Additive effects of climate and vegetation structure on the altitudinal distribution of greater white-toothed shrews Crocidura russula *in a Mediterranean mountain range*

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Acta Theriologica

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ORIGINAL PAPER

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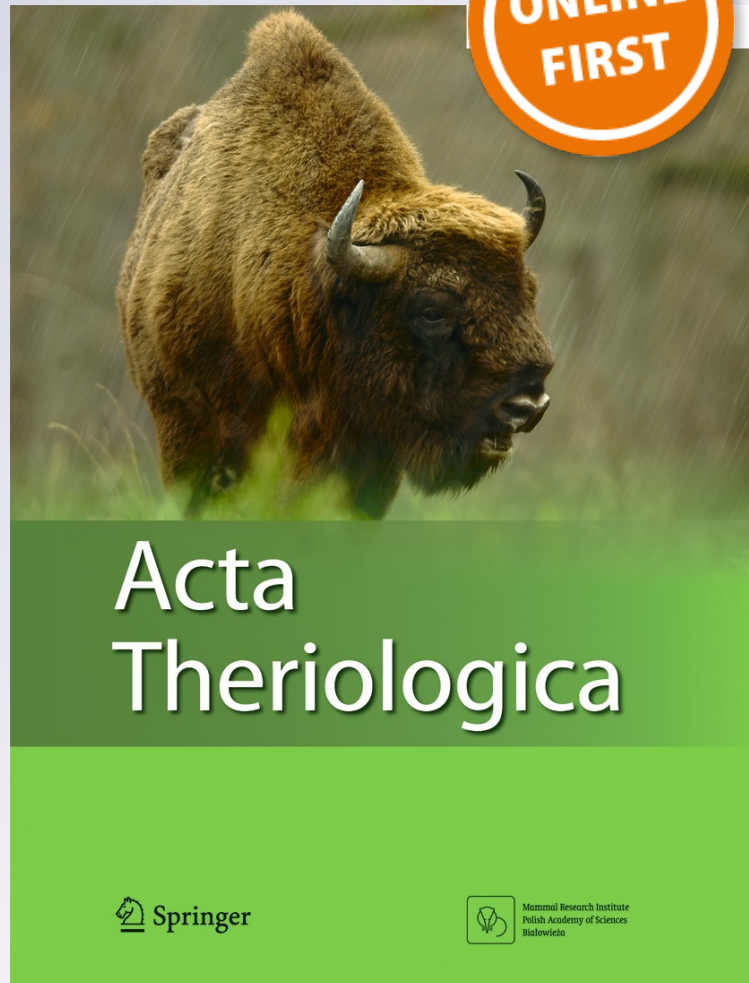
Ignasi Torre · Mario Díaz · Antoni Arrizabalaga

Abstract Environmental variation along geographic gradients determines the distribution of animals and plants trough both direct and indirect effects. We analyze the relative contribution of climate and vegetation structure variations along a Mediterranean altitude gradient on the patterns of abundance and occurrence of the greater white-toothed shrew *Crocidura russula*, a generalist small mammal whose distribution is constrained by cold conditions. Sampling was performed from February 1995 to July 1997 on nine plots covering a wide altitudinal gradient (540–1550 ma.s.l.). Structural equation models for the direct and indirect effects of climate and vegetation on shrew density and occupancy rates showed a stronger effect of vegetation structure (53 %) than direct climate effects (38 %) on shrew distribution. Shrews were more abundant in the warmer lowland sites, but were able to colonize highland cold areas by selecting habitats with well-developed understory vegetation (low shrubs or bracken). Vegetation effects were additive to climatic restrictions, seemingly providing more favorable microclimatic, and presumably food, conditions under shrub cover. Results indicate that predictions of range changes for shrews under climate change scenarios may underestimate expected range expansions under the current conditions of general land abandonment and shrub encroachment.

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Introduction

The existence of patterns of distribution and abundance of organisms along environmental gradients has been known for centuries. Within areas delimited by dispersal barriers, the distribution of most widespread species appear to be bounded by latitudinal, longitudinal, or altitudinal changes in abiotic factors such as air temperature or water availability (Lomolino et al. 2010). Abiotic gradients can limit distribution ranges directly, by delimiting in space the range of abiotic conditions in which the physiological requirements of the involved species can be met, or indirectly, by influencing other habitat requirements such as food and shelter (Brown 1995). The relative importance of direct and indirect effects of abiotic gradients on range limits should depend on the behavioral and physiological flexibility of the involved species (Helmuth et al. 2005). Specifically, the importance of direct effects should decrease as organisms increase its ability to modulate its internal and external environment through physiological homeostasis and behavioral micro-habitat selection (Helmuth et al. 2005; Thuiller et al. 2011; Devictor et al. 2012). Plants and small ectothermic animals should then be more directly constrained by abiotic soil and climate gradients (Thuiller et al. 2011; Stefanescu et al. 2011), whereas large endothermic animals (birds and mammals) should respond mainly to the indirect effects of abiotic gradients on the distribution of their habitat requirements (Vallecillo et al. 2009; Møller et al. 2010; Devictor et al. 2012). Small endotherms, such as passerine birds, bats, and small mammals, would then show a mixed dependency to

direct and indirect effects of abiotic gradients (Møller et al. 2010; Rebelo et al. 2010).

