

EFFECT OF SPATIAL HETEROGENEITY ON ZOOPLANKTON DIVERSITY: A MULTI-SCALE HABITAT APPROXIMATION IN A FLOODPLAIN LAKE

G. CHAPARRO^{a*}, P. KANDUS^b AND I. O'FARRELL^a^a *Departamento de Ecología, Genética y Evolución, Facultad de Ciencias, Exactas y Naturales, Universidad de Buenos Aires - IEGEBA (CONICET-UBA), Buenos Aires, Argentina*^b *Instituto de Investigación e Ingeniería Ambiental (3iA), Universidad Nacional de General San Martín, Prov. de Buenos Aires, Argentina*

ABSTRACT

Environmental heterogeneity is an essential quality of ecosystems as it has important implications in community structure. Macrophytes are a main component of environmental heterogeneity in floodplain lakes, and their dynamics are highly influenced by water level changes. In this context, we analysed at different spatial scales the relationship among hydrological variations, environmental heterogeneity associated to macrophytes and zooplankton regional diversity (γ diversity) in a South American floodplain lake adjacent to the Paraná River, and we also compared the local zooplankton diversity (α diversity) among the different environments that comprised the lake heterogeneity. At very low waters, the environmental heterogeneity was reduced as the lake was mainly limited to open water areas with low zooplankton diversity. At high waters, the profuse vegetation development (emergent and free-floating), in mixed or homogeneous patches, determined a higher lake environmental heterogeneity with enhanced regional zooplankton diversity; littoral species increased over limnetic ones. Zooplankton α diversity was higher in environments with free-floating macrophytes than in those without these plants. The structural complexity in the water column provided by plant roots would be closely related to the enhanced diversity found under free-floating mats. This study contributes to the knowledge on the effects of strong water level variations on environmental heterogeneity, which is strongly associated to macrophytes and on zooplankton diversity, and highlights the role of free-floating plants as diversity hosts and 'key structures' in floodplain lakes. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: zooplankton; macrophytes; spatial patterns; water level; diversity; remote sensing

Received 6 March 2013; Revised 26 May 2013; Accepted 16 September 2013

INTRODUCTION

Environmental heterogeneity occurs in ecosystems along a broad range of scales, and this is an essential quality to population dynamics and community organizations (Levin, 1992). It is hypothesized that more heterogeneous habitats offer more niches and possibilities to exploit resources, enhancing species turnover (Cramer and Willig, 2005) and the regional diversity of species known as γ diversity (Bazzaz, 1975). The processes through which environmental heterogeneity causes an increase in biodiversity are scale dependent and varied (McClain and Barry, 2010). In this sense, landscape ecology refers to the causes and effects of heterogeneity, and a basic question of this discipline is whether a given phenomenon is manifested over a wide range of scales or if it is limited to a narrow range (Levin, 1992). Both spatial and temporal changes in environmental heterogeneity (eg. those that occur during ecological succession) have effects on the biodiversity of species (Bazzaz, 1975; Ward and Tockner, 2001; Tews *et al.*, 2004, Yeager *et al.*, 2011).

In floodplains, the flood pulse produces a dynamic mosaic of terrestrial and aquatic habitats causing high environmental heterogeneity, which is characteristic of these ecosystems and affects all communities that inhabit them (Junk, *et al.*, 1989; Tockner *et al.*, 2000; Amoros and Bornette, 2002). Macrophytes are important components of habitat heterogeneity in these ecosystems, and their composition is largely determined by the water level regime (Boschilia *et al.*, 2008). Particularly in aquatic habitats, they dominate littoral zones of shallow lakes and host numerous communities including zooplankton (Serafim *et al.*, 2003; Maia-Barbosa *et al.*, 2008), macroinvertebrates (Thomaz *et al.*, 2008; Fontanarrosa *et al.*, 2012) and fishes (Agostinho *et al.*, 2007; Neiff *et al.*, 2009). The physical complexity added by macrophytes provides not only more niches but also food resources (Thomaz and Ribeiro da Cunha, 2010), refuge areas against predators (Padial *et al.*, 2009), breeding (Iglesias *et al.*, 2008), feeding (Casatti *et al.*, 2003) and oviposition areas (Merritts and Cummins, 1998). On the other hand, macrophytes of different habits and architectures exert different effects on water quality and the associated communities. Submerged macrophytes reduce water turbidity and nutrients availability for phytoplankton (Scheffer *et al.*, 1993; Burks *et al.*, 2006)

*Correspondence to: G. Chaparro, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias, Exactas y Naturales, Universidad de Buenos Aires - IEGEBA (CONICET-UBA) C1428EHA, Buenos Aires, Argentina.
E-mail: grichaparro@gmail.com

and constitute a refuge for numerous zooplankton and planktivorous fish species (Meerhoff *et al.*, 2003; Teixeira de Mello *et al.*, 2009). Emergent macrophytes play a similar role, especially in turbid ecosystems, where submerged macrophytes are limited (Iglesias *et al.*, 2007; Cazzanelli *et al.*, 2008). Finally, free-floating macrophytes reduce light penetration and oxygen availability in the water column (de Tezanos Pinto *et al.*, 2007; O'Farrell *et al.*, 2009) and while reducing phytoplankton diversity (O'Farrell *et al.*, 2009) are associated to rich communities of zooplankton (Serafim *et al.*, 2003; Gazulha *et al.*, 2011; Villabona-González *et al.*, 2011), macroinvertebrates (Poi de Neiff, 2003; Fontanarrosa *et al.*, 2012) and fishes (Agostinho *et al.*, 2007; Teixeira de Mello *et al.*, 2009).

Zooplankton is an important component in floodplain lakes due to its role in matter and energy transfer from primary producers to higher trophic levels (Lansac-Tôha *et al.*, 2009) and are also involved in the microbial loop (Work and Havens, 2003; Costa Bonecker and Aoyagui, 2005). Zooplankton is constituted by numerous groups (mainly rotifers, cladocerans and copepods), which can show great diversity (José de Paggi, 2004; Paggi, 2004; Maia-Barbosa *et al.*, 2008). Among the factors affecting its richness and diversity, studies indicate the influence of disturbance caused by a changing macrophyte cover (Fontanarrosa *et al.*, 2010) or by frequent flooding (Paidere, 2009), water level variations (Crome and Carpenter, 1988; Borges and Pedrozo, 2009), system connectivity (Jose de Paggi and Paggi, 2007; Lansac-Tôha *et al.*, 2009), macrophytes presence (Meerhoff and Mazzeo, 2004; Meerhoff *et al.*, 2007; Maia-Barbosa *et al.*, 2008) and architecture (Meerhoff *et al.*, 2007; Lucena-Moya and Duggan, 2011).

The relationship between environmental heterogeneity and species diversity is a concept well accepted in community ecology; however, there are severe limitations in its empirical support (Tews *et al.*, 2004). Studies are biased towards vertebrates and anthropogenic habitats, and less attention has been given to invertebrates in natural environments (Tews *et al.*, 2004). One useful tool for studying the relationship between environmental heterogeneity and biodiversity at broad scales is remote sensing. This technique allows to directly distinguish the spatial distribution of habitats or even species or to estimate environmental parameters closely related to species diversity (Turner *et al.*, 2003). The combined use of satellite and field data allows us to explore the relationship between environmental heterogeneity and landscape or regional zooplankton diversity (hereinafter γ diversity) at the lake scale and to compare the zooplankton local or within habitat diversity (hereinafter α diversity) among the environments comprising the lake heterogeneity.

The aim of this study is to understand the complex relationship between environmental heterogeneity associated

to macrophytes and zooplankton diversity in a floodplain lake adjacent to a large river with marked hydrological fluctuations. Considering that macrophytes are strongly affected by the water level fluctuations characteristic of these systems, the hypotheses here addressed are as follows: (i) the lake's environmental heterogeneity increases with water level; (ii) zooplankton γ diversity is enhanced in scenarios with high lake environmental heterogeneity; and (iii) environments covered with macrophytes will be associated with higher α zooplankton diversities than those without plants.

