

## Orthoptera assemblages associated with macrophytes of floodplain lakes of the Paraná River

Soledad Capello<sup>1,4</sup>, Mercedes Marchese<sup>1,2</sup> & María L. De Wysiecki<sup>3</sup>

<sup>1</sup> Instituto Nacional de Limnología (INALI-CONICET-UNL), Laboratorio de Vegetación, segundo piso. Ciudad Universitaria, Santa Fe (3000), Argentina. solecapello1@yahoo.com.ar

<sup>2</sup> Facultad de Humanidades y Ciencias-UNL. Ciudad Universitaria, Paraje El Pozo, 3000 Santa Fe, Argentina. mmarchese@inali.unl.edu.ar

<sup>3</sup> Centro de Estudios Parasitológicos y de Vectores (CEPAVE) (CCT-La Plata-CONICET-UNLP), Calle 2 n° 584, 1900 La Plata, Argentina. mlw@cepave.edu.ar

<sup>4</sup>Corresponding author.

---

**ABSTRACT.** Orthoptera assemblages associated with macrophytes of floodplain lakes of the Paraná River. The Orthoptera assemblage composition varies considerably, depending on habitat type. This study examines the spatiotemporal relationship between plant diversity, hydrometric level, environmental variables and the Orthoptera richness and abundance in floodplain lakes connected permanently or temporarily with the main channel of the Paraná River. The grasshoppers were collected fortnightly (April 2006–May 2007). A total of 17 species were recorded and classified according to their frequency of occurrence in constant (7), accessory (4), or accidental (6) species. In the two lakes, the greater species richness and abundance was recorded in summer, thereby coinciding with the highest water level of the Paraná River. The most significant correlation between the orthopteran richness and abundance was with the water level. The aquatic plant richness was significantly different between the lakes, but the vegetation was dominated by *Eichhornia crassipes* (Mart.) Solms. (Liliales, Pontederiaceae). The lake, which was connected permanently, presented the highest values of diversity and abundance, proving to be a more diverse assemblage. The beta diversity was higher in the temporary connected lake than in the permanently connected one. The orthopteran assemblages were different between the lakes, *Cornops aquaticum* and *Tucayaca gracilis* were the species that contributed more to the level of dissimilarity. *C. aquaticum* was more representative in the lake temporarily connected, while *T. gracilis* in the permanent connected one. The water level of the Paraná River and the connectivity of the floodplain lakes play an important role to explain the abundance and richness of their orthopteran assemblages.

**KEYWORDS.** Acrididae; aquatic plants; diversity index; hydrological level; Insecta; Tettigonidae.

---

Composition of Orthoptera assemblages vary considerably, depending on habitat type (Kemp *et al.* 1990). Many biotic and abiotic variables influence orthopteran populations and assemblages: plant species composition (Strohecker *et al.* 1968; Kemp *et al.* 1990), vegetation structure (Clarke 1993), soil type (Pdaft 1984), temperature, radiation, humidity, food availability, oviposition sites, shelters from predators (Kemp *et al.* 1990), or biotic interactions such as predation or parasitism (Joern & Pruess 1986). Vegetation is one of the key factors that determine Orthoptera distribution and composition, as different species occupy specific habitats according to the food availability and their microhabitat thermal requirements (Fielding & Brusven 1992; Squitier & Capinera 2002).

In aquatic systems the habitat structure is often provided by macrophytes, and the significance of a habitat is demonstrated by a far greater abundance of macroinvertebrates than in water bodies without aquatic plants (Heck & Crowder 1991). The abundance and richness of the macroinvertebrate assemblages appears to be proportional to the density or biomass of the freshwater macrophytes (Crowder & Cooper 1982; Stoner & Lewis 1985). However, this relationship is less clear when referring to the structure type or shape rather than to the density of structural elements, because various

macrophytes species tend to support different epiphytic communities (Rooke 1986; Chilton 1990; Humphries 1996).

The water-level fluctuations constitute the most important macrofactor that should be considered while explaining species richness, distribution, and abundance of organisms in aquatic systems (Lewis *et al.* 1987; Junk & Piedade 1993; Casco *et al.* 2005; Thomaz *et al.* 2007). On the other hand, as pointed out by Neiff (1996), the number and type of species in different hydrological stages change, and only a few can bear both phases (flood and drought). Variations in the hydrological regime lead to substantial temporal biotic and abiotic changes. During the low water level, the floodplain aquatic habitats become more isolated from each other and are subjected to local driving forces. Flood events increase the connectivity and similarities among habitats, thus overriding local factors by regional scale drivers (Ward & Tockner 2001; Thomaz *et al.* 2007). Water-level fluctuations of distinct frequencies, magnitudes, and durations cause different physical and biotic impacts on habitats that are strongly associated with habitat connectivity (*e.g.* distance from the main river, topography), thereby creating a shifting mosaic state that is characterized by habitats at different successional stages (Amoros & Bornette 2002; Palijan *et al.* 2008).

The concept of connectivity originally referred to gene flow between subpopulations of a metapopulation (Merriam 1984). Connectivity is a relatively new concept in ecology and has only recently caught the attention of ecologists. Hydrological connectivity (*sensu* Amorós & Roux 1988) refers to the exchange of matter (including organisms) and energy via the aqueous medium between different units of the riverine landscape. Floodplain water bodies differing in connectivity with surface waters of the main channel exhibit different successional trajectories and contain different biotic communities.

Several general hypotheses have been proposed that explain the relationships between plant and herbivore species richness (Hawkins & Porter 2003; Haddad *et al.* 2009), with insect herbivore diversity often viewed as generally increasing in its relationship to higher plant species richness due to an increased resource diversity (Haddad *et al.* 2001, 2009). Although habitat associations with grasshoppers have been studied since the early 1900s (Vestal 1913), understanding patterns of species diversity remains a continuing challenge in grasshopper ecology (Torrusio *et al.* 2002; Joern 2005). Many studies have examined the relationships between grasshopper community composition and vegetation patterns in grassland ecosystems worldwide (Kemp *et al.* 1990; Fielding & Brusven 1993; Sanchez & de Wysiecki 1993; Torrusio *et al.* 2002; Joern 2005; Branson 2011), but the relationships between the Orthoptera and macrophytes in floodplain environments are scarcely known.

This study examines the spatiotemporal relationship between plant species diversity, hydrometric level and the diversity of Orthoptera in aquatic plant communities belonging to different floodplain lakes of the middle Paraná River. The primary objectives were to (1) determine the alpha diversity in two lakes with a different connectivity; (2) ascertain the species composition of the orthopterans associated to macrophytes and establish the dominant, accessory, or accidental species; (3) determine the beta diversity between the lakes with different connectivity to the main channel of the Paraná River.

