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Long-term variations in rodent abundance in a rural landscape of the Pampas, Argentina

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Abstract The goal of this study was to analyze the variations in abundance of rodent communities over the last 24 years in a rural area, and their relation to possible changes in climatic variables and land use. The principal change in the area observed along the study period was an increase in the area covered by soybean. The habitats studied were crop fields and borders. The total abundance of rodents did not show a significant trend of variation over time in crop fields while in borders the abundance in autumn–winter (A–W) showed a significant trend to decrease over time. The different rodent species showed a differential response over time. While *Calomys laucha* and *C. musculinus* showed a decrease between the period before and after the soybean expansion, *Akodon azarae* did not change its abundance over time. The mean minimum temperature increased over time while the number of days with frost decreased. Total rodent abundance in A–W was positively associated with the cumulated precipitation of the previous spring–summer period and negatively with the cumulated precipitation of the same period. We conclude that rodent abundance variations in crop fields and borders of the study area are influenced by precipitation, but the observed trends of variation over time are better explained by changes in agricultural practices than by meteorological variables.

Keywords Rodent communities · Land use · Climate variation · Agroecosystems

Introduction

The structure and function of ecosystems vary both in time and space, depending on intrinsic mechanisms as well as on variations in the abiotic environment. In addition to the natural fluctuation in environmental variables, most ecosystems of the earth have some degree of human influence. The growth of the human population and the expansion of the power of technology has increased drastically the scope and nature of human modification of the ecosystems. These modifications involve land-use transformations, alter the major biochemical cycles, and add or remove species in most of the earth's ecosystems (Wolman 1993; Vitousek et al. 1997), and nowadays the use of land represents the most substantial human alteration of the earth systems (Vitousek et al. 1997).

In terrestrial ecosystems, the agricultural expansion is the most relevant change in land use (Paruelo et al. 2005), and temperate grasslands are probably the most altered ecosystems by man-made activities. Climate change is also expected to have an impact on temperate terrestrial ecosystems (Sala et al. 2000), both directly on organisms, or indirectly through the ecosystem processes that effect vegetation cover and food availability (Stenseth et al. 2002a). Among the expected changes are the variations in plant communities, with the replacement of native perennial by exotic annuals, woody invasions, and changes in the phenology. Animals are also affected through the effects on plant communities that cause changes in habitat and food availability, or directly by human activities, as hunting or exploitation.

Although there are few long-term studies of the effects of environmental variables on the population dynamics of rodents (Ernest et al. 2000; Lima et al. 2001; Stenseth et al. 2002b; Zhang et al. 2003), many studies showed the influence of temperature and precipitation

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patterns on rodent abundance. In the northern hemisphere, population cycles have been related to climate variations that influence resource availability as well as to top-down interactions with predators (Garsd and Howard 1981; Hanski et al. 1991; Singleton et al. 2001; Stenseth et al. 2003). In the southern hemisphere, rodent population fluctuations have been associated with the “Niño” oscillation (ENSO) and associated changes in precipitation patterns (Lima et al. 2002). In multispecies communities, the effect of environmental conditions may differ among species, and then community composition vary continuously over time, reflecting the responses of species and groups of species to different environmental variables (Lima et al. 2002).

In addition to climate fluctuations, most farming and agricultural practices affect the distribution and habitat use of small mammals, but their response may differ depending on the type and intensity of the disturbance (MacDonald et al. 2000; Todd et al. 2000; Jacob 2003; Jacob and Hempel 2003; Millan de la Pena et al. 2003; Michel et al. 2006). The differential effects on different species cause community changes in species composition and relative abundance, favoring some species that are preadapted to the changes, and reducing others.

In the Pampean region, native rodent species show seasonal and interannual variations in abundance that have been associated with natural variations in climatic variables that affect the availability of resources (Andreo et al. 2009). Variations in autumn winter temperatures affect survival and the duration of the reproductive season. Spring–summer precipitation affects the availability of plant resources and favors rodent population growth, while an increase in precipitations during winter cause a higher mortality. On the other hand, in recent years, environmental changes associated with human activities may have caused directional variations in rodent communities.

One of the most important changes observed during the 20th century has been in land use, with an intensification of agriculture and the replacement of the mixed annual cropping-grazing system by double cropping (de la Fuente et al. 2006), along with the fragmentation of natural habitats. According to recent estimates in the Rolling Pampas, more than 50% of the land is devoted to crops such as soybean, wheat, maize, and sunflower (Viglizzo et al. 2001; Paruelo et al. 2005). The increase in agriculture was associated with an increase in the abundance of rodents of the genus *Calomys* and a decrease in *Akodon* (Kravetz et al. 1986). Variations in rodent communities according to the type of crop and technology were also described (Busch et al. 1984; Mills et al. 1991), while Bilenca et al. (2007) found a strong effect of the presence or not of weeds on rodent abundance, but not an effect of the type of crop. During the last 40 years, the proportion of area devoted to different crops changed with a decrease in winter crops such as wheat and linen, in summer crops such as sorghum and sunflower, and an increase in the area planted with soybean. Soybean was a marginal crop in the Pampean

