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Regional and local determinants of rodent assemblages in agroecosystems of the Argentine Pampas

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Here, we characterize and compare rodent assemblages from crop fields and rangelands of the 4 Pampa districts included in Buenos Aires province, Argentina, to analyze the role of regional context, land use, and vegetation structure in determining the structure of rodent assemblages at the plot scale. Habitat generalist species (*Calomys laucha* and *Mus musculus*) tended to be more abundant in crop fields, whereas habitat specialists (*Akodon azarae* and *Oxymycterus rufus*) tended to be more abundant in rangelands. However, the degree of spatial segregation between habitat generalists and specialists and the associations between particular rodent species and land use differed among districts. The abundance of the dominant species (*C. laucha* and *A. azarae*) was positively associated with vegetation height. We also found a positive association between the abundance of the dominant species in a certain land use and the representation of that land use in the Pampa district, which suggests an effect of the regional context on local assemblages. Our results show that the structure of the rodent assemblage in a certain plot is the result of the interaction between the district the plot is in and the land use (and management) it is under. Future studies could shed light to the mechanisms behind the district effect observed in this study.

En este trabajo caracterizamos y comparamos los ensambles de roedores en campos agrícolas y ganaderos de las cuatro subregiones pampeanas incluidas en la provincia de Buenos Aires (Argentina), con el objetivo de analizar el papel que juegan el contexto regional, el uso de la tierra y la estructura de la vegetación en definir la estructura del ensamble de roedores a la escala de lote. Los resultados muestran que las especies generalistas (*Calomys laucha* y *Mus musculus*) suelen ser las más abundantes en los campos de cultivo, mientras que las especialistas (*Akodon azarae* y *Oxymycterus rufus*) tienen a serlo en los campos ganaderos. Sin embargo, el grado de segregación espacial entre especies generalistas y especialistas, y las asociaciones entre las especies de roedores y el uso de la tierra varían entre subregiones. La abundancia de la especie dominante (*C. laucha* y *A. azarae*) estuvo positivamente asociada con la altura de la vegetación. También encontramos una asociación positiva entre la abundancia de la especie dominante en un cierto uso de la tierra y la representación de dicho uso en la subregión. En resumen, nuestros resultados muestran que, en la región Pampeana, la estructura del ensamble de roedores en un determinado lote es el resultado de la interacción entre la subregión en la que se encuentra el lote y el uso (y manejo) al que está sujeto. Futuros estudios podrían echar luz sobre los mecanismos detrás de el "efecto subregión" observado en este estudio.

Key words: Argentina, farmland biodiversity, land use, Pampas, seasonality, small mammals

In agroecosystems, many biophysical processes and patterns are altered—directly and indirectly—by agricultural practices and management decisions (e.g., which crop is grown in a particular plot affects vegetation structure and its seasonal variations). In turn, those decisions are guided and constrained by the biophysical characteristics of the plot (e.g., some crops are better suited for certain environments). Some species can benefit from these changes from natural to agricultural vegetation, whereas others are affected negatively by them. Thus, the changes that take place in agroecosystems can affect the distribution of species at different spatial scales (Gonthier et al. 2014; Newbold et al. 2015). In general, species with narrow habitat requirements (specialists) tend to be more affected than those with wider requirements (generalists—Butler et al. 2007). However, the degree a species is affected by these changes would also depend on the differences between the original habitat and the one that replaced it (i.e., it is not the same if a wheat field replaces a grassland or a forest).

Furthermore, different plots can present differences in management, land-use history, and their surrounding context, which also can affect the species found on the particular plot (Abba et al. 2006; Bilenca et al. 2007). The characteristics of the region a plot is in will determine the pool of species that could potentially occupy the plot, and the relative abundances of those species. These influences could be mediated by the distance to the closest habitat that harbors a particular species (metapopulation dynamics) and by the number of such sources that are close by (mass effect—Weiher and Keddy 2001).

Several studies have shown the sensitivity of rodent assemblages to land-use changes in temperate agroecosystems (Gorman and Reynolds 1993; Love et al. 2001; Millán de la Peña et al. 2003; Heroldová et al. 2007; Gentili et al. 2014) and that vegetation structure is one of the main determinants of rodent abundance at the habitat-patch scale (Jacob 2008). In particular, several studies have investigated the effects of land use and farming practices on rodent assemblages from the Pampas in central Argentina (Busch et al. 1984; Mills et al. 1991; Bilenca and Kravetz 1998; Cavia et al. 2005; Bilenca et al. 2007; Fraschina et al. 2012, 2014; González Fischer et al. 2012; Coda et al. 2015; Gomez et al. 2015). Rodent species present varying degrees of habitat specialization; for example, *Calomys* spp. and *Mus musculus* are more generalists, whereas *Akodon azarae*, *Oligoryzomys flavescens*, and *Oxymycterus rufus* are more specialists (Ellis et al. 1997; Martínez et al. 2014). These assemblages are hierarchically structured: grassland specialists (e.g., *A. azarae*) occupy more stable habitats and competitively displace more generalist species (e.g., *C. laucha*) to the interior of crop fields (Mills et al. 1991; Busch and Kravetz 1992).

The Pampas included in Buenos Aires province (277,000 km^2) are classified into 4 ecological units or districts that can be distinguished according to differences in geomorphology, soils, drainage, physiography, vegetation, and land use: the Rolling Pampa, the Southern Pampa, the Flooding Pampa, and the Inland Pampa (Soriano et al. 1992). Interest in the rodent assemblages from the Pampas was prompted by the discovery of their role as hosts of Argentine hemorrhagic fever (AHF, a disease that mainly affects rural workers—Busch et al. 1984). Thus, most of the studies were performed at the endemic area of AHF (i.e., the Rolling Pampa) and regional information for other Pampa districts is lacking (but see Dalby 1975; Busch et al. 2012; Hodara and Poggio 2016). Rodent assemblages can differ in species composition and relative abundances among Pampa districts (Galliari et al. 1991; Pardiñas et al. 2010; González Fischer et al. 2011), and it is not clear whether the associations of land use and rodent species vary among districts (Mills et al. 1991; Busch and Kravetz 1992; Busch et al. 1997).

