



Grasshopper (Orthoptera: Acridoidea) diversity in the Pampas region of Argentina: status as revealed by long-term sampling

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Abstract

This study, spanning 37 years, assessed the diversity of grasshopper communities across much of the Pampas region. Ninety-five sampling sites were established in Buenos Aires and La Pampa provinces. Five zones were defined: Northeast (NE), Northwest (NW), Southeast (SE), Southwest (SW), and West (W). Each site was categorized according to the dominant vegetation. A total of fifty grasshopper species from three families were collected. Acrididae was the most diverse (41 species). Rarefaction analysis indicated that the SE was the zone with the lowest species richness (Q0). The NE, SW, and W showed higher diversity (Q1), while NE was less diverse according to Q2. The PCA revealed varying abundances of species across zones, with some species more abundant in specific areas (e.g., *Dichroplus maculipennis* and *Borellia bruneri* in SE). The highest species count (50) was in grassland with grass dominance. The CA showed significant associations between grasshopper species and different grasslands (e.g., *Covasacris pallidinota*, *Dichroplus maculipennis*, and *Parorhphula graminea* in Halophilous grassland). Beta diversity highlighted species turnover as key component in the SW, W, and NE, while in the SE it was nestedness. In the NW, turnover and species loss components affected beta diversity. Communities were dominated by a few species, with three or four species representing over 50% of the community. Some abundant species declined or disappeared over time, while others appeared later. These results provide the first quantitative analysis of the grasshopper fauna across much of one of South America's most heavily modified ecosystems, the grasslands of the Argentine Pampas region.

Implications for insect conservation For decades, the Pampas grasslands have been undergoing a significant transformation, with the replacement of grasslands by highly productive agroecosystems. Grasshoppers are among the most abundant insects in grasslands. Therefore, understanding whether this transition to intensive agroecosystems has affected the richness and diversity of grasshoppers is an important question. The results of this study highlight the importance of long-term ecological research (37 years), which has coincided with a period of significant agricultural intensification across the region. This intensification has resulted in a homogenization and fragmentation of natural grasslands, with consequent impacts on associated fauna. The observed trends of this study probably reflect the current state of the grasshopper fauna in the Pampas during the last decades, in an increasingly managed agroecosystem context.

Keywords Grasshopper communities · Grasshopper diversity · Grasslands · Agroecosystem

Introduction

The grasslands of the Pampas region represent approximately 15% of Argentina's land area and are considered one of the most modified biomes due to the intense livestock and agricultural use to which they have been subjected since the nineteenth century (Viglizzo et al. 2011; Piquer-Rodríguez et al. 2018; Ricard et al. 2019). Given the productive capacity of this region, the Pampas grasslands have been strongly replaced by agroecosystems that substantially modified their structure and functioning (Viglizzo et al. 2001;

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Baldi and Paruelo 2008; Bilenca et al. 2009). Until the early 1990s, production in the Pampas increased by taking over still existing natural lands. Production was characterized by extensive livestock farming on native grasslands, annual crop rotations under multi-pass tillage coupled with extensive livestock ranching, and annual crops expansion to land that still remained covered by grasslands and perennial pastures. Once this option was exhausted, additional increase in productivity was achieved through more intensive use of external inputs, technology, and management (Viglizzo et al. 2011; Modernel et al. 2016; Piquer-Rodríguez et al. 2018; Ricard et al. 2019). Diverse studies indicate that among the most important changes that occurred in production systems during the 1990s were the discontinuation of crop-livestock rotation, the incorporation of new crop varieties (genetically modified cultivars), the widespread use of new-generation pesticides, the adoption of no-till farming, and a strong tendency towards monoculture (Ghersa 2005; Aizen et al. 2009; Andrade et al. 2017; Leguizamón 2016). Changes in land use were also associated with increased livestock production via feedlots (Gavier-Pizarro et al. 2012; González-Roglich et al. 2015). Extensive areas are cultivated with soybean as summer crop and wheat as winter crop followed by oats, corn, sunflower, and natural or semi-natural grassland for cattle grazing (Lara and Gandini 2014).

The replacement of natural systems such as grasslands by agroecosystems is one of the main forces of change and loss of biodiversity on a global scale (Fumy et al. 2020). The loss, homogenization, and fragmentation of habitats resulting from agroecosystem development translate directly into a decrease in diversity (Benton et al. 2003; Tscharrntke et al. 2005; Fahrig 2019) by means of reductions in number of species, their abundance, and by variations in the distribution of populations (Fahrig 2003; Horváth et al. 2019), affecting ecological functions and the ecosystem services that these systems provide (Foley et al. 2005; Paruelo et al. 2007; Carreño and Viglizzo 2011; Mastrangelo et al. 2015).

Insects are the largest and most diverse group of animals. They are key components in the provision, regulation, and dynamics of many ecosystem services such as pollination, herbivory, and pest control, among others (Schowalter 2013; Ebeling et al. 2018; Noriega et al. 2018; Wagner 2020). Grasshoppers are dominant insect herbivores in grassland ecosystems worldwide and play a key role as primary consumers, as components of the trophic network, and in the cycling of nutrients and energy (Song et al. 2018). Like other groups of insects, grasshopper communities usually exhibit great variability in the composition and abundance of species (Jonas and Joern 2007). Some are considered of economic importance due to the damage they cause to pastures and crops in times of outbreaks (Lecoq and Zhang 2019). Grasshopper communities are also sensitive to disturbances (Gebeyehu and Samways 2003; Fartmann et al.

2022). They respond with variations in diversity, abundance, and composition to different management practices such as grazing intensity, fire frequency, and agriculture activities (Joern 2005; Hochkirch and Adorf 2007; Bazelet and Samways 2011). In general, as a consequence of these activities, the diversity of plant communities decreases, generating a simplification of species in grasshopper communities (Guo et al. 2006; Joern and Law 2013). This situation is frequently observed in overgrazed natural pastures (Joern 2005) and in crops where the richness of plant species decreases to a minimum (Carrasco et al. 2012). Several authors point out that agriculturalization in the Pampas has affected biodiversity patterns across different taxa (Medan et al. 2011, Codesido et al. 2011; Weyland et al. 2014).

Considering the ecological and economic importance of grasshoppers in grassland ecosystems and the agricultural intensification process of the last decades in the Pampas, it is important to question whether this transition to highly productive agroecosystems has caused a change in the richness and diversity of grasshoppers in different areas of the region over time. Thus, the main objective of this study was to evaluate the diversity of grasshopper communities in different areas of the Pampas region (Buenos Aires province and eastern La Pampa province) over a period of 37 years.

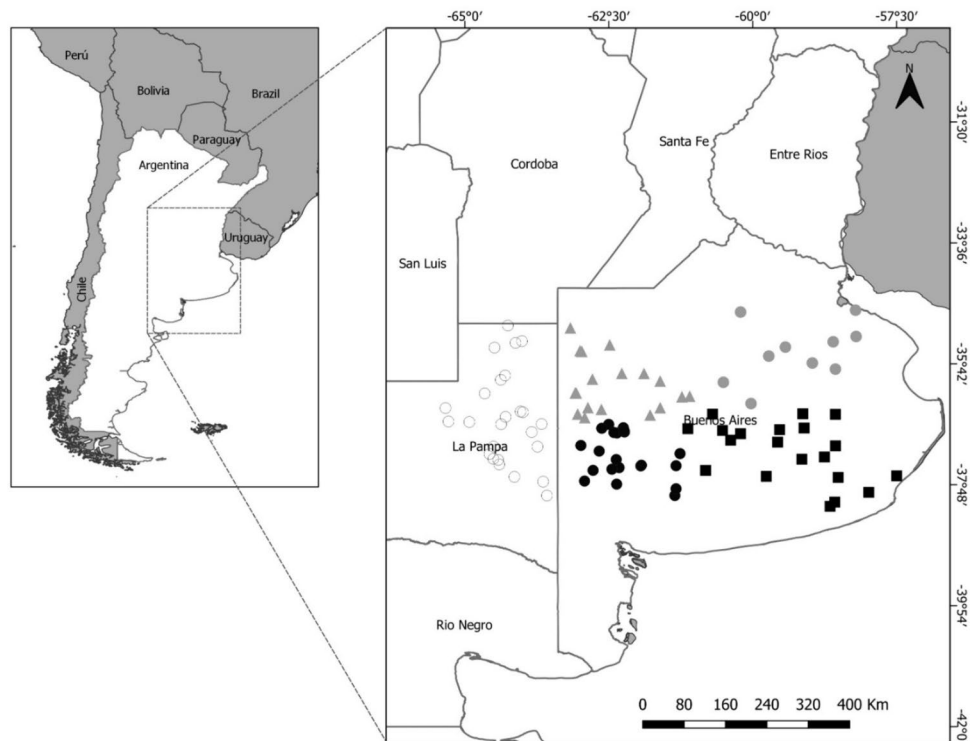
Methods

Study area and sampling sites

The Pampas region (30–40°S, 55–65°W), one of the world largest grasslands (Bilenca and Miñarro 2004; Oyarzabal et al. 2020), comprises an extension of land of around 52 million ha where a temperate climate with a hot summer predominates. The average temperature varies between 17 °C in the North and 14 °C in the South, and the rainfall, mostly concentrated in spring and summer, ranges from 1000 mm in the NE to 600 mm in the SW. The variability of rainfall increases from NE where crops predominate to SW, where lands are mainly allocated to mixed cattle–crop activities (Viglizzo et al. 1997; Oyarzabal et al. 2020). The Pampas region can be subdivided into six vegetation units, that is, areas with relatively homogeneous physiognomy and floristic composition, sharing geomorphic, hydrologic, and edaphic features (Soriano et al. 1992; Oyarzabal et al. 2018). The units are the Rolling Pampa, Mesopotamic Pampa, Flat Inland Pampa, West Inland Pampa, Flooding Pampa, and Southern Pampa.

Ninety-five sampling sites were established in different areas of Buenos Aires and La Pampa provinces. They were grouped into five areas: Northeast (NE) with 11 sites, Northwest (NW) with 18, Southeast (SE) with 20, Southwest (SW) with 21, and west (W) with 25 sites (Fig. 1), The sampling

Fig. 1 Distribution of the sampled sites in different zones of “Buenos Aires” and “La Pampa” provinces. On the left, a map of Argentina and neighboring countries, and on the right, a detailed view of the provinces and the sampled sites



sites were categorized according to the dominant vegetation in five categories: grazed grassland with grass dominance (GG), grazed grasslands with native and exotic dicotyledonous dominance (DG), halophilous grassland (HG) that comprised a short grass steppe dominated by a sparse cover of the grass *Distichlis spicata*, sown pastures (P), and summer crops (C) (mainly soy, corn, and sunflower) (Torrusio et al. 2002; Mariottini et al. 2013).

Grasshopper sampling

Grasshoppers were sampled in summer from 1982 to 2018. Sampling was conducted in either January or February when most of grasshopper populations are at their peak. The sites of sampling were visited multiple times during the study period, at least 6 times each of them. Species composition of communities and abundance of each species were determined from a total of 604 samples, each containing all the grasshoppers captured with 200 sweeps of entomological nets (diameter: 40 cm, depth: 75 cm, arc of sweep: 180°) along transects at each site as described by Evans (1988), a method acknowledged to provide representative samples of grasshopper communities (Larson et al. 1999). Four transects of 50 net sweeps each were made from a central point at 90° from each other as described by Bardi (2013). Grasshoppers collected were placed in plastic bags, kept in portable coolers, and taken to the laboratory for identification of species. Species richness was quantified as the total number of species present in a community and the relative

abundance of grasshopper species was calculated as the abundance of species relative to the total abundance of all species collected at each site.