region by 1970, increasing by 2003/2004 to approximately 38% of the cultivated area (Derpsch 1997; Paruelo et al. 2005). Along with an increase in the area devoted to soybean, there was a replacement of the traditional method by no-tillage practices. In Argentina, between 1987 and 1988, no-tillage cropping systems covered less than 25,000 ha, while in 2004 this grew to 15 million ha. Associated with no-tillage methods, there was an increase in the use of herbicides to control weeds (Satorre 2005). In consequence, there was a 160-fold increase in the use of glyphosate along with a 30-fold increase in the area cultivated with no-tillage systems in Argentina (Bilenca et al. 2007). Another change was the increase in more intensive activities in the region, as poultry breeding (Miño et al. 2007), which favored the presence of commensal rodent species as *Rattus rattus*, *Rattus norvegicus*, and *Mus musculus* (Timm 1994; Pockock et al. 2004), which may become pests in rural habitats and near human dwellings, and may affect another species by competition or predation (Pefaur et al. 1968).

The goal of this study is to analyze the variations in abundance of rodent communities over the last 24 years in a rural area, and to analyze their relation to possible changes in environmental variables and land use. Specifically, we wanted:

1. To assess if there was a trend of variation in the abundance of the different rodent species;
2. To assess if abundance variations were related to variations in climatic variables such as temperature and precipitation;
3. To compare rodent abundance between the periods prior to and after the expansion of the soybean.

Materials and methods

Study area

The study was conducted in the Exaltación de la Cruz Department (34°08'S, 59°14'W), Buenos Aires Province, in central Argentina. The study area is located in the Rolling Pampas within the large plains called Rio de la Plata Grasslands, which cover more than 700,000 km² of central-eastern Argentina, Uruguay, and southern Brazil (Baldi et al. 2006). The climate is sub-humid temperate with a mean summer temperature of 22.5°C and a mean winter temperature of 9.8°C. The warmest month is January, with a mean temperature of 23.4°C and a maximum of 41.5°C (Hall et al. 1992). The winter is characterized by having more than 5 days with frost per month, which is considered critical for rodent survival (Crespo 1944). The annual average rainfall is 1,000 mm, with higher values in summer than in winter (Hall et al. 1992). In this region, most of the native vegetation has been replaced by croplands, which covers more than 55.2% of the area, while the percentage of

grasslands is 34.1%. Water bodies cover less than 12% and the urban areas less than 0.4% (Baldi et al. 2006). There are no forests or shrubs (Viglizzo et al. 2010).

The landscape of the study area is composed of a matrix of crop fields and pastures surrounded by fences, and are representative of land use in the Rolling Pampa. The region is devoted mainly to agriculture, with crop fields of about 20 ha. Weed communities of spontaneous vegetation less affected by agrarian labors are developed along crop field fences covering a strip of about 2 m (Soriano et al. 1991). There are also patches of natural pastures, railways, roads, streams, and small urban areas with houses grouped in small villages or isolated within fields and poultry farms (Crespo 1966). The most frequent crops in the area are soybeans, maize (warm-season crops) and wheat (cold-season crop). Some of the plant species present along the crop field fences (borders) are: *Stipa neesiana*, *S. papposa*, *Paspalum dilatatum*, *Bromus unioloides*, the forbs *Solidago chilensis* and *Senecio grisebachii* and the thistles *Carduus acanthoides*, *Cirsium vulgare*, and *Cynara cardunculus* (Bonaventura and Cagnoni 1995; Bilenca and Kravetz 1998).

Rodent communities in the study area are mainly composed of the sigmodontines *A. azarae*, *C. laucha*, *C. musculus*, *Oligoryzomys flavescens*, *Oxymycterus rufus*, the caviidae *Cavia aperea*, and the introduced murines *Rattus rattus*, *R. norvegicus*, and *Mus musculus*. These species are omnivorous, with a high proportion of plant material (both green parts and seeds) and insects in their diet (Ellis et al. 1998; Bilenca et al. 1992). They show a differential habitat use, probably related to particular adaptations to perturbations and to interspecific interactions (Busch and Kravetz 1992). *A. azarae*, *O. flavescens*, *O. rufus*, and *C. aperea* are more abundant in less-disturbed habitats like road and crop field borders, railways, and riparian habitats. *C. laucha* is more frequent in crop fields and *C. musculus* in crop field borders. Habitat use of both species of *Calomys* is restricted by the competitive dominance of *A. azarae* (Busch et al. 2000, 2001), which prefers less-disturbed habitats with high plant cover. *M. musculus* and *Rattus* spp. are present in farms and around human dwellings, but they are rare in rural and sylvan habitats (Crespo 1966; Kravetz et al. 1986; Mills et al. 1991; Busch and Kravetz 1992). In rural habitats, native rodents show seasonal variations in abundance with a minimum in spring, a peak in autumn–early winter and a decrease in late winter after frosts (Crespo 1966). Seasonal changes in plant phenology and in the stage of development of crops determine qualitative and quantitative variations in resources both in crop fields and their borders that in turn cause changes in habitat use by rodents. *A. azarae* increases the use of crop fields in the reproductive period when these habitats offer green plant cover, while all species increase the use of borders during the agrarian labors in fields (Kravetz et al. 1981; Busch et al. 1984, 1997; Mills et al. 1991; Hodara and Busch 2006).

