Journal of Mammalogy, 2024, **105**, 404–416
https://doi.org/10.1093/jmammal/gyad133
Advance access publication 6 February 2024
Research Article

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Landscape and farm environmental structure determinants of small mammal assemblages in agroecosystems of central Argentina

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Associate Editor was Karen Mabry

Abstract

Natural processes and patterns are altered by human activity at different spatial and temporal scales, affecting species assemblages and population traits, modifying mechanisms or regulating dynamics at different scales. However, little is known about the influence of landscape structure on small mammal assemblages and populations on farms. Thus, in this work, we aimed to study the effect of landscape and environmental characteristics at the farm scale on the assemblage and populations of native and introduced small mammals in pig and dairy farms located in Buenos Aires province, Argentina. Our results showed that farms in contexts of higher environmental diversity at the landscape scale have higher species richness. Our results also showed that variations in assemblage composition were associated with the quantity of water body surfaces, cattle food, small mammal refugia, and impervious surfaces at the farm scale—and with woodland, grassland, and natural vegetation cover at the landscape scale. The abundance of commensal murids was higher on farms near towns, with higher vegetation cover at the farm scale and/or in landscape contexts with fewer crops. The abundance of *Akodon azarae* was higher on farms with a lower amount of cattle food at the farm scale and crop patches in the landscape. The abundance of *Didelphis albiventris* was higher during spring on farms with a low proportion of bare ground, while that of *Lutreolina crassicaudata* was higher on farms with high vegetation cover and a lower number of water body surfaces. These results show the relevance of multiscale determinants in the development of ecologically based management strategies to control pest small mammals.

Key words: agroecosystems, cover classes, dairy farms, EBRM, habitat, landscape ecology, opossum, pig farms, rodents, spatial ecology.

Resumen

Los procesos y patrones naturales se ven alterados por la actividad humana a distintas escalas espaciales y temporales, afectando tanto a los ensambles de especies como a sus poblaciones, modificando mecanismos o regulando sus dinámicas en distintas escalas. Poco es lo que se sabe acerca de la influencia de la estructura del paisaje sobre dichos ensambles y poblaciones. En este trabajo, estudiamos el efecto del paisaje y de variables ambientales dentro de las granjas sobre el ensamble y las poblaciones de pequeños mamíferos nativos e introducidos, en criaderos de cerdos y tambos de la provincia de Buenos Aires, Argentina. Nuestros resultados muestran que establecimientos en contextos de mayor diversidad ambiental a escala de paisaje poseen mayor riqueza específica. Además, muestran que las variaciones en la composición de los ensambles estuvieron asociadas a las proporciones de agua, comida para ganado, refugio para pequeños mamíferos y superficies impermeables a escala de granja y a las proporciones de árboles, pastizales y parches de vegetación natural a escala del paisaje. Las poblaciones de múridos comensales fueron mayores en establecimientos cercanos a las ciudades, con mayor cobertura vegetal alta y en contextos de paisajes sin cultivos. Las abundancias de *Akodon azarae* fueron menores en verano y mayores en establecimientos con menor proporción de comida para ganado y de parches de cultivo en el paisaje. La abundancia de *Didelphis albiventris* fue mayor durante la primavera en establecimientos con baja proporción de suelo desnudo, mientras que la abundancia de *Lutreolina crassicaudata* fue mayor en granjas con coberturas vegetales altas y con menor proporción de agua. Estos resultados muestran la pertinencia de los análisis multiescala para la elaboración de estrategias de manejo de pequeños mamíferos plagas basadas en fundamentos ecológicos.

Palabras claves: agroecosistemas, clases de coberturas, criaderos de cerdos, EBRM, ecología de paisaje, ecología espacial, hábitat, roedores, tambos, zarigüeyas.

Submitted 6 September 2022; Accepted 9 January 2024
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Human activity causes modifications in natural processes and patterns, either directly or indirectly. In turn, modifications to mechanisms that affect assemblages of species and populations at different spatial and temporal scales (Turner 1989; Pickett and Cadenasso 2006). In addition, modifications can affect different species differently. One of the effects of human activity is to homogenize habitats. Some species benefit from habitat homogenization, while others require a combination of heterogeneous patches, in terms of biotic and abiotic components, to maximize their fitness (Huston and McBride 2002; Soberón 2007). A greater diversity of habitats—both at local and landscape scales—together with differential habitat selection would allow the coexistence of a greater number of species with different habitat requirements (Kotliar and Wiens 1990; Duelli 1997; Darmon et al. 2012). Thus, the assemblage structure of communities—and population abundance of each species—depends on local conditions, landscape context, historical events, and evolutionary processes (Wiens et al. 1993; Pulliam 2000). The study of spatial and temporal patterns of variation in environmental characteristics and their relationship with changes in animal populations and assemblages provide a basis for understanding which factors are determinants at different levels of species organization (Kotliar and Wiens 1990; Alard and Poudevigne 2002). In rural landscapes, management decisions could act in 2 ways, according to the degree of anthropization: (1) either lead to completely homogenized landscapes, and thus to a decrease in species diversity (e.g. species richness); or (2) promote landscape heterogeneity, leading to an increase in species diversity (Soriano and Aguiar 1998; Alard and Poudevigne 2002; Filloy et al. 2010).

The Pampas ecoregion in central Argentina was originally characterized by a matrix of vegetation belonging to the Pampas grassland, but that has been largely replaced by a mosaic of crop fields and pastures (agroecosystems) and—to a lesser extent—by patches of planted forests, farmhouses, and intensive livestock farms (Bilenca and Miñarro 2004; Fraschina et al. 2014). These changes have resulted in an anthropogenically fragmented and heterogeneous landscape. Several studies conducted in the region have found associations between the degree of landscape heterogeneity or environmental gradients and the structure of assemblages of birds (Vaccaro et al. 2019), ants (Ramos et al. 2018), and small mammals (González Fischer et al. 2012; Serafini et al. 2019).

Among small mammals, the Order Rodentia represents the most successful group regarding abundances, diversity, and distribution (Solari and Baker 2007). Such has been their success that they have achieved a wide diversification of life forms and the occupation of a wide variety of habitats in natural, urban, and rural environments throughout the world (Coto 1997; Byron et al. 2002; Pocock et al. 2004; Cavia et al. 2009; Brown et al. 2017). Small mammals reported in Pampean agroecosystems include native sigmodontine and cavy species (Bilenca et al. 2007; González Fischer et al. 2012, 2017). Other small mammal species described in the regional small mammal assemblage include some marsupials (Perez Carusi et al. 2009; Muschetto et al. 2011).

