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Grasshopper (Orthoptera: Acridoidea) species diversity in the Pampas, Argentina

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Abstract. A study was conducted to describe the major features of geographical and temporal variation in the diversity of grassland grasshopper species (Orthoptera: Acridoidea) in different sites of the Pampas, Argentina. Species richness and relative abundance were assessed at 12 sites in eastern La Pampa and western Buenos Aires provinces, from 1994 through 1999. Mean species richness at the regional level was 10, and 34 grasshopper species were collected throughout of the study. Comparison with grasshopper species diversity from the Great Plains of North America is discussed. An evaluation of the proportions of species in each of the three distribution groups (broad, intermediate and narrow) revealed that, over all sites, broadly distributed species made up 14.7% of species composition and intermediately and narrowly distributed species made up 26.5% and 58.8%, respectively. The three top-ranked species in the studied sites were *Dichroplus elongatus*, *D. pratensis* and *Staurorhectus longicornis*. Results showed that, contrary to what was expected, one of the widely distributed species in the region (i.e. *Baeacris punctulatus*) does not always constitute one of the most abundant species. Finally, the loss of one of the historically most common species in the Pampas, *D. maculipennis*, is also discussed.

Key words. Acridoidea, diversity, grasshoppers, Orthoptera, Pampas grasslands.

INTRODUCTION

Ecologists and biogeographers have struggled to understand spatial and temporal variations in the abundance, distribution, and number of species. At the community level, the structure of an assemblage with time may greatly change in terms of both number and relative abundance of the species. Many populations of herbivorous insects fluctuate in size, although some others are relatively constant from year to year. Grasshopper communities exhibit large temporal oscillations in abundance (Gage & Mukerji, 1977; Joern & Pruess, 1986; Kemp, 1987; 1992a; 1992b; Cigliano *et al.*, 1995b) mostly attributed to changes in weather conditions (Dempster, 1963; Uvarov, 1966, 1977; Capinera & Horton, 1989; Joern & Gaines, 1990; Kemp & Cigliano, 1994; Lockwood, 1997; Schell & Lockwood, 1997).

Grasshoppers are among the most important native herbivores throughout much of the Pampas. Of the 230 grasshopper species known for Argentina, about 110 inhabit grasslands (Cigliano & Lange, 1998). The Pampas region covers approximately 15% of the country, and in the last few decades most of it has undergone increasing change in land use. Grazing and agricultural activities have been intensified, and natural pasture areas have been drastically reduced or altered (Llorens, 1995). Grasshoppers are a recurrent pest of the natural and artificial pastures of Argentina, inflicting damage on grazing systems and competing for food with the stock (Hemming & Waloff, 1972; Liebermann, 1972; De Wysiecki & Sánchez, 1992; Cigliano *et al.*, 1995a; Cigliano & Lange, 1998).

Despite the importance of grasshoppers in the Pampas, little work has been conducted on analysing the relative abundance and species composition of grasshopper communities in the area (Sánchez & de Wysiecki, 1993). The goal of this paper is to describe the major features of spatial and temporal variation in the diversity of species in different sites of this grassland region.

MATERIALS AND METHODS

Study area and collections

The study area was located in western Buenos Aires and eastern La Pampa provinces (Fig. 1) in the Pampas biogeographic region as defined by Cabrera & Willink (1973). This region encompasses a large proportion of available grassland habitat types in the country. Two sites (Santa Rosa and Carhué) were monitored from 1994 through 1999. The remaining sites were visited during 1 year (Villa Sauri, Guatraché, Padre Buodo, General Acha and El Durazno), 2 years (Alta Italia and Ojeda) or 3 years (América, Pehuajó and Castex).