Rodent and environmental data

We used data of samplings performed by our working group in the study area between 1984 and 2008, and bibliographic data from studies conducted in the same area by other authors that formerly belong to the group. All samplings were conducted with Sherman live traps that capture rodents up to approximately 100 g (adult rats and cavies were not included in the study because of their larger size). Animals captured were given an individual mark with an ear tag and released at the site of capture. Trapping design was either with one trap line in borders and one line in the crop field at 20 m of the border, or with grids of one line in the border and a variable number of traps in the crop field (Table 1). In all cases, the distance between traps within a line was 20 m, and each line had between 15 and 20 traps. The size of grids was 10 × 15 or 15 × 15 traps. Data were grouped according to the season in a spring–summer period (S–S) with low to medium density and reproductive activity of rodents, and the autumn–winter period (A–W) with medium to high densities and no reproductive activity. We estimated rodent abundance separately for each habitat, because climatic effects would be the same for both habitats, but land use may affect differentially crop fields and borders. Table 1 summarizes the years, periods, and habitats for which we have rodent data.

Unfortunately, we do not have data for all the years of the time series, and, consequently, we cannot assess the effect of endogenous processes on rodent abundance variations, but we consider that our data covers a sufficient time range to respond to our main questions about the effect of environmental variables and the existence of a trend of change in rodent abundance along the studied period. For each time considered, we had information from 3–6 different sites (between 100 and 3,480 trap-nights). Studied sites were evenly distributed within a total area of 1,000 km², independently of the time period. This area was homogeneous with respect to climatic, topographic, and land use, since the Rolling Pampa does not have elevation gradients, and is subject to similar uses. In consequence, we consider that spatial variation will not be creating artificial temporal patterns. In the analyses, we did not discriminate between different types of crops because we consider that rodent abundance responds to the history of use independently of the actual crop implanted, as was observed for weed and insect communities (de la Fuente et al. 2006). Before the expansion of the soybean, each crop field was cultured with different types of crops or supported livestock, while after the expansion of the soybean, each individual field is cultured with this crop a high proportion of the time (de la Fuente et al. 2006), and this effect is cumulative on rodent abundance. Soybean increased at the expense of other summer crops, but also of livestock and winter crops, which are harvested after the moment when soybean is usually sown. In a survey of wheat fields in the Rolling Pampa, de la Fuente et al. (2006) observed that approximately 57% were previously implanted by soybean or by a wheat/soybean rotation.

Table 1 Years and seasons (A–W: autumn–winter and S–S: spring–summer) for which we have data of rodent abundance in crop fields (C) and/or in their borders (B)

Year	Habitat	Period	Source	Trap design	<i>n</i>
1984	B/C	A–W	Bonaventura et al. (1988)	Grid	2
1984–85	B/C	S–S	Busch, own data	Lines	16
1988–89	B	S–S	Busch, own data	Lines	6
1989	B	A–W	Cittadino et al. (1994)	Lines	12
1989–90	B	S–S	Busch, own data	Grid	6
1990	B	A–W	Cittadino et al. (1994)	Lines	6
1993	B/C	A–W	Busch et al. (2000, 2001); Hodara et al. (2001)	Grid	18
1993–94	B/C	S–S	Busch et al. (2000, 2001); Hodara et al. (2001)	Grid	18
1994	B/C	A–W	Busch et al. (2000, 2001); Hodara et al. (2001)	Grid	18
1998	B/C	A–W	Cavia et al. (2005)	Lines	10
1998–1999	B/C	S–S	Cavia et al. (2005)	Lines	4
1999	B/C	A–W	Suárez et al. (2003)	Lines	4
1999–2000	B/C	S–S	Courtalon and Busch (2010)	Grid	12
2000	B/C	A–W	Courtalon and Busch (2010)	Grid	6
2000–01	B	S–S	Suárez et al. (2003)	Lines	4
2001	B	A–W	Suárez et al. (2003)	Lines	4
2002	B/C	A–W	Busch, own data	Lines	6
2002–03	B/C	S–S	Bilenca et al. (2007)	Lines	16
2004	B	A–W	Fraschina et al. (2009)	Lines	12
2004–05	B	S–S	Bilenca et al. (2007)	Lines	20
2006	B/C	A–W	Our data	Lines	32
2006–07	B/C	S–S	Our data	Lines	36
2007	B/C	A–W	Our data	Lines	24
2007–08	B/C	S–S	Our data	Lines	24

