

# SPECIES RICHNESS AND ABUNDANCE OF SMALL MAMMALS ALONG AN ELEVATIONAL GRADIENT OF A MEDITERRANEAN MOUNTAIN

I. TORRE\*, A. ARRIZABALAGA

Museu de Granollers-Ciències Naturals, C/ Francesc Macià 51, 08400 Granollers, Barcelona, Spain

\* Corresponding author: i.torre@museugranollers.org

ABUNDANCE  
CLIMATE  
ELEVATION  
MID-DOMAIN EFFECT  
SMALL MAMMALS  
SPECIES DENSITY  
SPECIES RICHNESS  
VEGETATION

**ABSTRACT.** – Spatial patterns of species richness and abundance were studied on a local scale (alpha-diversity) along an elevational gradient (540-1550 m a.s.l.) within a Mediterranean mountain in the Montseny Natural Park and Biosphere Reserve (NE Spain). Eight sampling stations consisting of 49 Sherman trap plots were sampled 11 times between 1995 and 1997. Values of cumulative species density, and species richness estimates (interpolated and extrapolated), were calculated to ascertain alpha diversity patterns. Species richness showed no consistent patterns along elevation, since patterns changed depending on the diversity measure used. Species richness (the number of species once controlling for the number of individuals sampled) showed a moderate increase with elevation, whereas a richness estimator (Jack 2) showed that alpha diversity peaked at middle elevations (1000-1200 m a.s.l.). Interpolation of species ranges suggested a mid-elevation peak in species diversity. Further, a null model provided moderate evidence of the influence of the geometrical constraints of species' ranges on the observed pattern, lending weight to a hump-shaped pattern of diversity with elevation. Nonetheless, the most consistent pattern observed was the strong decrease of small mammal abundance with elevation. Structural equation modeling confirmed that species density and species richness were associated with the mean climatic features of the plots, although vegetation structure profiles were also seen to influence patterns (cover and plant height). Species richness increased from the warm and relatively dry lowlands to the colder and moister uplands, with the highest levels of species richness being found at the divide between the Mediterranean and Eurosiberian climatic zones and plant communities. However, patterns of species richness were not related to patterns of vegetation richness at plot level, which decreased significantly with elevation. The abundance of small mammals also decreased with elevation due to climatic harshness and possibly also to the decreasing productivity associated with greater elevations. We hypothesized that the combined effects of geographical (mid-domain effect), abiotic (climatic), and biotic (vegetation composition and structure, density of small mammal individuals, interdigitation of biotic communities) factors would seem to be responsible for the mid-elevation peak in small mammal alpha diversity in the Montseny mountain.

## INTRODUCTION

Small mammals (insectivores and rodents) have been used as models to study patterns of diversity along elevational gradients. Species richness has been seen to increase (Rickart *et al.* 1991) or decrease with elevation (Patterson *et al.* 1989, 1996), and even in some cases to show no significant pattern (Heaney *et al.* 1989). However, most recent studies have detected peaks of diversity at mid-altitudes (Heaney 2001, Li *et al.* 2003, McCain 2004, Md Nor 2001, Rickart 2001, Sánchez-Cordero 2001), confirming that associations of small mammal diversity with elevation are hump-shaped (McCain 2005). These peaks are mainly caused by climate and other related variables, although the spatial constraints of species' ranges also explain part of the observed patterns (mid-domain effect, MDE, McCain 2005). The MDE is the pattern that

results from the random overlap in the distribution of species ranges along bounded domains (Colwell & Hurt 1994, Colwell & Lees 2000).

The heterogeneous patterns found in elevational studies of small mammal communities are to be expected if the full complexity of the interactions between ecological, historical, and evolutionary processes is taken into account (Rahbek 1997). Nonetheless, observed patterns may be partially due in some cases to sampling biases (Grytnes & Vetaas 2002, Rahbek 1995) or to the differing ways of measuring species diversity that can complicate comparisons between studies. Despite recent attempts to clarify concepts in species diversity, disagreement still occurs regarding the meaning and interpretation of related terms (see definition of species richness by Whittaker *et al.* 2001 and by Gotelli 2001).

Species density (i.e., the number of species in a stan-

standardized sample or area, Lomolino 2001) is normally used as a surrogate of species richness, the former being a more precise measure of diversity (Whittaker *et al.* 2001). However, it is preferable to use species richness (i.e., the number of species controlling for the number of individuals sampled, Gotelli & Colwell 2001) when testing models and evaluating predictions in ecology because species density is a function of species richness and the density or abundance of individuals, and the measurement of species density depends on the assumption that samples of individuals are taken from populations at comparable densities (Gotelli & Colwell 2001). Owing to the fact that in some mountain ranges small mammal abundance decreases with elevation (Patterson *et al.* 1989, Li *et al.* 2003) and that in some other species density covariates with abundance (Heaney 2001, Md Nor 2001), the evidence suggests that small mammal communities at different altitudes do not exist at comparable densities. This effect could be particularly challenging when investigators try to deal with alpha diversity, that is, the quantification of diversity at a local scale (Whittaker *et al.* 2001), and when individuals are sampled from communities with differing density of individuals despite the use of equal sampling areas or standardized effort.

At small spatial scales it has been shown that animal species richness is positively associated with vegetation richness (Hawkins & Pausas 2004, and references therein) and heterogeneity (reviewed by Tews *et al.* 2004). Likewise, small mammal abundance in Mediterranean habitats is associated with vegetation structure, which provides food and shelter against predators (Torre & Díaz 2004, and references therein). Most of the studies about small mammals and elevation did not consider vegetation attributes of plots, and we are able to suspect that vegetation may affect the distribution of species along elevation.

In this study we aimed to analyze the effects of climate and vegetation changes with elevation on the species richness and abundance of small mammals at a local scale (alpha diversity) on a Mediterranean mountain. Furthermore, we aimed to analyze how the use of different measures of diversity can affect the observed pattern of small mammal diversity along elevation. The influence of vegetation and of small mammal abundance on species density estimates were not analyzed in most of the studies about small mammals diversity and elevation (reviewed by McCain 2005). Changes in small mammal density with elevation may alter estimates of species density simply because of changes in sampling chances (Gotelli & Colwell 2001, Tews *et al.* 2004). We analyzed patterns of species richness by using rarefaction curves (Colwell & Coddington 1994) and non-parametric estimators to take into account variations in individual density with elevation (Gotelli & Colwell 2001, Tews *et al.* 2004).

