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Does the effect of aquatic plant types on invertebrate assemblages change across seasons in a subtropical wetland?

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ABSTRACT

Does the effect of aquatic plant types on invertebrate assemblages change across seasons in a subtropical wetland?

Habitat complexity is one of the fundamental factors determining the distribution of invertebrate assemblages due to the different architectures and growth forms of aquatic plants, which affect their density, species richness, biomass, and trophic structure. In this paper, we compared the density and richness of macroinvertebrates present in two species of aquatic plants with different architectures (*Salvinia biloba* and *Egeria najas*) across seasons. Samples of aquatic plants and associated invertebrates were collected seasonally in a wetland located in Corrientes (Argentina) with a net area of 962 cm^2. To characterize the different habitat types, we selected 12 traits of aquatic plants, including fractal complexity. A total of 15 225 invertebrates from 13 major groups were recorded from both habitat types (41 families and 24 genera in *S. biloba* and 24 families and 22 genera in *E. najas*). Significant differences in the total density (number of invertebrates per 1000 g plant dry weight) and taxa richness at family level were found between habitat types. Non-metric multidimensional scaling reflected differences in the seasonal patterns of 16 macroinvertebrate genera selected between both habitat types. A Similarity Analysis showed statistically significant differences between the habitat types and seasons. Structurally more complex habitat (*S. biloba*) supported a greater number of taxa and the highest number of individuals per plant dry weight. The differences in the density and richness of the invertebrate assemblages between *S. biloba* and *E. najas* were maintained throughout the seasons. The habitat structuring of aquatic macrophytes is a key factor in macroinvertebrate assemblages, and it is important to keep in mind when comparing wetlands with different aquatic vegetation.

Key words: Habitat types, habitat complexity, aquatic plants, *Salvinia biloba*, *Egeria najas*, invertebrates, subtropical wetland, temporal variation.

RESUMEN

¿El efecto de los tipos de plantas acuáticas sobre los ensambles de invertebrados cambia en las distintas estaciones en un humedal subtropical?

*La complejidad del hábitat es uno de los factores fundamentales que determinan la distribución de los ensambles de invertebrados debido a que las diferentes arquitecturas y formas de crecimiento de las plantas acuáticas afectan su abundancia, riqueza de especies, biomasa y estructura trófica. En este trabajo comparamos la abundancia y riqueza de los macroinvertebrados presentes en dos especies de plantas acuáticas con diferente arquitectura (*Salvinia biloba* y *Egeria najas*) en distintas estaciones del año. Las muestras de plantas acuáticas y los invertebrados vinculados fueron recolectadas estacionalmente en un humedal localizado en la provincia de Corrientes (Argentina) con una red de 962 cm^2 de área. Para caracterizar los diferentes tipos de hábitats, se seleccionaron 12 rasgos de las plantas acuáticas, incluyendo la dimensión fractal. Un total de 15 225 invertebrados de 13 grupos mayores fueron registrados en ambos tipos de hábitats (41 familias y 24 géneros en* S. biloba *y 24 familias y 22 géneros en* E. najas*). Se hallaron diferencias estadísticamente significativas en la abundancia total (número de invertebrados por 1000 g de peso seco de vegetación) y la riqueza de taxones a nivel de*

*familias entre tipos de hábitats. El análisis de Escalamiento Multidimensional No Métrico (NMDS) mostró diferencias en los patrones estacionales de 16 géneros de macroinvertebrados seleccionados entre ambos tipos de hábitat. El análisis de Similaridad mostró diferencias estadísticamente significativas entre tipos de hábitat y estaciones. El hábitat que presentó mayor complejidad estructural (*S. biloba*) albergó mayor número de taxones y de individuos por peso seco de vegetación. Las diferencias en la abundancia y riqueza de las comunidades de invertebrados entre* S. biloba *y* E. najas *fueron mantenidas en las distintas estaciones. La estructuración del hábitat por parte de las macrófitas acuáticas es un factor clave para los ensambles de macroinvertebrados y necesita ser tenida en cuenta cuando se realizan comparaciones entre humedales con diferente vegetación acuática.*

Palabras clave: *Tipos de hábitat, complejidad del hábitat, plantas acuáticas,* Salvinia biloba, Egeria najas, *invertebrados, humedal subtropical, variación temporal.*

INTRODUCTION

Aquatic plants provide required conditions for feeding, breeding, spawning and rearing of animals as well as shelter against predators for invertebrates and small sized fish (Lachavanne & Juge, 1997; Esteves, 2011). The macrophyte growth forms influence dominant fish in subtropical shallow lakes and have a cascading effect on other communities such as plankton (Meerhoff *et al.*, 2003).

