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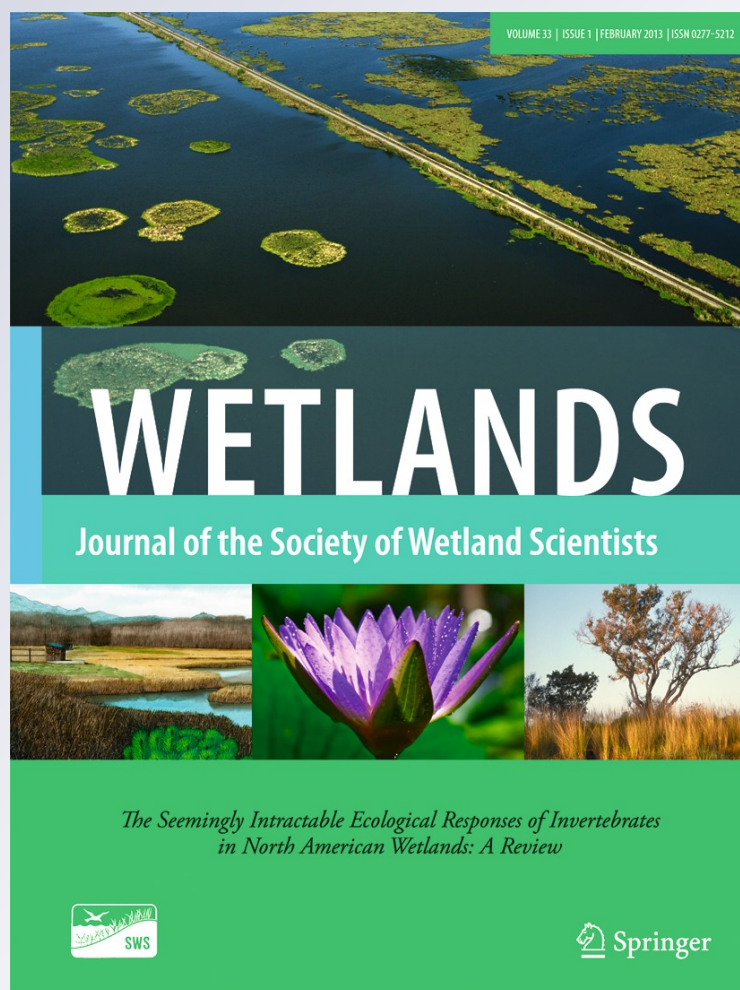
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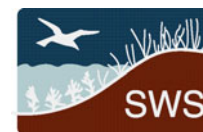
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Temporal and Spatial Patterns of Macroinvertebrates Associated with Small and Medium-Sized Free-Floating Plants

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Abstract Macrophytes play an important role in structuring communities in aquatic ecosystems due to their influence on ecological processes and attributes of biological aquatic assemblages. Freshwater macroinvertebrates comprise a functionally and taxonomically diverse group in shallow lakes, which serve as food for fish, amphibians, and water birds, and are involved in the breakdown of organic matter and nutrients. Here, we investigated macroinvertebrate assemblages associated with small and medium-sized free-floating plants (FFP) by describing their structure, analyzing functional aspects (considering functional feeding groups and habits), and determining how much of the variation in fauna composition is explained by environmental factors, mainly FFP. Differences in structure, functional feeding groups and habits of macroinvertebrate assemblages were associated with different compositions and percentages of cover of FFP. Gradients of richness and diversity of macroinvertebrates were positively related to the complexity of FFP mats, which was associated with the structure of roots and leaves.

Keywords Wetlands · Diversity · Community structure · Habitat complexity

Introduction

Macrophytes affect the ecological processes and attributes of biological aquatic assemblages, influencing their outcomes through structural, behavioral and chemical interactions

(Burks et al. 2006). Habitat structure is generally considered to influence local species abundance and diversity (Warfe et al. 2008). In this sense, the role of macrophytes as physical structures that increase the complexity or heterogeneity of habitats is widely recognized (Thomaz and Ribeiro da Cunha 2010). Moreover, this vegetation represents an important food resource for aquatic organisms, providing both living (grazing food webs) and dead organic matter (detritivorous food webs) (Thomaz and Ribeiro da Cunha 2010). It also serves as an indirect food resource by providing support for epiphytic biomass (Gosselain et al. 2005), which constitutes an important food source for higher trophic levels (Lamberti 1996). Macrophytes are used by some organisms (e.g. aquatic insects) as oviposition sites (Merritt and Cummins 1984), and may offer protection for small individuals against visual predators (Scheffer 1998). Their influence on different assemblages or trophic levels depends on the type of macrophyte (e.g. submerged, free-floating) (e.g. Meerhoff et al. 2003).

The presence of macrophytes usually increases the richness, biomass and density of macroinvertebrates (Scheffer 1998; Thomaz and Ribeiro da Cunha 2010). Macroinvertebrates comprise a functionally and taxonomically diverse group in shallow lakes, which serve as food for fish, amphibians, and water birds (de Szalay and Resh 2000) and are involved in the breakdown of organic matter and nutrients (Vanni 2002). They are important contributors to ecosystem functions occupying different spatial niches and showing diverse feeding modalities and habits (Bazzanti et al. 2009). The colonization of macrophytes by macroinvertebrates may be influenced or limited by the biology of organisms as well as by the architecture of plant structures such as leaves and stems (Laurindo da Silva et al. 2011). Changes in macrophyte species composition could then indirectly modify the composition and biomass of the macroinvertebrate community altering the biotic relationships among species (Warfe and Barmuta 2004; Cremona et al. 2008;

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Thomaz and Ribeiro da Cunha 2010; de Ávila et al. 2011). When analyzing beta diversity of macroinvertebrates in neotropical wetlands, de Ávila et al. (op. cit.) observed that different plant species in similar habitat types may have influenced macroinvertebrate community composition. Despite the fact that changes in macrophyte species composition and abundance may reflect the functional organization of macroinvertebrate assemblages, the influence of hydroperiod is paramount in floodplain systems. Water level not only affects the dynamics of the macroinvertebrate community, but it is correlated with other abiotic (e.g. dissolved oxygen, salinity, pH, depth) and biotic (e.g. primary production, detritus breakdown) factors that affect macroinvertebrates (Wissinger 1999; Grillet et al. 2002; Williams 2006).

The hypothesis that macrophyte structure shapes invertebrate communities has been repeatedly tested on submerged vegetation (e.g. Cremona et al. 2008; Thomaz et al. 2008; Warfe et al. 2008; Ferreira et al. 2011). In contrast, studies focused on invertebrate assemblages related to free-floating plants are less common. Free-floating macrophytes may be equally or more important than submerged macrophytes in many ecological processes in subtropical and tropical lakes (Meerhoff et al. 2003). Meerhoff et al. (2007) found higher densities of plant-associated macroinvertebrates in free-floating plants than in submerged ones. These authors also suggested that the relevance of free-floating plants is increasing due to the fact that areas dominated by this type of vegetation are likely to expand to temperate climates as a consequence of the warmer winters induced by the climate change. Studies including free-floating plants and invertebrates have been performed mainly on species of great size such as *Eichhornia* spp., with a neotropical native distribution (e.g. Poi de Neiff and Carignan 1997; Rocha-Ramírez et al. 2007; Padial et al. 2009; Villamagna and Murphy 2010; Kouamé et al. 2011; Ohtaka et al. 2011). Few works have considered free-floating plants of medium and small size like *Pistia*, *Azolla* or *Lemna* (e.g. Poi de Neiff and Neiff 2006; Mustapha 2008). Small and medium-sized free-floating plants, such as *Lemna* spp., *Ricciocarpus natans* and *Pistia* spp., have a cosmopolitan distribution (Sculthorpe 1967; Mendoza Ruiz 2008), whereas species of *Azolla* are widely distributed in tropical, subtropical and warm temperate regions (Sculthorpe 1967). Interestingly, certain species, particularly *A. filiculoides*, have become invasive in Europe and Scandinavia (Aragónés et al. 2009; Hussner 2010).