Data analysis

A linear discriminant analysis was performed in order to evaluate if grouping of sampling sites by zones (NE, NW, SE, SW, W) was sound according to the degree of homogeneity in terms of climatic variables. Different variables of precipitation and temperature were taken into account, such as the mean annual temperature (BIO1), the annual precipitation (BIO12), the seasonality in precipitation (coefficient of variation) (BIO15), the maximum temperature of the warmest month (BIO5) and the minimum temperature of the coldest month (BIO6). Temperature and precipitation of sites in each zone were obtained from Worldclim (Fick and Hijmans 2017) and Argentina's National Meteorological site (<https://www.smn.gob.ar/>).

In order to know the species richness of each sampling zone and the presence and abundance of rare species, the nonparametric estimators Chao1 and ACE were used. Chao1 uses the numbers of singletons and doubletons to estimate the number of undetected species because undetected species information is mostly concentrated on those low-frequency counts (Chao and Chiu 2012, 2016). The estimator abundance-based coverage estimator (ACE) proposes that the observed species are separated into rare (those with an abundance of less than 10 individuals) and abundant groups.

Only data in the rare group is used to estimate the number of undetected species (Chao et al. 1992). The Spade online software was used (<https://chao.shinyapps.io/SpadeR/>).

The comparison of grasshoppers' diversity between the different zones was performed by means of Hill numbers and rarefaction-extrapolation curves (Chao et al. 2014). For this analysis, the total abundance of every grasshopper species in each zone was considered. Three indexes from Hill numbers were used: Species richness ($Q=0$), the diversity of rare and common species ($Q=1$, the exponential of Shannon entropy), and the diversity of dominant species ($Q=2$, Simpson diversity). These indexes are widely accepted as being the most meaningful measures of species diversity (Ellison 2010). The significance of the comparisons between indexes was made through rarefaction/extrapolation curves and the overlapping of their confidence intervals. The 95% confidence intervals were built using the bootstrap method (100 replicates) and each curve was extrapolated to double the overall abundance (sample size) (Hsieh et al. 2016). Rarefaction and extrapolation were performed for sample size and for sample coverage. The first is the traditional method of applying rarefaction and extrapolation, but using sample coverage has recently been shown to be more reliable (Chao and Jost 2012). While the sample size is simply the number of individuals in a sample, sample coverage is the proportion of individuals in a community that belongs to the species represented in the sample. In addition, the sampling effort was evaluated by the sample coverage estimator, which indicates the proportion of the total number of individuals in a community that belongs to the taxa represented in the sample (Chao et al. 2014). The analyses were done using iNext online software: iNEXT.4steps https://chao.shinyapps.io/iNEXT_4steps/ (Chao et al. 2020).

In addition, in order to analyze the abundance of the species in different zones and the structure of covariation between them, a principal components analysis was carried out taking the study zones as a classification factor. Due to the fact that in most of the sampling sites, the abundance of some species was very low, or they were not present, a species selection criterion was proposed. Those species in which the accumulated relative abundance along samplings exceeded the value of 50% were considered. Consequently, 19 of the 50 species were used in the analyses. In the rest of analyzes we worked with all the species.

To analyze the association between the presence of different grasshoppers and the type of plant community a simple correspondence analysis was performed. It worked with the contingency of both variables, the type of plant community, and the abundance of the registered species.

Finally, to assess the degree of differentiation in terms of species composition over time in each study area, a beta diversity analysis was performed. Beta diversity may reflect two different phenomena, spatial species turnover and

nestedness of communities, which result from two opposite processes, namely species replacement and species loss, respectively. For these analyses, the Baselga method was used (Baselga 2010; Baselga and Orme 2012), applying the Sørensen and Jaccard indexes (β_{sor} and β_{jac}) and their respective turnover (β_{sim} and β_{jtu}) and nestedness (β_{sne} and β_{jne}) components. We compute the proposed indexes pairwise (Functions: beta. pair; beta) and multiple (Functions: beta. multi) comparisons. Statistical analysis was performed with GNU R statistical software (FactoMineR Packages for multivariate analysis and betapart packages for Beta diversity analysis).

In order to obtain an estimation of the changes in agricultural dynamics that occurred during the study period data were retrieved from the Ministry of Agriculture, Livestock and Fisheries web site (<https://datosestimaciones.magyp.gob.ar/reportes.php?reporte=Estimaciones>). Total cultivated area (ha), production (tons), and yield (kg/ha) were graphed for the most significant crops (oat, barley, corn, sunflower, soybean, wheat) over time for the counties where sampling sites were located.

Results

Results of the linear discriminant analysis based on climatic variables of the 95 sites agreed with the initial grouping of sites into the five different zones (NE, NW, W, SE, SW), suggesting a sound classification of the sites with a minimum error of 12.75% (11 sample sites) (Fig. 2). The climatic variables that mainly contributed to the discrimination of zones in the first canonical axis were BIO 01 (2.83) and BIO 05 (− 2.19) (Table 1). The sites in the NW had an average performance concerning these variables, while the sites in the W displayed an opposite behavior to those in the NE and SE. In the second discriminant axis, the variables that contribute the most to the classification were BIO 05 (0.73) and BIO 15 (− 0.64). In this axis, the NE was positively associated with the average annual temperature, while the SE and SW were associated with greater precipitation seasonality.

Throughout the entire study, a total of 85,956 grasshoppers were collected, belonging to 50 species in three families (Acrididae, Ommexechidae, Romaleidae). Acrididae was the most diverse family with 41 species (82%) followed by Romaleidae with 8 (16%) and Ommexechidae with one (2%). Within Acrididae, the subfamily Melanoplinae was the most abundant and species-rich with 19 species, Gomphocerinae with twelve, and Acridinae with five. Copiocerinae and Leptysminae had two species each, and Oedipodinae had only one (Table 2). The species richness registered in each zone varied between 29 in the NE and 42 in the W (Tables 2 and 3). According to the ACE estimator, the proportion of rare species in the

Fig. 2 Results of the linear discriminant analysis based on climatic variables of the different sampled sites sampled. SW southwest, SE southeast, W west, NW northwest, NE northeast

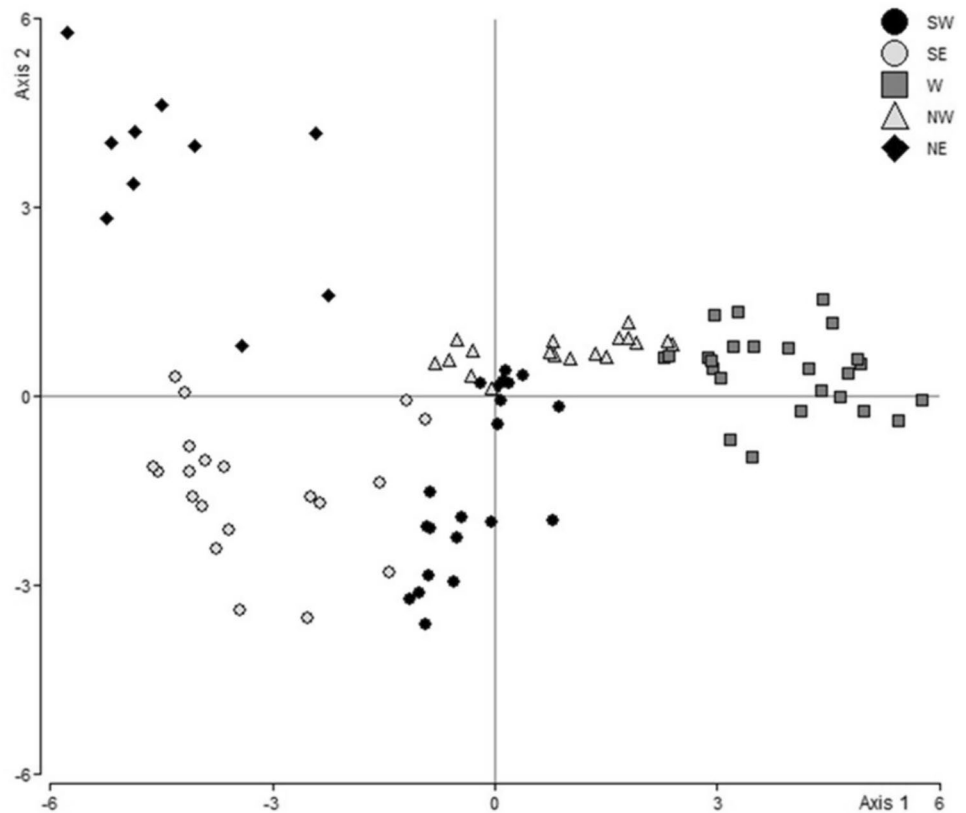


Table 1 Discriminant functions of linear analysis of different climatic variables mean annual temperature (BIO1), maximum temperature of the warmest month (BIO5) and the minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), seasonality in precipitation (coefficient of variation) (BIO15)

	Axis 1	Axis 2
BIO01	2.83	0.39
BIO05	-2.19	0.73
BIO06	-1.78	0.36
BIO12	-1.23	0.30
BIO15	0.97	-0.64

total species of each zone was higher in the sites located in the NE (16 of the 29 collected species had less than 10 individuals: 55.17%) (Table 3). In the NW, rare species represented 44.1%, while in the W, SW, and SE they represented 39.1%, 33%, and 28.5%, respectively.

The sampled completeness profiles (Fig. 3) showed that for $Q=0$, the estimated sample completeness for the NW zone was 69%, indicating a higher proportion (31%) of rare species (singletons and doubletons) that was not detected. In contrast, the NE had a lower percentage of species not detected at 15%, while the W and SW zones had 5%, and the SE had 3%. Curves for diversity orders $Q=1$ and $Q=2$ stabilized, and the sample completeness profile reached 100%, meaning that the asymptotic diversity estimates for these two indexes worked satisfactorily to infer true diversities and

nearly all abundant and highly abundant species had been found for each assemblage.

The rarefaction and extrapolation curves based on the individuals' number suggest that the stabilization of Q_0 occurred at approximately 2000 individuals in each zone. There was a significant difference in species richness between the SE and the other sampling zones when the same number of individuals was considered. However, when Shannon diversity (Q_1) was taken into account, the NE, SW, and W zones exhibited significantly higher diversity and richness than the NW and SE zones (Fig. 4). In terms of Simpson diversity (Q_2), only the NW zone had significantly lower diversity compared to the other zones (see Fig. 4). When standardized coverage of 99.9% was applied, the species richness, Shannon diversity, and Simpson diversity results between the four zones were consistent with the rarefaction curves by individuals, with the NW zone exhibiting the lowest diversity. These differences were statistically significant as indicated by non-overlapping 95% confidence bands.

