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Long-term human-induced landscape changes and small mammal communities in a Mediterranean place

Cambios temporales en el paisaje inducidos por el hombre y comunidades de micromamíferos en un ambiente mediterráneo

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Abstract

The small mammal community (Orders Rodentia and Eulipotyphla) was evaluated in one single locality in coastal Catalonia in relation to human-induced changes in land use. Low detectability of some species drove us to assess the small mammal assemblages analysing barn owl (*Tyto alba*) pellets sampled in the same nesting site for a period of thirty years. The objectives were to 1) describe variations in landscape use, 2) document small mammal community changes and 3) relate these changes to those in land use. Species richness did not seem to vary with changes in land use, however, when species were separated into guilds (open, forest and synanthropic), significant differences could be observed. The open guild decreased by 6%, while the forest and synanthropic guild increased by 5% and 2% respectively. Abandonment of arable land, expansion of forested areas and an increase in urbanisation were closely linked to these guild changes, while some individual species showed variations which paralleled climatic changes. Loss of adequate open habitat for this raptor was highlighted by a species substitution, with the tawny owl (*Strix aluco*) occupying the nesting site previously used by the barn owl during the last years of the study. Barn owl diet monitoring therefore proves to be a useful tool to analyse small mammal community responses to changes in the environment, allowing for more specific and viable conservation plans for both small mammals and barn owls.
Keywords: Barn owl, human-induced change, local extinction, Mediterranean, small mammal community.

Resumen

La comunidad de micromamíferos (órdenes Rodentia y Eulipotyphla) fue evaluada en una sola localidad cercana a la costa catalana, en relación con los cambios antrópicos en el uso del suelo. La baja detectabilidad de algunas especies nos condujo a evaluar el conjunto de micromamíferos analizando egagrópilas de lechuza común (*Tyto alba*) extraídas del mismo punto de anidación durante un período de treinta años. Los objetivos fueron: 1) describir las variaciones paisajísticas, 2) documentar cambios en la comunidad de micromamíferos y 3) relacionar estos cambios con los paisajísticos. La riqueza en especies no pareció variar con los cambios en el uso del suelo, sin embargo, cuando éstas se separaron en gremios (abierto, forestal y antrópico), se pudieron observar diferencias significativas. El gremio abierto disminuyó en un 6%, mientras los gremios forestal y antrópico se incrementaron un 5% y un 2% respectivamente. El abandono de terreno cultivable, la expansión de áreas forestales y el incremento en urbanización se vieron vinculados a estos cambios en los gremios, mientras que las especies, de forma individual, mostraron cambios relacionados con los climáticos. La pérdida de hábitat abierto adecuado para este ave se vio reflejada en la sustitución de la lechuza por el cárabo común (*Strix aluco*), ocupando su lugar de anidación. Por lo tanto, el seguimiento de la lechuza común resulta ser una herramienta útil para analizar respuestas al entorno en la comunidad de micromamíferos, posibilitando planes de conservación más viables y específicos para ambos.
Palabras clave: cambio inducido por el humano, comunidad de micromamíferos, extinción local, lechuza común, Mediterráneo.

Introduction

Mediterranean ecosystems are considered as highly sensitive to global changes, which are known to affect drastically the animal community (Sala *et al.* 2000, Doblas-Miranda *et al.* 2015), with climate change and land-use change being the most studied factors to date. The latter, which was the factor investigated in this report, has caused fluctuations in both the ecology and biology of animal and plant communities (Debussche *et al.* 1999, Szpunar *et al.* 2008). Land-use change is also considered one of the most important threats to biodiversity (Sala *et al.* 2000).

Many studies concerning climate or land use change have centred upon plants, birds, insects or fish, while small mammal species are not often addressed in biodiversity studies. There have been few investigations directed to identifying the response of small mammal communities to changing landscapes (e.g. Cagnin *et al.* 1998, Millán de la Peña *et al.* 2003, Rodríguez & Peris 2007, Torre *et al.* 2015). These species are directly related to the abundance and diversity of their depredators (Butet & Leroux 2001, Salamolard *et al.* 2000), being essential in the maintenance of a stable food web not only as prey (Korpimaki & Norrdahl 1991), but also as seed dispersers (Gómez *et al.* 2008, Morán-López *et al.* 2015). Therefore, forecasting small mammal species' responses to changes in climate or land use is of pressing concern (Barnard & Thuiller 2008). The complexity of these responses requires a deep understanding of the climatic and ecological factors driving these changes in diversity to predict the variations and to conserve the biodiversity of small mammal communities (Rubidge *et al.* 2011).