With the aim to give further insights into the composition and relevance of macroinvertebrate assemblages associated with small and medium-sized free-floating plants (FFP), we 1) describe the structure of these assemblages associated with different types of FFP, 2) analyze the temporal and spatial variation of functional aspects of macroinvertebrate communities by considering functional feeding groups and habits in relation with different types of FFP, and 3) determine how

much of the variation in fauna composition is explained by the environmental factors here analyzed. We hypothesized that FFP mats dominated by species of medium size: 1- are associated with richer and more diverse assemblages of macroinvertebrates, and 2- support more diverse feeding modalities and habits of macroinvertebrates than FFP mats dominated by small species. The rationale of this hypothesis is that FFP species have different architectures which may constitute a gradient of habitat complexity, from small to medium-sized species, for macroinvertebrates assemblages.

Materials and Methods

Study Area

Studies were conducted in the Natural Reserve Otamendi, a RAMSAR floodplain wetland 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 region has a temperate climate, without a dry season and with hot summers according to the updated Köppen-Geiger classification (Peel et al. 2007). The mean annual temperature ranges between 16.7 and 18 °C and precipitations occur during the whole year, with mean annual values of 950 mm. In particular, the wetland systems of the region moderate the extreme temperatures and the temporary hydrological deficit, creating conditions more similar to those of the humid subtropical zone (Malvárez 1999). The area has a limited drainage and is subject to the influence of a high and fluctuating water table, being permanently or periodically flooded due to rainfall (Chichizola 1993).

The water bodies studied in the wetland complex include a large shallow lake (Laguna Grande (LG); ~156 ha; Z<1 m), and two oxbow lakes (ROLs; ~17 ha; Z<0.5 m each one) (Fig. 1); these systems are not directly connected with rivers and are usually isolated from them. The water bodies in the wetland exhibit profuse aquatic vegetation mainly composed of rooted and floating species, whose spatial distribution and biomass experience marked fluctuations during the year and between years. The littoral zone of LG and the ROLs exhibit high development of the emergent *Schoenoplectus californicus*, followed by *Typha latifolia* and *Scirpus giganteus*. These water bodies also have a variable coverage of different free-floating macrophytes, including small species of *Lemna* spp., *Ricciocarpus natans* and *Azolla filiculoides*, and the medium-sized species *Pistia stratiotes*.

Sampling Methodology

Samples were taken from May 2007 to April 2008 (May 31, Jul 16, Sep 20, Oct 29, Dec 17, Jan 31, Mar 15, Apr 22), on two occasions per season, at sites where FFP are usually encountered (Izaguirre et al. 2004). Three sampling sites were

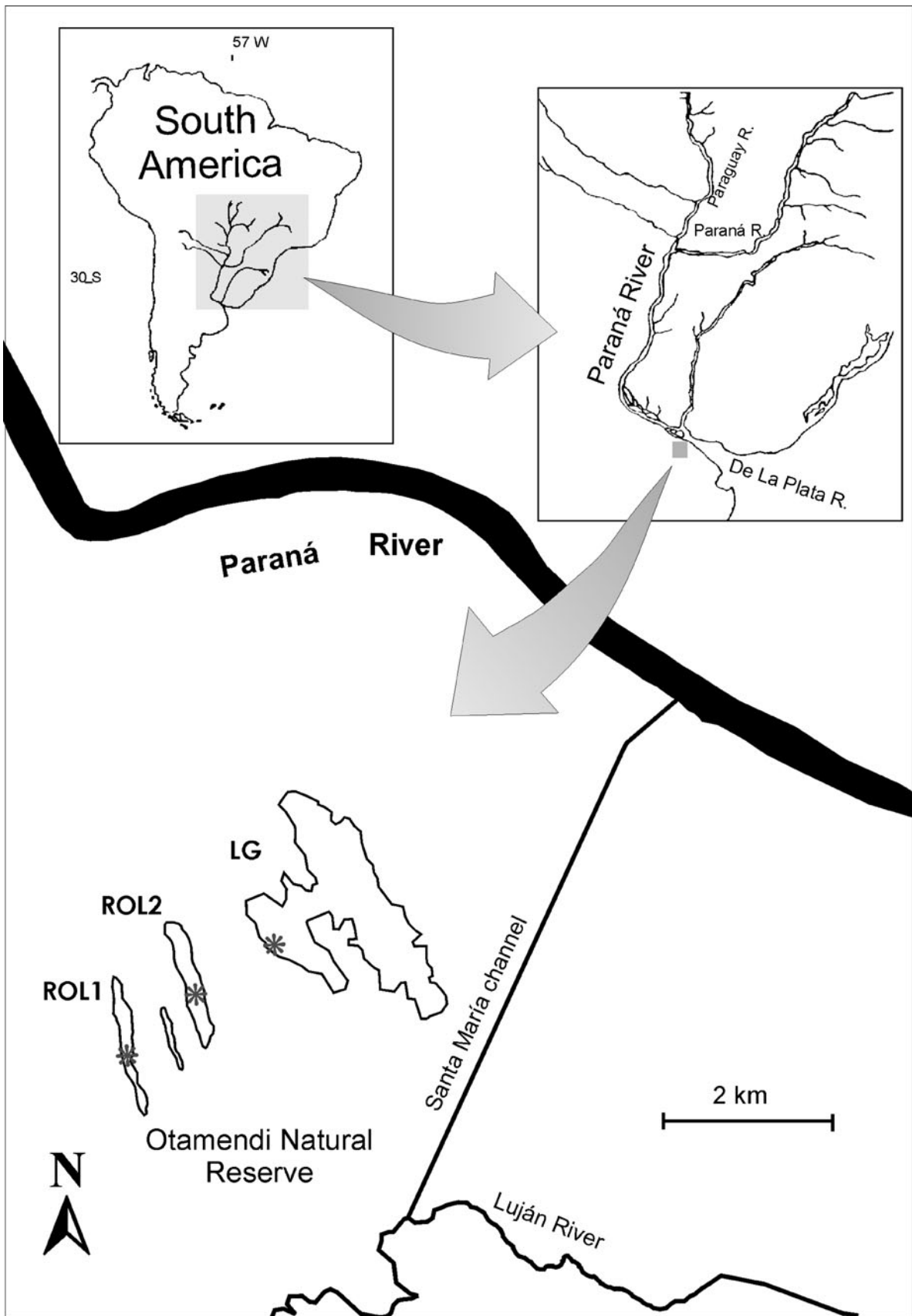


Fig. 1 Geographic location of the study area. The *asterisks* indicate the sampling area. LG: Laguna Grande; ROL1: Oxbow lake 1; ROL2: Oxbow lake 2

established in each ROL and three in the littoral zone of Laguna Grande (LG) (Fig. 1), along transects across the entire width of the ROLs and from the littoral margin to the limnetic area in LG; most sites were usually covered with FFP mats, dominated by small or medium-sized species. The percentage of cover of the entire mat of FFP and of each individual species was visually estimated in the field. For each sampling occasion, we corroborated the FFP species cover estimation performed in the field using digital photography of each site with a grid drawn on the image. Macroinvertebrate samples were taken with a hand net (30×25 cm; 290 µm mesh). A 1-m long sweep was performed on each sampling site and occasion to collect macroinvertebrates; FFP were collected whenever present.

In the laboratory, plants were thoroughly rinsed with tap water, and then filtered through a 290-µm mesh sieve to trap dislodged macroinvertebrates. Each sweep sample was sorted separately and preserved in ethanol 80 %. The macrophytes collected were dried at 60 °C until constant weight to estimate FFP biomass (dry weight) (FFP-DW). The macroinvertebrates were separated, counted and identified under a stereomicroscope to the lowest possible taxonomic level. Taxonomic identifications were performed using the appropriate systematic keys and specialized literature on local fauna: Insects: Merritt and Cummins (1984) and Lopretto and Tell (1995); Coleoptera: Archangelsky (1997), Grosso (1993) and Oliva et al. (2002); Diptera: Alexander and Byers (1981), Downes and Wirth (1981), James (1981), Darsie (1985), Paggi (2001), and Rossi et al. (2002); Heteroptera: Schnack (1976), Bachmann (1981), Bachmann and López Ruf (1994), and Estévez and Polhemus (2001); Odonata: Rodrigues Capítulo (1992); Eumalacostraca: Lopretto and Tell (1995) and Peralta (2001).

On each sampling date and habitat, the following physical and chemical water variables were measured in situ: temperature, pH, conductivity (with a Hanna HI 991301 meter), dissolved oxygen (with a Hanna HI 9143 portable instrument), and water depth (with a portable meter). Daily temperature and rainfall data were provided by the Servicio Meteorológico Nacional (Argentina).