Regarding the presence of species in the different zones, the PCA revealed that the first three components explained 94.2% of the total variation, the first plane alone accounting for 75% of the total variation (Fig. 5). The three planes were used to observe the species performance. Species with higher abundance according to zone were: *Aleuas*

Table 2 Total grasshopper species collected in each study zone (Buenos Aires and La Pampa provinces, Argentina) between 1986 and 2018

	NE	NW	SE	SW	W
ACRIDIDAE					
Acridinae					
<i>Allotruxalis gracilis</i>	*	*	*	*	*
<i>Cocytotettix argentina</i>		*	*		
<i>Covasacris pallidinota</i>	*	*	*	*	*
<i>Metaleptea adspersa</i>	*	*	*		
<i>Parorphula graminea</i>	*	*	*	*	*
Copiocerinae					
<i>Aleuas linneatus</i>	*	*	*	*	*
<i>Aleuas vitticolis</i>		*	*	*	*
Gomphocerinae					
<i>Amblytropidia australis</i>	*	*	*	*	*
<i>Borellia bruneri</i>	*	*	*	*	*
<i>Borellia pallida</i>	*	*	*	*	*
<i>Dichromorpha australis</i>				*	*
<i>Euplectrotettix ferrugineus</i>				*	*
<i>Euplectrotettix schulzi</i>		*		*	*
<i>Laplatacris dispar</i>	*	*	*		*
<i>Orphulella punctata</i>	*	*	*	*	*
<i>Rhammatocerus pictus</i>		*	*	*	*
<i>Scyllinula variabilis</i>	*	*	*	*	*
<i>Sinipta dalmani</i>	*	*	*	*	*
<i>Staurorhectus longicornis</i>	*	*	*	*	*
Leptysminae					
<i>Leptysma argentina</i>	*	*	*	*	
<i>Tucayaca gracilis</i>	*	*	*		
Melanoplinae					
<i>Atrachelacris gramineus</i>					*
<i>Atrachelacris unicolor</i>					*
<i>Baeacris pseudopunctulata</i>	*	*	*	*	*
<i>Baeacris punctulata</i>	*	*	*	*	*
<i>Dichroplus conspersus</i>	*	*	*	*	*
<i>Dichroplus elongatus</i>	*	*	*	*	*
<i>Dichroplus exilis</i>					*
<i>Dichroplus maculipennis</i>			*	*	*
<i>Dichroplus obscurus</i>			*		
<i>Dichroplus pratensis</i>	*	*	*	*	*
<i>Dichroplus schulzi</i>				*	*
<i>Dichroplus vittatus</i>				*	*
<i>Leiotettix pulcher</i>	*	*	*	*	*
<i>Neopedies brunneri</i>	*	*	*	*	*
<i>Ronderosia bergii</i>	*	*	*	*	*
<i>Ronderosia forcipata</i>		*		*	*
<i>Scotussa cliens</i>	*		*		*
<i>Scotussa daguerrei</i>		*	*	*	*
<i>Scotussa lemniscata</i>	*	*	*	*	*
Oedipodinae					
<i>Trimerotropis pallidipennis</i>			*	*	*

Table 2 (continued)

	NE	NW	SE	SW	W
OMMEXECHIDAE					
<i>Spathalium audouini</i>			*	*	
ROMALEIDAE					
<i>Alcamenes granulatus</i>			*		
<i>Chromacris speciosa</i>			*		*
<i>Diphontus argentinus</i>		*		*	*
<i>Diphontus clarazianus</i>				*	
<i>Staleoclera viridicata</i>	*				*
<i>Xileus laevipes</i>	*	*		*	*
<i>Zoniopoda omnicolor</i>		*			*
<i>Zoniopoda tarsata</i>	*	*			*

SW southwest, SE southeast, W west, NW northwest, NE northeast

lineatus, *Amblytropidia australis*, *Dichroplus elongatus*, *Scotussa lemniscata*, and *Ronderosia bergii* in the NE, *D. elongatus*, *R. bergii*, *Baeacris pseudopunctulata*, and *Staurorhectus longicornis* in the NW, *Borellia bruneri*, *Borellia pallida*, *Covasacris pallidinota*, *Dichroplus maculipennis*, *Dichroplus pratensis*, and *Parorphula graminea* in the SE, *D. pratensis*, *Dichroplus vittatus*, *Neopedies bruneri*, *Rhammatocerus pictus*, *Baeacris punctulatus*, and *B. pseudopunctulata* in the W, and *D. elongatus*, *D. pratensis*, *Leiotettix pulcher*, *S. longicornis*, and *B. pallida* in the SW. *Dichroplus elongatus* and *D. pratensis* occurred in all of the sampling areas.

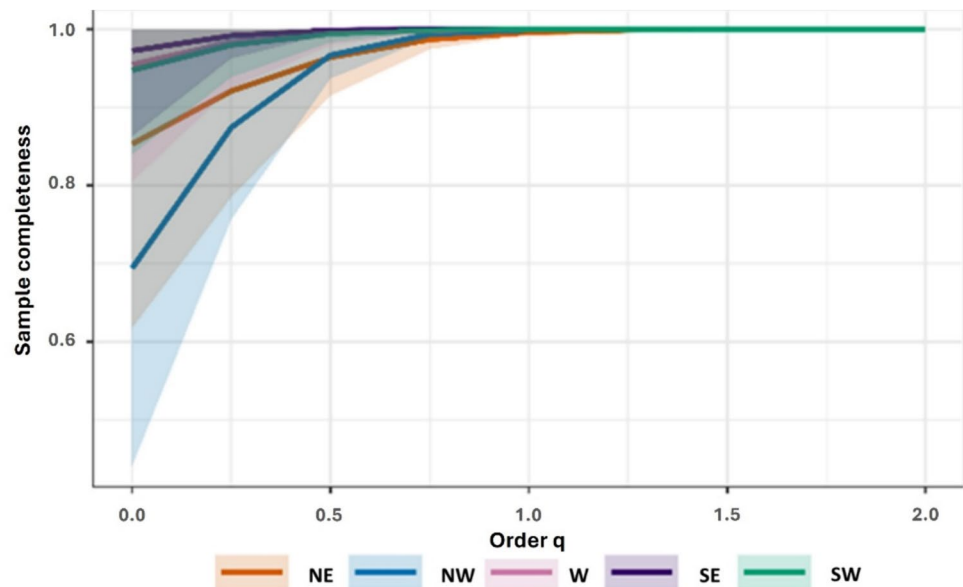
Of the 50 collected species, 25 were recorded in at least three of the plant communities sampled while the remaining 25 were found only in one or two. The highest number (50 species) was collected in GG followed by 33 in DG, 23 in both HG and C, and 17 in P. Crops exhibited the lowest number of individuals, representing only 2.51% of the total number collected while GG had the highest number, representing 51.87%. The correspondence analysis revealed a significant relationship between species and grassland, accounting for over 88% of the variance (Fig. 6) and showing how species were associated among the various plant communities. The HG contributed the most to the first dimension, accounting for 73.9% of the variation followed by the GG (21.3%) whereas P contributed the most to the second dimension, accounting for 79% of the variation (Table 4). Concerning species abundance by plant community, *B. bruneri* (10 in Table 5), *B. pallida* (11), *C. pallidinota* (14), *D. maculipennis* (19), and *P. gramineae* (34) were more abundant in the HG (Table 5). In P, *S. lemniscata* (40 in Table 5) was the most abundant species. *Dichroplus elongatus* (17) was the most frequently found species, and it was present in all environments, with the highest abundance in GG (56.32%) and DG (24.69%). *Dichroplus pratensis* (21) was also one of the most abundant species, mainly found in the GG.

Table 3 Species richness (S) and nonparametric estimators Chao 1 and ACE

Study zones	Sample size (n)	S	N° individuals in rare group	N° species for a rare group	N° individuals in abundant group	N° species for the abundant group	Estimated species richness
Northwest	6010	34	67	15	5943	19	Chao1: 48.998 ACE: 39.296
West	7860	42	68	16	7792	26	Chao1: 43.500 ACE: 43.428
Northeast	1412	29	42	16	1370	13	Chao1: 33.497 ACE: 34.986
Southwest	6594	36	56	12	6538	24	Chao1: 38 ACE: 37.02
Southeast	64,080	35	33	10	64,047	25	Chao1: 35.33 ACE: 36.48

Number of observed individuals for rare group, Number of observed species for rare group (Species with a number less than ten individuals), number of observed species for abundant group and number of observed individuals for abundant group according to ACE estimator

Fig. 3 Estimated sample completeness curves as a function of order Q between 0 and 2 for grasshopper species collected in the sampled sites in each study zone NE northeast, NW northwest, W west, SE southeast, SW southwest



In the Beta diversity analysis carried out to measure the species composition differences over time in each zone, it was observed that in SW, W, and NE, the species turnover (β_{sim} and β_{jtu}) was the key component that showed differentiation between years. Specifically, in the SW, the highest values were observed between the periods 1990–95/2001–05 (50% β_{sim} , 66% β_{jtu}) (Table 6). In the NE, the highest values of the species turnover β component were recorded between 1996–2000 and the rest of the periods, and in 2001–05, 2006–10, and > 2010. In the W, between 45 and 68.9% of differentiation was observed over all considered periods. In the SE, the Sorenson and Jaccard turnover indexes had lower values, and the highest diversity component was species loss, with values between 31.7 and 35.5% β_{jne} observed between 1996/2000 and 2006/2010, and 1996/2000 with > 2010. Additionally, between 2001/05

and 2006/2010, 40.7% β_{jne} was registered. In the NW, beta diversity between periods was affected by both the turnover component and the loss of species (Table 6).

In each zone, there were between 5 and 7 more abundant species that appear across the analyzed periods. Besides, it was observed that communities were structured with few dominant species, the three or four most abundant generally representing more than 50% of the community (Table 7). Moreover, some of the most frequent species were also the most abundant. While there were some abundant species recorded in the early years and then decreased or did not appear, there were others that showed up in later periods that were not initially collected. *Baeacris punctulata* decreased its abundance throughout the study in the SW, NW, W, and SE, and it was only found in one study period in the NE. Other species that decreased their abundance over the years

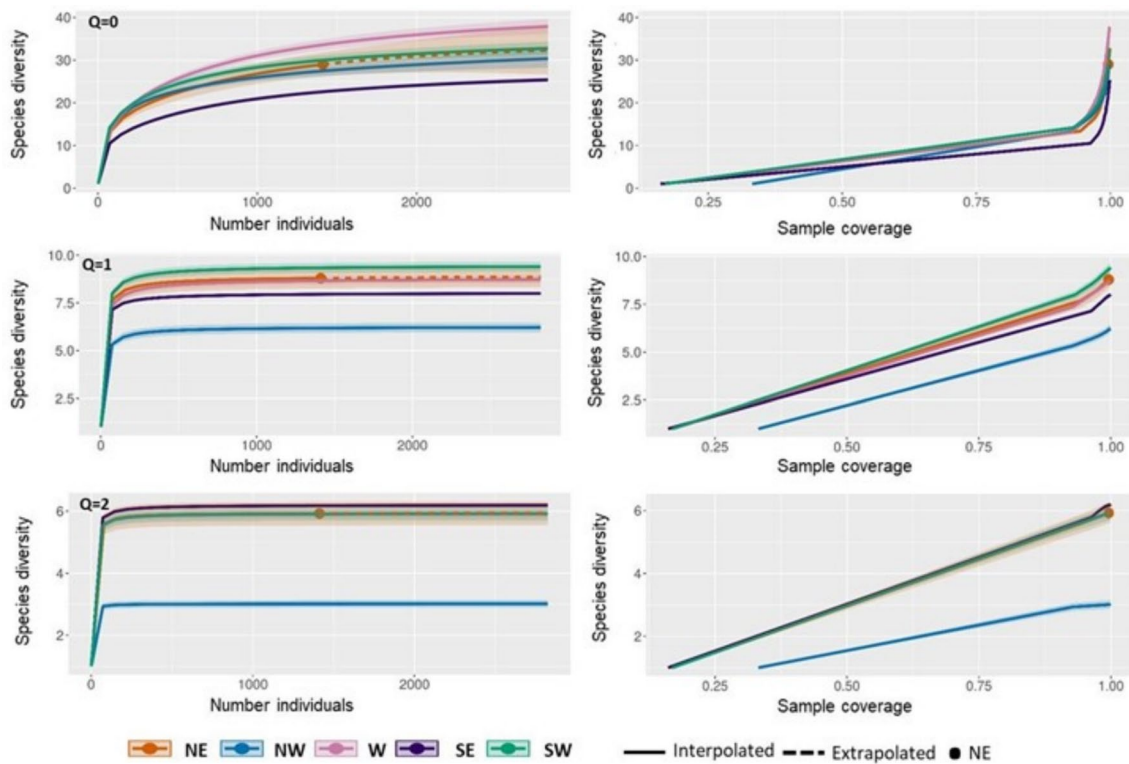


Fig. 4 Size-based rarefaction curves by individuals in the left and Coverage-based rarefaction by sample coverage in the right. Rarefaction (solid lines) and extrapolation (dashed lines), curves with 95%

