

Article

Long-term data from a small mammal community reveal loss of diversity and potential effects of local climate change

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Abstract

Climate change affects distribution and persistence of species. However, forecasting species' responses to these changes requires long-term data series that are often lacking in ecological studies. We used 15 years of small mammal trapping data collected between 1978 and 2015 in 3 areas at Doñana National Park (southwest Spain) to (i) describe changes in species composition and (ii) test the association between local climate conditions and size of small mammal populations. Overall, 5 species were captured: wood mouse *Apodemus sylvaticus*, algerian mouse *Mus spretus*, greater white-toothed shrew *Crocidura russula*, garden dormouse *Eliomys quercinus*, and black rat *Rattus rattus*. The temporal pattern in the proportion of captures of each species suggests that the small mammal diversity declined with time. Although the larger species (e.g., *E. quercinus*), better adapted to colder climate, have disappeared from our trapping records, *M. spretus*, a small species inhabiting southwest Europe and the Mediterranean coast of Africa, currently is almost the only trapped species. We used 2-level hierarchical models to separate changes in abundance from changes in probability of capture using records of *A. sylvaticus* in all 3 areas and of *M. spretus* in 1. We found that heavy rainfall and low temperatures were positively related to abundance of *A. sylvaticus*, and that the number of extremely hot days was negatively related to abundance of *M. spretus*. Despite other mechanisms are likely to be involved, our findings support the importance of climate for the distribution and persistence of these species and raise conservation concerns about potential cascading effects in the Doñana ecosystem.

Key words: climate change, count data, N-mixture models, rodents, Spain.

Our planet is experiencing dramatic environmental and climatic change. In the past 100 years, anthropogenic activities have raised the concentration of greenhouse gases in the atmosphere, leading to an increase in the Earth's average annual temperature of 0.6 °C (Parmesan

2006), threatening the integrity of ecosystems (Walther et al. 2002). Besides global warming, extreme and sudden changes of seasonal temperatures are currently occurring worldwide and, in particular, in the Mediterranean region (Barros et al. 2014). In this area, climate models

predict increasing mean and maximum temperatures and a reduction in precipitation (Giorgi and Lionello 2008).

Recent studies on ecological effects of climate change have mainly focused on how they affect the species geographical distribution, physiology, phenology, and local abundances (Jonzen et al. 2006; Parmesan 2006; Teplitsky et al. 2008; Myers et al. 2009). As well as long-term trends, unpredictable and fast changes in local climate conditions over short periods (so-called “extreme events”) have an important but often overlooked effect on the distribution and persistence of species (Easterling et al. 2000; Moreno and Moller 2011). Many studies have shown that the species geographical distributions are already changing in response to global warming, in particular by shifting toward higher latitudinal and altitudinal ranges (Walther et al. 2002; Chen et al. 2011). Changes of duration, seasonality, and intensity of rainfall have also been related to life-history changes among mammals, birds, and amphibians (Carey and Alexander 2003; Moritz et al. 2008; Altwegg and Anderson 2009).

Because of their short lifespan and fast life-history responses to environmental changes, small mammals are ideal model species for studying climatic effects on animal population dynamics. Furthermore, they play an important role in their ecosystems as seed dispersers, predators, and main preys of several mammalian carnivores and raptors (Delany and Delany 1974). Recently, it has been shown that the elevational limits of many small mammal species in the Yosemite National Park (N America) have shifted northward consistent with the $\sim 3^{\circ}\text{C}$ increase of minimum temperature during the last century (Moritz et al. 2008). A study (Myers et al. 2009) with collections’ records of small mammals in the Great Lakes region has shown a marked decline in the presence of northern species accompanied by an increase of southern species over a period similar to the present study. Others have shed light on some mechanisms that modulate the effects of climate on small mammals dynamics. For instance, Kausrud et al. (2008) found that reduction and duration of the subnivean space induced by warming-climate had a negative impact on survival and reproductive performance of Fennoscandian rodents consequently altering their cycles. Moreover, studies from paleontological data have linked ancient climate change on the distribution of small mammal species (Sesé Benito 1994; Casanovas-Vilar et al. 2010).

The present study evaluates the long-term species composition and the possible role of local climate change in the small mammal community at the Doñana National Park (DNP), a large protected area located in southwest Spain which is part of the Mediterranean Basin hotspot. According to the hypothesis of climate effect on species distribution and abundance, we expect that species’ abundance vary in response to long-term climate change consistently with their climatic requirements. Therefore we predict that, with local climate warming, the abundance of species for which Doñana represents the southern limit of the distribution range will decrease whereas abundance of species at the northern limit will increase. We used 15 years of trapping data from a period spanning 37 years (1978–2015). First, we described the community dynamics as shown by the proportion of species captures for each campaign. Then, we tested the relationship between climate variation and temporal changes in the small mammal species abundances.

