Contents lists available at ScienceDirect





Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Global change effects on Mediterranean small mammal population dynamics: Demography of Algerian mice (*Mus spretus*) along land use and climate gradients



Ignasi Torre ^{a,*}, Xavier Puig-Montserrat ^a, Mario Díaz ^b

^a BiBio Research Group, Natural Sciences Museum of Granollers, C/ Francesc Macià 51, E-08402 Granollers, Spain

^b Department of Biogeography and Global Change (BGC-MNCN-CSIC), National Museum of Natural Sciences, C/ Serrano 115 Bis, E-28006 Madrid, Spain

HIGHLIGHTS

G R A P H I C A L A B S T R A C T

- Modelling effects of global change drivers on demography may improve predictive power.
- Mediterranean species can be favoured by warming but affected by land use change.
- Population dynamics of Algerian mice was disturbed by both climate and land use change.
- Mice abundance declined while occupancy was more resilient to change.
- Negative land use change effects overcompensated positive effects of climate warming.

ARTICLE INFO

Editor: Rafael Mateo Soria

Keywords: Afforestation Climate warming Interacting global change drivers Land abandonment Occupancy analyses Population size



ABSTRACT

Climate and land use change are key global change drivers shaping future species' distributions and abundances. Negative interactions among effects of drivers can reduce the accuracy of models aimed at predicting such distributions. Here we analyse how climate and land use affected population dynamics and demography of the Algerian mouse (*Mus spretus*), an open-land thermophilic Mediterranean small mammal. Change to a warmer and drier climate would facilitate the expansion of the species, whereas landscape change (forest encroachment following extensive land abandonment) would produce its retreat. We correlated abundance and demography parameters computed from captures obtained in 16 plots during a 10-years period (2008–2017; SEMICE small mammal monitoring) with climate, vegetation and land use change. Climate became warmer and dryer, and afforestation due to encroachment occurred in 81 % of plots. Expected positive effects of climate warming, derived from bioclimatic niche models, were counterbalanced by negative effects of both increasing hydric deficit and changes in vegetation and landscape structure. Abundance showed a slight but significant decline (-5 %). The species' range was more resilient to change, as shown by occupancy analyses, apparently due to strong local effects of vegetation structure on occupancy. This result highlighted that negative population trends would not necessarily produce range retractions. Simultaneously analysing both abundance trends and occupancy patterns may thus allow for deeper understanding and more accurate predictions of expected population trends in response to interacting global change drivers.

1. Introduction

* Corresponding author. E-mail addresses: itorre@mcng.cat (I. Torre), mario.diaz@ccma.csic.es (M. Díaz). Land-use and climate change are among the primary drivers of global change (Sage, 2020), and together with biological invasions,

http://dx.doi.org/10.1016/j.scitotenv.2022.160875 Received 2 September 2022; Received in revised form 7 December 2022; Accepted 8 December 2022 Available online 15 December 2022 0048-9697/© 2022 Elsevier B.V. All rights reserved. overexploitation, and extirpation, are the main causes of biodiversity loss worldwide (Loehle and Eschenbach, 2012; Li et al., 2022). Predictions of climate change effects on local extinctions due to climate-driven range changes are now routinely approached using bioclimatic niche envelope models (Peterson et al., 2011), based on the assumption that the distribution of a species is mostly determined by climate (Araújo and Peterson, 2012). The spatial distribution of a species is however a more complex function of environmental tolerance, biotic favourability, and dispersal conditions (Peterson and Soberón, 2012), factors that are critically influenced by land-use change, the main driver of diversity loss (Newbold et al., 2015). Land use change has in fact been progressively incorporated to bioclimatic niche modeling (Huntley et al., 2010).

In spite of rapid refinement of models, their predictive ability is still poor at fine scales (Devictor et al., 2012), a fact that can be due to several compensatory mechanisms to global change drivers such as phenotypic and ecological plasticity (Valladares et al., 2014b), food web resilience (Stouffer and Bascompte, 2010) or behavioural flexibility (Díaz et al., 2021). Compensatory (or synergic) responses to the effects of several drivers can be best detected by analysing how demographic parameters change along spatial and temporal gradients (Matesanz et al., 2009; Torre et al., 2020). Demographic, rather than presence-absence approaches, are better grounded on the mechanisms of local and global extinctions, that are always preceded by a period of sustained or catastrophic decline (Caughley, 1994).

The Mediterranean basin is a prime example of rapid climate and land use change (Doblas-Miranda et al., 2015). Mediterranean climate is becoming drier, warmer and more variable, affecting negatively both plants and animals (Valladares et al., 2014a). Secular, long-term interactions between humans and ecosystems resulted in the regression of natural forest habitats and the expansion of more open grassland, cropland and scrub (Blondel, 2006). Land use changes followed a complex spatial and temporal pattern, creating a mosaic of open and closed habitats that allowed the coexistence of forest species and species adapted to drylands and shrublands at several spatial scales (Blondel et al., 2010; Moreno et al., 2016). Reversed landscape change trends due to new socio-economic conditions (land abandonment in mountain protected areas, and crop intensification and urbanization in the lowlands; (Pereira and Navarro, 2015; Ricotta et al., 2000) are however threatening high-diversity land mosaics in the Mediterranean basin, considered as a biodiversity hot spot (Myers et al., 2000).

