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Abstract Human-induced landscape changes are expected to have strong effects on the composition and structure of terrestrial small mammal communities (Orders Rodentia and Soricomorpha). However, testing such expectations is difficult due to low detectability of these animals. We used analyses of barn owl (*Tyto alba*) pellets sampled in the same roosting places during 1977–1991 and again in 2011–2014 to (a) document small mammal community changes and (b) relate them to changes in land use. Forest and synanthropic small mammals increased by a 7 % between both periods, whereas open-land species decreased by 13 %. Man-made loss (crops and meadows) and expansion (forest and urban) of relevant habitat types were closely related to these changes. Localities with land use changes opposite to the general trend showed also an opposite trend in small mammal community change. Land use heterogeneity increased and dominance decreased between both sampling periods, and this pattern was paralleled by an increasing trend in diversity and a decreasing trend in dominance in small mammal communities. Decreasing trends of some generalist northern species with restricted ranges may have been due to climate change. Diet monitoring of barn owls are thus valuable tools for both documenting and analyzing fine-grained small mammal responses to global change.

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Keywords Barn owl · Global change · Human-use trends · Mediterranean · Small mammal guilds

Introduction

Mediterranean ecosystems are currently considered as natural laboratories to study global change effects on wildlife, due to its high sensitivity to several global change drivers and their interactions (Sala et al. 2000; Doblas-Miranda et al. 2015). The two drivers more studied to date have been climate change and land-use change. Temperature is increasing and precipitation is decreasing, two factors that would largely determine the fauna and flora of a territory (Thuiller et al. 2011). Changes in land use are causing wide variations on the ecology and biology of animal and plant communities (Debussche et al. 1999; Pausas 2004; Szpunar et al. 2008). Such changes basically consist of the abandonment of agricultural and grazing land, caused by the acceleration of rural exodus during the second half of the twentieth century (Duguy 2003). Often, natural vegetation grows back in these abandoned lands, transforming former open habitats into forest areas (Debussche et al. 1999). Complex interactions among these drivers are expected, through processes such as changes in animal-plant, plant–plant or animal–animal interactions (competition, predation and dispersal), or in disturbance (fire) regimes (Doblas-Miranda et al. 2015). Just documenting patterns of change in relation to drivers is currently a priority in Mediterranean-type ecosystems, as it is essential to both build-up and test models for the effects of global change and the ways to ameliorate or adapt to it (Doblas-Miranda et al. 2015).

To date, most work on effects of global change on Mediterranean biodiversity has been focused on plants and birds (Devictor et al. 2012; Parmesan et al. 2013; Matesanz and Valladares 2014), in showy insects such as butterflies (Devictor et al. 2012) or in socially-important freshwater fish (Almodóvar et al. 2012). Small mammals, however, have been less studied, probably because of the problems associated to just detecting their presence in a given area (Torre et al. 2004). Nevertheless, many papers have proven the dependence of small mammals on habitat structure and land use (Seamon and Adler 1996), and on climate (Szpunar et al. 2008). Furthermore, small mammals are keystone prey, herbivores or even seed dispersers in terrestrial Mediterranean ecosystems (Torre 2004; Avenant 2005; Szpunar et al. 2008; Morán-López et al. 2015). This project aims to determine changes in the composition of the communities of small mammals in a Mediterranean area, and relate such changes to the observed changes in local landscapes. Community changes were determined using analyses of barn owl *Tyto alba* pellets to compensate for low detectability of small mammals with conventional sampling methods (livetrapping: Torre et al. 2004). This method, although known since long to analyze spatial patterns of small mammal abundance and community structure, has been still rarely used to document temporal changes in relation to global change (Szpunar et al. 2008). Barn owls are mostly considered as open habitat foragers avoiding large forests areas (Millán de la Peña et al. 2003). Our main hypothesis is that generalized abandonment of practices maintaining open habitats during the last 30 years (Debussche et al. 1999) would have favored forest species in detriment of open-habitats species, thus leading to a change in community structure somewhat opposite to that expected from climate change effects (see Seoane and Carrascal 2008, for birds). If this was true, small mammals, as other endotherms, will be proven to be more influenced by land use than from climate change (Thuiller et al. 2011; Devictor et al. 2012; review in Torre et al. 2014). Accordingly, three main objectives were followed: (1) to characterize landscape use and landscape changes in the study localities; (2) to determine if the small mammal communities of these localities have experienced any significant variations in a similar period of time; and (3) to analyze whether the two patterns of change were consistent, on the basis of the habitat requirements of the involved species (e.g. Torre et al. 2013).