confidence intervals (shaded areas) for the five different zones, separately by diversity order: Q0 (species richness), Q1 (Shannon diversity) and Q2 (Simpson diversity)

were *A. gracilis*, *B. bruneri*, *D. maculipennis*, *Orphulella punctata* and *P. graminea* in the SW, *A. australis* in the NW, *Parorphula graminea* and *Zoniopoda tarsata* in the W, *A. australis*, *B. bruneri*, *Laplatacris dispar*, and *Sinipta dalmani* in the NE, and *Tucayaca gracilis* and *S. dalmani* in the SE. On the other hand, species such as *R. bergii* and *R. forcipata* increased their abundance towards the end of the study in the SW, NW, and W. Also, in the different zones, species that appear in only one or two sampling periods were recorded, such as *D. vittatus* in the SW; *B. bruneri*, *Cocitotettix argentina*, *P. graminea*, and *Scotussa darreguei* in the NW; *O. punctata*, *S. daguerrei*, *Chromacris speciosa*, *Xileus laevipes*, *L. dispar* in the W; *P. graminea*, *Syllinula variabilis*, *T. gracilis*, *L. pulcher*, *N. bruneri*, *O. punctata* in the NE; and *C. argentina*, *A. gracilis*, *Aleuas vitticolis*, *R. pictus*, *Trimerotropis pallidipennis* in the SE (Figs. 7 and 8) (Appendix, Tables S8–S12).

Considering the agricultural dynamics during the study period, an increase in cultivated area, production, and crop yield was observed across all sampling zones (Appendix, Figs. S9–S13). Some selected examples *per* zone are mentioned. In the NE, approximately three times more land was sown during the 2010/11 season compared to 2000/01 (2000/01: 72,630 ha; 2010/11: 208,230 ha). The increase

in area sown with soybean was approximately 600% between 2000/01 (19,660 ha) and 2010/11 (116,420 ha). Soybean production rose from 45,300 tons in 2000/01 to 344,070 tons in 2010/11. In the NW, there was a significant increase in sown area and production, reaching a peak in 2018/19 of 10,880,465 tons, with 40% of this amount being soybean (4,370,761 tons) and 39.8% corn (4,334,339 tons). In this zone, the sown area during the 1982/83 season was 1,270,010 ha, and soybean cultivation represented 1.60% of the total sown area at that time, while in 2000/01 it represented approximately 40% of the total sown area. In the SW, wheat was the most important crop from the early years (1982/83), representing 68.4% of the total sown area, while the area sown with soybean had been increasing since 2000/01, reaching 28.8% of the total sown area in 2012/13. In the SE, the total sown area in 1982/83 was 872,600 ha, with a maximum in these 37 years in 2016/17 of 1,693,228 ha. Soybean crop in 1982/83 accounted for less than 1% of the total cultivated area while in 2012/13 it represented 68.14% of the total. The highest production in this zone was achieved in 2018/19 (5,307,602 tons), coinciding with one of the years of the largest sown area. Finally in the W, corn, wheat, and oats were the most sown crops during the study. Taking into account all crops, total production in

Fig. 5 Biplot from PCA (Principal component analysis) for more abundant grasshopper species between 1986 and 2018 in the different zones of the Pampas regions NE northeast, NW northwest, W west, SE southeast, SW southwest. **a** PC1 vs. PC2, **b** PC1 vs PC3, **c** PC2 vs PC3

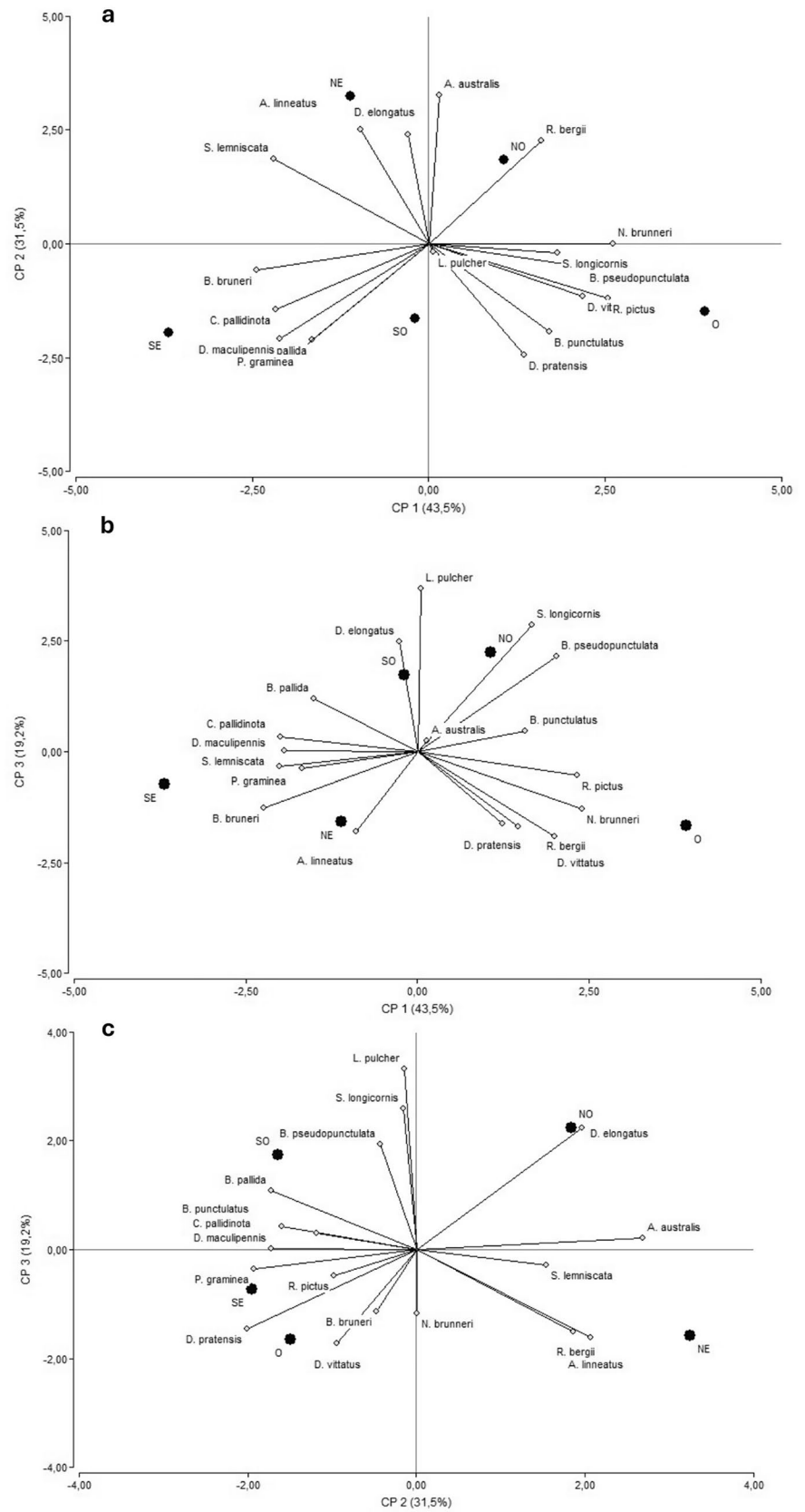
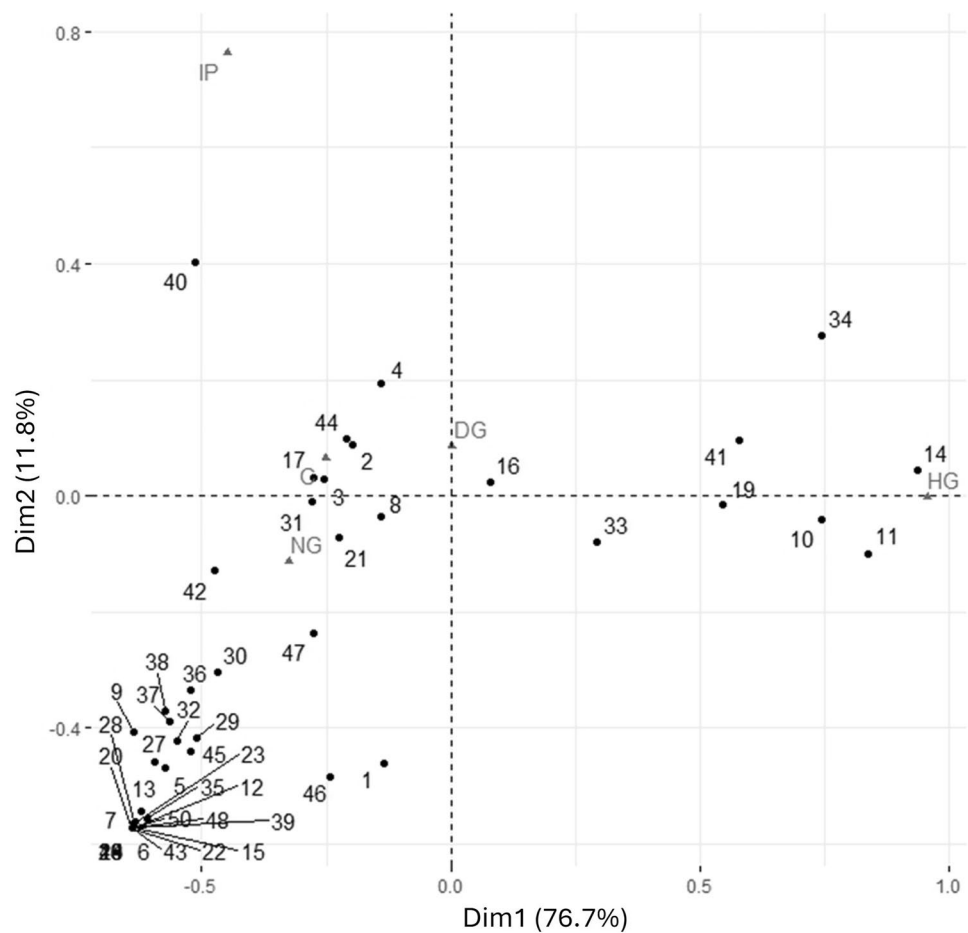


Fig. 6 Biplot from CA (Correspondence analysis) between the abundance of grasshopper species collected and the plant communities in the Pampas regions from 1986 to 2018. Grazed grassland with native grass dominance (GG), grazed grasslands with native and exotic dicotyledonous dominance (DG), Halophilous grassland (HG) sown pastures (P), and summer crops (C)



this area was highest in the 2004/05 (1,503,158 tons) and 2016/17 (1,490,501 tons) seasons.