Mountain ranges have been frequently used to investigate how abiotic gradients influence the distribution of organisms, as altitudinal and latitudinal patterns are assumed to respond to roughly the same environmental factors (Jump et al. 2009; Lomolino et al. 2010). Altitudinal changes in abiotic conditions also produce changes in vegetation and land uses, which in turn can influence the distribution of animal and plants (Koerner 2007). The distribution of many organisms has been found to be strongly associated to altitudinal climatic gradients, to the extent that their elevation ranges are shifting upwards in response to global climate change (Dirnbock et al. 2011). Analyses on the dependency on climatic and vegetation variables along elevation gradients may thus help to disentangle direct and indirect effects of climate change on species distributions.

The greater white-toothed shrew *Crocidura russula* is a small insectivorous mammal widely distributed in southwestern Europe, ranging from Iberia to northern Germany and the Netherlands (López-Fuster 2007). The species seems to have originated in Africa under warm climatic conditions, then spreading northwards following glacial retreat (Brändli et al. 2005). These origins, together with small body size and endothermy, implies a high dependency on thermal conditions (Cantoni and Vogel 1989), to the extent that its distribution appears to be limited by its inability to tolerate colder northern climates (Churchfield 1990). Nonetheless, greater white-toothed shrews have been able to colonize cold regions due to its generalist food habits and opportunistic microhabitat selection (Genoud and Hausser 1979; Churchfield 1990; Alcántara 1992; Alonso et al. 1996; Jaquiéry et al. 2008). Likewise, the species has wide distributions along elevation gradients throughout its range, usually showing declining trends with altitude (Ehinger et al. 2002) and overwintering dependence of human settlements high in northern mountains (i.e., Jaquiéry et al. 2008) as well as limitations linked to water availability in southern lowlands (Sans-Coma et al. 1987; López-Fuster 2007).

Greater white-toothed shrew distributions along altitudinal gradients are thus good study systems to analyze the relative contribution of direct and indirect effects of abiotic conditions on patterns of animal distribution. In this paper, we tested whether the patterns of occurrence and abundance of this species across a strong environmental gradient on a Mediterranean mountain range were associated to climatic and vegetation structure gradients, also analyzing indirect associations among climate, vegetation, and shrew patterns. Direct responses to climatic factors (i.e., temperature) would produce a progressive decrease of the abundance and occurrence of shrews with elevation, whereas indirect effects mediated by selection of suitable microhabitats would modulate this gradient allowing shrews to occupy cold highlands. Variance partitioning among direct and indirect effects will measure the relative dependency of the species on climatic and habitat traits.

Materials and methods

Study area

The study was carried out in the Montseny Natural Park and Reserve of the Biosphere (Barcelona province, NE Spain; 41° 46′ N, 2°23′ E; 29,960 ha; Fig. 1). The main orographic unit in the study area reaches moderate elevation (Turó de l'Home, 1,714 m a.s.l.) and is partially isolated from the surrounding mountains. The topography and climate vary markedly with elevation, and nearness to the sea produces a mild climate without strong thermal oscillations. Rainfall peaks in spring and fall, with moderate drought periods in summer (typical of the Mediterranean climate). Average annual rainfall rises from 700 mm in the lowest Mediterranean localities to 1,200 mm at mountaintops. Mean annual temperatures range from 7 to 15 ° C. Almost all the surface of the area is covered by forests (80 %) and other natural habitats (scrublands, grasslands, 15 %). A small fraction of the area is devoted to agriculture (4 %), and only 1 % is covered by human settlements. This mountain range has particular topographic and climatic characteristics that confer remarkable biogeographic interest to the plant and animal communities typical of northern, mid-European latitudes that are also found in this Mediterranean massif (de Bolòs 1983; Terradas and Miralles 1986).

Small mammal sampling

Sampling was performed from February 1995 to July 1997 on nine plots during eleven trapping sessions of 3 days each, collectively lasting 33 days. Every plot was sampled by a 7×7 trapping grid, with 49 Sherman traps (Sherman folding small animal trap; $23 \times 7.5 \times 9$ cm; Sherman Co., USA) mostly spaced 15 m apart (covering 1 ha), and opened for three consecutive nights. Plots had an effective surface of 1.1 ha (Krebs 1999). The plant communities sampled were characteristic of the three biogeographic regions found in the massif (de Bolòs 1983). Mediterranean vegetation was represented by three plots covered by evergreen oak woodlands of *Quercus suber* and *Quercus ilex* and a wide riparian forest of *Alnus glutinosa*. Eurosiberian vegetation was represented by four plots covered by *Fagus sylvatica*, *Quercus petraea*, or *Populus nigra* forests, and *Calluna vulgaris–Erica scoparia* shrubland. Finally, the Boreo-subalpine vegetation was represented by an *Abies alba* forest plot and a *Juniperus communis nana* scrub plot. The nine plots sampled were situated along an elevation gradient from 540 to 1,550 m a.s.l.