## MATERIAL AND METHODS

**Study site.** The floodplain of the Middle Paraná River is 600 km in length (Paoli *et al.* 2000), thereby providing a heterogeneous mosaic of aquatic environments. We selected lakes that differ in their degree of connectivity with the main channel, being lakes that were connected either permanently (*LCPer*) (31°38' 43.77"S; 60°34' 35.07"W) or temporarily to the Paraná River (*LCTemp*) (31°40' 14.40"S; 60°34' 44.43"W) (Fig. 1).

The vegetation of these floodplain lakes is directly associated with the hydrologic regime of the Paraná River, because the species richness varies according to the water level. The most important macrophytes in the Middle Paraná River are *Eichhornia crassipes* (Mart.) Solms., *Paspalum repens* (Elliott) Kunth, *Salvinia* sp. Seg., *Pistia stratiotes* L., *Azolla* sp. Lam., *Ludwigia peploides* (Kunth) P.H. Raven, *Echinochloa* sp. P. Beauv., and *Polygonum* sp. L. (Sabattini & Lallana 2007).

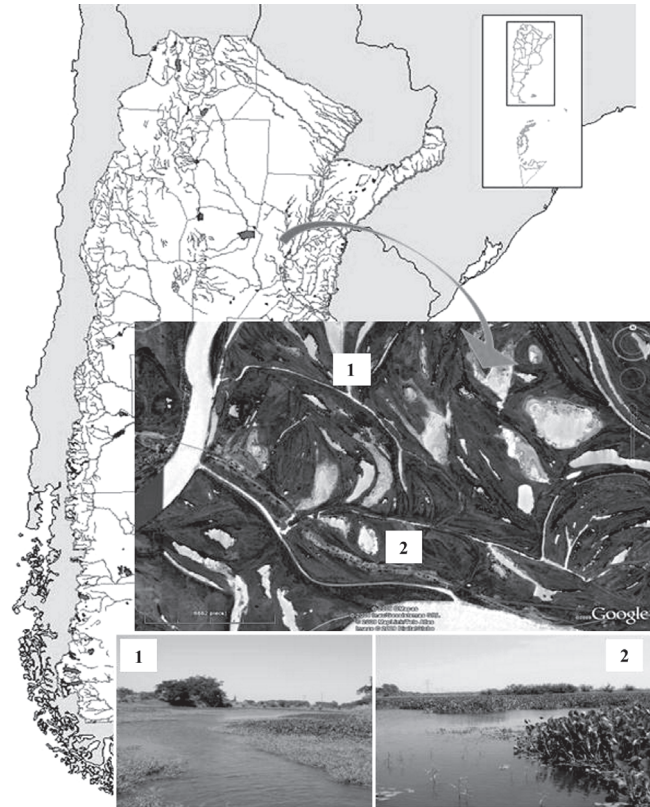


Fig. 1. Hydrographic system of Argentina. The arrow indicates the place of sampling: the Middle Paraná River. The photographs belong to the floodplain lakes studied. 1: lake connected permanently (*LCPer*) and 2: lake connected temporarily to the main channel of the Paraná River (*LCTemp*).

During the studied period, the hydrometric level of the Middle Paraná River presented a range of variation of 3.92 m. The lowest value (1.54 m) was recorded in September 2006, while the highest value (5.46 meters) was recorded in March 2007.

**Data collection.** The Orthoptera are usually not considered aquatic insects, but some of these species are linked to freshwater habitats mainly by a relation to an aquatic host plant. The orthopterans that cannot develop without aquatic plants, especially for egg laying and nymph development, are considered the primary inhabitants of freshwater biota (Amédégno & Devriese 2008).

The grasshoppers were collected fortnightly in each of the floodplain lakes from April 2006 to May 2007. For each sampling moment, we had chosen similar days in relation to climatic conditions, avoiding the days with strong winds and rain, so that there would not be an underestimation of the results.

The collection of individuals was carried out from a boat, using an entomological nylon net (500 µm mesh) of 70 cm in diameter, 1 m in depth and the net handle length was 1.30 m. The sampling was carried out for a total period of 15 minutes sweeping on the aquatic plants. In order to know what plant species were dominant and while analyzing the possible variations of floristic composition between the lakes, the specific composition and vegetation of the macrophytes

was analyzed by using the square method (70 x 70 cm). According to Foster *et al.* (1991), photo quadrates are more precise in estimating cover quadrates rather than point quadrates. For this reason, we obtained photographic records of each square. In each sampling, 10 photographs were randomly taken. The camera was maintained at a constant high during each photograph, and the photographic images were taken perpendicular to the substrate. These images were carefully analyzed by obtaining the proportion of each macrophyte.

All the captured Orthoptera were brought to the laboratory and preserved in the freezer for later and correct identification of taxonomic level by using different keys: Carbonell (1957, 2000), Carbonell *et al.* (2006), Montealegre-Zapata (1996), Roberts & Carbonell (1979), and Salto (1999).

**Data analysis.** Grasshoppers species richness and total abundance (total number of orthopterans/sampling) in each lake at each sampling moment were calculated. Species richness accumulated during the period studied (2006–2007) was obtained.

The Bodenheimer Index (Bodenheimer 1955) was applied for analyzing orthopteran species constants, using the following formula:  $c = p \times 100/P$ , where  $p$  is the number of samples where the specie  $i$  is recorded, and  $P$  is the total number of samples. In relationship to the  $c$  value obtained, the orthopterans were classified in the following manner: Constant species: > 50%, Accessory species: between 25 and 50%, and Accidental species < 25%.

To establish which Orthoptera species contributes to observed differences in the data and to determine which species characterizes and discriminates each Orthoptera assemblage area, we used SIMPER (Similarity Percentage). This is a simple method of assessment in which taxa are primarily responsible for an observed difference between groups of samples, and it is based on the analysis of Bray–Curtis similarity matrices that are derived from the species compositions between stations (Clarke 1993). The PRIMER v6 (Clarke & Gorley 2006) was used for this analysis.

In order to ascertain the relationship between species richness, abundance of orthopterans, climatic variables (temperature, mean temperature, minimum temperature, humidity, and precipitation), hydrometric level, and macrophytes species richness (expressed as special heterogeneity) were estimated using correlations. The statistical software XLSTAT 7.5.3 was used.

Orthopterans diversity was calculated as the Shannon–Wiener Index and Hulbert's PIE Index (Colwell 2005). Hulbert's PIE is the probability that two randomly sampled individuals from the same community pertain to two different species. It is an evenness index that combines the two mechanistic factors affecting diversity: dominance and species abundance. In addition, the dominance was also calculated. All these indexes were generated by a randomization process using EcoSim (Gotelli & Entsminger 2009).