n number of grids or lines of the trap design

The meteorological variables considered were selected according to the results of previous works about their effect on rodent abundance (Garsd and Howard 1981; Hanski et al. 1991; Lima et al. 2002; Andreo et al. 2009). Mean minimum temperature (TMIN) and mean maximum temperature (TMAX) in °C, the cumulated precipitation (PP) in millimeters, and the number of days with frost (FROST) for each year and period were obtained from the San Pedro Meteorological Station, which is located approximately 70 km from the center of the study area, in the same ecoregion. We also included an ENSO index (ENSO) obtained on basis of a sea-surface temperature (SST) index called ‘Niño 3.4’ for the region 5°N to 5°S, 120°E to 170°W. Monthly SST anomalies were obtained from the Climate Prediction Center (CPC, NOAA). Anomalies are departures from the 1971 to 2000 adjusted oscillation index climatology (AOIC) (Smith and Reynolds 1998). The average of the monthly index was calculated for the A–W and S–S periods.

Data from land use in the area were obtained from samplings conducted by the authors in the study area in the years 1988–1989 (prior to the soybean expansion) and 2006–2010 (after the soybean expansion). These samplings were conducted registering the type of use of fields along main and secondary roads. The area covered was of approximately 1,000 km².

In order to analyze the effect of the increase in soybean culture on rodent abundance, we considered the mean abundance for the years 1984–1996 (before the expansion) and the mean abundance for the years 1998–2008 (after the expansion), because since 1997 there was a strong increase in the area covered by soybean as a consequence of the introduction of transgenic varieties (Begenesic 2002).

Data analysis

Rodent abundance was estimated through a trap success index (TS = number of different individuals captured/number of traps × number of nights), because trapping efforts differed among samplings.

We analyzed the temporal trend in rodent abundance by simple linear regressions between rodent abundance and years (1984–2008), taking into account the habitat and season (crop fields and their borders in A–W and S–S). We analyzed the total rodent abundance (total TS) and the abundance of each species.

We also conducted simple linear regressions separately for the two periods (A–W, S–S) in order to assess if there were significant trends of variation over the years of study in the TMIN, TMAX, PP, and FROST.

In order to fulfill the assumptions of the model, in some cases we deleted outliers (two cases for TMIM in A–W, TMAM in A–W, FROST in S–S, and one case for TMIM and TMAM in S–S, and FROST in A–W) or transformed variables (we used square root in: *O. flavescens* in S–S for crop fields and their borders, *C. musculinus* in A–W and S–S for borders, *C. laucha* in A–W for borders). Analyses were conducted with the program InfoStat (2009).

In order to assess the effect of environmental variables on rodent abundance, we conducted stepwise multiple linear regressions (InfoStat 2009). The dependent variables were the total rodent abundance and the abundance of each species in each habitat (border and crop field) and time period (S–S and A–W). The independent variables were TMIN, TMAX, and FROST of the corresponding season, while for the PP and the ENSO index we considered both the values of the cor-

responding and the previous season. We conducted a correlation analysis among environmental variables in order to assess which were associated, although the stepwise analysis does not include correlated variables.

The proportion of area devoted to maize and soybean (with respect to the area covered by all crops that included linen, wheat, oat, sorghum and sun flower) between the periods before and after the expansion of the soybean were compared by means of a test of difference between proportions (Zar 1996).

In order to compare the abundance of rodent species in crop fields and borders between the period before and after the increase in soybean culture, we conducted a two-factor analysis of variance (ANOVA). We considered the mean rodent abundance for the years before and after 1997 (Factor 1: before/after) and separately for season (Factor 2: S-S and A-W). We conducted a posteriori Tukey contrasts when we found significant results for the ANOVA.

Results

Temporal trends in rodent abundance and climatic variables

The total abundance of rodents did not show a significant trend of variation over time in crop fields in none of

the periods of the year while in borders, the abundance in the A-W period showed a significant trend to decrease over time, but S-S numbers did not change (Fig. 1; Table 2a).

Different rodent species showed a differential response over time. *A. azarae* did not show significant abundance variations over time in any period of the year or habitat (Table 2b). *O. flavescens* showed a trend to an increase in borders in the S-S period but a decrease in crop fields in both seasons (Table 2c). Both species of *Calomys* showed a decrease in abundance over time in A-W in both habitats, but there were no significant changes in the S-S period (Table 2d, e).

TMIN tend to increase over time in both periods of the year, while FROST showed a significant decrease in S-S, and marginally significant in A-W. The TMAX and the PP did not show any significant trends of variation in either season (Table 3).

