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Population dynamics of small endotherms under global change: Greater white-toothed shrews *Crocidura russula* in Mediterranean habitats

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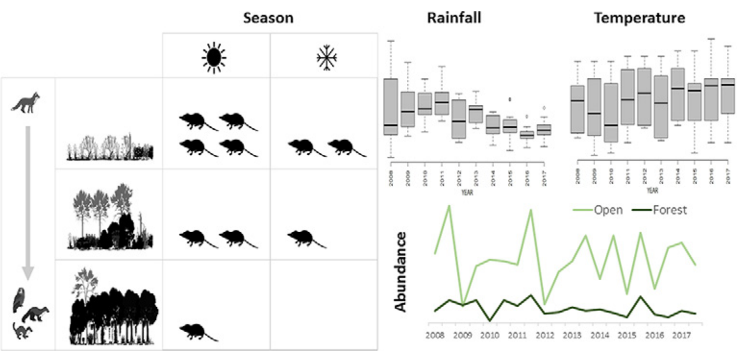
HIGHLIGHTS

- Shrews' populations were mainly affected by habitat and season in the Mediterranean.
- Abundance, occupancy and colonization were always higher in shrublands than in woodlands.
- Population growth rates were intrinsically regulated by density-dependence.
- Humidity and rainfall variance negatively affected populations.

GRAPHICAL ABSTRACT



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ABSTRACT

Small endotherms would be especially exposed to main global change drivers (habitat and climate changes) but would also be able to withstand them by adjusting population dynamics locally to changing climate- and habitat-driven food and predation conditions. We analyse the relative importance of changes in climate (mean and variability, including relevant time-lags) and habitat conditions on the abundance, age structure and growth rate of Mediterranean populations of a small endotherm, the greater white-toothed shrew *Crocidura russula*, along a 10-year period (2008–2017). Habitat type and season were the key factors shaping shrew population dynamics, which showed consistent peak numbers in open habitats in autumn, after the spring-summer reproductive period. Significant increases in aridity (increasing temperature and decreasing rainfall) along the study period did not explain variation in shrew numbers, although short-term variations in abundance were negatively related to relative air humidity and temperature over three last months prior to the surveys. Overall, ongoing climate change have not yet affected shrew population dynamics in its core areas of the Mediterranean region, in spite of expectations based on climate change rate in this region and small endotherm sensitivity to these changes. Reliance on open habitats with lower predation pressure would explain the resilience of shrew populations to climate change. However, current trends of land use change (land abandonment and afforestation) threaten Mediterranean open habitats, so that resilience would not last for long if these trends are not counteracted.

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1. Introduction

Human activity is reducing biodiversity through overuse of the natural resources and the destruction of many habitats (Hatfield et al., 2018; Newbold et al., 2015; Rockström et al., 2009). Negative effects on biodiversity also results from human-driven climate change, which include global warming and more extreme climate conditions (Bonada and Resh, 2013; Woodward et al., 2015). Action against the causes of climate change needs mainly consider long-term imbalances of greenhouse gases and other pollutants, but its effects on local biodiversity may be attenuated by short-term habitat management (Tanner-McAllister et al., 2017), providing we have enough knowledge on population responses to habitats and climate conditions (Drake, 2005; Thornton et al., 2014).

Mediterranean ecosystems are, and will be, among the most affected by climate change (Doblas-Miranda et al., 2015), with expected increases in temperature and decreases in rainfall much larger than the world's average (Mariotti et al., 2015). In addition, the region has experienced changes in land use like forest losses due to wildfires and loss of open habitats -croplands and grasslands- due to urbanization and encroachment after land abandonment (Doblas-Miranda et al., 2015). Furthermore, freshwater systems are affected directly by reduced rainfall, but also indirectly by land-use changes influencing water quality in whole catchments (Fernandes et al., 2019a, 2019b). Mediterranean wildlife is both extremely diverse and sensitive to recent changes, so that the region qualified as hot spot of biodiversity and biodiversity loss worldwide (Myers et al., 2000). Action to halt Mediterranean biodiversity loss is then especially urgent (Doblas-Miranda et al., 2015).

Responses of wildlife to the combined effects of climate and land use change may be purely additive or interactive, if climate change effects are attenuated or enhanced by habitat changes (Matesanz et al., 2009). Plants and small ectothermic animals seem to be directly affected by climate trends (Stefanescu et al., 2011; Thuiller et al., 2011), whereas mobile endothermic animals could mitigate direct climate effects by means of behavioral and physiological flexibility (Helmuth et al., 2005; Dunn and Møller, 2019). Small endotherms, such as passerine birds, bats, and small mammals, would show mixed responses to climate and habitat changes (Torre et al., 2015).

The greater white-toothed shrew, *Crocidura russula*, is a small mammal of the family Soricidae, whose distribution spans from South-West of Europe and the North of Africa to central Europe (López-Fuster, 2007; Aulagnier et al., 2016). Shrew's sensitivity to climate change stands from their dependency on climate to regulate their metabolism and adjust the phenology of energy-demanding processes like reproduction (Bronson, 2009). As invertebrate feeders, they also depend on climate effects on the abundance on their ectothermic prey; in addition, vegetation structure and biomass conditions food supply, and protects shrews from their own predators (Torre et al., 2013, and references therein). Their short life span and fast breeding cycle (López-Fuster, 2007) involves quick population responses to environmental changes, and even the possibility of local evolutionary adaptation (Balloux et al., 1998). Further, this species showed high detectability to standard sampling methods (Torre et al., 2018) so that long-term time series of shrew abundance are barely biased by methodological concerns.