Discussion

Results of the present study represent the first quantitative analytical attempt at describing the status of the grasshopper fauna in much of one of the most heavily modified ecosystems in South America, the grasslands of the Argentine Pampas region. Previous contributions on the subject were either limited in space and time or not based on analyses of long-term monitoring (Ronderos 1959; Cigliano et al.

2000; De Wysiecki et al. 2000, 2004; Mariottini et al. 2012, 2022). Although admittedly not exhaustive due to the large area considered, we feel the strength of the study resides in the unusual long-term sampling effort (37 years) conducted on the dominant plant communities over a period of significant agricultural intensification throughout the region with consequential heavy homogenization and fragmentation of habitats (Viglizzo and Jobbagy 2010; Bilenca et al. 2012; Ricard et al. 2019; Zhang et al. 2021). The trends that emerged might constitute a likely representation of the actual status of the grasshopper fauna in the Pampas in recent decades under an increasingly managed agroecosystem.

As expected, Acrididae was the most diverse family and within it the subfamilies Melanoplinae and Gomphocerinae (species of which are generally associated with grassland systems; Pocco et al. 2010) were the most diversified and abundant, representing 38% and 24% of the collected species, respectively. This agrees with various studies carried out timely and spatially restricted in different areas of the Pampas (Cigliano et al. 2000; Torrusicio et al. 2002; De Wysiecki et al. 2004; Mariottini et al. 2015). Therefore, this trend emerged at both local and regional scales.

Table 4 Results of the correspondence analysis carried out between the 50 grasshopper species collected between 1986 and 2018 and the dominant plant communities in the study zone

Dimensions	Dim1	Dim2	Dim3	Dim4
Eigenvalues	0.256	0.040	0.030	0.009
Percentage of variance	76.686	11.839	8.893	2.582
Cumulative percentage of Variance	76.686	88.525	97.418	100

Table 5 Relative abundance of grasshopper species collected during all study period (1996–2018) in each plant community

N	Species collected	C	IP	DG	NG	HG	Total ind/collected
1	<i>Alcamenes granulatus</i>				80	20	5
2	<i>Aleuas linneatus</i>	2,07	7,58	23,80	54,50	12,05	3046
3	<i>Aleuas vitticollis</i>			59,68	40,32		124
4	<i>Allotruxalis gracilis</i>		12,94	8,82	59,41	18,82	170
5	<i>Amblytropidia australis</i>			10,24	89,76		293
6	<i>Atrachelacris gramineus</i>				100		1
7	<i>Atrachelacris unicolor</i>				100		14
8	<i>Baeacris pseudopunctulatus</i>	6,59	6,04	11,29	58,98	17,10	1275
9	<i>Baeacris punctulatus</i>	1,62	3,10	1,47	93,81		678
10	<i>Borellia bruneri</i>	0,33	1,59	17,44	30,23	50,42	10,278
11	<i>Borellia pallida</i>	0,62	1,64	7,67	33,47	56,61	1461
12	<i>Chromacris speciosa</i>				100		8
13	<i>Cocytotettix argentina</i>			2,88	97,12		104
14	<i>Covasacris pallidinota</i>	0,30	2,28	18,75	20,97	57,70	4955
15	<i>Dichromorpha australis</i>				100		17
16	<i>Dichroplus conspersus</i>	0,69	3,22	33,10	42,76	20,23	435
17	<i>Dichroplus elongatus</i>	4,45	6,09	24,69	56,32	8,45	25,811
18	<i>Dichroplus exilis</i>				100		3
19	<i>Dichroplus maculipennis</i>	3,76	1,58	21,97	31,51	41,17	9590
20	<i>Dichroplus obscurus</i>				100		115
21	<i>Dichroplus pratensis</i>	0,69	4,65	22,45	61,09	11,12	10,409
22	<i>Dichroplus schulzi</i>				100		179
23	<i>Dichroplus vittatus</i>			0,82	99,18		730
24	<i>Diphontus argentinus</i>				100		36
25	<i>Diphontus clarazianus</i>				100		1
26	<i>Euplectrotettix ferrugineus</i>				100		59
27	<i>Euplectrotettix schulzi</i>				100		50
28	<i>Laplatacris dispar</i>				100		95
29	<i>Leiotettix pulcher</i>	1,45		13,29	83,57	1,69	418
30	<i>Leptysma argentina</i>		26,67	73,33			15
31	<i>Metaleptea adspersa</i>	19,23		36,54	40,38	3,85	52
32	<i>Neopedies bruneri</i>	1,09		13,82	85,09		646
33	<i>Orphulella punctata</i>	3,66		29,27	37,80	29,27	82
34	<i>Parorphula graminea</i>	2,29	10,91	3,93	28,24	54,63	917
35	<i>Rhammatocerus pictus</i>			0,96	98,08	0,96	208
36	<i>Ronderosia bergii</i>	2,62	1,05	16,27	79,53	0,52	383
37	<i>Ronderosia forcipata</i>	9,57		9,57	80,87		115
38	<i>Scotussa cliens</i>	14,29		7,14	78,57		14
39	<i>Scotussa daguerrei</i>				100		25
40	<i>Scotussa lemniscata</i>	1,79	48,08	14,37	32,75	3,01	8945
41	<i>Scyllinula variabilis</i>	0,00	6,19	14,16	34,51	45,13	113
42	<i>Sinipta dalmani</i>	5,76	5,24	14,14	71,73	3,14	191
43	<i>Spathalium audouini</i>				100		4
44	<i>Staleocloria viridicata</i>			66,67	33,33		3
45	<i>Staurorhectus longicornis</i>	2,93		9,11	85,74	2,22	3689
46	<i>Trimerotropis pallidipennis</i>				84,21	15,79	19
47	<i>Tucayaca gracilis</i>	2,90	2,90	11,59	71,01	11,59	69
48	<i>Xileus laevipes</i>				100		7
49	<i>Zoniopoda omnicolor</i>				100		5
50	<i>Zoniopoda tarsata</i>				100		94
	Total number of individuals	2115	4613	16,781	44,591	17,816	85,956

GG grazed grassland, DG grazed grasslands with native and exotic dicotyledonous dominance, HG halophilous grassland, P pastures, C summer crops

Table 6 Results of the Beta diversity analysis of grasshopper species collected in the sampled sites of the Pampas regions between different periods of time

Zones	1990–1995			1996–2000			2000–2005			2006–2010		
Southwest												
Sørensen	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}
1996–2000	0.125	0.097	0.222									
2001–2005	0.5	0.029	0.529	0.33	0.035	0.368						
2006–2010	0.187	0.221	0.409	0.05	0.158	0.208	0.22	0.169	0.391			
> 2010	0.131	0.108	0.421	0.25	0.035	0.285	0.33	0.066	0.400	0.136	0.103	0.240
Jaccard	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}
1996–2000	0.222	0.141	0.363	–	–	–	–	–	–	–	–	–
2001–2005	0.666	0.025	0.693	0.500	0.038	0.538	–	–	–	–	–	–
2006–2010	0.315	0.265	0.580	0.095	0.249	0.345	0.363	0.198	0.562	–	–	–
> 2010	0.476	0.116	0.592	0.400	0.040	0.444	0.500	0.071	0.571	0.240	0.147	0.387
West												
Sørensen	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}
1996–2000	0.416	0.00	0.416	–	–	–	–	–	–	–	–	–
2001–2005	0.214	0.206	0.421	0.357	0.168	0.526	–	–	–	–	–	–
2006–2010	0.166	0.119	0.285	0.208	0.113	0.321	0.142	0.335	0.478	–	–	–
> 2010	0.304	0.015	0.319	0.434	0.012	0.446	0.285	0.173	0.459	0.086	0.149	0.236
Jaccard	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}
1996–2000	0.588	0.000	0.588	–	–	–	–	–	–	–	–	–
2001–2005	0.353	0.239	0.592	0.526	0.163	0.689	–	–	–	–	–	–
2006–2010	0.285	0.158	0.444	0.344	0.141	0.486	0.250	0.397	0.647	–	–	–
> 2010	0.466	0.017	0.483	0.606	0.011	0.617	0.444	0.185	0.629	0.160	0.222	0.382
Northeast												
Sørensen				β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}
2001–2005	–	–	–	0.333	0.051	0.384	–	–	–	–	–	–
2006–2010	–	–	–	0.428	0.100	0.529	0.250	0.187	0.437	–	–	–
> 2010	–	–	–	0.300	0.116	0.416	0.300	0.063	0.363	0.100	0.300	0.400
Jaccard				β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}
2001–2005	–	–	–	0.500	0.055	0.555	–	–	–	–	–	–
2006–2010	–	–	–	0.600	0.092	0.692	0.400	0.208	0.608	–	–	–
> 2010	–	–	–	0.461	0.126	0.588	0.461	0.071	0.533	0.181	0.389	0.571
Northwest												
Sørensen				β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}
2001–2005	–	–	–	0.000	0.481	0.481	–	–	–	–	–	–
2006–2010	–	–	–	0.200	0.133	0.333	0.000	0.600	0.600	–	–	–
> 2010	–	–	–	0.350	0.045	0.395	0.000	0.533	0.533	0.134	0.085	0.215
Jaccard				β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}
2001–2005	–	–	–	0.000	0.650	0.650	–	–	–	–	–	–
2006–2010	–	–	–	0.333	0.166	0.500	0.000	0.750	0.750	–	–	–
> 2010	–	–	–	0.518	0.048	0.566	0.000	0.696	0.695	0.231	0.124	0.355
Southeast												
Sørensen				β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}	β_{sor}
2001–2005	–	–	–	0.125	0.026	0.151	–	–	–	–	–	–
2006–2010	–	–	–	0.058	0.214	0.273	0.0	0.256	0.256	–	–	–
> 2010	–	–	–	0.058	0.245	0.304	0.0	0.288	0.288	0.074	0.033	0.107
Jaccard				β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}	β_{jtu}	β_{jne}	β_{jac}
2001–2005	–	–	–	0.222	0.040	0.263	–	–	–	–	–	–
2006–2010	–	–	–	0.111	0.317	0.428	0.000	0.407	0.407	–	–	–
> 2010	–	–	–	0.111	0.355	0.466	0.000	0.448	0.448	0.055	0.055	0.193

Table 6 (continued)Sørensen and Jaccard indexes (β_{sor} y β_{jac}) and their respective turnover (β_{sim} and β_{jtu}) and nestedness (β_{sne} and β_{jne}) components

In each of the five sampling zones, a high proportion of rare species was recorded. Rare species are defined as those with restricted distribution, low population abundance, or a combination of both (Dee et al. 2019). The highest number of rare species (16) was recorded in the NW and W, followed by the SE with 10 species (each with fewer than 10 individuals). Furthermore, the NW zone exhibited the lowest completeness profile in terms of species richness, suggesting that approximately 31% of the rare species went undetected in the samples. In spite of relatively recent contributions on the structure and dynamics of grasshoppers in the Pampas (Torrusio et al. 2002; De Wysiecki et al. 2004, 2011; Mariottini et al. 2011, 2012, 2022), our understanding of ecological aspects concerning rare species remains limited because such contributions were mostly focused on agriculturally harmful species, usually those that are the most abundant, frequent or common. In this sense, results of the indexes we employed (ACE) showed that the grasshopper communities in each of the zones were structured with relatively few dominant species in terms of abundance and many rare species. However, as Dee et al. (2019) mentioned, rare species can have subtle or hidden (i.e. difficult to detect) direct and indirect impacts on ecosystem services through species interactions. Different authors (Flynn et al. 2009; Bracken and Low 2012; Vincent et al. 2020) pointed out that changes in land use (along with climate conditions) have had a significant impact on the decline of rare species and that the ecological consequences of losing rare species for the ecosystem functioning are still poorly understood.