Materials and Methods

Study area

This study was conducted in DNP (37°N , $6^{\circ}10'\text{W}$), a plain area (0–106 m a.s.l.), located in the southwest of the Iberian Peninsula,

in the Guadalquivir River mouth on the Atlantic ocean. This area is one of the most important natural reserves in Europe, designated as a Biosphere Reserve in 1980 with a special protection status. The climate is Mediterranean sub-humid with 2 marked seasons: wet mild winters (mean temperature in January $\approx 10^{\circ}\text{C}$) and dry warm summers (mean temperature in August $\approx 25^{\circ}\text{C}$) (Suso and Llamas 1993). The rainy period occurs between October and April, with a peak in December–January (yearly average precipitation $\approx 600\text{ mm year}^{-1}$). Three main biotopes can be distinguished in DNP: (1) marshes on a clay area with a regular flood pattern during winter; (2) mobile sand dunes parallel to the sea coast; and (3) scrubland that, according to proximity to the water table, is either xerophytic Mediterranean scrubland (drier), or hygrophytic Atlantic scrubland (more humid) (Moreno and Kufner 1988).

The present study was located in the xerophytic Mediterranean scrubland, which is 65–70% covered by xerophytic shrubs (e.g., *Halimium halimifolium*, *Cistus* spp., *Ulex* spp., *Genista anglica*, *Lavandula stoechas*, *Rosmarinus officinalis*, and *Thymus mastichina*). Trapping was carried out in 3 different areas (Figure 1) named “San Agustín”, “Las Pajareras”, and “Las Monjas”. During the study period the land use of these areas was not altered so that no artificial environmental changes occurred.

Study species

The small mammal community is characterized by low species diversity compared with other areas in the European mainland (Moreno and Rouco 2013), and is limited to 8 species: garden dormouse *Eliomys quercinus*, black rat *Rattus rattus*, wood mouse *Apodemus sylvaticus*, algerian mouse *Mus spretus*, mediterranean pine vole *Microtus duodecimcostatus*, western hedgehog *Erinaceus europaeus*, greater white-toothed shrew *Crocidura russula*, and pygmy white-toothed shrew *Suncus etruscus* (Palomo et al. 2007). The first 5 are rodents and the others insectivores. Throughout the study period, *E. europaeus* and *S. etruscus* were never caught as the used traps are not appropriate for these species.

For *E. quercinus*, a generalist species present in the Mediterranean scrubland (Moreno 2002), Doñana represents the southern limit of its geographical distribution. *Crocidura russula* is a small insectivorous rodent adapted to Mediterranean climate and widely distributed in Europe and North Africa (LópezFuster 2007). *Rattus rattus* is a very widespread species with an average body mass of 300 g. *Apodemus sylvaticus* shows a wide distribution throughout the western Palearctic with a southern limit corresponding to the west Mediterranean coast of Africa (Montgomery 1999). *Mus spretus* is associated with the Mediterranean climate and can survive even very dry conditions that no other rodent species can (Palomo et al. 2007). *Apodemus sylvaticus* and *M. spretus* overlap in their distribution range, and in habitat and food preferences (Bauduin et al. 2013). However, *M. spretus* prefers open habitats, whereas *A. sylvaticus* prefers greater vegetation cover (Khidias et al. 2002).

Trapping

Each trapping area was approximately 1 hectare, and separated from the other sites by at least 1,000 m to ensure independence of data (i.e., no interchange of individuals among sites, Kufner and Moreno 1989). Sites were of similar soil type and distance to marshes. The trapping method was consistent throughout the study period. We used 2 types of live-traps that yielded similar capture rates (personal observation): Sherman’s live-traps and similar traps

