Carolina Massa*, Pablo Teta and Gerardo Ruben Cueto

Effects of regional context and landscape composition on diversity and composition of small rodent assemblages in Argentinian temperate grasslands and wetlands

Abstract: This study aims to describe landscape evolution in two contiguous ecoregions with different land use intensity, to assess changes in small mammal assemblages. Rodent remains in pellet samples from barn owls were used to estimate the attributes of rodent assemblages. Two major biomes were considered in this study, a mosaic of wetlands (Delta and Paraná Islands ecoregion) and a mosaic of grasslands and cultivated fields (Pampa ecoregion). Environmental characterization was based on the analysis of satellite images and weather data. Fourteen rodent species in 28 sampling sites were identified, totaling 7645 prey items. Linear combinations of variables that characterized the landscape explained 66.6% of variation in the composition of rodent assemblages. A positive linear relationship between rodent diversity and the number of different patches was found in the Pampa. Our results suggest that landscape disturbances caused by agricultural intensification favor the increase of generalist and competitively subordinated species. In turn, changes in rodent diversity at the Paraná Delta were negatively associated with the percentage of water-covered area and the number of patches. The hydrological regime of this ecoregion acts as a filter for species establishment, restricting the richness of the rodent assemblages.

Keywords: land cover; micromammals; Sigmodontinae; *Tyto alba*.

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Introduction

Changes in land use represent a complex environmental, socio-economic and technological problem, causing not only a reduction in the area of the original cover type, but also changes in landscape structure (Baldi and Paruelo 2008). Natural landscapes are disappearing rapidly due to land use changes, following a general trend towards replacement of natural habitats by crop-lands and pasture (Klein Goldewijk et al. 2011). Several studies have shown habitat fragmentation and decreasing landscape heterogeneity to be associated with a loss of biodiversity in agricultural landscapes (Steffan-Dewenter and Tscharntke 1999, Weibull et al. 2003, Holzschuh et al. 2007).

One of the most human-modified biomes of the world is grassland (Hannah et al. 1995). In temperate southern South America, the extensive plains known as Río de la Plata Grasslands (RPG) have been transformed into cropland at high rates since the beginning of the 20th century (Baldi and Paruelo 2008). In the last two decades (1990s and 2000s), the rate of agricultural expansion increased considerably because of technological factors (e.g., non-tillage techniques and genetically modified crops) and market conditions (i.e., the increase in the demand for soybean by Asian countries and monetary exchange policies) (Baldi and Paruelo 2008). Agricultural intensification and expansion to monocultures, mainly soybean, compromise the long-term sustainability of the region and the provision of vital ecosystem services such as carbon sequestration, soil preservation, and regional climate amelioration (Baldi and Paruelo 2008).

A different scenario can be found in temperate wetlands surrounded by the RPG region. This area is environmentally heterogeneous, the product of past geomorphological and hydrological processes (Holocene marine ingressions and regressions) and current processes (fluvial modeling) (Ringuelet 1961). Traditional productive activities in this area are extensive cattle ranching and plantation forestry of Salicaceae (willows and poplars) (Vicari et al. 2006).

According to Bó and Malvárez (1999), overgrazing and cropping on unsuitable land, the use of unsuitable techniques and the advance of the agricultural frontier are contributing to soil degradation and erosion, and to habitat fragmentation in this region. In addition, the widespread use of different methods of water management (dykes, canals and drainage systems) also affects the structure and function of these wetlands (Bó and Malvárez 1999).

Small mammals are consumers of seeds, non-crop plants and insects (Ness and Morin 2008, Baraibar et al. 2009), but they can also be reservoirs of zoonoses (Cueto et al. 2008) and agricultural pests of various crops (Brown et al. 2007). In addition, they serve as a food supply for a large number of predators, and can exert significant influence on predator population cycles (Taylor 1994, Salamolard et al. 2000). Blois et al. (2010) suggest that recent climate change, in combination with human influences, could cause decreases in richness, increasing species turnover, and local increases in the abundance of generalist species in communities that are already more susceptible to perturbation. Millán de la Peña et al. (2003) investigated changes that occurred in rodent communities along a gradient of agricultural intensification in a European temperate grassland. The authors showed that intensification of agriculture tended to favor the most common and generalist species, while rare and habitat-specialist species were more numerous in low-intensity farmland landscapes. However, there are no studies describing the effect of changes in land use in wetlands on rodent assemblages, nor on how the responses of assemblages differ in different regional contexts.

We hypothesize that the attributes of rodent assemblages are influenced by the degree of agricultural land use, but in different ways according to the regional context. In grasslands with a strong history of land use, we expect to observe a loss of diversity of rodents associated with the increase of agricultural land use. In contrast, in regions with less land use history, like South American wetlands, human activity could increase the diversity of rodents due to increasing availability of new habitats. This study aims to characterize landscape along two contiguous regions with different land use intensity in order to assess changes in small-mammal assemblages. The specific aims of this study are: 1) to understand how the composition, abundance, species-richness and diversity of small mammal assemblages respond to changes in land cover; 2) to identify the species that are associated with the different landscape patterns, as well as the species that can be used to evaluate ecological problems arising from changes in land use; and 3) to determine how the response of rodent assemblages to agricultural land use changes according to the land-use history of each region.