Most rodent and small mammal community studies conducted in the Pampas ecoregion have been carried out in agroecosystems (Hodara and Busch 2006; Courtalon and Busch 2010; González Fischer et al. 2017), poultry farms (Gómez Villafañe et al. 2003; Fraschina et al. 2012; León et al. 2018), natural grasslands, and/or urban environments (Cavia et al. 2009; Massa et al. 2014; Maroli et al. 2015)—and have focused on aspects of their ecology including habitat use and selection (Busch et al. 1997), assemblage structure and diversity (Kravetz and Bilenca 1995; Bilenca et al. 2007), and distribution and seasonal variation of populations (Bilenca and Kravetz 1998; Gómez Villafañe and Busch 2007; Miño et al. 2007). However, although the Pampas ecoregion concentrates 99% of the dairy production and 70% of the swine production in Argentina (SENASA 2014a, 2014b), few studies have been conducted in intensive dairy cattle and/or pig farming systems (e.g. Lovera et al. 2015, 2017, 2019; Montes de Oca et al. 2017; Alonso et al. 2020). These studies have focused on microscale ecological and parasitological aspects, but not on the influence of the landscape context of the farm on small mammal assemblages and/or population structure and abundance—and in addition not on the influence of environmental characteristics at multiple scales (e.g. landscape and habitat characteristics).

The aim of this study was to analyze the influence of environmental characteristics of dairy and pig farms and surrounding landscapes on the structure and abundance of small mammal assemblages. We expected that both farm and landscape characteristics influence small mammal assemblages, and in particular expected that: (i) farms with greater environmental heterogeneity at both farm and landscape scales have greater diversity of small mammals; (ii) higher proportions of natural environments are associated with higher abundances of native small mammals, while higher proportions of modified or anthropized environments are associated with higher abundances of commensal species, at both farm and landscape scale; and (iii) at the landscape scale, farms surrounded by environments with natural elements have higher abundances of native small mammals and, in contrast, farms surrounded by anthropized or modified environments or associated with urban and peri-urban elements have higher abundances of commensal species.

Materials and methods

Study area

Fieldwork was conducted on pig and dairy farms located in the departments of Exaltación de la Cruz, Cañuelas, San Andrés de Giles, Las Heras, and Marcos Paz, in the northeast of Buenos Aires province, Argentina (34°S, 58.5°W; Fig. 1). The study area belongs to the Rolling Pampas, a subdivision of the Pampas ecoregion (Soriano 1991; Morello et al. 2012). The climate is temperate, with a mean annual temperature of 16.4 °C (Portela et al. 2009) and a mean annual precipitation of 1,005.2 mm (Pérez et al. 2015). The Rolling Pampas was originally dominated by multiple grassland communities (original Pampas grassland), which have been replaced mainly by crops. At present, only 28.5 ± 3.5% of the 7.4 million ha of the Rolling Pampas preserves the original Pampas grasslands (Bilenca et al. 2013; Modernel et al. 2016), being replaced by a landscape mosaic dominated by crops and livestock fields.

Small mammal assemblage

The small mammal assemblage on agroecosystems of the study area includes at least 7 rodent native species: the sigmodontines *Akodon azarae* (Fischer 1829), *Calomys laucha* (Fischer 1814), *C. musculinus* (Thomas 1913), *Necromys obscurus* (Waterhouse 1837), *Oligoryzomys flavescens* (Waterhouse 1837), and *Oxymycterus rufus* (Fischer 1814); the cavy *Cavia aperea* Erxleben 1777; 3 species of commensal introduced murids—*Rattus norvegicus* (Berkenhout 1769), *R. rattus* (Linnaeus 1758), and *Mus musculus* (Linnaeus 1758); and 3 species of didelphids—*Didelphis albiventris* (Lund 1940), *Lutreolina crassicaudata* (Desmarest, 1804), and *Monodelphis dimidiata* (Wagner 1847). The sigmodontines and the cavy have been

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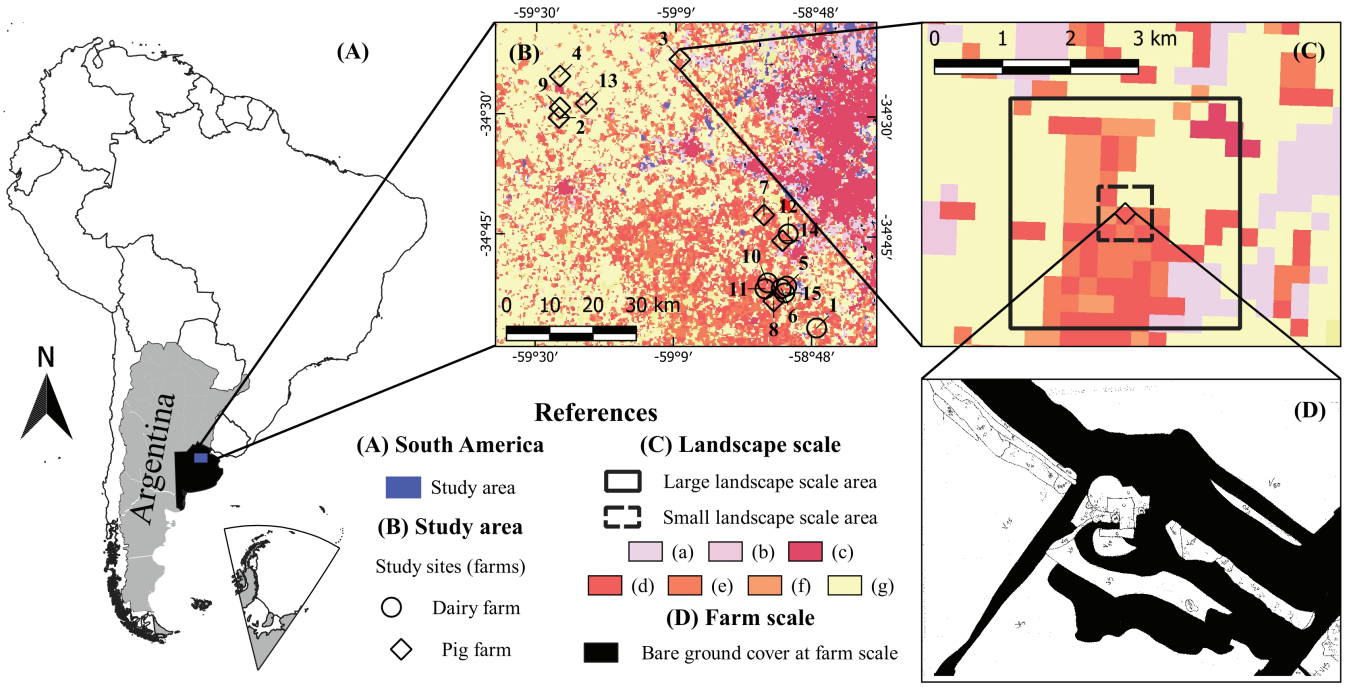