Materials and methods

Study area

The survey was carried out in eight localities in the counties of Osona and Vallès Oriental, an area of some 1,200 km^2 in the province of Barcelona (Catalonia, NE Spain; Table S1). Climate is Mediterranean but with variation related to orographic heterogeneity. Study sites were located between 200 and 850 m elevation (Table S1). Between 1950 and 2008, but mostly from the 1980s onwards, temperature in Catalonia has increased at an average rate of 0.21 °C/decade, reaching 0.35 °C/decade in the summer months. On the other hand, the mean annual rainfall has decreased about 1 % during the XX century (Llebot 2012). According to data analysed by the former authors, the distribution of temperature increase is fairly uniform on the territory.

Small mammal sampling

We sampled exactly the same eight places for which data on barn owl diets were obtained in the 1970′s and 1980′s according to published reports and unpublished data (Table S1). In some sampling locations we did not find evidence of barn owl presence despite there were active nests in previous decades (Arrizabalaga et al. 1986). The absence of barn owl activity in these locations is in agreement with the decreasing trend of this bird of prey in the study area (Estrada et al. 2004; Ribas 2014) as well as in Catalonia (Estrada et al. 2004) during the last three decades. We include old data from all localities in the Supplementary material to facilitate future analyses if sites are recolonized by owls. The average time elapsed between old and current samples was 30 years (range: 23–37 years), a period long enough to detect significant changes in the small mammal communities due to either landscape and/or climate change (Love et al. 2000; Szpunar et al. 2008).

Pellets produced by barns owls accurately reflect changes in its diet and such diet is considered to reflect accurately changes in prey availability both in space and in time owing to the generalist-opportunistic predator behavior of this owl (Tores et al. 2005; Bernard et al. 2010). Dry pellets were scattered, separating skull remains with tweezers and a teasing needle. Remains were cleaned with a brush (Gosálbez 1987) and identified following Gosálbez (1987) and Arrizabalaga et al. (1999), using the reference collection held at the Museu de Ciències Naturals de Granollers when necessary. Minimum numbers of individual prey were established from single and paired skull remains following standard procedures. We used the 4,277 prey items collected from four sites during 1977–1991 (1,069.3 ± 321.6; mean ± SD; $n = 4$), and 1,804 prey items collected from the same sites during 2011–2014 (451 ± 304.1). Samples sizes are considered as representative to characterize the small mammal fauna within a locality (Love et al. 2000; Torre 2001; Millán de la Peña et al. 2003). Considering a daily food intake of 60 g for adult barn owls (Marti 1973), and an average body mass of 15 g for their main prey in the study area (own data), pellet samples would include the remains of the prey caught during at least 112 days (mean recent samples) and 267 days (mean old samples) by owls at each site previous to pellet collection dates. In the old sample of La Vola (Culí et al. 1989) it has not been possible to determine the different species of *Apodemus* (*A. sylvaticus* or *A. flavicollis*).