The composition and trophic structure of macroinvertebrates is often affected by plant community types that occur in a wetland (Batzer & Wissinger, 1996; Kratzer & Batzer, 2007; Fontanarrosa *et al.*, 2013). Habitat structuring is one of the fundamental factors determining the distribution of organisms at all spatial scales, and vegetation is of primary importance in shaping the structural environment for invertebrates in a variety of systems (McAbendroth *et al.*, 2005). The abundance of phytophilous invertebrates was found to be related to plant biomass, macrophyte bed characteristics, and sampling date during an intensive survey of submerged aquatic plants in temperate lakes (Cyr & Downing, 1988). The invertebrate species richness on free and rooted floating plants in floodplain wetlands connected to the Paraná River (Poi de Neiff & Neiff, 2006; Thomaz *et al.*, 2008; Fontanarrosa *et al.*, 2013) was affected by the specific composition of the macrophytes and was related to plant biomass (Poi de Neiff & Neiff, 2006), the percentage of plant cover, and the plant dry weight (Fontanarrosa *et al.*, 2013).

Under the same limnological conditions, growth forms and the macrophyte type had effects on macroinvertebrate abundance (Walker *et al.*, 2013) and biomass (Tessier *et al.*, 2004). The size, leaf area, morphology index, and rugosity of leaves are some of the morphological traits that indicate the complexity of the plant architecture (Vieira *et al.*, 2007; Warfe *et al.*, 2008; Monção *et al.*, 2012; Walker *et al.*, 2013). The fractal geometry theory emerged as a tool to measure habitat complexity and has been applied at large spatial scales in different environments (Dibble & Thomaz, 2009). The fractal index was related to invertebrate abundance (Ferreiro *et al.*, 2011), species richness (Thomaz *et al.*, 2008), biomass-body size scaling, and overall invertebrate biomass (McAbendroth *et al.*, 2005).

In subtropical wetlands fed by rain, the lack of strong temporal variation in macroinvertebrate assemblages is frequent (Kratzer & Batzer, 2007), but the seasonal pattern is highly variable in seasonally flooded wetlands (Miller *et al.*, 2008).

In this paper, we compared the abundance and richness of macroinvertebrates present in two species of aquatic plants with different morphology traits (*Salvinia biloba* and *Egeria najas*) inhabiting a subtropical lake across seasons. We tested the following hypotheses: *a*) free floating plants (*S. biloba*) provide a more complex habitat because of their submerged and aerial fronds, such as those of *E. najas*, which grows completely submerged, and *b*) the effect of habitat structuring on invertebrates (spatial pattern) is more important than the seasonal pattern because of the subtropical climate.

MATERIALS AND METHODS

Study Area

The study was carried out in a small (625 390 m^2), shallow (mean depth: 1.23 m) lake, located in Northeast Argentina (Sánches Lake, 28°10′07″ S; 58°38′37″ W). This chosen lake is representative of sub-rounded lakes fed by rain located in the great wetlands of Corrientes province (Poi & Galassi, 2013), which encompasses 35 660 km^2. The dominant plant species were *Salvinia biloba* Raddi, 1825 and *Egeria najas* Planch, 1849, which are indicative of two different habitat types characterized by their structural complexity. *Salvinia* spp. is an endemic genus of neotropical-river flood plains system that occurs in the disconnected lakes and is invasive in warm waters of different continents (Monção *et al*., 2012). *E. najas* is native to the Paraná system and typically occurs in high transparent ponds with remote influence on the Paraná river in Argentina (Neiff, 1986). This species forms large masses of vegetation and causes serious problems in reservoirs of tropical and sub-tropical regions (Bini *et al*., 1999).

Sampling Methods

Four samples of each aquatic plant (*S. biloba* and *E. najas*) and associated invertebrates were collected during spring (September 2010), summer (December 2010), autumn (April 2011), and winter (July 2011), using a net area of 962 cm^2 and a 500 µm mesh size (Poi de Neiff & Carignan, 1997). The plants and macroinvertebrates were removed from the net, transferred to plastic bags, and preserved with 95 % ethanol. On each date, we measured physical and chemical variables of the water such as temperature, dissolved oxygen, pH, salinity, conductivity, and transparency using specific measuring instruments.

In the laboratory, the aquatic plants were thoroughly washed to detach the invertebrates, and the suspensions obtained were filtered through 1 mm and 500 µm sieves. The invertebrates were sorted and re-preserved in 70 % ethanol, and the plants were dried to constant weight at 105 ºC

for 48 hours and weighed. The invertebrates were counted and identified to the lowest possible taxonomic level using keys from Angrisano, 1992; Lopretto & Tell, 1995; Trivinho-Strixino & Strixino, 1995; Thorp & Covich, 2001; Michat *et al*., 2008; Domínguez & Fernández, 2009; Ramírez, 2010; Libonatti *et al*., 2011. In tropical and subtropical aquatic habitats, the invertebrate diversity is poorly known and taxonomic identification becomes difficult (specifically to the species or genus level) because descriptions of some taxa are incomplete and specific taxonomic keys are scarce. Additionally, the dominance of immature forms (larvae, nymphs and pupae) of many insects with adult aerial life (Diptera, Odonata, Ephemeroptera, Lepidoptera and Trichoptera) makes identification more difficult. Therefore, the use of family or even morphospecies richness has been suggested by Jacobsen *et al*. (2008). The density of invertebrates was expressed as individuals per 1000 g plant dry weight, which allows for the comparison of both life forms. This reference unit is neither affected by the changes in the plant cover of free floating plants, nor by changes in *E. najas* volume. In *S. biloba*, the number of individuals per m^2 was also calculated.