We expected that winter can be a limiting season for shrews for, at least, two non-fully independent reasons. Cold temperatures will produce a negative energy balance for a species that has no way of accumulating fat reserves (Oliveira et al., 2016). Further, during this period most of the small ectotherm fauna is hibernating and unavailable for shrews which are fully dependent on live invertebrates for feeding. On the other hand, summer can be a favourable season, since hot temperatures will allow shrews for passive thermoregulation without high energetic costs. During this period, invertebrates are active and fully available for shrews. The effects caused by the limiting season on shrew's populations will be detected during the immediately following season (spring). Conversely, the positive effects of summer on populations will be detected in autumn.

In this paper, we analysed the relative importance of climate change and habitat on the abundance, age structure and growth rate of the shrew populations inhabiting five Mediterranean natural parks, using data of the long-term monitoring of small mammal populations in these parks that started in 2008 (SEMICE monitoring scheme, Torre et al., 2018). Climate change estimates during the 2008–2017 period were obtained from official sources. We expected strong effects of changes in mean climatic variables (rainfall, temperature, humidity) and its variability on the abundance, age structure and growth rates of shrew populations, either immediate or time-lagged according to the life history traits of the species (longevity and generation time; Diaz et al., 2010). Habitat type and structure, and their changes, may however modulate climate effects by, at least, three main mechanisms (changes in primary productivity, in predator abundance and predation risk, and in microclimatic conditions; Huey et al., 2012; Torre et al., 2018). This fact should influence conservation actions for small endotherms as shrews under global change scenarios.

2. Materials and methods

2.1. Study area and sampling design

We carried out field work within five Natural Parks of Barcelona province (Catalonia, NE Spain, Fig. 1). The study area has undergone a general afforestation process in the last decades (Gil-Tena et al., 2010), so that woodlands are now the main habitat types (60%) followed by open natural habitats (shrublands and grasslands, 31%). Non-natural habitats are minority (urban areas, 5%, and croplands, 3%, Pino et al., 2013). Sampling was performed from spring 2008 to fall 2017, surveying 16 different plots during 20 trapping sessions (two sessions per year) following the SEMICE monitoring scheme (Torre et al., 2018). Sampling plots consisted on grids of 36 traps (6 × 6 trapping scheme), alternating in position 18 Sherman traps (Sherman folding small animal trap; 23 × 7.5 × 9 cm; Sherman Co., USA) with 18 Longworth traps (Penlon Ltd., Oxford, UK; Caceres et al., 2011; Nicolas and Colyn, 2006). Both traps are made on aluminium, but the Sherman trap is made on a single rectangular piece, and the Longworth trap is composed by a tunnel and a nest box (Sibbald et al., 2006). Traps were spaced 15 m, baited with a piece of apple and a mixture of tuna, flour and oil, and insulated by including hydrophobic cotton for bedding (Sikes and Gannon, 2011). Traps were operated during three consecutive nights and revised during the early morning of the first, second and third day. Shrews were identified, weighed, marked with fur clips (Sikes and Gannon, 2011) and released at the point of capture (Gurnell and Flowerdew, 2006). Two sampling sessions per year were carried out, in spring (April to June) and autumn (October to December), according to the biology of the target species (Jeanmaire-Besançon, 1988).

The SEMICE scheme is a volunteer-based monitoring program that ensures enough detectability and no sampling bias (low inaccuracies related to sampling) for population estimates of the target species (Torre et al., 2018), despite some qualitative bias regarding volunteer experience (ability to determine some individual traits, Torre et al., 2019). Research on live animals followed ethical guidelines (Sikes and Gannon, 2011), and captures were performed under special permission of the Catalan Government (Generalitat de Catalunya).

Climate data were obtained from the nearest active meteorological station to each sampling plot (Servei Meteorològic de Catalunya, www.meteo.cat, Fig. 1). Distances between stations and plots ranged from 0.7 to 12 km. Variables obtained were temperature, relative humidity, rainfall and solar radiation. Drought conditions were estimated through an hydric deficit (HD = rainfall-potential evapotranspiration, calculated with the Hargreaves methodology; Bandyopadhyay et al., 2008; Sánchez, 2017). These variables were chosen to reflect the ecological effects of a changing climate on the environmental conditions for a