Relationship between rodent abundance variations and climatic variables

The power of explanation of the models for the abundance variations of rodents according to climatic variables ranged between 0 (for *O. flavescens* in crop fields in S-S) and 0.94 (for total TS in fields in A-W). Abundance variations in A-W (period of high density) were

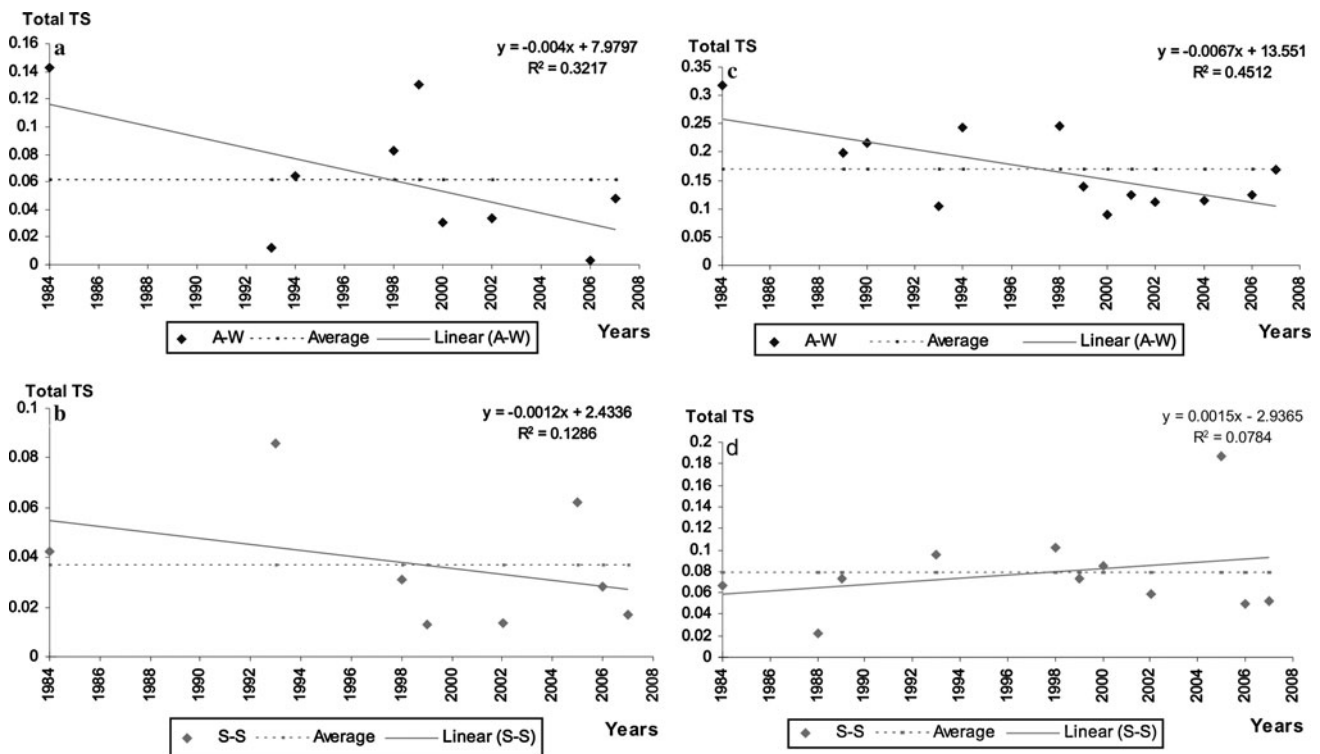


Fig. 1 Total TS variation over time (1984–2008) and the corresponding linear regression equation. **a** Crop fields in A-W ($p = 0.1112$), **b** crop fields in S-S ($p = 0.3831$), **c** crop field borders in A-W ($p = 0.0119$), **d** crop field borders in S-S

($p = 0.3185$). A-W autumn–winter season, S-S spring–summer season. Dotted line average of the total TS variation between years 1984 and 2008

Table 2 Regression summary for the relation between rodent abundance and years in the two habitats (borders and crop fields) and periods A–W (autumn–winter) and S–S (spring–summer); n is the number of years considered for the regression, (a) total TS, (b) *A. azarae*, (c) *O. flavescens*, (d) *C. musculus* and (e) *C. laucha*