Data Analysis

The species of FFP recorded were classified into three categories of habitat complexity according to their size, number and architecture of leaves and roots: complex (numerous large leaves and dense cluster of roots), intermediate (small leaves and single roots) and simple (small simple leaf and root). The macroinvertebrate specimens collected were assigned to different Functional Feeding Groups (MFFGs) and habits, following Merritt and Cummins (1984) and the mentioned literature on local fauna. The percentages of individual abundances of each MFFG and habit were recorded. Taxa that feed on more than one food type were categorized by their predominant food source. The macroinvertebrates abundance were expressed as

number of individual per liter; on each occasion the sampling volume was estimated considering the area of the net, the length of the sweep (1 m) and, if necessary, corrected by depth. For each sampling site, we calculated species richness (as the number of taxa observed), the Shannon Diversity Index (H) and evenness (based on the Shannon Index) (Zar 1999).

Spearman's rank non-parametric correlations (r_s) were performed between pairs of environmental variables, and between each environmental variable and taxa richness, the Shannon Index and individual abundance.

Determining total richness is often not practically possible, and even when it is, it may be a laborious and costly process; as there are undiscovered species in almost every taxonomic survey or species inventory, non-parametric techniques that estimate species richness are usually applied (Foggo et al. 2003). The non-parametric estimators of richness Chao1 and ACE (Abundance-based Coverage Estimator) were calculated for each habitat (α diversity). The EstimateS program version 8.2 (Colwell 2009) was used to calculate non-parametric estimators over 500 randomized iterations of the species accumulation. To evaluate β diversity or taxa turnover between sites (in space) and over the time within each habitat (in time), we used the Whittaker index (β_w) (Magurran 2004):

$$\beta_w = S/\alpha_{\text{mean}}$$

where S is the total number of species recorded (γ diversity) and α_{mean} is the average sample diversity. β_w ranges from 1 to 2, but values will be shown subtracting 1; thus, the results here presented range between 0 (minimum β diversity) and 1 (maximum β diversity), a more intuitively meaningful scale (Magurran 2004).

To determine the relative importance of environmental variables on species distribution, a Canonical Correspondence Analysis (CCA) was performed using the CANOCO program, version 4 (ter Braak and Smilauer 1998). The analysis included the abundance of macroinvertebrate taxa, the percentages of cover of each macrophyte species and the physical and chemical water variables. Forward analysis of the variables was used, considering the explained percentage of the variance and its significance. The Monte Carlo test was used for the statistical validation of the association between the ordination values of species, samples and environmental variables. A total of 199 iterations were performed for this test and considered to be significant at $p \leq 0.05$.

Results

Temporal Changes in the Habitat

The marked water level fluctuations of this system during the study period reflected the temperature and rainfall changes (Fig. 2a and b); the progressive drop of the water

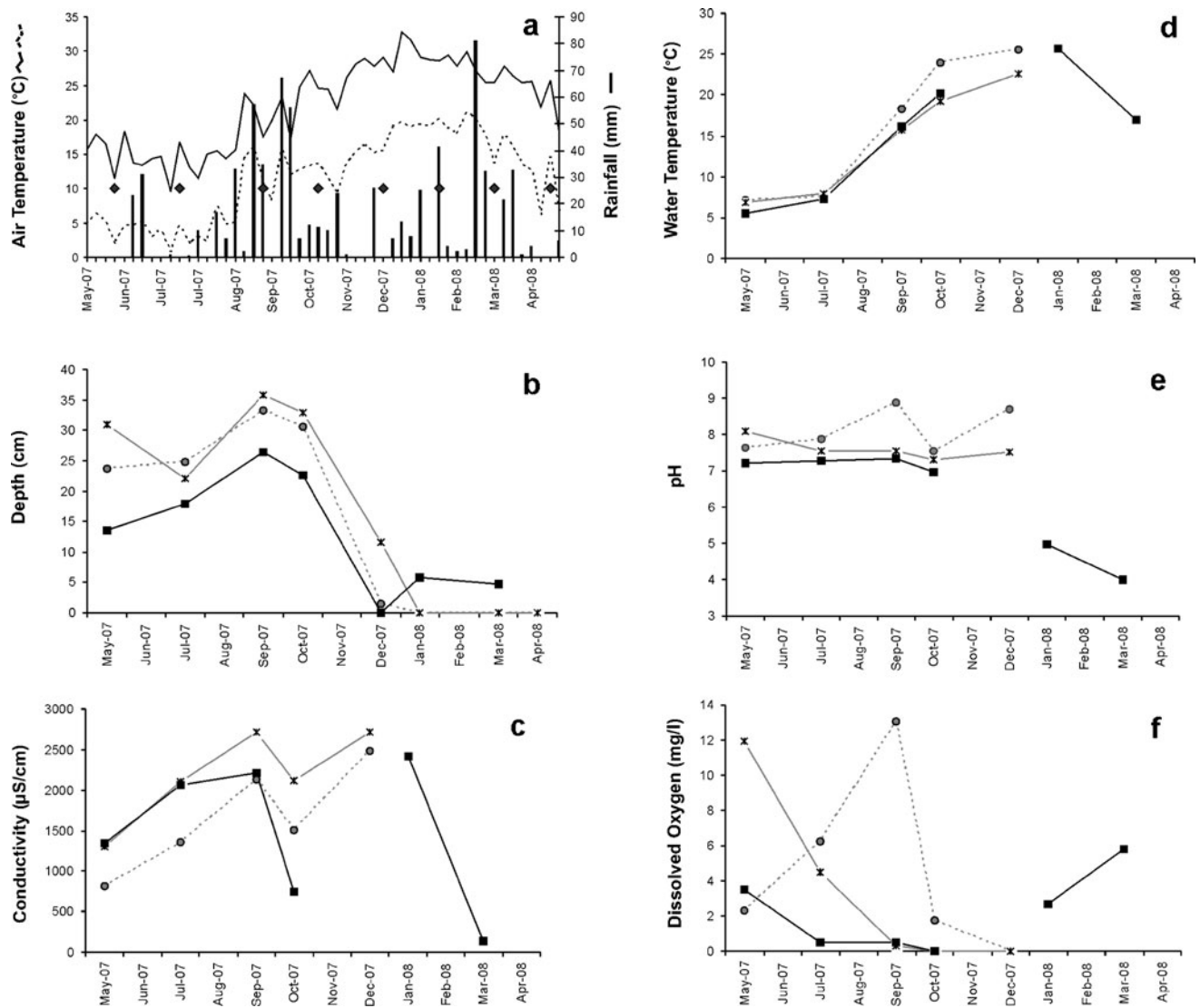


Fig. 2 Dynamics of the physico-chemical parameters evaluated during the study period. **a** Maximum and minimum weekly mean air temperatures (°C), weekly mean rainfall (mm), and ♦ sampling date; **b** Water

depth (cm); **c** conductivity (µS/cm); **d** water temperature (°C); **e** pH; **f** dissolved oxygen (mg/l). ○ LG (Laguna Grande); ■ ROL1 (Oxbow lake 1); ✕ ROL2 (Oxbow lake 2)

level up to the onset of the drought period by late spring was parallel to an increase in conductivity (Fig. 2c). Water temperature increased from 5.5 to 25.7 °C (Fig. 2d) in accordance to the season. The highest pH values were recorded in LG (mean 8.1) and the lowest in ROL1 (mean 6.3) (Fig. 2e). The maximum depth values and conductivities were usually found in ROL2, whereas the lowest O₂ concentrations were usually found in ROL1 (Fig. 2b, c, and f).

The FFP observed throughout the study period presented very different size and architecture according to their leaves and roots development (Table 1). Thus, among the species recorded, *Pistia stratiotes* had the most complex plant architecture whereas *Ricciocarpus natans* and *Lemna* spp. the simplest one.

Species composition and percentage of cover of the FFP varied from May (late autumn) to December (spring) in each of the habitats studied (Fig. 3). During late autumn and





winter, the littoral zone of LG was characterized by the dominance of the medium-sized *P. stratiotes*, which was replaced by species of smaller size during warmer months (Fig. 3). ROL2 was covered mainly by *Lemna* spp. and *R. natans*, while ROL1 was permanently covered by *A. filiculoides* until it dried out in December. This site was then partially colonized by herbs and shrubs, and when later flooded in January, no FFP were observed.