To characterize the different habitat types, we selected 12 traits of aquatic plants according to the criteria proposed by Willby *et al*. (2000) and Monção *et al*. (2012). To calculate fractal dimensions of *S. biloba* and *E. najas*, four representative portions of each aquatic plant species were photographed with a Canon Rebel T3/EOS 1100D (12.2 megapixels, zoom lens EF-S 18-55 mm) digital camera, capturing an area of (100.47 × 150.71 cm^2). A minimum of four pictures of each portion was taken. The programme Adobe Photoshop CS5 Extended 12.0 was used to transferred selected TIFF images to greyscale and bits map to produce a black and white image and then modified to adjust background shades to improve resolution of plants features (Dibble & Thomaz, 2009). The fractal dimensions (D) of both area and perimeter were calculated using the box counting method (Sugihara & May, 1990) with the program ImageJ 1.49 v (Rasband, 2015). A series of grid sizes of 2, 4, 6, 8, 12, 16, 32, 64,

Table 1. Traits of aquatic plants that characterize the different habitat types. *Rasgos de las plantas acuáticas que caracterizan los diferentes tipos de hábitats*.

Traits	*Salvinia biloba*	*Egeria najas*
Size	≤ 15 cm	≤ 200 cm
Growth form	Free-floating, surface	Anchored, submerged and/or floating leaves
Frond/leaf features	Bilobed, opposite, with hairy emergencies on upper surface	Entire, curl down and serrated, typically in whorls of 5 at each node
Rhizome/stalk	Creeping and hairy rhizome	Stalk of 0.5 to 1.5 cm diameter
Frond/leaf area	Medium (1-20 cm^2)	Small (< 1 cm^2)
Maximum width of the leaf	2 ± 0.39 cm	0.25 ± 0.03 cm
Frond/leaf perimeter	10 ± 2.05 cm	3.88 ± 0.42 cm
Plant biomass	132.43 ± 26.48 g/m^2	290.14 ± 44.96 g/m^2
Submerged fronds length	4 ± 0.76 cm	—
Fractal Dimensions	1.84 ± 0.04 (area) 1.58 ± 0.05 (perimeter)	1.81 ± 0.02 (area) 1.44 ± 0.03 (perimeter)
Sexual/asexual reproduction	Spores/Rhizomes	Seeds/Stem fragments
Perennation	Perennial	Perennial

128 and 256 pixel widths (Thomaz *et al*., 2008) were used to estimate fractal dimensions.

Data Analysis

To compare the abundance and family richness of invertebrate assemblages found in *S. biloba* and *E. najas* across seasons, a Kruskal-Wallis test was carried out. To assess annual patterns in invertebrate assemblages, the density of 16 dominant genera/species were ordered using a Nonmetric Multidimensional Scaling (NMDS). The results were confirmed by a Similarity Analysis (ANOSIM), Clarke (1993), using the Bray Curtis distance. To examine the spatial and temporal β diversity, we used the Complementary Coefficient (Colwell & Coddington, 1994). The statistical analysis was performed using PAST 2.08
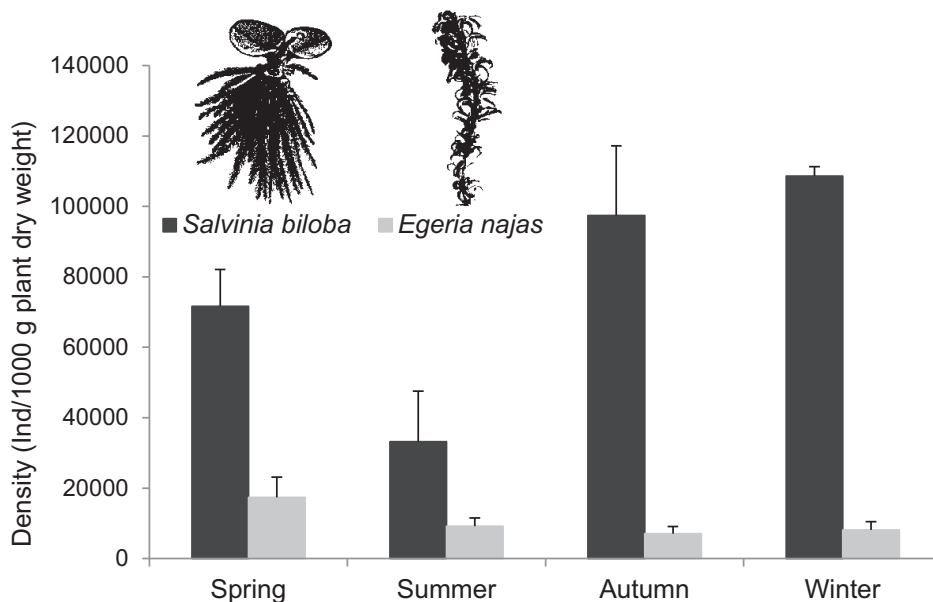