METHODS

Study area

The study was conducted in the Otamendi Natural Reserve, a Ramsar floodplain wetland that comprises several water bodies (Figure 1). It is delimited by the Paraná de las Palmas and Luján Rivers, Buenos Aires Province, Argentina (34°10'–34°17'S; 58°48'–58°53'W). The area is influenced by a high and fluctuating water table, being periodically flooded by rainfall (Chichizola, 1993). In periods of high waters, the river pulse contributes to the higher hydrometric levels of the water bodies, because they are connected underground with the Paraná de las Palmas and Luján Rivers (<http://atlasdebuenosaires.gov.ar>). Silva Busso and Santa Cruz (2005) analysed the stratigraphy and hydrostratigraphy of the aquifers of the hydrogeological region of the Paraná River in the study area and revealed a hydrodynamic relationship between aquifers and surface water resources (river and lakes). Rivers feed the aquifers during floods producing a high net recharge and an increase in the water table (Auge, 2004). The main lake, Laguna Grande (~156 ha, $Z < 1$ m), is eutrophic and exhibits profuse aquatic vegetation, both rooted emergent and free-floating species. The region has a temperate climate, with hot summers and without a dry season, according to the updated Köppen–Geiger classification (Peel and Huisman, 2009). The mean annual temperature ranges between 16.7 and 18 °C, and precipitations occur during the whole year with a mean annual value of 950 mm; however, a marked drought affected this region through 2008, which ended on March 2009.

Field survey

The entire lake was explored during an extensive field survey that included 33 points georeferenced with global positioning system, reached either by boat in the open pelagial waters or by wading the littoral vegetated areas. A brief description was obtained for each point: water depth, presence and life form of prevailing macrophytes (emergent

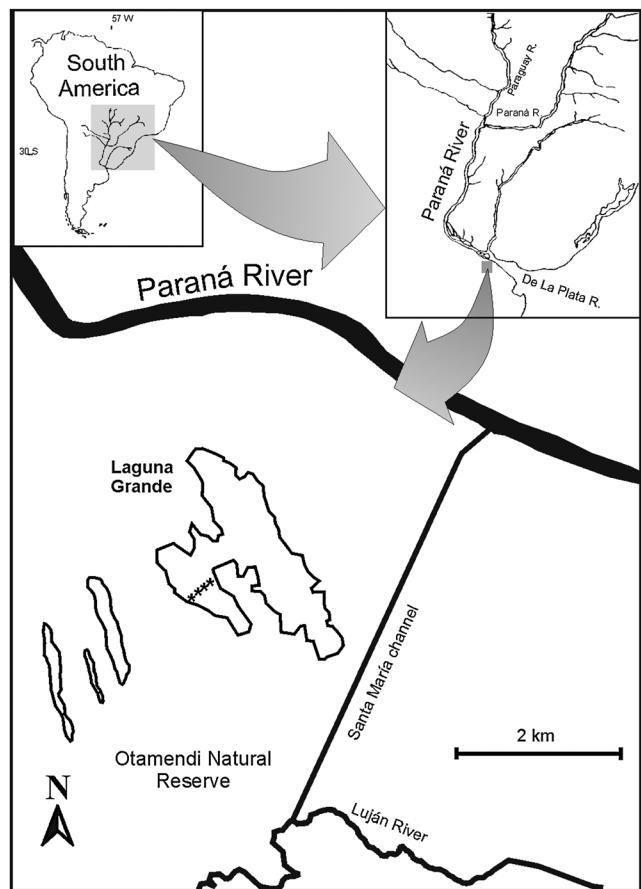


Figure 1. Geographic location of the study area. Asterisks indicate the sampling points

or free-floating, no submerged vegetation was detected). A temporal intensive sampling was performed in a subarea containing representative environments of the lake. Samples were taken monthly from September 2008 to February 2010 and then bi-monthly until August 2010, making a total of 19 campaigns. A transect of 300 m perpendicular to the coastline was established, covering areas with different macrophytes. In four fixed points of this transect, the presence and life form of macrophytes species were determined according to Sculthorpe (1967), and *in situ* parameters were measured: temperature, pH, conductivity and dissolved oxygen using HI 991301 Hanna® and HI 9143 Hanna® (Hanna Instruments, Woonsocket, RI, USA) portable instruments. Samples for the phytoplankton chlorophyll *a* were taken and filtered through Whatman GF/F filters (Whatman, Florham Park, New Jersey, USA); ethanol was used for pigment extraction, and the concentration was calculated following Marker *et al.* (1980). The water level of the lake was registered by a fixed scale located at the littoral area; water levels <0.45 m were classified as 'low waters' and those >0.45 m as 'high waters', according to O'Farrell *et al.* (2011). Daily rainfall data were provided by the Servicio

Meteorológico Nacional (Argentina) and the monthly water level of the Paraná de las Palmas River by the Subsecretaría de Puertos y Vías Navegables at the nearest gauge (Zárate).

Satellite imagery

Eight Landsat 5 TM images (path 225, row 84) available for the study period from the closest dates to the samplings were used. A subarea of the natural reserve was extracted; the images were georeferenced with a first-order polynomial transformation and nearest neighbour resampling method, with a root mean square error below 0.5 pixel. Digital numbers were transformed into surface reflectance considering that the influence of the atmosphere limits to additive effect of Rayleigh dispersion (Stumpf 1992). Then, a hybrid classification technique (unsupervised-supervised) was utilized in order to estimate the per cent of cover of the main classes (environments) of the lake during the study. Eight classes could be differentiated by the unsupervised classifications performed by ISODATA clustering, and their spectral signatures constituted the basis for the supervised classifications. The latter was performed by the minimum distance method: each pixel was assigned to the class whose signature had the minimum distance with respect to the spectral signature of the pixel. All classifications were performed into an 'area of interest' delimited by the lake perimeter. Classifications accuracy was evaluated at each sampling site on each scene on the basis of the field data. The image pre-processing and analyses were performed by ERDAS Imagine 9.1 software.

Environmental heterogeneity parameters

At the broad scale (entire lake), two environmental heterogeneity parameters were calculated for each scene on the basis of information obtained from the image classifications (Table I): richness of aquatic environments (Senv), as the total number of aquatic classes registered, and the Shannon Diversity Index of aquatic environments (Henv) (the classes *mud* and *terrestrial vegetation* were excluded from these calculations as these do not involve aquatic classes). In order to examine the relationship between environmental heterogeneity and γ zooplankton diversity, a small area corresponding to the intensive sampling was established within an area of interest of around 33 pixels (2.97 ha). At this finer scale, these same environmental heterogeneity parameters, Senv, Henv and also the number of aquatic patches (N° patches), considering a patch as each homogeneous class area, were calculated within this section.

Zooplankton

Integrated water column samples for zooplankton analyses were collected by duplicate at each sampling point, with a

Table I. Description of the representative classes (environments) of Laguna Grande during the study period obtained by the classification of Landsat 5 TM images

Class	Description
Open clear water	Water with low phytoplanktonic chlorophyll <i>a</i> concentrations (mean <14 µg/L)
Open turbid water	Water with high phytoplanktonic chlorophyll <i>a</i> concentration (mean >300 µg/L)
Macrophytes in patches	Areas partially covered by free-floating or emergent macrophytes surrounded by water
Emergent macrophytes	Areas totally covered by emergent macrophytes
Free floating + emergent macrophytes	Areas totally covered by mixed stands of free-floating + emergent macrophytes
Free floating macrophytes	Areas totally covered by free-floating macrophytes
Terrestrial vegetation	Areas covered by terrestrial vegetation
Mud	Areas where sediments are exposed

transparent acrylic bottle adequate for sampling at both open water and vegetated areas (Paggi *et al.*, 2001). Twelve litres of water were filtered through a 40-µm mesh sieve and preserved with 4% formaldehyde. Microzooplankton (nauplii and rotifers) was counted in a 1-mL Sedgwick-Rafter counting cell using an optical microscope: subsamples were taken with a Hensel-Stempel pipette. Mesozooplankton (copepodites, adult copepods and cladocerans) was examined and enumerated in a 5-mL Bogorov chamber under a stereomicroscope and subsampled with a Russell device. The number of examined subsamples was the minimum required in order to obtain an estimation error of total zooplankton abundance below 10%. Zooplankton was identified to the maximum possible taxonomic level.

Regional zooplankton diversity (γ diversity) was estimated by total richness, as the sum of taxa recorded at all sites on each occasion, and the species were classified into *limnetic* or *littoral* following Costa Bonecker *et al.* (1998), Rossa and Costa Bonecker (2003), Viayeh (2010) and on the basis of the available information from Koste (1978) and Koste and Shiel (1990). For each sampling point and occasion, zooplankton within habitat richness (α diversity), Shannon Diversity Index, evenness and the abundance of zooplanktonic groups were calculated: rotifers, copepods and cladocerans, expressed as Ind L^{-1} . In order to examine possible differences among different environment types, these data were assigned to four categories of environments according to the presence and life form of macrophytes registered in the field (independently from the date): *open waters* (OW), *emergent macrophytes* (EM), *free-floating*

macrophytes (FFM) and *mixed free-floating and emergent macrophytes* (FFM + EM).