		Coefficient	p value
(a) Total TS			
A–W	Intercept	13.55	0.01
Borders ($n = 13$)	Year	–0.007	0.01
$R^2: 0.4513$			
A–W	Intercept	7.98	0.11
Crop fields ($n = 9$)	Year	–0.004	0.11
$R^2: 0.3217$			
S–S	Intercept	1.87	0.30
Borders ($n = 9$)	Year	–0.001	0.32
$R^2: 0.1414$			
S–S	Intercept	2.44	0.38
Crop fields ($n = 8$)	Year	–0.001	0.38
$R^2: 0.1286$			
(b) <i>A. azarae</i>			
A–W	Intercept	3.87	0.38
Borders ($n = 13$)	Year	–0.002	0.40
$R^2: 0.0655$			
A–W	Intercept	–1.57	0.55
Crop fields ($n = 9$)	Year	0.001	0.55
$R^2: 0.0547$			
S–S	Intercept	0.77	0.77
Borders ($n = 10$)	Year	–0.0004	0.78
$R^2: 0.0102$			
S–S	Intercept	0.02	0.99
Crop fields ($n = 8$)	Year	0.000	0.10
$R^2: 0.00$			
(c) <i>O. flavescens</i>			
A–W	Intercept	–0.18	0.78
Borders ($n = 12$)	Year	0.0001	0.77
$R^2: 0.0091$			
A–W	Intercept	0.60	0.02
Crop fields ($n = 9$)	Year	0.0003	0.02
$R^2: 0.5754$			
S–S	Intercept	–6.27	0.08
Borders ($n = 11$)	Year	0.003	0.08
$R^2: 0.2332$			
S–S	Intercept	4.91	< 0.01
Crop fields ($n = 7$)	Year	–0.002	< 0.01
$R^2: 0.9447$			
(d) <i>C. musculus</i>			
A–W	Intercept	8.85	0.02
Borders ($n = 12$)	Year	–0.004	0.02
$R^2: 0.4350$			
A–W	Intercept	0.92	0.02
Crop fields ($n = 9$)	Year	–0.0005	0.02
$R^2: 0.5455$			
S–S	Intercept	–3.60	0.26
Borders ($n = 11$)	Year	0.0018	0.25
$R^2: 0.1427$			
S–S	Intercept	–0.18	0.10
Crop fields ($n = 8$)	Year	0.0001	0.09
$R^2: 0.3963$			
(e) <i>C. laucha</i>			
A–W	Intercept	14.83	< 0.01
Borders ($n = 11$)	Year	–0.0074	< 0.01
$R^2: 0.8088$			
A–W	Intercept	7.69	0.04
Crop fields ($n = 9$)	Year	–0.0038	0.04
$R^2: 0.4736$			
S–S	Intercept	0.26	0.49
Borders ($n = 11$)	Year	–0.0001	0.50
$R^2: 0.0517$			
S–S	Intercept	2.41	0.18
Crop fields ($n = 8$)	Year	–0.0012	0.18
$R^2: 0.2788$			

Significant values are highlighted in bold

Table 3 Regression summary for the relationship between environmental variables and years (1984–2007)

Environmental variable		Coefficient	<i>p</i> value
TMIN A–W (<i>n</i> = 11) <i>R</i> ² : 0.6869	Intercept	–162.14	< 0.01
	Year	0.09	< 0.01
TMIN S–S (<i>n</i> = 10) <i>R</i> ² : 0.4492	Intercept	–127.53	0.04
	Year	0.07	0.03
TMAX A–W (<i>n</i> = 11) <i>R</i> ² : 0.2916	Intercept	–63.20	0.21
	Year	0.04	0.09
TMAX S–S (<i>n</i> = 10) <i>R</i> ² : 0.3105	Intercept	–61.42	0.22
	Year	0.04	0.09
PP A–W (<i>n</i> = 13) <i>R</i> ² : 0.0772	Intercept	–3,628.38	0.38
	Year	1.89	0.36
PP S–S (<i>n</i> = 10) <i>R</i> ² : 0.057	Intercept	2,367.79	0.47
	Year	–1.09	0.51
FROST A–W (<i>n</i> = 11) <i>R</i> ² : 0.3488	Intercept	409.46	0.05
	Year	–0.20	0.06
FROST S–S (<i>n</i> = 9) <i>R</i> ² : 0.6271	Intercept	664.81	0.01
	Year	–0.33	0.01

n is the number of years considered for the regression. Significant values are highlighted in bold

TMIN mean minimum temperature, *TMAX* mean maximum temperature, *PP* cumulated precipitation, *FROST* number of days with frost, A–W autumn–winter period, S–S spring–summer period

better explained than variations in S–S (low numbers), with the exception of *C. laucha* models (Table 4). The best model for the total TS in A–W in borders included the PP S–S and PP A–W. Precipitation of the previous spring summer had a positive effect on rodent abundance, while the effect of precipitation in the current season was negative (Table 4a). In crop fields, PP S–S also had a positive effect on the total TS, and the model also included ENSO A–W, and TMAX (both with a negative effect, Table 4a). The best model for the total TS in S–S in borders included the PP S–S with a negative effect, while in crop fields, the variable FROST had a marginal positive effect (Table 4a). This last variable was marginally associated with the TMAX (coefficient = –0.39, *p* = 0.07).

The best model for *A. azarae* in A–W in borders included the PP S–S (positive) and PP A–W (negative). In crop fields ENSO S–S had a positive effect, and ENSO A–W had a negative effect on *A. azarae* abundance (Table 4b). The models for *A. azarae* abundance variation in S–S had low explanatory value, in borders included the TMIN with a positive effect, while in crop fields, the variable that contributed to explain abundance variations was the ENSO A–W with a positive effect (Table 4b).

The best model for *O. flavescens* in A–W in borders included the PP S–S (positive) and TMIN (negative). In

crop fields in A–W and in crop fields and borders in S–S, the models did not explain the abundance variations of this species (Table 4c).