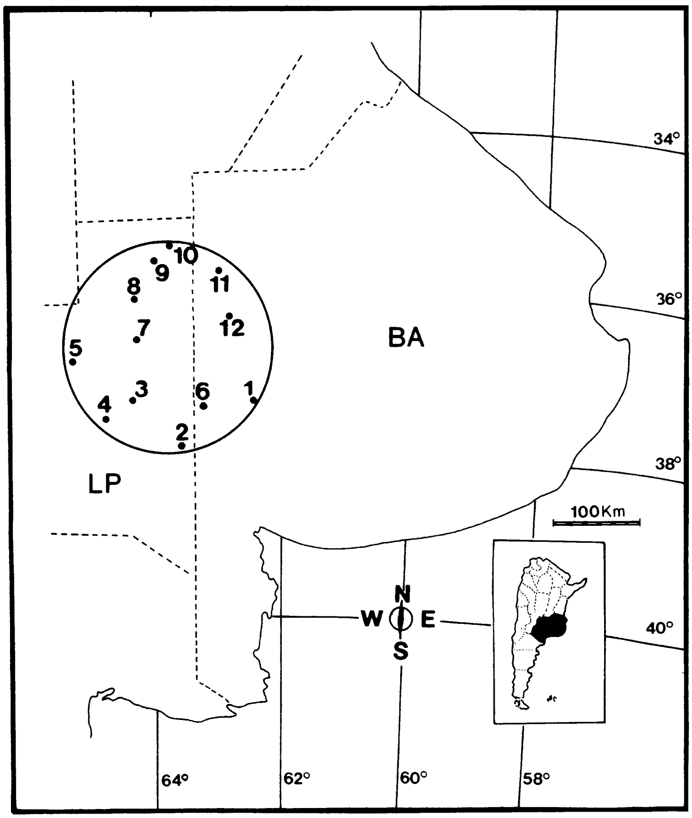

Fig. 1 Map showing sites used for collection of grassland grasshopper data 1994–99, Buenos Aires (BA) and eastern La Pampa (LP) provinces, Argentina. 1, Carhué; 2, Guatraché; 3, Padre Buodo; 4, General Acha; 5, El Durazno; 6, Villa Sauri; 7, Santa Rosa; 8, Castex; 9, Alta Italia; 10, Ojeda; 11, América; and 12, Pehuajó.

Sweep-net collections were made at each site, along vegetation transects. Sites were visited twice in the season (early January, early/mid-February) to ensure detection of species with different phenological patterns. Three hundred sweeps per site were made at each sampling period between 1000 and 1600 h under sunny sky and light winds. To reduce chances of variability caused by sampling error, collections were always made by the same two people. One should be aware of the existence of possible biases when testing hypotheses that rely on grasshopper community composition estimates obtained from sweep samples. However, studies have shown that sweep netting generally provide accurate estimates of grasshopper diversity on grasslands (Evans *et al.*, 1983; Larson *et al.*, 1999). Grasshoppers collected via sweep-net were placed in cages, and taken to the laboratory for identification to species and determination of development stages.

Analyses

Relative abundance

Of grasshopper species was calculated as the abundance of species *i* relative to the total abundance of all species collected at each site. For each year mean values from January–February were considered in the analysis.

Species distribution hierarchy

In order to examine whether the proportion of species in distribution hierarchy groups was constant over the entire region, the proportion of the species at each site that were narrowly (present at ≤ 25% of the 30 total site-years), intermediately (present at > 25 and < 75% of the 30 total site — years) and broadly (present at ≥ 75% of the 30 total site-years) distributed were computed.

Species richness

Species richness was quantified as the total number of species present in a community.

RESULTS

Grasshopper species richness

Thirty-four grasshopper species, belonging to two families and six subfamilies were recorded (Table 1). Average species richness ranged from four to 12 species per site among the 12 studied sites. Low numbers of grasshopper species per site were found in Villa Sauri (four species) and General Acha (five species). Higher values of species richness (12–16 species) were found in Ojeda (15), Alta Italia (12), Santa Rosa (16), Castex (15) and Pehuajó (12). Mean species richness at the regional level (all sites, all years) was 10.