Statistical analyses

Non-parametric Spearman correlations were performed in order to analyse the relationships between hydrometric parameters (river and lake water levels) and environmental heterogeneity both at the broad and fine scales. At the fine scale, γ zooplankton diversity was also included in the correlation analysis. To assess the relationship between the zooplankton community attributes (α diversity and the abundance of main groups) and the environmental parameters at the environments scale, a redundancy analysis (RDA) was performed; all variables not highly correlated ($r < 0.8$, $p < 0.05$) were included, and two additional categorical variables were used: presence-absence of emergent macrophytes and presence-absence of free-floating macrophytes. The significance of the ordination axes was assessed by the Monte Carlo test (499 permutations). The zooplankton community attributes (Shannon diversity Index, species richness and evenness) and limnological variables (water temperature, conductivity, pH, dissolved oxygen and chlorophyll *a* concentration) between the environment categories (OW, EM, FFM, FFM + EM) were compared by a one-factor analysis of variance and Tukey Kramer post-hoc comparisons (for non-balanced designs). The analyses concerning zooplankton variables were performed with the high waters data set that comprised all environmental categories and allowed their adequate comparison. In this way, we focused on the possible differences associated with macrophytes and minimized the effect of environmental changes associated with the hydrometric level. The ratios of limnetic and littoral zooplankton taxa to total zooplankton taxa were compared between *low* and *high* waters by one-factor analysis of variance. Normality and homocedasticity assumptions were tested by the Shapiro-Wilk and Levene tests. SPSS (SPSS Inc., Chicago, IL, USA) and CANOCO 4.5 (Wageningen UR, Wageningen, The Netherlands) software were used.

RESULTS

Analysis at different scales

The landscape of Laguna Grande varied along the 2-year survey that encompassed almost three vegetation growing seasons characterized by strong water level fluctuations. Accordingly, eight classes representative of the environments encountered in the lake were obtained through the ISODATA procedure (Table I); their spectral signatures are presented in Figure 2. These are distinguished by at least one spectral band, with the exception of the *free-floating macrophytes* and *terrestrial macrophytes* signatures, which

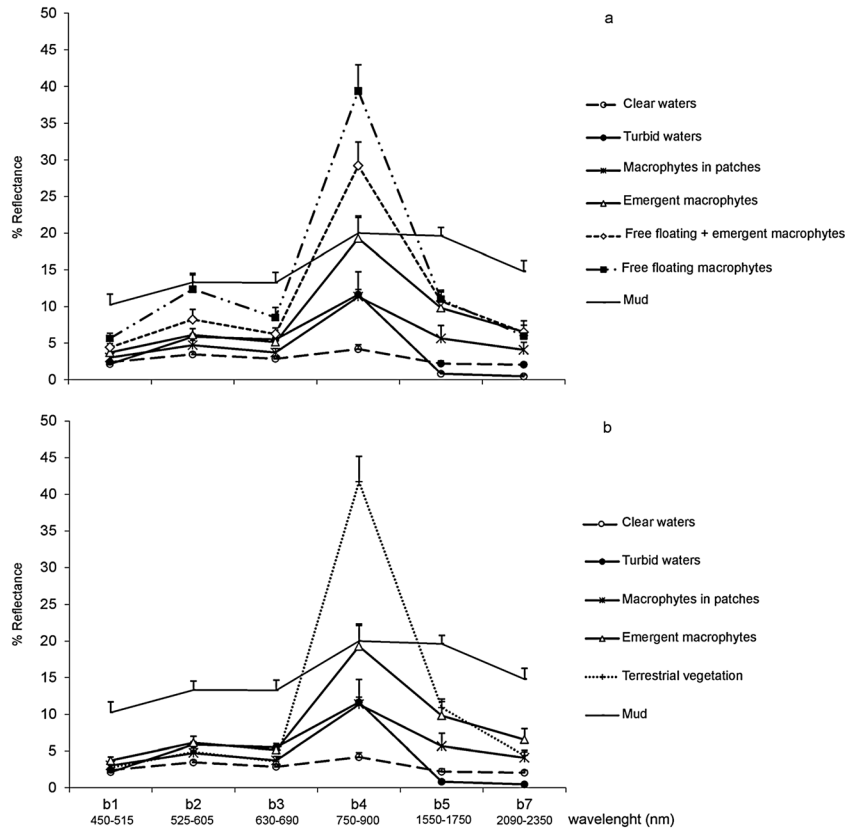


Figure 2. Spectral signatures of the different classes detected in the lake during the study. b1–b7: spectral bands of the Landsat 5 TM sensor. (A) *Low waters* spectral signature group, and (B) *high waters* spectral signature group

overlap in some bands. Considering that this single overlapping case involves classes that do not occur simultaneously (terrestrial vegetation occurs during extreme droughts, whereas free-floating macrophytes develop during mid or high waters), the supervised classifications were performed with two different spectral signature groups: one group excluding the *free-floating macrophytes* signature (in homogeneous or mixed patches) and the other excluding the *terrestrial vegetation* signature. When the eight scenes were classified with these two signature groups, it was corroborated that (i) the scenes that did not present the overlapping classes produced the same thematic map, independently of which signature group was used; and (ii) the only change registered involved the overlapping of the aforementioned signatures. Thus, the eventual presence of terrestrial vegetation and the absence of free-floating macrophytes were detected during *low waters* periods, whereas during *high waters* the opposite occurred, in concordance with field observations.

The water level at the littoral area of the lake strongly fluctuated between the early springs 2008 and 2010, ranging from -30 cm (beneath the sediment surface) to a water column of nearly 70 cm. During the austral spring–summer

2008–2009, an extremely *low water phase* occurred associated to the El Niño Southern Oscillation hydrometeorological event (<http://www.cpc.ncep.noaa.gov>), in correspondence to low hydrometric levels at the Paraná de las Palmas River and scarce precipitations in the area (Figure 3A). During this period, the lake’s aquatic environments were reduced and mainly represented by *turbid waters* and some patches of *emergent macrophytes*; a high contribution of *terrestrial vegetation* was registered (Figure 4A). During this phase, the mean Shannon Diversity Index and richness of aquatic environments were 1.2 and 4, respectively. On early February 2009, most of water surface dried (no water was registered at the sites located across the study transect), although isolated wet patches were detected by satellite imagery (Figure 3B).

The onset of the *high water* phase was associated to copious precipitations and increasing water level of the Paraná de las Palmas River by the end of February and beginning of March 2009 (Figure 3A). During this phase, clear waters prevailed, and the aquatic environments were gradually recovered; the entire lake was filled, and the terrestrial vegetation was replaced by emergent and free-floating macrophytes in the littoral areas (Figure 3B). By the end of the study (early Spring 2010), littoral

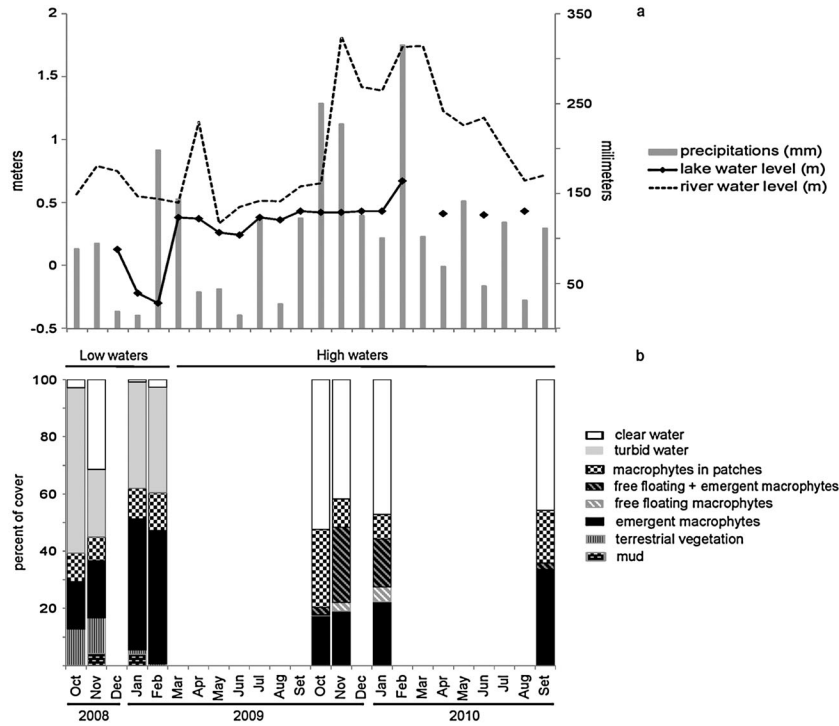


Figure 3. (A) Monthly accumulated precipitations and mean water levels of Laguna Grande (zero corresponds to the sediments level at a fixed point near the shore) and Paraná de las Palmas River. (B) Per cent of cover of each environment type (class) at the broad scale (entire lake) revealed by the satellite imagery classifications

macrophytes showed a profuse development in different stands of single or mixed life forms, and the presence of areas with different plant cover created a mosaic of environments (Figure 4B). The mean Shannon Diversity Index and richness of aquatic environments were 1.2 and 6, respectively. The emergent macrophytes most

commonly encountered were *Schoenoplectus californicus* and *Typha latifolia*, and among the free-floating, *Pistia stratiotes* prevailed.