Fig. 1. (A) South America and study area. (B) Study area, northeast of Buenos Aires province, central Argentina (34°S, 58.5°W). (C) Example of large and small landscape-scale buffers. Different colors in (A) represent different land cover classes from "Land Cover Map" ver. 2.0.7 (ESA 2017): (a) mosaic of shrublands; (b) shrublands; (c) urban; (d) mosaic of natural vegetation; (e) mosaic of crops; (f) grassland; and (g) crops. (D) Example of cover class recorded at farm scale. Farms survey period: sites 1, 2, 4, 8, 9, 13, and 14 = summer 2010 to spring 2011; site 3 = fall 2010 to summer 2011; sites 5, 6, 7, 10, 11, 12, and 15 = spring 2010 to winter 2011.

found associated with native grasslands or their relicts on crop field borders and rangelands (Fraschina et al. 2014; Massa et al. 2014; González Fischer et al. 2017), and the introduced murids with urban areas and farms where they are considered pest species due to their high abundance, the health risk they generate, and the economic losses they cause (Gómez Villafañe and Busch 2007; Cavia et al. 2009; Fraschina et al. 2012; Lovera et al. 2015). The opossum species have been found associated with forested and natural areas (Perez Carusi et al. 2009; Muschetto et al. 2011) and in the vicinity of natural water bodies (Regidor et al. 1999).

Trapping procedure

Trapping of small mammals was performed on 7 pig farms and 8 dairy farms from spring 2009 to spring 2011. Each farm was sampled once each season for 1 year. Small mammals were captured using cage traps (15 cm × 16 cm × 31 cm, LMG Taller, Haedo, Buenos Aires, Argentina) baited with carrot and meat, and Sherman traps (8 cm × 9 cm × 23 cm, H.B. Sherman Traps, Inc., Tallahassee, Florida) baited with a mixture of peanut butter, bovine fat, and rolled oats. Cage traps are wire mesh traps with 1 door that is locked open with a pin connected to a trigger device holding the bait. Both types of traps were set together every 10 m along trap lines of 50 to 100 m in different environments within the farms to include all the habitat variability present (e.g. breeding sheds, food storage sheds, drainage channels, vegetated patches, etc.), and were active for 3 consecutive nights on each trapping session. About 30 to 50 traps of each type were set on each farm in each seasonal trapping session and checked daily. The location and number of traps remained the same in all trapping sessions. For all captured animals, location, date of capture, sex, weight (g), and body length (mm) were recorded (see Lovera et al. 2015). Captured animals were handled in accordance with the national animal protection law 14346 and its amendments, as well as the Ethics Committee of the National Council for Scientific and Technical Research (CONICET 2005), and Sikes et al. (2016).

Farm and landscape environmental characteristics

Environmental characteristics of the farms were determined within their physical limits in each seasonal trapping session. Nine land cover types were mapped in the field using a printed Google Earth ver. 5.2.1.1588 (2010) satellite image of each farm (1:500 scale) as reference. Different cover classes were defined based on knowledge of habitat use and selection by small mammals on farms, as they are differentially selected by native and commensal species (e.g. vegetated areas and buildings, respectively), and could be mapped at this scale, following Montes de Oca et al. (2017) and Lovera et al. (2019; Table 1). After digitizing each map and 15 farms in 4 seasons (totaling 60 thematic maps), the proportion of each cover class on each farm and season was estimated using Photoshop CS 3 ver. 10 and Image J ver. 1.50i software (Schneider et al. 2012). Information obtained from these maps represents the farm scale, which was the smallest spatial scale of analysis in this study.

Environmental structure of the landscape surrounding each farm was based on a land cover classification from the "Land Cover Map" ver. 2.0.7, provided by the European Spatial Agency—Climate Change Initiative (ESA 2017). This free access map classified land uses into 22 cover classes, of which only 9 were included in the analyses since they occurred in the study area (Table 1). To assess the extent of landscape types around the farms having greater influence on small mammal assemblages, thematic maps were projected to UTM projection, and 2 square buffer areas around each farm were defined as areas of analyses: one of ≈61 ha ("small landscape scale") and the other of ≈1,141 ha ("large landscape scale"). These scales were chosen based on Massa et

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Table 1. Description of environmental variables recorded at each scale within and around the sites studied.

Scale	Variable	Mnemonic	Description
Farm scale	Water bodies	water	Proportion of surface covered by temporary or stable water bodies, natural or artificial, as drainage channels or waste ponds.
	Cattle food	—	Proportion of surface covered by food sources for livestock, crop residues, or waste, plausible to be used as food resources by small mammals.
	Small mammal's refugia	—	Proportion of surfaces covered by stored goods or scrap, plausible to be used by small mammals for protection or shelter, like piles of firewood, wood, iron sheets, or construction materials.
	Impervious surfaces	ip_sur	Proportion of impervious surface covered by built-up structures like houses, breeding sheds, asphalt, sidewalks, etc.
	Bare ground	bare_gd	Proportion of surface without vegetation.
	Sparse herbaceous vegetation	veg_spa	Proportion of surface covered by herbaceous vegetation between 0 and 5 cm high.
	Short herbaceous vegetation	veg_sho	Proportion of surface covered by herbaceous vegetation between 5 and 20 cm high.
	Medium herbaceous vegetation	veg_med	Proportion of surface covered by herbaceous vegetation between 20 and 50 cm high.
	Tall herbaceous vegetation	veg_tall	Proportion of surface covered by herbaceous vegetation over 50 cm high.
Small landscape and large landscape scale	Crops	—	Proportion of rainfed crops at the buffer.
	Shrublands	shrub	Proportion of shrublands at the buffer.
	Mosaic of grasslands with shrublands and trees	mos_grass	Proportion of surface with coverage by grasslands greater than 50% and coverage by shrublands and woodlands less than 50% at the buffer.
	Mosaic of natural vegetation	mos_ natveg	Proportion of surface with coverage by grasslands, shrublands, and woodlands greater than 50% and coverage by crops less than 50% at the buffer.
	Mosaic of crops	mos_crops	Proportion of surface with coverage by crops greater than 50% and coverage by grasslands, shrublands, and woodlands less than 50% at the buffer.
	Grassland	grass	Proportion of grasslands at the buffer.
	Distance to town	dis_town	Inverse of distance from each farm to the nearest town (km^{-1}).
Only at large landscape scale	Woodland	wood	Proportion of woodland areas at the buffer.
	Mosaic of shrublands	mos_ shrub	Proportion of surface with coverage by shrublands and woodlands greater than 50% and coverage by grassland less than 50% at the buffer.
	Urban	—	Proportion of urban areas at the buffer.

al. (2014) and Cavia et al. (2009) and on the pixel size of the land cover map (projected pixel size ≈ 6.76 ha). The proportion of each cover class within these areas was estimated using FRAGSTAT ver. 4 (McGarigal and Cushman 2012). The inverse distance (km^{-1}) between each farm and the closest town was also recorded.