Taxonomic diversity

From a taxonomic perspective, within the Acrididae the Melanoplinae was the most abundant and diverse subfamily (14 species belonged to this subfamily that represented 68.8% of the total grasshoppers' relative abundance) in our study, followed by the Gomphocerinae (nine species belonged to this subfamily, representing 23.8% of the total grasshoppers' relative abundance), Acridinae (three species belonged to this subfamily, representing 3.3% of the grasshoppers' relative abundance), Copiocerinae (two species of the grasshoppers caught were copiocerine representing 2.4% of the total grasshoppers' relative abundance) and Leptysminae (only one species of Leptysminae was caught representing 0.32% of the total). Only five species of Romaleinae (1.28% of the total relative abundance) were collected (Tables 1 and 2).

Relative abundance

Average relative abundance of grasshopper species from the 12 studied sites fluctuated among years (Table 1). For all the sites and years the most abundant three species (*D. elongatus*, *D. pratensis* and *S. longicornis*) constituted 63.4% of the grasshopper assemblage (Table 1).

Many species can be considered uncommon or rare. *B. punctulatus* was detected during most of the years but in low numbers (numerical rarity). Some species (*L. pulcher*) were found in reasonable numbers, in many years, but only in some locations (spatial rarity).

There were no major differences in grasshopper assemblages between the two sites that were monitored for a longer time. For Carhué the most abundant four species (*S. longicornis*, *D. elongatus*, *D. pratensis* and *L. pulcher*) constituted

Table 1 (A) Mean relative abundance (individuals/300 sweeps) patterns of grassland grasshopper species collected in Guatrache, Padre Buodo (P. Buodo), General Acha (G. Acha), El Durazno, Villa Sauri (V. Sauri), Castex, Alta Italia, Ojeda and América, in the Pampas, Argentina 1994–99

Family/subfamily/species	Guatrache 1994	P. Buodo 1994	G. Acha 1994	El Durazno 1995	V. Sauri 1995	Castex 1995	Castex 1996	Castex 1997	Alta Italia 1997	Alta Italia 1999	Ojeda 1997	Ojeda 1999	América 1997	América 1998	América 1999
ACRIDIDAE															
Acridinae															
Allotruxalis strigata (Bruner)	13	4	7							6	2	2	3	2	
Covasacris albitarsis Liebermann									1		4	5			
Parorphula graminea Bruner						1									
Leptysminae															
Leptysma argentina Bruner															
Melanoplinae															
Atrachelacris gramineus Bruner				1											
Baeacris pseudopunctulatus (Ronderos)										8				10	
B. punctulatus (Thunberg)	3	1	4	30	86	17	1	1	1	14	1		9		
Dichroplus conspersus Bruner										3					
D. elongatus G. Tos	6	31	68	9		16	22	31	1	31	8	22	75	65	51
D. pratensis Bruner	33	14	7	6	7	37	36	10	8	14	6	13	4	1	
D. vittatus Bruner	6	2		19		5	4	17	9						
Leiotettix pulcher															
Neopedies brunneri G. Tos	6	16	14	30					4	6	3			1	
Ronderosia bergii (Stal)							1	1					1		
R. forcipatus (Rehn)											3				
Scotussa cliens (Stal)											1				
S. daguerrei Liebermann		3													
S. lemniscata (Stal)					1			1					2	9	26
Gomphocerinae															
Amblytropidia australis Bruner								14	1		13		1	8	21
Borellia bruneri (Rehn)							1	1		6		5			
Dichromorpha australis Bruner												1			
Euplectrotettix ferrugineus Bruner				2											
Orphulella punctata De Geer					6									1	
Rhammatocerus pictus Bruner	1					2	1	1	5		4		1		
Scyllinula variabilis (Bruner)		1						1							
Sinipta dalmani Stal							1	1			1	1	1	1	
Staurorhectus longicornis G. Tos	28	25		3		21	17	19	63	3	42	43	2	1	
Copiocerinae															
Aleuas lineatus Stal	3	3					1	1	5	3	9	7		1	
A. vitticolis Stal									1		1	1			