At the fine scale, the different environments were more evenly represented, because open water was less important at the littoral zone, whereas vegetated areas dominated;

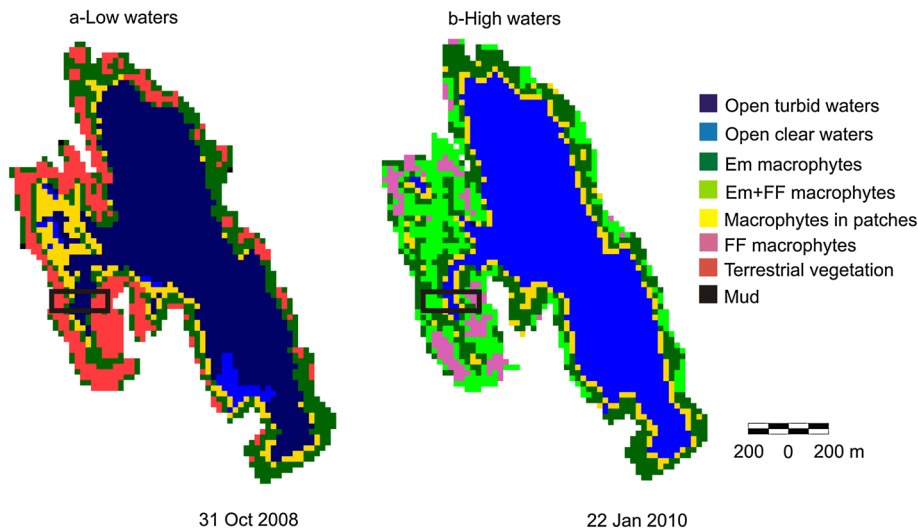


Figure 4. Thematic maps resulting from the hybrid classifications of the Landsat 5 TM images. The rectangle represents the small area (fine scale) where samplings were performed. Thematic maps: (A) representative of low waters, and (B) representative of high waters. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

however, regarding the dynamics of the different types of environments, the temporal patterns resembled those previously described for the entire lake. At this scale, the mean Shannon Diversity Index and richness of aquatic environments and the number of aquatic patches were 2, 0.4 and 4, respectively, during *low waters* and 4, 1.2 and 9 during *high waters*.

The analysis at a broad scale (entire lake) revealed that the water level of the river and the lake were positively correlated. Moreover, the river water level was positively correlated with the lake's environmental diversity while the lake water level with its richness of aquatic environments. At the fine scale (small area of interest), river and lake water levels were positively correlated, and in turn, these were positively correlated with environmental heterogeneity parameters: richness and diversity of aquatic environments and the number of aquatic patches. γ zooplankton diversity was also positively correlated with the environmental heterogeneity parameters and with the lake water level (Table II).

Comparison among environments

The occurrence of each type of environment differed between water phases at the sampling sites. During *low waters*, four sampling points corresponded to OW and three to EM. During *high waters*, 16 belonged to OW, 11 to EM, 10 to FFM and 18 to mixed EM + FFM. Water temperature varied seasonally in a similar way among the environments ($p > 0.05$), although slightly lower values were registered under floating mats (Table III). Conductivity, pH, dissolved oxygen and chlorophyll *a* concentrations were extremely high during *low waters* at OW and EM; values decreased during *high waters* ($p < 0.05$) and were similar among environments ($p > 0.05$), except pH that was higher at EM than at EM + FFM ($p < 0.05$). Total zooplankton abundance was high during *low waters* (especially at

EM) and lower during *high waters*; during the latter, abundances were similar among environments.

Zooplankton community was represented by 149 taxa, 120 rotifers, 21 cladocerans and 8 copepods (Table IV). Rotifers were the most abundant, followed by nauplii larvae of copepods. Thirty taxa were registered during *low waters*; the dominant species were the rotifers *Brachionus angularis*, *Brachionus ibericus*, *Brachionus plicatilis* and *Filinia saltator*; the copepod *Metacyclops mendocinus*; and the cladoceran *Moina wierzejskii*. The number of taxa increased markedly to 145 during *high waters*; the dominant species were the rotifers *Horaella* sp., *Lecane bulla*, *Lecane hamata*, *Lepadella patella*, *Lepadella imbricata* *Monommata* sp., *Polyarthra remata*, *Synchaeta oblonga*, *Testudinella patina*; copepods of the order Calanoidea; and the cladocerans *Ceriodaphnia* sp. and *Acroperus* sp. Interestingly, the ratios of limnetic and littoral taxa to total zooplankton taxa differed among water phases and showed opposite trends: the ratio of limnetic to total zooplankton taxa at *low waters* exceeded that of *high waters* (mean values 0.61 and 0.35, respectively) ($p < 0.05$), whereas the relation of littoral to total zooplankton taxa showed the opposite pattern (mean values 5.3 and 78 at *low* and *high waters*, respectively) ($p < 0.05$) (Figure 5).

The RDA performed with the zooplankton community attributes, and the environmental variables was significant ($p = 0.002$) (Figure 6). The first axis explains 62.1% of the variance, and it is positively correlated with conductivity ($r = 0.90$) and negatively with the presence-absence of free-floating macrophytes ($r = -0.40$). Samples with higher conductivity and higher abundance of all zooplankton groups are plotted at the right side of the figure and correspond to the early filling of the lake when all environments were represented. The second axis explains 27% of the variance, and it is negatively correlated with presence-absence of free-floating macrophytes ($r = -0.73$) and dissolved oxygen ($r = -0.70$). Samples with a higher

Table II. Spearman correlation coefficients between river and lake water levels (W-L) and environmental heterogeneity parameters (richness, S env; diversity, Sh env; number of patches, N° patches) at the broad (lake) and fine (small 'area of interest') scales and γ zooplankton diversity (γ zoo) at the fine scale

		S env	Sh env	N° Patches	γ zoo	W-L river
Lake	Sh env	-0.12				
	W-L river	0.46	0.71*			
	W-L lake	0.8*	0.41			0.82*
Small area of interest	SH env	0.97*				
	N° patches	0.98*	0.97			
	γ zoo	0.73**	0.75*	0.69**		
	W-L river	0.92*	0.95*	0.92*	0.54	
	W-L lake	0.85*	0.93*	0.85*	0.82*	0.82*

* $p < 0.05$.

** $p < 0.1$.

Table III. Mean values of limnological parameters and total zooplankton abundance registered at each hydrological phase and environment

		Temperature (°C)	Conductivity ($\mu\text{S cm}^{-1}$)	pH	O ₂ (mg L ⁻¹)	Chl <i>a</i> ($\mu\text{g L}^{-1}$)	Total zooplankton (Ind L ⁻¹)
Low waters	OW	26.7 (2.1)	4003 (2782)	8.6 (1.2)	10 (6.8)	261.3 (261.1)	6735 (4866)
	EM	24.9 (2.4)	4466 (2274)	8.4 (1.0)	6.6 (4.1)	231.2 (230.5)	15067 (9688)
High waters	OW	18.0 (7.1)	1699 (897)	7.1 (0.6)	4.7 (2.4)	33.5 (31.9)	1835 (3438)
	EM	16.4 (6.0)	2089 (762)	7.3 (0.3)	4.7 (2.7)	30.6 (42.6)	3110 (4346)
	FFM	13.5 (4.8)	1924 (768)	6.9 (0.5)	2.6 (2.4)	28.8 (45.0)	2279 (2497)
	EM + FFM	17.4 (7.0)	1644 (803)	6.6 (0.6)	2.3 (1.9)	27.1 (22.1)	1327 (1375)

Standard deviations are presented between parentheses.