Materials and methods

Study area

The study area is located in the lower Río de la Plata basin, approximately between 31°52′ and 33°54′ S and 58°12′ and 60°38′ W. It covers ca. 45,158 km^2 and is bounded to the west and south by the Paraná River, by the Uruguay River to the east and by the Río de la Plata estuary to the southeast (Figure 1).

The climate is temperate and humid, with mean annual temperatures between 17.6°C and 18.4°C. Average annual precipitation decreases towards the southeast from 1200 mm to 990 mm, with marked interannual variations (Engler et al. 2008). Altitude varies between 3 and 60 m above sea level, with the lowest altitudes being found in the south of the study region. According to characteristics of its geomorphology, soil, drainage, physiography and vegetation, this region can be classified in two natural subunits: a) Delta and Paraná islands, with an approximate area of 17,500 km^2, and b) Mesopotamic Pampas with a surface of 22,677 km^2 (Brown et al. 2006) (Figure 1). The Delta of the Paraná River ("Delta") is a macromosaic of wetlands, composed of permanent and temporary aquatic environments and land areas which form a gradient from the main water channels towards the edges of their flood plains. This geomorphologic characteristic, plus the flood and drought pulses confer a great "elasticity" (difference between the area occupied during the period of greatest flooding and/or inundation, and that occupied at the period of maximum drought) to this region (Neiff 1996). This elasticity could explain, in part, the distribution and abundance of animal and plant species (Neiff and Malvárez 2004).

The Paraná River and its large tributaries, such as the Paraguay, are important "corridors" (i.e., effective routes for active or passive migration) for tropical flora and fauna to temperate zones, where they can coexist with local species (Ringuelet 1961).

The Mesopotamic Pampa ("Pampa") is located between the Paraná and Uruguay rivers in the province of Entre Ríos, bordered to the north by the Espinal phytogeographical province, to the south by the Delta and to the east by the Uruguayan savanna. The land is mostly undulating, crossed by rivers and streams with gallery forests in their margins (Engler et al. 2008). It is characterized by a great abundance of subtropical grasses, interspersed with low shrubs and numerous herbs that increase with overgrazing. Woody vegetation is restricted to some relicts or patches of semixerophilous woodland, mainly in the
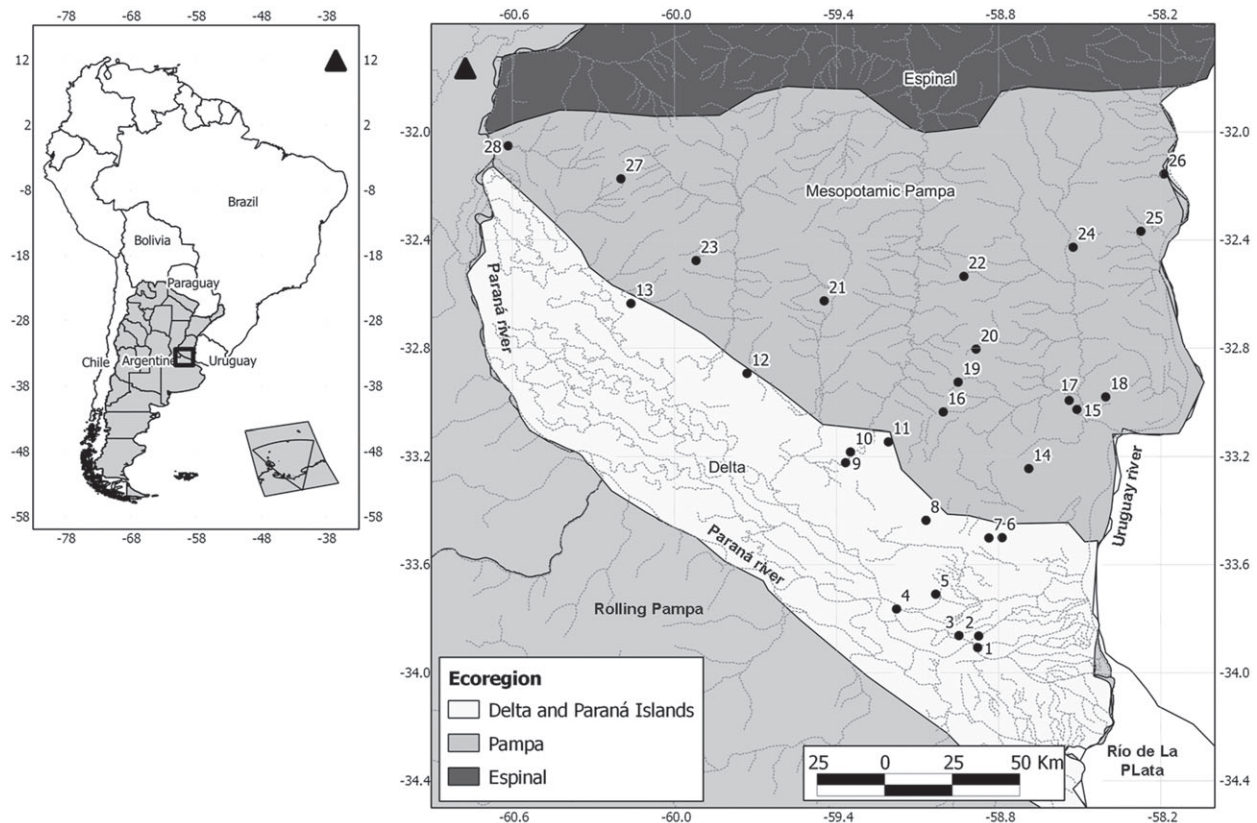
Figure 1 Map of the study area, lower Río de la Plata basin. Numbers correspond to those on Table 1.

transition towards the Espinal – at the northern limit of the ecoregion – and towards the gallery forests on narrow strips along rivers.