Table 1 (A) *continued.*

Family/subfamily/species	Guatrache 1994	P. Buodo 1994	G. Acha 1994	El Durazno 1995	V. Sauri 1995	Castex 1995	Castex 1996	Castex 1997	Alta Italia 1997	Alta Italia 1999	Ojeda 1997	Ojeda 1999	América 1997	América 1998	América 1999
ROMALEIDAE															
Romaleinae															
Diponthus argentinus Pictet & Saus.						1		1							
Chromacris speciosa Thunberg							1								
Xyleus laevipes (Stal)										3			1		2
Zoniopoda omnicolor (Blanchard)										3					
Z. tarsata (Serville)	1						14	1	1		2				
Total individuals/300 sweeps	98	74	85	159	279	821	792	405	233	35	302	259	226	169	72

Table 1 (B) Mean relative abundance (individuals/300 sweeps) patterns of grassland grasshopper species collected in Pehuajó, Carhué and Santa Rosa, in the Pampas, Argentina 1994–99

Family/subfamily/species	Pehuajó 1997	Pehuajó 1998	Pehuajó 1999	Carhué 1994	Carhué 1995	Carhué 1996	Carhué 1997	Carhué 1998	Carhué 1999	Santa Rosa 1994	Santa Rosa 1995	Santa Rosa 1996	Santa Rosa 1997	Santa Rosa 1998	Santa Rosa 1999
ACRIDIDAE															
Acridinae															
Allotruxalis strigata (Bruner)			2				1				1			1	
Covasacris albitarsis Liebermann									8						
Parorphula graminea Bruner					2	2		6		1					
Leptysminae															
Leptysma argentina Bruner		1	11												
Melanoplinae															
Baeacris pseudopunctulatus (Ronderos)		4	2						3					1	1
B. punctulatus (Thunberg)				2	4	7	5	4		8	8	3	1	3	1
Dichroplus conspersus Bruner							1							1	
D. elongatus G. Tos	86	22	18	18	50	8	20	35	38	10	25	17	15	13	20
D. pratensis Bruner		1		3	11	8	16	14	15	12	30	24	38	22	13
D. vittatus Bruner										21	13	22	6	1	
Leiotettix pulcher Rehn		2		12	2	10	22	2	6						
Neopedies brunneri G. Tos										12	3	2	3	2	6
Ronderosia bergii (Stal)	8									3	1	1		1	2
Scotussa daguerrei Liebermann				1	5	10		1	3	2	1	2	1	1	
S. lemniscata (Stal)	1	30	42	1	5			5	9	1	1				

Table 1 (B) *continued.*

Family/subfamily/species	Pehuajó			Carhué						Santa Rosa					
	1997	1998	1999	1994	1995	1996	1997	1998	1999	1994	1995	1996	1997	1998	1999
Gomphocerinae															
Amblytropidia australis Bruner	1	13	2					4	3				1	1	
Borellia bruneri (Rehn)														1	1
Rhammatocerus pictus Bruner								1		1	2	1	1	1	1
Sinipta dalmani Stal						2		1				1	1	1	
Staurorhectus longicornis G. Tos	11	16	13	62	18	48	35	24	6	26	12	21	27	47	52
Copiocerinae															
Aleuas lineatus Stal	1	1	6	1	2	4		3	9	2	2	5	6	3	2
A. vitticolis Stal		1										1			
ROMALEIDAE															
Romaleinae															
Diponthus argentinus Pictet & Saus.						1									
Chromacris speciosa Thunberg										1					
Xyleus laevipes (Stal)					1										
Zoniopoda omnicolor Blanchard			4								1				1
Z. tarsata (Serville)	1														
Total individuals/300 sweeps	430	352	47	232	98	153	129	112	30	122	254	440	296	628	409

Table 2 Relative abundance (%) of families and subfamilies registered at each site in the Pampas, Argentina 1994–99