OW = open waters; EM = emergent macrophytes; FFM = free-floating macrophytes; EM + FFM = emergent + free-floating macrophytes.

dissolved oxygen and chlorophyll *a* concentrations are plotted at the upper side of the figure; these correspond to the OW and EM environments and are characterized by low zooplankton richness (α diversity). On the contrary, the lower side of the graph shows those samples with free-floating and emergent macrophytes, associated to maximum zooplankton species richness.

Environments with free-floating macrophytes (F and EM + F) showed higher zooplankton diversity values (richness and Shannon Diversity Index) than those without them (OW and EM) ($p < 0.05$), although no differences were detected within these two groups ($p > 0.05$). On the contrary, significant differences were detected for evenness between OW–FFM and OW–EM + F (Figure 7).

DISCUSSION

Floodplain's ecological integrity depends upon a certain level of disturbance, which determines their high spatial and temporal heterogeneity and high species richness (Ward *et al.*, 1999). The floodpulse dynamics maintain these systems at different succession states, from semi-aquatic to lentic and lotic (Ward *et al.*, 1999). The results obtained in this study emphasize the role of water level fluctuations on the landscape changes of the floodplain lake, from a homogenous state with low zooplankton γ diversity to one more heterogeneous with enhanced macrophytes development and high zooplankton γ diversity.

Although Laguna Grande and the Paraná de las Palmas River are not superficially connected, the correlation between their hydrometric levels reveals a positive river influence on the lake, as it was previously suggested by O'Farrell *et al.* (2011). Moreover, associated to a strong negative El Niño Southern Oscillation hydrometeorological event, the extreme *low waters* determined a temporary drought that covered an extensive surface of the lake. Likewise, when both the Paraná de las Palmas River water level and its precipitations increased, the lake

recovered its hydrometric levels. These changes provoked deep transformations in the lake, regarding the elements of the landscape (this study) and the composition of its communities (Chaparro *et al.*, 2011).

At the landscape level of the wetland complex, the floodpulse increases the connectivity between floodplain environments and thus homogenizes them (Tockner *et al.*, 2000; Ward and Tockner, 2001; Thomaz *et al.*, 2007). A different perspective was obtained by the analysis performed at the lake scale in Laguna Grande, which shows that the effect of the flood within the water body is to increase its environmental heterogeneity. During low waters, the lake was reduced to open remaining pelagial areas free of macrophytes, because of a decline of aquatic littoral vegetation that was scarce. When water level rose, the lake recovered its total water surface, macrophytes recolonized and a mosaic of different environmental types characterized the lake. The physical and chemical changes occurring during floods allow macrophytes development. On the one hand, the fast colonization of free-floating macrophytes would be associated to the phosphorous increase registered on March in the water column (from 0.1 to 2 mg/L of P-PO₄), and to a marked decreasing salinity (Chaparro *et al.*, 2011), in agreement to observations described in other studies (Haller *et al.*, 1974; Thomaz *et al.*, 2006). On the other hand, emergent macrophytes are able to regenerate the aerial biomass lost during droughts (Esteves and Suzuki, 2008). Thus, the development of different macrophytes at advanced stages of the hydrological succession determined a higher environmental heterogeneity, represented by augmented richness of aquatic environments and patches. The relationship between discharge and landscape diversity is a functional characteristic of floodplains that is likely to exert a major control on biodiversity patterns (Ward and Tockner, 2001).

The increase of environmental heterogeneity that takes place along the succession was described for forests and related to enhanced biodiversity of the inhabiting plant communities (Bazzaz, 1975). Likewise, increased spatial

Table IV. Taxonomic list of zooplankton encountered in Laguna Grande during the study period

Rotifera	
<i>Asplanchna brightwelli</i>	<i>L. cf tenuiseta</i>
<i>Anuraeopsis fissa</i>	<i>L. spp. (2 species)</i>
<i>Brachionus angularis</i>	<i>Colurella obtusa</i>
<i>B. bidentata</i>	<i>C. uncinata</i>
<i>B. calyciflorus</i>	<i>C. sp. 1</i>
<i>B. caudatus</i>	<i>Lepadella acuminata</i>
<i>B. dimidiatus</i>	<i>L. imbricata</i>
<i>B. havanaensis</i>	<i>L. ovalis</i>
<i>B. ibericus</i>	<i>L. patella</i>
<i>B. nilsoni</i>	<i>L. cf. latusinus</i>
<i>B. quadridentatus</i>	<i>L. cf. benjamini braziliensis</i>
<i>B. plicatilis</i>	<i>L. triptera</i>
<i>B. urceolaris</i>	<i>L. sp. 1</i>
<i>B. zahniseri</i>	<i>Squatinella mutica</i>
<i>Keratella morenoi</i>	<i>Lindia sp.</i>
<i>K. tropica</i>	<i>Mytilina unguipes</i>
<i>K. spp. (2 species)</i>	<i>M. ventralis</i>
<i>Notholca sp.</i>	<i>Cephalodella forficula</i>
<i>Platyas quadricornis</i>	<i>C.cf. catellina</i>
<i>Platyonus patulus</i>	<i>C.spp. (11 species)</i>
<i>Dicranophorus sp. 1</i>	<i>Monommata sp.</i>
<i>D. sp. 2</i>	<i>Notommata spp. (2 species)</i>
<i>Beauchampiella sp.</i>	<i>Scaridium sp.</i>
<i>Euchlanis cf. dilatata</i>	<i>Polyarthra remata</i>
<i>E. cf. incisa</i>	<i>P. cf. vulgaris</i>
<i>Dipleuchlanis propatula</i>	<i>P. cf. dolichoptera</i>
<i>Gastropus sp.</i>	<i>Synchaeta cf. oblonga</i>
<i>Itura spp. (2 species)</i>	<i>S. pectinata</i>
<i>L. cf. aculeata</i>	<i>S. sp. 1</i>
<i>L. bulla</i>	<i>Trichocerca braziliensis</i>
<i>L. cornuta</i>	<i>T. bicristata</i>
<i>L. closterocerca</i>	<i>T. cf. iernis</i>
<i>L. curvicornis</i>	<i>T. inermis</i>
<i>L. elsa</i>	<i>T. rattus</i>
<i>L. flexilis</i>	<i>T. similis</i>
<i>L. hamata</i>	<i>T. tenuior</i>
<i>L. tenuiseta</i>	<i>T. vernalis</i>
<i>L. furcata</i>	<i>T. cf ruttneri</i>
<i>L. leontina</i>	<i>T. sp. 1</i>
<i>L. luna</i>	<i>Chonochilus sp.</i>
<i>L. lunaris</i>	<i>Filinia novaezelandiae</i>
<i>L. ludwigii</i>	<i>F. terminalis</i>
<i>L. rhytida</i>	<i>F. saltator</i>
<i>L. monostyla</i>	<i>F. pejlery</i>
<i>L. myersi</i>	<i>F. passa</i>
<i>L. papuana</i>	<i>Sinantherina semibullata</i>
<i>L. nana</i>	<i>S. spinosa</i>
<i>L. pyriformis</i>	<i>Testudinella patina</i>
<i>L. subtilis</i>	<i>Pompholix cf. triloba</i>
<i>L. halyclista</i>	<i>Horaella sp.</i>

(Continues)

heterogeneity associated to macrophyte cover and substrate characteristics was associated to higher macroinvertebrates diversity in ponds and streams (Heino, 2000; Brown, 2003; Verberk *et al.*, 2006). In floodplains, vegetated environments