## MATERIALS AND METHODS

*Study area:* The study was carried out in the Montseny Natural Park and Biosphere Reserve (Barcelona, Catalonia, NE Spain; 41° 46' N, 2° 23' E, 30.000 ha), whose main relief feature is Turó de l'Home, 1714 m a.s.l. This mountain of moderate elevation lies somewhat isolated from the surrounding mountains and is relatively near the Mediterranean Sea. Topography and climate vary markedly with elevation and its proximity to the sea implies a mild climate without strong thermal oscillations. Rainfall peaks in spring and fall and there are periods of moderate drought in summer, typical of Mediterranean climates. The average annual rainfall ranges from 800 mm in the lowest Mediterranean localities to 1200 mm at the top of the mountain.

Certain topographical and climatic characteristics bestow

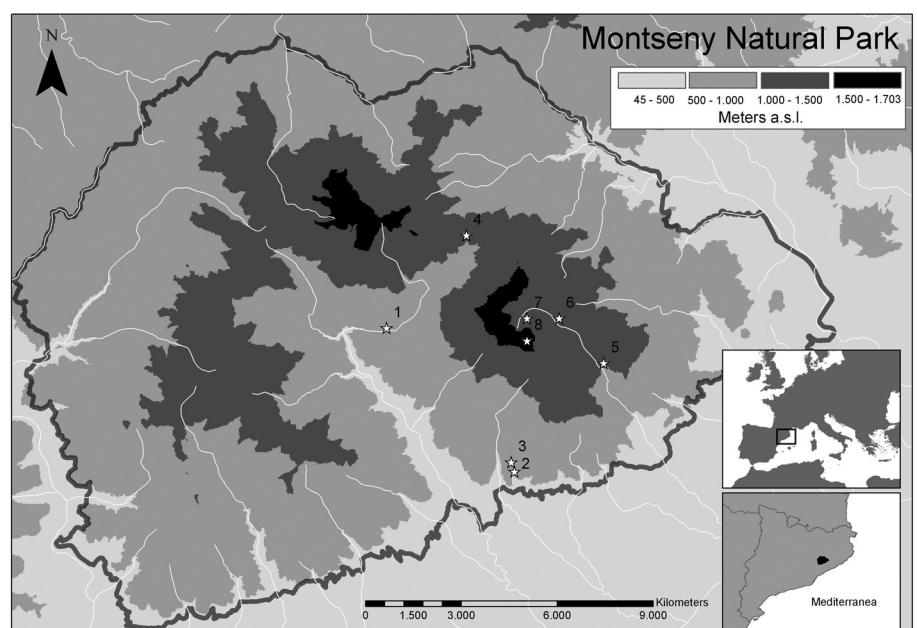


Fig. 1. – Location of the study area and location of the eight plots used for sampling small mammal communities with elevation (legend as in Table I).

Table I. – Climate and vegetation attributes of the eight trapping stations located along a 1010 m gradient of elevation in the Montseny mountains.

Habitat	Elevation (m a.s.l.)	Rainfall (mm)	Temperature (°C)	Potential evapotranspiration (mm)	Thornthwaite Index	Water deficit (mm)	Tree species	Tall shrubs species	Low shrubs species	Herbaceous species	Vegetation diversity
Riverbed forest (P1)	540	975	10.5	642	50	50	4	9	9	58	2.71
Cork Oak forest (P2)	550	825	13.5	642	30	150	3	1	10	70	1.78
Holm Oak forest (P3)	600	825	13.5	642	30	150	7	2	5	17	2.51
Black poplar (P4)	1060	1025	9.5	500	70	50	5	1	1	34	1.81
Oak forest (P5)	1070	1025	11.5	642	50	50	2	6	3	87	2.47
Beech forest (P6)	1150	1075	9.5	500	70	0	1	0	1	38	2.00
Fir forest (P7)	1450	1075	8.5	500	90	0	1	0	3	17	1.60
Juniper shrubland (P8)	1550	1075	7.5	500	90	0	0	0	4	41	1.00

upon the Montseny a remarkable biogeographical interest (Terradas & Miralles 1986) and the presence of well-established central European plant (de Bolòs 1983) and animal communities (Terradas & Miralles 1986) is well documented.

*Sampling design:* The alpha diversity dataset was obtained after sampling eight trapping stations (Fig. 1) that were established along an elevational gradient covering the three main bio-

geographical regions (Mediterranean, Eurosiberian, and Boreo-subalpine, de Bolòs 1983) in the Montseny mountain. The plant communities sampled were considered to represent the main natural habitats present along the elevational gradient (Heaney 2001, Rahbek 1995). Sampling was initiated at a relatively high elevation (540 m a.s.l.) because natural habitats are only found above 300 m on the southern face and at 500 m on the northern face. The areas around the mountain base are mainly cultivated and natural habitats are highly fragmented, so sampling was not considered in these areas. The mountain base is situated on the Tordera Valley at about 100–200 m a.s.l. on the southern face, and at about 500 m a.s.l. on the northern face. The gradient sampled in this study (1010 m) represents 67 % (southern face) and 86 % (northern face) of the entire mountain elevation (1714 m a.s.l.).

The mean climate data were obtained from the Catalan Climatic Atlas (Ninyerola *et al.* 2000, 2003), with a spatial resolution of 180 m. We used data regarding mean temperature, mean cumulative rainfall, mean evapotranspiration (as a measure of primary productivity, Brown 2001, Rosenzweig 1995), humidity, and water deficit from series obtained over the previous two decades (Ninyerola *et al.* 2000, 2003). The elevation, climate, and vegetation of the eight trapping stations are shown in Table I.

The vegetation composition of each plot was recorded in the summer of 1996 by means of three exhaustive inventories carried out in plots of 10 x 10 m (100 m<sup>2</sup>) with visually variable vegetation composition and structure. Plant composition was described in terms of four strata: trees, tall shrubs, low shrubs, and herbs. The total species richness for each group was computed as the number of different species recorded. The vegetation structure of each plot was characterized by estimating the values of 10 variables in a 5 m-radius circle centered on alternate traps in the trapping grid, and then by averaging out the values obtained from each plot (Torre & Bosch 1999). The variables measured were: the cover of rocks, trees, tall shrubs (> 1.5 m tall), low shrubs (< 1.5 m tall), herbaceous plants, and leaf litter, all measured as a percentage (%), and the height of trees, tall shrubs (> 1.5 m tall), low shrubs (< 1.5 m tall), and herbaceous plants measured in meters.