The degree of distinctness among the lakes was measured using the complementarity index suggested by Colwell & Coddington (1994). The value of this index, expressed as a

percentage, ranges from 0% for an identical species composition to 100% for an entirely different species composition. This measure of complementarity is, therefore, a direct measure of beta diversity. In addition, the rate of replacement of the species in each lake that was proposed by Whittaker (1972) was calculated. This index has proved to be more robust in measuring the replacement between communities (Wilson & Schmida 1984; Magurran 1989).

## RESULTS

**Orthoptera species richness and relative abundance of individuals.** A total of 17 orthopteran species representing two suborders, four families, and ten subfamilies were recorded. The individuals were classified according to their frequency of occurrence in constant (seven), accessory (four), or accidental (six) species. The constant species are considered aquatic due to their relationship with the freshwater environment (Table I).

Table I. Orthoptera species registered in the floodplain lakes of the Middle Paraná River. Based on Bodenheimer Index, the Orthoptera were categorized as constant (present in more than 50%), accessory (between 25% and 50%), and accidental (less than 25%) species while taking into account the presence of each species with regard to the total of the sampling carried out. Const.: constants; Acce.: accessory and Acci.: accidental species.

Species		Bodenheimer index
Caelifera		
Acrididae		
Acridinae	<i>Metaleptea adpersa</i> (Blanchard, 1843)	Acce
Copiocerinae	<i>Aleuas lineatus</i> Stål, 1878	Acce
Gomphocerinae	<i>Dichromorpha australis</i> Bruner, 1900	Acci
Leptysminae	<i>Leptysmia argentina</i> Bruner, 1906	Acci
	<i>Tucayaca gracilis</i> (Giglio-Tos, 1897)	Const
	<i>Cornops aquaticum</i> (Bruner, 1906)	Const
	<i>Haroldgrantia lignosa</i> Carbonell, Ronderos & Mesa, 1967	Acci
Melanoplinae	<i>Dichroplus elongatus</i> Giglio-Tos, 1894	Acci
Marellinae	<i>Marellia remipes</i> Uvarov, 1929	Acce
Paulinae	<i>Paulinia acuminata</i> (De Geer, 1773)	Const
Romaleidae		
Romaleinae	<i>Chromacris speciosa</i> (Thunberg, 1824)	Acci
	<i>Coryacris angustipennis</i> (Bruner, 1900)	Acce
	<i>Diponthus argentinus</i> Pictet & Saussure, 1887	Acci
Ensifera		
Tettigonidae		
Conocephalinae	<i>Conocephalus</i> sp.	Const
Meconematinae	<i>Phlugis</i> sp.	Const
Phaneropterinae	<i>Scudderia</i> sp.	Const
Gryllidae*		Const

\* The different species of this family were not identified.

The grasshoppers richness accumulated was to 17 species in the LCPer, while in the LCTemp, the richness accumulated was to 15 species. The species richness was significantly different between sites (U de Mann–Whitney  $Z = 2,355$ ;  $p = 0,019$ ).

In the two floodplain lakes, the greater species richness was recorded in late summer (February and March 2007), coinciding with the highest water levels of the Middle Paraná River (Fig. 2).

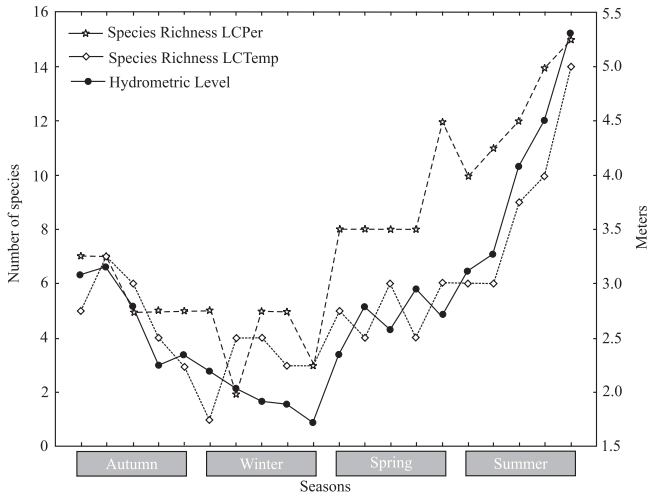


Fig. 2. Relationship between the hydrometric level of Middle Paraná River (Santa Fe city) and the species richness of each lake. LCPer: lake connected permanently; LCTemp: lake connected temporarily to the main channel.

A total of 5,236 individuals was collected throughout the study period sampled. The 60.30% (3,158 individuals) belong to the suborder Caelifera, while 39.70% (2,078 individuals) correspond of the suborder Ensifera.

The total abundance of Orthoptera in LCPer was greater (3,377 individuals), but there were no significant differences between the two lakes ( $p > 0.05$ ). The higher abundance was obtained in summer, whereas the lower abundance was obtained in winter (Table II).

Table II. Total abundance of Orthoptera according to the different seasons in each lake. LCPer: lake connected permanently; LCTemp: lake connected temporarily to the main channel of the Paraná River.

	Autumn	Winter	Spring	Summer	Total
LCPer	584	137	830	1826	3377
LCTemp	589	69	366	834	1858

The data obtained in this study showed that species richness was different between the two lakes with a different connectivity (U de Mann–Whitney  $Z = 2.355$ ;  $p = 0.019$ ), but this did not happen in the same manner with the abundances. However, the results obtained by SIMPER showed that these species abundances vary between sites, resulting in a dissimilarity value of 51.30 (average dissimilarity) between the lakes. The species that had major differences in the contribution for the total assemblage of Orthoptera in each lake were *Cornops aquaticum* Bruner, 1906 and *Tucayaca gracilis* (Giglio-Tos, 1897). In the first case, the

LCPer recorded a 21.29% contribution toward increasing this value in the LCTemp (46.02%). In opposition, *T. gracilis* had a greater contribution in the LCTemp than in the LCPer (20.23% and 4.18%, respectively). Thus, the orthopteran assemblage of LCPer was characterized by *Phlugis* sp. Stål, 1861, *C. aquaticum*, *T. gracilis*, Gryllidae, *Paulinia acuminata* (De Geer, 1773) and *Scudderia* sp. Stål, 1873 whereas in LCTemp by *C. aquaticum*, *Phlugis* sp., Gryllidae, *Scudderia* sp. and *T. gracilis* in abundance decrease (Fig. 3).