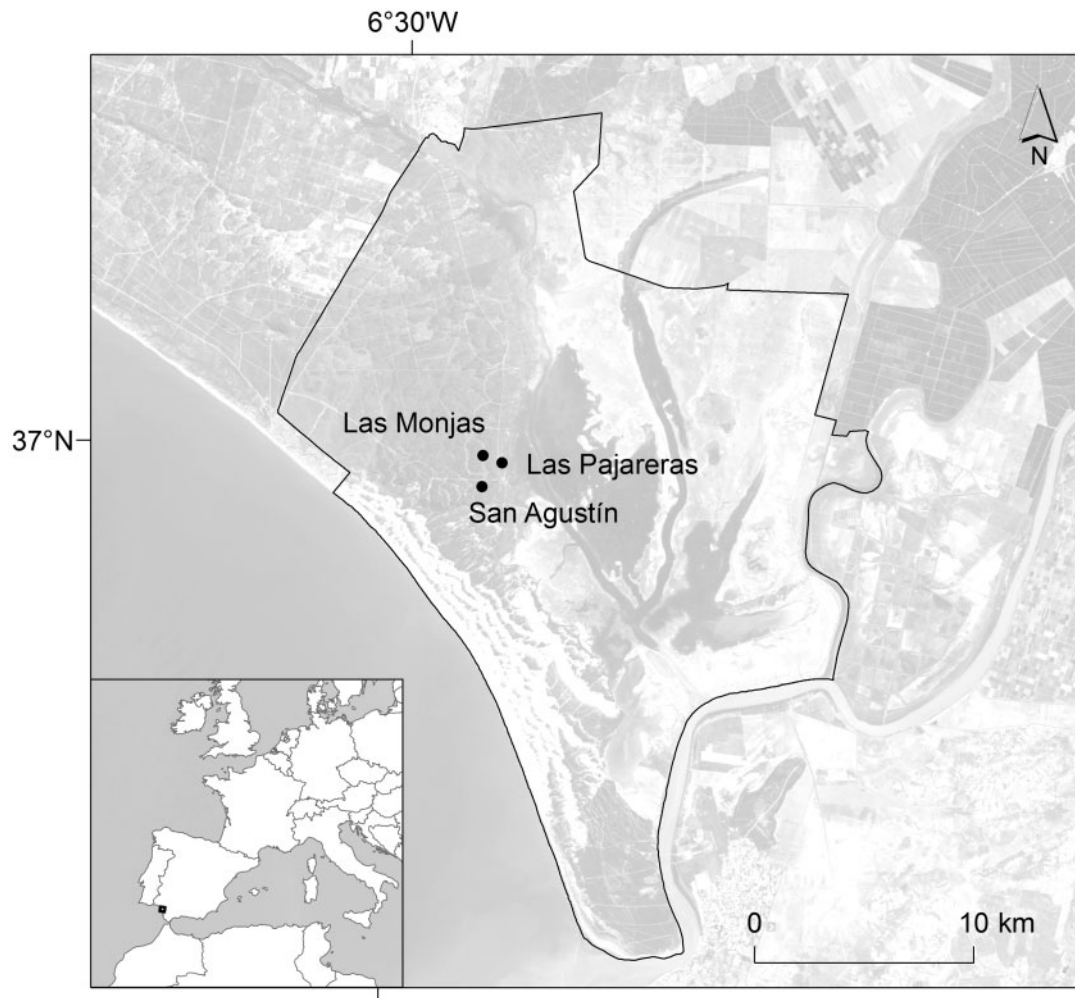


Figure 1. Study area. The 3 study sites position within the DNP (delimited by borders) located in southern Spain.

manufactured by the technical staff. All the traps were baited with bread soaked in fish oil and placed across a grid, 15 m apart. They were installed just before sunset of the first day and checked each day 2 h after sunrise. Each trapped specimen was individually marked when first captured. Three methods were used to mark animals: toe-clipping (1978–2007), subcutaneous microchip (2005–2007), and color points micro-tattooing in the tail (2012–2015).

Trapping was performed through 15 years within a period spanning 37 years (1978–2015). We carried out 5 *trapping campaigns*, that is, periods of consecutive years of sampling funded by different projects: 1978–1981 (Moreno 1984a), 1984–1985 (Kufner 1986), 1986–1987, 2005–2007, and 2012–2015. Trapping data were collected over the 4 seasons except from 2012 onward when sampling was not performed on summer due to the very small number of captures typically made in that season. During each season and site there was a variable number of *trapping sessions* which in turn consisted of a variable number of consecutive *trapping days* over which data were collected.

We focused on data at 2 different time-scales: (i) for the community species composition analysis we used the total number of captures for each species found at each *trapping campaign*, whereas (ii) for the analysis of species abundances at each site we used the number of captured individuals at each *trapping day* in winter. For the latter analysis, we focused on data from a single season because we

needed to define yearly time-intervals short enough to assume that the population size remained approximately constant. We used data from winter because of the higher number of captures and of years for which trapping data were available. For the analysis of species abundances at each site we disposed of a variable number of years (see [Supplementary Table S1](#)) as well as of *trapping sessions* (San Agustín, min: 1, max: 4; Las Pajareras, min: 1, max: 2; Las Monjas, min: 1, max: 1) and of consecutive *trapping days* (San Agustín, min: 3, max: 7; Las Pajareras, min: 4, max: 7; Las Monjas, min: 5, max: 7). Different numbers of traps were used in each area over the entire study period (min: 50, max: 150 traps/day, see [Supplementary Table S1](#) for details) but we accounted for this variation in the statistical analyses.

Community species composition analysis

To describe long-term changes at the community level, we used an index of relative abundance consisting of the number of captures for each species per 1,000 traps/days-of-sampling (Nelson et al. 1973) at each *trapping campaign*.

