Journal of Arid Environments 103 (2014) 80–84

Contents lists available at ScienceDirect

Journal of Arid Environments

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

Distribution of arid-dwelling land snails according to dryness

Gregorio Moreno-Rueda

Departamento de Zoología, Universidad de Granada, ES-18071 Granada, Spain

ARTICLE INFO

Article history:
Received 13 September 2013
Received in revised form
15 January 2014
Accepted 21 January 2014
Available online 12 February 2014

Keywords:
Autoregressive models
Habitat selection
Land snails
Mountain
Spatial autocorrelation
Spatially explicit models

ABSTRACT

Although land snails are hydrophilic animals, several species inhabit arid or semi-arid environments. Here, I hypothesize that, for arid-dwelling land snails, both relatively moist environments and extreme arid zones, within their distribution ranges, should be disadvantageous. Therefore, arid-dwelling land snails should show maximal probability of presence and maximal abundances at intermediate levels of aridity. I tested this hypothesis with two land-snails from Sierra Elvira mountain range (SE Spain), *Sphincterochila candidissima* and *Iberus gualterianus*. Given that environmental variables as well as snail distribution showed spatial autocorrelation, I performed spatially explicit models, specifically simultaneous auto-regressions (SAR). The results supported the hypothesis, with the distribution of *S. candidissima* and the abundance of *I. gualterianus* following a concave-down relationship with aridity. Moreover, both species were less abundant as elevation increased, and *I. gualterianus* showed a positive association with rocky surface. Therefore, this study highlights that, in arid environments, arid-dwelling land snails show maximal abundance and probability of presence at intermediate aridity levels. Although the reasons explaining why extreme aridity values limit the abundance and distribution of land snails are well detailed, it remains intriguing why these snails decrease in abundance when moisture increases.

1. Introduction

Arid environments present characteristically low moisture and scarce vegetation (Cox and Moore, 2005). Consequently, primary productivity is very low in arid environments (Hawkins et al., 2003), and this imposes restrictive living conditions on animals (Pianka, 2000). Arid environments are especially restrictive for hydrophilic animals, despite that several hydrophilic taxa inhabit arid environments. For example, terrestrial gastropods are very hydrophilic animals, since they have a permeable skin and undergo high rates of dehydration (Luchtel and Deyrup-Olsen, 2001; Prior, 1985). In fact, in temperate realms, their distribution is strongly affected by moisture, and a greater number of individuals are typically found in moist environments than in dry environments (Martin and Sommer, 2004). Nevertheless, several snail species inhabit arid zones, where they use behavioural, physiological, and/or morphological adaptations to minimise the risk of dehydration (Arad et al., 1989; Giokas et al., 2005; Moreno-Rueda, 2007).

As mentioned above, in relatively moist zones, land snails are typically more abundant in wetter zones. Therefore, it might be concluded that in arid or semi-arid zones, such as the Mediterranean region, arid-dwelling land snail distributions increase with moisture, even more markedly than in wet realms. However, the semi-arid Sierra Elvira mountain (SE Spain), in contrast to moist sites, shows higher abundances and diversity of land snails on its drier, southern slope (Moreno-Rueda, 2002). Although dry zones offer a clearly restrictive environment for land snails (also see Tryjanowski and Koralewska-Batura, 2000), wet zones may also be restrictive in some aspects, especially for animals not adapted to moist environments. Therefore, the dispersion of arid-dwelling land snails to moister zones may be limited by a number of factors. For example, parasites are more abundant in wet zones (Moyer et al., 2002). Given that species richness is higher in more productive zones (e.g. Moreno-Rueda and Pizarro, 2009), then more productive zones (i.e. moister zones) should harbour more predators and competitors. Competition with other species or subspecies may limit the distribution of land snails (Moreno-Rueda, 2006b). In fact, climatic selection strongly influences land snail distribution (Cowie, 1990; Cowie and Jones, 1985; Johnson, 2011).