In this paper, we characterize and compare rodent assemblages from crop fields and rangelands in the 4 Pampa districts included in Buenos Aires province (Rolling Pampa, Inland Pampa, Flooding Pampa, and Southern Pampa; Fig. 1a), to analyze the effects of district, land use, and vegetation structure on the structure of rodent assemblages at the plot level. We propose that generalist species will be more abundant in crop fields, where habitat structure is less similar to the original grassland cover, and that specialist species will be more abundant in rangelands, where habitat structure is more similar to the original grasslands. In addition, we propose that generalist species will be more abundant in crop fields from those districts with higher proportions of crop fields in the landscape, compared to crop fields from districts with lower proportions of crop fields. Accordingly, we also expect that specialists will be more abundant in rangelands from districts with higher proportions of rangelands in the landscape. Finally, we briefly discuss how recent trends in land-use change and management practices may influence the composition, abundance, and structure of rodent assemblages in the region.

Materials and Methods

Study area.—The Argentine Pampas are one of the most productive agricultural regions of the world, covering about 52 million hectares that were originally covered by grasslands (Soriano et al. 1992). It has transitioned since its origins as a livestock-raising area to one of the largest crop producers in the world (Paruelo et al. 2005). This process was accelerated after the introduction of glyphosate-resistant soybean varieties and the adoption of no-tillage practices at the end of the 1990s (Bilenca et al. 2009; Viglizzo et al. 2011). As other agroecosystems, the Pampas are continually changing as a result of land-use changes and new farming practices. For example, the use of cover-crop mulch is now an increasingly frequent practice in the region (Lorenzatti 2008).

Typically, mean temperature in July (austral winter) ranges from 7.5°C to 9.5°C, mean temperature in January (austral summer) ranges from 21.5°C to 23.0°C, and annual precipitation ranges from 700 to 1,000 mm. In the Rolling Pampa, crops have replaced most of the native vegetation and cover about 75% of the land, whereas in the Flooding Pampa grasslands or pastures prevail (> 85%). The Southern and the Inland Pampa have a mixed production system with both crops and animal husbandry (Baldi and Paruelo 2008). Soybeans (*Glycine max*) and maize (*Zea mays*) are the main crops in the Rolling, Inland,

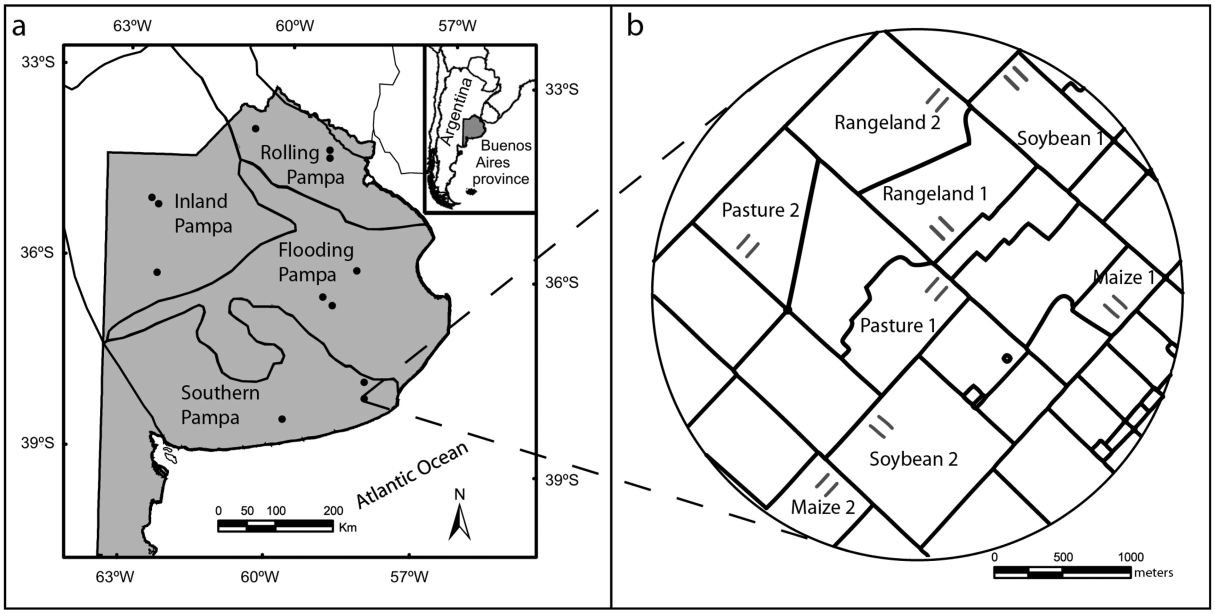

Fig. 1.—a) Map of the study area, showing the distribution of the 12 localities sampled in summer and winter 2010 (black dots) among the 4 districts of the Pampas in Buenos Aires province, Argentina. b) Example of the spatial distribution of the 8 plots sampled in 1 season in 1 of the 12 localities. The 2 parallel lines in each plot represent the traplines (each with 15 Sherman traps).

and Flooding Pampas, whereas in the Southern Pampa winter crops like wheat (*Triticum aestivum*) prevail (INDEC 2006).