All grids were sampled in five occasions in 1995, in late winter (February–March), spring (April–May), summer

Fig. 1 Situation of the nine plots within the study area (Montseny Natural Park). *Numbers* are the same as in Table 1. The *lower inset* shows the location of the study area within the Catalonia autonomous region (NE Spain), and the *upper inset*, the location of Catalonia within southwestern Europe
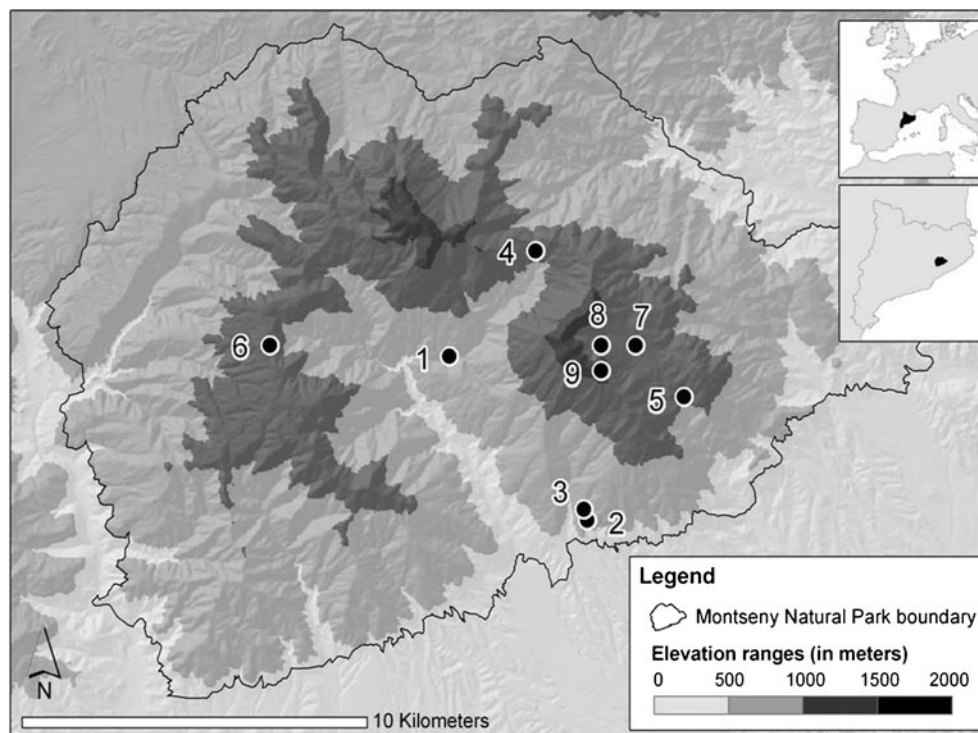
(June–July and August–September), autumn (October–November), and winter (December); in four occasions in 1996, in winter (January), spring (April–May), summer (June–July), and autumn (November–December); and in two occasions in 1997, in spring (March) and summer (July). The sampling calendar was determined by the availability of traps and manpower to sample grids close to new moon, to avoid moonlight effects on small mammal trappability (Díaz 1992). Low availability in 1995 and 1996 forced us to sample half grids during the new moon of a month and the other half in the following month, taking care to sample grids distributed along the whole altitudinal gradient in each month. Fortunately, weather, as well as moonlight, was roughly similar among months within the same altitudinal bands for each sampling occasion, so that we consider that this sampling shortcoming would have not biased results as compared to having sampled all altitudes during the same new moon period. Variation within altitudinal bands due to e.g., effects of aspect on temperature, radiation, and rainfall were included in the models used to generate the interpolated climatic data used here (see Ninyerola et al. 2003). Manpower limitations also precluded more than one revision of traps per sampling night. This revision was done early in the mornings of the days following each trapping night. Some mortality at traps was noticed but, unfortunately, we did not record it in detail at either the trap or the grid level. Every plot was then operative through 1,617 traps/night. All plots were situated within large habitat patches, and all habitats were interconnected by the extensive forest matrix. Minimum distance between

plots was 400 m and maximum 10,600 m, and all plots were situated within an area of 4,500 ha (Fig. 1). The *Calluna vulgaris–Erica scoparia* shrubland plot was located farther west and was slightly larger (2.25 ha, and 30-m spacing among traps) than the others because it comes from a monitoring scheme started in the early 1990s. White-toothed shrew abundances were recalculated to individuals per hectare to allow unbiased comparisons among the nine plots.