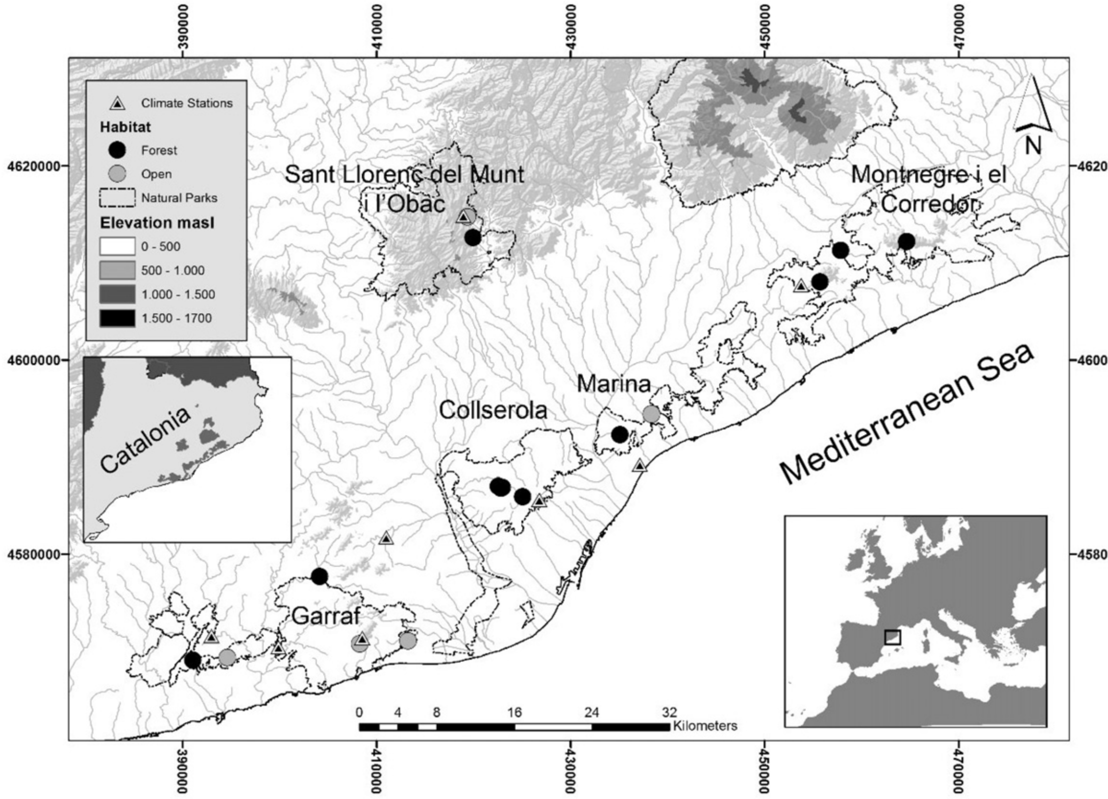

Fig. 1. Location of the small mammals sampling plots (black circles: forest locations; gray circles: open locations) and the associated climate stations (triangles) within five Natural Parks in the province of Barcelona (NE Spain).(shown in the inlet).

small endotherm, namely drought conditions affecting primary productivity and temperature and radiation potentially affecting thermoregulation. Habitats sampled in each plot were grouped in two classes (open-shrubby and closed-woody) according to shrew's habitat preferences (Torre et al., 2014). Three-dimensional vegetation structure of sampling plots was assessed by LiDAR (Light Detection and Ranging) technology, since variables obtained were better predictors than field-based variables for modelling ground-dwelling small mammal preferences (Jaime-González et al., 2017). Open habitats included post-fire vegetation communities dominated by Kermes oak *Quercus coccifera* scrublands. Closed woodlands included evergreen (*Pinus pinea*, *P. halepensis*, *Quercus ilex*) and deciduous (*Quercus pubescens*, *Alnus glutinosa*, *Salix* spp.) forests. All plots were located in the lowlands (95–750 m a.s.l.).

2.2. Data analysis

2.2.1. Population size and growth rate

Dependent (response) variables for analyses were the abundance of adults, the abundance of young individuals (weighing ≤7 g, Oliveira et al., 2016), the total abundance (adults + juveniles + undetermined), and the population growth rate (R_t):

$$R_t = \frac{\ln\left(\frac{N_{t+T}}{N_t}\right)}{T}$$

where N_t is the total abundance at the time t, N_{t+T} is the total abundance in the next sampling, and T is the weeks between the consecutive samplings (Diaz et al., 2010).

The independent (predictor) variables were altitude, habitat (categorical: forest or open area), sampling period (categorical: spring or autumn) and four meteorological variables (temperature, humidity, rainfall, and hydric deficit). Effects of the increase in the frequency and the intensity of extreme weather phenomena (Thomas et al., 2013; Datry et al., 2016) were tested by including the variance of meteorological variables as well as the mean. Three different time frames of three, six and 12 months before every sampling session were established to account for climatic effects on shrews' abundance. The three-month frame was based on the shrew breeding period, which is about seven weeks long from the gestation until weaning (López-Fuster, 2007), adding five more weeks owing the response of the surrounding vegetation and arthropods' population on shrew abundance (see Diaz et al., 2010, for a similar approach). The six-month frame analysed the period between consecutive sampling sessions, and the 12 months frame was used to account for the normal lifespan of shrews in the wild (Bouteiller and Perrin, 2000). The final selection of predictors incorporated to the models was assessed by paired correlations according to the strength of association (Spearman correlation: $\rho \geq 0.75$) and their ecological significance for the species. In addition, the multicollinearity was addressed by the Variation Inflation Factor (VIF) (Zuur et al., 2010), selecting sets of independent variables with VIF values <3. After the collinearity testing, the final set of suitable variables to model the abundance and growth rate responses for each time frame, 1) included season, altitude and habitat for all time frames; 2) excluded mean temperature and mean temperature for the three-month frame and 3) excluded mean temperature for the six-month frame.

Associations between response variables and environmental data were established using generalized linear mixed models (*glmer* function in R) assuming the distribution of Poisson errors for abundance data, and linear mixed models (*lmer* function in R) assuming Gaussian errors for population growth rate (Zuur et al., 2010, 2009). Sampling station was included as a random factor, and all independent predictors where scaled before fitting the models (Zuur et al., 2009, 2010). All possible model where built using the *dredge* function in the package MuMIn (Bartoń, 2015), and 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 where estimated (*model.avg* function from MuMIn package) including all best models, resulting in four final models, one for each dependent variable. Standardized estimates of significant predictors were obtained for all models (Zuur et al., 2009, 2010). Incidence rate ratios, which can be readily read as the changes in the response variable for a unit change in the continuous predictors, or as the factor by which the response variables change among the categories of the binomial predictors, where used to plot the effect of the significant predictors from the GLMMs. Estimates were used for the LMM. In all cases the standard error and the significance level was reported.