Determining land uses

The home range of barn owls varies from 2 to 7 km^2, but it is generally assumed that a radius of 3 km around resting/breeding sites is sufficient to characterize barn owl's habitat (Martínez and Zuberogoitia 2004; Bond et al. 2005; Szpunar et al. 2008). Consequently, we obtained environmental information from circles of 2.5 km of radius centered on each locality (Szpunar et al. 2008). Land uses in these circles were obtained from the ''Land use classification of Catalonia 1987'' (as representative to land uses in the 1970–1980s) and the ''Land use classification of Catalonia 2002'' (for land uses in 2014; Generalitat de Catalunya, Departament de Territori i Sostenibilitat: (http://www20.gencat.cat/portal/site/territori)). We considered that land use changes between the two mapping periods will be representative, albeit somewhat conservative, for changes in the last 30 years (see Estrada et al. 2004). Maps were created by Institut Cartogràfic i Geològic de Catalunya (ICGC: http://www.icc.cat) using the data processing by the TematicMapper (TM) sensor from the Landsat satellite. The cartography used consisted in maps with a 30 m × 30 m (900 m^2) resolution and 22 categories of land use. Variations occurring during the study period for each land use class were calculated by means of ArcMap v.9.3 (ESRI).

Data analysis

Small mammal species were assigned to three main guilds according to their habitat requirements (Gosàlbez 1987; Torre et al. 2004, 2013): (1) Forest guild, composed by *Apodemus flavicollis, A.sylvaticus,* and *Myodes glareolus;* (2) Open-land guild, with *Microtus agrestis, M.duodecimcostatus, Mus spretus, Crocidura russula,* and *Suncus etruscus*; and (3) Urban guild, composed by species closely associated to man such as *Mus musculus, Rattus norvegicus,* and *R. rattus*. *Sorex minutus, S.araneus, Arvicola sapidus* and *Eliomys quercinus* were not included in any guild due to their generalist behavior. Low abundance or absence in most localities of these habitat generalists (Table S2, Torre et al. 2004, 2013), and lack of coincidence with any kind of land use, precluded its meaningful inclusion and analysis as a separate guild. Accordingly, land uses were also grouped into four main categories in relation to habitat structure: (1) Forest, which included broad-leaved deciduous forests, broad-leaved evergreen forests, and coniferous forests; (2) Crops, that included fruit tree crops, vineyards, rainfed arable crops, and irrigated arable crops, which represented open human-induced habitats; (3) Scrub and meadows, which represented open natural habitats; and (4) Urban, which comprised commercial and industrial areas, roads, towns, and residential areas. ''Bare soil'' and ''Continental water'' land uses were not considered owing to their limited influence on small mammals and their very low occurrence in the study area. Habitats 2 and 3 were gathered in the category ''open'' for analysing small mammal-habitat relationships.

The fit of log-linear models to the multiway contingency tables generated by the factors period (old-current), land use type or guild (forest-crops-scrub-urban or forest-open land-urban, respectively) and locality (Llerona, Marata, L'Ajuda and La Vola) were used to determine whether land uses or small mammal communities differed significantly between the two periods considered, and whether temporal changes differed among localities. The units of frequency counts were number of hectares for land use types and number of individuals found in pellets for guilds, respectively. This procedure is analogous to an ANOVA in which total variance in frequency data is partitioned into factors and factor interactions thus permitting tests of the significance of their effects (Everitt 1992).

The influence of land use changes on small mammal communities was analyzed by testing predictions from null models, a method more robust than conventional statistical test to deal with low sample sizes (Gotelli and Entsminger 2001). Statistical rarefaction was used for comparison of the small mammal community parameters between sampling periods. Rarefaction uses probability theory to derive expressions for the expectation and variance of species richness for a sample of a given size (Gotelli and Entsminger 2001), providing a meaningful interpretation of species composition and abundance within localities when temporal samples differed in the total number of individuals collected (Rowe 2007). The community indexes used were the Shannon diversity index (H) and the Dominance índex (D, the fraction of the collection that is represented by the most common species), as both show high stability (i.e. asymptotic behavior) even with low sample sizes. We used Ecosim 7.0 software (Gotelli and Entsminger 2001) to generate individual-based rarefaction curves of the community parameters (H and D) and the associated variance for the two sampling periods. We also used rarefaction to compare the landscape composition between the considered periods in every locality due to differences in the number of total cells analysed.

In order to determine whether the small mammal communities were related to the land use composition, redundancy analysis (RDA) was performed with CANOCO 4.5 for Windows (Ter Braak and Smilauer 2002; Leps and Smilauer 2003). Due to low sample size, the number of variables was reduced by gathering small mammals and habitats in three groups (forest, urban, and open). The canonical axes extracted explain which part of the variance in the small mammal community composition can be explained by the land use variables.