Data analysis

The relative abundance of small mammals on each farm on each trapping session was estimated by the trap success ([trapped individuals/trap-nights] × 100; Mills et al. 1991). Since there were no differences in abundances of small mammal species between the sampled years (Lovera et al. 2015), data from 2 years were pooled for the statistics analysis.

To study the relationship between small mammal alpha diversity and environmental heterogeneity, stepwise forward multiple regression procedures were used with generalized linear models (GLMs), a Poisson distribution, a log link function, and the Laplace approximation method (McCulloch 2001; Bolker et al. 2009; Christ 2009; Crawley 2012). Small mammal species richness (S) was used as the diversity response variable, while environmental heterogeneity from each scale was used as explanatory variables. Environmental heterogeneity was estimated by the Shannon–Wiener and Simpson indexes (Krebs 2009) based on the proportion of different cover classes at the farm scale and at the small and large landscape scale separately, totaling 6 landscape heterogeneity measures: (1) Shannon–Wiener land cover index at the farm scale, (2) the small landscape scale, (3) the large landscape scale; and Simpson land cover index at (4) the farm scale, (5) the small landscape scale, and (6) the large landscape scale. For the stepwise forward selection criteria, the significant and greater change of deviance was used for a variable or interaction and the simplest significant models are reported. When more than 1 candidate model was found, the Akaike Information Criterion (AIC) was used for model selection, and only models with ΔAIC < 2 compared to the best model are reported (Burnham and Anderson 2002). Where appropriate, if overdispersion or underdispersion was observed, the Conway–Maxwell–Poisson (CMP) error structure was used (Shmueli et al. 2005). The packages *base*

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(R Core Team 2019) and *glmmTMB* (Brooks et al. 2017) were used to fit the models, while *visreg* (Breheny and Burchett 2017) and *ggplot2* (Wickham 2016) were used to plot the model results (R Core Team 2019).

Relationships between the small mammal assemblage structure and environmental characteristics, season, and type of production system were explored using multivariate analyses by canonical correspondence analysis (CCA; Borcard et al. 2008). For this analysis, annual mean trap success of each small mammal species on each farm was used as the response variable and explanatory variables were the environmental variables recorded at the 3 scales plus the type of production system (dairy farm or pig farm; Table 1). Since within-farm characteristics of each farm were estimated seasonally, annual mean proportion of the types of cover was used at this scale for this analysis. A forward selection procedure was used to include explanatory variables that explained the small mammal assemblage structure. This analysis was performed using the *vegan* package (Oksanen et al. 2019; R Core Team 2019).

To analyze the influence of environmental factors over the abundance of each small mammal species, stepwise forward multiple regression procedures using generalized linear mixed models (GLMMs) were used with a binomial distribution of errors, a logit-link function, and Laplace approximation method (McCulloch 2001; Bolker et al. 2009; Christ 2009; Crawley 2012). Trapping success of each small mammal species on each farm was used as the response variable, while all environmental variables of the 3 scales, season, and type of production system were used as explanatory variables. If any level of a factorial explanatory variable was included in the model, the levels that showed no significant differences between them were joined into a new level variable, and the model was fitted again (Nicholls 1991). The farm was included as a random effect because each farm was sampled repeatedly 4 times. When the random effect did not improve the model (based on the change of deviance between the model with and without the random effect), it was removed, and GLM regression analysis was used instead (Zuur et al. 2013). For the stepwise forward selection criteria, the significant and greater change of deviance was used for a variable or interaction and the simplest significant models are reported. The association between all predicted variables was assessed using the variance inflation factors (VIFs)—if any VIF value was larger than 5, the variable was removed, and the process was repeated until all the VIFs were smaller than 5 (Christ 2009; Zuur et al. 2010). When more than 1 candidate model was found, again AIC was used for model selection, and only models with $\Delta AIC < 2$ compared to the best model are reported (Burnham and Anderson 2002). If overdispersion or underdispersion was observed, the Poisson and/or CMP error structure were used, changing the response variable to the abundance of each small mammal species and adding the trap effort logarithm as offset (Shmueli et al. 2005; Christ 2009). The *base* (R Core Team 2019), *lme4* (Bates et al. 2015), *car* (Fox and Weisberg 2019), and *glmmTMB* (Brooks et al. 2017) packages were used to fit the models, while the *visreg* (Breheny and Burchett 2017), *sjPlot* (Lüdecke 2019), *rgl* (Adler et al. 2019), *LMERConvenienceFunction* (Tremblay and Ransijn 2015), and *ggplot2* (Wickham 2016) packages were used to plot results (R Core Team 2019).

Results

A total of 437 individuals belonging to 9 species of small mammals were captured on the 15 farms studied, with a total capture effort of 5,589 Sherman trap-nights and 5,342 cage trap-nights. The species captured were the introduced murids *R. norvegicus* ($n = 241$), *M. musculus* ($n = 72$), and *R. rattus* ($n = 16$); the native sigmodontines *A. azarae* ($n = 33$), *O. flavescens* ($n = 7$), and *C. laucha* ($n = 4$); the native cavy *C. aperea* ($n = 6$); and the native opossums *D. albiventris* ($n = 38$) and *L. crassicaudata* ($n = 20$). The introduced murids *R. norvegicus* and *M. musculus* were the dominant species in both dairy and pig farms, present in almost all farms and with the highest relative abundances (Supplementary Data SD1).

Farm environmental characteristics

Within farms, bare soil and herbaceous vegetation of different heights exhibited the highest proportions of coverage—whereas water bodies, cattle food, small mammal refugia, and impervious surface showed the lowest proportions of coverage. Additionally, the proportions of coverage of the herbaceous vegetation with different heights and bare ground showed a seasonal change—while those of water bodies, cattle food, small mammal refugia, and impervious surfaces were almost invariant across seasons. The proportion of tall herbaceous vegetation increased in summer and spring, while the proportions of bare ground and medium herbaceous vegetation increased during fall and winter (Supplementary Data SD2 and SD3).