Table IV. Continued

Cladocera	
<i>Bosmina sp.</i>	<i>Daphnia spinulata</i>
<i>Acroperus spp. (2 species)</i>	<i>Diaphanosoma birgei</i>
<i>Alona sp.</i>	<i>D. brevireme</i>
<i>Camptocercus sp.</i>	<i>Scaphoeleberis sp.</i>
<i>Chydorus sp.</i>	<i>Ilyocryptus sordidus</i>
<i>Euryalona sp.</i>	<i>Macrothrix spinosa</i>
<i>Leydigia sp.</i>	<i>Moina wierzejskii</i>
<i>Phryxura sp.</i>	<i>M. micrura</i>
<i>Pseudochydorus sp.</i>	<i>Moinodaphnia sp.</i>
<i>Ceriodaphnia cornuta</i>	<i>Simocephalus vetulus</i>
Copepoda	
<i>Metacyclops mendocinus</i>	Ciclopoida 3
<i>Acanthocyclops robustus</i>	Ciclopoida 4
Ciclopoida 1	<i>Notodiaptomus incompositus</i>
Ciclopoida 2	Harpacticoida

host richer fish communities (Gomes *et al.*, 2012), especially in those habitats with greatest complexity related to the life form and density of macrophytes (Petry *et al.*, 2003). In this study, we observed that the environmental heterogeneity related to the spatial distribution of macrophytes was positively correlated to zooplankton γ diversity. Particularly, an increase of littoral species associated to vegetation was registered, in concordance to what has been described in lakes during flooding periods (van den Brink *et al.*, 1994; Rossa and Costa Bonecker, 2003). These results would support the hypothesis that, at higher environmental heterogeneity (provided by macrophytes), and thus higher availability of niches, zooplankton diversity increases by enhanced occurrence of specialist species (*sensu* Cramer and Willig, 2005). Moreover, the increase of environmental heterogeneity at *high waters* coincided with marked limnological changes (mainly lower conductivity), which also affected zooplankton richness. In this sense, during *low waters* and extremely high conductivities, few euryhaline species

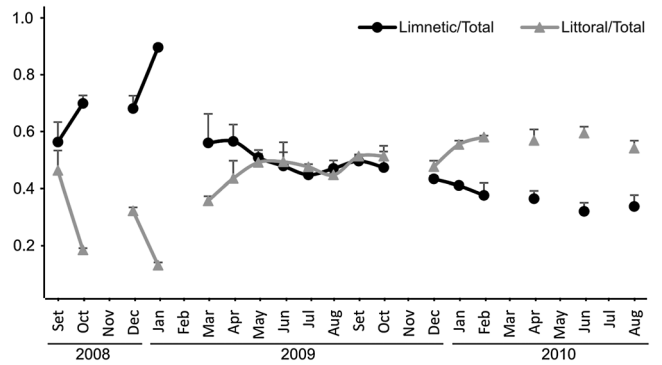


Figure 5. Ratio between limnetic and littoral to total zooplankton taxa recorded in Laguna Grande at each sampling date. Bars indicate the standard deviations

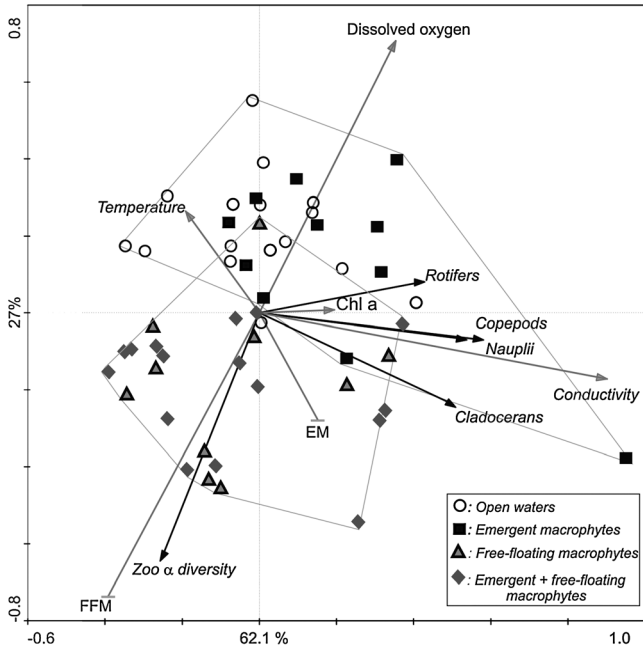


Figure 6. Redundancy analysis triplot of the zooplankton community attributes (abundance of rotifers, copepods, cladocerans and nauplii and α diversity—black arrows), environmental variables (dissolved oxygen, conductivity, water temperature, chlorophyll *a* (Chl *a*)—grey arrows), presence-absence of emergent macrophytes (EM) and free-floating macrophytes (FFM)—grey lines—and types of environments (○: open waters; ■: emergent macrophytes; ▲: free-floating macrophytes; ◆: emergent + free-floating macrophytes)

were registered in accordance to the patterns described for systems with high salinities (Schallenberg *et al.*, 2003), whereas during *high waters*, several oligohaline species occurred (Chaparro *et al.*, 2011).

The comparisons among different environments of this shallow lake during *high waters* indicate that zooplankton

α diversity was higher in environments with presence of free-floating macrophytes, both in homogeneous and mixed patches (F and EM + F). Interestingly, the environments did not differ in their limnological variables during this study, suggesting that such conditions played a minor role driving zooplankton richness differences during *high waters*. As it was described for macroinvertebrates (Thomaz *et al.*, 2008; Ohtaka *et al.*, 2011; Fontanarrosa *et al.*, 2012), the high zooplankton richness found at environments with free-floating plants would be strongly associated to the structural complexity provided by roots in the water column. The importance of habitat complexity provided by macrophytes on zooplankton diversity has been experimentally assessed by Lucena-Moya and Duggan (2011) and found that richness was greater on more complex macrophytes. Free-floating macrophytes increase the number of available niches (Thomaz and Ribeiro da Cunha, 2010), host rich epiphytic communities (Rodríguez *et al.*, 2011) which constitute food resources (Rodrigues *et al.*, 2003) and may modify the physical and chemical water (de Tezanos Pinto *et al.*, 2007; O’Farrell *et al.*, 2009). Despite it was argued that these macrophytes would not constitute a refuge for great and medium size zooplankters, as they may host predators as fishes and macroinvertebrates (Agostinho *et al.*, 2007; Iglesias *et al.*, 2007; Meerhoff *et al.*, 2007), our results indicate that such macrophytes constitute favourable habitats for a great variety of rotifers and even cladocerans and copepods. Considering our results and the fact that free-floating macrophytes host rich macroinvertebrate and fish communities (Iglesias *et al.*, 2007; Meerhoff *et al.*, 2007; Fontanarrosa *et al.*, 2012), within the frame of environmental heterogeneity and following the concepts by Tews *et al.* (2004), we propose that free-floating macrophytes constitute ‘key structures’ in vegetated floodplain shallow lakes, as they determine a quantitative change on the diversity of a variety of groups. Although

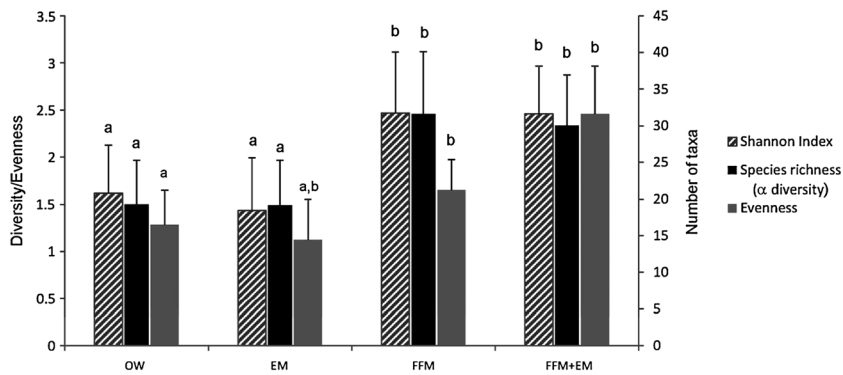


Figure 7. Mean values of Shannon Diversity Index, species richness (α diversity) and evenness for zooplankton assemblages at each type of environment. EM, emergent macrophytes; OW, open waters; FFM, free-floating macrophytes; EM + FFM, emergent + free-floating macrophytes. Bars indicate standard deviation. Different letters denote statistical differences in the post-hoc comparisons performed between the environmental categories ($p < 0.05$)

the role of free-floating macrophytes as zooplankton hosts has been explored (Serafim *et al.*, 2003; Gazulha *et al.*, 2011; Villabona-González *et al.*, 2011), rotifers were seldom considered, even though they are usually the most abundant and diverse group in subtropical and temperate shallow lakes (Meerhoff *et al.*, 2003; Iglesias *et al.*, 2007; Meerhoff *et al.*, 2007). More diverse communities comprise species with different strategies to exploit resources and thus are more efficient and stable (Ptacnik *et al.*, 2008; Cleland, 2011).

Finally, an additional effect of the presence of free-floating macrophytes was associated to lower zooplankton abundances, especially under anoxic or suboxic conditions (Figure 6). Previous experimental work indicated that low oxygen concentrations produced by simulating a floating macrophyte cover caused zooplankton demise in this lake (Fontanarrosa *et al.*, 2010). Accordingly, as shown in the RDA, free-floating macrophytes developed during the *high water* period at the same time as zooplankton abundance decreased in all environments evidencing a complex response related to chemical and physical processes (eg. redox conditions and flushing/dilution mechanisms). The inverse relationship between water level and zooplankton abundance was repeatedly reported in South American floodplain lakes (José de Paggi and Paggi, 2008; Lansac-Tôha *et al.*, 2009; Villabona-González *et al.*, 2011).