Figure 1. Macroinvertebrates mean density in both habitat types in different seasons. The bars show standard deviations. *Abundancia media de macroinvertebrados en ambos tipos de hábitat en diferentes estaciones. Las barras muestran los desvíos estándar.*

Table 2. Relative density (%) of macroinvertebrate families found in both habitat types in different seasons (Sp: spring, Su: summer, Au: autumn, Wi: winter). *Abundancia relativa (%) de las familias de macroinvertebrados halladas en ambos tipos de hábitat en diferentes estaciones (Sp: primavera, Su: verano, Au: otoño, Wi: invierno).*

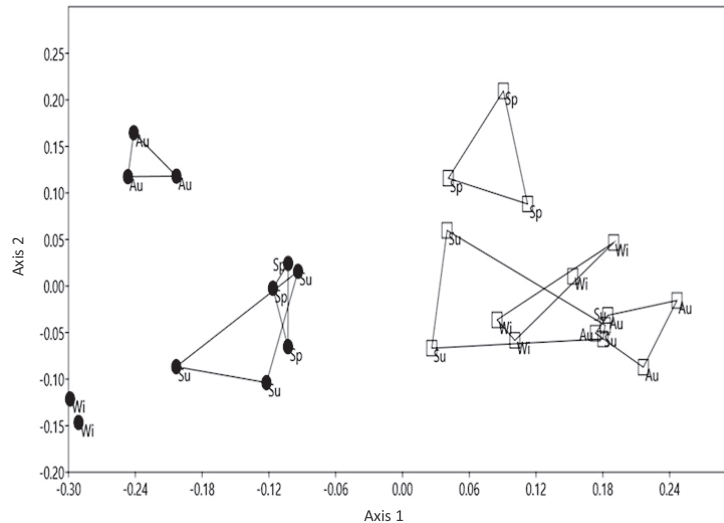| Taxa	Salvinia biloba Sp	Su	Au	Wi	Egeria najas Sp	Su	Au	Wi
INSECTA								
Lepidoptera			1.28					
Crambidae	0.15			0.04				
Nepticulidae				0.04				
Diptera								
Chironomidae	14.98	13.45	38.47	8.11	76.55	31.45	29.41	23.53
Ceratopogonidae	37.84	6.72	9.37	9.21	0.09	0.16	0.26	
Culicidae	0.78	1.38	2.93					
Tabanidae	0.30		0.05	0.51				
Stratiomyidae		0.53	1.64	0.51				
Ephydridae		1.01		0.17	0.95	0.61	2.16	0.34
Odonata								
Coenagrionidae	0.56	2.05	2.37	1.99	1.33	2.26	2.46	4.96
Libellulidae	0.61	0.55	0.44	1.00		0.75	0.12	0.34
Coleoptera								
Curculionidae	0.25	0.69	0.18		0.56	1.30	1.23	1.98
Hydrophilidae	1.82	12.54	8.01	10.57				
Dytiscidae	0.26	4.18	2.44	4.75		1.79		
Noteridae	0.70	1.64	1.74	2.57	0.32		0.19	
Hydrochidae				0.13				
Scirtidae		1.50	4.16	1.95				
Chrysomelidae				0.72				
Scarabeidae				0.04				
Staphylinidae	0.18	0.30	0.06	0.04				
Lampyridae		0.11	0.07	0.43				
Pselaphidae		0.58	0.03					
Heteroptera								
Lygaeidae		2.29		0.08				
Corixidae					0.57	1.72	0.22	
Naucoridae	0.13	0.38	0.45	0.55		0.45	1.06	
Pleidae	0.32	0.64	0.03	0.51	0.80	1.92	0.12	
Hebridae	1.18	5.68	3.95					
Belostomatidae	0.06	0.11	0.36	0.21				
Nepidae	0.02							
Aphididae				0.50				
Ephemeroptera								
Caenidae	1.39	0.50	0.03	0.55	0.38	0.42	0.93	0.19
Baetidae	0.04	0.07	0.09			0.44	0.82	0.13
Trichoptera							0.97	
Hydroptilidae	0.87							
Polycentropodidae				0.04				
Leptoceridae								0.44
Psychomyiidae		0.27	0.19					0.46
Orthoptera								
Acrididae			0.25					
ARACHNIDA								
Araneae				0.55				
HIDRACARINA	0.69	4.47	4.85	1.64	0.13	2.32	2.89	16.79
COLLEMBOLA				0.09				
OSTRACODA	1.97	3.10		0.76	2.79		2.30	0.76
AMPHIPODA								
Hyalellidae	6.20	14.52	0.26	34.68	3.21	11.99	0.59	10.23
DECAPODA								
Potamonidae				0.04				
Palaemonidae					6.10	0.87	4.58	6.78
CLADOCERA	1.55			1.76				
COPEPODA	4.89			7.18				
GASTROPODA								
Planorbiidae	0.79	1.40	1.72	0.59			0.12	
Ancylidae	0.42	0.66	0.03		1.81	12.93	29.63	25.92
Ampullaridae					0.15	1.41		
HIRUDINEA								
Glossiphonidae	0.26	0.43	0.67	1.22	0.81	0.21	0.49	0.10
OLIGOCHAETA								
Naididae	20.83	20.53	11.63	4.77	3.45	27.01	19.64	6.86
NEMATODA				1.44				
TOTAL ABUNDANCE	4040	1637	3243	2344	1227	526	937	797