Nowadays, the sustained increase in soy bean prices is displacing beef cattle production from traditional mainland areas to marginal ones. The islands along the Paraná main channel and Delta are the main receptors of these cattle, as most are federal or state lands and are near the most productive cattle-growing areas of the Pampa region.

Rodent sampling

The assemblages of small rodents (<300 g) were assessed through the collection of pellets and pellet debris of the barn owl, *Tyto alba*. Pellets are conglomerates of undigested prey parts (e.g., bones, feathers, hairs, etc.) consumed by the birds (Errington 1930) and which are regurgitated periodically, usually in nesting and roosting sites (Andrews 1990).

This method was considered the most suitable as it allows the study of large areas, and generates a large number of individuals per sample. Several authors agree that the number and frequency of prey found in these

pellets can be taken to be representative of the availability of micromammals present in a particular area (Errington 1930, Bonvicino and Bezerra 2003, Millán de la Peña et al. 2003, Pardiñas et al. 2003, Trejo and Lambertucci 2007, Fischer et al. 2012, Lyman 2012).

Bernard et al. (2010) documented for the first time the dietary response of *Tyto alba* to variations in prey density in temperate ecosystems, and observed significant correlations between the proportion of rodents in the diet of *T. alba* and their respective densities in the field. They showed that the frequency of a given species in the diet of *T. alba* depends not only on its own population density in the field, but also on the population density of other species present. In this study we used the analysis of the diet of *T. alba* to detect changes in the representation of rodent species in different assemblages. We did not attempt to estimate the population abundance of any of this species since the increase in representation of a given species according to this method does not allow discrimination between an increase in species abundance and a decrease in the representation of other species.

Between 2007 and 2009, the study area was explored looking for possible owl nesting and roosting sites (church belfries, abandoned buildings, bridges, water

tanks, train stations, etc.) (Del Hoyo et al. 1992, Taylor 1994). As the estimated home range of barn owls is within a radius of 2.5 km (Evans and Emlen Jr. 1947, Taberlet 1983, Taylor 1994), selected sampling sites were at least 6 km apart to avoid overlapping between different individuals. The chosen sites were those nests or roosts containing a number and age range of pellets, following the classification proposed by Doughty (2002), that ensured an amount of material accumulated for at least a year, in order to minimize the effect of seasonal fluctuations in the studied assemblages. The method of processing for pellets samples is the same as described in Love et al. (2000). Prey items were identified to species level by comparison of skull fragments and mandibles with reference collections housed at the Bernardino Rivadavia Natural Sciences Museum ("Museo Argentino de Ciencias Naturales Bernardino Rivadavia") in Buenos Aires, Argentina. The minimum number of individuals for each taxon, based on the quantification of the most common bone element, was calculated for each sample (Andrews 1990).

Landscape characterization

Maps of landscape variables for the study area were elaborated. Around each sampling site a circle of 2.5 km radius representing a mean owl home range was generated (Taberlet 1983), and the following variables were recorded from each map:

– altitude and its coefficient of variation, using a GTOPO30 grid with a 30 arc-second resolution (around 1×1 km) (http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/GTOPO30)
– cover type, determined from MODIS images that show ground cover types at a global scale (MCD12Q1) for 2008, at 500×500 m resolution.

The IGBP (International Geosphere-Biosphere Program Data and Information System) classification system was used. The images showed 17 cover types (Loveland and Belward 1997) that were reclassified as water, forest, shrubland, savanna, grassland, permanent wetlands, croplands, urban and cropland/natural vegetation mosaics. The five original forest types and the two savanna types were each unified into a single category to simplify the model. Bare soil, present in only one site, in only three of 98 pixels, and wetlands were joined, since comparison with previous years' (2001 and 2007) images and aerial photographs showed that they correspond to river flooding plains which in 2008 remained dry due to an intense drought (Paparotti and Gvozdenovich 2009).

Numbers of patches, numbers of classes, the proportion of cover types and landscape diversity were calculated.

Climatic variables

Climatic variables were obtained from the WorldClim data set (Hijmans et al. 2005, http://www.worldclim.org/), an interpolation of 30 arc-seconds resolution set of global data (approximately 1×1 km). The variables considered for the analysis were annual mean temperature, annual precipitation and the precipitation seasonality. All other available variables presented significant correlation with at least one of the three chosen variables (Pearson correlation coefficient; p<0.05 for all cases). The images were analyzed with the ArcView 3.2 program (Esri, 1999. ArcView GIS, 3.2a ed. Environmental Systems Research Institute, Inc., New York.) and landscape indices were calculated with its Spatial Analysis module (Esri, 2000. ArcView Spatial Analyst 2.0a.).