Climate and landscape changes can affect habitat suitability for particular species. Modified habitat conditions will impact rates of reproduction and survival that may lead to local extinction or colonization. Ultimately, such population-level changes will cause shifts in the occurrence and abundance of species across the landscape (Rowe, 2007). Understanding how these dynamic processes are affected by changes of habitat or climate may be important for the management of ecological systems (Mackenzie et al., 2018). Small mammals are ideal model organisms to analyse shortterm effects of climate and landscape change on their demography, distribution and populations dynamics, owing to their short life cycles, small home ranges, and limited dispersal (Paniccia et al., 2022; Umetsu et al., 2008).

Here we studied the factors affecting population dynamics and demography of a Mediterranean small mammal, the Algerian mouse (*Mus spretus*) (Fig. 1). As a thermophilic species with a North African origin, the Algerian mouse has spread towards southwestern Europe from Neolithic times (Palomo et al., 2009), probably due to increasing climate favourability (Lalis et al., 2019). In fact, recent climate envelope models predict an expansion of the species range in all future climate change scenarios (Araújo et al., 2011; Lalis et al., 2019). The Algerian mouse is an openhabitat species showing consistent habitat preferences throughout its distribution range (Khidas et al., 2002; Tarjuelo et al., 2011), that would have been also favoured by land use change until recently. Nonetheless, the process of land abandonment during the last century in Mediterranean areas may have decreased habitat suitability for open-land species due to habitat loss by natural afforestation, fragmentation due to wildfires, and recovery of small mammal predators (Navarro and Pereira, 2015; Torre et al.,



Fig. 1. Algerian mouse (*Mus spretus*) and scrubland in Garraf Natural Park (Photographs by I. Torre).

2022a, 2022b). As other short-lived small mammals, Algerian mice are opportunistic breeders showing fast responses to changes in food, water availability, and air temperature (Massoud et al., 2021). Climate warming will allow to expand the breeding period to encompass also the winter (Durán et al., 1987). Population dynamics of Algerian mice would be thus driven by climate change, that will facilitate the expansion of the species, and landscape change, that will produce its retraction. We analysed the relative effect of these two factors on a short-term times series (10-year) of abundance and demographic parameters to evaluate future range shifts from its mechanistic basis. This demographic approach will hopefully provide better predictions than current niche envelope models (Araújo et al., 2011), and may contribute to explain why small mammals showed so little response to the late-Pleistocene climatic change in terms of range shifts (Blois et al., 2010).

2. Materials and methods

2.1. Study area

Field work was conducted within five Natural Parks of the Barcelona province (Catalonia, NE Spain, Fig. 2). The study area has undergone a general process of shrub encroachment and afforestation in the last decades (Gil-Tena et al., 2010) (Regos et al., 2016), and woodlands are now the dominant habitat (60 %) followed by open natural habitats (shrublands and grasslands, 31 %). Open habitats have been mostly originated by huge wildfires at the end of the XXth century (Riera and Castell, 1997). Non-natural habitats (urban areas and croplands) are minority (<10 %, Pino et al., 2013; Baśnou et al., 2013).



Fig. 2. Situation of the 16 sampling plots (circles), classified as Forest sites or Open sites, and climate stations (triangles) on the five Natural Parks monitored in the Barcelona province (Catalonia, NE Spain).

2.2. Small mammal sampling

We used the database of the SEMICE small mammal monitoring program (www.semice.org; (Torre et al., 2021). The program monitors common species with high detectability (Torre et al., 2018), ensuring no sampling biases of population and occupancy estimates (Mackenzie et al., 2018).

The study plots were selected from available SEMICE stations, a nonrandom sample of natural Mediterranean habitats representative of the study area. We sampled 16 plots of 0.56 ha monitored twice a year, in spring and autumn, to cover the life cycle of the target species (Carrilho et al., 2017; Massoud et al., 2021). Time series included ten years, from spring 2008 to fall 2017. Sampling plots consisted of grids of 36 traps $(6 \times 6 \text{ and } 9 \times 6 \text{ scheme design})$, alternating in position the same number of Longworth (Longworth Scientific Instrument Co., Oxford, UK; Caceres et al., 2011; Nicolas and Colyn, 2006) and Sherman traps (Sherman folding small animal trap; 23 imes 7.5 imes 9 cm; Sherman Co., USA) to avoid sizespecific biases in small mammal community assessments (Torre et al., 2016). Traps were spaced 15 m, baited with a piece of apple (to avoid dehydration) and some energetic food (a mixed dough of tuna and flour), and were provided with hydrophobic cotton for bedding (Machtinger and Williams, 2020). Traps were operated during three consecutive nights and revised during the early morning of the first, second and third day. Mice were identified, weighed, marked with ear-tags (Style 1005-1, National Band Co. USA), and released at the point of capture (Gurnell and Flowerdew, 2006). Research on live animals followed ethical guidelines (Sikes and Animal Care and use Committee of the American Society of, 2016), and the project being approved and captures performed under special permission of the Catalan Government (Generalitat de Catalunya).