Results

The diet of the barn owl was mostly based on small mammal preys (93.6 % of all the preys consumed).

Small mammals were more frequent in the barn owl diet in recent than in old samples (Present: 97.03 % $\pm$ 3.53 SD; Old: 92.71 % $\pm$ 5.90 SD; Wilcoxon test: $Z = 1.82$, $p = 0.06$, $n = 4$). As a whole, 6,081 small mammal individuals from fifteen species were found in owl pellets (Table S2). Fourteen species were detected in the old samples, whereas only ten species were detected in current samples. Rarefaction analyses confirmed that species richness was higher in the old sample for the same number of individuals (Present: $R = 10$ species $\pm$ 0 (CI); Old: $R = 13.3$ species $\pm$ 2 species (CI); $n = 1{,}800$ individuals). Ten species decreased in frequency of appearance between periods (but only four were statistically significant), and the remainder five increased (Table S2).

Small mammal guilds changed their frequencies of occurrence between both study periods (Log-linear fit, Guild x Period interaction: $G^2 = 158.8$, d.f. = 2, $p < 0.0001$). As a whole, the open guild decreased by 13 % (Freeman-Tukey deviate: $G^2 = 32.9$, d.f. = 1, $p < 0.0001$), whereas both the forest and the synanthropic guilds increased by 7 % (Freeman-Tukey deviates: $G^2 = 21.5$, d.f. = 1, $p < 0.0001$ and $G^2 = 94.1$, d.f. = 1, $p < 0.0001$, respectively; Fig. 1). Changes in guild frequencies were not consistent across sampling localities, however (Guild × Period × Locality: $G^2 = 1317.1$, d.f. = 17, $p < 0.0001$, Table S3). Most localities showed the general trends described above, whereas one locality (La Vola) showed the opposite pattern (Fig. S1A, Table S3). Small mammal diversity tended to increase and dominance to decrease between periods (Fig. 1), although both trends were considered not significant (one-way ANOVA with randomization; $p = 0.24$ and $p = 0.19$, respectively).

Land-use changes were not consistent across localities for the period 1987–2002 either (Guild × Period × Locality: $G^2 = 7{,}606.5$; d.f. = 24; $p < 0.001$). Crops and urban areas showed the same pattern of change in all localities, with decreasing crop areas and increasing urban areas (Fig. 1; Fig. S1B). Forest areas increased and scrubs and meadows decreased in three areas, showing the opposite trend in the fourth, La Vola (Fig. S1B). Habitat heterogeneity (Shannon diversity Index) increased (Permutation test, $p = 0.023$) whereas dominance decreased during the study period with a marginally significant p value (Permutation test, $p = 0.057$).

The first axis extracted by redundancy analysis was significant (F-ratio = 17.4, $p = 0.036$; 81.3 % variance explained), and represented a gradient from open to forested localities (Fig. 2). The second axis added little variance explanation (1.6 %), but represented the main landscape changes observed between both sampling periods as it discriminated the old samples from the recent ones. This axis was mainly related to the amount of urban habitats. Redundancy analyses indicated that 82.9 % of the variance in the small mammal community composition was explained by land uses. The forward selection procedure after 499 permutations showed that

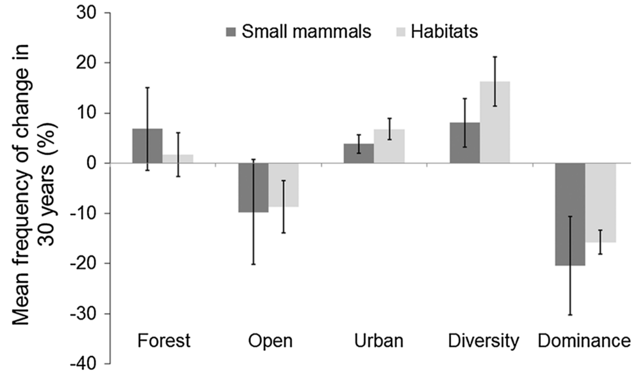

Fig. 1 Average frequency of change (% $\pm$ SE) per locality of small mammal guilds and their main associated habitats between 1977–1991 and 2011–2014