2.3. Population trends and demography

Population trends were assessed by means of TRIM software (Trends & Indices for Monitoring data, Pannekoek and Strien, 2005), which allows the analysis of time series of counts with missing observations. TRIM uses statistical procedures for estimation and testing that consider serial correlations and overdispersion of count data following a Poisson distribution. Since TRIM uses linear models for the logarithm of expected counts in contingency tables, indices of abundance of the species were Log $(X + 1)$ transformed to avoid error in calculations (Torre et al., 2018).

Multiple-season Occupancy models (Mackenzie et al., 2006) were used to ascertain parameters potentially influencing the population dynamics of shrews. These kinds of models allow Markovian changes in occupancy, in words, occupancy at a site in the present season depends on the state of occupancy at that site in the last season. In order to do so, models calculate some parameters like local colonization and local extinction probabilities to account for changes in occupancy between seasons. Following Mackenzie et al. (2006), colonization (γ) is the probability that an unoccupied site in season t is occupied by the species in season $t + 1$. Extinction (ε) is the probability that a site occupied in season t is unoccupied by the species in season $t + 1$. Furthermore, the models also take account of species imperfect detection by calculating detection probabilities (p).

The SEMICE monitoring program is especially suitable for applying such a kind of statistical models, since it consists in three surveys repeated in three consecutive days for every sampling site, and surveys are repeated in two annual seasons. Besides, detection probabilities for the involved species ($p = 0.77 \pm 0.03$: Torre et al., 2018) is much higher than the 0.3 threshold indicating high likelihoods for false negatives (Mackenzie et al., 2002).

We fitted 10 competing occupancy models (software PRESENCE, Mackenzie et al., 2002) to determine the parameters (local colonization and extinction probabilities) mostly affecting population dynamics of the species, once controlling for imperfect detectability. Two main factors were considered: habitat and season, owing the influence of these predictors in GLMM on species abundance and population growth rate. We started with a null model, considering that occupancy rate did not change along the study period, and conversely, the parameters colonization and extinction were zero, and setting detection probabilities constant. The models were improved adding habitat (site-dependent covariate) and sampling season, and also considering both altogether in the models (either additive or multiplicative effects).

3. Results

Almost 4600 small mammals were captured during the study period (2008–2017), belonging to seven different species: wood mouse (*Apodemus sylvaticus*, 59.9%), greater white-toothed shrew (*Crocidura russula*, 24.5%), Algerian mouse (*Mus spretus*, 8%), bank vole (*Myodes glareolus*, 4.1%), yellow-necked mouse (*Apodemus flavicollis*, 3%), common shrew (*Sorex araneus*, 0.4) and pygmy shrew (*Sorex minutus*, 0.04%). 813 individuals were identified as *C. russula* (1122 captures). Mean number of individuals in each sampling station and campaign was 3.21 ± 0.26 (SE, range 0–20) individuals. 61% of the captured individuals of *C. russula* were adults (495 individuals), followed by 25% of young (203 individuals) and 14% of individuals of undetermined age (115 individuals). Trap mortality only affected to 77 captures (6.9%). Annual rainfall decreased ($r = -0.46, p < 0.001$) and mean annual temperature increased ($r = 0.13, p = 0.04$) during the 10-year study period, thus hydric deficit increased ($r = -0.50, p < 0.001$). Mean relative humidity showed a curvilinear pattern, with maximums at both extremes of the series (Fig. S1). Rainfall variance ($r = -0.29, p < 0.001$) and temperature ($r = -0.16, p < 0.05$) decreased along the study period, whereas humidity variance increased ($r = 0.52, p < 0.001$).

Three-month time frame models for total shrew abundance considering all climatic predictors (temperature, humidity, hydric deficit, precipitation, and their variances) showed lower mean AIC values ($\overline{X}\,\text{AIC} = 829.06$), compared to the six-month ($\overline{X}\text{AIC} = 845.43$) and 12-month models ($\overline{X}$ AIC $= 842.77$, Table S1). Three-month models were also the best for juveniles and adults, suggesting that this was the time lag at which shrew populations responded more strongly to climate variation.

Habitat type and season were the main predictors of changes in shrew abundance and age structure (Table 1). Mean total abundance of shrews was four times higher in open habitats and the same was valid in the case of adults and juveniles (Table 2). Abundances were higher in autumn than in spring, especially in open habitats (Table 2, Fig. 2). In addition, shrew abundance was negatively affected by temperature and air humidity variance. The pattern was due to adult' responses, whereas juvenile abundance was not related to temperature but was negatively related to rainfall and altitude (Table 1, Fig. S2). Density-dependence was the main factor influencing seasonal changes in growth rates (Fig. 3). Open habitats were characterised by their higher vegetation cover and volume at the floor level, whereas forests showed most of the cover at the canopy (Table 2).

Mean abundance of shrews did not show a significant trend along the study period ($r^2 = -8.7\text{e} - 05$; $p = 0.32$; Fig. 3). TRIM analyses confirmed this result (imputed index: 0.00 ± 0.0064SE, $Chi^2 = 265.02$, $p = 0.02$, overdispersion = 1.02, serial correlation = 0.02). Nonetheless, including habitat as a fixed factor improved model fit ($Chi^2 = 207.86$, $p = 0.37$, covariate effect: Wald test = 35.44, $df = 19$, $p = 0.012$), suggesting that population dynamics may differ among habitat types. In fact, open habitats showed a slight increase ($r = 0.22$), whereas forest populations showed a decline ($r = -0.33$) along the study period, but none of the trends where statistically significant. Population dynamics showed a more consistent pattern in open habitats (clearer saw-tooth pattern, with maximum in autumn and minimum in spring) than in forests.