Two main habitat types were defined. Open habitats included post-fire vegetation communities dominated by Kermes oak *Quercus coccifera* scrublands (Fig. 1), and woodlands included evergreen (*Quercus ilex* with *Pinus*)

pinea and P. halepensis) and deciduous (Quercus canariensis, Alnus glutinosa, Salix spp.) forests. The more frequent short shrub species providing food and shelter to mice were Q. coccifera, Pistacia lentiscus, Rosmarinus officinalis, Cistus albidus, and resprouting Q. ilex. Tall shrub species were represented by Arbutus unedo, Erica arborea, Calicotome spinosa, and Juniperus oxycedrus. Scrublands originated from wildfires occurred between 1982 and 2003. All plots were located in the lowlands (95–750 m a.s.l.) to avoid the influence of northern climates on species diversity/abundance patterns (Torre and Arrizabalaga, 2009).

2.3. Climate and vegetation data

Climatic data were obtained from the eight meteorological stations located nearest to the sampling plots (1 to 15 km), provided by Servei Meteorològic de Catalunya (https://www.meteo.cat, Fig. 2). Mean monthly temperature and relative humidity, and monthly rainfall were downloaded directly. Mean monthly hydric deficit was computed as monthly rainfall minus potential evapotranspiration (Hargreaves and Samani, 1982), to estimate drought conditions (Torre et al., 2020).

Vegetation structure of plots was evaluated by ALS LiDAR (Lefsky et al., 2002; Simonson et al., 2014) obtained from flights 2016–2017 and downloaded from the Institut Cartogràfic i Geològic de Catalunya (https://www.icgc.cat/). LIDAR data provide better estimates than conventional field-based vegetation compositional surveys for analysis of small mammal-vegetation relationships (Garden et al., 2007; Jaime-González et al., 2017). We considered that differences in the periods of LiDAR and small mammal data collection would not bias results since all plots experienced similar vegetation change (Vierling et al., 2014), and no significant land-use changes were observed at the scales of the plots (see below). Height of vegetation is relevant for Algerian mice microhabitat selection (Gray et al., 1998), and 12 variables describing vertical vegetation structure

and height were obtained at the plot level (see Torre et al., 2021, for further details). Variables describing horizontal profiles of vegetation were not considered due to positive relationships between height and cover (Tarjuelo et al., 2011; Navarro-Castilla et al., 2017). The complexity of the vertical structure (six variables: CON x-y) was estimated, as a percentage, by the relative contribution of each vegetation layer (0.15–0.50 m, 0.50–1 m, 1–1.50 m, 0.15–1.50 m, 1.50–2.50 m, >2.50 m). Vegetation mean height (six variables: ALT x-y) was calculated as the mean of the heights of every laser return within each layer (Table S1).

Land-use changes around sampling plots were estimated at two spatial scales, 100–m buffer (plot area = 3.5 ha) and 500–m buffer (landscape area = 78.5 ha). Official land cover maps (González-Guerrero and Pons, 2020) were used to estimate change in forest and open habitat covers between 2007 and 2017.

2.4. Data analysis

2.4.1. Vegetation structure and land-use

The 12 LiDAR variables were summarised into structural gradients by means of a Principal Component Analysis (PCA). Varimax rotated components with eigenvalues > 1 (Kaiser criterion) were retained, interpreted as vegetation gradients from eigenvalues of variables and used as predictors in further analyses (Dytham, 2011). Land-use change was estimated by calculating the difference in land cover between 2007 and 2017 of the two natural (scrubland and forest) and the two anthropic habitats (crops and urban areas) at two spatial scales. Comparison between periods were performed with a Wilcoxon matched-pairs tests.

2.4.2. Population abundance

We defined three dependent (response) variables to analyse population responses to climate and land use changes: abundance of adults (mass > 10 g), abundance of juveniles (mass \leq 10 g), and total abundance (adults + juveniles + age unknown because some individuals were not weighted).

The independent (predictor) variables were sampling period (categorical: spring or autumn), vegetation profiles (PC-Lidar), land-use change, and four meteorological variables (temperature, humidity, rainfall, and hydric deficit). Means and variances of climatic variables were used to account for the increase in the frequency and intensity of extreme weather phenomena (Easterling et al., 2000) (Thomas et al., 2013; Datry et al., 2016). Three different time frames of three, six and 12 months before every sampling session were established to account for climatic effects on mice abundance (Díaz et al., 2010). Algerian mice develop rapidly, reaching sexual maturity during the first three months of life (Durán et al., 1987) Consequently, a three-month frame was adequate for testing the role of climate on recruitment. The six-month frame analysed the period between consecutive sampling sessions, and the 12 months frame was based on the maximum longevity reported in the wild (Palomo et al., 2009). For juveniles, only the three-month frame approach was considered because prior to three months the individuals will be absent from the population.

The final set of predictors was assessed by strength of pairwise correlations (Spearman correlation $\rho \geq 0.8$ was considered to indicate redundant predictors) and ecological significance for the species. In addition, multicollinearity was addressed by the Variation Inflation Factor (VIF) following Zuur et al. (2010), selecting sets of independent variables with VIF < 3. The final set of variables included season, altitude, LiDAR-PC1, afforestation rate, plus the climatic variables mean temperature, mean temperature variance, precipitation, precipitation variance, mean humidity, mean humidity variance and hydric deficit. Rainfall and humidity for the 3 months' time frame and temperature and humidity from the 6 months' time frame were eliminated to avoid multicollinearity effects.