Trapping was performed from February 1995 to July 1997 and the eight plots were sampled during eleven three-day trapping periods. Grids were sampled in February–March 1995, April–May 1995, June–July 1995, August–September 1995, October–November 1995, December 1995–January 1996, April–May 1996, June–July 1996, November–December 1996, March 1997, and July 1997 (eleven trapping sessions of three days each, collectively lasting 33 days). Each trapping period (eight plots sampled over three days) lasted for a month (two plots per week) due to limitations in the availability of researchers and traps. Each plot was sampled by a 7 x 7 trapping grid and 49 Sherman traps (Sherman folding small animal trap; 23 x 7.5 x 9 cm; Sherman Co., USA) were placed 15 m apart (covering one ha) and left open for three consecutive nights. The plant communities sampled were characteristic of the three biogeographical regions found in Montseny: *Quercus suber*, *Q. ilex*, *Alnus*

*glutinosa*, *Fagus sylvatica*, *Q. petraea*, *Populus nigra*, *Abies alba* and *Juniperus communis nana*. Taking into account the number of trapping periods, traps, and night traps were open; each plot was operative for 1617 trapping nights.

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, and were set under the cover of shrubs or dense herbs to conceal them and to provide some thermal insulation. The small mammals caught were identified to species, marked by toe-clipping (Adler *et al.* 1999, Gurnell & Flowerdew 1990), and released at the point of capture. We used the number of different individuals trapped within the three days as an index of the abundance of small mammal species in each study plot; this index is closely related to the density estimators for closed populations ( $M_{t+1}$ , Slade & Blair 2000).

**Data analysis:** Variations in small mammal abundance, species density, and species richness with elevation were assessed by path analysis, an extension of multiple regression analysis which was developed to break down correlations into different parts in order to interpret for effects (Everitt & Dunn 1991). We tested the significance of regression models with structural equation modeling software (SEM, Amos 4.01, Arbuckle 1994-1999). The appropriateness of the models was assessed with the Goodness of Fit Index (GFI), which ranges from 0 (maximum lack of fit) to 1 (maximum fit), and the matrix permutation test (Hesterberg *et al.* 2005). In all, 500 permutations of the matrix data were performed for every model. We obtained the number of permutations that improved the model fit, and those that resulted in a higher discrepancy function. If the model selected is perfectly fitted to the data, we would expect that the number of permutations improving the model to be zero; however, as a general pattern a good fit would be expected from models in which the number of permutations improving the fit divided by the number of permutations not improving the fit to be less than 0.05. Given that, species density is a function of species richness and the density of individuals (Gotelli & Colwell 2001); the density of individuals within plots was also used as an independent variable to assess its influence on estimates of species density. Due to low sample size and in order to test the reliability of the SEM parameter estimates, we used bootstrapping techniques to create resamples by repeatedly sampling with replacements from the random sample in order to obtain information about the sampling distribution (Hesterberg *et al.* 2005). To avoid the multicollinearity of independent variables, we used a Principal Components Analysis (PCA) to obtain orthogonal components that were interpreted as gradients of vegetation composition, vegetation structure, and climate.

Species richness estimates within habitats (alpha diversity) are influenced by species abundance and by sample size (Colwell *et al.* 2004, Gotelli & Colwell 2001, Ludwig & Reynolds 1988). We decided to control for differences in sample size (number of individuals sampled) between plots along the elevational gradient by using Ecosim 7.0 software to generate individual-based rarefaction curves for every plot (Gotelli & Entsminger 2001). This allowed us to compare the species rich-

ness of assemblages with equivalent numbers of individuals. The individual-based datasets were obtained after grouping replicated samples (11 sampling sessions) together into a single sample for each sampled plot (Gotelli & Colwell 2001). These values represent cumulative alpha diversity, that is, the sum of the species found between two time limits (Halffter & Moreno 2005). Rarefaction is the most basic and least controversial null model (Gotelli 2001) and is a conservative way of producing species richness estimates because it uses interpolation instead of extrapolation, but it eliminates data by reducing all sample sizes to the level of the poorest sample (Rosenzweig 1995). We also aimed to calculate the true species richness within plots (observed + unobserved species) by using the least-biased non-parametric richness estimator based on extrapolation (Jackknife 2, Colwell & Coddington 1994, see McCain 2004 for the same approach) and Estimate S Software (Colwell 1994-2004).

In all the analysis trapping stations were considered as independent sampling points due to evident differences in vegetation and small mammal composition and abundance, and also in climate.

Finally, we tested whether the observed diversity pattern was influenced by the geometrical constraints of species' ranges within a bounded domain, based on analytical-stochastic models (McCain 2005, and references therein). In order to do so, the diversity pattern was compared to a null model prediction with a Monte Carlo simulation procedure (Mid-Domain null, McCain 2004). The simulation boundaries were situated between 500 and 1600 m, and the diversity data were simulated in 100-m increments by using an interpolation of species' ranges on the basis that a species was present at one elevation if it was found at higher and lower altitudes (McCain 2004, 2005).

## RESULTS

### *Climate and vegetation patterns with elevation*

The elevational gradient sampled also has a marked climatic gradient (Table I). A principal components analysis (PCA) was performed to summarize the climatic attributes of the plots. This PCA accounted for 87 % of the variance in the original variables and only a single PC was extracted. This PC was negatively correlated to water deficit ( $r = -0.95$ ,  $P < 0.001$ ), temperature ( $r = -0.94$ ,  $P < 0.001$ ), and evapotranspiration ( $r = -0.89$ ,  $P = 0.003$ ), but was positively correlated to Thornthwaite's moisture index ( $r = 0.98$ ,  $P < 0.001$ ) and rainfall ( $r = 0.89$ ,  $P < 0.001$ ). This PC was also strongly correlated to elevation ( $r = 0.90$ ,  $P = 0.002$ ).

A second PCA was performed to summarize vegetation composition and structure within plots. This PCA accounted for 88 % of the variance in the original variables; the first, PC1, was positively correlated to vegetation richness ( $r = 0.87$ ,  $P = 0.004$ ) and the height of shrub-by vegetation ( $r = 0.87$ ,  $P = 0.004$ ). As well, PC1 was marginally correlated to vegetation diversity ( $r = 0.67$ ,