In accordance with this reasoning, I predict that in an arid or semi-arid zone, such as Sierra Elvira mountain range, the abundance and probability of detecting arid-dwelling land snails should show a concave-down relationship with aridity. In a cline of aridity, both extremes should impose restrictive situations for land snails by the aforementioned conditions, with their abundances maximized at intermediate aridity values. I test this prediction with the two main species of land snails in Sierra Elvira: *Sphincterochila candidissima* and *Iberus gualterianus* (Moreno-Rueda, 2002). In the present study, I measured in detail a number of environmental

---

E-mail address: gmr@ugr.es.

0140-1963/$ – see front matter © 2014 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jaridenv.2014.01.006

variables, and statistically tested whether the abundance values and probabilities of detection of the two snails show a concave-down relationship with plant cover, as an inverse indicator of micro-geographic aridity.

2. Methods

2.1. Study species

S. candidissima (Gastropoda; Sphincterochilidae) is widespread in the west side of the Mediterranean basin (Fechter and Falkner, 1993). All the species in Sphincterochilidae are well adapted to desert and subdesert environments (Arad et al., 1989; Shachak, 1981; Yom-Tov, 1971). On the other hand, the genus *Iberus* (Gastropoda; Helicidae) is endemic to Spain (García San Nicolás, 1957) and typically inhabits zones with Mediterranean climate (Ruiz Ruiz et al., 2006). *I. gualterianus* inhabits mainly arid and semi-arid zones such as the mountain range sampled in the present study (Moreno-Rueda, 2011).

2.2. Study area

Sierra Elvira (SE Spain; 37° 15′ N, 3° 40′ W), is a small karstic sierra within an elevational range of 600–1100 m a.s.l. It is characterized as having a Mediterranean climate with up five months of drought (Moreno-Rueda et al., 2009). The study area shows a mosaic of habitats composed mainly of scrubland of *Quercus coccifera*, *Juniperus oxycedrus*, *Stipa tenacissima*, *Cistus* ssp. and *Rosmarinus officinalis*, alternating with small patches of grasslands and bare soil.

2.3. Sampling

The sampling was performed between 2002 and 2004, during October and November, when detectability of snails is at its peak (Moreno-Rueda and Collantes-Martín, 2007; Moreno-Rueda and Pizarro, 2007). For the measurement of snail distribution and environmental variables, I studied 70 quadrats of 9 m^2 (3 × 3 m) randomly distributed on the mountain (Fig. 1). Quadrats were cordoned off, and I carefully searched for snails by the complete quadrat, especially scrutinizing rock crevices as well as searching inside and under scrubby vegetation, where these snails are frequently sheltered (Moreno-Rueda, 2007). Live specimens as well as empty shells were recorded. Since snails inhabit a low-productive environment, they are found at very low densities (Moreno-Rueda and Collantes-Martín, 2007; Moreno-Rueda and Pizarro, 2007). Therefore, I estimated relative abundance according to total live plus dead snails found. Previously, I tested whether this is a good estimation of relative abundance of live snails. For both species, density of live animals was significantly correlated with that of dead snails (for *I. gualterianus*: $r_s = 0.578$, $P < 0.001$; for *S. candidissima*: $r_s = 0.549$, $P < 0.001$; $n = 70$ quadrats). Slopes might encourage the accumulation of empty shells in lower flat areas (Baur et al., 1997). For this reason, I measured the slope angle of the quadrat with an inclinometer at 16 points homogeneously distributed, and estimated the average. The density of empty shells was uncorrelated with average inclination of the quadrat for both species (*I. gualterianus*: $r_s = 0.189$, $P = 0.117$; *S. candidissima*: $r_s = 0.143$, $P = 0.239$). Therefore, I considered a species to be present in a quadrat when I found at least one shell in the quadrat. The relative abundance was estimated as the total of empty shells plus live individuals found in the quadrat.