Associations between abundance variables and environmental predictors were tested using generalized linear mixed models (glmer function in R) with negative binomial distribution of errors (Zuur et al., 2010, 2009). Sampling station was included as a random factor, and all independent predictors were scaled before fitting the models (Zuur et al., 2009, 2010). All possible models where built using the dredge function in the package MuMIn (Barton, 2020). Model complexity (parsimony) was assessed by the Akaike information criterion (AIC) (Burnham and Anderson, 2004), retaining as meaningful models those with AIC values not higher than the minimum AIC value + 2. Average models were estimated (model.avg. function from MuMIn package) including all best models according to the described AIC criterion. Standardized estimates of significant predictors were obtained for all models.

2.4.3. Population trends and demography

TRIM software (Trends & Indices for Monitoring data, Pannekoek and Strien, 2005) was used to analyse population trends. TRIM analyses time series of log-transormed count data with missing observations, considering serial correlations and overdispersion (Torre et al., 2018, see Spooner et al., 2018, for a similar approach). We used the covariates scrubland, pinewood, and broad-leaved woodland to determine whether population trends differed among habitats. Multiple-Season Occupancy models (Mackenzie et al., 2018) were used to compute the demographic parameters occupancy, colonization, extinction, persistence turnover and detectability. Occupancy (ψ) is the proportion of sites that occupied by the target species. Colonization (γ) is the probability that an unoccupied site in season t is occupied in season t + 1. Extinction (ε) is the probability that a site occupied in season t is unoccupied in season t + 1. Persistence (\emptyset) is the probability of a site being occupied in successive seasons $(1-\varepsilon)$. Turnover is the probability of a site changing the occupancy status between seasons ($\tau = \psi \varepsilon + (1 - \psi)$ γ). And detectability (*p*) is the probability of detecting the species when actually present. These models allow to estimate first-order Markovian changes in occupancy, that is, when occupancy at a site in the present season is conditioned by the state of occupancy at that site in the last season (Mackenzie et al., 2018). We considered two temporal scales: A short one, consisting in the detection/non-detection of the species during the three consecutive trapping sessions conducted during a survey to account for species detectability; and a long one, consisting in the detection/non-detection of the species during consecutive (seasonal) surveys to account for changes in occupancy and the rest of parameters. The SEMICE program is especially appropriate for applying occupancy models (Torre et al., 2020), because it consists in three surveys repeated in three consecutive days for every sampling site (secondary occasions), and surveys are repeated in two annual seasons along the years (primary occasions). Furthermore, the Algerian mouse showed high detectability (Torre et al., 2018), well above the p =0.3 threshold indicating low probabilities for false negatives (Mackenzie et al., 2002).

Competing occupancy models were fitted with the software PRESENCE (MacKenzie, 2012). We started with a null model (setting all parameters constant), considering that occupancy rate and derived parameters did not change in space and time $[\psi(\cdot)\gamma(\cdot)\varepsilon(\cdot)p(\cdot)]$. The models were adjusted adding vegetation structure profiles of trapping plots (LiDAR-PC1, sitedependent covariate) and seasonal effects. We expected that initial occupancy (i.e., occupancy at the start of the study), as well as the other parameters (derived occupancy, colonization, extinction, detectability), were determined by vegetation structure profiles of trapping plots. These models were temporally static because vegetation structure descriptors were the same throughout the study period. In spite that vegetation profiles may change due to ecological succession, the absence of detectable and consistent land-use changes within a 100 m buffer centred on each plot (see Section 3.2) gave support to that approach. Nonetheless, alternative models were fitted considering that significant land-use changes were observed at the landscape level (within a 500 m buffer centred on each plot, see Section 3.2), and parameters could be affected by land-use change at a spatial scale larger than the limits of the sampling plots. Starting from the previous model, we added a new site dependent covariate to illustrate landscape change (total change of cover of open land and woodland between 2007 and 2017). We expected that initial occupancy will be mostly conditioned by vegetation structure profiles represented by the LiDAR-PC1, but colonization and extinction could be affected throughout the seasons by both vegetation structure and land-use change.

3. Results

During the study period 2645 small mammals were captured, belonging to five different species. Out of these, 294 individuals (11.1 %) were identified as *M. spretus* (364 captures), of which 76 % were considered adults (225 individuals). 82 % of individuals were captured in open land (scrubland). Trap mortality was very low (4 individuals, 1.4 %).

3.1. Vegetation structure and land-use of the sampling stations

The PCA yielded four significant factors with eigenvalues equal or greater than one (Table S1). The first two PCs accounted for 76.13 % of variance (54.35 % for PC1 and 21.78 % for PC2). PC1 was correlated with nine out of 12 variables measuring the contribution (~cover) and height of vertical vegetation profiles, and clearly segregated scrublands from woodlands, being interpreted as a gradient of vertical vegetation structural complexity. PC2 was mostly associated to contribution and height of short and tall shrubs (right end of the axis).