Traps were baited and rebaited when necessary (when the bait was eaten) with a piece of apple and a mixture of tuna, flour, and oil. This bait was proven to be effective for shrews at least in Mediterranean mountain conditions (e.g., Torre et al. 2007). The small mammals caught were identified to species, marked by toe clipping (Gurnell and Flowerdew 1990; Jaquiéry et al. 2008), and released at the point of capture. We used counts (e.g., the number of different individuals trapped within 3 days, Morris 1996) as an estimate of population size in each study plot, assuming that the unseen proportion of the population is constant and that counts and estimates yielded similar results (Slade and Blair 2000).

The vegetation structure of each plot was recorded in the summer of 1996 by visually estimating height and cover in a 5-m-radius circle centered on alternate traps in the trapping grid, and then by averaging the values obtained from each plot. The variables measured were: the cover of rocks, trees, shrubs, herbaceous plants, mosses and leaf litter, all measured as a percentage of area covered (in percent), and the height of trees, shrubs, and herbaceous plants measured in meters. We consider that these variables will show little temporal variation during our 3-year study period due to

the slow growing rates of Mediterranean woody plants and the strong correlations between rock and woody plant variables and variables related to herb, moss, and litter covers (see Torre and Arrizabalaga 2008 for further details).

Mean climatic data were obtained from the Catalan Climatic Atlas (Ninyerola et al. 2003), with a spatial resolution of 180 m. We used data on mean temperature, mean cumulative rainfall, mean evapotranspiration, mean humidity (Thornthwaite index) and mean water deficit, from series obtained during the last two decades (Ninyerola et al. 2003). Mean climate features of the sampling plots were obtained from the GIS Miramon (http://www.creaf.uab.es/miramon), after combination of the geographic coordinates of plots with isocline maps of environmental variables.

Data analysis

Mean density estimates of white-toothed shrews were calculated after the eleven sampling sessions conducted on the nine plots. We considered these estimates as good surrogates of real densities since sampling was performed along 3 years with strong interannual variation in rainfall and productivity (Díaz et al. 2010). We relied on population density as the simplest indicator of habitat quality for white-toothed shrews (Wheatley et al. 2002, and references therein). Other parameters, like breeding performance, survival, and immigration, may be more adequate than density to test for wildlife–habitat relationships (Van Horne 1983; Wheatley et al. 2002), but were not considered here due to the low number of individuals trapped in many plots throughout the study period. We also considered site occupancy rate as a dependent variable to check for either cyclical or directional altitudinal variations in distribution range along the study period (see Jaquiéry et al. 2008 for a similar approach). Site occupancy was the number of sampling sessions in which shrews were captured on a plot divided by the total number of sampling sessions (Jaquiéry et al. 2008).

Spatial variation of mean white-toothed shrew density in the Montseny mountain range was assessed by statistical path analysis, an extension of multiple regression which was developed to decompose correlations into different pieces for interpretation of effects (Everitt and Dunn 1991). Independent variables for analysis were vegetation structure and climate. The rationale of using path analysis instead of conventional regression was that climate may have both direct (mediated by physiological demands) and indirect (mediated by effects on vegetation structure and food supply) effects on the target species (see above). To avoid multicollinearity of independent variables, we used principal components analysis (PCA) to obtain orthogonal components that were interpreted as gradients of vegetation structure and climate. The Kaiser criterion (Kaiser 1960) was used to determine the number of principal components extracted (eigenvalues>1).

We tested the significance of regression models by means of structural equation modeling (SEM) software (Amos 5.0, Arbuckle 1983–2003). The appropriateness of models was assessed by means of the goodness of fit index (GFI) which ranges from 0 (maximum lack of fit) to 1 (maximum fit), and the matrix permutation test (using 1,000 permutations, Hesterberg et al. 2005). In order to test the reliability of the parameter estimates of the SEM, we used bootstrapping techniques creating many resamples by repeatedly sampling (200 resamples, the default option in the program used) with replacement from the only random sample to obtain information about the sampling distribution (Hesterberg et al. 2005). Permutations tests and bootstrapping estimates are implemented in the Amos software (Arbuckle 1983–2003).

Prior to analysis, all variables were transformed to reach homoscedasticity and normality. Frequency variables were arcsin-transformed, and continuous variables were log-transformed (Zar 1996).

Results

Climate and vegetation patterns

Mean values for climatic and vegetation structure variables measured at the nine plots are shown in Table 1. A PCA was performed to summarize climate attributes of plots. The single principal component extracted accounted for 82 % of the variance in the original variables and was positively correlated to water deficit, temperature, and evapotranspiration ($r=0.95$, 0.95, and 0.86, respectively, $p<0.05$), and negatively correlated to Thornthwaite's moisture index and rainfall ($r=-0.97$ and -0.91; $p<0.05$). This principal component was also negatively correlated with elevation ($r=-0.88$, $p<0.002$) and latitude ($r=-0.80$, $p=0.009$), but was not correlated with longitude ($r=-0.10$, $p=0.77$).