Rodent assemblages.—The rodent assemblage includes at least 11 species (Mills et al. 1991; González Fischer et al. 2012). The most abundant species (and the ones that are found in all 4 districts) are the sigmodontine rodents *C. laucha*, *C. musculinus*, *A. azarae*, *O. flavescens*, and *Holochilus brasiliensis*, and the murine *M. musculus*. Other species present in the area include *O. rufus* (present in the Rolling, Flooding, and Southern Pampas), *Necromys lasiurus* (Rolling and Southern Pampas), *N. obscurus* (only present in the Southern Pampa), and the commensal rats *Rattus rattus* and *R. norvegicus*, which are mostly restricted to poultry and pig farms and peridomestic habitats (Lovera et al. 2015).

Rodent sampling.—Rodent trapping was conducted at 12 localities, 3 in each of the 4 Pampa districts included in Buenos Aires province (Fig. 1a). In each of the 12 localities, 8 plots were selected in summer 2010 and 8 different plots were selected in the following winter: 4 maize or soybean crop plots ("crop fields") and 4 paddocks devoted to grazing cattle ("rangelands," including natural and seminatural grasslands, and old pastures colonized by native species; Fig. 1b). In this way, 96 crop fields (48 in summer and 48 in winter) and 96 rangelands (48 in summer and 48 in winter) distributed among 12 localities were sampled. In summer, crop plots were occupied by the standing crop, whereas in winter they were covered by the stubble of the previous crop. Different plots were used in each season to avoid potential effects of dependence among data and rodent removal (see below).

In each plot, 2 parallel lines separated by 20 m were placed perpendicularly to the field border (Fig. 1b). Each line consisted of 15 Sherman-style traps (8 × 9 × 23 cm) spaced 10 m apart. Traps were baited with a mixture of peanut butter, rolled oats, and bovine fat, and checked daily for 3 consecutive nights. The species of each individual was identified by external morphology and, in some cases, confirmed by an analysis of the skull. All captured rodents were removed and tissues samples were collected for other studies. Handling of animals throughout the study followed the ASM guidelines (Sikes et al. 2016) and the Argentine Law for Animal Care (National Law 14346).

Characterization of vegetation structure.—Simultaneously with rodent sampling, 3 to 5 1-m^2 plots were randomly placed in each trapping plot to describe the vegetation and microhabitat structure. Vegetation was characterized by recording the height of the 1st stratum and visually estimating the proportion of total vegetation cover, herb cover, green (photosynthetically active) cover, bare ground, and mulch cover. All the measurements for 1 trapping plot were averaged to obtain 1 value for each variable. Since all these measures were highly correlated (Spearman $r \geq |0.5|$, $P \leq 0.05$, for all pairs of comparisons), and it has been previously reported to affect small mammals in agroecosystems (Jacob 2008), the height of the 1st stratum of vegetation was finally used as the sole descriptor of the vegetation structure.

Data analysis.—The abundance of each rodent species was estimated based on its trap success ([trapped individuals/trap-nights] × 100—Cavia et al. 2012). The relationships between the structure of the rodent assemblage and land use, season, and district were explored using a canonical correspondence analysis (CCA—Borcard et al. 2011). For this analysis, the response variables were the abundances of each rodent species and the explanatory variables were land-use type, season, and Pampa district. Since in some plots there were no rodents captured, all captures from the same locality, land use, and season were pooled. The significance of the CCA and each canonical component were evaluated by means of a permutation test

(Borcard et al. 2011). These analyses were done using the *vegan* package for R (Oksanen et al. 2016). In addition, we performed a Cochran–Mantel–Haenszel test to analyze differences in rodent composition and relative abundance between crop fields and rangelands, considering the 4 Pampa districts as different strata (Quinn and Keough 2002; for this analysis, the number of individuals captured in both seasons were pooled).

Rodent abundances were compared between crop fields and rangelands from the 4 districts in both seasons by means of general linear models with estimations of variances for each group (Di Rienzo et al. 2012). In addition, the effect of vegetation height on the abundance of rodents was incorporated as a covariable in these models. These analyses were done using the *nlme* package for R (Pinheiro et al. 2011), running background in Infostat (Di Rienzo et al. 2012).

Results

After a total trapping effort of 16,944 trap-nights, 156 rodents of 6 species were captured: *Calomys laucha* (representing 51.3% of total individuals), *A. azarae* (23.7%), *C. musculinus* (9.6%), *M. musculus* (7.1%), *O. rufus* (6.4%), and *O. flavescens* (1.9%).

The first 2 axes of the CCA were significant ($P < 0.01$ for both axes) and explained 38.5% of the variation in rodent composition according to land use, Pampa district, and season. The 1st axis (23.5%) separated rodent samples according to land use and season, and also was partially related to district (Fig. 2a). *A. azarae* was associated with rangelands, especially in winter at the Flooding Pampa, whereas at the opposite extreme of axis 1, *C. laucha* was associated with crop fields (*C. laucha* was the dominant species in crop fields of the Inland, Flooding, and Rolling Pampas) along with *M. musculus* (which was the dominant species in crop fields of the Southern Pampa). The 2nd axis (15.0%) revealed a district effect, separating the Southern Pampa from the other Pampa districts (Fig. 2a), accounting for the higher abundance of *O. rufus* and *M. musculus* in that district.