Scrublands, showing negative factor coordinates, were characterized by their high vegetation cover of short shrubs (83.4 % of mean contribution of shrubs in the class 0.15–1.50 m tall), but low vegetation cover of tall vegetation (>2.50 m). Broad-leaved evergreen and deciduous woodlands, showing positive factor scores, revealed low vegetation cover of short shrubs (12.0 % of mean contribution of shrubs in the class 0.15–1.50 m tall), but high vegetation cover of tall vegetation (87.8 % of mean contribution of the class >2.5 m). Pinewoods of *P. halepensis*, with significant low canopy cover, showed high vegetation cover of short shrubs than denser broadleaved woodlands (28.2 % versus 8.2 %). Pinewood were then structurally intermediate between scrubland and broad-leaved woodland.

Landscape descriptors in 500–m buffers around sampling plots differed between the three habitats considered: At the start of the study (2007), scrublands were mostly surrounded by open land (75 %), and broadleaved woodlands were surrounded by forest (83 %), whereas pinewoods showed an intermediate situation (42 % open land, 47 % of forest). Factor coordinates of LiDAR-PC1 were significantly correlated (Spearman rank correlation coefficient) with land-use at the plot and the landscape scales in both periods and for both main habitats: LiDAR-Open land 2007: r = -0.95 and -0.83; LiDAR-Open land 2017: r = -0.94 and -0.83; LiDAR-Woodland 2007: r = 0.94 and 0.84. Vegetation structure profiles summarised by LiDAR-PC1 were then associated to land-use composition at the scales of the trapping plot and landscape.

3.2. Patterns of climate and landscape change

Most of the climatic variables showed significant change along the study period (2008–2017): mean annual temperature increased (r = 0.13, p = 0.04), whereas annual rainfall decreased (r = -0.46, p < 0.0001), strongly increasing hydric deficit (r = -0.50, p < 0.0001). Rainfall variance (r = -0.29, p < 0.001) and temperature variance (r = -0.16, p < 0.05) decreased along the study period, whereas humidity variance increased (r = 0.52, p < 0.0001) (Fig. S1).

Land-use changes between 2007 and 2017 at the 16 trapping plots were clear-cut at the landscape-level scale: Open natural habitats (grassland and shrubland) decreased by 4.9 % on average (z = 2.85, p = 0.004, n = 16), forest increased by 3.2 % (z = 2.79, p = 0.005, n = 16), urban areas increased by 0.9 % (z = 3.17, p = 0.001, n = 16), and crops remained unchanged (+0.8 % change, z = 1.21, p = 0.22). These patterns were similar in both scrubland and forest plots, indicating that landscape change was consistent among vegetation types. In fact, 13 out of 16 plots (81 %) showed scrubland regression and afforestation, two plots showed no change, and only one plot showed a reversed pattern (scrubland increase and forest decrease, Fig. 3). Rate of change of scrubland and woodland were negatively correlated (r = -0.92, p < 0.001, n = 16), suggesting that scrubland regression was associated to afforestation. Nonetheless, land-use changes at the 100-m buffer plot scale were non-significant

(forest: z = 0.56, p = 0.57, n = 16; open land: z = 0.91, p = 0.36, n = 16), possibly due to heterogeneity in patterns of land-use change within plots (Fig. 3). Six plots showed no change, four showed forest regression and scrubland expansion, and three showed scrubland regression and afforestation. Interestingly, pinewood plots suffered the stronger land-use changes at the landscape-level scale: Open land decreased (-10.7%) and woodland increased (+10.2%), followed by scrubland (-4% open land, +2.7% woodland) and broad-leaved forests (-2.8% open land, +2.1% woodland).

3.3. Algerian mouse associations to climate, vegetation structure profiles, and land-use change

Twelve-month time frame GLM models for total mice and adult abundance considering all climatic and habitat predictors showed lower mean AIC values and explained higher variance than models for six- and threemonth time frames (Fig. 4, Table S2). Vegetation structure (LiDAR-PC1) was the main predictor for the abundance change of both adults, juveniles and total. Increased vegetation complexity was negatively associated to abundance. Total and adult abundance were also negatively associated to hydric deficit and humidity variance. Juvenile recruitment was lower in landscapes with higher increases of forest habitat around plots.

The abundance of Algerian mice showed a significant (p = 0.01) but moderate (5 %) decline along the study period (TRIM; imputed index: -0.0535 ± 0.0103 SE, Chi² = 216.8, p = 0.15, overdispersion = 1.1, serial correlation = 0.02, df = 197). Model fit improved when habitat type (scrubland/pinewood/broad-leaved forest) was included a covariate (Chi² = 211.7, p = 0.20, covariate effect: Wald test = 6.54, df = 19, p = 0.038, df = 195). Trends were more negative in woodland than in shrubland (Fig. S2).