Throughout this study the pellets produced by the barn owl were analysed and used to evaluate changes in small mammal species during a given time span. This method is used to compensate for the low detectability of some small mammals when using other sampling procedures such as live-trapping (Torre *et al.* 2004, 2018). The barn owl often selects open land such as grasslands or recently cleared areas to find prey, avoiding dense forest habitats (Shawyer 1998, Millán de la Peña *et al.* 2003). Nonetheless, habitats available for owls are declining due to the afforestation process observed during the last decades in Western Europe. Changes in land use were caused by the abandonment of agricultural lands during the second half of the twentieth century (Duguy 2003), transforming these former open habitats into forested areas (Debussche *et al.* 1999). This has induced the barn owl to become more dependent on rough grasslands, field margins, hedgerows and forest ecotones (cf. Tomé & Valkama 2001, Salvati *et al.* 2002). Furthermore, this succession towards closed habitats causes a general loss of suitable habitat for barn owls (Green 1990).

The main goals in this study were: (1) to describe the variations in landscape use in the study area; (2) to assess if there have been significant changes in the small mammal community diversity in the same area during a similar length of time; and (3) to observe if there is a relationship between these two patterns of change (e.g. Torre *et al.* 2013, 2015). We therefore hypothesise that, following the general afforestation throughout the region and the subsequent loss of suitable foraging habitat for barn owls; their diet will be increasingly dependent on small mammal species related to closed areas and decreasingly so on those related to open areas.

Materials and Methods

Study site

The study was performed in a single locality in the county of Maresme (41° 33' 53"N; 2° 24' 40"E; elevation: 118 m asl) at about 25 km NE from Barcelona (Catalonia, NE Spain). The climate is typically Mediterranean with temperatures ranging from 23.9°C in July, the warmest month of the year, to 8.9°C in January, the coldest. More than 25% of rainfall is concentrated in the months of September and October, being the annual amount of rainfall 658 mm.

Small mammal sampling

A large deposit of disaggregated barn owl pellets was sampled from a single roost located in an abandoned turret of a XVI century 'masia'. The material was found to be compacted and composed of four visibly distinct layers, which could be easily separated when collected. These strata were assumed to belong to different periods of occupation of the nesting site due to clear differences in the pellet remains, with the bottom and oldest stratum containing heavily fragmented material and dust, in contrast with the most recent stratum. A first collection of this sample had been done prior to 2011, so that stratum four corresponds to the period between 2011 and 2016. Barn owls are considered generalist predators of small mammals whose diet reflect changes in relative prey abundance (Love *et al.* 2000, Bernard *et al.* 2010), which is mainly based on small mammals, mostly rodents (Brown *et al.* 1982). The study of the owl's pellet analysis has consequently been shown to reflect changes in prey availability in space and time (Bernard *et al.* 2010, Meek *et al.* 2012). Due to the large magnitude of the sample extracted, it was decided that a subsample would be necessary. To do so, the remains of each stratum were scattered over a sieve, to separate the fur/feather matrix from the skeletal material, and organised into quadrants, which were later chosen randomly. The jaws were then handled with tweezers and a teasing needle and cleaned with a brush (Gosàlbez 1987). The mammalian remains were identified to species using a magnifying lens following Gosàlbez (1987) and Arrizabalaga *et al.* (1999). Birds and reptiles were identified to class while invertebrate species were not recorded as they are not considered an important food source to the barn owl (Shawyer 1998). The minimum number of prey individuals per subsample was determined from the highest number of mandible items present (see Granjon & Traoré 2007).

Carbon Dating

The carbon dating procedure was used to date the oldest stratum (stratum 1), as its age was unknown. A small sample of postcranial bones were sent to the C-14 laboratory of the Universidad de Granada where it underwent treatment. The results concluded that it dated later to 1950 (modern age), even though the magnitude of the remains found could have suggested an extended period of breeding.

Land use determination

The barn owl has a predation range of 2 to 7 km^2, but a radius of 3 km around the nesting location is enough to characterise the owl's habitat (Bond *et al.* 2004, Szpunar *et al.* 2008). The area comprised inside the 3 km radius was 2087.4 ha which is sufficient to consider it as representative of the barn owl's foraging range (Taylor 1994). Maps were created from the Institut Cartogràfic i Geològic de Catalunya (ICGC: http://www.icc.cat) processing the data by the TematicMapper™ sensor from the Landstat satellite. The cartography used maps with a 30 m resolution and 8 different categories of land use. A buffer was created for every 10 years since 1986 until 2016. The differences between land usage categories of each period were calculated using ArcMap v.10.2.2 (ESRI).