Landscape environmental characteristics

At the small landscape scale, the proportion of crops and mosaic of natural vegetation coverage were the most representative (Supplementary Data SD4 and SD5), followed by grassland and the mosaic of crops. Alternatively, at the large landscape scale we observed a similar trend but with the proportion of crops showing the highest coverage, followed in descending order by the proportions of mosaic of natural vegetation, mosaic of crops, and grasslands. Shrubs and mosaics of grasslands with shrublands and trees also showed low proportions, but this scale included 3 other cover classes: woodlands, urban, and mosaic of shrublands (Supplementary Data SD4 and SD6).

Small mammal assemblage diversity and structure

As expected, on farms small mammal species richness increased as the complexity of the landscape increased (Simpson index) at the small landscape scale (coefficients ± standard error: intercept = 0.70 ± 0.27, slope = 1.50 ± 0.52; P intercept = 0.01, P slope = 0.004; null AIC = 58.50, model AIC = 53.13; Supplementary Data SD7). However, this pattern was not found at the farm scale nor at the large landscape scale, in contrast to our predictions.

Small mammal assemblage structure was associated with characteristics of the farm scale and landscape scale according to the CCA. According to this analysis, farms with higher proportions of water body surfaces had assemblages with higher abundance of the introduced rodents *M. musculus* and *R. rattus*, and the native opossum *D. albiventris*—while farms with lower proportions of water bodies had assemblages with higher abundance of the native rodents *A. azarae*, *O. flavescens*, *C. laucha*, and *C. aperea*, and the introduced murid *R. norvegicus*. In turn, according to the second CCA axis, farms with low proportions of cattle food within the farms and low proportion of woodland cover around the farms at the large landscape scale had assemblages with higher abundances of *A. azarae*, *C. laucha*, *R. rattus*, and *O. flavescens*. Farms with higher proportions of these cover classes had assemblages with higher abundances of *D. albiventris*, whereas those with intermediate proportions had higher abundances of *R. norvegicus*, *C. aperea*, and *L. crassicaudata* (Fig. 2).

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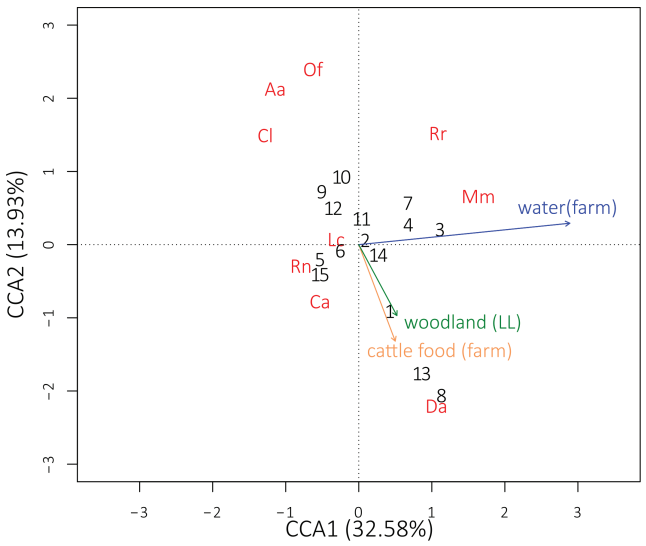


Fig. 2. Triplot of canonical correspondence analysis (CCA) for the mean annual abundances of small mammal species on each farm (1 to 15). The simplest model ($\mathbf{F}_{3,11} = 3.66$, $P < 0.001$) explained 49.98% of the total variance, and the first 2 axes of the CCA explained 46.51% of it. Aa = *Akodon azarae*; Ca = *Cavia aperea*; Da = *Didelphis albiventris*; Lc = *Lutreolina crassicaudata*; Mm = *Mus musculus*; Of = *Oligoryzomys flavescens*; Rn = *Rattus norvegicus*; Rr = *R. rattus*. Parentheses in the axes show the percentage of total variance explained. The proportion of woodlands at large landscape scale was negatively correlated with the proportion of grasslands and positively correlated with the proportion of mosaic of natural vegetation ($r_{\text{wood(LL)–grass(SL)}}$: −0.38; $r_{\text{wood(LL)–mos_natveg(SL)}}$: 0.58, $P < 0.05$).

Species abundance models

Predictions about the association between farm and landscape characteristics and abundances of different small mammal species were partially confirmed for all 3 scales of study. As expected, commensal species *M. musculus* and *R. rattus* were associated with anthropized environments at the landscape scale, while abundances of native opossums were associated with natural environments at the farm scale. However, contrary to predictions, abundance of the commensal *R. norvegicus* was associated with natural environments at the farm scale, while abundance of the native rodent *A. azarae* was related with anthropogenic environments at the landscape and farm scale.

Rattus norvegicus abundance showed seasonal changes, and changes with both the proportion of medium and tall herbaceous vegetation (Table 2) at farm scale. Abundance of this species was positively correlated with tall herbaceous vegetation and with medium herbaceous vegetation in winter, although not in non-winter seasons (Fig. 3A). No association was found between *R. norvegicus* abundance and landscape variables.

In contrast, *M. musculus* abundance on farms was influenced by characteristics at both the farm and landscape scales. Their abundance changed with distance to the nearest town, proportion of crops around farms, and proportion of medium herbaceous vegetation within farms (Table 2). Regarding the influence of distance to nearest town, *M. musculus* abundance on farms was higher when they were closer to towns—whereas regarding the influence of the proportion of crops and proportion of medium herbaceous vegetation, when both proportions were low or high at the same time *M. musculus* abundance was higher. However, if only 1 proportion was high, abundance was lower, and if proportions were intermediate, abundance was also intermediate (Fig. 4A). Furthermore, *M. musculus* abundance was also higher in fall than in other seasons.

Rattus rattus abundance, like that observed for *M. musculus*, was driven by both farm-scale and landscape-scale variables. Their abundance was related to proportion of herbaceous medium vegetation and distance to nearest towns. In addition, it was higher when proportion of medium herbaceous vegetation within the farms was higher or when farms were near towns (Table 2).

In turn, *A. azarae* abundance changed with season as well as with characteristics at farm and landscape scales. Abundance of this native species was associated with proportion of cattle food within the farm, and proportion of mosaic of crops at the small landscape scale (Table 2). Regarding seasonality, *A. azarae* abundance was lower in summer than in other seasons. *Akodon azarae* was less abundant in farms with a higher proportion of mosaic of crops at the small landscape scale and a higher proportion of cattle food within the farm (Fig. 4B).