Species abundances analysis

Methodological issues typically hinder the study of climate effects on dynamics of populations, species, and communities. First, these

Box 1. HMs in a nutshell

According to the definition that Kery and Royle (2016) propose in their book, an HM is a sequence of models ordered by their conditional probability structure. Typically, an HM involves at least one model (or level of the HM model) that refers to a latent (unobserved) variable. The latent variable can consist of: (i) a random effect, where an ecological measurement like presence/absence or count replicates are more similar within than among groups (e.g., site) or (ii) a state variable like the site-specific (real) presence or absence of a species or its population size. The first example resembles the classical random effects models (also called multi-level, or mixed models) with an unobservable latent variable which accounts for non-independence and similarity of sampling replicates within groups. Here, we focus on HMs as that described in the second example where the latent variable is the outcome of natural processes and therefore consists of a real quantity as the occupancy state or the population abundance at a certain site. Royle (2004) proposed an HM for count replicates collected at a number of sites through a period short enough to assume that population sizes do not vary over the study period. This 2-level HM considers the observed counts as a function of an observation process which in turn depends on the population size at each site. In mathematical terms it is:

$$y_{ij}|N_i \sim \text{Binomial}(N_i, p),$$

where y_{ij} , that is the counts at site i at the j th occasion is conditional on the local population size (N_i) and follows a binomial distribution where p is the individual-level probability of detection. The local population size follows a distribution such as:

$$N_i \sim \text{Poisson}(\lambda).$$

Notably, N-mixture models like that illustrated allow for the direct estimation and hypotheses-testing of the factors that affect the spatial structure of abundance (λ) and/or the detection probability (p).

studies require long-term data collected over a time span broad enough to include climate variations. Second, analyses of counts and presence/absence data should account for imperfect detection to avoid spurious findings (Mackenzie and Kendall 2002; Dénes et al. 2015). Even where encounter histories of individually marked animals are available, estimates of population size by capture-mark-recapture analyses (Lebreton et al. 1992) may be difficult to be obtained because of data sparseness and/or limited sample sizes. In these cases, another class of models, so-called Hierarchical Models (HMs, see Mackenzie and Kendall 2002; Kery and Royle 2016) represent a valid alternative if spatial and/or temporal replicates (presence/absence or counts) are available. These models can tease apart variation of the latent (unobserved) variable/s (e.g., abundance, species occurrence) by variation in the observation process (e.g., imperfect detection of individuals or species). More details on the conceptual framework behind HM are given in Box 1.

We adapted the Royle (2004) HM to the case where temporal (among-years) instead of spatial replicates were drawn so that species' abundance estimates at 1 site were obtained. Due to the short lifespans of the studied species and to the large time intervals between *trapping campaigns* we assumed that the within-species temporal correlation among population sizes was negligibly small. For this analysis, we did not use data collected during the 1986–1987 *trapping campaign* because for that period we only knew the number of captures for each species per 1,000 traps/days-of-sampling. Due to the small number of captures for some species, we could analyze data from only 3 species: *M. spretus*, *A. sylvaticus*, and *E. quercinus* (this species at San Agustin only). HM analyses were run in R (R Core Team 2013) using the function “*pcount*” from the “*unmarked*” package (Fiske and Chandler 2011). A separate analysis was run for each area and species (R code in Supplementary Appendix S1).

As predictors of abundance in winter, we considered local climatic data collected by a weather station in close proximity to the study areas (downloaded from <http://icts-rbd.ebd.csic.es/>) in the

immediately preceding autumn, during which both *A. sylvaticus* and *M. spretus* have a reproductive peak at DNP (Moreno 1984b). We considered: (i) the average daily mean temperatures, (ii) the total rainfall, and (iii) the number of extremely hot days, that is, with a mean temperature higher than the 90th percentile of the daily mean temperatures in autumn calculated throughout the entire study period (Barros et al. 2014). Over this time, the autumn mean temperatures showed an increasing trend, the total rainfall decreased (Supplementary Figure S1), and the number of extremely hot days increased (Supplementary Figure S2), as expected by climate change predictions (Thibault and Brown 2008). As predictors of individual capture probability we considered 3 variables: daily rainfall and mean temperature during trapping days and number of traps.

Model selection

For each case study (area and species), we used Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002), considering the number of trapping days as sample size (see details in Supplementary Appendix S1). To avoid inflated type I error, we considered models separated by less than 2 AICc as equally plausible (Burnham and Anderson 2002). First, we modeled the capture probability by considering models with all the possible combinations of the above mentioned predictors (3, 2, 1, or no effect) and holding the abundance constant (only intercept). Then, we retained the model structure for the capture probability from the model with the lowest AICc value and used it to model abundance. For the sake of parsimony, we only considered models with one abundance predictor for each model. By doing so, we finally attained a list of models sorted by growing AICc values, each one representing a specific hypothesis about abundance changes. This approach allowed us to keep the number of tested models as low as possible and address simple hypotheses (Burnham and Anderson 2002).