Calomys laucha abundance variations in S–S were better explained than A–W variations by climatic variables (Table 4d). The best model for *C. laucha* in A–W in borders included ENSO A–W with a negative effect while in crop fields there were no significant effects of climatic variables. The best model for *C. laucha* in S–S in borders included TMAX, ENSO A–W, and FROST with a positive effect. This last variable was also included in the model for crop fields (Table 4d).

For *C. musculus*, in borders we could not conduct the multiple regressions because the data did not fulfill the assumptions of the model. The best model for these species in A–W in crop fields included the PP S–S (positive) and PP A–W (negative), while in S–S, the model showed a low value of *R*², and only included TMAX with a positive effect, but its effect was not statistically significant (Table 4e).

Another rodent species present in the area is the sub tropical *O. rufus* (Pardiñas et al. 2010; Busch and Hodara 2010), which showed an increase in abundance through the study period (0 individuals captured between 1984 and 1997, nine individuals captured in samplings conducted between 1998 and 2004, and 51 individuals in the 2006–2008 samplings). The low abundance in the past did not allow for conducting statistical analysis.

Rodent abundance and land-use changes between the periods before/after soybean expansion

In crop field borders, there was a significant interaction between the effect of years and seasons on total rodent abundance (total TS). There were no differences between the periods before/after soybean increase in any season, while before the increase in soybean there was a seasonal effect, which disappeared after this increase. For *A. azarae*, there was only a significant seasonal effect. For *O. flavescens*, there was a significant interaction between factors, but there were no differences between before/after 1997 and no seasonal effects (Table 5a). *C. musculus* showed a significant decrease between before/after 1997 only in A–W, while after the increase of soybean there was not a seasonal effect. *C. laucha* abundance was significantly higher before than after 1997 in both seasons, and did not show any seasonal effects (Table 5a).

In crop fields, the total and *C. musculus* TS did not show any significant seasonal effects nor differences between before/after periods, while *C. laucha* showed marginal differences between the period before (with higher abundance) and the period after soybean increase. The other species showed low numbers in crop fields that prevented conducting statistical analysis (Table 5b).

Table 4 continued

<i>C. musculus</i>	Variable	Intercept	TMAX	PP S-S	PP A-W
(e)					
A-W	Coeff	-0.001		0.00004	-0.00004
Crop fields (<i>n</i> = 9)	<i>p</i> value	0.80		0.01	0.03
<i>R</i> ² : 0.84					
S-S	Coeff	-0.02	0.001		
Crop fields (<i>n</i> = 8)	<i>p</i> value	0.1262	0.1120		
<i>R</i> ² : 0.37					

Significant values are highlighted in bold

TMIN mean minimum temperature, *TMAX* mean maximum temperature, *PP* cumulated precipitation, *FROST* number of days with frost, *ENSO* ENSO Index

Table 5 Two-factor ANOVA

	Before/after	Season S-S/A-W	Interaction	A-W before	A-W after	S-S before	S-S after
(a) Border							
Total TS	-	-	<i>p</i> = 0.0405	b	a; b	a	a
<i>A. azarae</i>	NS	(<i>p</i> = 0.0024) A-W > S-S	NS				
<i>O. flavescens</i>			<i>p</i> = 0.0334	b	b	a	a; b
<i>C. musculus</i>			<i>p</i> = 0.0203	b	a	a	a
				>			
<i>C. laucha</i>	<i>p</i> = 0.0117 before > after	NS	NS				
(b) Crop fields							
Total TS	NS	NS	NS				
<i>C. musculus</i>	NS	NS	NS				
<i>C. laucha</i>	(<i>p</i> = 0.069) Before > after	NS	NS				

Significant values are highlighted in bold; *NS* no significant values

Factor 1, before and after the soybean expansion accompanied by no-tillage labor; Factor 2, A-W (autumn-winter period) and S-S (spring-summer period) for (a) borders and (b) crop fields; total TS, total rodent abundance; *Aa*, *Akodon azarae*; *Of*, *Oligoryzomys flavescens*; *Cm*, *C. musculus*; *Cl*, *Calomys laucha*

Discussion

Rodent abundance showed consistent variation between seasons (higher abundance in A-W with respect to S-S) and although showed irregular variations among years, there was a trend to decrease in total rodent abundance in crop field borders and in both habitats for the *Calomys* species.

Along the studied period, we observed a significant increase in *TMIN* in A-W and S-S, along with a decrease in the number of days with frost in the S-S period (from September to February), result, which is consistent with the predictions of the models of climate change (IPCC 2009), although higher variations are expected in the cold than in the warm season.