	Carhué	Sta. Rosa	Castex	Guatraché	P. Buodo	G. Acha	El Durazno	V. Sauri	Alta Italia	Ojeda	América	Pehuajó	x ± SE
ACRIDIDAE													
Acridinae	3.10	0.41	0.16	13.00	4.00	7.00	—	—	3.50	6.50	1.60	0.66	3.30 ± 1.10
Leptysminae	—	—	—	—	—	—	—	—	—	—	—	3.85	0.32 ± 0.32
Melanoplinae	59.30	62.20	66.70	53.00	67.00	93.00	95.00	93.50	49.50	28.50	85.40	72.74	68.80 ± 5.87
Gomphocerinae	34.00	33.60	26.70	29.50	26.00	—	5.00	6.50	39.00	55.00	11.60	18.50	23.80 ± 4.64
Copiocerinae	3.10	3.50	0.66	3.00	3.00	—	—	—	4.50	9.00	0.16	2.76	2.40 ± 0.75
ROMALEIDAE													
Romaleinae	0.40	0.41	5.80	1.50	—	—	—	—	3.50	1.00	1.24	1.50	1.28 ± 0.50

77% of the grasshopper assemblage. The most abundant four species (*D. elongatus*, *D. pratensis*, *S. longicornis* and *D. vittatus*) at Santa Rosa constituted 82.2% of the assemblage.

Species distribution hierarchy

With the arbitrary break-points that were selected in this study for the grassland grasshopper species distribution hierarchy for the Pampas (identical to the groupings suggested by Kemp, 1992a), results suggest that there are five broadly, nine intermediately, and 20 narrowly distributed species. From a taxonomic perspective, of the 14 species of Melanoplinae collected, three fell within the broadly distributed species group, five in the intermediatelly distributed species group, and six within the narrowly distributed group (Table 3). Of the nine species of Gomphocerinae collected, one fell within the broad species group, three fell within the intermediate, and five fell within the narrowly distributed species group. The Acridinae and Romaleinae showed strong representation in the narrowly distributed species group, but were conspicuously absent from the broadly and intermediately distributed species group. Of the two species of Copiocerinae collected one fell within the broad species group and the other one fell within the narrowly distributed species group. The only Leptysminae species collected fell within the narrowly distributed group.

DISCUSSION

Species richness values documented in this study are consistent with those observed by Sánchez & de Wysiecki (1993) in different pastures of La Pampa province, where species richness values ranged from seven to 12.

Species richness values reported from other grassland regions of the world seem to be slightly higher than the values recorded in the Argentine Pampas. Kemp (1992b) analysed the interspecific associations of rangeland grasshoppers in the Gallatin Valley, Montana, USA, during 1988–90 when regional densities were low. He found that although 40 rangeland species were collected valley-wide throughout the study, mean species richness at the habitat type level ranged from 10 to 17 (Kemp, 1992b). Similar values were found in previous studies from the sandhills grassland of Nebraska (Joern & Pruess, 1986) and from shortgrass prairie in north-eastern Colorado (Capinera & Thompson, 1987). Kemp (1992a) has shown that species richness increases with grasshopper population density; presumably, rare species become sufficiently abundant to reach the detection threshold. Although grasshopper population densities were not estimated in this study, variations in the total of individuals collected in 300 sweep-nets were observed between years. In those localities that were visited for longer periods (Santa Rosa and Carhué) the number of specimens collected varied from 122 to 628 in Santa Rosa and from 30 to 232 in Carhué (Table 1). However, grasshopper species richness values did not varied markedly, ranging from eight to 10 in Carhué and from 13 to 16 in Santa Rosa.