As observed for *R. norvegicus*, *D. albiventris* abundance was only related to characteristics at the farm scale and seasonality (Table 2). In fact, abundance of *D. albiventris* was driven by the proportion of bare ground in relation to seasons—their abundance was lower when the proportion of bare ground on farms was higher in spring (Fig. 3B). No association was found between *D. albiventris* abundance and landscape variables.

Lastly, *L. crassicaudata* abundance also was associated with characteristics at the farm scale (Table 2). Abundance of *L. crassicaudata* was related to proportions of water body surfaces, as well as medium and tall herbaceous vegetation. Abundance was higher when the proportion of these herbaceous vegetation categories was higher and associated with lower proportions of water body surfaces within the farm. No association was found between *L. crassicaudata* abundance and landscape variables.

Discussion

In this study, we found that diversity, structure, and species abundance of small mammal assemblages were influenced by farm and landscape characteristics, as expected. Intensive livestock farms were dominated by introduced murids over native species (Gómez Villafañe and Busch 2007; Miño et al. 2007; Fraschina et al. 2014; Lovera et al. 2015; Montes de Oca et al. 2017, 2020). This dominance in small mammal communities may be driven by the amount of cattle food available (Timm 1987; Smith and Meyer 2015; Lovera et al. 2019), since farms with average proportional values of cattle food showed the highest abundance of *R. norvegicus* and *M. musculus*. In addition, other management decisions within farms would act like disturbance factors that impact differentially on each species, on their abundances, and on rodent assemblages. The frequency and intensity of disturbances produced by anthropogenic activity within farms decrease the chances of establishment of native rodents (Sauvajot et al. 1998; Cavia et al. 2005; Miño et al. 2007; Rickart et al. 2007). The inability of native rodent species to occupy certain sites would create vacant spaces that could be occupied by commensal species, as experimentally shown Busch et al. (2005). However, our results showed that the small mammals assemblage is influenced by the landscape context in which farms are immersed, as expected. The predominant components shaping landscape context around the farms were crops and rangelands, but their representation was heterogeneous in the study area. Native rodent assemblage composition changes among agroecosystem habitats such as grasslands, rangelands, crop fields and their edges, and railway

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Table 2. Summary of the GLMM or GLM simplest models for each small mammal trap success (TS). Binomial (Bi) or Conway–Maxwell–Poisson (CMP) distribution errors were used. The farm was included as a random effect if doing so improved the model (see text). Season were grouped as: (1) winter versus non-winter; (2) fall versus non-fall; (3) summer versus non-summer, (4) spring versus non-spring. SE = standard error; AICn = Akaike Information Criterion of null model; LRT = likelihood ratio test; df = degree of freedom; %dev: percentage of deviance explained. See Table 1 for mnemonics and a full description of each explanatory variable.

Model (Bi)	***Rattus norvegicus* TS ~ veg_med * season(1) + veg_tall + (1|farm)**							
	Coefficients	**SE**	**P**	**AICn**	**AIC**	**LRT**	**df**	**%dev**
Intercept	−5.53	0.57	<0.0001	292.6	272.1	33.4	6	9.84
veg_med	10.22	2.09	<0.0001					
non-winter	1.14	0.40	0.004					
veg_tall	1.56	0.62	0.012					
veg_med:non-winter	−8.59	2.28	0.0001					
Model (Bi)	***Mus musculus* TS ~ season(2) + dis_town + mos_crops(LL) * veg_med**							
	Coefficients	**SE**	**P**	**AICn**	**AIC**	**LRT**	**df**	**%dev**
Intercept	−4.54	0.63	<0.0001	274.0	108.9	175.1	6	80.9
fall	0.88	0.26	<0.0001					
dis_town	4.40	0.47	<0.0001					
mos_crops(LL)	−20.04	4.17	<0.0001					
veg_med	−8.06	2.91	0.005					
mos_crops(LL):veg_med	63.20	17.20	0.0002					
Model (CMP)	***Rattus rattus* TS[a] ~ veg_med + dis_town + (1|farm)**							
	Coefficients	**SE**	**P**	**AICn**	**AIC**	**LRT**	**df**	**%dev**
Intercept	−9.10	0.85	<0.0001	74.5	61.0	18.1	4	24.8
veg_med	6.66	2.13	0.001					
dis_town	4.23	0.86	<0.0001					
Model (Bi)	***Akodon azarae* TS ~ cattle food * mos_crops(SL) + season(3) + (1|farm)**							
	Coefficients	**SE**	**P**	**AICn**	**AIC**	**LRT**	**df**	**%dev**
Intercept	−3.57	0.53	<0.0001	132.5	102.0	18.06	4	30
cattle food	−291.14	70.98	<0.001					
mos_crops(SL)	−3.17	1.81	0.08					
summer	−1.75	0.75	0.019					
cattle food:mos_crops(SL)	464.15	130.2	0.0003					
Model (Bi)	***Didelphis albiventris* TS ~ season(4) * bare_gd + (1|farm)**							
	Coefficients	**SE**	**P**	**AICn**	**AIC**	**LRT**	**df**	**%dev**
Intercept	−4.87	0.84	<0.0001	146.8	138.07	14.68	5	10.30
spring	3.29	0.91	0.001					
bare_gd	−4.24	3.25	0.1919					
spring:bare_gd	−14.44	6.29	0.021					
Model (CMP)	***Lutreolina crassicaudata*[a] TS ~ veg_med + water + veg_tall + (1|farm)**							
	Coefficients	**SE**	**P**	**AICn**	**AIC**	**LRT**	**df**	**%dev**
Intercept	−8.07	3.09	0.009	74.2	62.1	18.1	6	26.6
veg_med	12.78	0.69	<0.0001					
water	−32.64	7.29	<0.0001					
veg_tall	2.58	0.35	<0.0001					

[a]Since the trapping effort was used as the offset for models with CMP distribution of errors, the estimates for these models corresponded to a trap effort of 83 trap-nights (the mean number of trap-nights set in each farm and season).