Figure 2. Non-metric multidimensional scaling (NMDS) plot showing macroinvertebrate density between habitat types (*S. biloba* and *E. najas*) and between seasons. References: ● *S. biloba*, □ *E. najas*, Sp: spring, Su: summer, Au: autumn, Wi: Winter. *Gráfico de Escalamiento Multidimensional No Métrico (NMDS) mostrando la abundancia de los macroinvertebrados entre tipos de hábitat (*S. biloba *and* E. najas*) y entre estaciones. Referencias:* ● S. biloba, □ E. najas, *Sp: primavera, Su: verano, Au: otoño, Wi: invierno.*

(Hammer, 2001) and InfoStat (Di Rienzo *et al.*, 2013) software.

RESULTS

Study area

During the studied period, the water was transparent and its dissolved oxygen concentration was high (mean 8.02 ± 0.71 mg/L). The water temperatures were generally high (13.9 °C in winter and 31 °C in summer), pH values were around neutrality (between 6.5 and 7.4), and the electrical conductivity ranged between 57 and 73 μS/cm. The phosphorus and total nitrogen content varied between 95 and 105 μg/L and 25 and 38 μg/L, respectively.

Salvinia biloba comprised a narrow stripe in all of the littoral area in the study lake, while *E. najas* covered 35 % of the lake area. Both species coexisted under the same limnological conditions in monospecific stands. *S. biloba* had more complex plant architecture and habitat complexity (aerial and submerged fronds) than *E. najas* (Table 1). However, the values obtained from fractal dimension estimation of both area and perimeter,

were slightly higher. The number of plants per unit surface changed during the sampling period in the free floating mats of *S. biloba*, mainly due to wind action. The plant biomass per m^2 varied across seasons, and its mean value is shown in Table 1.

Abundance and taxa richness of invertebrate assemblages

A total of 15 225 invertebrates from 13 major groups were recorded from both habitat types (*S. biloba* and *E. najas*). We found 41 families and 24 genera in *S. biloba* and 24 families and 22 genera in *E. najas*. There were seasonal variations in the relative abundance and specific arrangement of invertebrate taxa in both habitats (Table 2). In addition, significant differences in taxa richness ($H = 5.33$; $p < 0.0286$) were found between habitat types. The most abundant families on *S. biloba* were Chironomidae, Ceratopogonidae, Hyalellidae and Naididae. The invertebrate density of *E. najas* was dominated by Chironomidae, Naididae and Ancylidae (Table 2).

When density was expressed as invertebrates/1000 g plant dry weight, the total number was significantly higher ($H = 18.33$; $p < 0.0001$)

in *S. biloba* than in *E. najas* (Fig. 1). The maximum density was found in *S. biloba* during winter (108 605 ind/1000 g plant dry weight), whereas *E. najas* reached 17 374 ind/1000 g plant dry weight in spring. When the density was expressed as invertebrates/m^2, the total mean number on *S. biloba* varied between 5672 (± 138.43) in summer and 13 998 (± 5747.57) in spring.