Data analysis

According to the preferred habitats of the small mammal species, they were designated to one of three general guilds (Gosàlbez 1987, Torre *et al.* 2013, 2015): (1) Open guild, including the species *Microtus duodecimcostatus*, *Mus spretus*, *Crocidura russula* and *Suncus etruscus*; (2) Forest guild, with *Apodemus sylvaticus* and *Myodes glareolus*; and (3) Urban guild, comprising *Mus musculus* and *Rattus rattus*, closely related to anthropic activity. *Eliomys quercinus* was not classified into any of these categories due to its mainly generalist behaviour in habitat selection (Torre *et al.* 2015). Land uses extracted from the cartographic analysis enabled the formation of three analogous guilds relating habitat structure: (1) Open, conformed by natural habitats such as scrubs and meadows, as well as human-influenced habitats including irrigated and rain-fed arable crops, vineyards, fruit tree crops and abandoned fields; (2) Forest, with dense and sparse coniferous forests and broad-leaved evergreen forests; (3) Urban, comprising roads, towns, residential areas and commercial and industrial zones. A 'bare soil' category was also included in the classification of land uses during the map-making process, but it was finally dismissed owing to its minimal influence on the small mammal community (Torre *et al.* 2015).

Only one value was extracted for each stratum and time period, therefore, to evaluate the significance of the differences between each stratum (1,2, 3 and 4) and land use and guild (open, forest and urban), log-linear models were fitted to the multiway contingency tables generated by each category (Torre *et al.* 2015). The units used were hectares of each certain land use category, per time period, and number of individuals of each guild, per stratum, for the small mammal count. This method is considered equivalent to an ANOVA, which separates total variance between data into factors and their interaction allowing for tests of significance between their effects (Everitt 1992). The statistical analysis was carried out using the software Statistica 12 (StatSoft Inc.). The residuals extracted from this technique were correlated with Pearson's correlation coefficient to evaluate the significance of the relationship between the mammalian guilds and land uses, setting the level of significance for the refusal of the null hypothesis at $p < 0.05$.

To estimate the actual species richness of the samples obtained from the pellets, species accumulation curves were calculated (Gotelli & Colwell 2001). The curves were generated using EstimateS (Colwell 2013), after 100 randomizations of the number of species observed in this sample. The Clench equation was used to verify the inventory's completeness, fitting the function provided by EstimateS and following the procedure presented by Jiménez-Valverde & Hortal (2003) using the non-linear estimation module in Statistica 12. Accumulation curves grant more reliability to biological inventories, enabling their comparison and allowing the extrapolation of the number of individuals to estimate the total number of species in an area (Colwell & Coddington 1994, Gotelli & Colwell 2001).

Results

Species richness analysis

A total of 4,537 prey items were identified from the four strata (1,134.3 ± 130.7; mean ± SD; *n*= 4). If only small mammals were considered, a total of 4,367 individuals were identified from the mandible remains, which represents the 96.25% of the whole prey sample. The remaining 3.75% was composed by birds, a lizard and a bat, which were merely classified to class and order as they were not the focus of this study. Invertebrates, fruit and seeds were not considered. Through mandible analysis 94.34% of small mammal individuals could be identified to species. The rest were classified to genus (in the case of *Rattus*) or family (in the case of Muridae) since some of the remains were incomplete, impeding exhaustive identification using mandibles alone.

The accumulation curves showed a very close approach to the asymptote in all four strata; however, due to the presence of only one individual of *E. quercinus* in stratum 3, this curve was less stable (dashed line in Fig. 1). The Clench equation fitted all four species accumulation curves closely (R^2= 0.95; 0.93; 0.90; 0.94 for stratum 1 to 4, respectively) and estimated species richness was 8.07, 8.99, 8.67, and 7.96, at the end of the species accumulation curve, meaning that 99%, 97%, 97%, and 98% of all small mammal species were sampled in each inventory, respectively. *E. quercinus* was absent from both the first and last stratum, whereas the remaining species were shared by all strata.