Statistical analysis

In order to evaluate the minimal sample size (number of individuals), cumulative species frequencies were computed from five independents series of different sample sizes (from 1 to 300 rodents) extracted from two whole samples, one from Pampa (site 20, n=417), and the other from Delta (site 5, n=347), and were compared against species frequencies of the whole samples by using the Percentage Similarity index (PS) (Krebs 1999). Mean values of this index were computed for each of the five independent series following Millán de la Peña et al. (2003).

The following attributes of rodent assemblages for each site were compared: species composition, species richness (S) and Simpson diversity (D) (Magurran 1988). To describe the landscape and the degree of association between variables, a PCA (principal component analysis) based on the correlation matrix was conducted. The percentage of the variability in representation of different species in the rodent assemblages explained by changes in landscape variables was estimated through redundancy analysis (RDA) (Lepš and Šmilauer 2003), and the statistical significance of that percentage was determined using the Monte Carlo permutation test. Most relationships between species and explanatory variables were approximately linear. Forward selection was used to choose landscape variables, taking into account the inflation index (lower than 13) and the collinearity between them (Lepš and Šmilauer 2003).

Finally, to analyze the association between landscape variables and the assemblage diversity, stepwise multiple linear regressions were carried out. This analysis was performed both for sites of each of the two ecoregions separately and for all sites together.

The validity of the models assumptions was tested using graphical methods (Q-Q plots to evaluate normality and plots of residuals against predicted values to study homogeneity of variances). The autocorrelation of residuals of the final model was also analyzed.

Results

Taxonomic composition and relative species abundance of rodent assemblages

Similarities obtained from samples over 100 individuals with the whole sample was over 0.95 (Figure 2). We concluded that samples containing more than 100 rodents adequately represented relative species abundance in assemblages.

The rodent assemblages were described for a total of 28 sites, 13 in the Delta, mainly in the southern portion denominated Lower Delta (Iriondo 1979), and 15 in the Pampa (Figure 1); based on the analysis of approximately 2600 pellets containing 7645 rodents of 14 different species. The presence and relative abundance data for each site are summarized in Table 1. Mean assemblage richness was eight species, with a minimum of six and a maximum of 12. Seventy-nine percent of all surveyed sites had between seven and nine species (Table 1).

Sites located in the Pampa were characterized by the dominance of *Calomys* cf. *laucha* (Fischer 1814) and *Calomys callidus* (Thomas 1916), while in the Delta the dominant species was *Oligoryzomys flavescens* (Waterhouse 1837) accompanied by *Deltamys kempi* (Thomas 1917) and *Scapteromys aquaticus* (Thomas 1920) (Table 1).

In the center of the Pampa the assemblages were dominated by *Calomys* cf. *laucha* with a relative abundance higher than 70%. The assemblages with the lowest rodent diversity were recorded in this area. The proportion of *Calomys callidus* increased towards the west, while to the east, on the Uruguay River shores, there was an increase of *Akodon azarae* (Fischer 1829) and *Oligoryzomys flavescens*. These grassland sites had the highest rodent diversity (Table 1).

In the Delta region the lowest rodent diversity was found in the south, and *Oligoryzomys flavescens* was its dominant species. To the north and west, the proportion of *Calomys* cf. *laucha* increased, together with *Akodon azarae*, while an increase in the diversity of the rodent assemblages was also registered (Table 1).

Landscape characterization

The first two axes of the principal component analysis, that sorted the sites according to the environmental variables, explained 54% of the association between these variables (Table 2). The first component (39%) was positively associated with the number of patches, the number of classes and the percentage of the area covered with forest, water, wetlands, shrub land and savanna, and negatively with the percentage of cropped area, mean
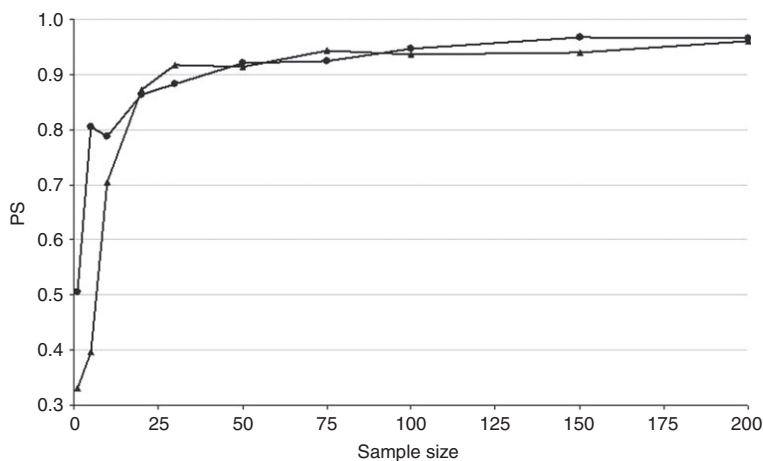
Figure 2 Similarity of species frequencies obtained through percentage similarity index (PS), five independents series of different sample sizes (from 1 to 300 rodents) extracted from two samples of 423 and 417 individuals, one belonging to Pampa (circle) and the other to Delta (triangle).

Table 1 Relative abundance of small mammals contained in pellets of *Tyto alba* at 28 sites of the study area.