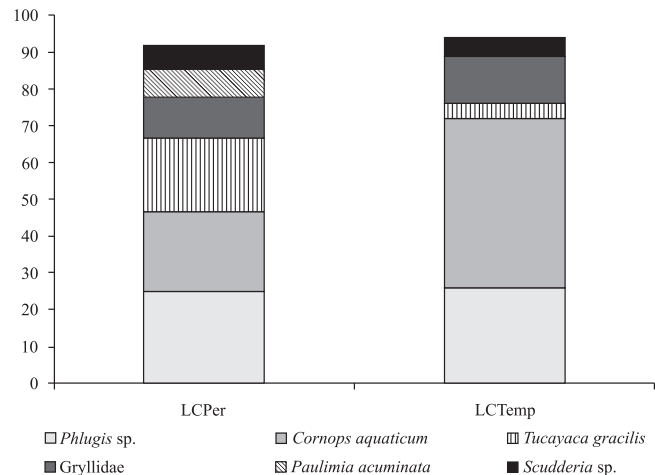


Fig. 3. The most representative species of Orthoptera assemblage in each lake of different connection to the main channel of the river. The species mentioned involve 90% of the ensemble of Orthoptera are associated with aquatic plants. LCPer: lake connected permanently; LCTemp: lake connected temporarily to the main channel of the Paraná River.

The correlation between the richness and abundance obtained with the hydrometric level and the precipitations was significant ( $p < 0.001$ ). The correlation between the vegetal cover (measured as water hyacinth proportion) and the habitat heterogeneity (measured as the plant species) was not significant ( $p > 0.05$ ) (Table III).

**Macrophyte cover.** The accumulative species richness of the macrophytes was low, with a total of 20 species detected across sites (Table IV). The vegetation was dominated by *Eichhornia crassipes* (Mart.) Solms, and this macrophyte was a unique aquatic plant registered in all the samples.

The plant richness was significantly different between the two lakes (U de Mann–Whitney  $Z = -1.984$ ;  $p = 0.047$ ), as well as the proportion of *E. crassipes* between the environments (U de Mann–Whitney  $Z = -3.628$ ;  $p \leq 0.0001$ ).

In the LCTemp, the species richness of the macrophytes was positively correlated with the hydrometric level of the river ( $r = 0.630$ ;  $p = 0.003$ ) and with the species richness of Orthoptera ( $r = 0.448$ ;  $p = 0.048$ ). In contrast to this, in the LCPer, there were no significant correlations between these variables.

On the other hand, the correlations between plant richness and Orthoptera abundance were not significant ( $p > 0.05$ ) in the two lakes with a different connectivity (Table III).

Table III. Correlations (Spearman) between species richness and abundance of Orthoptera with different variables. The asterisks indicate significant values.

	Hydrometric level	Precipitation	Temperature			Humidity			Waterhyacinth proportion	Spatial Heterogeneity
			Maximum	Mean	Minimum	Maximum	Mean	Minimum		
Species richness	r: 0.835 p < 0.0001*	r: 0.621 p < 0.0001*	r: 0.282 p: 0.077	r: 0.538 p: 0.000	r: 0.508 p: 0.001	r: 0.334 p: 0.035	r: 0.323 p: 0.042	r: 0.319 p: 0.045	r: 0.225 p: 0.163	r: 0.048 p: 0.767
Abundance	r: 0.779 p < 0.000*	r: 0.573 p: 0.000*	r: 0.263 p: 0.101	r: 0.464 p: 0.003	r: 0.417 p: 0.007*	r: 0.350 p: 0.027	r: 0.494 p: 0.001*	r: 0.483 p: 0.002*	r: 0.093 p: 0.570	r: 0.176 p: 0.276

Table IV. List of aquatic plants recorded in the floodplain lakes of the Middle Paraná River. The crosses indicate the macrophyte presence in LCPer (lake connected permanently) and/or LCTemp (lake connected temporarily).

Family	Specie	LCPer	LCTemp
Pontederiaceae	<i>Eichhornia crassipes</i> (Mart.) Solms.	X	X
Pontederiaceae	<i>Eichhornia azurea</i> (Sw.) Kunth	X	-
Araceae	<i>Pistia stratiotes</i> L.	X	X
Graminae	<i>Paspalum repens</i> (Elliott) Kunth	X	X
Hydrocaritaceae	<i>Limnobiium spongia</i> (Bosc) Rich. ex Steud.	X	X
Poligonaceae	<i>Poligonum</i> sp.	X	X
Onagraceae	<i>Ludwigia peploides</i> (Kunth) P.H. Raven	X	X
Compuesta	<i>Enhydra anagallis</i> (Gardner)	-	X
Araliaceae	<i>Hydrocotile</i> sp.	X	X
Gramineae	<i>Panicum prionitis</i> Nees	X	-
Cyperaceae	<i>Oxicarium cubense</i> (Poepp. & Kunth) Lye	X	X
Azollaceae	<i>Azolla filiculoides</i> Lam.	X	X
Salviniaceae	<i>Salvinia</i> sp.	X	X
Meniantaceae	<i>Nymphaoides</i> sp.	X	X
Haloragaceae	<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	-	X
Nimphaceae	<i>Victoria cruziana</i> A.D. Orb.	X	X
Amarantaceae	<i>Alternanthera philoxeroides</i> (Mart) Griseb.	X	X
Limnocaritaceae	<i>Hydrocleys nymphaoides</i> (Humb. & Bonpl. ex Willd.) Buchenau	X	X
Commelinaceae	<i>Commelina</i> sp.	X	X
Lemnaceae	<i>Lemna</i> sp.	X	X

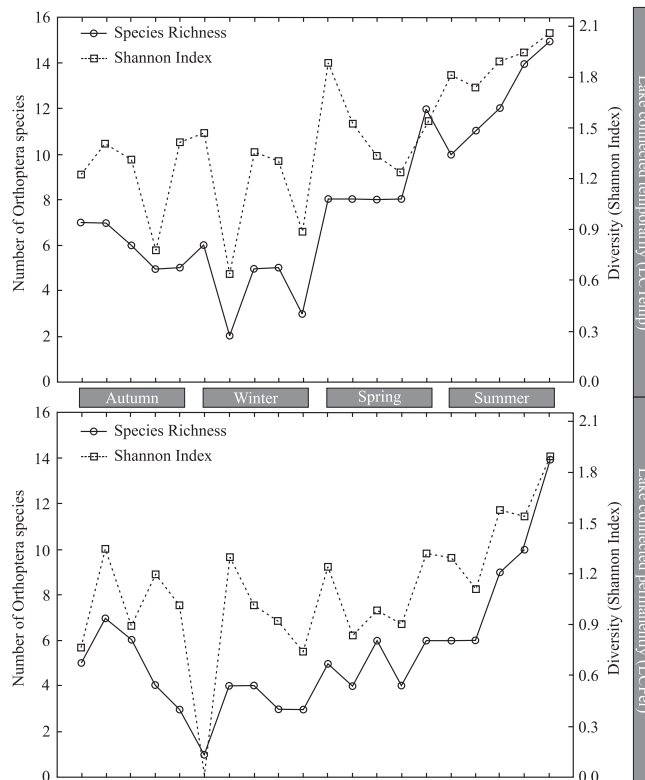


Fig. 4. Diversity (Shannon-Wiener Index) and species richness in each lake.