Regarding the environmental variables, I measured: (1) Plant cover, which was measured by subdividing the quadrat in 225 squares of 20 × 20 cm. For each square, I recorded whether it was mainly (>50%) covered by vegetation or not. The percentage of cover was calculated as number of squares covered by vegetation divided by 2.25. Aridity of the quadrats was approached as the absence of vegetation, estimated as 100 minus plant cover, that is, the percentage of the quadrat not covered by vegetation. (2) Elevation, with the use of a GPS device. Elevation was measured because previous studies show that it affects the presence at least of *I. gualterianus* (Moreno-Rueda, 2006c). (3) Rocky substrate. In the study area, substrate may be divided basically into bare soil and rocky substrate. I measured the type of substrate, because it has been proved to be important for the distribution of *I. gualterianus*

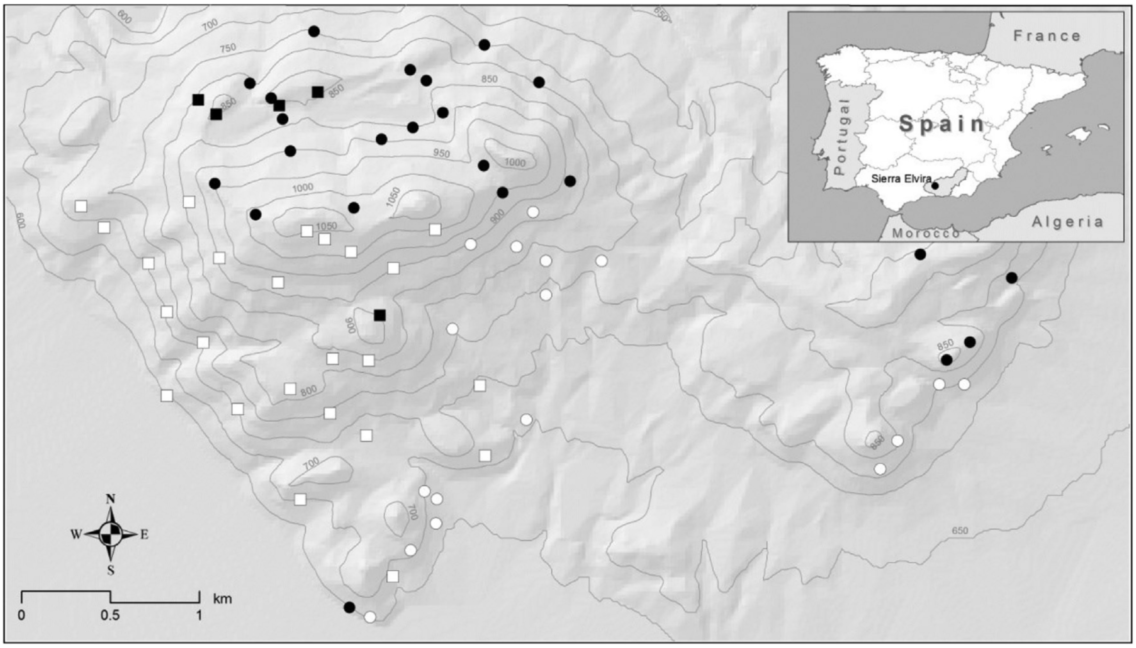

Fig. 1. Geographic location of study quadrats in Sierra Elvira mountain range (SE Spain). White indicates quadrats in which *Sphincterochila candidissima* was present, black in which *S. candidissima* was absent, squares indicate that *Iberus gualterianus* was present, while circles indicate that it was absent.