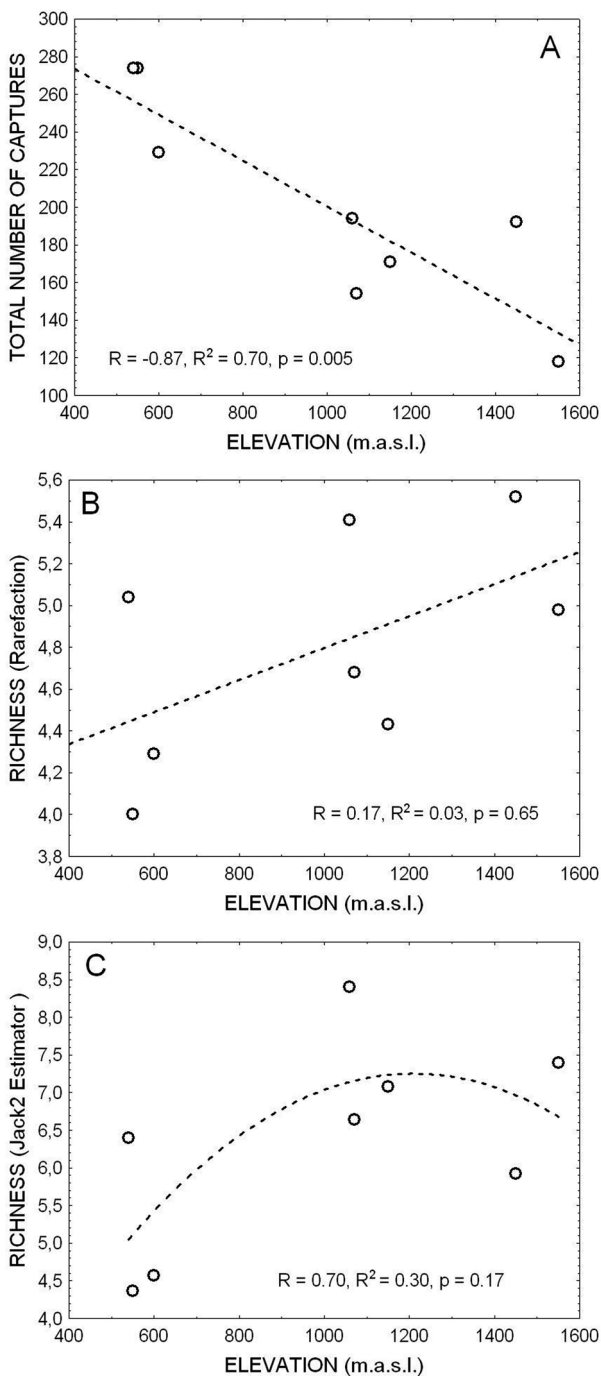


Fig. 2. – Total number of small mammals captured (A), interpolated species richness (rarefaction, B), and extrapolated species richness (Jack 2 estimator, C) along the elevation gradient sampled (540–1550 m a.s.l.).

$P = 0.06$ ). PC2 was positively correlated to the cover and height of herbaceous plants ( $r = 0.94$  and  $r = 0.95$ ,  $P < 0.0001$ ). The third, PC3, was negatively correlated to shrub cover ( $r = -0.96$ ,  $P < 0.0001$ ). PC1 was negatively correlated to elevation ( $r = -0.83$ ,  $P = 0.01$ ), whereas PC2 and PC3 were uncorrelated ( $r = 0.35$ ,  $P = 0.38$ , and  $r = -0.02$ ,  $P = 0.95$ ).

### *Patterns of small mammal density, species density, and species richness with elevation*

During the study period, 1606 small mammals belonging to nine species (3 insectivores and 6 rodents) were captured on 12 936 trapping-nights (an average trapping success of 12.41 %). The mean (and total) small mammal abundance per plot decreased over the height gain of 1010 m from 25.00 individuals per plot in the lowlands (275 individuals at 550 m) to 10.72 individuals per plot in the highlands (118 individuals at 1550 m,  $r = -0.87$ ,  $n = 8$ ,  $P = 0.005$ , Fig. 2A). Small mammal mean and total abundances decreased from the warm and dry lowlands to the cold and rainy uplands, and overall the small mammal abundance was negatively correlated to the PC summarizing climate ( $r = -0.74$ ,  $n = 8$ ,  $P = 0.03$ ).

The observed cumulative species density per plot, rarefied species richness, and extrapolated species richness, showed no significant correlation with elevation (Fig. 2B, C). However, elevation was strongly correlated to the PC summarizing the climatic attributes of the plots; rarefied species richness was positively correlated to moisture (Thorntwaite's index,  $r = 0.75$ ,  $P = 0.03$ ) and negatively to temperature ( $r = -0.76$ ,  $P = 0.02$ ) at plot level. Species richness calculated by using Jack 2 non-parametric estimator correlated to the PC summarizing the climatic attributes of plots in both a linear and non-linear way. Both models explained higher variance for the second order polynomial than for the linear fit (Climate, Jack2: adjusted  $r^2$  0.79 vs 0.47,  $P = 0.008$  and  $P = 0.03$ , respectively).

A structural equation model (SEM) was built with all the independent variables (PC climate, PC 1 to PC 3 of vegetation composition and structure, and small mammal abundance) and species density (observed number of species within plots) as the dependent variable. This model explained 81% of variance and gave a high goodness of fit ( $\chi^2 = 1.42$ ,  $d.f. = 3$ ,  $P = 0.70$ ) and marginal significance (permutation test,  $P = 0.07$ ). The model with all the regression paths and their significance, obtained by means of percentile confidence intervals after bootstrapping, are shown in Fig. 3A. Five path coefficients were significant: Climate (PC) showed a direct positive effect on species density and herbaceous cover and height (PC2), but had a negative effect on small mammal abundance, vegetation richness, and height of shrubs (PC1). Small mammal abundance had a positive effect on species density. Vegetation composition and structure did not have any significant effect on either small mammal abundance or species density. Species density was mainly and positively affected by climate changes produced by the altitudinal gradient. This model, taking into account the influence of small mammal abundance on species density, may be equivalent to the model using species richness after rarefaction.

Another SEM using the PC summarizing climate and the PCs summarizing vegetation composition and structure as independent variables and with the species rich-