FINAL REMARKS

Our results highlight the influence of water level variations on environmental heterogeneity and zooplankton diversity in vegetated floodplain lakes adjacent to large rivers. Water pulses trigger environmental heterogeneity by promoting the development of different macrophyte life forms, which is associated with enhanced zooplankton diversity as well as to declining abundances. We emphasize the role of free-floating macrophytes as key components of environmental heterogeneity as these plants host high zooplankton diversity by providing distinct habitats that can support populations of different species.

ACKNOWLEDGEMENTS

We thank the staff of the Limnology Laboratory (UBA) and the personnel of Reserva Natural Otamendi for the field assistance. We thank the Servicio Meteorológico Nacional for providing meteorological data, the Subsecretaria de Puertos y Vías Navegables for the hydrological data, the Comisión Nacional de Actividades Espaciales (Argentina) and the Instituto Nacional de Pesquisas Espaciais (Brazil) for the satellite imagery. This study was financially supported by Agencia Nacional de Promoción Científica y Tecnológica

(PICT 536) and Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 5355), Argentina.

REFERENCES

- Agostinho AA, Thomaz SM, Gomes LC, Baltar SLSMA. 2007. Influence of the macrophyte *Eichhornia azurea* on fish assemblage of the upper Paraná River floodplain (Brazil). *Aquatic Ecology* **41**: 611–619.
- Amoros C, Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* **47**: 761–776.
- Auge M. 2004. Vulnerabilidad de acuíferos. *Revista Latino-Americana de Hidrogeología* **4**: 85–103.
- Bazzaz FA. 1975. Plant species diversity in old-field successional ecosystems in Southern Illinois. *Ecology* **56**: 485–488.
- Borges MG, Pedrozo C. 2009. Zooplankton (cladocera, copepoda and rotifera) richness, diversity and abundance variations in the Jacuí Delta, RS, Brazil, in response to the fluvio-metric level. *Acta Limnologica Brasiliensis* **21**: 101–110.
- Boschilia SM Oliveira EF, Thomaz SM. 2008. Do aquatic macrophytes co-occur randomly? An analysis of null models in a tropical floodplain. *Oecologia* **156**: 203–214.
- Brown G. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters* **6**: 316–325.
- Burks RL, Mulderij G, Gross E, Jones I. 2006. Center stage: the crucial role of macrophytes in regulating trophic interactions in shallow lake wetlands. In: *Wetlands: Functioning, Biodiversity Conservation and Restoration*, Bobbink R, Beltman B, Verhoeven JTA, Whigham DF (eds). Springer-Verlag: Heidelberg: 37–59.
- Casatti L, Mendes HF, Ferreira KM. 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana Reservoir, Paranapanema River, Southeastern Brazil. *Brazilian Journal of Biology* **63**: 213–222.
- Cazzanelli M, Warming TP, Christoffersen KS. 2008. Emergent and floating-leaved macrophytes as refuge for zooplankton in a eutrophic temperate lake without submerged vegetation. *Hydrobiologia* **605**: 113–122.
- Chaparro G, Marinone MC, Lombardo R, Guimarães AS, Schiaffino MR, O'Farrell I. 2011. Zooplankton succession during extraordinary drought–flood cycles: a case study in a South American floodplain lake. *Limnologia* **41**: 371–381.
- Chichizola SE. 1993. Las comunidades vegetales de la Reserva Natural estricta de Otamendi y sus relaciones con el ambiente. *Parodiiana* **8**: 227–263.
- Cleland EE. 2011. Biodiversity and ecosystem stability. *Nature Education Knowledge* **2**: 2.
- Costa Bonecker C, Lansac-Tôha FA, Rossa DC. 1998. Planktonic and non planktonic rotifers in two environments of the Upper Paraná River floodplain, State of Mato Grosso do Sul, Brazil. *Brazilian Archives of Biology and Technology* **41**: 447–456.
- Costa Bonecker C, Aoyagui ASM. 2005. Relationships between rotifers, phytoplankton and bacterioplankton in the Corumbá Reservoir, Goiás State, Brazil. *Hydrobiologia* **546**: 415–42.
- Cramer MJ, Willig MR. 2005. Habitat heterogeneity, species diversity and null models. *Oikos* **2**: 209–218.
- Crome FHJ and Carpenter SM. 1988. Plankton community cycling and recovery after drought-dynamics in a basin on a flood plain. *Hydrobiologia* **164**: 193–211.
- de Tezanos Pinto P, Allende L, O'Farrell I. 2007. Influence of free-floating plants on the structure of a natural phytoplankton assemblage: an experimental approach. *Journal of Plankton Research* **29**: 47–56.
- Esteves BS, Suzuki MS. 2008. *Typha domingensis* pers. subject to interactions among water level and fire event in a tropical lagoon. *Acta Limnologica Brasiliensis* **20**: 227–234.