The trend that is apparent by the results of the rarefaction analyses is that the SE and NW zones showed a lower diversity of grasshoppers which could be explained either by the own characteristics of the zones as well as the process of agricultural intensification. In the case of the SE, most sampling sites were located in what is called the Flooding Pampa sub-region which even at present is the area with less agricultural activity and thus conserving to a considerable extent grasslands for livestock (Bilenca et al. 2012). However, the most widespread plant community in this zone is the HG which is of very low plant diversity (Perelman et al. 2007) and was shown to depict also low grasshopper diversity in previous studies (Torrusio et al. 2002; Mariottini et al. 2013). On the contrary, the sampling sites in the NW were within the sub-regions of the Rolling Pampa and the Inland Pampas where over decades heavy, increasing agricultural intensification has completely modified the natural landscape (Viglizzo et al. 2011). The area of land under agriculture (crop and stubble) represents the dominant pattern. Fields are cultivated

along fences, road edges, and primary and secondary roads. This type of cultivation has reduced the connectivity of patches of spontaneous vegetation that can develop in the region and consequently the animal biodiversity associated with these ecosystem (Bilenca and Miñarro 2004; Codesido et al. 2011; Andrade et al. 2017).

Most of the 19 grasshopper species considered in the PCA analysis were recorded in different study zones but with different abundance. Such variability in abundance could potentially suggest a preference for specific habitats, zones, or alternatively, a lower abundance due to changes in land use over the past 37 years. Several of these 19 species are considered pests (Carbonell et al. 2024) and it is relevant to know the areas where they are particularly abundant. For example, *Dichroplus maculipennis*, a melanopline showing some clear expressions of density-dependent phase polyphenism (Mariottini et al. 2015), is predominantly abundant in the SE in association with the HG. From there, when outbreaks occur, it is capable of invading neighboring areas with mass-migrating adults. Along with *D. maculipennis*, the gomphocerine *B. bruneri*, which is recognized as a pest in the Pampas region of Uruguay (Lorier et al. 2010; Miguel et al. 2014), was also most abundant in the SE. On the other hand, *Dichroplus elongatus*, a major pest of several crops (Carbonell et al. 2024) like *D. maculipennis*, resulted to be frequently found in high abundance across all study areas possibly due to its known great adaptability (De Wysiecki et al. 1997; Cigliano et al. 2014).

Regarding the estimated beta diversity, the temporal composition patterns at the SW, W, and NW sites was mostly defined by species turnover over the years. This variability in species composition could be linked to changes in land use as well as environmental variables that favor the life cycle of some species more than others (Mariottini et al. 2022). Distinctly, in the SE nestedness was the main component. As already pointed out, in this zone land use change was not as extensive as in the other zones. However, it needs to be mentioned that many of the sites in the SE suffered significant droughts in 2008–2010 and 2018 that affected grasshopper richness (Mariottini et al. 2011, 2012). Climate change is increasingly mentioned as a significant threat to insects (Cardoso et al. 2020). Some thermophilous species may expand their range with rising temperatures (Poniatowski et al. 2020) while others, in contrast, are expected to suffer from global warming (hygrophilous species). Given these possibilities, it would be important to study in the near future the distribution, abundance, dispersal ability, and degree of habitat specialization of grasshoppers in the Pampas region in response to global warming.

Table 7 The four grasshoppers' species more abundant (relative abundance in percentage) in different time periods for each study zone

Zones	1990–95	1996–2000	2001–2005	2006–2010	2010 onwards					
SW										
	<i>Baeacris punctulata</i>	24,52	<i>Covasacris pallidinota</i>	6,80	<i>Dichroplus elongatus</i>	34,73	<i>Baeacris pseudopunctulata</i>	10,66	<i>Dichroplus elongatus</i>	20,54
	<i>Borellia bruneri</i>	10,55	<i>Dichroplus elongatus</i>	29,77	<i>Dichroplus schulzi</i>	9,42	<i>Dichroplus elongatus</i>	43,65	<i>Dichroplus pratensis</i>	25,64
	<i>Dichroplus pratensis</i>	20,65	<i>Dichroplus pratensis</i>	20,62	<i>Scotussa lemniscata</i>	11,47	<i>Dichroplus pratensis</i>	8,12	<i>Scotussa lemniscata</i>	6,37
	<i>Staurorhectus longicornis</i>	16,05	<i>Staurorhectus longicornis</i>	11,93	<i>Staurorhectus longicornis</i>	18,48	<i>Staurorhectus longicornis</i>	14,09	<i>Staurorhectus longicornis</i>	26,49
	Total	71,77	69,12	74,11	76,52	79,04				
NW										
	-	-	<i>Amblytropidia australis</i>	6,76	<i>Aleuas linneatus</i>	10,69	<i>Baeacris pseudopunctulatus</i>	4,45	<i>Dichroplus elongatus</i>	36,30
	-	-	<i>Dichroplus elongatus</i>	56,60	<i>Baeacris pseudopunctulatus</i>	9,92	<i>Dichroplus elongatus</i>	59,84	<i>Dichroplus pratensis</i>	9,59
	-	-	<i>Scotussa lemniscata</i>	12,54	<i>Dichroplus elongatus</i>	66,41	<i>Scotussa lemniscata</i>	5,95	<i>Scotussa lemniscata</i>	6,99
	-	-	<i>Staurorhectus longicornis</i>	10,47	<i>Scotussa lemniscata</i>	9,92	<i>Staurorhectus longicornis</i>	7,91	<i>Staurorhectus longicornis</i>	20,55
	-	-		86,37		96,95		78,15	73,42	
W										
	<i>Baeacris punctulata</i>	8,80	<i>Amblytropidia australis</i>	4,26	<i>Aleuas linneatus</i>	4,67	<i>Baeacris pseudopunctulata</i>	6,13	<i>Dichroplus elongatus</i>	18,96
	<i>Dichroplus elongatus</i>	14,57	<i>Dichroplus elongatus</i>	27,47	<i>Dichroplus elongatus</i>	47,91	<i>Dichroplus elongatus</i>	37,32	<i>Dichroplus pratensis</i>	42,44
	<i>Dichroplus pratensis</i>	31,73	<i>Dichroplus pratensis</i>	32,99	<i>Dichroplus pratensis</i>	9,83	<i>Dichroplus pratensis</i>	9,38	<i>Dichroplus vittatus</i>	5,12
	<i>Staurorhectus longicornis</i>	20,68	<i>Dichroplus vittatus</i>	9,96	<i>Staurorhectus longicornis</i>	28,26	<i>Dichroplus vittatus</i>	19,39	<i>Staurorhectus longicornis</i>	15,80
	Total	75,78	74,69	90,66	72,22	82,32				
NE										
	-	-	<i>Borellia bruneri</i>	36,83	<i>Aleuas linneatus</i>	29,39	<i>Aleuas linneatus</i>	37,18	<i>Dichroplus elongatus</i>	36,14
	-	-	<i>Dichroplus elongatus</i>	26,34	<i>Amblytropidia australis</i>	8,02	<i>Covasacris pallidinota</i>	3,27	<i>Dichroplus pratensis</i>	26,51
	-	-	<i>Dichroplus pratensis</i>	5,12	<i>Dichroplus elongatus</i>	34,73	<i>Dichroplus elongatus</i>	29,95	<i>Scotussa lemniscata</i>	16,27
	-	-	<i>Laplatacris dispar</i>	14,63	<i>Scotussa lemniscata</i>	20,61	<i>Scotussa lemniscata</i>	9,64	<i>Staurorhectus longicornis</i>	3,61
	-	-		82,92		92,75		80,03	82,55	
SE										
	-	-	<i>Borellia bruneri</i>	13,58	<i>Covasacris pallidinota</i>	15,28	<i>Borellia bruneri</i>	27,21	<i>Dichroplus elongatus</i>	30,67
	-	-	<i>Covasacris pallidinota</i>	30,60	<i>Dichroplus elongatus</i>	45,15	<i>Covasacris pallidinota</i>	9,65	<i>Dichroplus maculipennis</i>	12,94
	-	-	<i>Dichroplus elongatus</i>	15,63	<i>Dichroplus pratensis</i>	8,34	<i>Dichroplus elongatus</i>	22,99	<i>Dichroplus pratensis</i>	13,97
	-	-	<i>Scotussa lemniscata</i>	13,25	<i>Scotussa lemniscata</i>	9,98	<i>Dichroplus maculipennis</i>	19,06	<i>Scotussa lemniscata</i>	15,96
	-	-		73,06		78,75		78,90	73,55	

NE northeast, NW northwest, W west, SE southeast, SW southwest



Fig. 7 Some of the abundant grasshopper species in the Pampas region during 1986–2018. **a** *Dichroplus maculipennis*, **b** *Borellia bruneri*, **c** *Aleuas lineatus*, **d** *Parorophula gramineae*, **e** *Dichroplus elongatus*, **f** *Scotussa lemniscate*, **h** *Baeacris pseudopunctulata*, **g**

Dichroplus pratensis. Images not to scale. Photos by M. Mancini (**a**, **b**, **d** and **h**), M.L. de Wysiecki (**c**, **e**), and M.M. Cigliano (**f**, **g**) from Carbonell et al. (2024)



Fig. 8 Some of the grasshopper species with less abundance in the Pampas region during 1986–2018. **a** *Neopedies bruneri*, **b** *Leptysmia Argentina*, **c** *Chromacris speciosa*, **d** *Metaleptea adspersa*, **e** *Diponthus argentinus*, **f** *Dichroplus vittatus*, **g** *Spathalium audouinii* Images

not to scale. Photos by M.L. de Wysiecki (**a**, **f**), M. Mancini (**b**), M.M. Cigliano (**c**–**e**) from Carbonell et al. (2024) and Y. Mariottini (**g**)

As observed from the rarefaction analysis the grasshopper communities were structured with few dominant species and a higher percentage of either rare species or few (up to four) abundant species comprising more than 70% of the community. Moreover, it was also observed that the dominant species were practically the same during all sampling years, while less abundant species varied their abundance in the different periods considered. For example, *B. punctulata* was more abundant during the first years of sampling and then decreased or did not appear in later periods. It was a common species in the early sampling years in the SW, NW, W, and SE. The opposite happened with *R. bergii* which

occurred in later sampling years in the SW, NW, and W but showed low abundance in the first years of sampling.

Several studies conducted in the Pampas show how habitat modification affected the distribution and abundance of species. Medan et al. (2011) have summarized the available information on the effects of agriculture on biodiversity of several groups of animals. In the case of birds, loss of grassland area is one of the main factors for the decline in species richness and abundance (Cerezo et al. 2010; Codesido et al. 2011; Weyland et al. 2014). Increase of agrochemical use during recent decades, notably insecticides, is another major factor affecting bird populations in the Pampas region,

possibly even underestimated (Bernardos and Zaccagnini 2011). Likewise, several studies were performed in the Pampas on the diversity of arthropods and insects. De La Fuente et al. (2003, 2010) examined insect communities in wheat (*Triticum aestivum*) and soybean (*Glycine max*) in the Rolling Pampas with varying cropping histories. They found that lower richness of insect communities can be attributed to intensified agricultural practices and landscape homogenization. Similarly, several studies highlight the negative impact of intensified agricultural practices on pollination services in the Pampas region (Marrero et al. 2016; Aizen et al. 2019; Torreta et al., 2021). All these works, like ours, dealt with taxonomic diversity, but also it is also of importance to consider how habitat modification impacts genetic diversity. Ortego et al. (2015) predict that agricultural lands constitute barriers to gene flow and hypothesize that fragmentation has restricted inter-population dispersal and reduced local levels of genetic diversity. The results of their work confirmed the expectation that isolation and habitat fragmentation have reduced the genetic diversity of local populations. Landscape genetic analyses showed that agricultural land offers ~ 1000 times more resistance to gene flow than semi-natural habitats, indicating that patterns of dispersal are constrained by the spatial configuration of remnant patches of suitable habitat. Overall, semi-natural habitat patches function as important corridors for gene flow and should be preserved for their significant ecological role despite their small size in human-modified landscapes.