**Diversity indexes.** The LCPer presented the highest values of the Shannon–Wiener Index (1.96), Hulbert’s PIE Index (0.81), and the lowest dominance (0.35), proving to be a more diverse assemblage. The values recorded for the LCTemp were 1.59, 0.71, and 0.46, respectively. The species richness and diversity was higher in summer in both the lakes, with the permanently connected lake showing more variation in the values (Fig. 4).

Diversity beta between the floodplain lakes (spatial diversity), according to the complementarily index, was 0.12. This means that both lakes have a similar composition of species, and only 11.7% of the species of Orthoptera are complementary between environments.

The results obtained from the Whittaker Index in each lake, that is, the replacement of species throughout the year, showed that LCTemp presented a higher turnover (1.73) than LCPer (1.19).

## DISCUSSION

The results of this study allowed an analysis of the simultaneous and comparative Orthoptera assemblages between floodplain lakes permanently and temporarily connected to the Paraná River. The species richness in the Orthoptera is determined by a complex relationship between external factors, such as the climate and vegetation, and internal factors, such as population dynamics (Joern 2005; Zhong-Wei *et al.* 2006).

Based on the results obtained, only seven of the 17 Orthoptera species found associated to the water hyacinth can be considered constant species of aquatic habitats. Three of them are Acrididae: *Paulinia acuminata*, *Cornops aquaticum* and *Tucayaca gracilis*. The first two species have been widely studied for their use as potential agents of biological control of weeds: *Salvinia auriculata* Aubl., 1775 (Thomas 1980;

Sands & Kassulke 1986; Vieira & Adis 1992) and *Eichhornia crassipes* (Bennett & Zwölfer 1969; Silveira-Guido & Perkins 1975; Hill & Oberholzer 2000; Oberholzer & Hill 2001; Adis & Junk 2003), respectively. On the other hand, the three species of Ensifera that were registered were described as the insects that inhabit moist places and those near to the water: *Phlugis* sp., *Conocephalus* sp., and *Scudderia* sp. The crickets collected in this study were cited by other authors as being a part of the insect community living on floating aquatic plants (Carbonell 1980; Albertoni *et al.* 2007).

The number of recorded orthopterans associated to the aquatic plants with adaptive strategies to live in wet environments were 13 species (Acrididae and Romaleidae), whereas Carbonell *et al.* (2006) reported a higher species richness (75 acridids) including terrestrial habitats. *C. aquaticum* and *P. acuminata* have been considered the most aquatic species according to Bentos-Pereira & Lorier (1991). In agreement, we classified the same acridids as constants in the macrophytes in the floodplain lakes studied. In addition, Bentos-Pereira & Lorier (1991) mentioned that *T. gracilis* is a species that frequently occurs in aquatic environments; but in our study, this grasshopper has attained great abundance while being placed within the constant species found on the aquatic vegetation.

On the other hand, *Marellia remipes* Uvarov, 1929, well adapted to the freshwater environments (Uvarov 1929, 1930; Carbonell 1957; Bentos-Pereira & Lorier 1991), was registered in low abundance, with 30 individuals captured during the study period. This result may be explained, because these acridids are related to *Hydrocleis nymphoides* (Humb. & Bonpl. ex Willd.) Buchenau (Butomaceae), an aquatic plant growing in quiet and clean waters (Carbonell & Arrillaga 1958), which was observed only occasionally owing to the suspended sediments load, the exposition of the wind, and the hydrologic dynamics of the lakes studied.

The species richness of insect herbivores is positively correlated with the area covered by their host plants (Strong *et al.* 1984), and it is independent of the habitat heterogeneity (Greze 1992). However, we did not find the same relation with the plants richness in the floodplain lakes studied. Thus, a significant correlation between habitat heterogeneity (plants richness) and species richness of orthopterans was obtained in the temporary connected lake (LCTemp), whereas no significant correlation was observed in the permanently connected lake (LCPer). Therefore, the connectivity between the floodplain lakes and the channels plays an important role in the orthopteran richness associated to aquatic plants. In addition, the water level of the river was the variable that was considered more important in the grasshopper abundance and species richness variation, attaining the highest values along with the maximum water level. By coincidence, the hydrologic effect was reported by Nunes & Adis (1992), Nunes *et al.* (2005), Vieira & Adis (1992), for others Orthoptera in central Amazonia, at the alluvial plain of the Amazonas-Solimões River. Thus, *P. acuminata* presented more abundance of nymphs and adults in high water than low water

(Vieira & Adis 1992). On the other hand, the water level had an indirect effect on the populations of *Phlugis teres* (De Geer, 1773), because the macrophyte abundance was regulated (Nunes *et al.* 2005).

The macrophyte composition and abundance in floodplain lakes is largely determined by the water level regime (Junk 1970; Junk & Piedade 1993, 1997; Neiff 1979, 1990a, 1990b, 1999; Neiff *et al.* 2001; Piedade & Junk 2000; Parolin *et al.* 2004; Thomaz *et al.* 2004). In addition, the macrophyte represents the habitat and trophic resources for herbivorous insects, the aquatic plant communities are the support for aquatic orthopteran assemblages, and their abundance and richness depends on the abundance and distribution of the vegetation.

Instead, the temporal variation of plant communities (biomass, structure and diversity) in their relationships with drought or floods affects the distribution, density and composition of the orthopterans (Evans 1988; Kemp 1992a,b; Cigliano *et al.* 1995, 2000; Branson *et al.* 2006; Branson & Sword 2009).

The macrophyte composition showed significant differences between the floodplain lakes with a different connectivity with the main river. The highest species richness was attained in the permanently connected lake during the low water level, whereas the lowest species richness was obtained in the temporary connected lake. In addition, the hydrologic regime has a different effect on the aquatic plants richness in the lakes that are connected or disconnected with the river. By coincidence, Boschilia *et al.* (2008) showed that macrophyte assemblages are organized differently depending on the degree of connectivity.