FFP cover and FFP-DW were negatively and significantly correlated with dissolved oxygen ($r_s: -0.59, p < 0.01$ and $r_s: -0.37, p: 0.04$ respectively).

Temporal Changes in Macroinvertebrate-FFP Relationships

The macroinvertebrate assemblages were represented by 68 taxa belonging to 10 families of Diptera, seven of Coleoptera,

Table 1 Description of the macrophyte species recorded during the study period, size class and complexity classification according to plant architecture

Macrophyte	Leaves / thallus	Roots	Size class ^a	Complexity (macrophyte architecture)	
<i>Pistia stratiotes</i>	fleshy leaves forming a rosette of 20–165 mm in diameter (mean 82 mm)	dense clusters of principal adventitious roots covered with fine lateral roots of 30–237 mm in length (mean length 122 mm)	medium	complex	 100 mm
<i>Azolla filiculoides</i>	a polygonal shape of 15 mm in diameter	simple roots (mean length 50–60 mm)	small	intermediate	 50 mm
<i>Ricciocarpus natans</i>	small thallus of less than 10 mm in diameter	scales and very short fine root-like structure (rhizoids) (length 1–2 mm)	small	simple	 6 mm
<i>Lemna</i> spp.	very small thallus which is leaf-like (mean diameter 2 mm)	a single root (mean length 6 mm)	small	simple	 3 mm

a- sensu Cabrera and Fabris 1948

seven of Heteroptera, three of Odonata, one Hyalellidae, one Palaemonidae and five Gastropoda (Table 2). A total of 32,141 individuals, 80 % of which corresponded to *Hyalella curvispina*, were collected. Nevertheless, this species clearly dominated only in ROL2, representing 91 % of the macroinvertebrates collected over the study period. In LG, dipterans were more abundant (66 %), followed by coleopterans (14 %) and *H. curvispina* (16 %), while in ROL1, Coleoptera and *Hyalella* were the best represented (37 and 39 % respectively) and only 18 % corresponded to dipterans. In all the habitats surveyed, other macroinvertebrate groups represented less than 4 % of the individuals collected. The highest macroinvertebrate richness was recorded in the littoral zone of LG, which differed significantly from that of ROL2 (Fig. 4a). The highest number of macroinvertebrate taxa and diversity were recorded during late autumn and winter (Fig. 4), when the littoral zone of LG was covered mainly by FFP of medium size (*P. stratiotes*) (Fig. 3). By late winter, the macrophyte composition changed to smaller sized species, its cover diminished to 33 %, and the lowest richness of macroinvertebrate taxa was detected. In spring, when small macrophytes still persisted but the FFP cover increased, the macroinvertebrate richness also increased, but did not achieve the autumn-winter levels (Fig. 4). The lowest richness was recorded in ROL2, with a FFP cover lower than 20 % and composed of

small-sized plants. The lowest diversity value was also observed in this habitat in response to the dominance of *H. curvispina*, and with no apparent relationship with the FFP covers (Figs. 3 and 4). ROL1 showed similar richness and diversity over time, under a stable and dense *A. filiculoides* mat (Figs. 3 and 4).

The percentage of cover of FFP was positively and significantly correlated with richness and abundance ($r_s:0.52$, $p<0.01$ and $r_s:0.55$, $p<0.01$ respectively) but not to the Shannon Index ($r_s:-0.08$; $p:0.64$); FFP-DW was positively and significantly correlated with taxa richness and the Shannon Index ($r_s:0.76$, $p<0.01$ and $r_s:0.60$, $p<0.01$ respectively) but not with individual abundance ($r_s:0.29$, $p:0.07$).

Differences in the percentage of macroinvertebrate functional feeding groups (MFFGs) were observed between the habitats studied. In LG, the dominance of predators and collector-gatherers alternated, accompanied by lower abundances of scrapers and shredders. In ROL1 and ROL2, collector-gatherers were the dominant group, followed by predators, whereas in ROL1, the shredders were better represented only in October (Fig. 5a). The highest diversity of habits was recorded in LG and ROL1 (Fig. 5b). Nevertheless, a more even distribution of habits was detected in LG, principally under the *P. stratiotes* mats.

Fig. 3 Temporal variation of composition, percentage of cover and dried weight of FFP (FFP-DW g/m^2) on the habitats studied. LG: Laguna Grande; ROL1: Oxbow lake 1; ROL2: Oxbow lake 2