For the first 3 winters at San Agustin, we disposed only of the total number of individuals captured during each *trapping session*.

Table 1. GOF analyses of the best model for *Apodemus sylvaticus*, *Mus spretus*, and *Eliomys quercinus* in each sampling area: San Agustin (SA), Las Pajareras (PJ), and Las Monjas (MN)

Species	Sampling area	t_0	mean ($t_0 - t_B$)	StdDev ($t_0 - t_B$)	Pr ($t_B > t_0$)
<i>Apodemus sylvaticus</i>	SA	33.645	4.18	10.11	0.320
	PJ	33.0	-15.7	21.2	0.802
	MN	35.1	16.5	8.54	0.079
<i>Mus spretus</i>	SA	1,384	1,284	73.5	0*
	PJ	1,409	1,305	45.2	0*
	MN	41.7	-33.2	23.8	0.931
<i>Eliomys quercinus</i>	SA	39.2	25.1	8.4	0.0198*
	PJ	—	—	—	—
	MN	—	—	—	—

Notes: Values of $\text{Pr}(t_B > t_0) > 0.05$ (remarked by *) indicate lack of > model fit to the data. t_0 , statistic computed for the real data; t_B , statistic computed for the bootstrap samples; $\text{StdDev}(t_0 - t_B)$, difference between standard deviation of t_0 and t_B .

We obtained 100 plausible data sets for which the first 3 years *trapping day* counts of individuals were drawn by a multinomial distribution whose sum matched that of individuals captured at the *trapping sessions* level (details in [Supplementary Appendix S1](#)). Model selection was performed for each data set separately.

Goodness of fit

We used parametric bootstrapping (function “parboot” in “unmarked”) to test the goodness of fit (GOF) of the best model (Fiske and Chandler 2011). The GOF test allows validation of the model and provides an estimate of how well a model fits with a set of observations (Burnham and Anderson 2002). We used a significance threshold of 0.05 as a cutoff for determining adequate model fit, which was attained in only 4 cases: for *A. sylvaticus* in the 3 areas and for *M. spretus* at Las Monjas (Table 1).

Results

Community species composition

Species proportional composition has varied substantially over the study period (Figure 2). *Eliomys quercinus* showed a marked decline between the 1978–1981 and 1986–1987 campaigns, after which the species was never trapped again. *Rattus rattus* was captured only in the first campaign. Low numbers of *C. russula* were captured during all the campaigns except the last (2014–2015), when it was not captured at all. Although the number of *A. sylvaticus* trappings was substantial throughout the first 3 campaigns, it declined markedly in the last 2 (from 2005 onward). The only species that showed a marked increase over the 5 campaigns was *M. spretus*, which represented only a small fraction of total captures in the first campaign to become the most captured species in the last 2 (2005–2015).

Species abundances

For *A. sylvaticus* at San Agustin, the inverse relationship with mean temperature was selected as the most parsimonious model for abundance (Table 2). However, a positive relationship with rainfall and the number of extremely hot days could not be ruled out ($\Delta\text{AICc} < 2$). Based on the lowest AICc model, we estimated the mean abundance for each sampling year that varied between a minimum of 2.05 individuals ($SE = 1.55$; Temperature = 16.86°C) and

a maximum of 4.95 individuals ($SE = 3.971$; Temperature = 15.19°C) (Figure 3).

At Las Pajareras and Las Monjas, we found strong support for a model that accounted for a positive relationship of rainfall with abundance of *A. sylvaticus* (Table 2). From these models, we estimated at Las Pajareras a minimum abundance of 2.29 individuals ($SE = 1.14$; rainfall = 91.8 mm) and a maximum of 92.59 individuals ($SE = 22.26$; rainfall = 338.5 mm) and at Las Monjas a minimum of 12.06 individuals ($SE = 9.86$; rainfall = 37.32 mm) and a maximum of 88.99 individuals ($SE = 22.13$; rainfall = 103.85 mm) (Figure 3).

Finally, we found that abundance of *M. spretus* at Las Monjas was inversely related to the number of extremely hot days in autumn (Table 2). From this model, we obtained a minimum abundance of 20.40 individuals ($SE = 10.83$; number of extremely hot days = 16) and a maximum of 88.07 individuals ($SE = 39.61$; number of extremely hot days = 6).

Species capture probability

At San Agustin, we found that for some of the simulated data sets (see Materials and Methods), the capture probability was inversely related to the higher daily mean temperature, while in others it was positively related also to the number of traps (Supplementary Table S2). The estimated daily average capture probability for *A. sylvaticus* at this site was 0.164 ($SE = 0.073$).