The Cochran–Mantel–Haenszel test revealed significant differences in the rodent assemblage structure between land uses ($\chi^2_4 = 47.00$, $P < 0.001$; Fig. 2b). These differences were observed in all Pampa districts, except the Inland Pampa, where *C. laucha* was the only species captured in either land use (Fig. 2b). Differences in the Southern Pampa ($\chi^2_4 = 19.15$, $P < 0.001$) were related to *M. musculus* being the most abundant species in crop fields and absent from rangelands, whereas *O. rufus* was exclusively captured in rangelands. Differences in the Flooding Pampa ($\chi^2_4 = 30.73$, $P < 0.001$) were related to the dominance of *A. azarae* in rangelands and its absence from crop fields, in contraposition to the dominance of *C. laucha* in crop fields and its absence from rangelands. Finally, differences in the Rolling Pampa ($\chi^2_4 = 11.00$, $P = 0.027$) were related to the dominance of *C. laucha* in crop fields, while it was codominant with *A. azarae* in rangelands (Fig. 2b).

Plot vegetation height was lower in the Inland Pampa (19.0 ± 2.2 cm) than in the other districts, where it ranged from 21.0 ± 4.8 cm in the Southern Pampa to 35.7 ± 5.8 cm in the Flooding Pampa ($F_{3,176} = 4.51$, $P = 0.005$).

Comparisons of abundance were only performed for *A. azarae* and *C. laucha*, since these 2 species were the only ones that were abundant enough to allow for statistical analysis. There was a significant interaction effect between land use, Pampa district, season, and vegetation height on abundance of *A. azarae* ($F_{3,156} = 5.22$, $P = 0.002$). To further interpret this interaction, a posteriori correlation analyses revealed

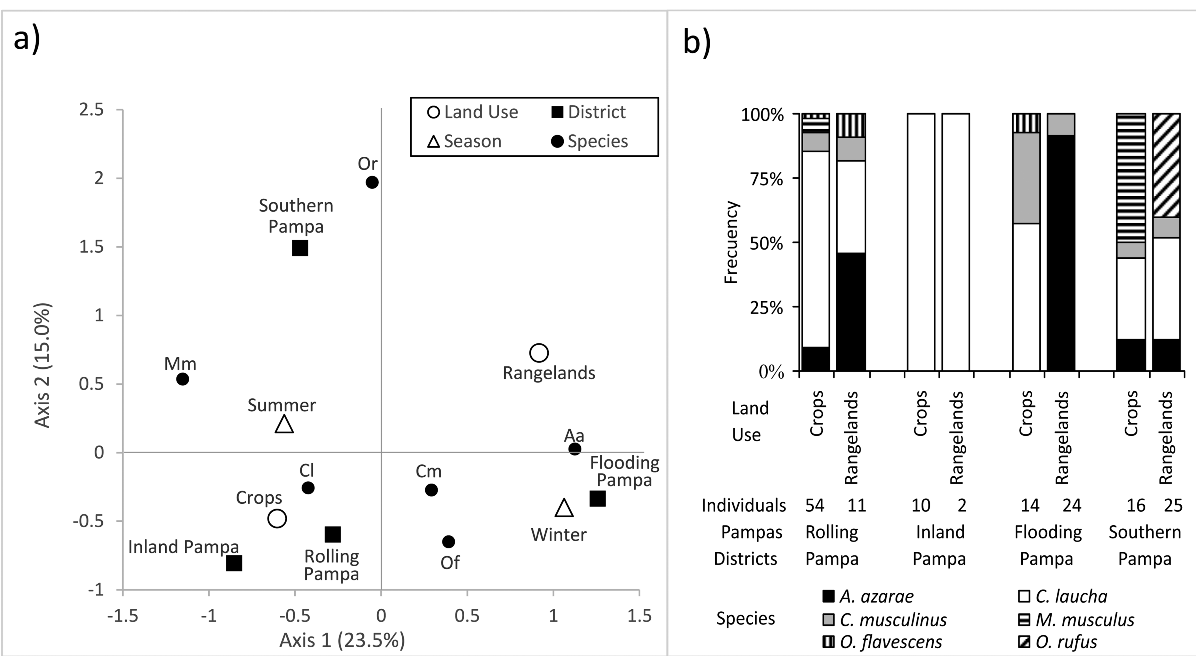

Fig. 2.—a) Diagram of the first 2 axes of the multiple correspondence analysis. Cl: *Calomys laucha*; Aa: *Akodon azarae*; Cm: *Calomys musculinus*; Mm: *Mus musculus*, Or: *Oxymycterus rufus*; Of: *Oligoryzomys flavescens*. b) Relative abundance of each rodent species (in %) in crop fields and rangelands in each of the Pampa districts of Buenos Aires province, Argentina, 2010.

that *A. azarae* increased its abundance with vegetation height in rangelands from the Flooding Pampa in winter (Pearson $r = 0.79$, $P = 0.002$) and in the Southern Pampa in summer (Pearson $r = 0.92$, $P < 0.001$). The highest abundance of *A. azarae* was observed in rangelands of the Flooding Pampa in winter (Fig. 3a). We also detected a significant interaction effect between land use, Pampa district, and vegetation height on the abundance of *C. laucha* ($F_{3,156} = 4.24$, $P = 0.007$), as it increased with vegetation height in crop fields of the Rolling Pampa in both seasons (winter Pearson $r = 0.55$, $P = 0.06$; summer Pearson $r = 0.56$, $P = 0.04$). The highest abundance of *C. laucha* was observed in crops of the Rolling Pampa in summer (Fig. 3b).