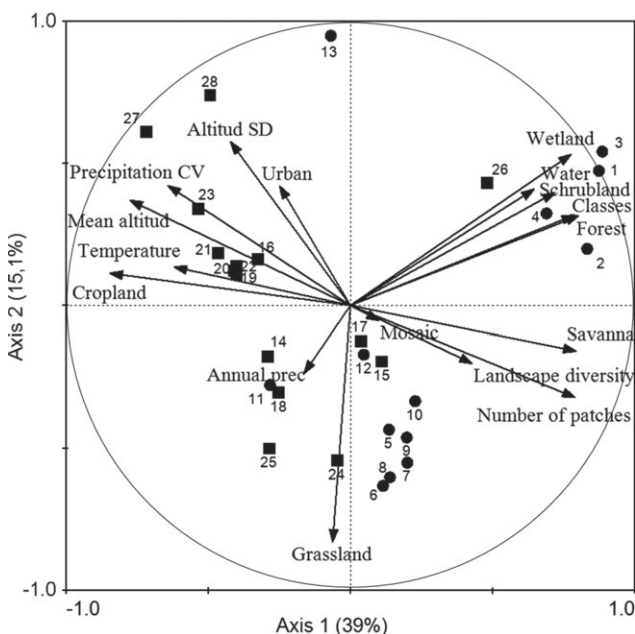| Site	Name	LAT	LONG	Aa	Dk	Or	Sa	Hc	Hb	On	Of	Cl	Cc	Rt	Mm	R.spp.	Ca	N	S	D
1	Pte Urquiza	-33°55'	-58°53'	0.06	0.04	0.01	0.04	–	0.07	–	0.68	0.09	–	–	0.01	–	–	180	8	0.51
2	Brazo Chico	-33°52'	-58°52'	0.08	0.05	0.03	0.05	–	–	0.05	0.65	0.03	–	–	0.05	–	–	150	8	0.55
3	Brazo Largo	-33°52'	-58°57'	0.09	0.02	0.01	0.03	–	0.03	0.02	0.78	0.03	–	–	–	<0.01	–	388	9	0.39
4	Ibicuy	-33°46'	-59°11'	0.03	0.02	–	0.05	–	0.03	–	0.61	0.26	–	–	–	–	–	262	6	0.55
5	San Martín	-33°43'	-59°02'	0.10	0.03	0.03	0.05	–	0.01	<0.01	0.33	0.45	–	–	–	–	–	347	8	0.68
6	Ceibas	-33°30'	-58°47'	0.06	0.04	0.11	0.04	–	0.05	<0.01	0.66	0.02	–	–	–	<0.01	–	220	9	0.54
7	Ea. La Peregrina	-33°30'	-58°50'	0.07	0.01	0.01	0.07	–	0.05	<0.01	0.35	0.37	–	0.07	<0.01	–	<0.01	981	11	0.72
8	Medanos	-33°26'	-59°04'	0.12	–	–	0.01	0.03	0.03	–	0.53	0.27	–	–	–	–	–	338	6	0.63
9	Pto Ruiz	-33°13'	-59°22'	0.08	–	–	0.01	0.01	–	–	0.10	0.4	0.17	0.24	–	–	–	189	7	0.74
10	Ea. Los Tres Palos	-33°11'	-59°21'	0.17	–	–	–	0.01	–	–	0.07	0.6	0.07	0.08	–	–	–	133	6	0.59
11	Carbó	-33°09'	-59°13'	0.21	0.01	–	0.02	–	–	–	0.28	0.25	0.01	0.05	0.03	0.14	–	173	9	0.79
12	Ea. El Estribo	-32°53'	-59°44'	0.12	–	0.03	–	0.07	0.03	–	0.20	0.36	0.16	0.03	–	–	–	116	8	0.78
13	Victoria	-32°38'	-60°10'	0.03	–	–	–	0.44	0.03	–	0.25	0.17	0.07	–	–	0.01	–	104	7	0.71
14	Perdices	-33°14'	-58°41'	0.33	–	0.04	–	–	0.02	0.02	0.15	0.44	–	–	–	0.01	–	107	7	0.68
15	Gualeguaychú	-33°02'	-58°31'	0.04	–	–	<0.01	–	<0.01	0.03	0.18	0.72	–	–	0.02	–	<0.01	423	8	0.44
16	Larroque	-33°02'	-59°01'	0.13	–	–	–	–	<0.01	–	0.07	0.7	0.07	0.01	0.01	–	–	355	7	0.48
17	Cem. Gualeguaychú	-32°59'	-58°32'	0.28	–	–	–	–	0.03	0.03	0.26	0.2	–	–	0.15	0.02	0.03	102	8	0.79
18	Cnia. Ubajay	-32°59'	-58°24'	0.05	–	0.01	0.01	–	–	–	0.02	0.88	–	–	0.02	0.01	–	170	7	0.22
19	Irazusta	-32°56'	-58°57'	0.09	–	0.01	–	–	–	–	0.03	0.78	0.07	0.02	–	–	0.01	160	7	0.39
20	Parera	-32°48'	-58°53'	0.04	–	0.02	–	–	<0.01	–	0.03	0.79	0.10	–	<0.01	–	–	417	7	0.36
21	Remonta	-32°38'	-59°27'	0.05	–	0.01	–	–	0.01	–	0.03	0.77	0.10	0.04	–	–	–	300	7	0.39
22	Gilbret	-32°32'	-58°56'	0.06	–	–	–	–	–	–	0.02	0.78	0.12	0.01	0.02	–	–	324	6	0.37
23	Febre	-32°29'	-59°55'	0.19	–	0.03	–	<0.01	<0.01	0.01	0.16	0.39	0.18	<0.01	0.01	<0.01	0.01	472	12	0.75
24	Palacio San José	-32°26'	-58°31'	0.22	–	0.09	–	–	0.04	0.05	0.08	0.37	–	–	0.12	0.02	0.03	199	9	0.78
25	Ruta 14	-32°22'	-58°16'	0.08	–	–	0.01	–	–	–	0.11	0.76	–	0.02	0.01	<0.01	0.01	225	8	0.40
26	Liebig	-32°10'	-58°11'	0.19	–	–	0.01	–	0.04	0.05	0.41	0.28	–	–	–	<0.01	0.02	253	8	0.71
27	Ramírez	-32°10'	-60°12'	0.05	–	–	–	–	–	–	0.05	0.75	0.14	0.01	0.01	0.01	–	198	7	0.41
28	Strobel	-32°03'	-60°37'	–	–	0.01	<0.01	0.01	–	–	0.12	0.65	0.16	–	0.01	0.01	–	359	9	0.53