Small mammal community changes

Small mammal species did not seem to follow a stable trend throughout the four different strata;

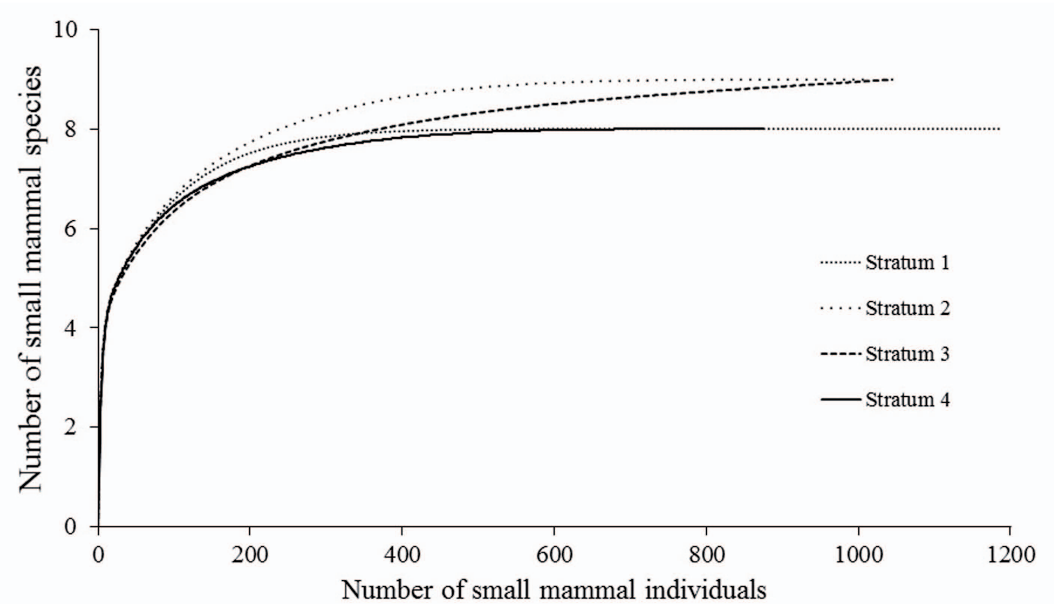

Figure 1. Small mammal species accumulation curves for all four strata after individual-based rarefaction of abundance data.

nevertheless, considering the first and last strata, four species increased in occurrence, four decreased, and *E. quercinus* remained the same. From stratum one to four the frequency of occurrence of *A. sylvaticus* increased by 5.60% and *M. duodecimcostatus* increased by 1.05%, while both synanthrophic species *M. musculus* and *R. rattus* increased by 0.77% and 0.70%, respectively. On the other hand, *C. russula* decreased by 3.97%, followed by *M. spretus*, which decreased by 2.29%, *S. etruscus* by 0.60% and *M. glareolus* by 0.36%. A log-linear analysis showed significant differences in the frequency of occurrence of the nine species between the four strata (χ^2= 64.2; d.f.= 24; p< 0.001).

When species were grouped into guilds, the log-linear analysis also showed significant differences between guilds and strata (χ^2= 16.7; d.f.= 6; p= 0.01; Fig. 2). From stratum one to four, the open guild decreased by 5.81% (from 68.11% to 62.3%), whilst both the forest and synanthropic guilds increased by 5.24% and 1.80% respectively (forest guild from 24.11% to 29.35% and the synanthropic guild from 2.31% to 4.11%; Table 1, Fig. 3).

Land use changes

The changes in land use were calculated by extracting data provided by the mapping process and using Ha as the habitat occupation measure and a percentage as the frequency of occurrence (Table 2). The habitats were assembled into three main groups: open, forest and urban, and their frequencies evaluated. The year 1986 was assumed to correspond to the age of the oldest stratum as land use composition matched the relatively low frequencies of open area small mammal species predated on by the barn owl (following data in Torre *et al.* 2015). This allowed also for an easier comparison between the four land-use maps and four strata remaining, meaning that each stratum corresponded to one map and year (stratum 1 to 1986, stratum 2 to 1996, stratum 3 to 2006 and stratum 4 to 2016).