Occupancy models showed strong associations of populations parameters to vegetation structure profiles (Table 1). Occupancy changed between sites but not among seasons or years, as well as colonization and extinction probabilities. Detectability differed among seasons. Occupancy, colonization and persistence were negatively associated to vegetation structure complexity, whereas extinction was positively associated (Fig. 5). Occupancy was higher in scrubland ($\psi = 0.92 \pm 0.07$, n = 5), followed by Aleppo pinewoods ($\psi = 0.42 \pm 0.10$, n = 2), and broad-leaved evergreen and deciduous woodlands ($\psi = 0.16 \pm 0.06$, n = 9). Probability of colonization was higher in scrubland (γ = 0.29 ± 0.26), followed by pinewoods ($\gamma = 0.15 \pm 0.06$) and broad-leaved forests ($\gamma = 0.10 \pm 0.05$). Persistence of populations was higher in open habitats due to high colonization and low extinction probabilities along the gradient of vertical structure complexity. Detectability was higher in open habitats ($p = 0.57 \pm 0.14$, range 0.07–0.94) than in forests ($p = 0.30 \pm 0.13$, 0.02–0.83) throughout the seasons and years (Fig. S2). Detectability declined along the study period (r = -0.44, p < 0.05) due to its positive association with abundance (Fig. S2). Landscape change around sampling plots slightly increased model fit. Initial occupancy was only influenced by vegetation structure profiles, but colonization/extinction probabilities depended on both vegetation structure and land-use change around sampling plots at the landscape scale. Probability of occupancy did not change along the study period in plots with moderate landscape change around (-5 % decrease of occupancy in scrubland, and + 4 % increase in broad-leaved woodland), but it decreased strongly in the habitat showing greater landscape change (-43 % in pinewood). Colonization probability was significantly lower when including landscape change in pinewood models ($\gamma_{Landscape}$ = 0.05 ± 0.05 vs. $\gamma = 0.14 \pm 0.06$) but it did it not change in the remaining habitats (broad-leaved forests: $\gamma_{Landscape} = 0.11 \pm 0.05$ vs. $\gamma = 0.10 \pm$ 0.04; scrubland: $\gamma_{Landscape} = 0.32 \pm 0.29$ vs. $\gamma = 0.29 \pm 0.25$).

4. Discussion

Abundance and short-term dynamics of Algerian mice populations were strongly associated to climate and land use changes. No evidence for positive effects of climate warming (Araújo et al., 2011) was found. Warming



LiDAR-PC1 (Scrublands to Woodlands)

Fig. 3. Landscape change (%) at two spatial scales (100 and 500 m buffers centred in the 16 sampling plots) in the period 2007–2017. Percent change of the two structural habitats considered (open land-scrubland and forest-woodland) are shown. Plots were ordered along the x-axis according to the factor scores of LiDAR-PC1, representing a structural gradient of vertical complexity of vegetation, from scrubland to woodland.

was moderate although significant along the study period, and may have increased hydric deficit, together with decreasing rainfall, a factor negatively associated to population parameters. Changes in vegetation and landscape structure driven by afforestation, which negatively affected habitat suitability for the target species (Holland and Bennett, 2007), showed much stronger negative effects on demography. Hence, a reduction rather than an expansion of the species' range might be expected, contrary to predictions from bioclimatic models (Araújo et al., 2011).

Climate change not only implies warming, but also a decrease in rainfall, at least in the Mediterranean areas (Penuelas and Boada, 2003; Seoane and Carrascal, 2008). A mean decline of 240 mm in rainfall and an increase of 0.6 °C in temperature was detected along a short (10 years) time series, that combined into an increased hydric deficit, as also found for other Spanish forests (Khoury and Coomes, 2020). Increasing drought conditions have deleterious effects on many animal and droughtintolerant plant populations (Selwood et al., 2015a; Morán-Ordóñez et al., 2021). Increased hydric deficit may have decreased vegetation productivity and availability of food resources (ephemeral vegetation and their seeds, Previtali et al., 2009) for herbivore and granivore species like the Algerian mouse, thus counteracting expected positive effects of increasing temperature.

Apart from trends in means, climate change in the Mediterranean region typically involve increased frequency of extreme events that increase climatic variance (Easterling et al., 2000). Rainfall variance raises were associated to population decline, although no significant associations with population size were detected. Variance in relative humidity variance was negatively associated to population size (as observed in other thermophilic small mammals, Torre et al., 2020), suggesting that extreme climatic events might are playing a role in Algerian mice demography (Drake, 2005).

Habitat changed at the landscape scale along the study period following the expected pattern for Mediterranean vegetation under the lack of disturbances (Koniak and Noy-Meir, 2009). Open land cover decreased (-4.9 % on average) and forests increased (+3.2 %) around most sampling plots, and these changes were associated to significant declines in habitat suitability for the target and other common small mammal species (Torre et al., 2022a; Torre and Díaz, 2022), as well as for other animal groups (Seoane and Carrascal, 2008; Regos et al., 2016; Stefanescu et al., 2011). Landscape changes (afforestation, urbanization, etc.) have been related to changes in the composition of small mammal communities over longer time periods (30 years, Torre et al., 2015), with a decrease of open land species and an increase of forest species. Occupancy analysis suggested, however, that the target species was resilient to change, at least in most of the plots (14 out of 16) and on the most representative habitats (broad-leaved forest and scrubland). Average occupancy was slightly higher at the start (2008: ψ = 0.48 ± 0.05 SE) than at the end of the period (2017: ψ = 0.43 ± 0.08 SE), although the difference was not significant. Negative population trends that are not accompanied by a spatial retraction of the species range could be more easily reverted than changes affecting both population and occupancy trends, as it usually occurs (Schulz et al., 2020). Analysing simultaneously both abundance trends and occupancy patterns may thus allow for deeper understanding of expected population trends in response to global change drivers (Billman et al., 2021) while controlling for population variability on observed patterns (McCain et al., 2016).