Fitted occupancy models (Table 3) indicate the overwhelming importance of habitat type, since the seven first selected models included this factor in combination to other parameters, always showing a better fit than the null model. The first model showed high statistical support (63.4%). Occupancy (Ψ) was static along seasons and years, as well as colonization (γ) and extinction (ε) probabilities, whereas detectability (p) changed along seasons. Occupancy rates were higher in open habitats ($\Psi = 0.96 \pm 0.02$) than in forests ($\Psi = 0.65 \pm 0.07$) throughout the study period (Fig. 4). Accordingly, colonization and extinction (and, hence, persistence) were also affected by habitat with no change along the study period (lower support for models including either additive -habitat+season- or interactive – habitatxseason- factors; Table 3). Probability of colonization was three times higher in open habitats ($\gamma = 1.0 \pm 0.0$) than in forests ($\gamma = 0.34 \pm 0.07$) and probability of local extinction was five times lower ($\varepsilon = 0.039 \pm 0.031$ and $\varepsilon = 0.152 \pm 0.046$ for open and forest, respectively). Persistence of

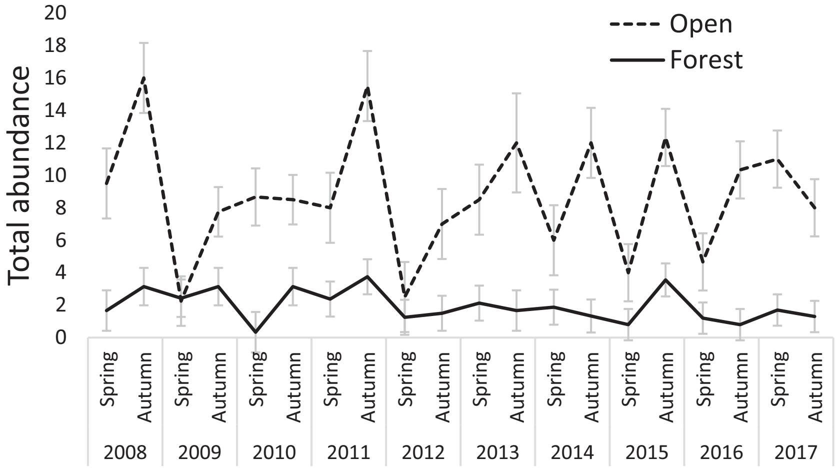

Fig. 2. Mean total abundance (±SE) of shrews along the study period (2008–2017) according to habitat type (open of forest plots). Two sampling sessions per year were conducted in relevant seasons for the species (spring and autumn).

populations was always guaranteed in open habitats due to high colonization rates and low extinction probabilities, but persistence was less guaranteed in forests due to low colonization rates and relatively high local extinction probabilities. In fact, shrew's populations in some sampling sites surrounded by dense forest matrices have become locally extinct during this study (Oak-tree forest; $r = -0.72$, $p < 0.001$, $n = 20$). Detectability was higher in open habitats ($p = 0.85 \pm 0.06$, range 0.64–0.96) than in forests ($p = 0.55 \pm 0.11$, 0.26–0.86) throughout the years (Fig. 4). Detectability was associated to abundance in both habitats (Open: $r = 0.49$, $p < 0.05$; Forest: $r = 0.66$, $p < 0.01$). The model with most support informed about the state of the population dynamics: a system in equilibrium, where the occupancy levels expected ($\psi_{eq} = \gamma/(\gamma + \varepsilon)$) were similar to the observed occupancy rates in both habitats.

4. Discussion

This is, to our knowledge, the first study dealing with population dynamics of the Greater white-toothed shrew in Mediterranean natural habitats. A relatively long time series (10 years), along with a moderate number of sampling sites (18), allowed reaching consistent patterns about the role of either exogenous (climate, habitat) and endogenous (density-dependence) factors on the population dynamics of *C. russula*. Advances on population dynamics of this shrew have been performed in Central Europe, where occupancy mostly depends on non-natural habitats (i.e., gardens) and human settlements during the unfavourable seasons (Ehinger et al., 2002; Jaquiéry et al., 2008). These authors realised that habitat quality was certainly to affect all processes determining metapopulation dynamics in greater white-toothed shrews. However, since populations in Central Europe are considered as marginal (i.e., at the elevation limit of its range) and frequently fragmented due to spatial isolation (Ehinger et al., 2002), wild generalisation of dynamics towards the main distributional area of the greater white-toothed shrew (Mediterranean Spain and France) could be unlikely.

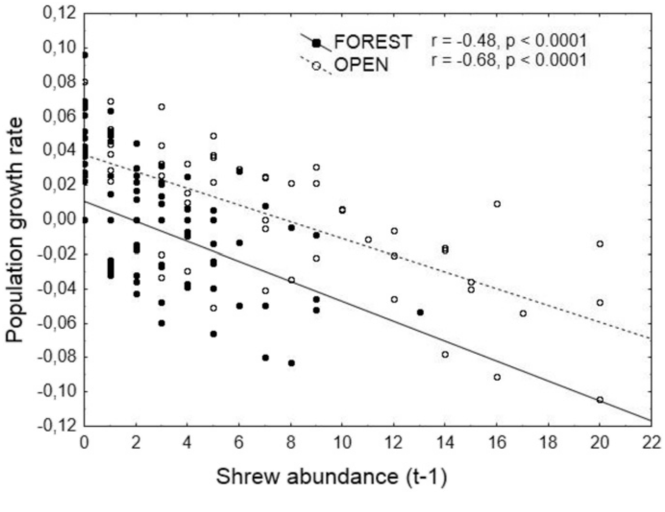

Fig. 3. Density-dependence in population growth rates according to habitat type.