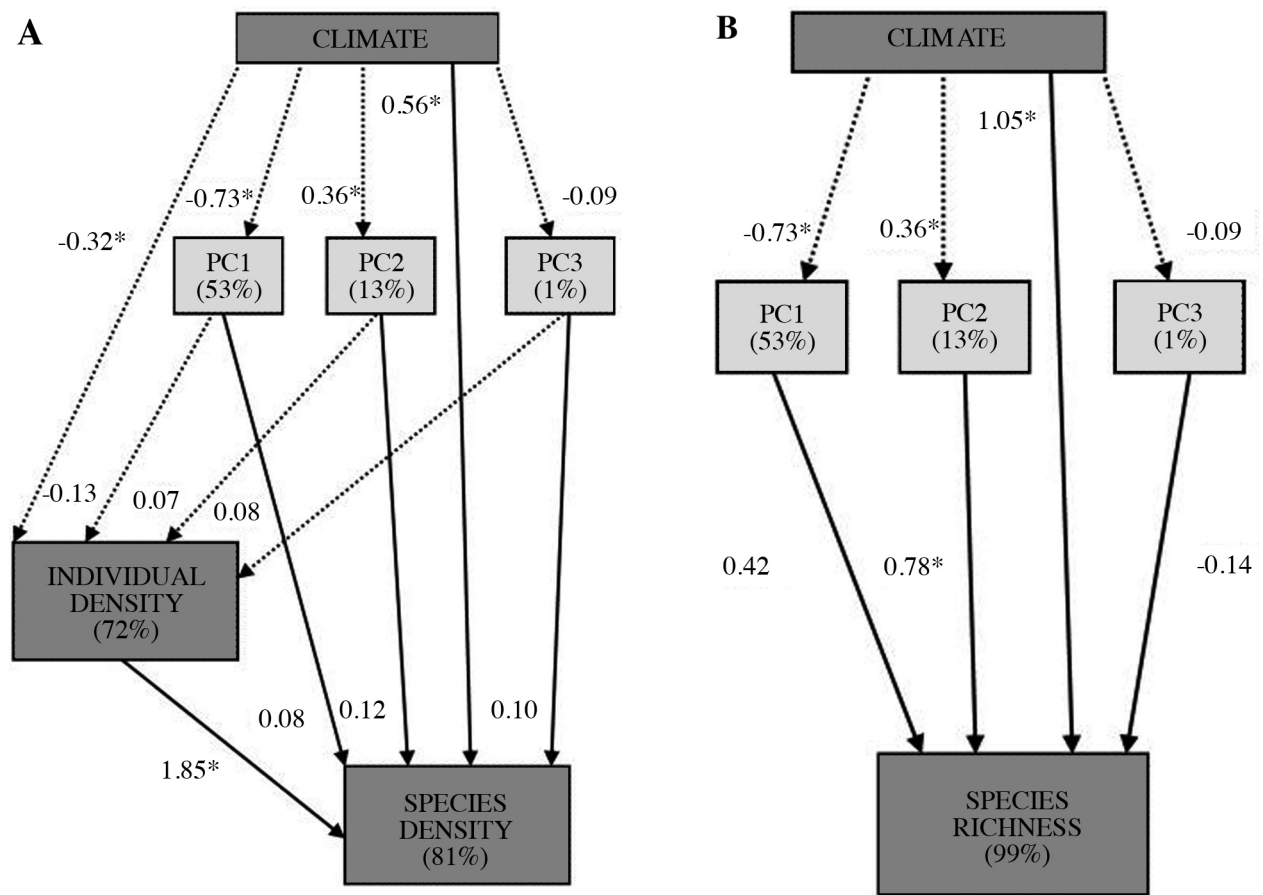


Fig. 3. – Structural Equation Models built to determine the effects of environmental variables (climate, and vegetation composition, and structure, PC1 to PC3, see results for definition of these principal components) and individual density on species density (A), and the effects of environmental variables (climate, and vegetation composition and structure, PC1 to PC3) on species richness estimated by Jack 2 estimator (B). All the regression coefficients and their statistical significance are shown (\*  $P < 0.05$ ); the explained variance by predictors on dependent variables is also shown.

ness calculated by extrapolation (Jack2 estimator) as the dependent variable explained almost all the variance in species richness (99 %) and gave a high goodness of fit ( $Chi^2 = 1.42$ ,  $df = 3$ ,  $P = 0.70$ ) with marginal significance (permutation test:  $P = 0.06$ ). The model with all the regression paths and their significance is shown in Fig. 3B. Four path coefficients were significant: climate showed a direct positive effect on species richness and herbaceous cover and height (PC2), and a negative effect on vegetation richness and height of shrubs (PC1). Herbaceous cover and height (PC2) showed a positive effect on species richness. Despite the richness estimator showed better fit to the climatic gradient with non-linear than with linear regression models, SEM are based on linear relationships between variables.

Finally, a mid-elevation peak in alpha diversity was observed for the dataset after using interpolation of species' ranges (Figs 4 and 5). The 95 % prediction curves from 50,000 simulations by the program Mid-Domain Null demonstrated a significant but moderate fit to the predictions of the null model ( $r^2 = 0.40$ ,  $P < 0.01$ ). The peak of alpha diversity was situated around the mid-point of the gradient sampled but above the mid-point of the

mountain elevation and coincided with the transition between the Mediterranean and Eurosiberian biogeographical regions (Fig. 4). Nonetheless, the second order polynomial fit of species richness with elevation was non-significant ( $r = 0.65$ ,  $r^2 = 0.28$ ,  $p = 0.10$ ).

## DISCUSSION

The study of the patterns of small mammal alpha diversity with elevation in the Montseny mountains pointed out heterogeneous results, as far as we observed different patterns depending on the way diversity was measured. Furthermore, species diversity was affected by abiotic factors, like climate and geography, but also by biotic factors, like vegetation and small mammal density. So, in the Montseny mountain, the small mammal diversity pattern with elevation seems to have a multifactorial origin. As has been argued by many ecologists and biogeographers, general patterns in nature may result from the combined effects of convergent processes rather than independent effects (Heaney 2001, Lomolino 2001, and references therein).

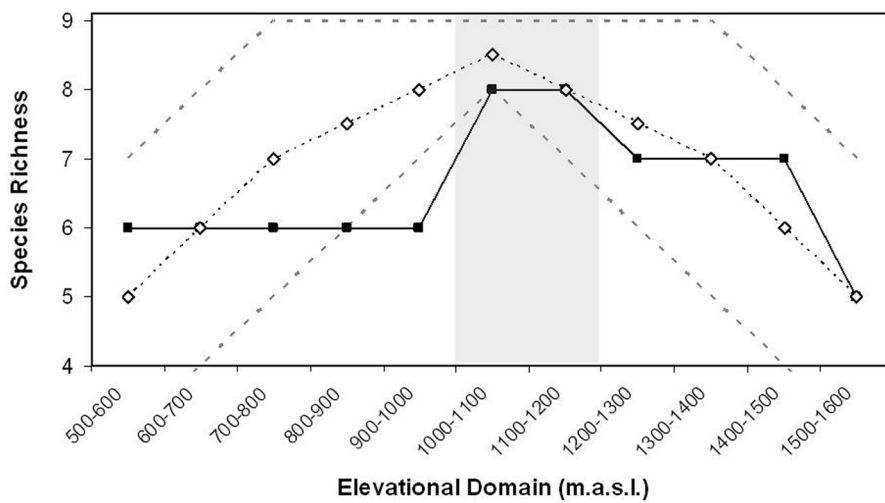


Fig. 4. – Observed alpha diversity curve based on interpolated species ranges (line with closed squares), predicted alpha diversity curve (line with open diamonds), and 95 % prediction curves (dotted lines) obtained after sampling without replacement from the program Mid-Domain Null (50 000 simulations). The alpha diversity curve showed a significant but moderate fit to the predictions of the null model ( $r^2 = 0.40$ ,  $P < 0.01$ ). The shaded area represents the transition between the Mediterranean and the Eurosiberian regions.