The beta diversity was higher in temporary connected lakes than in the permanently connected ones, suggesting a greater change among the species of Orthoptera between different sampling dates. This phenomenon probably gives rise to the fact that this environment has more unstable hydrological conditions, thereby indirectly affecting the diversity of the grasshoppers and tettigonids present on the macrophytes.

In summary, our results show that the water level of the Paraná River and the connectivity of the floodplain lakes are the most important forces that should be considered to explain the abundance and richness of orthopteran assemblages. The floodplain lakes were characterized by different orthopteran assemblages, the richest ones found in the floodplain lakes with a permanent connection with the main channel. The effect of the high water level in increasing the abundance and species richness of orthopterans in the lakes may also be explained by the fact that semi-aquatic or terrestrial grasshoppers may use the macrophytes as food, shelter, and so on, during the floods.

#### ACKNOWLEDGMENTS

We thank Language Edit for the revision of our manuscript. This work was funded by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Argentina.

## REFERENCES

- Adis, J.A. & Junk, W. 2003. Feeding impact and bionomics of grasshopper *Cornops aquaticum* on the water hyacinth *Eichhornia crassipes* in the Central Amazonian floodplains. **Studies on Neotropical Fauna and Environment** **38**: 245–249.
- Albertoni, E.F., Prellvitz, L.J. & Palma-Silva, C. 2007. Macroinvertebrate fauna associated with *Pistia stratiotes* and *Nymphoides indica* at subtropical lakes (South Brazil). **Brazilian Journal of Biology** **67**: 499–507.
- Amédégnato, C. & Devriese, H. 2008. Global diversity of true and pygmy grasshoppers (Acridomorpha, Orthoptera) in freshwater. **Hydrobiologia** **595**: 535–543.
- Amoros, C. & Bornette, G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. **Freshwater Biology** **47**: 761–776.
- Amoros, C. & Roux, A.L. 1988. Interactions between water bodies within the floodplains of large rivers: function and development of connectivity, p. 125–130. In: Schreiber, K.F. (ed.). **Connectivity in Landscape Ecology**. Volume 29, Münstersche geographische Arbeiten. Münster, Universität Münster, Institut für Geographie, 255p.
- Bennett, F.D. & Zwölfer, H. 1969. Exploration for natural enemies of the water hyacinth in northern South America and Trinidad. **Hyacinth Control Journal** **7**: 44–52.
- Bentos-Pereira, A. & Lorier, E. 1991. Acridomorfos acuáticos (Orthoptera, Acridoidea) I. Adaptaciones morfológicas. **Revista Brasileira de Zoologia** **35**: 631–653.
- Bodenheimer, F.S. 1955. **Precis d'Écologie Animale**. Paris, Payot, 315 p.
- Boschilia, S.M., Oliveira, E.F. & Thomaz, S.M. 2008. Do aquatic macrophytes co-occur randomly? An analysis of null models in a tropical floodplain. **Oecologia** **156**: 203–214.
- Branson, D.H. & Sword, G.A. 2009. Grasshopper herbivory affects native plant diversity and abundance in grassland dominated by the exotic grass *Agropyron cristatum*. **Restoration Ecology** **17**: 89–96.
- Branson, D.H. 2011. Relationships between plant diversity and grasshopper diversity and abundance in the Little Missouri National Grassland. **Psyche** **2011**, 7 p. doi:10.1155/2011/748635
- Branson, D.H., Joern, A. & Sword, G.A. 2006. Sustainable management of insect herbivores in grassland ecosystems: New perspectives in grasshopper control. **Bioscience** **56**: 743–755.
- Carbonell, C.S. 2000. Taxonomy and a study of the phallic complex, including its muscles, of *Paulinia acuminata* (Acrididae, Pauliniinae) and *Marellia remipes* (Acrididae incertae sedis). **Journal of Orthoptera Research** **9**: 161–180.
- Carbonell, C.S. & Arrillaga, B. 1958. Sobre la relación anatómica de las ootecas de *Marellia remipes* Uvarov (Orthoptera, Acrid. Pauliniidae) con las hojas de su planta huésped, y su posible significación fisiológica. **Revista de la Sociedad Uruguaya de Entomología** **3**: 45–56.
- Carbonell, C.S., Cigliano, M.M. & Lange, C.E. 2006. Especies de acridomorfos (Orthoptera) de Argentina y Uruguay [CD-ROM]. Publications on Orthopteran Diversity, The Orthopterists Society at "Museo de La Plata", Argentina/USA.
- Carbonell, C.S. 1957. The external anatomy of the South American semiaquatic grasshopper *Marellia remipes* Uvarov (Acridoidea, Pauliniidae). **Smithsonian Miscellaneous Collections** **137**: 61–97.
- Carbonell, C.S. 1980. Orthoptera (Part I. Arthropoda), p. 92–99. In: Hurlbert, S.H., Rodriguez, G. & dos Santos, N. D. (eds). **Aquatic biota of tropical South America**. San Diego, San Diego State University, 342 p.