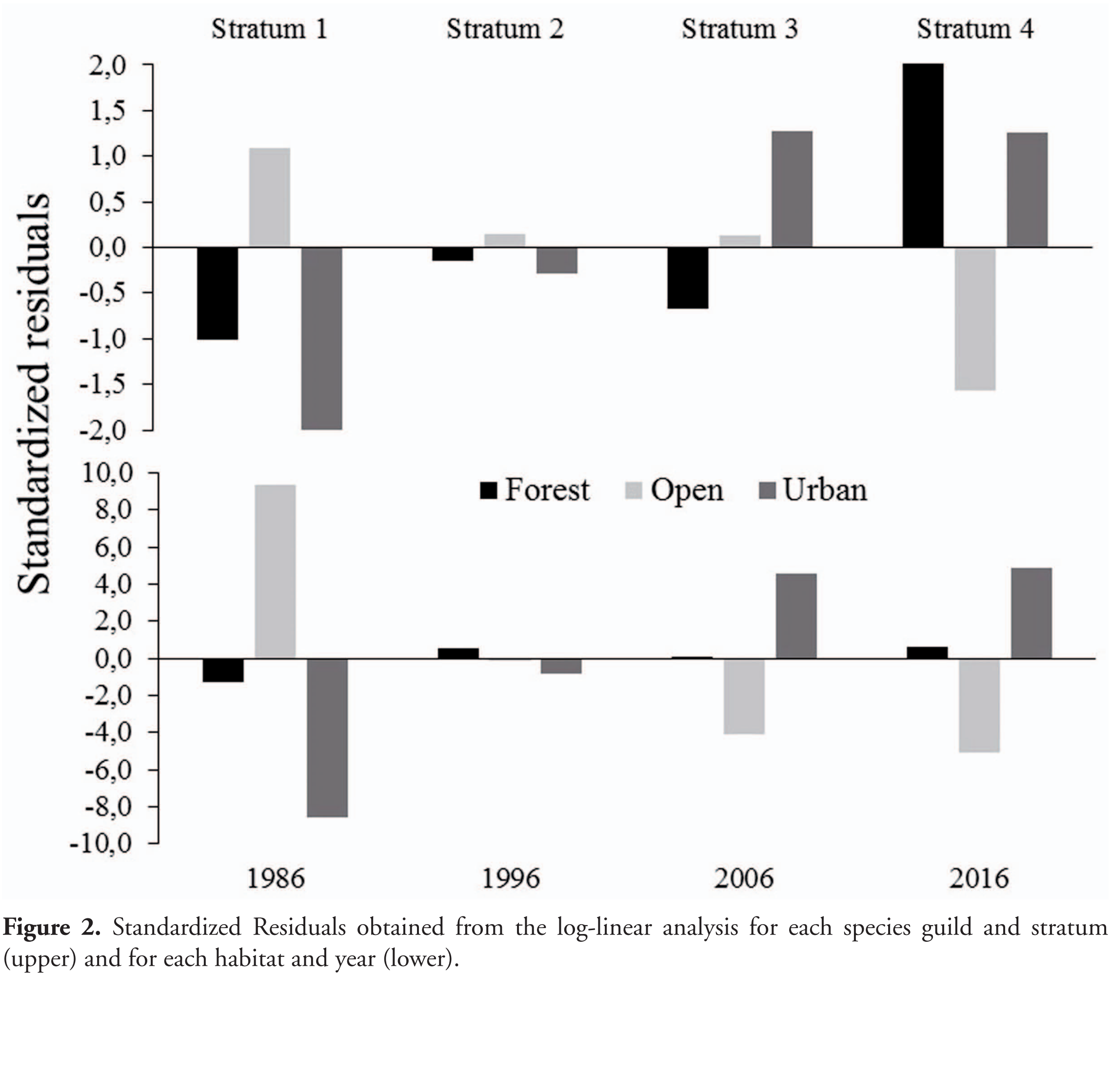

Figure 2. Standardized Residuals obtained from the log-linear analysis for each species guild and stratum (upper) and for each habitat and year (lower).

A log-linear analysis showed that the differences between the land uses of the four periods grouped into the three main habitat categories were significant ($\chi^2 = 251.4$; d.f.= 6; $p < 0.001$). A clear pattern of habitat changes from the year 1986 to 2016 was shown by the residuals obtained from this test (Fig. 2): open areas decreased by 13.21%, forested areas increased by 2.61%, and urban areas increased by 10.56%.

Correlation between land use and small mammal community changes

A Pearson correlation coefficient between the residuals obtained from the log-linear analyses of the three habitats (open, forest and urban for the maps from 1986 to 2016) and the three different guilds, for stratum one to four, was significant (r= 0.76, p= 0.003, n= 12, Fig. 4). This means that temporal change of frequencies of occurrence of both habitats and guilds showed a similar trend during the study period (Fig. 3).

Table 1. Total number of individuals (*N*) and the relative frequency (%) for each small mammal species and stratum.

Species	Stratum 1		Stratum 2		Stratum 3		Stratum 4	
	N	%	*N*	%	*N*	%	*N*	%
Microtus duodecimcostatus	202	16,02	204	19,01	217	19,50	157	17,07
Myodes glareolus	10	0,79	5	0,47	4	0,36	4	0,43
Crocidura russula	305	24,19	214	19,94	171	15,36	186	20,22
Suncus etruscus	13	1,03	4	0,37	4	0,36	4	0,43
Apodemus sylvaticus	294	23,31	267	24,88	270	24,26	266	28,91
Mus spretus	339	26,87	287	26,31	345	30,99	226	24,58
Mus musculus	16	1,28	17	2,02	14	1,26	19	2,05
Muridae	69	5,47	54	5,03	56	5,03	39	4,24
Rattus rattus	9	0,71	11	1,03	18	1,62	13	1,41
Rattus sp.	4	0,32	6	0,56	13	1,17	6	0,65
Eliomys quercinus	0	0,00	4	0,37	1	0,09	0	0,00
RICHNESS	8		9		9		8	
Total	1261	100,00	1073	100,00	1113	100,00	920	100,00