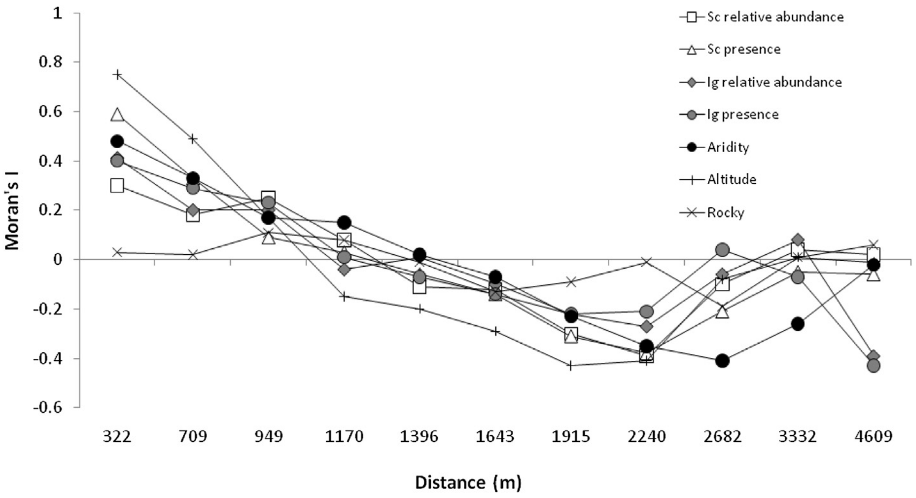

Fig. 2. Moran's *I* index of spatial autocorrelation for each variable considered in this study (*Sphincterochila candidissima* as well as *Iberus gualterianus* presence and abundance, aridity, elevation, and rocky surface). Sc indicates *S. candidissima*, and Ig indicates *I. gualterianus*. Positive values of Moran's *I* index indicate that values for close sampling plots are similar as a consequence of proximity (positive spatial autocorrelation). Spatial autocorrelation decreases as sampling plots are more dispersed (at about 1 km for most of variables).

(Moreno-Rueda, 2002, 2006a,c; Moreno-Rueda et al., 2009). For measuring substrate type, I recorded whether the substrate was mainly bare soil or rock for every 225 squares. The percentage of rocky substrate was estimated as the number of squares covered mainly by rock divided by 2.25. The vegetation cover might be expected to decrease with increased rocky surface. However, this was not the case in the study area ($r_s = 0.013$, $P = 0.89$), suggesting that variation in vegetation cover is mainly the result of variation in moisture. (4) The coordinates of the quadrat, in UTM, were recorded by using the GPS device.

2.4. Statistical analyses

To test the hypothesis that relative abundance and probability of presence of arid-dwelling species is maximized at intermediate levels of aridity in their distribution range, I was interested in regressing the probability of presence and relative abundance of the two species against aridity (measured as percentage of ground bare of vegetation). For this, I used a polynomial regression (Quinn and Keough, 2002). According to a polynomial regression, a negative quadratic term indicates a concave-down relationship between the dependent variable and the predictor (aridity in this case). However, covariation between the distribution of species and any environmental variable may be simply a consequence of distribution and environment to be spatially co-structured, this called spatial autocorrelation, which increases type-I statistical error (Legendre, 1993). Therefore, I first tested whether the distribution of the two species and environmental variables showed spatial autocorrelation according to Moran's *I* (Dormann et al., 2007). Spatial autocorrelation was tested with Spatial Analysis in Macroecology (SAM) program (Rangel et al., 2010). Given that the two species as well as some environmental variables showed spatial autocorrelation (see Results), I performed spatially explicit models, specifically simultaneous autoregressive (SAR) models, which account for most of spatial autocorrelation (Lichstein et al., 2002). As dependent variables, I introduced presence as well as relative abundance of the two land snails. Predictors of the presence and relative abundance were aridity and its quadratic term (both arcsine-transformed), as well as elevation and percentage of rocky substrate (arcsine-transformed), which also affect snail distribution (see above). Variables measured in percentage were arcsine-transformed for a better fitting of the models (Quinn and Keough, 2002). For the analyses performed to test the effect of aridity on snail presence, I used the 70 quadrats, with values of 0 and 1 for non-present and present, respectively. To analyse the effect of aridity on relative abundance, I used only the quadrats where each species was present ($n = 29$ for *I. gualterianus* and $n = 41$ for *S. candidissima*). As the objective of these models is to examine what determinates snail abundance (in contrast with previous models, examining what determinates snail presence), only zones where the snails are effectively present were considered, since by including quadrats where the species is absent, the model generated would not substantially differ from a model examining the effect of environment on presence distribution. The normality as well as the spatial autocorrelation of model residuals was checked, and the relative abundance of *S. candidissima* was log-transformed for a better fitting of the model.