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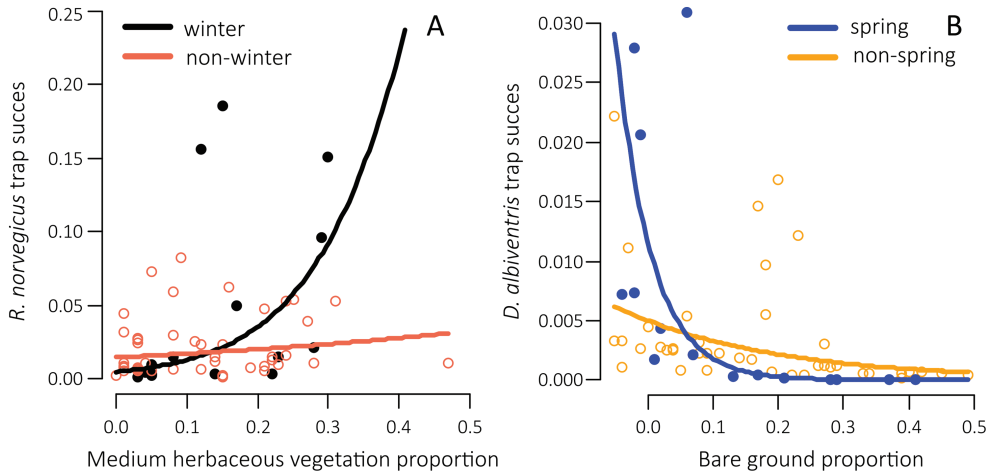


Fig. 3. (A) Plot of the interaction term between winter/non-winter seasons and the proportion of medium herbaceous vegetation in the *Rattus norvegicus* trap success model. (B) Plot of the interaction term between spring/non-spring seasons and the proportion of bare ground in the *Didelphis albiventris* trap success model.

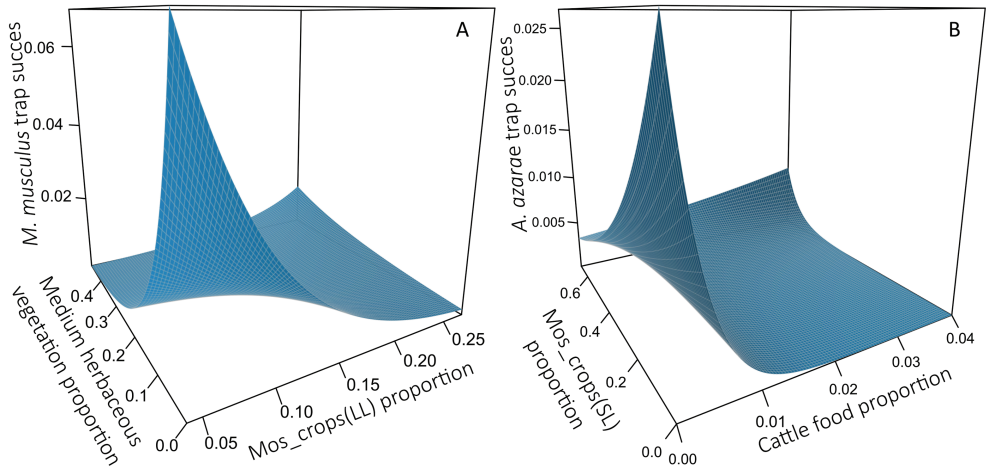


Fig. 4. (A) Plot of the interaction term between proportion of medium herbaceous vegetation at farm scale and proportion of mosaic of crops [mos_crops(LL) proportion] at large landscape scale in the *Mus musculus* trap success model. (B) Plot of the interaction term between cattle food proportion at farm scale and proportion of mosaic of crops [mos_crops(SL) proportion] at small landscape scale in the *Akodon azarae* trap success model.

embankments (Kravetz and Bilenca 1995; Busch et al. 1997; Bilenca and Kravetz 1998; Fraschina et al. 2017; González Fischer et al. 2017; Gorosito et al. 2017). We found that landscape heterogeneity, the abundance of some landscape components such as crops and woodlands, as well as proximity to urban areas influenced the relative abundances of both commensal and native species within farms.

Species diversity is expected to increase with spatial heterogeneity ("mosaic concept"; Duelli 1997). Our results support this idea, showing the expected diversity pattern at the small landscape scale. If the diversity of habitats around the farms included woodlands, grasslands, and other types of habitats, colonization by native rodent and marsupial species increased farm species diversity. However, this expected pattern was not found for the farm scale or the large landscape scale, probably because of the effect of other factors or processes that were not evaluated in the present study, such as farmers management decisions or the presence of predators (Gómez Villafañe et al. 2009; León et al. 2009, 2018; Montes de Oca et al. 2017). Also, methodological aspects such as the cover classification schemes used may be masking the association (Turner and Gardner 2015). Regarding the structure of small mammal assemblages, the association between higher abundances of *M. musculus* and *R. rattus* in farms with higher water body surfaces could result from the fact that the metabolism of these species requires consumption of large quantities of water (Fertig and Edmonds 1969; Marsh 1994; Timm 1994; Ylönen et al. 2003). On the other hand, although water body surface was considered an important factor according to the CCA model, it could also reflect the influence of impervious surfaces, short herbaceous vegetation, or bare ground coverages on the small mammal assemblage due to lack of independence between them. Impervious surfaces represent anthropogenic structures within farms, which are nesting and breeding sites for these species (Timm 1987; Marsh 1994; Feng and Himsworth 2014). Lovera et al. (2019) found that these species select sites with walls, impervious surfaces, and different vertical elements at the microhabitat scale. Additionally, short vegetation habitats are usually avoided by some small mammal species (Busch et al. 1997; Jacob and Hempel 2003; Gómez Villafañe et al. 2009; Montes de Oca et al. 2017). On the other hand, the association between assemblages with higher abundances of *A. azarae*, *O. flavescens*, and *C. laucha* and lower proportions of cattle food, water body

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surfaces, and woodlands could indicate that these species avoid farms that reduce coverages of these habitats. As previously mentioned, woodlands are of anthropogenic origin—trees were nearly absent in this region and have been planted in patches to provide shade and shelter from the wind for rural infrastructure (Soriano 1991; Bilenca and Miñarro 2004). As such, the correlation between assemblages with higher abundances of didelphids and higher woodland cover could be explained because these marsupials build nests in trees and wooded hills, which, in the study area, have been described as sites with the highest abundances of these species (Perez Carusi et al. 2009). The large home range of these opossums—7.04 ha for *D. albiventris* (Sanches et al. 2012) and 0.95 ha for *L. crassicaudata* (Cajal 1981), would allow them to live in areas that include 1 or more breeding sites and adjacent woodland patches.