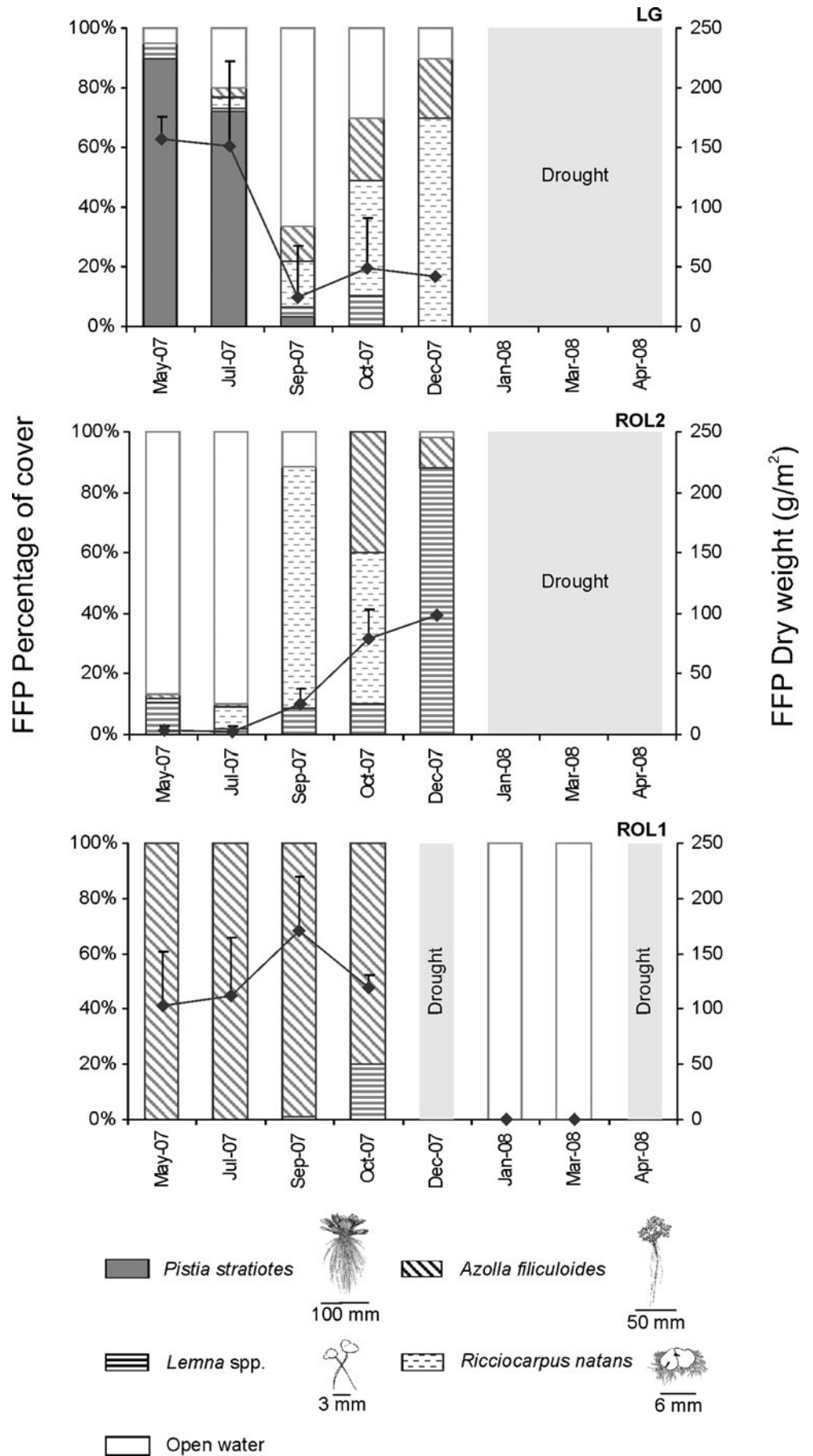


Table 2 Macroinvertebrate taxa collected from the different habitats

Taxa	LG	ROL 1	ROL 2	Habit	MFFG
Diptera					
Ceratopogonidae (l,p)	+	+	+	BU	PR
Chironomidae (l,p)	+	+	+	BU	CG
Tanypodinae (l)	+	+	+	SP-SW	PR
Chironominae (l)	+	+	+	BU-CL	CG
Orthocladinae (l)	+			BU	CG
Culicidae					
<i>Ochlerotatus albifasciatus</i> (l,p)		+		SW	CG
<i>Culex (Cx.) eduardoi</i> (l)			+	SW	CF
<i>Mansonia indubitans</i> (l)	+			CN	CG
Ephydriidae (l,p)	+		+	SP-BU	CG
Muscidae					
morpho 1 (l,p)	+	+	+	SP	PR
morpho 2 (l,p)		+	+	SP	PR
morpho 3 (p)		+		SP	PR
Psychodidae					
Pshychodinae (l)	+	+		BU	CG
Stratiomyidea					
<i>Hedriodiscus</i> sp. (l)	+	+	+	CL	SC
Syrphidae (l,p)	+			BU	CG
Tipulidae					
<i>Limonia</i> sp. (l,p)	+	+	+	SP-BU	SH
Tabanidae					
<i>Chrysops</i> sp. (l)	+	+		SP-BU	CG
<i>Hybomitra</i> sp. (l)	+	+		SP-BU	PR
Coleoptera					
Hydrophilidae					
<i>Helochaers</i> sp. (l)	+	+	+	CL	PR
<i>Berosus</i> sp. (l)					
<i>Berosus bruchianus</i> (a)	+			SW-DI	CG
<i>Berosus (Auriceps) ethmonotus</i> (a)		+		SW-DI	CG
<i>Derallus</i> sp. (l,a)	+			SW-DI	CG
<i>Derallus paranensis</i> (a)	+	+	+	SW-DI	CG
<i>Derallus argentinensis</i> (a)		+		SW-DI	CG
<i>Enochrus</i> sp. (l)	+	+	+	CL	PR
<i>Enochrus (Hugoscottia) variegatus</i> (a)	+	+	+	SP-BU	CG
<i>Enochrus (Methydus) vulgaris</i> (a)	+	+	+	SP-BU	CG
<i>Enochrus (Methydus) circumcinctus</i> (a)	+	+	+	SP-BU	CG
<i>Helochaers (Sindolus) femoratus</i> (a)	+	+	+	SW-DI	CG
<i>Helochaers (Sindolus) talarum</i> (a)			+	SW-DI	CG
<i>Paracymus</i> sp. (a)	+	+	+	BU	CG
<i>Tropisternus</i> sp. (l)	+	+	+	CL	PR
<i>Tropisternus (T.) dilatatus</i> (a)	+	+		SW-DI	CG
<i>Tropisternus (T.) ignoratus</i> (a)	+	+	+	SW-DI	CG
<i>Tropisternus (T.) laevis</i> (a)				SW-DI	CG
<i>Tropisternus (T.) setiger</i> (a)			+	SW-DI	CG
<i>Tropisternus (T.) ovalis</i> (a)	+	+		SW-DI	CG
Hydrochidae					
<i>Hydrocus orchymonti</i> (a)		+		CL	SH

Table 2 (continued)

Taxa	LG	ROL 1	ROL 2	Habit	MFFG
Dytiscidae					
<i>Liodessus</i> sp. (l,a)	+	+	+	SW-CL	PR
<i>Hemibidesus bifasciatus</i> (a)		+		SW-CL	PR
<i>Hydaticus</i> sp. (l)		+		SW-DI	PR
<i>Desmopachria</i> sp. (a)	+	+	+	SW-CL	PR
<i>Megadytes</i> sp. (l)	+			CL	PR
<i>Laccophilus</i> sp. (a)	+			SW-DI	PR
Noteridae					
<i>Hydrocanthus</i> sp. (l,a)	+	+	+	CL	PR
<i>Suphis cimicoides</i> (a)	+			CL	PR
<i>Suphis notaticollis</i> (a)			+	CL	PR
<i>Suphisellus</i> sp. (a)	+	+	+	CL	PR
Lampyridae (l)					
	+	+		BU	PR
Curculionidae (a)					
	+	+	+	SP-CN	SH
Chrysomelidae (l,a)					
	+	+	+	CN(l)-SP(a)	SH
Heteroptera					
Belostomatidae					
<i>Belostoma elegans</i> (l,a)	+	+		SW-CL	PR
<i>Belostoma plebeyum</i> (a)	+			SW-CL	PR
<i>Belostoma elongatum</i> (a)	+			SW-CL	PR
Corixidae					
<i>Sigara (T.) chrostowskii</i> (l,a)	+			SW-CL	CG
<i>Sigara (T.) denseconscripta</i> (l,a)	+			SW-CL	CG
<i>Sigara (T.) platensis</i> (l,a)	+			SW-CL	CG
Hebridae					
<i>Lipogomphus lacuniferus</i> (l,a)	+	+	+	CL	PR
Lygaeidae					
<i>Lipostemmata humeralis</i> (l,a)		+	+	CL	PR
Naucoridae					
<i>Ctenipocoris</i> sp. (a)	+			CN-SW	PR
Notonectidae					
<i>Buena fuscipennis</i> (l,a)	+		+	SW	PR
Pleidae					
<i>Neoplea maculosa</i> (l,a)	+	+	+	SW-CL	PR
<i>Neoplea argentina</i> (a)			+	SW-CL	PR
Odonata					
Aeshnidae					
<i>Aeshna</i> sp. (l)	+	+		CL	PR
Libellulidae					
<i>Sympetrum</i> sp. (l)	+	+		SP-CL	PR
Coenagrionidae (l)	+	+	+	CL	PR
Orthoptera					
Gryllidae					
<i>Phylloscyrtus</i> sp. (a)	+	+		SP	SH
Eumalacostraca					
Hyalellidae					
<i>Hyaella curvispina</i> (j,a)	+	+	+	SW	CG
Palaemonidae					
<i>Palaemonetes argentinus</i> (j,a)	+	+		SW	PR

Table 2 (continued)

Taxa	LG	ROL 1	ROL 2	Habit	MFFG
Gastropoda	+	+	+		
morpho 1	+	+		SP	SC
morpho 2 (<i>Gundlachia</i> sp.)	+	+		SP	SC
morpho 3 (<i>Drepanotrema bermatoides</i>)	+	+	+	SP	SC
morpho 4	+	+		SP	SC
morpho 5	+	+		SP	SC

LG Laguna grande; ROL1 oxbow lake 1; ROL2 oxbow lake 2. (l): larva, (p): pupa, (a): adults and (j): juvenile. **Habits** assigned to the taxa collected: BU burrowers, SP sprawlers, SW swimmers, CL climbers, CN clingers and DI divers; and **MFFGs**: Macroinvertebrate Functional Feeding Groups assigned to the taxa collected: CF collector-filterers, CG collector-gatherers, PR predators, SC scrapers and SH shredders

Burrowers, mainly represented by chironomids, prevailed in December due to the low depth recorded (<2 cm). Great abundance of free-swimmers (mainly *H. curvispina*) and swimmer-divers was found in all the habitats over time.

β Diversity in Time and Space

Analysis of the Whittaker index over time revealed different patterns for each habitat. β diversity in LG increased (Fig. 6a), and the lowest species turnover was detected between samples corresponding to a stable mat of *P. stratiotes*, reflecting a lower species replacement (Fig. 3). In ROL2, an important turnover of species was detected between July and September (Fig. 6a), in coincidence with a marked increase in FFP richness and cover (Figs. 3 and 4). Conversely, β diversity in ROL1 decreased slightly until the habitat dried out in December (Fig. 6a).

β diversity values among sites indicated higher species turnover between ROL2 and the other two water bodies (Fig. 6b), thus revealing high dissimilarity of their macroinvertebrate assemblage composition. In other words, LG and ROL1 were more similar, although they are spatially more distant. The Whittaker index exceptionally evidenced the lowest β diversity between LG and ROL2 (similarity increase) in September, when FFP cover and richness were lowest in LG.