3. Results

Presence as well as relative abundance of the two land snails showed spatial autocorrelation (Fig. 2). Spatial autocorrelation was significantly positive below 1000 m and tended to be negative between 1500 and 2500 m. A logistic regression showed that *S. candidissima* presence is correlated with latitude ($\chi^2 = 33.57$, $p < 0.001$), being more frequent at the south of the mountain (see Fig. 1). However, *I. gualterianus* probability of presence increased towards the east ($\chi^2 = 31.25$, $p < 0.001$; see Fig. 1 and Moreno-Rueda (2006c)). When counting for spatial autocorrelation, the presence of the two land snails was not significantly correlated (Spearman correlation, $r_s = -0.163$, corrected $P = 0.083$, $n = 70$; *P*-value corrected following Dutilleul (1993)). Relative abundance between the two species was also not significantly correlated ($r_s = 0.158$, corrected $P = 0.334$).

Similar patterns of spatial autocorrelation were found for aridity (Fig. 2). Elevation also showed spatial autocorrelation, but surface coverage by rocky substrate did not (Fig. 2). Therefore, a simple relation between aridity and snail distributions might be due to spatial autocorrelation between the two set of variables. This implies the need to apply spatially explicit models, such as simultaneous autoregressive models (SAR), in order to control for most of the spatial autocorrelation (Lichstein et al., 2002).

The SAR models indicated that the probability of finding *S. candidissima* increased with aridity, following a concave-down relationship, as the quadratic term was significant and negative (Table 1). The probability of finding *S. candidissima* also decreased with elevation. Space explained more variance than did environment in the distribution of this land snail (Fig. 3). For *I. gualterianus*, similarly, the probability of presence increased with aridity, and tended to follow a concave-down relationship (Table 1). Nevertheless, for this species, the quadratic term was not significant ($P = 0.061$). As previously found with no spatially explicit models (Moreno-Rueda, 2006c), the probability of finding an *I. gualterianus* increased with the percentage of surface area covered by rocky substrate (Table 1). Environment and space accounted for similar quantities of variance in the distribution of this snail (Fig. 3).

Regarding the effect of aridity on relative abundance, the model showed that the abundance of *S. candidissima* decreased as elevation increased. For aridity, the trend was the same as for presence, but the *P*-values were not significant (Table 1). Space and environment account for similar quantities of variance in abundance of this snail (Fig. 3). For *I. gualterianus*, the abundance of individuals increased with aridity, following a significant concave-down relation (Table 1). Moreover, *I. gualterianus* abundance decreased with elevation and increased with the surface area covered by rocky substrate (Table 1). The geographic variance in abundance of this snail was explained almost exclusively by environment variation, with spatial structure accounting for only 3% of the variance (Fig. 3).

4. Discussion

The results of this study show that both the presence and abundance of the two snail species (*S. candidissima* and *I. gualterianus*) tended to follow concave-down relationships with aridity, being statistically significant for *S. candidissima* presence and *I. gualterianus* abundance. In a previous study (Moreno-Rueda, 2011), I had found a significant concave-down relationship between *I. gualterianus* presence and percentage of surface uncovered by vegetation, by using a logistic regression. However, that analysis did not account for spatial autocorrelation, and in the present study, when spatial autocorrelation is considered, the concave-down relationship between *I. gualterianus* presence and aridity turned out to be non-significant. This detail emphasizes the importance of control for spatial structure in studies of species distribution. The two land snails are typical of arid and semi-arid environments (Moreno-Rueda, 2007). However, extreme values of aridity seem to negatively affect the distribution of these species. Even for a land snail as well adapted to desert environments as is *S. candidissima* (Moreno-Rueda, 2008), extreme aridity values in Sierra Elvira limited its distribution.