Discussion

Associations between rodent species and land use.—Habitat generalists (*C. laucha* and *M. musculus*) were more abundant in crop fields, whereas habitat specialists (*A. azarae* and *O. rufus*) were more abundant in rangelands. Furthermore, in the Rolling Pampa—where most previous knowledge about these assemblages comes from—our results are in agreement with previous studies showing that *C. laucha* is the dominant species in crop fields, with a tendency to show higher abundances in summer than in winter, and *A. azarae* is dominant in habitats that are less disturbed by farming practices (like rangelands), being more abundant in winter than in summer (Mills et al. 1991; Busch and Kravetz 1992; Busch et al. 1997; Fraschina et al. 2012, 2014). However, when we look at the other districts, our results show some differences regarding the association between rodent species and land use. In the Southern Pampa, *M. musculus* and *O. rufus* replaced *C. laucha* and *A. azarae* as the dominant species in crop fields and rangelands, respectively. Furthermore, in the Flooding Pampa, *C. laucha* and *A. azarae* were absent from rangelands and crop fields, respectively, even though in the Rolling Pampa both species were common in both land uses. Moreover, *C. laucha* was the only species caught in either land use in the Inland Pampa. The latter is in agreement with previous studies remarking the paucity of rodent species richness in this district (Pardiñas et al. 2010). Considering that small mammals are sensitive to vegetation height in pampean agroecosystems (Ellis et al. 1997; Fraschina et al. 2009), it is possible that the overall lower abundance and species richness in the Inland Pampa are at least partially related to the significantly lower vegetation height recorded in plots of this district. In that regard, Busch et al. (2012) found that after many years of cattle exclusion, some grasslands of the Inland Pampa were dominated by *A. azarae* followed by *O. flavescens*, *C. musculinus*, and *C. laucha*.

Relatively high abundances of *M. musculus* in the Southern Pampa had already been reported by studies based on barn owl pellets (Kittlein 1994; Leveau et al. 2006; González Fischer et al. 2012) and trapping (Dalby 1975). All the individuals trapped in this study were far away from any buildings, which reinforces the idea that there is an established wild population of *M. musculus* in the fields of the region.

The effect of regional context.—Our results suggest a positive association between the abundance of the dominant species in a certain land use and the representation of that land use in the district. The highest abundance of *C. laucha* was found in crop fields of the Rolling Pampa (the district with the highest percentage of land occupied by crops), whereas the highest abundance of *A. azarae* was found in the rangelands of the Flooding Pampa (the district with the highest percentage of rangelands—Baldi and Paruelo 2008). This result reinforces the hypothesis that the abundance of these species in a certain paddock or plot is influenced by both land use and regional context (González Fischer et al. 2012). The effect of this regional context on local

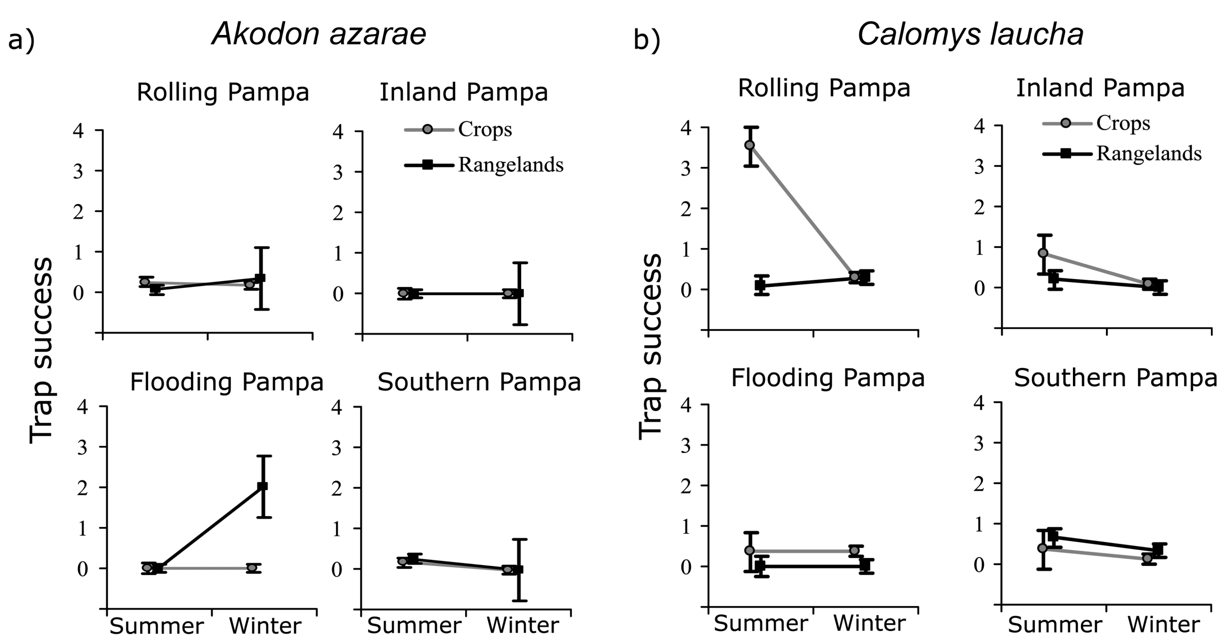

Fig. 3.—Mean trap success (± *SE*) of a) *Akodon azarae*, and b) *Calomys laucha* classified by Pampa district, land use, and season in Buenos Aires province, Argentina, 2010.

faunal assemblages has also been reported for birds in pampean agroecosystems (Filloy and Bellocq 2007; Codesido et al. 2011, 2013). Furthermore, the positive association between the abundances of *C. laucha* and crop fields observed in this study supports the hypothesis that the relatively recent and fast geographical expansion of *Calomys* spp. in the Pampas has been favored by the increase of the area dedicated to crops (de Villafañe et al. 1988; Mills et al. 1991; Busch and Kravetz 1992; Bilenca and Kravetz 1995a).