Contrary to expectations, population size and dynamics of a small endotherm were little affected by ongoing climate change in its Mediterranean core area. Expectations were based on significant recent changes in climate, predicted indeed by models (Mariotti et al., 2015), and on the sensitivity and fast response of the species to environmental conditions (Ehinger et al., 2002; Jaquiéry et al., 2008; Torre et al., 2014). Rather, habitat traits and strong density dependence were the main predictors of populations fluctuations. Mitigation of climate change effects by means of habitat selection are usually interpreted as based on the benign microclimate effects of complex vegetation (i.e. forest habitats; Scheffers et al., 2014; De Frenne et al., 2019). In addition, forests encroachment on former open habitats due to land abandonment have further increased these mitigation effects of climate change in the case of the Mediterranean region (Seoane and Carrascal, 2008; Torre et al., 2015). Open habitats can also buffer potential negative effects of climate change, as demonstrated by the case study presented here.

Patterns observed can be considered as robust, bearing in mind that population parameters were calculated considering imperfect detection. Indeed, *C. russula* can be considered a good study model owing its high trappability (and detectability) with live-trapping methods both in the study area and elsewhere (Bouteiller and Perrin, 2000; Torre et al., 2018). Detectability reached mean values well above the minimum threshold ($p = 0.3$, Mackenzie et al., 2002) to avoid underestimates in occupancy even in periods/habitats with low abundance.

Shrew population dynamics in the study area showed relatively regular seasonal oscillations, with lows in spring and highs in autumn, suggesting a relationship between demography and the environment (Reed and Slade, 2006). This pattern is consistent with shrew's breeding phenology (early spring to early autumn, López-Fuster, 2007) that implies recruitment of juveniles to the population in autumn (Jeanmaire-Besançon, 1988). Spring lows were reached after winter, considering that the latter could be a limiting season due to less food available (invertebrates are less active) and harsher climatic conditions (Fargallo et al., 2009). This pattern was fully expected considering that shrews

Table 1
Best mixed models for categorical and continuous predictors on shrew abundance and population growth rate (only three-months time frame models are shown). Standardized estimates are given for fixed effects of the models and the SD of the estimates in parenthesis. P(z) indicates significant estimates.

	Abundance			Adults				Juveniles	Growth ratio
Models built	64			64				64	128
Model family	GLMM			GLMM				GLMM	LMM
Data distribution	Poisson			Poisson				Poisson	Gaussian
Model number	**1**	**2**	**3**	**1**	**2**	**3**	**4**	**1**	**1**
(Intercept)	−0.32	−0.31	−0.31	−0.61*	−0.54	−0.61*	−0.61*	−1.89***	−0.01*
	(0.30)	(0.29)	(0.30)	(0.29)	(0.29)	(0.29)	(0.29)	(0.28)	(0.00)
Season-Autumn	0.67***	0.67***	0.66***	0.43***	0.28**	0.43***	0.44***	1.19***	
	(0.10)	(0.10)	(0.10)	(0.12)	(0.10)	(0.12)	(0.12)	(0.19)	
Habitat-open	1.56**	1.54**	1.55**	1.52**	1.55**	1.52**	1.52**	1.44***	0.04***
	(0.51)	(0.49)	(0.51)	(0.47)	(0.48)	(0.47)	(0.47)	(0.37)	(0.01)
Humidity variance	−0.18**	−0.18**	−0.18***	−0.15*	−0.18**	−0.15*	−0.15*	−0.32**	
	(0.05)	(0.05)	(0.05)	(0.07)	(0.06)	(0.07)	(0.07)	(0.12)	
Temperature variance	−0.19***	−0.19***	−0.18**	−0.13		−0.13	−0.14	−0.27*	
	(0.05)	(0.05)	(0.06)	(0.07)		(0.07)	(0.07)	(0.11)	
Altitude		−0.20				−0.11		−0.50*	
		(0.23)				(0.22)		(0.20)	
Cumulative rainfall			−0.03				0.02	−0.24*	
			(0.05)				(0.06)	(0.09)	
Abundance(t-1)									−0.03***
									(0.00)
Log likelihood	−408.04	−407.67	−407.87	−344.45	−346.25	−344.32	−344.36	−229.41	415.15
AIC	828.09	829.34	829.75	700.90	702.50	702.64	702.71	474.81	−820.31
Delta	0.00	1.25	1.66	0.00	1.60	1.74	1.81	0.00	0.00
Weight	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Num. obs.	211	211	211	211	211	211	211	211	188

*** $p < 0.001$.
** $p < 0.01$.
* $p < 0.05$)

can reproduce only during the most energetically favourable part of the year as determined by ambient temperature as well as food availability (Bronson, 2009). This may also explain the small and negative short-term effects of climate variables (variability in air temperature and humidity, and rain fell three months before sampling) on shrew abundance, recuitment and growth rate: this variability may have precluded the adjustement of reproductive effort to environmental conditions thus decreasing effort, increasing juvenile mortality, or both (Campbell et al., 2012).