Non-metric multidimensional scaling (NMDS) reflected differences in the seasonal patterns of the 16 genera selected between both habitat types (*S. biloba* and *E. najas*). The first axis of NMDS analysis differentiates invertebrate density between the habitat types, whereas the second axis shows differences between seasons (Fig. 2). The NMDS assemblage ordination had an acceptably low final stress (12 %). The genera associated with *S. biloba* and *E. najas* are grouped on the left and right of the first axis, respectively. In *S. biloba*, the assemblage was similar in spring and summer and differed in autumn and winter, while in *E. najas*, the invertebrate assemblage found in spring was different than that found in other seasons. These results were confirmed by
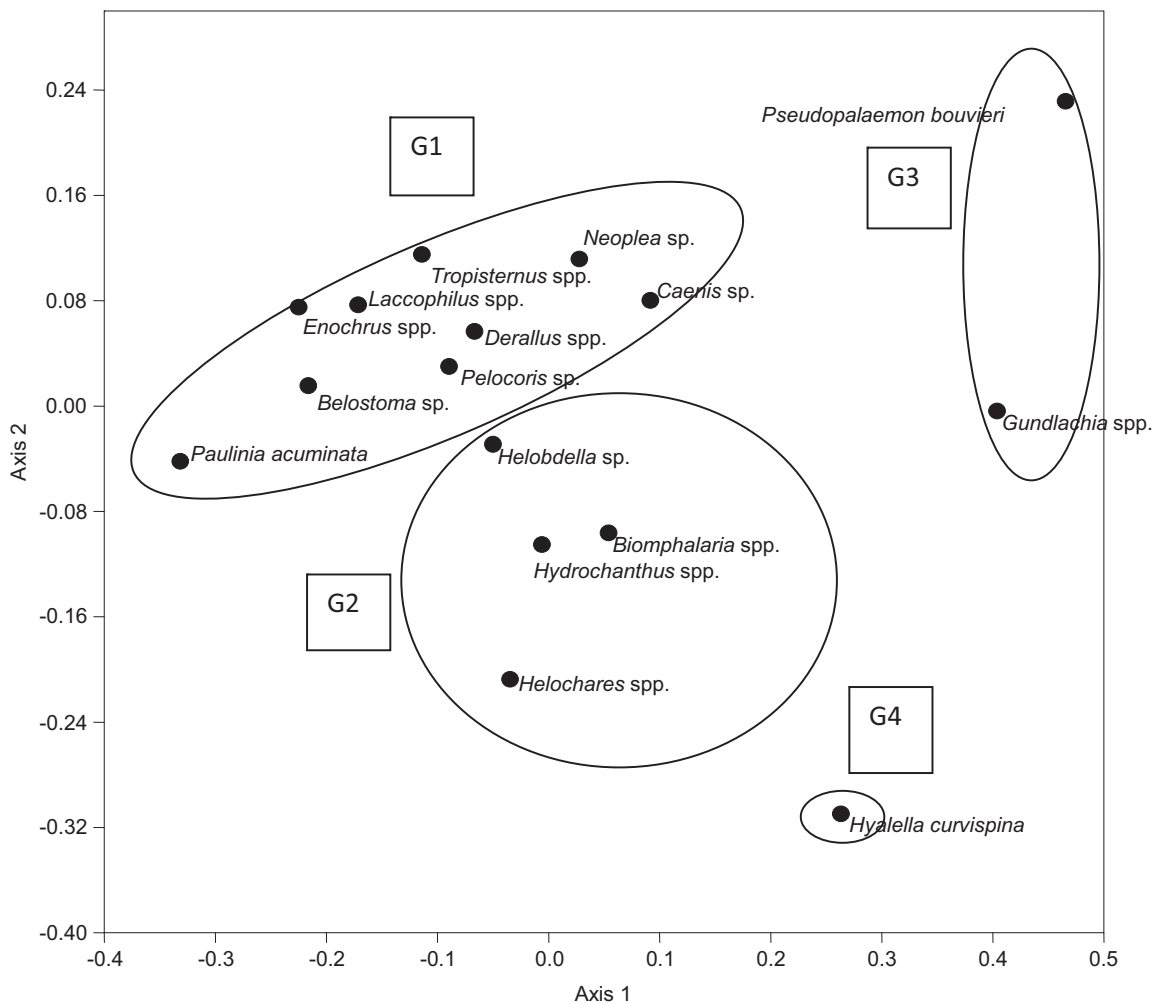