At Las Pajareras, the best model for capture probability of *A. sylvaticus* accounted for a positive relationship with the number of traps (Supplementary Table S3). From this model, we estimated an average daily capture probability that resulted to be the highest we found (0.524; $SE = 0.073$) among all the species and sites. For *A. sylvaticus*, we found a positive relationship of number of traps on capture probability also at Las Monjas (Supplementary Table S4). The average daily probability of capture was 0.223 ($SE = 0.096$).

For *M. spretus* at Las Monjas, the capture probability was inversely related to the number of traps (Supplementary Table S5) and the average daily probability of capture was 0.454 ($SE = 0.084$).

Discussion

Trapping records indicate that from late 1970s to the present time the small mammal community at DNP has exhibited a marked change in species composition. In the last 4 years *M. spretus*, the species most adapted to dry conditions, accounts for almost all captures. In addition, for all the cases where sufficient data were available, we found a relationship between local climate change and abundance (*A. sylvaticus* in the 3 study areas and *M. spretus* in 1). Simultaneously, there was a trend toward increased temperatures and decreased rainfall (Supplementary Figures S1 and S2). Although other non-exclusive environmental factors are likely to be involved, our findings support the hypothesis that long-term climate change played a role in the local small mammals population dynamics.

Climate effect hypothesis

Climate change may affect individuals and populations either directly or indirectly (Myerud et al. 2002). Indeed, physiological mechanisms can be directly triggered by climate change (Parmesan 2006). Besides, indirect climate effects may operate by affecting the species' ecological niches by means of changes in the environment where they live or in the interspecific relationships (Tylianakis et al. 2008; Gilman et al. 2010). Climate warming is affecting the

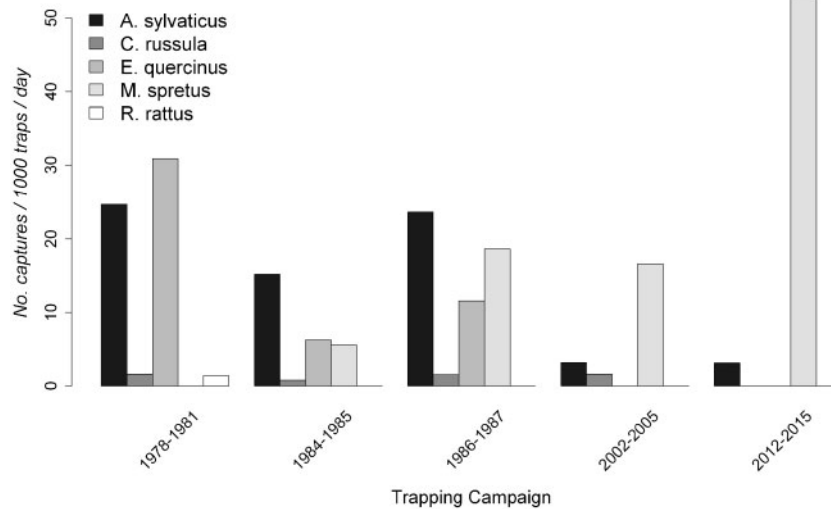


Figure 2. Number of captures (per 1,000 traps/day) by species for each trapping campaign.

Table 2. Modeling abundance changes for *Apodemus sylvaticus* and *Mus spretus*

Species	Sampling area	lam (Int)	lam (rain)	lam (temp)	lam (tmextr)	df	log L	AICc	Δ AICc	AICc weight
<i>Apodemus sylvaticus</i>	SA	1.241	—	-0.343	—	4.27	-56.817	122.836	0	0.429
		1.378	—	—	-0.058	4.27	-57.211	123.623	0.787	0.288
		1.384	0.046	—	—	4.27	-57.234	123.669	0.833	0.283
		1.778	—	—	—	3.27	-88.888	184.723	61.887	0
	PJ	1.141	1.708	—	—	4	-37.984	85.146	0	0.926
		0.599	—	—	-1.123	4	-41.041	91.259	6.113	0.043
		0.871	—	1.213	—	4	-41.411	91.998	6.851	0.030
	MN	1.208	—	—	—	3	-46.392	99.469	14.322	0.001
		3.392	0.911	—	—	4	-31.449	72.438	0	0.676
		4.338	—	—	—	3	-34.018	74.926	2.488	0.195
3.927		—	0.475	—	4	-33.634	76.807	4.369	0.076	
<i>Mus spretus</i>	MN	4.288	—	—	-0.075	4	-33.994	77.527	5.089	0.053
		3.718	—	—	-0.615	4	-47.061	103.661	0	0.872
		2.001	0.530	—	—	4	-49.777	109.092	5.431	0.057
		2.714	—	-0.994	—	4	-49.934	109.406	5.745	0.049
		2.067	—	—	—	3	-52.106	111.101	7.440	0.021