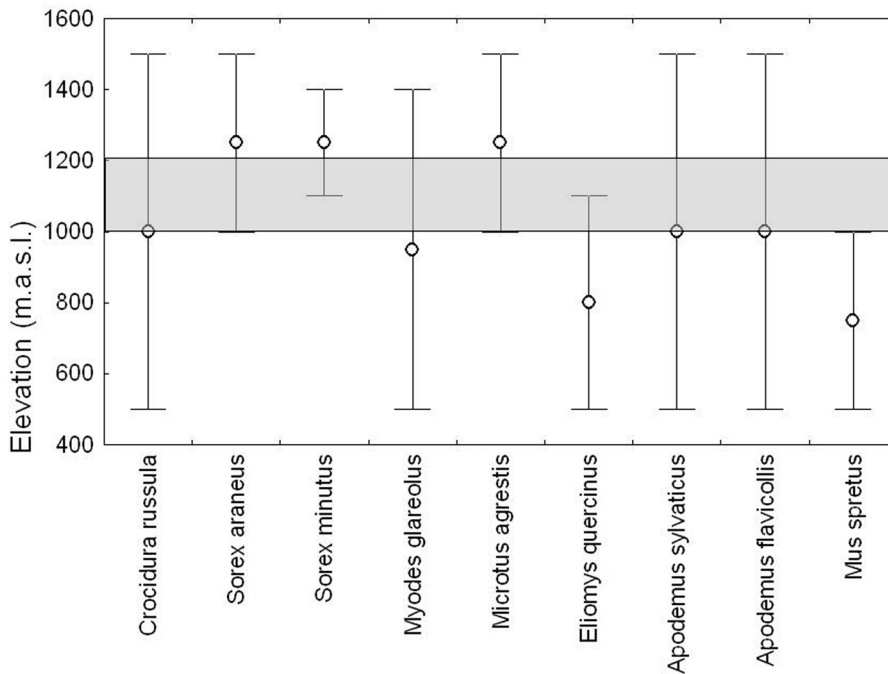


Fig. 5. – Interpolated small mammal species ranges along elevation in the Montseny mountain (shaded area represents the transition between the Mediterranean and the Eurosiberian regions).

Nonetheless, we observed a strong decreasing pattern of small mammal abundance along elevation, so the influence of changes in abundance along elevation on species density estimates need to be controlled. Species richness estimates within habitats (alpha diversity) are influenced by species abundance and by sample size (Colwell *et al.* 2004, Gotelli & Colwell 2001, Ludwig & Reynolds 1988), but these influences were not considered in most of the studies about small mammal diversity and elevation (Heaney 2001, Li *et al.* 2003, McCain 2004, 2005, Md Nor 2001).

Path analysis pointed out some climatic influences on species density and species richness (controlling for the number of individuals sampled, Gotelli & Colwell 2001) showing a moderate increase with changes in climate associated to the elevation gradient. In general, mammal species richness appears to vary positively with precipitation,

moisture, and other related variables (Hawkins & Pausas 2004, Ruggiero & Kitzberger 2004, Tognelli & Kelt 2004), and similar results have been found elsewhere for small mammals (Heaney 2001, Md. Nor 2001, Li *et al.* 2003). In our case, the areas with the highest species richness coincided with the areas of greatest rainfall. This pattern coincides with that observed by Hawkins & Pausas (2004) in Catalonia. They studied the relationship between mammal richness, vegetation richness, and climate at a larger spatial scale and concluded that climatic variables (Thornthwaite's index) were more important than vegetation in determining mammal species richness (see Boone & Krohn 2000, for similar results in Maine, USA).

Changes in species richness with elevation have often been hypothesized to be related to changes in productivity (Rahbek 1997, Rosenzweig 1992) and this relationship has been observed in the case of small mammals (Li *et al.*

2003). However, the use of two surrogates of productivity (evapotranspiration and rainfall, which were negatively correlated) yielded contrasting interpretations of the species richness pattern, although these surrogates may differ in the extent to which they correlate to productivity (Mittelbach *et al.* 2001). Rainfall is an easy-to-quantify measure of productivity and has been used to interpret the seasonal and annual changes in productivity available to small mammals (Lima & Jaksic 1999, Lima *et al.* 2001, Meserve *et al.* 1995). Evapotranspiration is closely related to net aboveground productivity (Rahbek 1997, Whittaker & Field 2000), which in turn can be used as an estimate of the potential productivity available at higher trophic levels (i.e., herbivores, Mittelbach *et al.* 2001). Nonetheless, productivity is a biological process affected by abiotic stress (Brown & Lomolino 1998) and stressful conditions for life such as decreasing temperatures with elevation usually result in low plant productivity and plant species diversity on mountain tops (Brown & Lomolino 1998). In the Montseny Park, the richness of vascular plants (species of trees and shrubs) and plant diversity (species of trees, shrubs, and herbaceous plants) at plot scale decreased with increasing elevation. These patterns of diversity could be interpreted as a response to increasing harshness and, perhaps, to decreasing productivity with elevation, since it is generally observed that vegetation diversity is closely related to changes in primary productivity with elevation in mountain ranges (Li *et al.* 2003, Md Nor 2001). According to the observed patterns of vegetation we are able to suspect that productivity was negatively affected by elevation in the Montseny mountain, and evapotranspiration rather than rainfall would be a more meaningful surrogate for productivity.

Small mammal species richness has been correlated to vegetation diversity in some mountain ranges (Li *et al.* 2003, Md Nor 2001), although this seems not to be the case at Montseny, where small mammal species richness and vegetation diversity showed relatively contrasting patterns with elevation. Patterns of association between vegetation and mammal diversity have not been found at higher spatial scales in Catalonia (NE Spain, Hawkins & Pausas 2004) and our results at a smaller spatial scale agree with these findings. On the other hand, vegetation does provide small mammals with structure for nest sites and anti-predator refuges, and a relationship between vegetation structure and small mammal richness may exist (Williams *et al.* 2002 & references therein). Shrubby plant cover has been observed to correlate with small mammal richness and abundance in Mediterranean habitats (Torre & Díaz 2004), although this factor was unrelated to small mammal richness in the elevation gradient studied in Montseny. However, small mammal species richness was affected positively by the cover and height of the herbaceous vegetation. This pattern could be explained by the presence of habitat specialists in the Mid-European small mammal community that mainly feeds in grasslands (i.e.,

field vole *Microtus agrestis*) and/or on herbaceous vegetation (bank vole *Myodes glareolus*) (Gurnell 1985).