As expected, at the population level abundances of commensal rodents were associated with anthropized landscapes, but also with natural habitat characteristics. Our results suggest that towns and cities may act as sources for *M. musculus* and *R. rattus* recolonization. Pocock et al. (2005) found that *M. musculus* often travels as stowaways in vehicles carrying agricultural and waste products. Studies in mixed agriculture and poultry farms have shown evidence of immigration of *M. musculus* by movements among farms (Pocock et al. 2004; León et al. 2010). Lovera et al. (2019) provided a complete description of habitat selection and use at microhabitat scale of small mammals on pig and dairy farms but did not consider their spatial use at a macrohabitat level. Until now, the role of landscape structure on *M. musculus* in these production systems was unknown, except for that described by Fraschina et al. (2014) who showed an increase in *M. musculus* abundance in a hypothetical scenario of an increased number of commensal habitats (poultry farms) in the landscape—and Singleton et al. (2007) who showed the role of agricultural landscapes and farms in Australia as possible source habitats during outbreaks of house mouse populations. Although we did not find any relationship between landscape characteristics and *R. norvegicus* abundance, Gómez Villafañe et al. (2019) found that individuals of *R. norvegicus* captured in poultry farms within an area of 110 km^2 showed high population gene flux due to dispersal patterns. Future studies of population genetic diversity across the landscape would further insight into the functions of different landscape elements (e.g. corridors, resistance, isolation) on dispersal processes and patterns and assist with development of effective rodent management plans. Abundance of commensal species was favored by medium and tall vegetation, particularly *R. norvegicus* during the unfavorable season. It has been proposed that vegetation cover would provide shelter from predators and would be used as a source of food for rodents (Gómez Villafañe and Busch 2007; Miño et al. 2007; Lovera et al. 2015, 2019; Montes de Oca et al. 2017). Thus, herbaceous vegetation cover could be playing a key role for maintenance of sustainable populations of these introduced species.

Contrary to what we expected for native species, abundance of *A. azarae* was not related to natural habitats at any of the study scales. In fact, abundance increased inversely with farm cattle food and mosaic of crop covers in the landscape, indicating that this species likely avoids sites with higher abundance of commensal species such as *R. norvegicus* that could prey on it. In this respect, the more dominant behavior of commensal species could severely affect the abundance of native rodent species (Harris 2009; Stokes et al. 2009; Feng and Himsworth 2014). Moreover, some studies indicate that this species selects patches of herbaceous vegetation in agroecosystems (Busch et al. 1997; Hodara and Busch 2006, 2010; Lovera et al. 2019)—however, those studies were conducted at the microhabitat scale, indicating that the response patterns of *A. azarae* could be "scale-dependent" (Turner 1989) and that, at the farm scale, the proportion of area occupied by medium or tall herbaceous vegetation may not be decisive for this species.

The didelphids showed the expected pattern for the native species, being negatively related with anthropized habitats and positively related with natural habitats. At population level, *D. albiventris* used farms with less bare ground proportions—indicating that it could use farms with resources for shelter, nesting, or gestation—mainly during the reproductive season (Perez Carusi et al. 2009). Regarding *L. crassicaudata*, it has been captured almost exclusively in water habitats on intensive livestock farms (Lovera et al. 2015) and has also been associated with water bodies (Santori et al. 2005). Since the water bodies present in dairy cattle and pig farms are generally used as dumping grounds for animal waste, thus favoring the development of bacteria and organisms harmful to animal health, they are probably avoided by *L. crassicaudata*.

Abundance models showed, in general, that species with a higher home range and dispersal capability (e.g. *L. crassicaudata* and *D. albiventris*), or more common species (e.g. *R. norvegicus*) would be less influenced by the surrounding landscapes of farms. In contrast, habitat specialist species (e.g. *A. azarae*; Busch et al. 2001) or with limited dispersal in rural landscapes (e.g. *R. rattus* and *M. musculus*) are more influenced by landscapes surrounding the farm. Levin (1976) described 3 main factors that could explain population dynamics and their relationship with spatiotemporal variation: (1) the local uniqueness of a site on a landscape, given by microhabitat trait changes; (2) phase differences, associated with the differential effect of disturbances on different sites; and (3) species dispersal effect across the landscape, which lead to a particular pattern of movement (e.g. patch-matrix pattern). Delattre et al. (1999) showed the importance of these factors in studies on the population dynamics of *Microtus arvalis*. Our study, together with those developed by Lovera et al. (2015, 2017) and Montes de Oca et al. (2017, 2020), addresses these issues, providing elements to understand the ecology of small mammals and, particularly, providing tools for the ecologically based rodent management (EBRM) of pest species (Singleton et al. 1999). This EBRM should involve both modifications of the natural environment (mainly grass cutting in unfavorable seasons) and security measures on available food (such as tear-resistant bags and use of rodent barriers in animal feeders). However, based on our results, the location of pig and dairy farms should be part of land-use planning and management, since infestation of pest rodents was directly related to proximity to urban areas, which could favor rodent colonization.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Small mammal occurrence and trap success in dairy and pig farms.

Supplementary Data SD2.—Boxplots of the farm-scale proportions of cover classes by season.

Supplementary Data SD3.—Pearson's correlation matrix between the proportions of cover classes recorded at farm scale.

Supplementary Data SD4.—Boxplots of the small and large landscape-scale proportions of cover classes.

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Supplementary Data SD5.—Pearson's correlation matrix between the proportions of cover classes at small landscape scale.

Supplementary Data SD6.—Pearson's correlation matrix between the proportions of cover classes at large landscape scale.

Supplementary Data SD7.—Summary of the generalized linear model between small mammals species' richness and cover classes diversity.

Acknowledgments

We express our sincere thanks to the workers, managers, professionals, and owners of each farm. We are also grateful to Daniela P. Montes de Oca, Violeta Rimieri, M. Victoria Vadell, Vanina León, María Busch, Noelia Campallo, Emiliano Muschetto, Isabel Gómez Villafañe, Mariano González King, Ignacio Gould, Florencia Mallaou, and Laura Calfayan for their assistance in the fieldwork, and to Santiago Carrizo for language revision. Our special thanks to the staff of "San Marco Veterinary" for their assistance. This paper is dedicated to the memory of Dr. Daniela P. Montes de Oca.

Author contributions

RJA contributed to conceptualization, data curation, formal analyses, investigation, methodology, supervision, visualization, writing, review, and editing; RL contributed to conceptualization, formal analyses, investigation, methodology, supervision, review, and editing; MSF contributed to the formal analyses, investigation, methodology, project administration, review, and editing; RC contributed to conceptualization, formal analyses, funding acquisition, investigation, methodology, project administration, supervision, review, and editing.

Funding

This study was supported by the Universidad de Buenos Aires, Agencia Nacional de Promoción Científica y Tecnológica, and Consejo Nacional de Investigaciones Científicas y Técnicas.

Conflict of interest

None declared.

Data availability

Data available from authors upon request.

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