Notes: Models are ranked by Akaike's Information Criterion corrected by small sample size (AICc); the lowest value of AICc corresponds to the best-fitting model. Lam, parameter value; df, number of estimated parameters; log L, logarithm of maximum likelihood; Δ AICc, difference between the AICc of the current model and the AICc of best model; AICc weight, Akaike weight for each predictor; int, intercept; temp, mean temperature in autumn; rain, cumulative rainfall in autumn, tmextr, number of days with extremely hot temperature in autumn. Note that for *A. Sylvaticus* at San Agustín a mean value for each parameter has been reported from 100 simulated data sets. For this reason, the number of estimated parameters (df) may be not an integer.

distribution of species toward higher latitudes and elevations (Moritz et al. 2008; Myers et al. 2009; Chen et al. 2011). As an example, a recent study based on barn owl *Tyto alba* pellet analysis from multiple locations in Italy showed a consistent increase of xerothermophilic species in the small mammal communities since late 70s (Szpunar et al. 2008). Coherent with this scenario we found that, *E. quercinus*, a species more related to colder climates than that of Doñana which represents the southern limit of its distributional range, has gradually disappeared from the trapping records. Conversely, *M. spretus*, distributed in the warm climates of southwest Europe and the western Mediterranean coast of Africa, currently represents nearly all of the species captured. The hypothesis

of climate effect was also supported by the observed relationships between abundances of *A. sylvaticus* and *M. spretus* with, respectively, the amount of rainfall and the number of extremely hot days in the preceding autumn. Our study cannot reveal which mechanisms, if any, modulated the effects (direct or indirect) of climate variation on the DNP small mammal diversity and abundances. It is possible that their fate at Doñana depended on different physiological responses to climate change (Chen et al. 2011). For instance, lower rainfall during the reproductive peak (autumn) might have determined a reduction in the undergrowth and shrubs that are crucial for *A. sylvaticus* and not for *M. spretus* which prefers open habitats (Khidias et al. 2002).

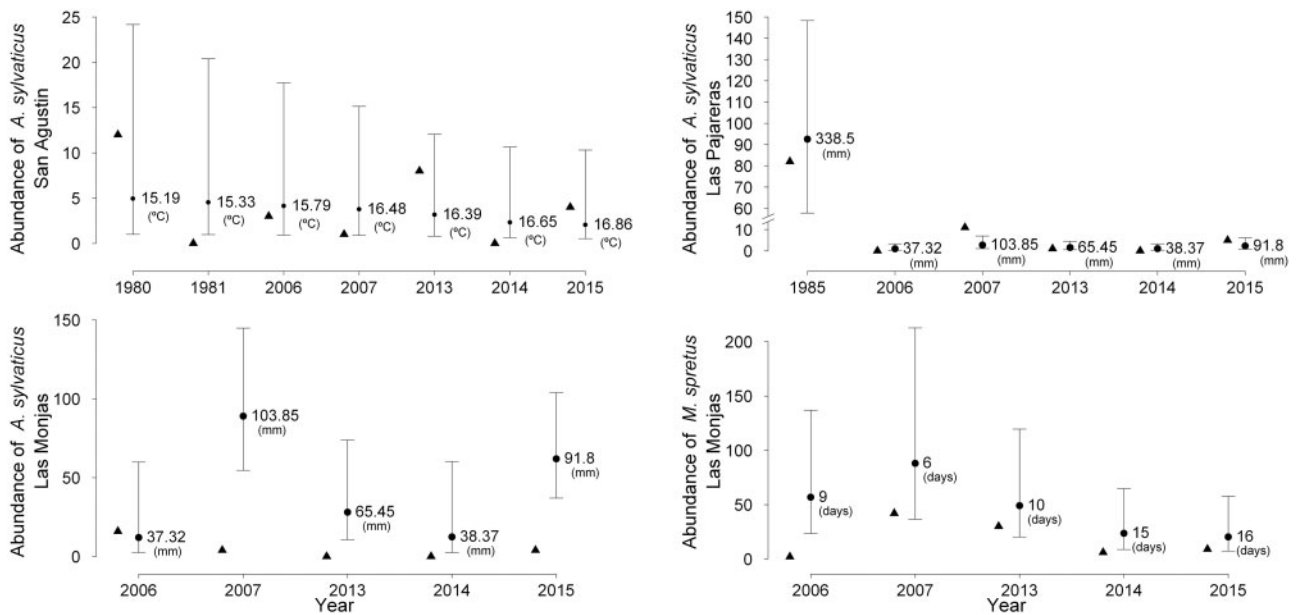


Figure 3. Predicted abundance (full black circles), and total captures (full black triangles) for *Apodemus sylvaticus* and *Mus spretus*. Abundance was estimated by the lowest AICc abundance model. Predictors of species abundance were: (i) for *A. sylvaticus* at San Agustín the daily mean temperature, (ii) for *A. sylvaticus* at Las Pajareras the total autumn rainfall, (iii) for *A. sylvaticus* at Las Monjas the total autumn rainfall, and (iv) for *Mus spretus* at Las Monjas the number of extremely hot days in autumn. Beside each point the estimated value of the corresponding predictor is shown.