On the other hand, besides habitat fragmentation and modification, animal biodiversity is affected by the indiscriminate and continuous use of chemical pesticides in agroecosystems. In Argentina, particularly in the Pampas region, the increase in the volume of pesticides used *per* unit area in recent times has been mainly due to the high use of the herbicide glyphosate associated with the practice of no-till farming and the use of RR cultivars of soybean and corn. Additionally, the emergence of resistant weeds has led to increased doses of glyphosate and the use of product mixtures (Andrade et al. 2017). The percentage of pesticides in the least hazardous categories (green and blue bands) grew from 31 in 1985 to 85% in 2016 (Satorre and Andrade 2021). During periods of high grasshopper population densities, the predominant control method is the use of chemical insecticides, affecting not only the target species but also other grasshopper species and their natural enemies (Pelizza et al. 2019; Lange et al. 2020).

Andrade et al. (2017) discusses the problem of biodiversity loss and the decline of ecosystem services that accompanied the process of agricultural expansion and intensification in Argentina. He attributes this to at least four critical components: the extent or magnitude of the process, its homogeneity, the lack of landscape and farm-scale design to protect critical areas, and the excessive reliance on input-based

technologies. Our long-term, space-wide effort seems to concur with the above-mentioned studies in that the process of agriculture intensification in the Pampas has modified the distribution pattern and abundance of grasshoppers possibly favoring generalist species over others. In this sense, we agree with Bilenca et al. (2012) who highlight that the effects of agriculture and land use changes are not uniform for all species but rather differential, so that the particular characteristics of each species determine the spatial scales of their eventual responses.

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Author contributions YM, MLDW, and CEL have carried out the conceptualization of the manuscript, the sampling design, the field data collection, and conducted the taxonomic determination of the grasshopper species. CJB collaborated with the field data collection. RC, CM, and YM have carried out the statistical analysis and the figure editing. YM, MLDW, and CEL wrote the original draft. All authors reviewed and edited the final version of the manuscript and agreed to send it for publication.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

References

- Aizen MA, Garibaldi LA, Dondo M (2009) Expansión de la soja y diversidad de la agricultura Argentina. *Ecol Aust* 19:45–55
- Aizen MA, Aguiar S, Biesmeijer JC, Garibaldi LA et al (2019) Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Glob Change Biol* 25:3516–3527. <https://doi.org/10.1111/gcb.14736>
- Andrade JF, Poggio SL, Ermacora MR, Satorre EH (2017) Land use intensification in the Rolling Pampa, Argentina: diversifying crop sequences to increase yields and resource use. *Eur J Agron* 82:1–10
- Baldi G, Paruelo JM (2008) Land-use and land cover dynamics in South American temperate grasslands. *Ecol Soc* 13(2):6
- Bardi CJ (2013) Biología y biocontrol de *Dichroplus elongatus* Gigliot-Tos (Orthoptera: Acrididae: Melanoplinae), acridio plaga del agro en Argentina. Phd Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Glob Ecol Biogeogr* 19:134–143
- Baselga A, Orme CDL (2012) Betapart: An R package for the study of beta diversity. *Methods Ecol Evol* 3:808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Bazelet CS, Samways MJ (2011) Identifying grasshopper bioindicators for habitat quality assessment of ecological networks. *Ecol Indic* 11:1259–1269

- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol Evol* 18:182–188
- Bernardos J, Zaccagnini ME (2011) El uso de insecticidas en cultivos agrícolas y su riesgo potencial para las aves en la Región Pampeana. *Hornero* 26(01):055–064
- Bilenca D, Codesido M, Fischer C, Carusi LP (2009) Impactos de la actividad agropecuaria sobre la biodiversidad en la ecorregión pampeana. INTA, Buenos Aires
- Bilenca D, Codesido C, Fischer C, Pérez Carush P, Zufiaurre E, Abba A (2012) Impactos de la transformación agropecuaria sobre la biodiversidad en la provincia de Buenos Aires. *Rev Del Museo Arg De Cs Naturales* 14:189–198
- Bilenca D, Miñarro F (2004) Identificación de Áreas valiosas de Pastizal. En las Pampas y Campos de Argentina, Uruguay y Sur de Brasil (AVPs). Programa de Pastizales. Fundación Vida Silvestre
- Bracken ME, Low NH (2012) Realistic losses of rare species disproportionately impact higher trophic levels. *Ecol Lett* 15(5):461–467. <https://doi.org/10.1111/j.1461-0248.2012.01758.x>
- Carbonell CS, Cigliano MM, Lange CE (2024) *Acridomorph* (Orthoptera) species from Argentina and Uruguay, Version II. <https://bio-dar.unlp.edu.ar/acridomorph/>
- Cardoso P, Barton PS, Chichorro F, Deacon C et al (2020) Scientists' warning to humanity on insect extinctions. *Biol Conserv* 242:108426. <https://doi.org/10.1016/j.biocon.2020.108426>
- Carrasco A, Sánchez N, Tamagno L (2012) Modelo agrícola e impacto socio-ambiental en la Argentina: monocultivo y agronegocios. Universidad Nacional de La Plata, La Plata
- Carreño L, Viglizzo E (2011) Provisión de servicios ecológicos y gestión de los ambientes rurales en Argentina. Área estratégica de Gestión Ambiental. Ediciones INTA
- Cerezo A, Conde MA, Poggio SL (2010) Pasture area and landscape heterogeneity are key determinants of bird diversity in intensively managed farmland. *Biodivers Conserv*. <https://doi.org/10.1007/s10531-011-0096-y>
- Chao A, Chiu C (2012) Estimation of species richness and shared species richness. In: Balakrishnan N (ed) *Methods and applications of statistics in the atmospheric and earth sciences*. Wiley, New York, pp 76–111
- Chao A, Chiu CH (2016) *Nonparametric estimation and comparison of species richness*. Wiley, Chichester. <https://doi.org/10.1002/9780470015902.a0026329>
- Chao A, Jost L (2012) Diversity measures. In: Hastings A, Gross L (eds) *Encyclopedia of theoretical ecology*. University of California Press, Berkeley, pp 203–207
- Chao A, Lee SM, Jeng CL (1992) Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* 48:201–216
- Chao A, Gotelli NJ, Hsieh TC, Sander KH, Robert K, Colwell A, Ellison M (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr* 84:45–67. <https://doi.org/10.1890/13-0133.1>
- Chao A, Kubota ZD, Chiu CH, Li CF, Kusumoto B, Yasuhara M, Thorn S, Wei CL, Costello MJ, Colwell RK (2020) Quantifying sample completeness and comparing diversities among assemblages. *Ecol Res* 35:292–314
- Cigliano MM, De Wysiecki ML, Lange CE (2000) Grasshopper (Orthoptera, Acrididae) species diversity in the pampas. *Argentina Diver Distrib* 6:81–91
- Cigliano MM, Pocco ME, Lange CE (2014) Acrideos (Orthoptera) de importancia agroeconómica en la República Argentina. In: Roig Juárez S, Claps L, Morrone JJ (eds) *Biodiversidad de Artrópodos Argentinos*, vol 3. Sociedad Entomológica Argentina, La Plata, pp 11–36
- Codesido M, González-Fischer CM, Bilenca DN (2011) Distributional changes of land bird species in agroecosystems of central Argentina. *Condor* 113:266–273
- De la Fuente EB, Suarez SA, Ghera CM (2003) Weed and insect communities in wheat crops with different management practices. *Agron J* 95:1542–1549
- De la Fuente EB, Perelman S, Ghera CM (2010) Weed and arthropod communities in soybean as related to crop productivity and land use in the Rolling Pampa, Argentina. *Weed Res* 50:561–571
- De Wysiecki ML, Cigliano MM, Lange CE (1997) Fecundidad y longevidad de adultos de *Dichroplus elongatus* (Orthoptera: Acrididae) bajo condiciones controladas. *Rev Soc Entomol Argent* 56:101–104
- De Wysiecki ML, Sánchez N, Ricci S (2000) Grassland and shrubland grasshopper community composition in northern La Pampa province. *Argentina J Orthoptera Res* 9:211–221
- De Wysiecki ML, Torrusio S, Cigliano MM (2004) Caracterización de las comunidades de acridios del partido de Benito Juárez, sudeste de la provincia de Bs. As, Argentina. *Rev Soc Entomol Argent* 63:87–96
- De Wysiecki ML, Arturi M, Torrusio S, Cigliano MM (2011) Influence of weather variables and plant communities on grasshopper density in the Southern Pampas. *Argentina J Insect Sci* 11:109. <https://doi.org/10.1673/031.011.10901>
- Dee LE, Cowles J, Isbell F, Pau S, Gaines SD, Reich PB (2019) When do ecosystem services depend on rare species? *Trends Ecol Evol* 34(8):746–758. <https://doi.org/10.1016/j.tree.2019.03.010>
- Ebeling A, Hinesb J, Hertzog LR, Lange M, Meyer ST, Simons NK, Wissner W (2018) Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. *Basic Appl Ecol* 26:50–63
- Ellison AM (2010) Partitioning diversity. *Ecology* 91:1962–1963
- Evans EW (1988) Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influences of fire frequency, topography, and vegetation. *Can J Zool* 66:1495–1501
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Ann Rev Ecol Evol Syst* 34:487–515
- Fahrig L (2019) Habitat fragmentation: a long and tangled tale. *Glob Ecol Biogeogr* 28:33–41. <https://doi.org/10.1111/geb.12839>
- Fartmann T, Brüggeshemke J, Poniatowski D, Löffler F (2022) Summer drought affects abundance of grassland grasshoppers differently along an elevation gradient. *Ecol Entomol* 47:778–790
- Fick SE, Hijmans RJ (2017) WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315. <https://doi.org/10.1002/joc.5086>
- Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Trautman Richers B, Lin BB, Simpson N, Mayfield MM, DeClerck F (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecol Lett* 12(1):22–33. <https://doi.org/10.1111/j.1461-0248.2008.01255.x>
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH (2005) Global consequences of land use. *Science* 309(5734):570–574. <https://doi.org/10.1126/science.1111772>
- Fumy F, Löffler F, Samways MJ, Fartmann T (2020) Response of orthoptera assemblages to environmental change in a low-mountain range differs among grassland types. *J Environ Manage* 256:109919. <https://doi.org/10.1016/j.jenvman.2019.109919>
- Gavier-Pizarro GI, Calamari NC, Thompson JJ, Canavelli SB, Solari LM, Decarre J, Goijman AP, Suarez RP, Bernardos JM, Zaccagnini ME (2012) Expansion and intensification of row crop agriculture in the Pampas and Espinal of Argentina can reduce ecosystem service provision by changing avian density. *Agric Ecosyst Environ* 154:44–55
- Gebeyehu S, Samways MJ (2003) Responses of grasshopper assemblages to long-term grazing management in a semi-arid African savanna. *Agric Ecosyst Environ* 95(2–3):613–622
- Ghera CM (2005) La Sucesión ecológica en los Agrosistemas pampeanos. Sus modelos y Significado agronómico. In: Oosterheld