Geographical, evolutionary, and historical factors play a strong role in determining a community's composition, diversity and other attributes of its organization (Schluter & Ricklefs, 1993). The Pampas and the Great Plains of North America have a number of remarkable ecological similarities in grasshopper fauna (Gangwere & Ronderos, 1978; Vickery, 1989); however, there are some striking differences in their diversity. The fauna of the North American Great Plains includes 200–250 acridid species (Otte, 1981, 1984; Lockwood *et al.*, 1994). For the state of Wyoming only, 113 species of acridids are known (Shambaugh & Lockwood, 1993), compared to about 230 known species for all of Argentina (Cigliano & Lange, 1998). Although the US grasslands appear to have greater species diversity, the Pampas grasslands have a greater diversity of higher acridid taxa, two families (Acrididae and Romaleidae) and six subfamilies (Oedipodinae, Melanoplinae, Gomphocerinae, Acridinae, Cyrtacanthacridinae and Romaleinae), vs. three families (Acrididae, Romaleidae and Ommexechidae) and nine subfamilies (Melanoplinae, Gomphocerinae, Copiocerinae, Leptysminae, Cyrtacanthacridinae, Acridinae Romaleinae, Ommexechinae and Aucacrinae). In both regions, the Melanoplinae is one of the most common subfamily and, according to Gangwere & Ronderos (1978), one parallel between the two faunas is furnished by the North American genus *Melanoplus* and its ecological equivalent, the South American genus *Dichroplus*. Both include many species that are strikingly similar in ecology,

Table 3 Grassland grasshopper species based on their frequency distribution across the 12 sites, in the Pampas, Argentina 1994–99

	Broadly distributed (≥ 75–100% of all sites)	Intermediately distributed (> 25 < 75% of all sites)	Narrowly distributed (0- ≤ 25% of all sites)
ACRIDIDAE			
Acridinae			
Allotruxalis strigata		40	
Covasacris albitarsis			13
Parorphula graminea			17
Leptysminae			
Leptysma argentina			7
Melanoplinae			
Atrachelacris gramineus			3
Baeacris pseudopunctulatus			23
B. punctulatus	77		
Dichroplus conspersus			10
D. elongatus	97		
D. pratensis	90		
D. vittatus		40	
Leiotettix pulcher			23
Neopedies brunneri		47	
Ronderosia bergii		30	
R. forcipatus			7
Scotussa cliens			3
S. daguerrei		37	
S. lemniscata		47	
Gomphocerinae			
Amblytropidia australis		43	
Borellia brunneri			20
Dichromorpha australis			3
Euplectrotettix ferrugineus			3
Orphulella punctata			7
Rhammatocerus pictus		47	
Scyllinula variabilis			7
Sinipta dalmani		37	
Staurorhectus longicornis	90		
Copiocerinae			
Aleuas lineatus	77		
A. vitticolis			17
ROMALEIDAE			
Romaleinae			
Diponthus argentinus			10
Chromacris speciosa			7
Xyleus laevipes			13
Zoniopoda omnicolor			13
Z. tarsata			20

behaviour and economic importance (Gangwere & Ronderos, 1978; Vickery, 1989). The Gomphocerinae also play an important role in both faunas. However, there is one essential difference in the diversity of the two ecosystems. In terms of taxonomic richness, the US grasslands also have many Oedipodinae species (Otte, 1981, 1984; Capinera & Thompson, 1987; Pfadt, 1988; Kemp *et al.*, 1990) while the Argentine fauna has only one species of Oedipodinae (*Trimerotropis pallidipennis*), and it is not common in the Pampas region. On the other hand, the Acridinae subfamily, highly diversified in Argentina, is represented by only one species (*Metaleptea brevicornis*) in the Great Plains. The remaining subfamilies of Acrididae collected in our study are endemic taxa from South America. Finally, the Romaleidae, present in both ecosystems, is more diversified in the Pampas.