Interestingly, the use of richness estimators offered a different interpretation of the species diversity-elevation relationship, suggesting a middle elevation peak in diversity. This pattern was also observed when small mammal species ranges were interpolated between 500 and 1500 m.a.s.l. and the resulting pattern was compared to a null model testing for the mid-domain effect (McCain 2005 and references therein). The mid-elevation peak in the Montseny exactly coincided with the transitional area between Mediterranean and Eurosiberian communities (occurring at about 1000 m a.s.l. on the northern slope and at about 1200 m a.s.l. on the southern slope, de Bolòs 1983), lending weight to the hypothesis of the juxtaposition or interdigitation of communities (Heaney 2001, Lomolino 2001) on observed patterns. The plot with the greatest small mammal species richness was situated at the southern lower limit of the Eurosiberian Region (1060 m a.s.l.) but also possessed typical Mediterranean species of flora and fauna (i.e., holm oak *Quercus ilex* and Algerian mouse *Mus spretus*). Juxtaposition also may play a role in areas of the interdigitation of communities outside the limits of the Eurosiberian region since the habitat with the greatest species richness within the Mediterranean plots (riverbed) was also inhabited by many Eurosiberian species of flora (i.e., *Corylus avellana*, *Fraxinus excelsior*). Local micro-environmental features such as moisture will cause an enrichment of small mammal diversity in Mediterranean areas and significant penetrations of mid-European species occur as a result (Torre *et al.* 1996, Torre & Arrizabalaga 2008). Mid-European species present in Montseny seem to be tolerant of the mild Mediterranean conditions of the lowlands (relatively humid, > 800 mm rainfall, Sans-Fuentes & Ventura 2000) and moist habitats such as riverbeds allow small mammal species such as yellow-necked mouse *Apodemus flavicollis* and bank vole *Clethrionomys glareolus* to thrive in Mediterranean lowlands (Torre & Arrizabalaga 2008). A mid-elevation peak in species diversity is the most commonly observed pattern for non-flying small mammal fauna (McCain 2005) and our data, showed a moderate fit to the null model providing evidence for such a general pattern (Lomolino 2001). Despite the low sample size analyzed and moderate fit of the data, we are able to suspect that a mid-elevation peak in small mammal diversity would be a valid model in the Montseny mountain.

Small mammal abundance showed a significant decrease with elevation at the heights sampled (540-1550 m a.s.l.) in Montseny and this pattern was mainly caused by increasing climatic harshness with elevation. The areas with the greatest small mammal abundance were those with higher temperatures and water and evapotranspiration deficit. The decrease in small mammal abundance with elevation seems to be common place in the mountains of the Iberian Peninsula (Alcántara 1989, Delibes



1985, Fa *et al.* 1992) and has also been recorded in other temperate mountain ranges around the world (Li *et al.* 2003, Patterson *et al.* 1989). Decreases in abundance are generally attributed to increases in the severity of environmental conditions and to the decreasing availability of food resources with elevation (Fa *et al.* 1992, Li *et al.* 2003, Patterson *et al.* 1989). The high plant diversity of Mediterranean lowlands, with its great variety of fruit-bearing shrubs and trees (Fa *et al.* 1992), provides plenty of food resources for small mammals and may permit better breeding performance and individual survival and thus increase individual density.

We have shown that individual density influences species density estimates with elevation and thus in the areas with higher density of individuals (lowlands) species density may well be overestimated and likewise underestimated in areas of low individual density (highlands). We would expect species density to decrease in areas of lower individual density simply because fewer individuals are sampled (Gotelli & Colwell 2001) and, conversely, we would expect species density to increase in areas of higher individual density because there are more individuals to be sampled. Since individuals are the units that carry taxonomic information and by which biodiversity is measured (Gotelli & Colwell 2001), environmental factors that affect the density of individuals with elevation are also likely to cause changes in species density. The patterns of small mammal density with elevation and their influence (if any) on the observed alpha diversity patterns were not assessed in most of the studies about small mammal diversity and elevation (Heaney 2001, Li *et al.* 2003, McCain 2004, Md Nor 2001), and were not included in a recent meta-analysis (McCain 2005). Rarefaction would have to be used to control for individual differences between samples in order to have comparable measures of species richness along environmental gradients (Hurlbert 2004).

Summarizing, we hypothesized that the combined effects of geographical (mid-domain effect), abiotic (climatic), and biotic (vegetation composition and structure, small mammal density, interdigitation of biotic communities) factors would seem to be responsible for the suggested mid-elevation peak in small mammal alpha diversity in the Montseny mountain.

ACKNOWLEDGMENTS. – A Ribas collaborated in the field work. The comments of two anonymous referees greatly improved the final version of this article. This study received financial and logistic support from the Oficina Tècnica de Parcs Naturals, Diputació de Barcelona.

## REFERENCES

- Alcántara M 1989. Análisis de la distribución elevacional de la fauna de micromamíferos de la Sierra de Guadarrama. *Acta biol montana* 9: 85-92.
- Arbuckle JL 1994-1999. *AMOS 4.01*, Student Edition. Small Waters Corporation, Chicago, USA.
- Boone RB, Krohn WB 2000. Partitioning sources of variation in vertebrate species richness. *J Biogeogr* 27: 457-470.
- Brown JH 2001. Mammals on mountainsides: elevational patterns of diversity. *Global Ecol Biogeogr* 10: 101-109.
- Brown JH, Lomolino MV 1998. *Biogeography*. Second edition. Sinauer Associates, USA.
- Colwell RK 1994-2004. Estimate S: statistical estimation of species richness and shared species from samples, ver 7.50. User's guide and application published at <http://www.viceroy.ceb.uconn.edu/EstimateS>.
- Colwell RK, Coddington JA 1994. Estimating terrestrial biodiversity through extrapolation. *Philos Trans R Soc Lond B* 345: 101-118.
- Colwell RK, Hurt GC 1994. Nonbiological gradients in species diversity and a spurious Rapoport effect. *Am Nat* 144: 570-595.
- Colwell RK, Lees DC 2000. The mid-domain effect: geometric constraints on the geography of species diversity. *Trends Ecol Evol* 15: 50-76.
- Colwell RK, Mao CX, Chang J 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecol* 85: 2717-2727.
- De Bolós O 1983. La vegetació del Montseny. Diputació de Barcelona.
- Delibes J 1985. Distribution and abundance of small mammals in a gradient of elevation. *Acta Zool Fenn* 173: 53-56.
- Everitt BS, Dunn G 1991. *Applied multivariate data analysis*. London, Edward Arnold.
- Fa JE, Shaw E, Santana A 1992. Habitat associations of small mammals in a southern Spanish fir forest. *Mammalia* 56: 478-481.
- Gotelli NJ 2001. Research frontiers in null model analysis. *Global Ecol Biogeogr* 10: 337-343.
- Gotelli NJ, Colwell RK 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Letters* 4: 379-391.
- Gotelli NJ, Entsminger GL 2001. *Ecosim: Null Models Software for Ecology*. User's guide and application published at <http://homepages.together.net/~gentsmin/ecosim.htm>.
- Grytnes JA, Vetaas OR 2002. Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan elevational gradient, Nepal. *Am Nat* 159: 294-304.
- Gurnell J 1985. Woodland rodent communities. In *The Ecology of Woodland Rodents, Bank Voles and Wood Mice*, JR Flowerdew, J Gurnell, JHW Gipps ed. *Symp Zool Soc Lond* 55: 377-402.
- Gurnell J, Flowerdew JR 1990. Live trapping small mammals. A practical guide. *Occ Pub Mam Soc Lond* 3: 1-39.
- Halffter G, Moreno CE 2005. Significado biológico de las diversidades alpha, beta y gamma. In *Sobre Diversidad biológica. El significado de las Diversidades alpha, beta y gamma*. G Halffter, J Soberón, P Koleff, A Melic Ed. Monografías Tercer Milenio, vol 4. S.E.A., Zaragoza.
- Hawkins BA, Pausas JG 2004. Does plant richness influence animal richness?: the mammals of Catalonia (NE Spain). *Divers Distrib* 10: 247-252.
- Heaney LR 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecol Biogeogr* 10: 15-39.