Population growth rates further highlighted that seasonality was a relevant factor for shrew dynamics, although density-dependence was the most important factor. This could be expected according to the social organisation system of this shrew (territorial and mostly monogamous, Cantoni and Vogel, 1989) and to the fact that self-regulation was also affected by season (higher in autumn than in spring). During the breeding season pairs defended their territories, but during winter shrews gathered in communal nests (Cantoni and Vogel, 1989), thus relaxing interactions between individuals. Seasonal dynamics seems to be intrinsically determined since it is similar under contrasting climatic conditions (i.e., in mountains of Central Europe: Jeanmaire-Besançon, 1988). As small endothermic species, white-toothed shrews were constrained by cold temperatures so that climate warming would produce positive effects (i.e. range expansions both northwards and upwards). Despite future scenarios of thermal favourability, trends for other important variables like water availability (López-Fuster, 2007) will be negative. Indeed, the populations studied were negatively affected by short-term extreme climatic events as exemplified by humidity and temperature variance, although no longer-term trends in response to climate are still evident. Population growth rate links all aspects of density dependence, resource dependence, and interspecific and intraspecific interactions (Drake, 2005). Population growth rates were inversely related to climatic variability, suggesting that the increase in extreme weather events resulting from climate change (Woodward et al., 2015) might yield negative population outputs for the target species and other small endotherms.

Open habitats showed higher mean abundance (either for adults or juveniles), higher population growth rates, higher occupancy rates, higher colonization rates, and lower extinction rates, throughout seasons (spring and autumn) and years (2008 to 2017). Open habitats were a set of burned sites (the last plot was burned in the early years of this century) covered by re-sprouting short vegetation (shrubs <1.5 m tall) and without canopy cover. Forests were habitats covered by a thick canopy, and with short vegetation cover (short shrubs) almost lacking. These contrasting habitat profiles represented significant differences in suitability for shrews, regarding several biotic (food, cover, predation) and abiotic (climate) factors (Alcántara de la Fuente, 1992; Alonso et al., 1996). There are -at least- three (non-mutually exclusive) reasons why open-shrubby habitats could be considered as high-quality habitats for shrews, and forest could be considered as low-quality habitats. In open-shrubby habitats, shrews experienced low predation risk (more understory cover) and low predation pressure (less predators) than in forests (Torre and Diaz, 2004); high vegetation volume of short vegetation (understory vegetation) in open habitats

Table 2
Mean values for total shrew abundance (adults + juveniles + undetermined), adult and juvenile abundance according to habitats and seasons. Mean vegetation profiles and mean altitude of plots are also shown. SD in parentheses.

Variable	Open (n = 5)		Forest (n = 11)	
	Spring	Autumn	Spring	Autumn
Adults	4.15 (2.75)	6.15 (3.70)	1.09 (1.54)	1.27 (2.02)
Juvenils	1.42 (1.94)	3.11 (2.93)	0.27 (0.61)	0.64 (1.28)
Total	6.27 (4.70)	10.38 (5.32)	1.57 (1.99)	2.26 (2.79)
Altitude m	342 (156.15)		352.81 (158.51)	
Vegetation cover at 0.15–1.5 m (%)	54.52 (21.51)		4.93 (4.73)	
Vegetation cover at >1.5 m (%)	12.53 (13.02)		90.87 (8.29)	
Vegetation cover at >2.5 m (%)	6.09 (7.34)		87.92 (9.34)	

Table 3
Competing occupancy models for greater white-toothed shrews ordered according to their statistical fit based on Akaike Information Criterium (AIC). Model support (AIC weight%), Model Likelihood, and number of parameters are also shown (delta AIC ≤ 2 highlights models with equal support). Ψ: occupancy; γ: colonization; ε: extinction p: detectability.

No	Model	AIC	deltaAIC	AIC wgt (%)	Model Likelihood	no.Par.
1	$\psi(\text{hab})\gamma(\text{hab})\varepsilon(\text{hab})p(\text{hab} + \text{season})$	712.96	0	63.41	1	27
2	$\psi(\text{hab})\gamma(\text{hab})\varepsilon(\text{hab})p(\text{hab})$	715.21	2.25	20.59	0.3247	8
3	$\psi(\text{hab})\gamma(.)p(\text{hab})$	715.8	2.84	15.33	0.2417	5
4	$\psi(\text{hab})\gamma(\text{hab} + \text{season})\varepsilon(\text{hab})p(\text{hab})$	722.14	9.18	0.64	0.0102	26
5	$\psi(\text{hab})\gamma(\text{hab})\varepsilon(\text{hab} + \text{season})p(\text{hab})$	730.96	18	0.01	0.0001	26
6	$\psi(\text{hab})\gamma(.)\varepsilon(.)p(.)$	758.17	45.21	0	0	5
7	$\psi(\text{hab})\gamma(\text{hab} + \text{season})\varepsilon(\text{hab} + \text{season})p(\text{hab} + \text{season})$	760.54	47.58	0	0	104
8	$\psi(.)\gamma(.)\varepsilon(.)p(.)$	760.56	47.6	0	0	4
9	$\psi(\text{hab} + \text{season})\gamma(.)p(.)$	853.96	141	0	0	23
10	$\psi(\text{habxseason}),\gamma(.),p(.)$	879.84	166.88	0	0	42

could be related to primary production and food availability for shrews (Torre et al., 2007; Carrilho et al. 2017); Since shrews rely on energy saving mechanisms to cope with seasonal changes in a Mediterranean climate (Oliveira et al., 2016), thermal restrictions could be alleviated (either for cold or hot temperatures) using more favourable microclimatic conditions found under dense vegetation in open habitats. Predation risk and predation pressure seem to be lower in Mediterranean open-shrubby than in forests habitats (Torre and Diaz, 2004), where predator communities are well structured and composed by species whose diet is mostly based on small mammals (i.e., *Genetta genetta* and *Strix aluco*; Torre et al., 2013, 2018). A short study of the carnivore community performed by remote photography between January and August of 2019 in the study area showed that forests and tall shrublands showed high number of independent contacts of five species (*Martes foina*, *Vulpes vulpes*, *Meles meles*, *G. genetta* and *Mustela nivalis*), whereas short shrublands and crops showed less contacts of three species

