyer I. (2005) Predicting plant species' responses to river regulation: The role of water level fluctuations. *J. Appl. Ecol.* **42**, 239–50.

Liu W. T. & Juárez R. I. N. (2001) ENSO drought onset prediction in northeast Brazil using NDVI. *Int. J. Remote Sens.* **22**, 3483–501.

Mantovani W. & Martins F. R. (1990) O método de pontos. *Acta Botân. Bras.* **4**, 95–122.

McCune B. & Grace J. B. (2002) Analysis of Ecological Communities. MJM Software Design, Gleneden Beach.

Miranda L. E. & Hunt K. M. (2011) An index of reservoir habitat impairment. *Environ. Monit. Assess.* **172**, 225–34.

Nekola J. C. & White P. S. (1999) The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* **26**, 867–78.

O'Farrell I., Izaguirre I., Chaparro G. *et al.* (2011) Water level as the main driver of the alternation between a free-floating plant and a phytoplankton dominated state: A long term study in a floodplain lake. *Aquatic Sci.* **73**, 275–87.

Pianka E. R. (1970) On r- and K-Selection. *Am. Nat.* **104**, 592–7.

Pitelli R. L. C. M., Toffaneli C. M., Vieira E. A., Pitelli R. A. & Velini E. D. (2008) Dinâmica da comunidade de macrófitas aquáticas no reservatório de Santana, RJ. *Planta Dan.* **26**, 473–80.

Pivari M. O., Pott V. J. & Pott A. (2008) Macrófitas aquáticas de ilhas flutuantes (baceiros) nas sub-regiões do Abobral e Miranda, Pantanal, MS, Brasil. *Acta Bot. Bras.* **22**, 563–71.

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

Quinn G. & Keough M. (2002) Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Rangel T. F., Diniz-Filho J. A. F. & Bini L. M. (2010) SAM: A comprehensive application for Spatial Analysis in Macroecology. *Ecography* **33**, 46–50.

Renvoize S. A. (1984) The Grasses of Bahia. Royal Botanical Gardens, Kew.

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

Riis T. & Hawes I. (2002) Relationships between water level fluctuations and vegetation diversity in shallow water of New Zealand lakes. *Aquat. Bot.* **74**, 133–48.

Sculthorpe C. D. (1967) The Biology of Aquatic Vascular Plants. Edward Arnold Ltd, London.

Souza V. C. & Giulietti A. M. (2009) Levantamento das espécies de Scrophulariaceae sensu latu nativas do Brasil. *Pes. Bot.* **1**, 93–120.

Tabosa A. B., Matias L. Q. & Martins F. R. (2012) Live fast and die young: The aquatic macrophyte dynamics in a temporary pool in the Brazilian semiarid region. *Aquat. Bot.* **102**, 71–8.

The International Plant Names Index (2011) Available from URL: http://www.ipni.org. Accessed 25 April 2011.