Table 1

Results of the simultaneous autoregressive (SAR) models predicting the distribution of presences and abundance for the land snails *Sphincterochila candidissima* and *Iberus gualterianus* in Sierra Elvira mountain (SE Spain). Standardized beta coefficient, *t*-statistic and *P*-value indicate the "effect" of each environmental variable on each dependent variable. For each model, the R^2, *F*-statistic, sample size, and *P*-value are shown. In bold, significant effects.

	β coefficient	*t*	*P*
SAR model for *S. candidissima* presence			
$R^2 = 0.336$, $F = 8.212$, $n = 70$, $P < 0.001$			
Aridity	**1.265**	**3.903**	**<0.001**
$(\text{Aridity})^2$	**−1.070**	**−3.159**	**0.002**
Elevation	**−0.384**	**−2.818**	**0.006**
Rocky surface	0.071	0.805	0.424
SAR model for *I. gualterianus* presence			
$R^2 = 0.257$, $F = 5.620$, $n = 70$, $P < 0.001$			
Aridity	**0.946**	**2.723**	**0.008**
$(\text{Aridity})^2$	−0.693	−1.909	0.061
Elevation	−0.007	−0.045	0.964
Rocky surface	**0.249**	**2.637**	**0.010**
SAR model for *S. candidissima* abundance			
$R^2 = 0.275$, $F = 4.410$, $n = 41$, $P = 0.018$			
Aridity	0.854	1.776	0.084
$(\text{Aridity})^2$	−0.729	−1.437	0.160
Elevation	**−0.439**	**−2.423**	**0.021**
Rocky surface	−0.084	0.559	0.580
SAR model for *I. gualterianus* abundance			
$R^2 = 0.640$, $F = 10.647$, $n = 29$, $P < 0.001$			
Aridity	**1.552**	**3.494**	**0.002**
$(\text{Aridity})^2$	**−1.458**	**−3.214**	**0.004**
Elevation	**−0.486**	**−2.604**	**0.016**
Rocky surface	**0.614**	**−4.738**	**<0.001**

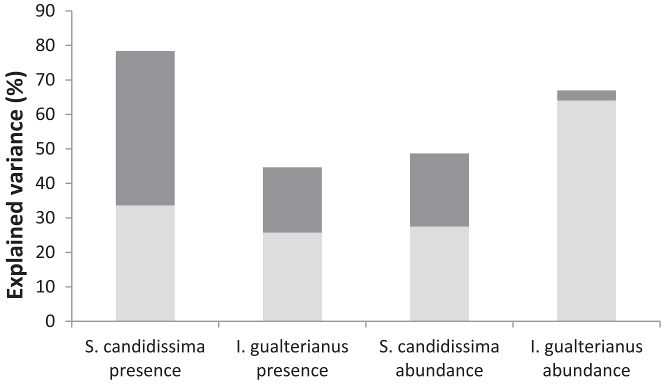

Fig. 3. Percentage of variance explained by the SAR models for both *Sphincterochila candidissima* and *Iberus gualterianus* presence and abundance. Pale grey indicates the variance explained by the environmental variables, while dark grey indicates the variance explained by spatial structure.

The question that arises is why moisture also limits the distribution of these species. There are various tentative explanations for this finding. First, these snails are generalist herbivores (Moreno-Rueda and Díaz-Fernández, 2003), and given that vegetation is more abundant in less arid zones, competition for food with other species (mainly arthropods, since snails are almost absent from moist zones in Sierra Elvira) does not seem to be the underlying cause that limits dispersion to moister zones of the mountain range. Nevertheless, competition among herbivores may be more important than expected (Baur and Baur, 1990).