Figure 3. Non-metric multidimensional scaling (NMDS) plot showing macroinvertebrate genera grouping. G1: group 1, G2: group 2, G3: group 3, G4: group 4. *Gráfico de Escalamiento Multidimensional No Métrico (NMDS) mostrando el agrupamiento de los géneros de macroinvertebrados. G1: grupo 1, G2: grupo 2, G3: grupo 3, G4: grupo 4.*
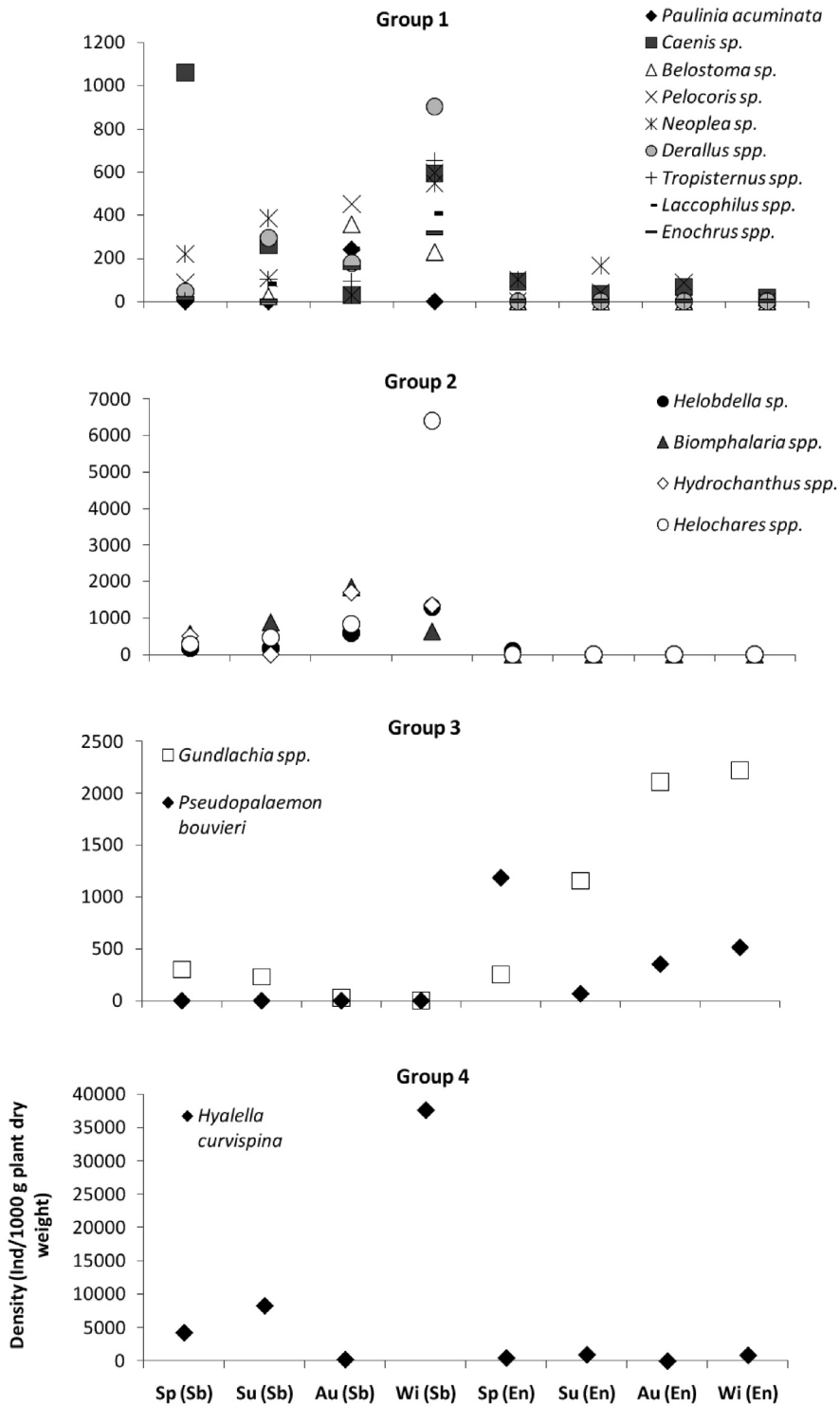
Figure 4. Temporal variation of the mean density of macroinvertebrate species of the 4 groups in both habitat types. Sp: spring, Su: summer, Au: autumn, Wi: winter, (Sb): *Salvinia biloba*, (En): *Egeria najas*. *Variación temporal de la densidad media de las especies de macroinvertebrados de los 4 grupos en ambos tipos de hábitat. Sp: primavera, Su: verano, Au: otoño, Wi: invierno, (Sb):* Salvinia biloba, *(En):* Egeria najas.

a Similarity Analysis (ANOSIM) that showed statistically significant differences between habitat types ($R = 0.94$, $p = 0.0001$) and seasons ($R = 0.55$, $p = 0.0001$).

In a second NMDS, the R stress value (10 %) was also acceptably low (Fig. 3). The invertebrate genera associated with *S. biloba* are grouped to the left of the first axis and those associated with *E. najas*, to the right. The plot shows the differentiation of 4 groups, with the first one (G1) placed in the upper left quadrant of the plot comprising 9 grouped invertebrate genera with low densities in autumn and winter. *Paulinia acuminata*, De Geer, 1773, *Belostoma* sp., *Tropisternus* spp., *Enochrus* spp., *Derallus* spp. and *Laccophilus* spp. were not found in *E. najas*. These genera peaked at winter except for *Belostoma* sp. (Fig. 4).

The second group (G2) presented a high mean density in *S. biloba* (Fig. 4) with genera peaking at winter (*Helochares* spp.) and autumn (*Hydrochanthus* spp. and *Biomphalaria* spp.). The third group (G3) presented two species (*Gundlachia* sp. and *Pseudopalaemon bouvieri*, Sollaud, 1911) that were registered with a major mean density in *E. najas* during winter (Fig. 4). *P. bouvieri* was not registered in *S. biloba*. The fourth group (G4) presented a unique species (*Hyalella curvispina*, Shoemaker, 1942) that appeared with major frequency and mean density in *S. biloba* (Fig. 4) during winter.