The PCA carried out to summarize vegetation structure accounted for 90 % of the variance in the original variables (Table 2). The first component was positively correlated to moss, tree, and rock cover; the second was positively correlated to tree height and to cover of litter; the third was positively correlated to herbaceous cover and height, and to cover of shrubs; and the fourth was negatively correlated to shrub height (Table 2).

Number of white-toothed shrews captured and patterns of density

During the study period, we captured 1,919 small mammals of nine species, 218 of which being white-toothed shrews (11.36 %). The study area received twice as rainfall in 1996 as during 1995 and 1997, being autumn the season with the highest cumulative rainfall (Díaz et al. 2010). Wood mice (*Apodemus* sp.) were dominant in all habitats studied, with

Table 1 Number of different greater white-toothed shrews captured, site occupancy rate (defined as the number of sampling sessions during which shrews were captured on a plot divided by the total number of sampling sessions, which was 11 in all cases), and mean values for climatic and vegetation structure variables measured at the nine plots

Variables / Plot Dominant Tree/Shrub species	1 Alnus glutinosa	2 Quercus suber	3 Quercus ilex	4 Populus nigra	5 Quercus petraea	6 Calluna vulgaris– Erica scoparia	7 Fagus sylvatica	8 Abies alba	9 Juniperus communis
No. captures (all species)	274	275	229	194	154	298	173	192	118
No. captures (C. russula)	38	35	19	27	3	68	1	4	23
Maximum density	7.41	9.88	4.94	9.88	2.47	6.67	1.23	2.47	8.64
Site occupancy rate	1.00	0.72	0.81	0.80	0.18	1.00	0.09	0.27	0.72
Elevation (m)	540	550	600	1060	1070	1150	1150	1450	1550
Rainfall (mm)	975	825	825	1025	1025	875	1075	1075	1075
Temperature (°C)	10.5	13.5	13.5	9.5	11.5	9.5	9.5	8.5	7.5
Water deficit	50	150	150	50	50	50	0	0	0
Rock cover (%)	18.05	2	7.24	1	15.85	7.24	8.65	31.76	18.4
Tree cover (%)	86.19	49.89	51.03	40.2	35	10	70.5	50.83	0
Tree height (m)	10.35	6.43	10.17	12.5	8.27	3	12.65	20.5	0
Shrub cover (%)	23.33	25.04	45.9	25.5	14.26	45.9	12.49	12.39	59.89
Shrub height (m)	1.24	1.22	0.77	0.76	1.01	1.25	0.3	0.35	0.32
Herbaceous cover (%)	41.58	11.58	3.02	87.7	21.88	25	18.23	15.15	33.26
Herbaceous height (m)	0.37	0.29	0.07	0.92	0.14	0.2	0.095	0.038	0.084
Mosses cover (%)	11.68	2	5.78	2	4.53	2	2.45	5.79	1.4
Litter cover (%)	78.66	45.6	73.14	69	53.4	25.3	69.52	40.39	10.62

1,356 individuals trapped (70.6 %). Numbers of shrews captured were significantly positively related to overall small mammal numbers among plots ($r=0.75$, $p=0.021$, $n=9$; Table 1), and not significantly to numbers of dominant *Apodemus* sp. mice ($r=0.53$, $p=0.142$). White-toothed shrews were trapped at least once in all plots during the study period. Nonetheless, frequency of occurrence strongly varied between habitats, from 0.1 % at the beech *F. sylvatica* forest plot to 100 % in the *Calluna-Erica* shrubland plot and in the *A.*

glutinosa forest plot (Table 2). Mean density along the study period ranged from 0.11 individuals/ha in the beech forest to 4.26 individuals/ha in the *Alnus* forest plot (Fig. 2).

Shrews showed higher densities in Mediterranean than in Eurosiberian and Boreo-subalpine plots (ANOVA: $F_{2, 89}=7.85$, $p=0.0007$; Fig. 2). Further, significant differences were observed among non-Mediterranean plots according to understory vegetation (Fig. 2). Eurosiberian and Boreo-subalpine forest plots (oak, beech, and fir), with few or no understory herbs and shrubs, showed the lowest shrew densities all over the study period (<0.5 individuals/ha on average; Fig. 2), whereas shrublands and the black poplar woodland showed mean densities that were only slightly lower than those found in the Mediterranean woodlands (2.5–3.5 individuals/ha on average; Fig. 2). These plots had a higher amount of understory vegetation than forests, i.e., short shrubs in heathland and juniper shrubland plots, and bracken *Pteridium aquilinum* in the poplar (Table 2).