Inter-annual fluctuations in rodent abundance were correlated with precipitation, but this effect varied according to the season, while precipitation in S-S was positively related to rodent abundance in the following A-W period, precipitation affected negatively the abundance in the same season. The effect of precipitation in the S-S season on rodent abundance in A-W is probably mediated through its effects on plant growth

and availability of resources (Lima et al. 1999, 2002; Andreo et al. 2009). On the other hand, precipitation during the cold season would have a direct effect because it increases the mortality caused by low temperatures. The effect of precipitation on rodent abundance in the Pampean region was mentioned in many works since a long time ago (Sarmiento 1885; Hudson 1903; Crespo 1944; Lima et al. 1999). Although precipitation explains rodent abundance variation among years, it does not account for the observed directional trends of decrease in total TS and *Calomys* abundance, because precipitation did not show a significant trend of variation over time. *C. laucha* abundance in the S-S period was positively related to the number of days with frost, which showed a significant decrease along the studied period along with an increase in the minimum temperature. Whether there is a real relation between *C. laucha* abundance and frost is a matter for future research, because this result may have been the consequence of another variable not considered in this study that may show a similar temporal trend.

The main change observed in land use in the area was the increase in the area covered each year with soybean, as a consequence of the replacement of other summer

crops (sunflower, sorghum) by soybean and because fields remained as fallows after the harvest of this crop, until the following spring when summer crops are implanted again, instead of being planted with winter crops. The effect of changes in agricultural practices on rodent abundance may have been related to several associated factors, such as a reduction in plant cover due to no-tillage farming, an increase in rodent vulnerability to avian predators (especially for the *Calomys* species, which use more open habitats), reduced food availability related to a decrease in weeds and insects, or a decrease in the abundance of rodent predators due to hunting, pesticides, and loss of habitats (Medan et al. 2011). A decrease in predators, however, may have caused an increase in rodent abundance, and in consequence does not explain the observed trend to decrease. With our data, we could detect changes in rodent abundance in two periods with different land use, but we were not able to discriminate among the effects of the different factors that may change along with agricultural practices, such as plant cover, predation risk, poisoning, or food availability.

In order to disentangle the effect of climatic and land-use effects, it would be necessary to follow over time similar areas with and without land-use change. This approach is out of the scope of this work, since practically all the study area was subject to modifications in land use, and areas that did not change are probably not useful for agriculture purposes, and then are not comparable.

A. azarae, which was numerically dominant in native grasslands and is competitive dominant in crop field borders, did not vary its abundance over time, while inter-annual fluctuations were associated with the pattern of precipitation, as was previously observed for this species in Río Cuarto (Andreo et al. 2009). *O. flavescens*, which also uses the borders but is competitive subordinate, showed a decrease in crop fields in both seasons, but an increase in borders in S–S. The observed decrease in crop fields may have been related to a decrease in green plant cover in A–W that causes changes in habitat use.

Calomys laucha and *C. musculinus* were the species that showed a greater change over time and between the periods prior to and after the expansion of soybean. These species, especially *C. laucha*, are associated with crop fields, and showed an increase in abundance with the expansion of agriculture and annual crops, which replaced grasslands and livestock fields (Kravetz et al. 1986; Viglizzo et al. 2010) but actual changes in agricultural practices seem to be affecting their populations and causing a decrease both in crop fields and borders. A lower abundance of the *Calomys* species in soybean fields with respect to other crops was reported by Busch et al. (1984) and Mills et al. (1991). Rodents show an annual abundance cycle with minimal numbers in spring at the beginning of the reproductive season, density increases during the summer as the maturation of summer crops, and reached peak numbers in autumn in fallows that are covered by weeds.

The observed changes in *Calomys* abundance in crop fields and borders seem to be more associated with changes in land use than by climatic variables. In this work, we did not discriminate between different types of crops, but we consider that after the expansion of the soybean, each individual field is cultured with this crop a high proportion of the time and this effect is cumulative on rodent abundance, independently of the crop implanted at a particular time.

Our results show the trends of variation in rodent abundance in crop fields and their borders, which may be different from the trends at a regional scale, in which the relative proportion of crop fields and other land uses determine the overall abundance of each rodent species. Bilenca et al. (2008) found an increase in the proportion of *Calomys* in the diet of raptor species in the same area over the same time period. Because the *Calomys* species are predominant in crop fields, the increase in the area covered by these habitats may have resulted in an increase in abundance of *Calomys* at a regional scale in spite of its decrease in abundance in crop fields. The difference in trends observed at different spatial scales reinforces the evidence that changes in rodent abundance are related to land-use changes, instead of climatic variables, which would have the same effect at different spatial scales.

In summary, returning to our goals, we conclude that (1) along the studied period, there was an increase in the mean minimum temperature and a decrease in the number of days with frost in the area; (2) rodent abundance in A–W decreased over the years, but each species showed a different pattern of variation; (3) rodent abundance variations were associated with precipitation (or to the ENSO index, which is associated with precipitation), but the observed trends of variation over time were not explained by these variables, which did not show a significant trend of variation over time; (4) the observed changes in agricultural practices are consistent with the observed trends of variations in rodent abundance in crop fields and borders, especially those species highly associated with crop fields.

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