Number of rodents, species richness and Simpson's dominance index was calculated for each site. Sites are sorted by latitude. Sites 1–13 belong to Delta e Islas del Paraná, and 14–28 to Pampa. *Aa: Akodon azarae*; *Dk: Deltamys kempi*; *Or: Oxymycterus rufus*; *Sa: Scapteromys aquaticus*; *Hc: Holochilus chacarius*; *Hb: Holochilus brasiliensis*; *On: Oligoryzomys nigripes*; *Of: Oligoryzomys flavescens*; *Cl: Calomys* cf. *C. laucha*; *Cc: Calomys callidus*; *Rt: Reithrodon typicus*; *Md: Mus musculus*; *R. spp.: Rattus* spp.; *Ca: Cavia aperea*; N: number of individuals; S: species richness; D: Simpson's diversity index.

Table 2 Factor loadings of the first two axes for principal component analysis.

Variable	Axis 1 (39%)	Axis 2 (15.1%)
Water	**0.6458**	0.4088
Forest	**0.8018**	0.3156
Shrublands	**0.7187**	0.3975
Savannas	**0.7929**	-0.1592
Grassland	-0.0617	**-0.8309**
Permanent wetlands	**0.7762**	**0.5319**
Croplands	**-0.8445**	0.1133
Urban and builllt-up	-0.2483	0.4194
Cropland/Natural vegetation mosaic	0.1006	-0.0528
Number classes	**0.7875**	0.3182
Number of patches	**0.7900**	-0.3220
Diversity	0.4282	-0.2023
Annual mean temperature	**-0.6194**	0.1353
Annual precipitation	-0.1629	-0.2369
Precipitation seasonality	**-0.6411**	0.4222
Mean Altitude	**-0.7743**	0.3702
Altitude coefficient variation	-0.4211	**0.5762**

Values above 0.5 in bold.

altitude and precipitation seasonality (Figure 3). In Figure 3, the southeastern sites of the Delta, as well as one Pampa site, are located at the positive extreme of axis 1, showing

high values of number of cover classes, number of patches and wetland, water, forest and savanna cover. The rest of the Delta sites displayed intermediate values on axis 1, forming a continuum with the Pampa ecoregion sites as the values of the variables mentioned above decreased and mean altitude, cropped area, seasonality and mean temperature increased (Table 2). At the other extreme of axis 1 only Pampa sites were located. The second component (15.1%) was positively associated with altitude standard deviation, and negatively with the percentage of grassland cover (Table 2). This axis showed a gradient from sites with high altitude variability, located on the escarpments of the big rivers (sites 13 and 28; Figure 3), to topographically homogeneous sites with a gradual increase in the percentage of grassland cover.

Species responses to the changes in landscape variables

On the basis of the linear combinations of variables that describe the landscape characteristics, the RDA explained a significant fraction of the variation in rodent species proportions (70.2%, Monte Carlo test: F=4.91, p=0.002), with the first axis explaining 87% of that amount. Most Delta sites were located towards the right, while the Pampa sites were on the left (Figure 4). *Oligoryzomys flavescens*, *Scapteromys aquaticus*, *Holochilus brasiliensis*
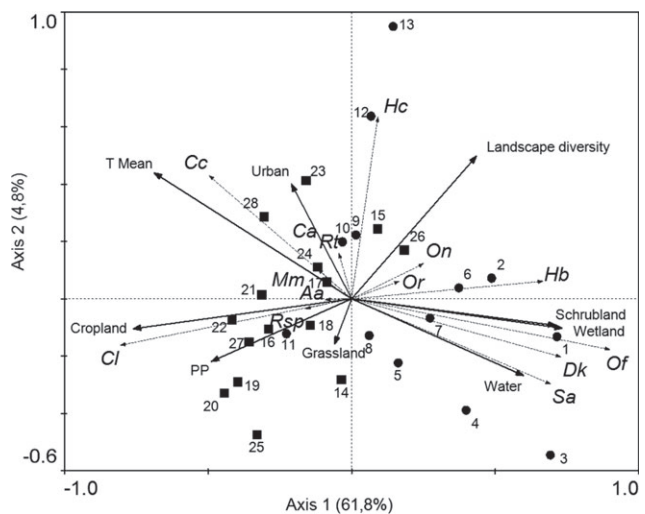

Figure 3 Ordination of study sites produced by principal component analysis (PCA) based on landscape variables. Numbers correspond to the sites in Figure 1 and Table 1. Sites 1 to 13 belong to Delta ecoregion (circles), and from 14 to 28 to Pampa (squares). Correlation circle indicates the influence of the different variables.