- Fontanarrosa MS, Chaparro G, O'Farrell I. 2012. Temporal and spatial patterns of macroinvertebrates associated with small and medium-sized free-floating plants. *Wetlands*, **33**: 47–63, DOI:10.1007/s13157-012-0351-3.
- Fontanarrosa MS, Chaparro G, Tezanos Pinto P, Rodriguez P, O'Farrell I. 2010. Zooplankton response to shading effects of free-floating plants in shallow warm temperate lakes: a field mesocosm experiment. *Hydrobiologia* **646**: 231–242.
- Gazulha V, Montú M, da Motta Marques D, Costa Bonecker C. 2011. Effects of natural banks of free-floating plants on zooplankton community in a shallow subtropical lake in Southern Brazil. *Brazilian Archives of Biology and Technology* **54**: 745–754.
- Gomes LC, Bulla CK, Agostinho AA, Vasconcelos LP, Miranda LE. 2012. Fish assemblage dynamics in a neotropical floodplain relative to aquatic macrophytes and the homogenizing effect of a flood pulse. *Hydrobiologia* **685**: 97–107.
- Haller W, Sutton D, Barlowe W. 1974. Effects of salinity on growth of several aquatic macrophytes. *Ecology* **55**: 891–894.
- Heino J. 2000. Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. *Hydrobiologia* **418**: 229–242.
- Iglesias C, Goyenola G, Jeppesen E. 2007. Horizontal dynamics of zooplankton in subtropical Lake Blanca (Uruguay) hosting multiple zooplankton predators and aquatic plant refuges. *Hydrobiologia* **584**: 179–189.
- Iglesias C, Mazzeo N, Goyenola G, Fosalba C, Teixeira de Mello F, García S, Jeppesen E. 2008. Field and experimental evidence of the effect of *Jenynsia multidentata*, a small omnivorous-planktivorous fish, on the size distribution of zooplankton in subtropical lakes. *Freshwater Biology* **53**: 1797–1807.
- José de Paggi S. 2004. Diversidad de rotíferos monogonta del litoral fluvial argentino. In: FG Aceñolaza (coord ed) Temas de la biodiversidad del Litoral Fluvial Argentino. Instituto Superior de Correlación Geológica, Tucumán, INSUNGEO. *Miscelánea* **12**: 185–194
- Jose de Paggi S, Paggi JC. 2007. Zooplankton. In: The Middle Paraná River: Limnology of a Subtropical Wetland, Iriondo MH, Paggi JC, Parma MJ (eds). Springer-Verlag: Berlin, Heidelberg: 229–249.
- José de Paggi SB, Paggi JC. 2008. Hydrological connectivity as a shaping force in the zooplankton community of two lakes in the Paraná River floodplain. *International Review of Hydrobiology* **93**: 659–678.
- Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river floodplains systems. Proceedings of the international large river symposium. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**: 110–127.
- Koste W. 1978. Rotatoria. Die rädertiere mitteleuropas. Bestimmungswerk begründet Von Max Voigt. Borntraeger: Stuttgart, Germany.
- Koste W, Shiell RJ. 1990. Rotifera from Australian inland waters V. Lecanidae (Rotifera: Monogononta). *Transactions of the Royal Society of South Australia* **113**: 119–143.
- Lansac-Tôha FA, Bonecker CC, Velho LFM, Simões NR, Dias JD, Alves GM, Takahashi EM. 2009. Biodiversity of zooplankton communities in the upper Paraná River floodplain: interannual variation from long-term studies. *Brazilian Journal of Biology* **69**: 539–549.
- Levin SA. 1992. The problem of pattern and scale in ecology. *Ecology* **73**: 1943–1967.
- Lucena-Moya, P, Duggan IC. 2011. Macrophyte architecture affects the abundance and diversity of littoral microfauna. *Aquatic Ecology* **45**: 279–287.
- Marker AFH, Nusch A, Rai H, Riemann B. 1980. The measurement of photosynthetic pigments in freshwater and standardization of methods: conclusions and recommendations. *Archiv für Hydrobiologie Beiheftung Ergebnisse der Limnologie* **14**: 91–106.
- Maia-Barbosa PM, Peixoto RS, Guimaraes AS. 2008. Zooplankton in littoral waters of a tropical lake: a revisited biodiversity. *Brazilian Journal of Biology* **68**: 1069–1078.
- McClain CR, Barry JP. 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* **91**: 964–976.
- Meerhoff M, Iglesias C, Teixeira de Mello T, Clemente JM, Jensen E, Lauridsen TL, Jeppesen E. 2007. Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biology* **52**: 1009–1021.
- Meerhoff M, Mazzeo N. 2004. Importancia de las plantas flotantes libres de gran porte en la conservación y rehabilitación de lagos someros de Sudamérica. *Ecosistemas* **13**: 13–22.
- Meerhoff M, Mazzeo N, Moss B, Rodríguez-Gallego L. 2003. The structuring role of free-floating versus submerged plants in a subtropical shallow lake. *Aquatic Ecology* **37**: 377–391.
- Neiff JJ, Neiff APD, Verón MBC. 2009. The role of vegetated areas on fish assemblage of the Paraná River floodplain: effects of different hydrological conditions. *Neotropical Ichthyology* **7**: 39–48.
- O'Farrell I, de Tezanos Pinto P, Rodríguez P, Chaparro G, Pizarro H. 2009. Experimental evidence of the dynamic effect of free-floating plants on phytoplankton ecology. *Freshwater Biology* **54**: 363–375.
- O'Farrell I, Izaguirre I, Chaparro G, Unrein F, Sinistro R, Pizarro H, Rodríguez P, de Tezanos Pinto P, Lombardo R, Tell G. 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 Sciences* **73**: 275–287.
- Ohtaka A, Narita T, Kamiya T. 2011. Composition of aquatic invertebrates associated with macrophytes in Lake Tonle Sap, Cambodia. *Limnology* **12**: 137–144.
- Padial AA, Thomaz SM, Agostinho AA. 2009. Effects of structural heterogeneity provided by the floating macrophyte *Eichhornia azurea* on the predation efficiency and habitat use of the small neotropical fish *Moenkhausia sanctaefilomenae*. *Hydrobiologia* **624**: 161–170.
- Paggi JC, Mendoza RO, Debonis CJ, Jose de Paggi SB. 2001. A simple and inexpensive trap-tube sampler for zooplankton collection in shallow waters. *Hydrobiologia* **464**: 45–49.
- Paggi JC. 2004. Importancia de la fauna de “cladóceros” (Crustácea, Branchiopoda) del litoral fluvial argentino. In: Temas de la Biodiversidad del Litoral Fluvial Argentino, Aceñolaza FG (coord ed), Instituto Superior de Correlación Geológica, Tucumán, INSUNGEO *Miscelánea* **12**: 239–246.
- Paidere J. 2009. Influence of flooding frequency on zooplankton in the floodplains of the Daugava River (Latvia). *Acta Zoologica Lituanica* **19**: 306–313.
- Peel HW, Huisman J. 2009. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* **11**: 1633–1644.
- Petry P, Bayley PB, Markle DF. 2003. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology* **63**: 547–579.
- Poi de Neiff AS. 2003. Macroinvertebrates living on *Eichhornia azurea* Kunth in the Paraguay River. *Acta Limnologica Brasiliensis* **15**: 55–63.
- Ptácnik R, Solimini AG, Andersen T, Tamminen T, Brettum P, Lepistö L, Willen E, Rekolainen S. 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. *Proceedings of the National Academy of Sciences* **105**: 5134–5138.
- Rodrigues L, Bicudo D, Moschini-Carlos V. 2003. O papel do perífiton em áreas alagáveis e nos diagnósticos ambientais. In: Ecologia e manejo e macrofitas acuáticas, Thomaz SM, Bini LM (eds). EDUEM, Maringá; 211–230.
- Rodríguez P, Tell G, Pizarro H. 2011. Epiphytic algal biodiversity in humic shallow lakes from the Lower Paraná River Basin (Argentina). *Wetlands* **31**: 53–63

- Rossa DC, Costa Bonecker C. 2003. Abundance of planktonic and non-planktonic rotifers in lagoons of the upper Paraná River floodplain. *Amazoniana* **17**: 567–581.
- Schallenberg M, Hall CJ, Burns CW. 2003. Consequences of climate-induced salinity increases on zooplankton abundance and diversity in coastal lakes. *Marine Ecology Progress Series* **251**: 181–189.
- Scheffer M, Houser SH, Meijer ML, Moss B, Jeppesen E. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* **8**: 275–279.
- Serafim M Jr, Costa Bonecker C, Rossa DC, Lansac-Tôha FA, Costa CL. 2003. Rotifers of the upper Paraná River floodplain: additions to the checklist. *Brazilian Journal of Biology* **63**: 207–212.
- Silva Busso A, Santa Cruz J. 2005. Distribución de elementos traza en las aguas subterráneas del partido de Escobar, Buenos Aires, Argentina. *Ecología Austral* **15**: 31–47.
- Stumpf RP. 1992. Remote sensing of water clarity and suspended sediments in coastal waters. In: Proceedings of the First Thematic Conference on Remote Sensing for Marine and Coastal Environments. SPIE, New Orleans, 293–305.
- Sculthorpe CD. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold Ltd., London.
- Teixeira de Mello F, Meerhoff M, Pekcan-Hekim Z, Jeppesen E. 2009. Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. *Freshwater Biology* **54**: 1202–1215.
- Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**: 79–92.
- Thomaz SM, Bini LM, Bozelli RL. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* **579**: 1–13.
- Thomaz SM, Dibble ED, Evangelista LR, Higuiri J, Bini LM. 2008. Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. *Freshwater Biology* **53**: 358–367.
- Thomaz SM, Pagioro TA, Bini LM, Murphy KJ. 2006. Effect of reservoir drawdown on biomass of three species of aquatic macrophytes in a large sub-tropical reservoir (Itaipu, Brazil). *Hydrobiologia* **570**: 53–59.
- Thomaz SM, Ribeiro da Cunha E. 2010. The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. *Acta Limnologica Brasiliensia* **22**: 218–236.
- Tockner K, Malard F, Ward JV. 2000. An extension of the flood pulse concept. *Hydrological Processes* **14**: 2861–2883.
- Turner W, Spector S, Gardiner N, Fladelan M, Sterling E, Steininger M. 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology and Evolution* **18**: 306–314.
- van den Brink FWB, van Katwijk MM, van der Velde G. 1994. Impact of hydrology on phyto- and zooplankton community composition in floodplain lakes along the lower Rhine and Meuse. *Journal of Plankton Research* **16**: 351–373.
- Verberk WCEP, van Duinen GA, Brock AMT, Leuven RSEW, Siepel H, Verdonschot PFM, van der Velde G, Esselink H. 2006. Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. *Journal for Nature Conservation* **14**: 78–90.
- Viayeh RM. 2010. An overview of the rotifers of the family Notommatidae (Rotifera: Monogononta: Ploima) from Iran. *Caspian Journal of Environmental Sciences* **8**: 127–139.
- Villabona-González SL, Jaime Aguirre RN, Estrada PAL. 2011. Influencia de las macrófitas sobre la estructura poblacional de rotíferos y microscrustráceos en un plano de inundación tropical. *Revista de biología tropical* **59**: 853–870.
- Ward JV, Tockner K. 2001. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology* **46**: 807–819.
- Ward JV, Tockner K, Schiemer F. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *River Research and Applications* **15**: 125–139.
- Work KA, Havens KE. 2003. Zooplankton grazing on bacteria and cyanobacteria in a eutrophic lake. *Journal of Plankton Research* **25**: 1301–1306.
- Yeager LA, Layman CA, Allgeier JE. 2011. Effects of habitat heterogeneity at multiple spatial scales on fish community assembly. *Oecologia* **167**: 157–166.