Fig. 4. Results of the GLMMs for the juvenile (upper), adult (middle), and total (lower) abundance of *Mus spretus* as response variables, and a set of scaled climatic and landuse predictors (see Methods for details). Coefficients differing from zero are marked in red (negative effect) or blue (positive effect), and their relative weights being directly comparable. r2m: marginal variance; r2c: conditional variance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Knowledge of the association between vegetation traits and the occurrence of a species is essential to guide conservation and restoration efforts (Holland and Bennett, 2007). Our results were in agreement with a strong and consistent habitat preference of the Algerian mouse, showing higher abundance, occupancy, and colonization probabilities in open habitats (i.e., scrubland, Palomo et al., 2009). Demographic parameters showed a decreasing rate of change along a structural gradient of vertical complexity of vegetation from scrubland to woodland. Algerian mice seemed to be more prone to local extinction in forest areas and to have a lower colonization capacity in scrubland than other open land small mammals (e.g., C. russula, Torre and Díaz, 2022). Population persistence of common and widely distributed small mammals can thus be severely affected by global change drivers, even more in the case of small seed-caching granivores (Yeakel et al., 2020). Bearing in mind the relevant roles of common species in ecosystems (Gaston and Fuller, 2008), these trends may cascade up and down through trophic chains, as has been shown for small mammal predators in the study region (Oro et al., 2021).

Mice-habitat associations presented here agree with conceptual and empirical frameworks raised to explain changes in habitat suitability for common small mammals along vegetation structural gradients in Mediterranean landscapes under a context of land abandonment (Paniccia et al., 2022; Torre et al., 2022a). In fact, patterns of abundance and demographic parameters of Algerian mice could be related to the influence of a number of biotic and abiotic factors changing along landscape gradients (Holland and Bennett, 2007), of which predators could be relevant drivers (Gallego et al., 2017; Torre and Díaz, 2004; Torre et al., 2022a; Torre et al., 2022b). Indeed, a rewilding process consisting in substantial expansion of top predators (carnivores and birds of prey) on abandoned land was noticed in several countries of western Europe (Navarro and Pereira, 2015), potentially increasing predation pressure on small mammals, particularly in the case of juveniles (Dickman et al., 1991). Because forests hold more species of small mammal predators with diets based on small mammals (Torre et al., 2018, 2022b), we predicted higher predation rates than in scrublands. These effects will be exacerbated in small and isolated patches of pinewoods placed at the periphery of the study area (Riera and Castell, 1997), with high fragmentation caused by land abandonment and wildfires (Torre et al., 2022a, 2022b), and influenced by edge effects and anthropogenic disturbances (Holland and Bennett, 2009). This will produce a higher concentration of forest predators and competitors than in continuous non-fragmented woodland.

The Algerian mouse has been considered as a sentinel for the assessment of environmental quality (da Silva Júnior et al., 2017). As an open-habitat species (Palomo et al., 2009), the process of land abandonment and predicted rewilding in Mediterranean areas (Navarro and Pereira, 2015) will produce a decline of habitat suitability for this and other open-land species, due to habitat loss associated to natural afforestation (Navarro and Pereira, 2015; Torre et al., 2022a, 2022b). Land use changes may thus counteract expected positive effects of warming, derived from bioclimatic niche models (Araújo et al., 2011). Further, negative effects of warming on



Fig. 5. Graphical representation of the probability of occupancy model selected using PRESENCE software. Dots indicate the changes in the modelled probability of five demographic parameters along vegetation structural gradients represented by LiDAR-PC1 (model AIC = 365.2: ψ LiDAR, γ (LiDAR), ϵ (LiDAR),p(LiDAR + season)). The underlying picture depicts the change in vegetation structure from scrublands to dense forests along the structural gradient. See Table 1 for details.

drought, especially in association with decreased rainfall, may further counteract expected positive effects of warming. Analyses of demographic parameters rather than presence data only, and developed at the appropriate spatial scales (smaller and adequate to the target species), were probably more precise and powerful than simpler bioclimatic models (Osorio-Olvera et al., 2016). Demographic models emphasised the role of vital rates as ultimate determinants of the persistence and extinction of the Algerian mouse populations in the study area (Srinivasan and Wilcove, 2021, and references therein). As suggested, the combined pressures of both land-use change and climate change may result in species declines and extinctions occurring faster than otherwise predicted (Selwood et al., 2015b). Unfortunately, new socio-economic circumstances are against some effects of global change, such as reversing afforestation, falling well outside the capacity of the land administrators even considering the increasing impact of wildfires in the present framework of climate change (Duane et al., 2019).