Direct and indirect effects of climate and vegetation on shrew density

The structural equation model relating mean shrew density with the principal components of the analyses of climate and vegetation structure received high statistical support (Fig. 3). The model explained 87 % of variance of shrew density and showed high goodness of fit ($\chi^2_6=1.56$, $p=0.96$, GFI=0.95).

Table 2 Results of the principal component analyses carried out with the vegetation structure variables estimated at the nine plots

| VARIABLES	PC1	PC2	PC3	PC4
Rock cover (%)	0.62*	−0.19	−0.38	0.58
Tree cover (%)	0.74*	0.46	0.11	−0.29
Tree height (m)	0.24	0.95*	−0.14	0.07
Shrub cover (%)	−0.12	−0.47	0.65*	0.10
Shrub height (m)	0.15	−0.04	0.02	−0.98*
Herbaceous cover (%)	0.06	0.02	0.93*	0.02
Herbaceous height (m)	−0.02	0.23	0.90*	−0.27
Mosses cover (%)	0.93*	0.25	−0.12	−0.10
Litter (%)	0.26	0.89*	0.16	−0.11
Moisture	0.72*	0.57	0.24	0.14
Explained variance (%)	26.00	25.00	24.00	15.00

Correlations marked with an asterisk are significant at $p<0.05$

Fig. 2 Mean (± SE) greater white-toothed shrew densities in the nine study plots. *Grey bars*: Mediterranean plots; *black bars*: Eurosiberian and Boreo-subalpine plots without understory vegetation; *stripped bars*: Eurosiberian and Boreo-subalpine areas with understory vegetation. Differences in mean density between plots in the Eurosiberian and Boreo-subalpine regions depending on the presence of understory vegetation were significant (ANOVA: F1, 61=37.12. *p*<0.0001)
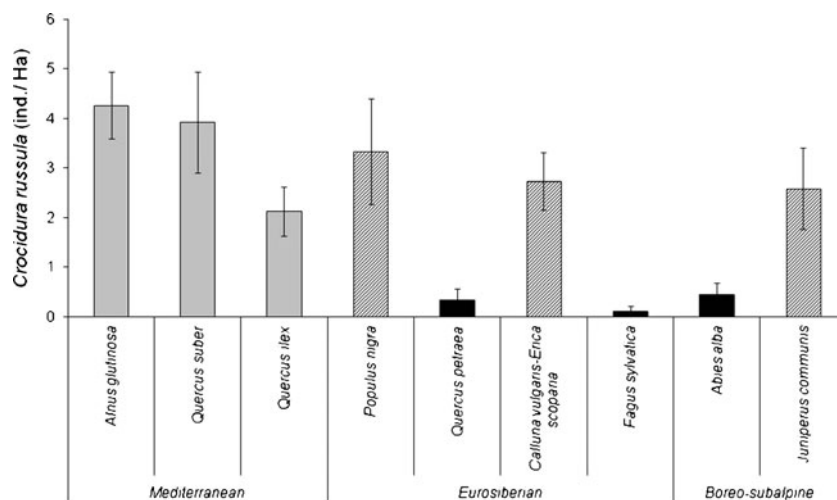
The permutation test showed that only 39 out of 1,000 permutations of the observed data improved model's fit, whereas the 961 remaining resulted in a higher discrepancy function (*p*=39/1000=0.039).

The saturated model included four significant path coefficients (obtained by means of percentile confidence intervals after bootstrapping), one measuring direct effects of climate on shrews, and three related to effects of climate on vegetation and effects of vegetation on shrews (Fig. 3). The only component derived from the PCA of climatic variables, that went from rainy and moist sites in northern highlands to hot dry
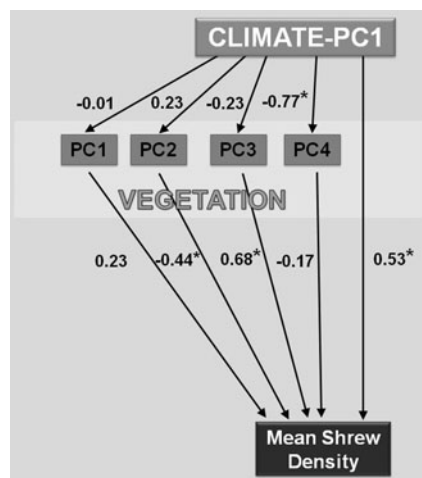
Fig. 3 Structural Equation Model (SEM) built up to determine the effects of environmental variables (a principal component of climate variation and four components of vegetation structure variation along the latitudinal gradient of the Montseny mountain range) on mean greater white-toothed shrew density. All the standardized partial regression coefficients and their statistical significance are shown (*p<0.05). Briefly: the climate component went from rainy and moist sites in northern highlands to hot dry sites in southern lowlands. The first vegetation component (*PC1*) was a gradient of moss, tree, and rock cover; *PC2* was a gradient of tree height and litter cover; *PC3*, a gradient of herb and shrub cover; and *PC4*, an inverse gradient of shrub height (see Table 2 and the main text for details)