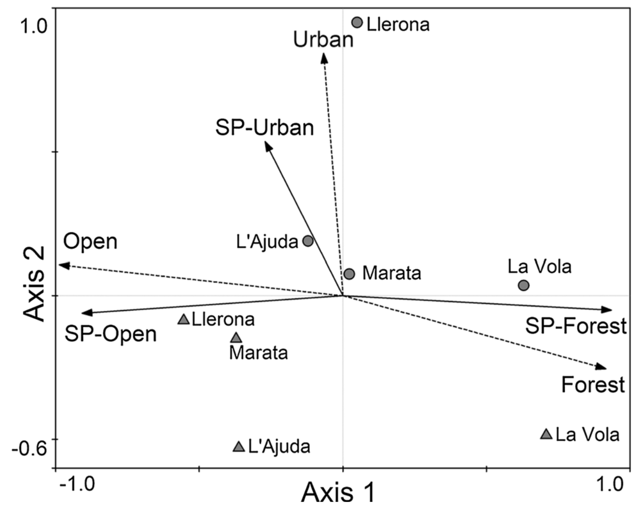

Fig. 2 Representation of the land uses (Open, Forest and Urban, *dashed lines*) and small mammal guilds (SP-, *solid lines*) in the two-dimensional space created by the first two axes extracted from the redundancy analysis. The location of the samples according to the period was also shown like *dots* (current) or *triangles* (old)

open habitats were the most influencing land use variables on small mammal community change (79 % of variance). Nonetheless, owing to the fact that open and forest variables were negatively correlated, changes of small mammal communities along the first axis were complementary. In any case, relationships among changes in small mammal guilds and in their associated habitats explained patterns of change in all localities, either following the most common trend linked to change from open to forest habitats or following the opposite (Fig. 2).

Discussion

Barn owl pellet analysis, a non-invasive sampling method, was able to detect significant shifts in the small mammal community composition and structure. The method has been proved efficient for detecting changes in the small mammal frequencies of occurrence in agricultural environments related to different farming practices (Cooke et al. 1996; Torre et al. 1997; Millán de la Peña et al. 2003; Rodriguez and Peris 2007), and is considered as a valuable method for assessing small mammal populations and their change over time (Love et al. 2000; Meek et al. 2012). Accuracy of the method is based on the well-established fact that barn owls are generalist predators of small animals whose diet closely track spatial and temporal changes in relative prey abundance (Tores et al. 2005; Bernard et al. 2010). Of course, such a track would not be perfect, as many other factors besides relative prey availability are expected to influence fine-scale variations in capture success and prey and habitat preferences (Embar et al. 2014). For instance, non-linear, type II and type III functional responses would imply saturation of responses above and/or below threshold values of prey availability (Holling 1965), and individual needs during e.g. breeding or even bird personality should also influence the exact relationship between diet and prey availability (Constantini et al. 2005), However, all these factors would have predicted mismatches between diet changes and land-use changes potentially influencing prey abundance rather than the close match found in our study. Besides, land use changes potentially affecting relative abundances of mammal guilds were measured only twice, and sample sizes were only moderate (four sites). Lack of strong effects of these sources of noise emphasized the strength of results, conclusions, and the proposal of using owl pellets to track small mammal community responses to global change.

In this study we have shown that small mammal changes over time documented with this method were strongly correlated with human-induced habitat changes, as expected from habitat preferences of the involved species. The decline of barn owls in the area (only half of the localities sampled during 1977–1991 were still occupied nowadays; Table S1) is also evident throughout Western Europe (Askew et al. 2007), and this fact may limit the applicability of the method to land-use changes that do not produce local extinctions of barn owls (e.g. complete substitution of open habitats by either closed forests or highy urbanized environments). However, we have also shown that the method produces clear-cut results even with small sample sizes, the four localities were barn owls survived the last 30-year period.