The degree of spatial segregation between specialists and generalists also changed between districts. In less-modified districts (Flooding Pampa), habitat generalists were restricted to crop fields and habitat specialists were only found in rangelands, whereas in more-modified districts (Southern and Rolling Pampas), both generalists and specialists were found in both habitats. These differences could be explained by metapopulation dynamics or by mass effects (Weiher and Keddy 2001). When a few crop fields appear in a region dominated by grasslands, they can be colonized by generalist species, while grassland specialists remain in grasslands. However, the generalist species are still competitively excluded from grasslands. When the proportion of crop fields grows, the populations of generalist species can grow in numbers and enough individuals may disperse into the surrounding grasslands to become established there (despite the competition with the dominant habitat specialists). Conversely, as the more stable habitats (native grasslands) become rarer, dispersing habitat specialists may have to settle for less optimal habitats and seek refuge in crop fields. In this scenario, the generalist species occur in grasslands as a result of mass effects, whereas the specialist species only occupy crop fields when dispersing individuals have difficulty locating available areas of their preferred habitat (native grassland). The latter may be an example of source–sink dynamics if survival or reproduction of the grassland specialist is low in the crop fields, and these populations would not persist without continued immigration.

Vegetation height.—In temperate ecosystems, the composition and structure of vegetation show seasonal fluctuations, and these seasonal changes are usually enhanced by farming practices. Seasonal changes in vegetation height and vegetative cover are, therefore, inherent to agricultural land use. The intensity of these changes depends on the cropping system and cultivation system (i.e., rotation and choice of crops). Seasonal reduction in vegetation height is drastic in grain-growing systems (e.g., soybeans and maize), and much less pronounced in rangelands and other grasslands (Jacob and Halle 2001). In the Pampas, we observed differences in vegetation height among districts and between land uses and seasons. We also observed that rodent abundances increased with vegetation height, even though this response was not generalized among districts, land uses, or seasons. Previous studies have already described the association between vegetation height and rodent abundances in pampean agroecosystems (Ellis et al. 1997; Fraschina et al. 2009) and lowering vegetation height has been proposed as a method for controlling rodent pests (Gómez Villafañe et al. 2001; Jacob 2008). Furthermore, it has been suggested that the association between declining rodent abundances and cropping intensification has been mediated by the diminished vegetation cover provided by crops in contrast with natural vegetation and pastures (Fraschina et al. 2012; Hodara and Poggio 2016).

Looking ahead.—Some studies of trends in land use in the Pampas suggest a further increase in the area dedicated to crops (Vega et al. 2009). This could mean an increase in the abundances of generalist species in detriment of habitat specialists. Our previous understanding of the associations between land use and rodents, coming mostly from the Rolling Pampa, would have indicated that rodent assemblages from crop fields throughout Buenos Aires province will have higher abundances of *C. laucha*. However, the "district effect" observed in this study suggests otherwise. If the area dedicated to crops increases in the Southern Pampa, we might see an increase in the abundance of *M. musculus* (the dominant species in crop fields from that district) instead of *C. laucha*. Both scenarios could have negative consequences for crop production, as both species are known crop pests (Bilenca and Kravetz 1995b; Singleton et al. 2010).

The use of cover-crop mulch is an increasingly frequent agricultural practice in the Pampas (Lorenzatti 2008), which may provide year-round vegetation cover in the fields. This improvement of vegetation structure provided by cover crops may favor higher abundances of rodents in crop fields, reversing the observed trend of diminishing rodent abundances (Fraschina et al. 2012; Hodara and Poggio 2016). In addition, making the habitat structure in crop fields more similar to that of the original grassland could turn the balance in favor of grassland specialists (*A. azarae* and *O. rufus*).

In summary, our results support the idea that in the Pampas of central Argentina, the composition of rodent assemblages and the abundance of rodent species in a certain plot are the result of the interaction between land use at that plot and the regional context. The regional effect could be related to differences in the regional pool of species, related to regional land use (Alard and Poudevigne 2002). Furthermore, at least for some species, this response is modulated by seasonal effects and management practices.

The high variability of our predictions regarding the future evolution of rodent populations highlights the need to monitor these populations across the different Pampa districts. Experimental assessment of the effect of cover crops and other management techniques on the structure rodent assemblages should be performed to better understand these assemblages and to anticipate possible negative consequences associated with their changes.

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Literature Cited

Abba, A. M., E. Zufiaurre, M. Codesido, and D. N. Bilenca. 2016. Habitat use by armadillos in agroecosystems of central Argentina: does plot identity matter? Journal of Mammalogy 97:1265–1271.

Alard, D., and I. Poudevigne. 2002. Biodiversity in changing landscapes: from species or patch assemblages to system organisation. Pp. 9–24 in Application of geographic information systems and remote sensing in river studies (R. S. E. W. Leuven, I. Poudevigne, and R. M. Teeuw, eds.). Backhuys Publishers, Leiden, The Netherlands.

Baldi, G., and J. M. Paruelo. 2008. Land-use and land cover dynamics in South American temperate grasslands. Ecology and Society 13:6. http://www.ecologyandsociety.org/vol13/iss2/art6/. Accessed 15 June 2016

Bilenca, D. N., M. Codesido, and C. M. González Fischer. 2009. Impactos de la Actividad Agropecuaria Sobre la Biodiversidad en la Ecorregión Pampeana: Impactos de la Expansión Agrícola y de la Intensificación de la Agricultura y de la Ganadería, con Algunas Recomendaciones de Manejo Para su Mitigación. Ediciones INTA, Buenos Aires, Argentina.

Bilenca, D., M. Codesido, C. M. González Fischer, L. Pérez Carusi, E. Zufiaurre, and A. Abba. 2012. Impactos de la transformación agropecuaria sobre la biodiversidad en la provincia de Buenos Aires. Revista del Museo Argentino de Ciencias Naturales 14:189–198.