- Casco, S.L., de Chiozzi N.I.B. & Neiff, J.J. 2005. La vegetación como indicador de la geomorfología fluvial. **Revista Brasileira de Geomorfologia** **6**: 123–136.
- Chilton, E.W. 1990. Macroinvertebrate communities associated with three aquatic macrophytes (*Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Vallisneria americana*) in Lake Onalaska, Wisconsin. **Journal of Freshwater Ecology** **5**: 455–466.
- Cigliano, M.M., Kemp, W.P. & Kalaris, T. 1995. Spatiotemporal characteristics of rangeland grasshopper (Orthoptera: Acrididae) regional outbreaks in Montana. **Journal of Orthoptera Research** **4**: 111–126.
- Cigliano, M.M., de Wysiecki, M.L. & Lange, C.E. 2000. Grasshopper (Orthoptera, Acrididae) species diversity in the pampas. Argentina. **Diversity and Distributions** **6**: 81–91.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. **Australian Journal of Ecology** **18**: 117–143.
- Clarke, K.R. & Gorley, R.N. 2006. PRIMER v6 (Plymouth Routines In Multivariate Ecological Research).
- Colwell, R.K. & Coddington, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. **Philosophical Transactions of the Royal Society B** **345**: 101–118.
- Colwell, R.K. 2005. EstimateS, Version 7.5: statistical estimation of species richness and shared species from samples (Software and User's Guide). Available at: <http://viceroy.eeb.uconn.edu/estimates>.
- Crowder, L.B. & Cooper, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. **Ecology** **63**: 1802–1813.
- Gotelli, N.J. & Entsminger, G.L. 2009. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. and Kesey-Bear. Jericho, VT 05465. Available at: <http://garyentsminger.com/ecosim.htm>.
- Evans, E.W. 1988. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tall grass prairie: influences of fire frequency, topography, and vegetation. **Canadian Journal of Zoology** **66**: 1495–1501.
- Fielding, D.J. & Brusven, M.A. 1992. Food and habitat preferences of *Melanoplus sanguinipes* and *Aulocara elliotti* (Orthoptera, Acrididae) on disturbed rangeland in southern Idaho. **Journal of Economic Entomology** **85**: 783–788.
- Fielding, D.J. & Brusven, M.A. 1993. Grasshopper (Orthoptera: Acrididae) community composition and ecological disturbance on Southern Idaho rangeland. **Environmental Entomology** **22**: 71–81.
- Foster, M.S., Harrold, C. & Hardin, D.D. 1991. Point vs photo quadrat estimates of the cover of sessile marine organisms. **Journal of Experimental Marine Biology and Ecology** **146**: 193–203.
- Greze, A. 1992. Riqueza de especies de insectos herbívoros y tamaño de parche de vegetación huésped: una contrastación experimental. **Revista Chilena de Historia Natural** **65**: 115–120.
- Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M. & Knops, J.M.H. 2001. Contrasting effects of plant diversity and composition on insect communities: a field experiment. **American Naturalist** **158**: 17–35.
- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H. & Tilman, D. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. **Ecological Letters** **12**: 1029–1039.
- Hawkins, B.A. & Porter, E.E. 2003. Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. **Global Ecology and Biogeography** **12**: 475–481.
- Heck, K. & Crowder, L. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems, p. 281–299. In: Bell, S., McCoy, E. & Mushinsky, H. (eds). **Habitat structure: the physical arrangement of objects in space**. Chapman and Hall, London, 438 p.
- Hill, M.P. & Oberholzer, I.G. 2000. Host specificity of the grasshopper, *Cornops aquaticum* a natural enemy of water hyacinth, p. 349–356. In: Spencer, N.R. (ed). **Proceedings of the X International Symposium on Biological Control of Weeds**. Bozeman, Montana State University.
- Humphries, P. 1996. Aquatic macrophytes, macroinvertebrate associations and water levels in a lowland Tasmanian river. **Hydrobiologia** **321**: 219–233.
- Joern, A. & Pruess, K.P. 1986. Temporal constancy in grasshopper assemblages (Orthoptera: Acrididae). **Ecological Entomology** **11**: 379–385.
- Joern, A. 2005. Disturbance by fire and bison grazing modulate grasshopper assemblages in tallgrass prairie. **Ecology** **86**: 861–873.
- Junk, W.J. 1970. Investigations on the ecology and production-biology of the "floating meadows" (Paspalo-Echinochloetum) on the Middle Amazon. I. The floating vegetation and its ecology. **Amazoniana** **2**: 449–495.
- Junk, W.J. & Piedade, M.T.F. 1993. Herbaceous plants of the Amazon floodplain near to Manaus: Species diversity and adaptations to the flood pulse. **Amazoniana** **12**: 467–484.
- Junk, W.J. & Piedade, M.T.F. 1997. Plant life in the floodplain with special reference to herbaceous plants, p. 147–186. In: Junk, W.J. (ed). **The Central Amazonian Floodplain: Ecology of a pulsing System, Ecological Studies**. Berlin, Springer, 548 p.