The values of Complementary Coefficient across seasons (β temporal diversity) were low for both habitat types (Table 3).When we analysed β diversity between habitat types (β spatial diversity), the values were higher in the winter (0.733) than those calculated for spring, summer (0.538) and autumn (0.625).

DISCUSSION

Our results indicate that *Salvinia biloba* supports a greater number of taxa and the highest number of individual per plant dry weight than *Egeria najas*. *S. biloba* is a structurally more complex habitat (aerial and submerged fronds), but the fractal dimensions do not reflected this complex-

Table 3. Complementary Coefficient values for both habitat types, comparing different time periods. *Valores del Coeficiente de Complementariedad para ambos tipos de hábitats, comparando diferentes períodos de tiempo.*

	Salvinia biloba	Egeria najas
spring-summer	0.285	0.250
summer-autumn	0.200	0.250
autumn-winter	0.133	0.375

ity. The values of fractal dimensions obtained in this work were similar to those mentioned in the bibliography for the same aquatic plants species (Dibble & Thomaz, 2009; Matsuda *et al.*, 2015). The differences in the abundance and richness of the invertebrate assemblages between *S. biloba* and *E. najas* were maintained along the seasons. Habitat complexity provided by the different architecture of aquatic plants affects both the number of taxa and density of invertebrates (Thomaz *et al.*, 2008). However, other studies indicate that macrophytes with greater complexity support a greater abundance of invertebrates but not a greater number of taxa (Ferreiro *et al.*, 2011; Walker *et al.*, 2013).

The taxa richness of *S. biloba* in Sánches Lake was similar to that reported by Poi de Neiff & Neiff (2006) in studies conducted in shallow lakes connected to the Paraná river floodplain using similar methods. With regards to *Egeria najas*, we found a greater number of genera and families of invertebrates compared with those reported by other investigators (Ferreiro *et al.*, 2011) for submerged aquatic plants in a stream of central Argentina, where amphipods and gastropods were the most abundant taxa.

The composition of invertebrate assemblages was different in the two types of habitat studied in Sánches Lake. *Salvinia biloba* has air fronds and supports semi-aquatic species such as *Paulinia acuminata*. This grasshopper feeds on the *S. biloba* air fronds (Vieira & Adis, 2000 and 2002), suggesting a high specificity for its host plant.

S. biloba also had a higher number of genera of Coleoptera (*Helochares* spp., *Enochrus* spp., *Derallus* spp., *Tropisternus* spp., *Paracymus* spp., *Berosus* spp., *Hydrochus* spp., *Desmopachria* spp., *Laccophilus* spp., *Liodessus* spp. and *Hy-*

drochanthus spp.) and Hemiptera (*Belostoma* spp., *Pelocoris* spp., *Neoplea* spp. and *Ranatra* sp.) than *Egeria najas*. The respiratory demands of some of these genera may be satisfied by a thin layer of air maintained along their body surface (plastron), which makes regular ascents to the water surface, and some others have a respiratory siphon to intake atmospheric oxygen. Gómez Lutz *et al*. (2015) found that the habitats and microhabitats (forming by different species of aquatic plants) directly influence the structure and the spatial and temporal variations of several species of *Tropisternus*.

Pseudopalaemon bouvieri is adapted to living in oligohaline waters of shallow lakes of Corrientes Province, and it is closely associated with *E. najas*. This freshwater prawn is known to have a relatively non-specific diet, feeding on algae, plant remains, Protozoa, Rotifera, Oligochaeta, Crustacea, Insecta, detritus, and other items (Carnevali *et al*., 2012).

The physical and chemical characteristics of the water varied in a narrow range during the sampling period, and the winter temperatures were sufficiently high for the development of aquatic plants and for allowing macroinvertebrate activity. However, the results of our study indicate a marked seasonal variability, both in terms of the total density, taxa richness, and the density of the populations of dominant taxa.

The largest number of invertebrate taxa was recorded during winter in the subtropical studied lake, a result that is in accord with another study (Fontanarrosa *et al*., 2013) carried out in the free floating plants of the Paraná river floodplain. The diversity and abundance of invertebrates are generally low in spring due to the early spring emergence of some species, but the total abundance cannot reflect these changes (Kratzer & Batzer, 2007). However, in other shallow lakes of the study area, some populations of crustaceans, such as *Hyalella curvispina* (Galassi *et al*., 2006), reach their population peak in spring. *Pseudopalaemon bouvieri* increases their populations in spring-summer due to breeding occurring at the end of spring (Carnevali, 2012).

The habitat structuring of aquatic macrophytes is a key factor in the macroinvertebrate assemblages that should be included in comparative studies about vegetated wetlands with different habitat types. The strong temporal variation across seasons was a surprise in a subtropical climate, where the pronounced seasonality is absent.

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