Bilenca, D. N., C. M. González Fischer, P. Teta, and M. Zamero. 2007. Agricultural intensification and small mammal assemblages in agroecosystems of the Rolling Pampas, central Argentina. Agriculture, Ecosystems and Environment 121:371–375.

Bilenca, D. N., and F. O. Kravetz. 1995a. Patrones de abundancia relativa en ensambles de pequeños roedores de la región pampeana. Ecología Austral 5:21–30.

Bilenca, D. N., and F. O. Kravetz. 1995b. Daños a maíz por roedores en la Región Pampeana (Argentina), y un Plan para su Control. Vida Silvestre Neotropical 4:51–57.

Bilenca, D. N., and F. O. Kravetz. 1998. Seasonal variation in microhabitat use and feeding habits of the pampas mouse *Akodon azarae* in agroecosystems of central Argentina. Acta Theriologica 43:195–203.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical ecology with R. Springer, New York.

Busch, M., M. R. Alvarez, E. A. Cittadino, and F. O. Kravetz. 1997. Habitat selection and interspecific competition in rodents in pampean agroecosystems. Mammalia 1:167–184.

Busch, M., C. Knight, C. N. Mazía, K. Hodara, E. Muschetto, and E. Chaneton. 2012. Rodent seed predation on tree invader species in grassland habitats of the inland Pampa. Ecological Research 27:369–376.

Busch, M., and F. O. Kravetz. 1992. Competitive interactions among rodents (*Akodon azarae*, *Calomys laucha*, *C. musculinus* and *Oligoryzomys flavescens*) in a two-habitat system. I. Spatial and numerical relationships. Mammalia 56:45–56.

Busch, M., F. O. Kravetz, R. E. Percich, and G. A. Zuleta. 1984. Propuestas para un control ecologico dela Fiebre Hemorragica Argentina a traves del manejo del habitat. Medicina 44:34–40.

Butler, S., A. J. Vickery, and K. Norris. 2007. Farmland biodiversity and the footprint of agriculture. Science 315:381–384.

Cavia, R., G. R. Cueto, and O. V. Suárez. 2012.Techniques to estimate abundance and monitoring rodent pests in urban environments. Pp. 147–172 in Integrated pest management and pest control - current and future tactics (M. L. Larramendy and S. Soloneski, eds.). InTech, Rijeka, Croatia.

Cavia, R., I. E. Gómez Villafañe, E. A. Cittadino, D. N. Bilenca, M. H. Miño, and M. Busch. 2005. Effects of cereal harvest on abundance and spatial distribution of the rodent *Akodon azarae* in central Argentina. Agriculture, Ecosystems and Environment 107:95–99.

Coda, J., D. Gomez, A. R. Steinmann, and J. Priotto. 2015. Small mammals in farmlands of Argentina: responses to organic and conventional farming. Agriculture, Ecosystems and Environment 211:17–23.

Codesido, M., C. M. González Fischer, and D. N. Bilenca. 2011. Distributional changes of landbird species in agroecosystems of central Argentina. The Condor 113:266–273.

Codesido, M., C. M. González Fischer, and D. N. Bilenca. 2013. Landbird assemblages in different agricultural landscapes: a case study in the Pampas of central Argentina. The Condor 115: 8–16.

Dalby, P. L. 1975. Biology of Pampa rodents, Balcarce, Argentina. Publication of the Museum of Michigan State University (Biological Series) 5:153–271.

de Villafañe, G., S. M. Bonaventura, M. I. Bellocq, and R. E. Percich. 1988. Habitat selection, social structure, density and predation in populations of Cricetine rodents in the pampa region of Argentina and the effects of agricultural practices on them. Mammalia 52:339–359.

Di Rienzo, J. A., et al. 2012. InfoStat. Grupo InfoStat FCA, Universidad Nacional de Córdoba, Córdoba, Argentina.

Ellis, A., J. N. Mills, J. E. Childs, M. C. Muzzini, K. T. Mckee, Jr., and G. E. Glass. 1997. Structure and floristics of habitats associated with five rodent species in an agroecosystem in Central Argentine. Journal of Zoology 243:437–460.

Filloy, J., and M. I. Bellocq. 2007. Patterns of bird abundance along the agricultural gradient of the Pampean region. Agriculture, Ecosystems and Environment 120:291–298.

Fraschina, J., C. Knight, and M. Busch. 2009. Foraging efficiency of *Akodon azarae* under different plant cover and resource levels. Journal of Ethology 27:447–452.

Fraschina, J., V. A. León, and M. Busch. 2012. Long-term variations in rodent abundance in a rural landscape of the Pampas, Argentina. Ecological Research 27:191–202.

Fraschina, J., V. A. León, and M. Busch. 2014. Role of landscape scale in the distribution of rodents in an agroecosystem of Argentina. Journal of Agricultural Science 6:22–35.

Galliari, C. A., W. D. Berman, and F. J. Goin. 1991. Mamíferos. Recursos y rasgos naturales en la evaluación ambiental. Situación ambiental de la provincia de Buenos Aires. Comisión de Investigaciones Científicas, La Plata, Argentina.

Gentili, S., M. Sigura, and L. Bonesi. 2014. Decreased small mammals species diversity and increased population abundance along a gradient of agricultural intensification. Hystrix, Italian Journal of Mammalogy 25:1–6.

Gomez, M. D., et al. 2015. Agricultural land-use intensity and its effects on small mammals in the central region of Argentina. Mammal Research 60:415–423.

Gómez Villafañe, I. E., D. N. Bilenca, R. Cavia, M. H. Miño, E. A. Cittadino, and M. Busch. 2001. Environmental factors associated with rodent infestations in Argentine poultry farms. British Poultry Science 42:300–307.