Relationship Between Macroinvertebrates and the Environment

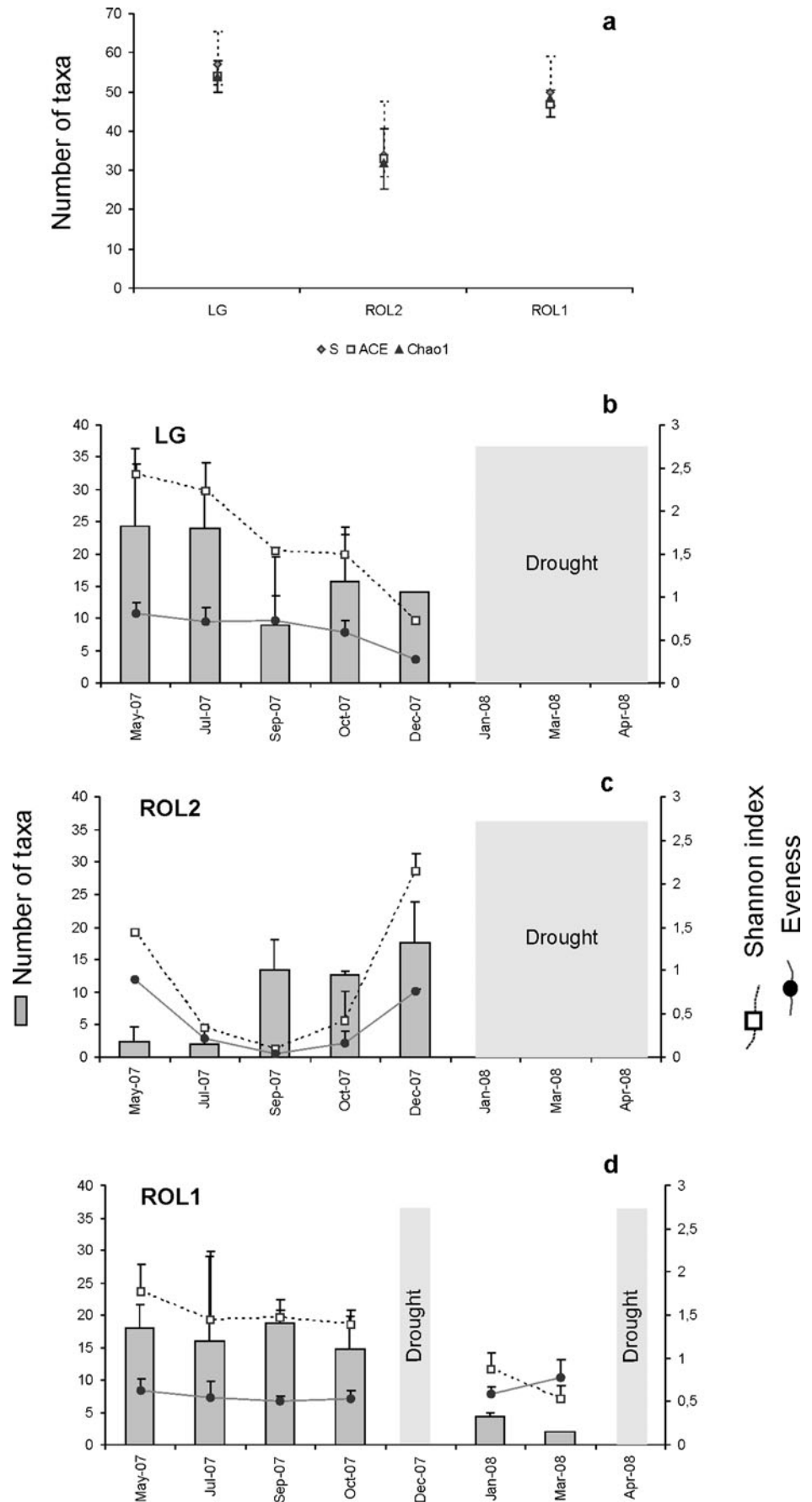
The CCA performed with macroinvertebrate species relative abundance and the environmental variables showed a high species-environment correlation ($r=0.99$); the first and second axis explained 65 % of variance in this relationship ($p=0.002$). The eigenvalues for the first and second canonical axes were 0.93 and 0.49, respectively; the Monte Carlo permutation test for the first axis was significant ($p=0.05$). The first axis represented the hydrological and seasonal changes in this wetland; this axis was positively associated

with water temperature (correlation coefficient =0.73) and negatively associated with depth ($cc=-0.94$) (Fig. 7). The second axis represented the variation in the species composition of FFP; *Ricciocarpus natans* ($cc=-0.85$) was negatively associated with this axis. The ordination revealed a remarkable similarity between LG and ROL1, characterized principally by higher abundance of coleopterans and dipterans (Fig. 7), with the exception of the LG December sample, which was separated by high water temperature and low depth. On this occasion this site was characterized by its great abundance of chironomid larvae and gastropods morpho 4. Samples from ROL2 were highly influenced by the dynamics of *R. natans*: when its cover was highest (October–September), the macroinvertebrate assemblages were dominated by *H. curvispina*, whereas when this species was absent or scarce (December), small coleopterans like *E. vulgaris*, *Liodes* spp. and *Paracymus* sp. dominated. May and July samples were separated due to the poor macroinvertebrate contribution associated with very low FFP cover.

Discussion

Free-floating plants are key macrophytes in this floodplain wetland as they occur in all water bodies and their cover becomes periodically dominant. Their effects on water quality and phytoplankton and zooplankton ecology have been thoroughly studied and the main findings are related to the FFP cover extension and dynamics (O'Farrell et al. 2009; Fontanarrosa et al. 2010; O'Farrell et al. 2011). In this study, we observed temporal changes in the extension of FFP cover and the fluctuations in its species composition that affected the structure of the associated macroinvertebrate assemblages. Such variation in FFP species composition may modify the habitat structure, as the species involved have distinct differences in size and root complexity. It has been suggested that the high habitat complexity provided by aquatic plants with different architectures may support

Fig. 4 **a** Overall taxa richness (S) and non-parametric estimators of richness Chao1 and ACE (Abundance-based Coverage Estimator) on each habitat studied; the standard deviation is indicated by *dashed and full error bars* for Chao1 and ACE, respectively. LG: Laguna Grande; ROL1: Oxbow lake 1; ROL2: Oxbow lake 2. **b, c, d** Temporal variation of mean number of taxa, Shannon diversity index and evenness; bars indicate standard deviations