Figure 4 Triplot of the 14 rodent species (indented arrows), 28 sites (circles) and nine quantitative environmental variables (full arrows) on the two first canonical axes of the redundancy analysis (RDA). Symbols of the variables: species, same as Table 1. Environmental variables, T Mean=mean temperature; PP=annual precipitation. Sites 1–13 belong to Delta ecoregion (circles), and from 14 to 28 to Pampa (squares).

(Desmarest 1819) and *Deltamys kempi* were positively correlated to axis 1, i.e., to sites with the highest percentage of wetlands, shrublands, water surfaces and with high landscape diversity. Species of the genus *Calomys*, *C.* cf. *laucha* and *C. callidus*, showed a high negative association with this axis. These species were positively associated with the percentage of the area covered by crops, mean annual temperature and precipitation. Axis 2 explained a low portion of the explainable variance (6.8%). *Holochilus chacarius* (Thomas 1906) was positively correlated with this axis, associated with sites with greater landscape diversity. *Mus musculus* (Linnaeus 1758), *Akodon azarae*, *Cavia aperea* (Erxleben 1777), *Rattus* spp. [*R. rattus* (Linnaeus 1758), *R. norvegicus* (Berkenhout 1769)], *Reihtrodon Typicus* (Waterhouse 1837), *Oligoryzomys nigripes* (Thomas 1917) and *Oxymycterus Rufus* (Fisher 1814) did not show a clear association with either of the two axes analyzed (Figure 3).

Response of rodent assemblage diversity (D) to spatial changes in landscape variables

A significant positive regression was found between rodent assemblage diversity and landscape diversity (R^2=0.26; p=0.0052; Table 3). The proportion of the variance explained in rodent assemblage diversity was greater when ecoregions were analyzed separately than when all data was pooled together. In the Delta, diversity decreased monotonically as the percentage area of water surfaces and the patch number increased (Table 3). These two variables explained 74% of the total variation. The sites at the southern Delta had high values for those two variables (sites in the positive portion of axis 1 of the PCA; Figure 3), and showed the lowest rodent diversity values. In the Pampa, rodent diversity increased with patch number. This last variable was also negatively associated with cropping area (Figure 3). This regression explained 31% of the total variability of rodent diversity (Table 3).

Discussion and conclusions

In this study we analyzed rodent assemblages in two ecoregions (Pampa and Delta) with two different regional contexts. The geographic distribution of 13 out of the 14 rodent species reported in this study included the complete study area (Massoia and Vetrano 1986, Udrizar Sauthier et al. 2005, 2008, Vadell et al. 2011). *Deltamys kempi* present a distribution restricted to the Delta (Massoia and Fornes 1964, González and Pardiñas 2002, Teta et al. 2007).

Although the pool of species, with the exception of *Deltamys kempi*, was the same in both ecoregions, we did find differences in the relative abundance of each species between ecoregions. *Calomys* cf. *laucha* was frequently dominant in grasslands and agroecosystems of Pampa while *Oligoryzomys flavescens* was frequently dominant in Delta wetlands. A similar scenario has already been reported by Pardiñas et al. (2010) and Leveau et al. (2006) for the Delta and another subunit of Pampa (rolling Pampa) in Buenos Aires province.

Our results for the RPG show that as the proportion of area occupied by crops increases, landscape becomes simpler, i.e., landscape diversity, patch number and the number of cover types decreases. Ryszkowski (2002) reported impoverished animal communities in cultivated fields. In our grasslands, while we did not find a decrease in species richness associated with landscape simplification, we did find a decrease in rodent assemblage diversity. Sites with fewer patches (associated with greater agricultural land use) had lower rodent diversity due to the dominance of species of the genus *Calomys*, particularly *C.* cf. *laucha*. This condition is common to most of the Pampas territory, south of the Paraná River, where *C. laucha* and *Calomys musculinus* (Thomas 1913) are the dominant species of micromammal communities (Pardiñas et al. 2010, Teta et al. 2010, Fischer et al. 2011).

Table 3 Stepwise multiple linear regressions of Simpson index using 19 landscape variables for each ecoregion (Delta and Pampa), and for the study area as a whole.