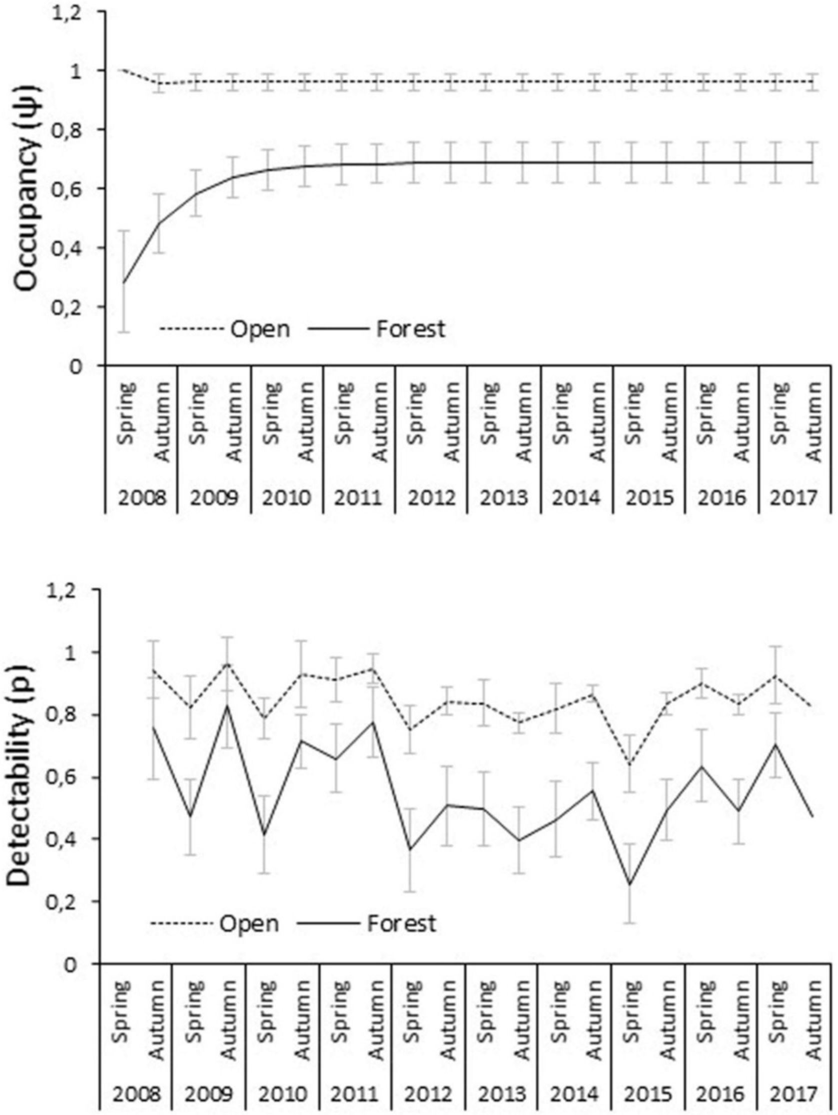

Fig. 4. Occupancy probabilities (ψ) and detectability (p) of shrews according to habitat type along the study period. Whiskers indicate standard errors.

(*V. vulpes*, *M. foina* and *M. meles*). Predators negatively affected population growth rates of shrews in semi-natural Mediterranean grasslands (Fargallo et al., 2009), and the lack of interactive effects between habitat and season on abundance and population growth rates pointed out at predation rather than food or termorregulation as explanatory factors. Predation is usually a density-independent factor if mostly due to generalist predators (see Fargallo et al., 2009 and references therein), whose effects should then be additive to density-dependent factors. Food or shelter availability are instead density-dependent, so that interactive rather than additive affects of habitat type should have been expected if these factors would have mediated among-habitat differences in habitat quality.

High-quality habitats for shrews (i.e., those with higher mean abundance and occupancy) may sustain populations with lower extinction rates and/or higher colonization rates (Torre et al., 2014), apparently due to good conditions for population growth during favourable seasons and/or years (Jaquiéry et al., 2008). Nonetheless, apart from habitat quality, populations can be affected by the suitability of habitat patches and by landscape factors such as the isolation or connectedness of the habitat fragments (Reed et al., 2014), surely affecting dispersal and genetic structure (Vuilleumier and Fontanillas, 2007). We did not attempt to analyse these topics, which would also affect population dynamics of shrews. However, we might expect that open habitats will be considered as sources in the metapopulation system studied, owing the high persistence (1 – local probability of extinction, Mackenzie et al., 2006) of populations in these habitats, whereas forest will be considered as sinks due to lower values of persistence. Expected increasing rates of forest maturation and afforestation (Gil-Tena et al., 2010) will affect negatively the species (re)colonization process through unbalanced source–sink dynamics according to the lower availability of source habitats (i.e., open-shrubby). This could be particularly true in low quality forest patches surrounded by extensive forest matrices, where the species will be more prone to local extinctions due to lower colonization probability and higher distance to a neighbouring source. Reverting this natural process to recover open habitats will effectively fight against potential range changes associated with landscape dynamics resulting from rural land abandonment (Regos et al., 2016).

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

Conceptualization and sampling design: IT; Field work: IT; Project Administration and funding: AA; Formal analyses: IT & JB-L; Initial draft: IT & JB-L; Supervision, edition, and writing of the final draft: IT & MD.

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