Other hypotheses

We cannot discard that other processes could have been involved in the observed changes in the small mammal diversity and abundances. At DNP small mammals play a key role in the trophic chain being the secondary prey of many mammalian carnivores and raptors (Kufner 1986) after rabbits *Oryctolagus cuniculus*. In the late 1980s, a greater than 60% decline in the rabbit population at DNP was caused by an outbreak of rabbit hemorrhagic disease (Delibes-Mateos et al. 2008) and small mammals have gained importance as a food resource for other predators (e.g., for the Iberian lynx, Palomares et al. 1996). Therefore, the observed changes in the DNP small mammal community might have resulted also from top-down control (Palomares et al. 1995), a hypothesis that we could not test due to lack of suitable data about time-changing predation pressure on these species.

Cascading effects

The observed reduction of small mammal diversity and abundance should warn ecologists and conservationists against the possible cascading effects this might cause in the Doñana ecosystem. Such a negative impact on ecosystem may occur by altering the dynamic of its predators and other ecological roles of small mammals in the ecosystem (e.g., seed dispersal). For instance, a recent marked decline of wild rabbits in Spain has been shown to reflect higher number of road-killed (due to increased displacements), and lower breeding success of, Iberian lynx *Lynx pardinus* (Delibes-Mateos et al. 2014).

Apodemus Sylvaticus

The positive association between rainfall and *A. sylvaticus* abundance was consistent in all 3 areas, regardless of any difference in study period and habitat. In the San Agustín area, the lowest AICc model for abundance was for the negative association with increased mean temperature; nonetheless, the positive relationship with rainfall was also supported. The positive effect of rainfall is in line with

findings from other studies on small mammals in arid and semi-arid regions (Lima et al. 2002; Díaz et al. 2010). A study conducted in the Mediterranean coast of the Iberian Peninsula suggested the positive effect of rainfall on both abundance and reproduction of *A. sylvaticus* (Díaz et al. 2010) which may be explained by higher availability of food resources (vegetative growth, enhanced seed production, and accessibility).

Mus spretus

The number of extremely hot days correlated negatively with the abundance of *M. spretus* at DNP. Although caution is needed as data from only 5 years were modeled, this finding is surprising as *M. spretus* is adapted to high temperatures (Palomo et al. 2009). However, extreme high temperatures are known to be a cause of heat stress in birds (Jenouvrier 2013) and even mortality for some species of mammals (Greenville et al. 2012). Although the ecological impacts of extreme events are still poorly understood (Thibault and Brown 2008), it has been proposed that they might turn local systems into ecological traps by increasing the extent of trophic mismatches (Jiguet et al. 2011). In the future, extreme events are going to increase in multitude and magnitude (Easterling et al. 2000); this pattern was already evident at DNP for the study period (Supplementary Figure S2). We encourage that further studies on small mammal diversity at Doñana explicitly address the potential effects of extreme climatic events.

Counts: abundance and detectability

Although often not appreciated in past ecological research, counts can provide little information on ecological processes if the level of detectability is not maintained over time and space. HMs overcome this problem by accounting for changes in the observational process (Kéry and Royle 2016). HMs are gaining popularity among ecologists as a robust approach for studying changes in abundance and distribution also with historic records (see e.g., Iknayan et al. 2014).

Using HMs, we found that probability of capture varied according to the number of traps or daily mean temperature. Although such effects were in the expected directions (negative effect of temperature and positive of number of traps) for most cases, we cannot explain why the capture probability for *M. spretus* at Las Monjas decreased with an increasing number of traps. We cannot discard it was a stochastic result of limited data set rather than reflecting a causal effect.

Final remarks

Albeit other processes such as top-down control and species competition were likely to be involved, our findings support a relationship between changes in the local climate conditions and small mammal community whose diversity declined remarkably at DNP. Such a reduction in diversity and abundance of small mammals is alarming especially for species like, among others, *T. alba* and *Genetta genetta* whose diet, breeding success, and other ecological parameters depend on small mammals abundance.

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Supplementary material

Supplementary material can be found at <http://www.cz.oxfordjournals.org/>.

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