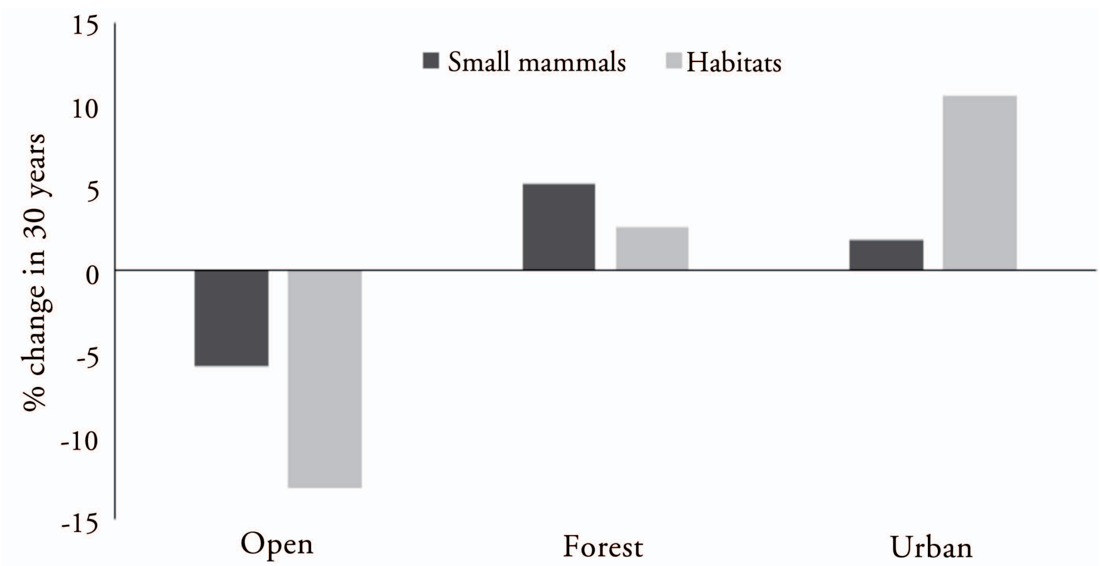

Figure 3. Rate of change (%) of the small mammal guilds and their associated habitats between strata 1 to 4 (barn owl diet) and years 1986 – 2016 (land-use).

Table 2. Total area (ha) and the relative frequency (%) for each habitat type and year corresponding to a land-use map.

Habitat	Year 1986		Year 1996		Year 2006		Year 2016	
	Ha	%	Ha	%	Ha	%	Ha	%
Open	907,47	32,10	651,21	23,03	559,73	19,80	533,98	18,89
Forest	1537,40	54,37	1582,81	55,98	1586,56	56,11	1611,13	56,98
Urban	300,68	10,63	464,57	16,43	591,13	20,91	599,37	21,20

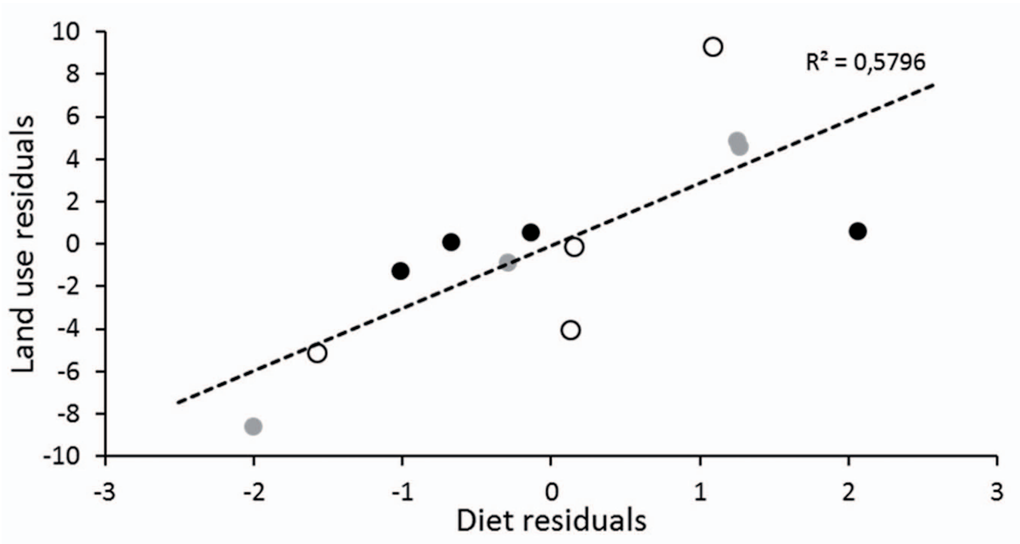

Figure 4. Correlation of the residuals obtained from two log-linear tests analysing temporal changes in small mammal guilds in barn owl diet and their associated habitats (open circles: open habitat; light grey: synanthropic habitat; black: forest habitat).