5. Conclusions

Precise predictions of populations trends at relevant spatial scales are increasingly needed due to accelerated change in global change divers. This study addresses demographic responses of a thermophilic small mammal species to two key global change drivers, climate and land use. Both showed significant change along a short, 10-year time frame (2008–2017): climate became warmer and dryer, and land experienced a process of natural afforestation. Warming had no measurable associations with Algerian mice population parameters, whereas afforestation and increased hydric deficit (in part associated to warming) showed significant negative associations. Overall, expected trends in population size would be opposite than expected from bioclimatic niche models. Further, we found that population declines were associated to a stable rather than to a retreating occupancy. This result highlighted that negative population trends would not necessarily produce spatial retractions of species' ranges.

Table 1

Single-species, Multiple-season occupancy models for the Algerian mouse ordered according to their statistical fit based onAkaike Information Criterium (AIC). Model support (AICweight%), Model Likelihood, and number of parameters are also shown (delta AIC \leq 2 highlights models with equal support). Ψ : occupancy; γ : colonization; ϵ : extinction p: detectability. Predictors: LiDAR = Structural vertical complexity of vegetation summarised by PC1; Landscape = Absolute landscape change around sampling plots (500 m-buffer) between 2007 and 2017; Land-use₂₀₀₇ = Land-use in the precedent year of the start of the study (2007, 500 m-buffer).

Order	Model	AIC	deltaAIC	AIC wgt%	Model likelihood	No.Par.
1	ψ LiDAR, γ (LiDAR + Landscape), ε (LiDAR + Landscape), p (Season + LiDAR)	364.96	0.00	0.3370	1	29
2	ψ LiDAR, γ (LiDAR), ε (LiDAR), p (Season + LiDAR)	365.19	0.23	0.3004	0.8914	27
3	ψ LiDAR + Landscape, γ (LiDAR + Landscape), ε (LiDAR + Landscape), p (Season + LiDAR)	366.96	2.00	0.1240	0.3679	30
4	ψ LiDAR + Land-use ₂₀₀₇ , γ (LiDAR), ε (LiDAR), p (Season + LiDAR)	367.19	2.23	0.1105	0.3279	28
5	ψ Land-use ₂₀₀₇ , γ (Land-use ₂₀₀₇), ε (Land-use ₂₀₀₇), p (Season + LiDAR)	368.26	3.30	0.0647	0.1920	27
6	ψ LiDAR, γ (LiDAR + Land-use ₂₀₀₇), ε (LiDAR + Land-use ₂₀₀₇), p (Season + LiDAR)	369.17	4.21	0.0411	0.1218	29
7	ψ LiDAR + Land-use ₂₀₀₇ , γ (LiDAR + Land-use ₂₀₀₇), ε (LiDAR + Land-use ₂₀₀₇), p (Season + LiDAR)	370.40	5.44	0.0222	0.0659	30
8	ψ (LiDAR), γ (LiDAR + Land-use), p (Season + LiDAR)	386.04	21.08	0.0000	0.0000	26
9	ψ Landscape, γ (Landscape), e (Landscape), p (Season + LiDAR)	392.44	27.48	0.0000	0.0000	27
10	$\psi, \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	414.27	49.31	0.0000	0.0000	4

Simultaneously analysing both abundance trends and occupancy patterns may thus allow for deeper understanding and more accurate predictions of expected population trends in response to interacting global change drivers.

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2022.160875.

Data availability statement

The data that support the findings of this study are available upon request to the corresponding author.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ignasi Torre reports financial support was provided by Barcelona Provincial Council (Diputació de Barcelona).

Acknowledgements

We are grateful to the Barcelona Provincial Council (Diputació de Barcelona) and Collserola Natural Park for financial and logistic assistance throughout the years. We thank Antoni Arrizabalaga (Labs' head) for providing administrative support and guarantee to the SEMICE program all over the years. We also recognize the role of volunteers and professionals in charge of SEMICE stations which kindly recorded data in the study area: Tomàs Pulido, Dolors Escruela, James Manresa, Joan Manuel Riera, Marc Vilella, Marçal Pou, and Alfons Raspall (also provided the picture of the Algerian mouse). Carlos Jaime-González provided LiDAR information of plots. The SEMICE project had additional support by Fundación Biodiversidad (2015), Ministerio de Medio Ambiente de España, Conselh Generau d'Aran, and SECEM (Sociedad Española para la Conservación y Estudio de los Mamíferos). The positive comments of two reviewers greatly improved the final version of the article.

CRediT authorship contribution statement

Conceptualization, IT; investigation, IT; methodology, IT and XP-M; software, IT and XP-M; formal analysis, IT and XP-M; data curation, IT and XP-M; writing—original draft preparation, IT; writing—review and editing, IT and MD; All authors have read and agreed to the published version of the manuscript.

Funding

This research was funded by the Barcelona Provincial Council (Diputació de Barcelona: reference numbers 2015/3456).

Institutional review board statement

Investigations regarding small mammals followed the ethical guidelines for the use of wild mammals in research and education (Sikes and Animal Care and use Committee of the American Society of, 2016). All surveys were approved and conducted with special permission issued by the Catalan Government (Generalitat de Catalunya): 2008-SF/317; 2009-SF/398; 2010-SF/446; 2011-SF/389; 2012-SF/285; 2013-SF/519; 2014-SF/617; 2015-SF/778; 2016-SF/687; 2017-SF/891. The authors declare that there is no conflict of interest regarding the publication of this article.

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