According to Ricklefs & Latham (1993) contemporary patterns of diversity may originate in part from the unique history and biogeography of each region. Amedegnato & Descamps (1979) considered that the South American Acridoidea fauna includes 70% of autocthonal elements developed before or during the Tertiary and 30% elements resulting from a recent Plio-Pleistocenic immigrants. As several authors suggested (Amedegnato, 1977; Carbonell, 1977; Amedegnato & Descamps, 1979) the South American Acridoidea fauna seems to be constituted by the superposition of various faunistic strata corresponding to different evolutionary stages and geological periods. The Romaleidae and the endemic South American Ommexechidae are included in the first of these strata, and both are considered to have their origin in the South American part of Gondwana (Carbonell, 1977), or the Romaleidae may have resulted from an ancient vicariance event separating South America from North America and the Old World, while the Ommexechidae may be from southern South America (Amedegnato & Descamps, 1979; Amedegnato, 1993). The Leptysminae and the Copiocerinae subfamilies belong to the second stratum that is constituted by five exclusively Neotropical subfamilies of Acrididae (Carbonell, 1977). Finally, the Melanoplinae, Gomphocerinae and Acridinae subfamilies are included in the most recent of the faunal strata. Amedegnato (1977) and Carbonell (1977) hypothesized that these three subfamilies are recent elements of the Neotropical acridomorph fauna which must have invaded South America from the Nearctic region during the late Cenozoic.

In our study, the evaluation of the proportions of the species in each of the three distribution groups (broad, intermediate and narrow) revealed that, over all sites, broadly distributed species made up 14.7% of species composition and intermediately and narrowly distributed species made up 26.5% and 58.8%, respectively. Broadly distributed species were primarily melanoplines; coincident results were obtained by Kemp (1992b).

Results showed that few species can be considered common, and many species uncommon or rare. In fact, we found that there may be more than one form of rarity involved in the Pampas. Some species (such as *B. punctulatus*) were collected every year, from almost all sites but in low numbers (numerically rarity), while some others (*L. pulcher*) were found in reasonable numbers, in many years, but only in some locations (spatial rarity). As Brown (1988) has noted, the distribution of abundances within different biotas tends to be quite similar. Although the same specific species–abundance relationship may not characterize all assemblages, virtually all floras and faunas are comprised of a few common species and many are rare ones.

The three top-ranked species in the studied sites appear to be *D. elongatus*, *D. pratensis*, and *S. longicornis*. Results showed that *D. vittatus* in Santa Rosa, and *L. pulcher* in Carhué play an important role in these communities together with the other three top-ranked species already mentioned.

Also, our results showed that one of the most widely distributed species in the region (i.e. *B. punctulatus*) do not always constitute one of the top rank species. Notably, this pattern is not congruent with the positive relationship between the distribution and abundance of species that have been observed by ecologists. According to Hanski *et al.* (1993) species with more extensive distributions tend to be more abundant locally than species with more restricted distributions. It is worth mentioning that *B. punctulatus* is the most widely distributed species of South American Melanoplinae, occurring in Brazil, Argentina, Uruguay, Paraguay, Bolivia, Peru, Ecuador, Colombia, Venezuela and Guyanas (Ronderos & Cigliano, 1991).

Finally, an interesting outcome of this study becomes obvious when comparing our results with grasshopper diversity patterns observed in the past. Liebermann (1972) described eight acridological regions for Argentina based on the distribution and abundance of what he considered the 12 most economically important grasshopper species. In his scheme, the western half of Buenos Aires and eastern La Pampa ('region II') was characterized by the presence, among other species, of what he called 'one of the most harmful grasshopper species in South America', *Dichroplus maculipennis* (Liebermann, 1966, 1972). It is worthy of particular note that although this species is still extremely abundant in the valleys of western Patagonia, it was not collected in our study or in earlier studies at other sites of La Pampa and Buenos Aires provinces (de Wysiecki & Sánchez, 1992; Lange, 1992; Sánchez & de Wysiecki, 1993; Cigliano *et al.*, 1995a). Indeed, a surprising aspect of this study is not the loss of a rare species, but of one of the most common species. According to MacArthur & Wilson (1967), the number of species in a habitat should represent a balance between forces that allow species to invade and persist and forces that drive species to local extinction. Thus, it would be interesting to investigate which are the forces that have driven populations of *D. maculipennis* so low that they were not sampled in the studied years or that have driven this species to local extinction.

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