Discussion

In this investigation barn owl pellets were used as an alternative to live-trapping, since it is considered a non-invasive sampling technique for detecting changes in the small mammal abundance and community composition (Torre *et al.* 2015). Even though both methods have certain biases and disadvantages, the pellet analysis was efficient for detecting shifts in species frequencies of occurrence in agricultural habitats in relation to different land uses (Millán de la Peña *et al.* 2003, Rodríguez & Peris 2007, Torre *et al.* 2015). At the landscape scale, using live-trapping would imply establishing many plots to encompass habitat heterogeneity, whereas using barn owl pellets seemed a better choice since owls cover large areas while exploring hunting places, being able to capture a larger and more heterogeneous sample of prey items than live-traps (Paillat 2000, Torre *et al.* 2004).

It is important to note that land use changes affecting relative guild and species frequencies were measured only once per stratum and although sample size was large, only one location was used (resulting in no spatial replicates nor variation). Therefore, only general trends shall be considered in this study and additional data will be needed for complete validation. A species replacement from barn owl to tawny owl also took place during the period corresponding to mid stratum four (authors unpub.), which emphasized the general barn owl abundance decrease due to habitat loss in Catalonia as well as throughout Western Europe (Askew *et al.* 2007, Torre *et al.* 2015). The tawny owl is known to prefer closed and forested areas but has also shown remarkable flexibility colonising urban environments (Goszczynski *et al.* 1993) in contrast to the open grasslands frequented by barn owls.

Our results showed that human-induced landscape changes caused variations in the small mammal community and species frequency. A strong correlation between the owl's diet and the change in land use was observed. Landscape changes were evident, with open areas decreasing in frequency and urban areas increasing, complementing the recognized pattern throughout Catalonia (Estrada *et al.* 2004, Parcerisas *et al.* 2012) and the Mediterranean region (Debussche *et al.* 1999). However, a large increase in forested areas was expected (only a 2,6% increase between 1986 and 2016) as is happening in most Mediterranean regions (Debussche *et al.* 1999), but in other areas forest decreased (Torre *et al.* 2015). These results point out that temporal interactive responses of landscape change can be found at small spatial scales (i.e. at the locality level), and their influence on the small mammal communities can be overlooked when considering higher spatial scales of analysis (Torre *et al.* 2015). These small variations were enough to cause slight changes in the barn owl's diet, with a 5.8% decrease in species belonging to the open guild, and a 5.2% increase in those conforming the forest guild, in congruence to our hypothesis. The synanthropic guild increased only by 1.8%. These changes were not as marked as those found in spatially replicated studies (Torre *et al.* 2015), but nevertheless significant and following the same variation pattern. These results suggested a parallel trend between land use changes and small mammal community variations.

The most noticeable change in barn owl diet between stratum one and four was the increase in the frequency of occurrence of *A. sylvaticus* in the diet. This could be due to increasing woodland cover with time, since forests are the preferred nesting habitats (Telleria *et al.* 1991, Rosalino *et al.* 2011, Torre *et al.* 2015). The wood mouse is also widely considered a habitat generalist, capable of colonising arable habitats as well as forests and scrublands and benefiting from heterogeneous landscape patches (Rodríguez & Peris 2007), which may also explain the rapid adaptation to changing landcover in contrast to competing species (Love *et al.* 2000). The wood mice increment was especially pronounced during the fourth stratum, which could also be due to the introduction of the tawny owl in the nesting site (authors unpub.), as it is known to depend on this murid species for breeding success (Southern & Lowe 1968).