Gonthier, D. J., et al. 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proceedings of the Royal Society of London, B. Biological Sciences 281:20141358.

González Fischer, C. M., G. Baldi, M. Codesido, and D. N. Bilenca. 2012. Seasonal variations in small mammal-landscape associations in temperate agroecosystems: a study case in Buenos Aires province, central Argentina. Mammalia 76:399–406.

González Fischer, C. M., M. Codesido, P. Teta, and D. N. Bilenca. 2011. Seasonal and geographic variation in the diet of Barn Owls (*Tyto alba*) in temperate agroecosystems of Argentina. Ornitología Neotropical 22:295–305.

Gorman, M., and P. Reynolds. 1993. The impact of land-use change on voles and raptors. Mammal Review 23:121–126.

Heroldová, M., J. Bryja, J. Zejda, and E. Tkadlec. 2007. Structure and diversity of small mammal communities in agriculture landscape. Agriculture, Ecosystems and Environment 120:206–210.

Hodara, K., and S. L. Poggio. 2016. Frogs taste nice when there are few mice: do dietary shifts in barn owls result from rapid farming intensification? Agriculture, Ecosystems and Environment 230:42–46.

Instituto Nacional de Estadística y Censos [INDEC]. 2006. Censo Nacional Agropecuario 2002. Resultados Generales. 1st ed. Presidencia de la Nación, Buenos Aires, Argentina.

Jacob, J. 2008. Response of small rodents to manipulations of vegetation height in agro-ecosystems. Integrative Zoology 3:3–10.

Jacob, J., and S. Halle. 2001. The importance of land management for population parameters and spatial behaviour in common voles (*Microtus arvalis*). Pp. 319–330 in Advances in vertebrate pest management II (H. Pelz, et al., eds.). Filander Verlag, Fürth, Germany.

Kittlein, M. J. 1994. Predación por lechuzas sobre poblaciones de roedores. Ph.D. dissertation, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina.

Leveau, L. M., P. Teta, R. Bogdaschewsky, and U. F. J. Pardiñas. 2006. Feeding habits of the Barn Owl (*Tyto alba*) along a longitudinal-latitudinal gradient in central Argentina. Ornitologia Neotropical 17:353–362.

Lorenzatti, S. 2008. La importancia de las buenas prácticas agrícolas en la mitigación del daño ambiental. Chapter 12 in Agro y Ambiente: una agenda compartida para el desarrollo sustentable (O. Solbrig and J. Adamoli, eds.). Foro de la Cadena Agroindustrial Argentina, Buenos Aires, Argentina.

Love, R. A., C. Webon, D. E. Glue, and S. Harris. 2001. Changes in the food of British Barn Owls (*Tyto alba*) between 1974 and 1997. Mammal Review 30:107–129.

Lovera, R., M. S. Fernández, and R. Cavia. 2015. Wild small mammals in intensive milk cattle and swine production systems. Agriculture, Ecosystems & Environment 202:251–259.

Martínez, J. J., V. Millien, I. Simone, and J. W. Priotto. 2014. Ecological preference between generalist and specialist rodents: spatial and environmental correlates of phenotypic variation. Biological Journal of the Linnean Society 112:180–203.

Millán de la Peña, N., et al. 2003. Response of the small mammal community to changes in western French agricultural landscapes. Landscape Ecology 18:265–278.

Mills, J. N., B. A. Ellis, K. T. Mckee, J. I. Maiztegui, and J. E. Childs. 1991. Habitat associations and relative densities of rodent populations in cultivated areas of central Argentina. Journal of Mammalogy 72:470–479.

Newbold, T., et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Oksanen, J., et al. 2016. Vegan: community ecology package. R package version 2.3-5. https://CRAN.R-project.org/package=vegan. Accessed 26 July 2016.

Pardiñas, U. F. J., P. Teta, and D. N. Bilenca. 2010. Análisis biogeográfico de los roedores sigmodontinos de la provincia de Buenos Aires. Pp. 35–57 in Biología y ecología de pequeños roedores en la región Pampeana de Argentina (J. J. Polop and M. Busch, eds.). Universidad Nacional de Córdoba, Córdoba, Argentina.

Paruelo, J. M., J. P. Guerschman, and S. R. Verón. 2005. Expansión agrícola y cambios en el uso del suelo. Ciencia Hoy 15:14–23.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2011. The R Development Core Team 2011 nlme: linear and nonlinear mixed effects models. R package version 3.1-102. R Foundation for Statistical Computing, Vienna, Austria. http://cran.r-project.org/web/packages/nlme/index.html. Accessed 26 July 2016.

Quinn, G. G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, United Kingdom.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Singleton, G. R., S. R. Belmain, P. R. Brown, and B. Hardy. 2010. Rodent outbreaks: ecology and impacts. International Rice Research Institute, Metro Manila, Philippines.

Soriano, A., et al. 1992. Río de la Plata Grassland. Pp. 367–407 in Ecosystems of the world 8A. Natural grasslands. Introduction and Western Hemisphere (R. Coupland, ed.). Elsevier, Amsterdam, The Netherlands.

Vega, E., G. Baldi, E. G. Jobbágy, and J. Paruelo. 2009. Land use change patterns in the Río de la Plata grasslands: the influence of phytogeographic and political boundaries. Agriculture, Ecosystems and Environment 134:287–292.

Viglizzo, E. F., et al. 2011. Ecological and environmental footprint of 50 years of agricultural expansion in Argentina. Global Change Biology 17:959–973.

Weiher, E., and P. A. Keddy. 2001. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, London, United Kingdom. Vol. 1.

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