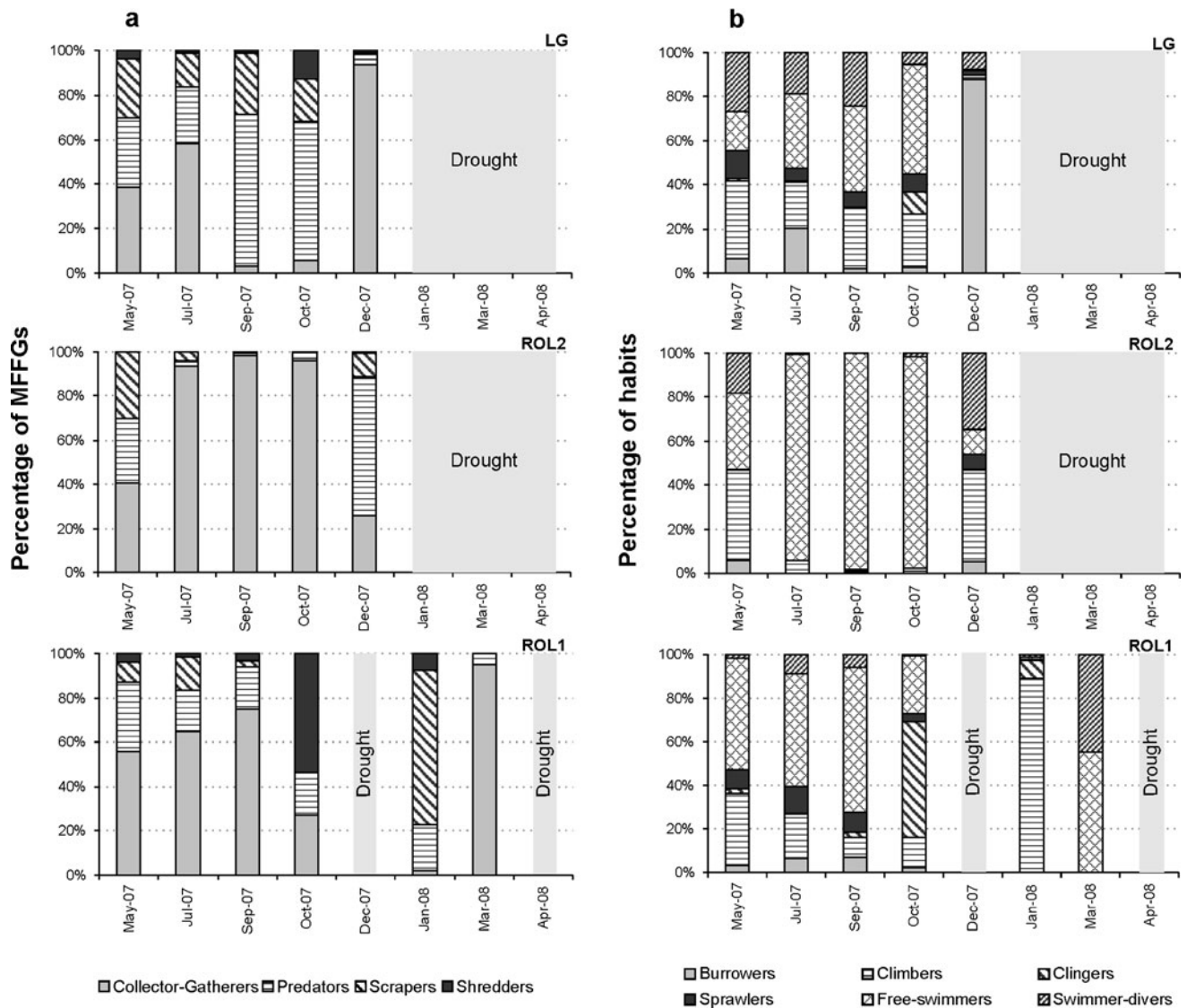


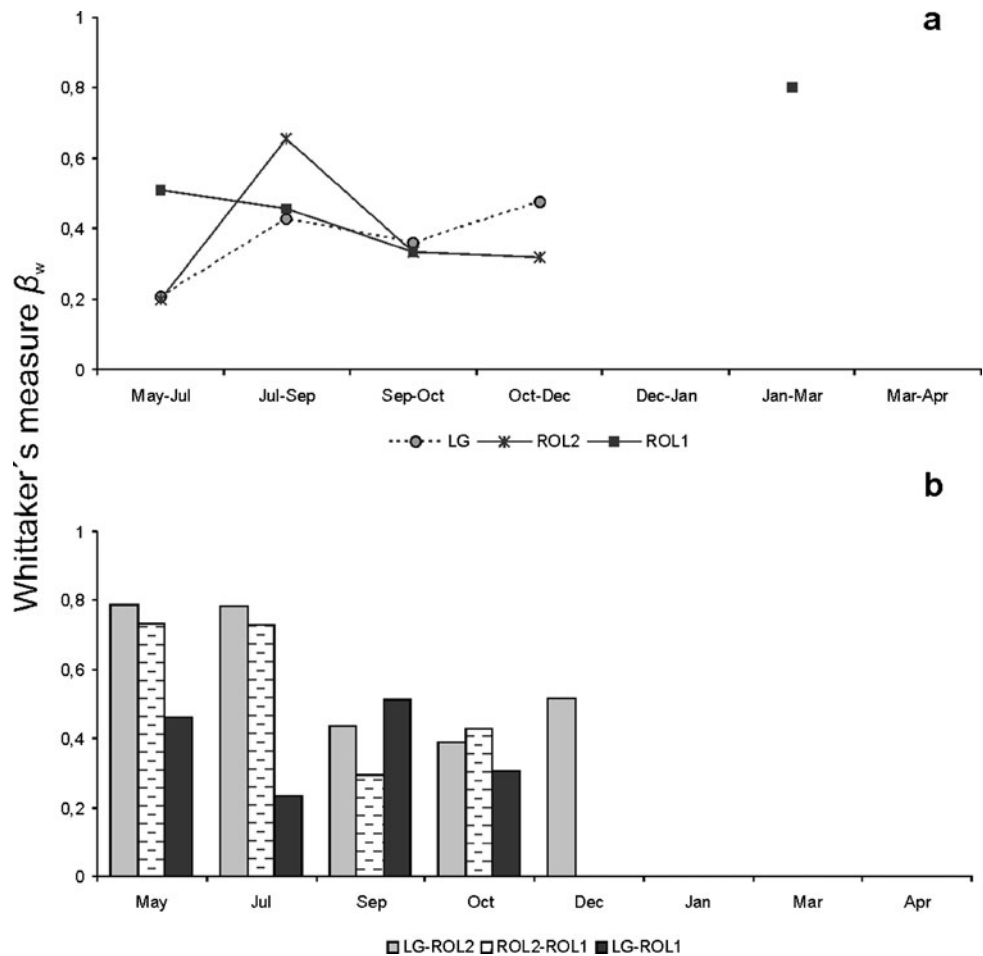
Fig. 5 Temporal variation in the percentage of macroinvertebrate functional feeding groups (MFFPs) and habits on each habitat studied. LG: Laguna Grande; ROL1: Oxbow lake 1; ROL2: Oxbow lake 2

greater invertebrate richness and density (Thomaz et al. 2008; Warfe et al. 2008). This pattern has been attributed to different factors, including refuge availability related to the shape of the plant, development of periphyton depending on light penetration, and retention capacity of particulate matter by roots (Poi de Neiff and Neiff 2006). Particularly, the submerged parts of the floating vegetation form a complex intertwined root and rhizome system, making a special biotope that can harbor diverse aquatic organisms (Ohtaka et al. 2011).

In this wetland complex we recorded a decreasing pattern of macroinvertebrate richness from the lake (LG) to the adjacent oxbow lake (ROL2); this result was reinforced by the outcome of non-parametric estimators. Among the FFP found in the littoral zone of LG, *Pistia stratiotes* was

characterized by the highest biomass and the most complex structure of roots and leaves. In this habitat, the highest macroinvertebrate richness and diversity corresponded to the occurrence of dense mats of this macrophyte; values dropped when its cover diminished drastically, and coincidentally, a great species turnover was recorded (higher β diversity). A recovery of taxa richness was observed associated with re-establishment of a FFP mat of the small-sized *Ricciocarpus natans*. Conversely, the lowest richness was recorded in ROL2 when it was covered by FFP of small size like *R. natans* and *Lemna* spp. Thus, habitat complexity in terms of macrophyte architecture could be one of the most important factors influencing macroinvertebrate assemblages. Accordingly, FFP-DW was related to macrophyte species with higher complexity in this wetland complex

Fig. 6 **a** Temporal variation in Whittaker index (β_w) on each habitat studied. **b** Temporal variation in Whittaker index (β_w) between habitats. LG: Laguna Grande; ROL1: Oxbow lake 1; ROL2: Oxbow lake 2



(Fig. 3) and a positive correlation was observed between FFP-DW and both macroinvertebrate taxa richness and the Shannon diversity index. Nevertheless, it should be kept in mind that macrophytes-DW may not correctly represent the different complexities of associated macroinvertebrate assemblages because a simple thin macrophyte with only one leaf can weigh the same as shorter ones with many leaves (Attrill et al. 2000). Poi de Neiff and Neiff (2006) also reported a gradient of macroinvertebrate richness associated with FFP biomass: richness increased as macrophyte size increased. On the other hand, as shown in previous studies (Attrill et al. 2000; Schultz and Dibble 2012), FFP-DW was not significantly correlated with macroinvertebrate density, probably due to the great abundance of *H. curvispina* in ROL2, where FFP of smallest size thrived.