Predictors	R²	R²aj	b	F/t	P-value
Delta (n=13)					
Model	0.78	0.74		9.069	0.0050
Water			-2.601	-4.614	0.0010
Number of patches			-0.005	-3.129	0.0107
Constant			0.811	16.943	<0.0001
Pampa (n=15)					
Model	0.36			7.533	
Number of patches			0.001	2.690	0.0187
Constant			0.360	5.270	0.0002
Delta+Pampa (n=28)					
Model	0.26			9.285	0.0052
Landscape diversity			0.703	3.470	0.0052
Constant			0.126	0.858	0.3988

For a variable to be considered and retained in the model, the significance level used was 10% (p<0.1) for the Delta and Pampa models, and 15% (p<0.15) for the model of the entire area as a whole. The selected predictors, coefficient of determination (R²), adjusted coefficient of determination (R²aj), partial regression coefficient (b), model statistics (F), variables statistic (t) and P-value of each model are shown.

The sites with the highest number of patches (indicative of greater landscape diversity) showed an increase in assemblage diversity. This could be due to the decrease in *Calomys* cf. *laucha* representation, commonly associated with the decrease in crops and the increased availability of sites suitable for grassland species such as *Akodon azarae* (Zuleta et al. 1988), and riverside species such as *Oligoryzomys nigripes* (Massoia and Fornes 1965, Weksler and Bonvicino 2005) and *Scapteromys aquaticus* (Cueto et al. 1995b). Studies at habitat scale showed that these species are spatially segregated: *C. laucha* is most abundant in crop fields while *A. azarae* and *Oligoryzomys flavescens* inhabit field edges (Hodara et al. 2000). This habitat segregation is due as much to a differential habitat selection as to interspecific competition, with *A. azarae* dominating over *O. flavescens* and *C. laucha* (Busch and Kravetz 1992, Cueto et al. 1995a).

Our results suggest that disturbances caused by agricultural intensification would favor the increase of representation of generalist and competitively subordinated species such as *Calomys* cf. *laucha*. This scenario is similar to that of the rolling Pampa (Kravetz et al. 1987, Pardiñas 1999, Pardiñas et al. 2010). Millán de la Peña et al. (2003) observed that intensification of agriculture in temperate European grasslands seems to favor more common, generalist and sometimes more unstable rodent species, while rare and threatened species appear to be more frequent in unmodified traditional farmland ecosystems. These results are also consistent with empirical findings suggesting that the decline of specialist species observed worldwide is likely to be related to human-induced landscape degradation (Devictor et al. 2008, Blois et al. 2010, and references therein).

In wetlands, the advance of the agricultural frontier had a different effect on the diversity of rodent assemblages from those observed in grasslands. In low-lying, seasonally flooding terrains where livestock farming and cropping is not very developed, low rodent diversity was recorded. Those sites showed a high representation of *Oligoryzomys flavescens*, a species adapted to flood pulses (Udrizar Sauthier et al. 2010). According to Bó and Malvárez (1999), in natural wetlands only those species adapted to seasonal flood pulses can persist. This hydrological regime acts as a filter for species establishment, restricting the richness of the rodent assemblages.

Changes in altitude were associated with changes in the representation of those species typically found in agroecosystems or on well-drained soils, such as *Calomys* cf. *laucha*, *Calomys callidus*, *Akodon azarae* (Pardiñas 1999) and *Reithrodon typicus* (Pardiñas and Galliari 2001), increasing the assemblage diversity with altitude. This

is related to the decrease in the impact of flooding with altitude, allowing an increase of agricultural land use as elevation increases.

Taking into account the time scale, comparing the current assemblages of southern Delta sites with those published by Massoia and Fornes (1964), Massoia et al. (1989), and Teta et al. (2006) obtained using the same sampling method, there was an increase in rodent richness. This change is associated with the appearance of *Calomys* cf. *laucha* and two species of commensal muroid rodents – *Mus musculus* and *Rattus* spp. The arrival of these species, not previously recorded in the Delta wetlands (Massoia and Fornes 1964), may be related to water management practices. Currently, 11% of this area is affected by dykes (Kandus and Minotti 2010). These practices, related to plantation forestry (Bó and Malvárez 1999) and transport activities, create corridors and suitable habitats for these species (Kravetz and De Villafañe 1981, Mills et al. 1991, Hodara 1998). In addition, as a result of these water management practices, flood pulses would stop acting as a filter for species establishment.

The rodent assemblage response to anthropogenic activity varied according to the regional context considered. In grasslands, where there has been an intensification of agricultural activity leading to landscape simplification, rodent assemblages responded negatively, decreasing their diversity and increasing representation of generalist and competitively subordinated species. This situation highlights the need for generating patterns of management strategies in these ecosystems which help to reverse or minimize the loss of diversity of habitats in order to preserve biodiversity. Some alternatives to be implemented include the return to cattle grazing-cropping, mixed systems, and the creation of spontaneous vegetation strips at the edges of arable fields. This last measure is of great importance; given the fact that, in Pampa agroecosystems, field edges provide shelter, food, nesting sites and protection against terrestrial and avian predation to a great variety of small mammal species (Medan et al. 2011 and references therein), it would be wise to implement the creation of grass strips at the edges of arable fields. As Marshall et al. (2006) observed, these techniques have positive effects on the diversity of plants and animals.

In contrast, in wetlands where there has been less anthropogenic activity, livestock farming and water management could be the cause of the increase in rodent diversity. The current magnitude of human activity in the area would favor the increase in the diversity of rodent assemblages due to an increase in niche diversity. However, an increase in human activity, especially in water management, enables agricultural intensification, leading to

landscape simplification, resulting in a decreased rodent diversity, as is observed in grasslands.

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