- Heaney LR, Heideman PD, Rickart EA, Uzzurum RB, Klompen JSH 1989. Altitudinal zonation of mammals in the central Philippines. *J Trop Ecol* 5: 259-280.
- Hesterberg T, Moore DS, Monaghan S, Clipson A, Epstein R 2005. Bootstrap Methods and Permutation Tests, 2nd edition, W H Freeman, NY.
- Hurlbert AH 2004. Species-energy relationships and habitat complexity in bird communities. *Ecol Letters* 7: 714-720.
- Li JS, Song YL, Zeng ZG. 2003. Elevational gradients of small mammal diversity on the northern slopes of Mt Qilian, China. *Global Ecol Biogeogr* 12: 449-460.
- Lima M, Jaksic FM. 1999. Population rate of change in the leaf-eared mouse: the role of density-dependence, seasonality and rainfall. *Aust J Ecol* 24: 110-116.
- Lima M, Julliard R, Stenseth NC, Jaksic FM. 2001. Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climatic factors. *J Anim Ecol* 70: 761-775.
- Lomolino MV 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecol Biogeogr* 10: 3-13.
- Ludwig JA, Reynolds JF 1988. Statistical Ecology. A primer on methods and computing. John Wiley & Sons, New York.
- McCain CM 2004. The mid-domain effect applied to elevational gradients: richness of small mammals in Costa Rica. *J Biogeogr* 31: 19-31.
- McCain, CM 2005. Elevational gradients in diversity of small mammals. *Ecol* 86: 366-372.
- Md Nor S 2001. Elevational diversity patterns of small mammals on Mount Kinabalu, Malaysia. *Global Ecol Biogeogr* 10: 41-62.
- Meserve P, Yunker JA, Gutiérrez JR, Contreras LC, Milstead WB, Lang BK, Cramer KL, Herrera S, Lagos VO, Silva SI, Tabilo EL, Torrealba MA, Jaksic FM 1995. Heterogeneous responses of small mammals to an El Niño southern oscillation event in Northcentral semiarid Chile and the importance of ecological scale. *J Mammal* 76: 580-595.
- Mittelbach G, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381-2396.
- Ninyerola M, Pons X, Roure JM 2000. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *Int J Climatol* 20: 1823-1841.
- Ninyerola M, Pons X, Roure JM 2003. Atlas Climàtic Digital de Catalunya. Univ Autònoma Barcelona and Generalitat de Catalunya.
- Patterson BD, Meserve PL, Lang BK 1989. Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. *J Mammal* 70: 67-78.
- Patterson BD, Pacheco V, Solari S 1996. Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. *J Zool Lond* 240: 637-658.
- Rahbek C 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18: 200-205.
- Rahbek C 1997. The relationship among area, elevation, and regional species richness in neotropical birds. *Am Nat* 149: 875-902.
- Rickart EA, Heaney LR, Uzzurum RB 1991. Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines. *J Mammal* 72: 458-469.
- Rickart EA 2001. Elevational diversity gradients, biogeography and the structure of montane mammal communities in the intermountain region of North America. *Global Ecol Biogeogr* 10: 77-100.
- Rosenzweig ML 1992. Species diversity gradients: We know more and less than we thought. *J Mammal* 73: 715-730.
- Rosenzweig ML 1995. Species diversity in space and time. Cambridge University Press.
- Ruggiero A, Kitzberger T 2004. Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. *Ecography* 27: 401-416.
- Sánchez-Cordero V 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. *Global Ecol Biogeogr* 10: 63-76.
- Sans-Fuentes MA, Ventura J 2000. Distribution patterns of the small mammals (Insectivora and Rodentia) in a transitional zone between the Eurosiberian and the Mediterranean regions. *J Biogeogr* 27: 755-764.
- Slade NA, Blair SM 2000. An empirical test of using counts of individuals captured as indices of population size. *J Mammal* 81: 1035-1045.
- Stevens GC 1992. The elevational gradient in elevational range: an extension of Rapoport's latitudinal rule to elevation. *Am Nat* 140: 893-911.
- Terradas J, Miralles J 1986. El patrimoni biològic del Montseny. Catàlegs de flora i fauna 1. Diputació de Barcelona, Spain.
- Tews J, Brose U, Grimm V, Tielbörger K, Wiechmann MC, Schwager M, Jeltsch F 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of key-stone structures. *J Biogeogr* 31: 79-92.
- Tognelli MF, Kelt DA 2004. Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography* 27: 427-436.
- Torre I, Tella JL, Arrizabalaga A 1996. Environmental and geographic factors affecting the distribution of small mammals in an isolated Mediterranean mountain. *Z Säugetierkd* 61: 365-375.
- Torre I, Bosch M 1999. Effects of sex and breeding status on habitat selection by feral House mice (*Mus musculus*) in a small Mediterranean island. *Z Säugetierkd* 64: 176-186.
- Torre I, Díaz M 2004. Small mammal abundance in Mediterranean post-fire habitats: a role for predators? *Acta Oecol* 25: 137-142
- Torre I, Arrizabalaga A 2008. Habitat preferences of the bank vole (*Myodes glareolus*) in a Mediterranean mountain range. *Acta Theriol* 53: 241-250.
- Whittaker RJ, Field R 2000. Tree species richness modelling: an approach of global applicability. *Oikos* 89: 399-402.
- Whittaker RJ, Willis KJ, Field R 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J Biogeogr* 28: 453-470.
- Williams SE, Marsh H, Winter J 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* 83: 1317-1329.

Received May 2, 2008

Accepted November 18, 2008

Associate Editor: E Magnanou