sites in southern lowlands (Table 1), influenced directly shrew density (*p*<0.05; R^2=28.1 %). The climate gradient was strongly negatively related to the fourth vegetation component (*p*<0.01, R^2=59.3 %), which was inversely related to shrub height (Table 1); this vegetation gradient had no significant effects on shrew density, though (Fig. 3). Shrew density was positively affected by the third vegetation component (*p*<0.01, R^2=46.2 %), a direct gradient of herb and shrub cover (Table 2), and negatively affected by the second vegetation component (*p*<0.01, R^2=19.4 %), a gradient of tree height and cover of litter (Table 1). These vegetation gradients were not related to climatic variation (Fig. 3). The first vegetation gradient was not influenced by climate, and it did not influence shrew density.

Overall, both vegetation structure and climate influenced directly shrew density along the studied altitude gradient, but vegetation effects were stronger and there was no evidence for indirect effects of climate through its effect on vegetation structure. Shrew density was higher in habitats with developed understory vegetation and lower in habitats with high covers of tall trees and litter, and these traits were not influenced by climate. Vegetation traits accounted for 60.8 % of the variance in shrew density explained by the full model

$$\left(R^2 = \left(\sum \text{vegetation} - \text{shrew density coefficients} \right)^2 \right).$$ In addition to these vegetation effects, direct climatic effects accounted for an additional 43.4 % ($R^2 = ((\text{climate} - \text{shrew}) - (\sum (\text{climate} - \text{vegetation} \times \text{vegetation} - \text{shrew}))^2$; Arbuckle 1983–2003). Shrew numbers increased with increasing water deficit, temperature, and evapotranspiration, and decreased with moisture and rainfall. Indirect effects mediated by effects of climate on vegetation accounted together for 5.2 % of variance (composite path coefficient values for each climate–vegetation component were 0.00, −0.1, 0.16, and 0.13, respectively, and its corresponding R^2=0.0, 1.0, 2.4, and 1.7; R^2 values can be summed up as vegetation components

were statistically independent by PCA constraints). A SEM using site occupancy rate as the dependent variable yielded almost the same results than the one using the mean numbers ($p=0.040$, $R^2=83$ %). In fact, mean density of shrews per plot was strongly correlated with occupancy rate ($r=0.89$, $p=0.001$, $n=9$), as also was maximum density ($r=0.78$, $p=0.013$, $n=9$; Table 2).

Discussion

In spite of a number of logistic shortcomings, mostly due to low manpower availability, we were able to obtain unbiased samples of the mean abundance and occupancy rate of plots located in a wide altitudinal gradient (500–1,550 m) during a 3-year period. Logistic constraints precluded larger sampling plots and hence number of captures, as well as more frequent trap revisions to document movements of marked individuals and, of course, experimental manipulations. For these reasons, the discussion of patterns found in terms of mechanisms is necessarily based on narrative arguments rather than on direct evidence. However, patterns found were clear-cut enough to reach some valid conclusions, as well as to suggest directions for further research.

The greater white-toothed shrew was found in all the nine habitats studied in the Montseny mountain range, as already documented for other Mediterranean mountains (Alcántara 1992). Nonetheless, significant differences in density and occurrence were observed between plots, suggesting a preference for some habitats and avoidance of others. The highest mean densities were recorded in Mediterranean lowlands (i.e., alder riverbeds and evergreen oak woodlands), and the lowest in Eurosiberian and Boreo-subalpine highlands, as also found in other studies (Genoud and Hausser 1979; Alcántara 1992; Sans-Fuentes and Ventura 2000; Jaquiéry et al. 2008). However, some highland plots reached densities as high as those found in Mediterranean lowlands as far as plots provided well-developed understory vegetation (i.e., thick bracken or scrub). These results suggest that the unfavorable highland environmental conditions for this small insectivore (Cantoni and Vogel 1989; Ehinger et al. 2002; Jaquiéry et al. 2008) can be alleviated by vegetation structure traits such as dense herb or shrub cover.

Occupancy rates were higher throughout the study period in the habitats with the higher mean densities, suggesting an association between habitat quality and population dynamics (Jaquiéry et al. 2008). This association to high-quality habitats was also supported by positive among-plot correlations between overall shrew abundance and the abundance of other small mammals (Table 1, Torre and Arrizabalaga 2008; Díaz et al. 2010), a fact that suggested little or no interspecific competition for resources such as food or refuges (e.g., Torre et al. 2007). Positive associations between the abundances of shrews and other small mammals also indicate that trap saturation (i.e., the inability of Sherman traps to capture more than one individual; Anderson 1976) was unlikely to have biased results, as negative effects of small mammal abundance on shrew captures would have been expected otherwise. Only two plots showed a continuous presence of shrews throughout the study period, whereas the others showed a discontinuous presence of the species directly related to mean and maximum shrew densities. This pattern suggested that local extinctions and recolonizations were mostly related to habitat quality, providing evidence for a high turnover rate typical of a metapopulation dynamics system (Jaquiéry et al. 2008). According to our results, we hypothesize that high-quality habitats benefited from lower extinction rates and/or higher colonization rates, besides good conditions for population growth during favorable seasons and/or years, as suggested by Jaquiéry et al. (2008). Further studies based on capture–recapture data form a large number of individuals are, however, required to test this hypothesis properly.