- M, Aguiar MR, Ghersa CM, Paruelo JM (eds) La heterogeneidad de la vegetación de los agroecosistemas. Editorial Facultad de Agronomía, Buenos Aires, pp 195–212
- González Roglich M, Swanson J, Villareal D, Jobbagy Gampel EG, Robert J (2015) Woody plant-cover dynamics in Argentine savannas from the 1880s to 2000s: the interplay of encroachment and agriculture conversion at varying scales. *Ecosystems* 18:481–492
- Guo ZW, Li HC, Gan YL (2006) Grasshoppers (Orthoptera: Acrididae) biodiversity and grassland ecosystems. *Insect Science* 13:221–227
- Hochkirch A, Adorf F (2007) Effects of prescribed burning and wildfires on Orthoptera in Central European peat bogs. *Environ Conserv* 34:225–235
- Horvath Z, Ptacnik R, Vad CF, Chase JM (2019) Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. *Ecol Lett* 22:1019–1027. <https://doi.org/10.1111/ele.13260>
- Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol* 7:1451–1456
- Joern A (2005) Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86:861–873
- Joern A, Laws AN (2013) Ecological mechanism underlying arthropod species diversity in grasslands. *Annu Rev Entomol* 58:19–36
- Jonas JL, Joern A (2007) Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison grazing and weather in North American tallgrass prairie: a long-term study. *Oecologia* 153:699–711
- Lange CE, Mariottini Y, Plischuk S, Cigliano MM (2020) Naturalized, newly-associated microsporidium continues causing epizootics and expanding its host range. *Protistology* 14:32–37. <https://doi.org/10.21685/1680-0826-2020-14-1-4>
- Lara B, Gandini M (2014) Quantifying the land cover changes and fragmentation patterns in the Argentina Pampas, in the last 37 years (1974–2011). *GeoFocus* 14:163–180
- Larson DP, O’Neill KM, Kemp W (1999) Evaluation of the accuracy of sweep sampling in determining grasshopper (Orthoptera: Acridae) community composition. *J Agron Urban Entomol* 16(3):207–214
- Lecoq M, Zhang L (2019) Encyclopedia of pest orthoptera of the World. China Agricultural University Press Ltd, Beijing
- Leguizamon A (2016) Disappearing nature? Agribusiness, biotechnology and distance in Argentine soybean production. *J Peasant Stud* 43:313–330
- Lorier E, Miguel L, Zerbino MS (2010) Manejo de tucuras. In: Altier N, Rebuffo M, Cabrera K (eds) Enfermedades y plagas en pasturas. INIA, Montevideo, pp 51–71
- Mariottini Y, Wysiecki ML, Lange CE (2011) Seasonal occurrence of life stages of Grasshopper (Orthoptera: Acridoidea) in the Southern Pampas. *Argentina Zool Stud* 50:737–744
- Mariottini Y, De Wysiecki ML, Lange CE (2012) Variacion temporal de la riqueza, composicion y densidad de acridios (Orthoptera: Acridoidea) en pastizales del Sur de la region Pampeana. *Rev Soc Entomol Arg* 71(3–4):275–288
- Mariottini Y, De Wysiecki ML, Lange CE (2013) Diversidad y distribucion de acridios (Orthoptera:Acridoidea) en pastizales del sur de la region Pampeana. *Argentina Rev BiolTrop* 61(1):111–124
- Mariottini Y, Scatollini MC, Cigliano MM, Lange CE (2015) Morphometric differentiation in a field population of *Dichroplus maculipennis* (Orthoptera: Acrididae: Melanoplinae) under outbreak and non-outbreak situations. *J Orthop Res* 24(2):67–75
- Mariottini Y, Marinelli C, Cepeda R, De Wysiecki ML, Lange CE (2022) Relationship between pest grasshopper densities and climate variables in the southern Pampas of Argentina. *Bull Entom Res*. <https://doi.org/10.1017/S000748532100119X>
- Marrero HJ, Medan D, Zarlavskyb GE, Torrettab JP (2016) Agricultural land management negatively affects pollination service in Pampean agro-ecosystems. *Agric Ecosyst Environ* 218:28–32. <https://doi.org/10.1016/j.agee.2015.10.024>
- Mastrangelo ME, Weyland F, Herrera LP, Villarino SH, Barral MP, Auer AU (2015) Ecosystem services research in contrasting socio-ecological contexts of Argentina: critical assessment and future directions. *Ecosyst Serv* 16:63–73
- Medan D, Torretta JP, Hodara K, de la Fuente EB, Montaldo N (2011) Effects of agriculture expansion and intensification on the vertebrate and invertebrate diversity in the Pampas of Argentina. *Biodivers Conserv* 20:3077–3100
- Miguel L, Lorier E, Zerbino S (2014) Caracterizacion y descripcion de los estadios ninfales de *Borellia bruneri* (Rhen, 1906) (Orthoptera: Gomphocerinae). *Agrocienc Urug* 18(72–81):72
- Modernel P, Rossing WA, Corbeels M, Dogliotti S, Picasso V, Tittonell P (2016) Land use change and ecosystem service provision in Pampas and Campos grasslands of southern South America. *Environ Res Lett* 11(11):113002. <https://doi.org/10.1088/1748-9326/11/11/113002>
- Noriega JA, Hortal J, Azcarate FM, Berg MP, Bonada N, Briones MJI, Del Toro I, Goulson D, Ibanez S, Landis DA et al (2018) Research trends in ecosystem services provided by insects. *Basic Appl Ecol* 26:8–23
- Ortego J, Aguirre M, Nogueras V, Cordero P (2015) Consequences of extensive habitat fragmentation in landscape-level patterns of genetic diversity and structure in the Mediterranean esparto grasshopper. *Evol Appl* 8:621–632. <https://doi.org/10.1111/eva.12273>
- Oyarzabal M, Clavijo J, Oakley L, Biganzoli F, Tognetti P, Barberis I, Maturro HM, Aragon R, Campanello PII, Prado D, Oesterheld M, Leon RJ (2018) Unidades de vegetacion de la Argentina. *Ecol Aust* 28(1):040–063. <https://doi.org/10.25260/EA.18.28.1.0.399>
- Oyarzabal M, Andrade B, Pillar VD, Paruelo JM (2020) Temperate Subhumid grasslands of Southern South America. In: Goldstein MI, Della Sala DA (eds) Encyclopedia of the World’s Biomes, vol 2. Elsevier, Amsterdam, pp 577–593. <https://doi.org/10.1016/B978-0-12-409548-9.12132-3>
- Paruelo JM, Jobbagy EG, Oesterheld M, Golluscio RA, Aguiar MR (2007) The grasslands and steppes of Patagonia and the Rio de la Plata plains. In: Veblen T, Young K, Orme A (eds) The physical geography of South America. Oxford University Press, Oxford, pp 232–248
- Pelizza SA, Mariottini Y, Russo ML, Vianna MF, Scorsetti AC et al (2019) Application of *Beauveria bassiana* using different baits for the control of grasshopper pest *Dichroplus maculipennis* under field cage conditions. *J King Saud Univ* 31(4):1511–1515
- Perelman SB, Batista WB, Chaneton E, Leon RJC (2007) Habitat stress, species pool size, and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. *J Ecol* 95:662–673
- Piquer-Rodriguez M, Butsic V, Gartner P, Macchi L, Baumann M, Gavier Pizarro G, Volante JN, Gasparri IN, Kuemmerle T (2018) Drivers of agricultural land-use change in the Argentine Pampas and Chaco regions. *Appl Geogr* 91:111–122
- Pocco ME, Damborsky MP, Cigliano MM (2010) Comunidades de ortopteros (Insecta, Orthoptera) en Pastizales del Chaco Oriental Humedo, Argentina. *Anim Biodivers Conserv* 33:119–129
- Poniatowski D, Beckmann C, Loffler F, Munsch T, Helbing F, Samways M, Fartmann T (2020) Relative impacts of land-use and climate change on grasshopper range shifts have changed over time. *Glob Ecol Biogeogr* 29:2190–2202. <https://doi.org/10.1111/geb.13188>
- Ricard F, Berhongaray G, Viglizzo E (2019) The Argentine Pampas: a novel ecosystem at the crossroad. *Encycl World Biomes*. <https://doi.org/10.1016/B978-0-12-409548-9.12060-3>
- Ronderos RA (1959) Identificacion de las especies de tucuras mas comunes en la Provincia de Buenos Aires. *Agro* 1:1–31
- Satorre EH, Andrade FH (2021) Cambios productivos y tecnologicos de la agricultura extensiva argentina en los ultimos quince aos. *Ciencia Hoy* 29 (173):19–27.

- Schowalter TD (2013) *Insects and sustainability of ecosystem services*. CRC Press/Taylor and Francis Group, Boca Raton
- Song H, Mariño-Pérez R, Woller DA, Cigliano MM (2018) Evolution, diversification, and biogeography of grasshoppers (Orthoptera: Acrididae). *Insect Syst Diver* 2(4):1–25. <https://doi.org/10.1093/isd/ixy008>
- Soriano A, León R, Sala O, Deregibus V, Cauhépé M, Scaglia O, Velásquez LJ (1992) Río de La Plata Grasslands. In: Coupland RT (ed) *Ecosystems of the world*. Elsevier, Holanda, pp 367–407
- Torretta JP, López MC, Marrero HJ (2021) Flower flies (Diptera: Syrphidae) in Pampean agroecosystems: a study case. *Rev Soc Entomol Argentina* 80:23–34
- Torrusio SA, Cigliano MM, De Wysiecki ML (2002) Grasshopper (Orthoptera: Acrididae) and plant community relationships in the Argentine pampas. *J Biogeog* 29:221–229
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol Lett* 8:857–874
- Viglizzo EF, Roberto ZE, Lértora F, Lopez Gay E, Bernardos J (1997) Climate and land use change in Field-crop ecosystems of Argentina. *Agric Ecosyst Environ* 66:61–70
- Viglizzo EF, Lértora FA, Pordomingo AJ, Bernardos J, Roberto ZE, Del Valle H (2001) Ecological lessons and applications from one century of low external-input farming in the pampas of Argentina. *Agric Ecosyst Environ* 81:65–81
- Viglizzo EF, Frank FC, Carreño LV, Jobbagy EG, Pereyra H, Clatt J, Pincén D, Ricard F (2011) Ecological and environmental footprint of 50 years of agricultural expansion in Argentina. *Glob Change Biol* 17:959–973
- Viglizzo EF, Jobbágy E (2010) *Expansión de la frontera agropecuaria en Argentina y su impacto ecológico-ambiental*. Ediciones INTA ISBN N° 978-987-1623-83-9.
- Vincent H, Bornand C, Kempel A, Fischer M (2020) Rare species perform worse than widespread species under changed climate. *Biol Conserv* 246:108586. <https://doi.org/10.1016/j.biocon.2020.108586>
- Wagner DL (2020) Insect declines in the Anthropocene. *Annu Rev Entomol* 65:457–480
- Weyland F, Baudry J, Ghera CM (2014) Rolling Pampas agroecosystem: which landscape attributes are relevant for determining bird distributions? *Rev Chil Hist Nat* 1:1–14
- Zhang S, Zhang Q, Yan Y, Han P, Liu Q (2021) Island biogeography theory predicts plant species richness of remnant grassland patches in the agro-pastoral ecotone of northern China. *Basic Appl Ecol* 54:14–22

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