Likewise, changes in macrophyte species composition and the extension of FFP mats affected functional composition of macroinvertebrates. We observed increasing abundance of macroinvertebrates when FFP extended the area colonized and also registered different MFFGs and habits composition in the three habitats throughout the study period. Poi de Neiff and Neiff (2006) indicated that FFP with low biomass and small roots, such as *Lemna* spp. and *R.*

natans, have low capacity of particulate matter retention and support more predator and herbivorous species than collector-gatherers. Surprisingly, ROL2 colonized by FFP of small size had the highest proportion of collector-gatherers mainly by the abundance of *H. curvispina* (which was the main representative of this MFFG in all habitats). This apparently contradictory result in ROL2, as well as the overall high contribution of collector-gatherers in all three habitats, could be explained by the great connectivity between roots and sediments in these very shallow systems (depth <35 cm), which increases the availability of detritus to this MFFG, as asserted by Saigo et al. (2009). Moreover, roots and stems of macrophytes in shallow aquatic habitats allow greater interactions between bottom-dwellers and plankton, acting as corridors for invertebrates between the surface and bottom of the environment (Neiff 1990; Williams 2006). LG presented the most complex functional structure of macroinvertebrate assemblages, with the highest proportion of predators. In particular, the presence of macroinvertebrate predators of great size like *Belostoma* spp. and odonate larvae were mainly recorded in LG and ROL1, in coincidence with larger FFP species. In this sense, Meerhoff et al. (2007) asserted that the architecture of macrophytes is

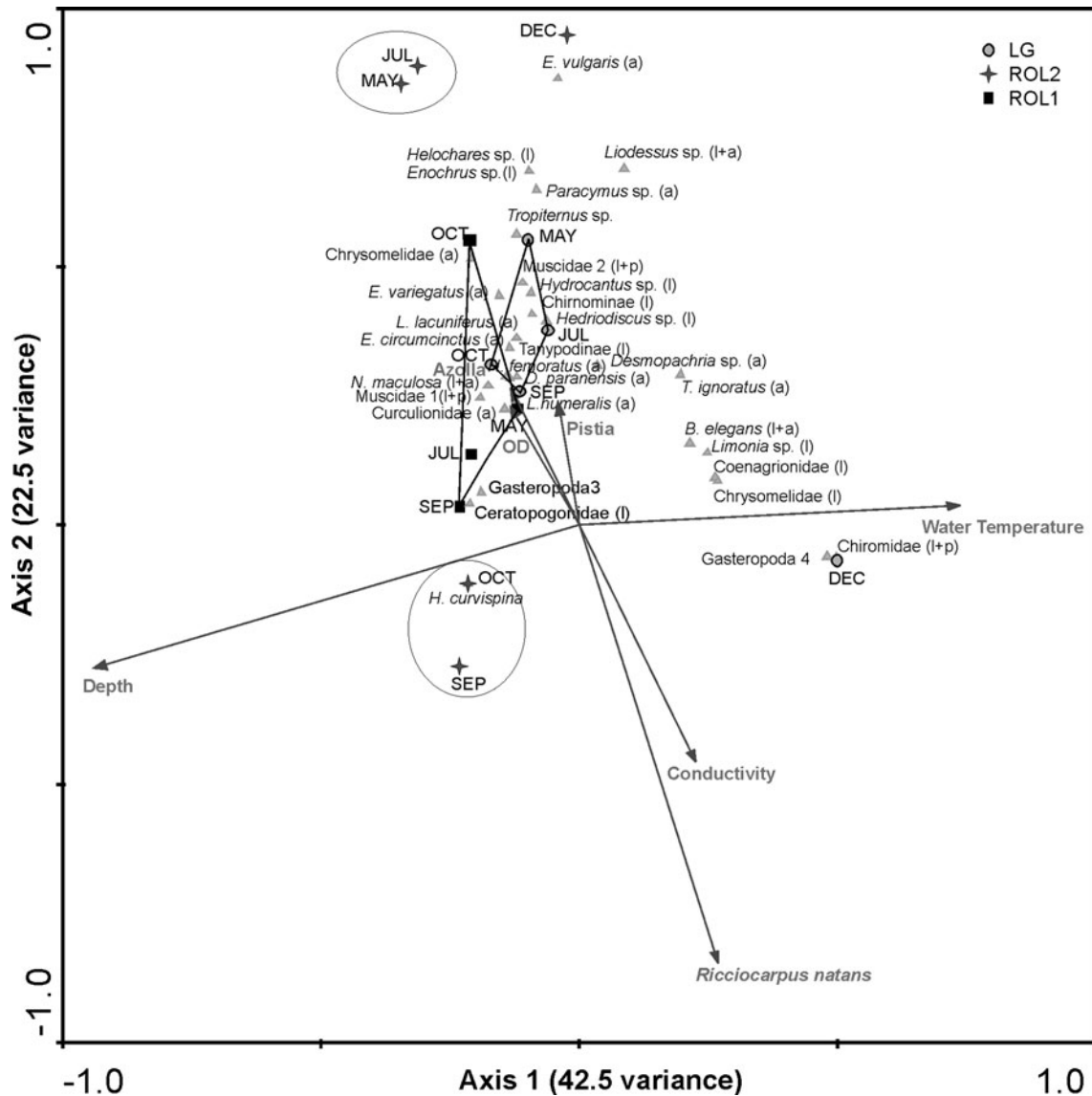


Fig. 7 CCA triplots of environmental variables, macroinvertebrate species and sample sites. *Arrows* indicate environmental variables; Δ macroinvertebrate species (l: larvae; p: pupa; a: adult); the sampling month is indicated next to the symbols of each habitat

highly relevant due to its impact on trophic dynamics, which they stated is principally mediated by the structure of the predator assemblages. Regarding the macroinvertebrate habit organization, LG presented different habits in more even proportions than both ROLs, particularly under *P. stratiotes* mats, which reflect the highest microhabitat availability. In ROL2, the clear dominance of free swimmers and swimmer-divers may be explained by the availability of space to swim between very short roots of small FFP. The presence of climbers in May and December was correlated with the presence of small coleopteran species (*Liodessus* and *Desmopachria*), which are agile swimmers and whose small size allows them to climb on these macrophytes. The occurrence of dense mats of *A. foliculoides* was also

associated with the establishment of macroinvertebrates with diverse habits; the structural complexity of this plant may be considered as intermediate between *Pistia* and *Lemna*. In brief, it is not surprising that LG and ROL1 showed a higher similarity than each of them individually compared with ROL2. In this wetland complex, the gradients in richness and diversity of macroinvertebrate assemblages were influenced by the size of FFP species, from medium to small-sized, which is closely related to the complexity of the structure of root and leaves.

As stated above, it is well accepted that substratum (FFP in our case) is a primary factor influencing the abundance and distribution of macroinvertebrates, but it is also true that it never has influence in isolation (Minshall 1984).

Hydrological changes are an important factor largely accepted to affect macroinvertebrate assemblages (Batzer et al. 2004; Bazzanti and Della Bella 2004; Cremona et al. 2008). The floodplain habitats studied here recorded an unusually dry period during our survey; a strong drought affected the system in correspondence to El Niño Southern Oscillation meteorological phenomenon (O'Farrell et al. 2011). The CCA revealed that both hydrological fluctuations and changes in the taxonomic composition and relative abundances of macrophyte species affected the structure of macroinvertebrate assemblages. Moreover, hydrological dynamics were associated with changes in depth, water temperature, dissolved oxygen and conductivity among other limnological variables, which were significantly related to the ordination of macroinvertebrate taxa. Minshall (1984) indicated, several important factors that alter the response of invertebrates to substratum: flow regime, water temperature, and chemical composition of the water operate on a broad scale, whereas light, food, oxygen content and interactions with other organisms are imposed primarily at local or microhabitat levels. Moreover, marked water level fluctuations are becoming increasingly important, as climate change models predict increased droughts or flooding cycles for many regions of the world (Jentsch et al. 2007; Williamson et al. 2009; IPCC 2010). In this sense, it is relevant to understand how FFP and hydroperiod affect the aquatic invertebrate community structure as well other groups inhabiting wetlands.

This research contributes information on the role of medium and small-sized FFP on the dynamics of macroinvertebrates of shallow lakes. This knowledge may be useful for the assessment of the effect of climate warming, as areas dominated by these macrophytes are likely to expand to temperate climates (Meerhoff et al. 2007), and because trends in average temperature have shown to induce profound impacts on aquatic invertebrates (Burgmer et al. 2007). At regional scale, the diversity and dynamics of invertebrates in marginal wetlands of the Paraná River system are poorly known (Ezcurra de Drago et al. 2007). To our knowledge, the present study is the first contribution about macroinvertebrates associated with FFP in the lower Paraná River floodplain. Further studies on habitat complexity and influence of top predators (fish and birds) are necessary for a better understanding of the macroinvertebrate dynamics and trophic structure in vegetated wetlands.

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