- Kemp, W.P. 1990. Habitat and insect biology revisited. **American Entomologist** **36**: 44–49.
- Kemp, W.P. 1992a. Temporal variation in rangeland grasshopper (Orthoptera: Acrididae) communities in the steppe region of Montana, USA. **Canadian Entomologist** **124**: 437–450.
- Kemp, W.P. 1992b. Rangeland grasshopper (Orthoptera: Acrididae) community structure: a working hypothesis. **Environmental Entomology** **21**: 462–470.
- Lewis, W. M.; S. K. Hamilton; S. L. Jones & D. D. Runnels. 1987. Major element chemistry, weathering and element yields for the Caura River drainage, Venezuela. **Biogeochemistry** **4**: 159–181.
- Magurran, E.A. 1989. **Diversidad ecológica y su medición**. Barcelona, Vedra, 200 p.
- Merriam, G. 1984. Connectivity: a fundamental ecological characteristic of landscapes. **Proceedings of the International Association for Landscape Ecology** **1**: 5–15.
- Montealegre-Zapata, F. 1996. Key for the identification of the Tettigoniidae (Orthoptera: Ensifera) from Escalarete (Buenaventura). **Cespedesia** **21**: 29–40.
- Neiff, J.J. 1979. Fluctuaciones de la vegetación acuática en ambientes del valle de inundación del Paraná Medio. **Physis** **38**: 41–53.
- Neiff, J.J. 1990a. Aspects of primary productivity in the lower Paraná and Paraguay riverine system. **Acta Limnologica Brasiliensis** **3**: 77–113.
- Neiff, J.J. 1990b. Ideas para la interpretación ecológica del Paraná. **Interciencia** **15**: 424–441.
- Neiff, J.J. 1996. Large rivers of South America: toward a new approach. **Verhandlungen des Internationalen Verein Limnologie** **26**: 167–181.
- Neiff, J. J. 1999. El régimen de pulsos en ríos y grandes humedales de Sudamérica, p. 97–145. In: Malvárez, A.I. & Kandus, E.P. (eds.). **Tópicos sobre grandes Humedales Sudamericanos**. ORCYT-MAB (UNESCO), 229 p.
- Neiff, J.J.; de Neiff, A.P. & Casco, S.L. 2001. The effect of prolonged floods on *Eichhornia crassipes* growth in Paraná River floodplain lakes. **Acta Limnologica Brasiliensis** **13**: 51–60.
- Nunes, A.L. & Adis, J. 1992. Observaciones sobre el comportamiento sexual y la oviposición de *Stenacris fissicauda fissicauda* (BRUNER, 1908) (Orthoptera, Acrididae). **Etología** **2**: 59–63.
- Nunes, A.L., Adis, J. & Mello, J.A.S.N. de 2005. Fenología de *Phlugis teres* (DE GEER, 1972) (Orthoptera: Tettigoniidae) e abundância de Artrópodos em populações de *Eichhornia crassipes* (Pontederiaceae) em um lago de Várzea na Amazônia Central. **Boletim do Museu Paraense Emílio Goeldi, Série Ciências Naturais**, **1**: 271–285.
- Oberholzer, I.G. & Hill, M.P. 2001. How safe is the grasshopper *Cornops aquaticum* for release on water hyacinth in South Africa?, p.82–88. In: Julien, M.H., Hill, M.P., Center, T.D. & Jianqing, D. (eds.). **Biological and integrated control of water hyacinth, *Eichhornia crassipes***. ACIAR Proceedings, 152 p.
- Palijan, G., Bogut, I. & Vidaković, J. 2008. The impact of inundation-isolation cycles on the culturable bacterioplankton in the Danube River floodplain. **Polish Journal of Ecology** **56**: 391–403.
- Paoli, C., Iriando, M. & García, M. 2000. Características de las cuencas de aporte, p. 27–68. In: Paoli, C. & Schreider, M. (eds.). **El río Paraná en su Tramo Medio**. Santa Fe, Universidad Nacional del Litoral.
- Parolin, P., De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Schmidt, W., Piedade, M.T.F. & Junk, W. 2004. Central Amazon floodplain forests: tree survival in a pulsing system. **Botanical Review** **70**: 357–380.
- Pdaft, R.E. 1984. Species richness, density, and diversity of grasshoppers (Orthoptera: Acrididae) in a habitat of the mixed grass prairie. **Canadian Entomologist** **116**: 703–709.
- Piedade, M.T.F. & Junk, W.J. 2000. Natural Grasslands and Herbaceous plants in the Amazon Floodplain and their Use, p. 269–290. In: Junk, W.J., Ohly, J.J., Piedade, M.T.F. & Soares, M.G.M (eds.). **The Central Amazon Floodplain: Actual Use and Options for a Sustainable Management**. Leiden, Backhuys Publishers, 584 p.
- Roberts, H.R. & Carbonell, C.S. 1979. A revision of the Genera *Stenopola* and *Cornops* (Orthoptera, Acrididae, Leptysminae). **Proceedings of the Academy of Natural Sciences of Philadelphia** **131**: 104–130.
- Rooke, J.B. 1986. Macroinvertebrates associated with macrophytes and plastic imitations in the Eramosa River, Ontario, Canada. **Archiv für Hydrobiologie** **106**: 307–325.
- Sabattini, R.A. & Lallana, V.H. 2007. Aquatic Macrophytes, p. 205–226. In: Iriando, M.H., Paggi, J.C. & Parma, M.J. (eds.). **The Middle Paraná River: Limnology of a Subtropical Wetland**. Berlin, Springer, 394 p.
- Salto, C. 1999. Manejo y Reconocimiento de Tucuras: Centro Oeste de Santa Fe y Centro Este de Córdoba. **INTA, Publicación Técnica** **59**: 1–23.
- Sánchez, N. & Wysiecki, M.L. de 1993. Abundancia y diversidad de acridios (Orthoptera: Acrididae) en pasturas de la Provincia de La Pampa, Argentina. **INTA Revista Investigaciones Agropecuarias** **24**: 29–39.
- Sands, D.P.A. & Kassulke, R.C. 1986. Assessment of *Paulinia acuminata* (Orthoptera: Acrididae) for the biological control of *Salvinia molesta* in Australia. **Biocontrol** **31**: 11–17.
- Silveira-Guido, A. & Perkins, B.D. 1975. Biological and host specificity of *Cornops aquaticum* (BRUNER) (Orthoptera: Acrididae), a potential biological control agent for waterhyacinth. **Environmental Entomology** **4**: 400–404
- Squitier, J.M. & Capinera, J. 2002. Host selection by grasshoppers (Orthoptera: Acrididae) inhabiting semi-aquatic environment. **Florida Entomologist** **85**: 336–340.
- Stoner, A.W. & Lewis, F.G. 1985. The influence of quantitative aspects of habitat complexity in tropical seagrass meadows. **Journal of Experimental Marine Biology and Ecology** **94**: 19–40.
- Strohecker, H.F., Middlekauff, W.W. & Rentz, D.C. 1968. The Grasshoppers of California (Orthoptera: Acridoidea). **Bulletin of the California Insect Survey** **10**: 1–167.
- Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984. **Insects on plants. Community Patterns and Mechanisms**. London, Blackwell, 313 p.
- Thomas, P.A. 1980. Life cycle studies on *Paulinia acuminata* (DE GEER) (Orthoptera: Pauliniidae) with particular references to the effects of constant temperature. **Bulletin of Entomological Research** **70**: 381–389.
- Thomaz, S.M., Pagiolo, T.A., Bini, L.M., Roberto, M.C. & Rocha, R.R.A. 2004. Limnological characterization of the aquatic environments and the influence of hydrometric levels, p. 75–102. In: Thomaz, S.M., Agostinho, A.A. & Hahn, N.S. (eds.). **The Upper Paraná River and its floodplain: physical aspects, ecology and conservation**. Leiden, Backhuys Publishers, 393 p.
- Thomaz, S.M., Bini, L.M. & Bozelli, R.L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. **Hydrobiologia** **579**: 1–13.
- Torrusio, S., Cigliano, M.M. & de Wysiecki, M.L. 2002. Grasshopper (Orthoptera: Acridoidea) and plant community relationships in the Argentine Pampas. **Journal of Biogeography** **29**: 221–229.
- Uvarov, B.P. 1929. Studies in the Iranian Orthoptera. I: Some new or less known Tettigoniidae. **Annuaire du Musée Zoologique de l'Académie des Sciences de l'USSR** **31**: 623–639.
- Uvarov, B.P. 1930. Saltatorial Orthoptera collected by Mr. C. L. Collenette in British Somaliland. **Annals and Magazine of Natural History** **10**: 176–185.
- Vestal, I.G. 1913. Local distribution of grasshopper in relation to plant associations. **Biological Bulletin** **25**: 141–180.
- Vieira, M.F. & Adis, J. 1992. Abundância e biomassa de *Paulinia acuminata* (DE GEER, 1773) (Orthoptera, Pauliniidae) em um lago de várzea da Amazônia Central. **Amazoniana** **12**: 337–352.
- Ward, J.V. & Tockner, K. 2001. Biodiversity: towards a unifying theme for river ecology. **Freshwater Biology** **46**: 807–819.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. **Taxon** **21**: 213–251.
- Wilson, M. V. & A. Schmida. 1984. Measuring beta-diversity with presence – absence data. **Journal of Ecology** **72**: 1055–1064.
- Zhong-Wei, G., Hong-Chang, L.I. & Ya-Ling, G. 2006. Grasshoppers (Orthoptera: Acrididae) biodiversity and grassland ecosystems. **Insect Science** **13**: 221–227.

Received 03 July 2012; accepted 13 November 2012

Associate Editor: Rodrigo F. Krüger