Relative proportions of small mammal species in owls' diets are not independent from each other, since factors such as prey abundance and behaviour also play an important role in prey selection (Love *et al.* 2000). The apparent increase in *A. sylvaticus* could therefore explain the general decrease in Algerian mouse, greater white-toothed shrew (*C. russula*) and Etruscan shrew (*S. etruscus*) in the owl's diet. Interspecific competition between *A. sylvaticus* and *M. spretus* has been well documented (Boitani *et al.* 1985, Khidas *et al.* 2002), which could explain the slight decrease in the latter species, although more arid environments and cultivable land are associated to *M. spretus*. These relative abundance changes, however, could be due to a decrease in open habitat in the study area, both for the shrew species and *M. spretus*. Shrews showed a positive association to understorey vegetation due to thermal restrictions, food availability, and predator avoidance (Torre *et al.* 2014). Bank voles (*M. glareolus*) are more strictly restricted to forest habitats, therefore an increase of this species' abundance in pellets was expected (Torre *et al.* 2015), strengthened by the replacement of the barn owl by the tawny owl, which bases its diet mainly on this species as well as on *Apodemus sp*. (Southern & Lowe 1968). Nevertheless, this was not observed in our results. In fact, a decrease was perceived, although the results were not significant. Bank voles are not a predominant species in the study area however, as they find themselves in the lower limit of their distribution in Catalonia, preferring higher altitudes and humid woodlands (Torre & Arrizabalaga 2008).

In the case of the Mediterranean pine vole (*M. duodecimcostatus*), a slight increase was perceived, describing a negative pattern in relation to the expected results from a species belonging to the open guild. This may be attributed to the species' adaptation to the warmer and drier Mediterranean climate, experiencing an increment in its frequency of occurrence due to current climate change conditions in Catalonia instead of following the patterns of variation derived from land use change (Spzunar *et al.* 2008).

Synanthropic species such as the black rat (*R. rattus*) and house mouse (*M. musculus*) presented an increase in frequency throughout the samples analysed, following the urbanisation pattern experienced in the study area from 1986 to 2016. These species have no conservation value at all as they are closely related to human influence. The increase of species comprising the urban guild is as expected from an increasing urban environment. However, even in largely urbanised areas, it has been found that anthropic-related species do not necessarily abound in the barn owl's diet (Hindmarch *et al.* 2015) in congruence with our results.

Many of the dietary changes experienced by the barn owl during our investigation can be therefore attributed to land use changes in its habitat, which are a consequence of the agricultural abandonment occurring throughout the Mediterranean and Catalonia (Debussche *et al.* 1999, Estrada *et al.* 2004, Parcerisas *et al.* 2012), resulting in the loss of appropriate habitats for potential small mammal prey. However, it is important to note that significant changes in small mammal composition could be affected by the introduction of tawny owl in the nesting site. Nevertheless, this could be largely due to the land use changes occurring in the study area, favouring the latter's survival over the barn owl.

Likewise, suitable habitats for both small mammal communities and barn owls tend to be small and isolated patches with a high heterogeneity (Stoate *et al.* 2001), with edge habitats being of great importance for the maintenance of the barn owl in the area (Bond *et al.* 2004). Previous studies have shown that areas along woodland edges, river banks, hedgerows and field margins have been persistently used by barn owls when optimum unimproved grasslands were not available (Shawyer & Shawyer 1995, Tomé & Valkama 2001).

This study site seems to be no longer viable for barn owl breeding, which could be linked to 1) the loss of habitat suitability due to a general decrease in open land that was mostly substituted by urban areas (and forests to a lesser extent) and 2) to the strong interspecific competition with the tawny owl parallel to this afforestation in the area. Since the tawny owl breeds on average seven weeks before the barn owl (Roulin *et al.* 2009), it would occupy nesting sites prior to the latter species, replacing it in the ecosystem. Barn owls are particularly vulnerable to changes in food availability owing to their fast metabolism and then, greater energetic needs in comparison to other birds of prey (Massemin & Handrich 1997), recurring to less profitable prey (Krebs & Davies 1993), limiting their chances of survival in a no longer suitable area such as this. The method employed in this study can be, therefore, limited to the sites where land use variation in relation to the owl's diet does not produce local extinctions.

Summarising, the analysis of barn owl pellets was as a useful tool to assess changes in small mammal communities related to temporal land-use changes. Similar results were found throughout the Mediterranean region, where abandonment of arable land gave rise to afforestation and an increase in forest species, while the general increase in urbanisation provided the same effect for synanthropic species. The loss of open habitat also contributed to a notable decrease (but heterogeneous) in field-related species in the barn owl's diet. The predator substitution observed during this study (barn owl by tawny owl) also highlighted the importance of the effects caused by human-induced changes in habitat structure. However, future studies focused on smaller temporal scales and multiple study sites could apply both live-trapping and pellet analysis methods to complement our results. This would provide greater insight into the barn owl's habitat selection and the specific pressures causing its steady decline throughout the country, aiding in its much-needed conservation as an important small mammal predator.

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