Shrew density and occupation rates along the sampled altitudinal gradient were influenced by both local climate and vegetation structure. The general pattern of high density in Mediterranean lowlands and variable density in Eurosiberian and Boreo-subalpine highlands was related to the combined effects of vegetation structure and climate effects, as revealed by structural equation modeling. Direct effects of climate accounted for some 38 % of the variance in shrew densities found in the study area (43.4 % of the 87 % variance explained by the whole model). These direct effects could be caused by the physiological needs of shrews, which limit their ability to tolerate cold conditions (Cantoni and Vogel 1989; Churchfield 1990; Jaquiéry et al. 2008). Direct effects of vegetation structure accounted for a further 53 % of variance in shrew densities, and results obtained are in close agreement with general knowledge on the habitat preferences of greater white-toothed shrew in southwestern Europe for habitats with high herb and shrub cover at the ground level (e.g., Alcántara 1992; Alonso et al. 1996). Association with understory vegetation can be due to several, nonexclusive ecological processes. First, thermal restrictions can be alleviated by the use of more favorable microclimatic conditions found under dense vegetation cover. Second, small mammals are under the eye of several predators, and the association with understory vegetation could be an antipredatory strategy (Torre and Díaz 2004). And third, vegetation volume and height are closely related to primary production, and may also estimate food availability for small mammals (Torre et al. 2007). Remarkably, no evidences for indirect, interactive effects of climate and vegetation on shrew densities were found, as vegetation traits influenced by climate did not affect shrews, and vegetation traits influencing shrews were not affected by climate in the studied altitudinal gradient. Climate and vegetation effects on the altitudinal distribution of

greater white-toothed shrew were thus additive rather than interactive, as has been found for the combination of other ecological processes (i.e., predation and asymmetric competition) on the local abundance of shrews and other species in Mediterranean mountain habitats (Torre et al. 2007).

Habitat associations of greater white-toothed shrews in Mediterranean mountains differed somewhat to those found in mountains of Central Europe. In the Mediterranean case, the species is scarce or absent in highland habitats without herb or shrub cover, especially during winter, but occupy shrubby communities up to the mountain tops (1,500–2,000 m a.s.l.) throughout the year (Alcántara 1992, this study). In Central Europe, shrews select areas of dense understory vegetation during summer, shifting to human settlements during winter between 600 and 1,000 m, and being almost absent above 1,000 m (Churchfield 1990; Ehinger et al. 2002; Jaquiéry et al. 2008). Ehinger et al. (2002), using live-trapping, documented a significant decrease of shrew's density with elevation in the Jura Mountains, suggesting that populations living in highlands are smaller and sparser. Comparison of absolute altitudes reached by shrews in both areas, as well as recent evidences for physiological adaptation to colder environments in Central European highlands (Fontanillas et al. 2005), reinforce the most likely physiological basis for altitudinal range limitations for this species, i.e., its inability to tolerate cold temperatures. Ehinger et al. (2002) speculated that human settlements allow winter survival of shrews by providing sources of warmth and invertebrate food such as compost piles, stables, and farms. Higher temperatures in the Mediterranean region (see Table 1 and Ninyerola et al. 2003) would allow winter survival under the more favorable microclimatic, and presumably food, conditions found under shrubs, bracken, and dense herb cover (Alcántara 1992; Alonso et al. 1996). Vegetation effects on the distribution patterns of shrews along altitudinal gradients should hence be additive to thermal restrictions, allowing populations to thrive outside (above) limits imposed by climate. Within these limits, population abundance and long-term persistence would depend mainly on habitat quality, as defined by the effects of vegetation structure (cover of understory herbs or shrubs) on food availability and predation risk (Alcántara 1992; Alonso et al. 1996). Direct measurements of microclimate, food, and predator activity along altitudinal gradients, as well as manipulative experiments of these environmental traits, would be necessary to estimate the relative contributions of these non-exclusive mechanisms.

Vegetation structure had stronger influences than direct climate effects, allowing shrews to colonize areas outside its optimal climatic envelope. These results would indicate that the predicted range expansions for shrews both northwards and upwards due to climate warming may be underestimated at least in the Mediterranean region, especially under the current conditions of general land abandonment and shrub encroachment (Sirami et al. 2008). Although it has been found that climate changes would have stronger influences than land-use changes over large scales (Triviño et al. 2011), our results point to opposite expectations at smaller, regional scales, based on patterns of microhabitat selection by generalist species.

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