The localities studied can be considered as highly modified ecosystems regulated by human activities (agriculture-dominated ecosystems; Seiferling et al. 2014). Landscape changes from 1987 to 2002 were mostly consistent between localities. Crops decreased a 7.5 % on average (range 2–15 %), whereas urban areas increased a 6.8 % (range 4–13 %), following the patterns observed both in Catalonia (Estrada et al. 2004; Parcerisas et al. 2012) and throughout the Mediterranean Region (Debussche et al. 1999). Nonetheless, while forest cover increased in three localities, as in most Mediterranean regions (Debussche et al. 1999; Estrada et al. 2004), it decreased in La Vola, considered as a seminatural system (Seiferling et al. 2014). All these changes, although significant, were relatively small, and did not modify the general dominance of either open or forest habitats in the study localities. In spite of these small variations, patterns of change of small mammal species and guilds also differed among localities, closely tracking land-use changes according to mammal's habitat requirements. As a whole, the forest and synanthropic guilds increased a 7 % between both periods, whereas the open-land guild decreased by 13 %. *A. sylvaticus* increased in the three localities with increased forest cover, but decreased in the locality that experienced reduced forest cover between sampling periods. 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 (i.e. the whole sample). Parallel trends in land-use heterogeneity (diversity and dominance) and small mammal diversity trends also supported a key role of land-use change, as diversities increased and dominances decreased during the study period. Since heterogeneous environmental conditions provide more niches and resources, an increase in species diversity was to be expected (Tews et al. 2004). However, a trivialization of communities was observed (Szpunar et al. 2008), with increased frequencies of synanthropic species without any conservation value (i.e. *Rattus* sp., *Mus musculus*).

Land-use changes are being increasingly considered as key drivers of biodiversity change, especially at local scales (Doblas-Miranda et al. 2015 and references therein). Climate is warming in the study area (Peñuelas and Boada 2003; Llebot 2012), but the variations observed in the rodent community between sampling periods were opposite to expectations from climate change effects. Mediterranean species, which are adapted to warmer and drier climate regimes, showed a significant decrease (*M. duodecimcostatus, C. russula* and, to a lesser extent, *M. spretus* and *S. etruscus*), rather than the expected increase under current climate conditions. This pattern may be attributed to the loss of open habitats due to urbanization and afforestation. Conversely, forest-dwelling species adapted to cool and humid climates (*A. flavicollis* and *M. glareolus*) increased rather than decreased, most likely due to the fact that afforestation may favor its expansion across moist forest, a pattern that will ameliorate changes of global warming in small mammal communities (Rowe 2007). A similar pattern has been recently demonstrated for Spanish birds (Seoane and Carrascal 2008). Our results are just opposite for common species, but may suggest that the decline of habitat generalist species with mid-European requirements, such as *S. araneus* and *S. minutus*, may be associated to climate change effects. In fact, these species have been shown to decline in Italy likely as a consequence of climate warming (Szpunar et al. 2008).

Large samples of small mammal remains can be easily obtained from barn owl roosts (Love et al. 2000), so that community changes can be monitored with a high degree of certainty. The method perform better than traditional live-trapping due to lower effort and much weaker species-specific sampling biases (Millán de la Peña et al. 2003; Torre et al. 2004; Avenant 2005; McDonald et al. 2013). Recent work has shown that frequencies of occurrence of small mammals in barn owl's diets were strongly correlated with frequencies in the diet of generalist forest predators (genets *Genetta genetta*) along environmental gradients (Torre et al. 2013), so that forest-dwelling species can also be monitored from its presence in barn owl diets, although perhaps less accurately than open-habitat species. So, changes in the frequencies of occurrence of forest species in the barn owl diet can be also interpreted as responses of prey species to environmental variations due to the particular species requirements (Torre et al. 2015). Summarizing, the use of non-invasive pellet analyses can be especially suitable for detecting small mammal community changes and for analyzing its human-induced causes because of easy replication in time, as far as barn owl populations remain.

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