Second, predators may be more abundant in moister zones of the mountain, as these zones are more productive. Predation is an important factor limiting species distribution in general (Sih et al., 1985), and snail distribution in particular (e.g. Murray et al., 1988; Rosin et al., 2011). However, *S. candidissima* is barely depredated, due to the thick shell (Rosin et al., 2013). *I. gualterianus*, by contrast, is heavily preyed upon by rats in the study area (Moreno-Rueda, 2009). If predators are more abundant in moister zones, *I. gualterianus* may suffer less predation pressure in the driest zones of the mountain. In fact, the only land snails I have found in the wettest zone of the sierra (the northern slope) were seven individuals of *Iberus alcarazanus* depredated by rodents. Nevertheless, at this moment I have no data on how predator abundance varies with moisture on Sierra Elvira mountain.

Third, parasites seem to be more abundant in moist realms (Moyer et al., 2002), and land snails are hosts of several parasitic species, whose parasitism intensity varies geographically (Baur and Baur, 2005). Moister zones present higher productivity and species richness, and thus more potential vectors, so that they may impose a strong pressure through parasitism. In fact, some studies have shown that parasites may be major factors shaping the distribution of land snails (e.g. Cunningham and Daszak, 1998).

Also, this study showed that *I. gualterianus* was distributed mainly on rocky substrate. This finding coincides with previous studies, which did not use spatially explicit models (Moreno-Rueda, 2006c). This snail is found mainly on rocky substrate since it uses rocky crevices as shelters in order to survive aestivation and daylight periods (Moreno-Rueda, 2007). On the other hand, I have found that the abundance of the two land snails diminished with the elevation. A fall in temperature with a rise in elevation could explain the decline in *S. candidissima* abundance, since this species is rather thermophilic (Moreno-Rueda, 2007, 2008; Moreno-Rueda and Collantes-Martín, 2007). However, it is unlikely that decreasing temperature negatively affects *I. gualterianus* distribution, as this land snail remains active at lower temperatures than does *S. candidissima* (Moreno-Rueda, 2012; Moreno-Rueda and Collantes-Martín, 2007). Winds tend to be stronger at higher elevations (Körner, 2007), and this would discourage snail activity (Humphreys, 1976), so that stronger winds at high elevations might cause lower abundance at higher elevations for both species in Sierra Elvira.

In conclusion, although dry areas restrict the living conditions of land snails, the presence and abundance of two arid-dwelling land snails (*S. candidissima* and *I. gualterianus*) increased with aridity. This finding is probably a consequence of moist zones imposing restrictions for land snails adapted to aridity, such as increased competition, predation or parasitism. On the other hand, evidence of the restrictive conditions of arid environments, even for snails adapted to aridity, is that the distribution of both species decreased for high aridity. Therefore, arid-dwelling land snails avoid extreme values of both high and low aridity within their distribution range.

Acknowledgements

Fran Ruiz-Avilés, Rocío Márquez-Ferrando and Rubén Rabaneda-Bueno collaborated during fieldwork. Manuel Pizarro drew the Fig. 1. Jean Mattos-Reaño and David Nesbitt reviewed the English. Comments by Cristina Armas and anonymous referees improved the manuscript.

References

Arad, Z., Goldenberg, S., Heller, J., 1989. Resistance to desiccation and distribution patterns in the land snail *Sphincterochila*. J. Zool. 218, 353–364.

Baur, A., Baur, B., 2005. Interpopulation variation in the prevalence and intensity of parasitic mite infection in the land snail *Arianta arbustorum*. Invertebr. Biol. 124, 194–201.

Baur, B., Baur, A., 1990. Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. J. Anim. Ecol. 59, 301–315.

Baur, B., Ledergerber, S., Kothbauer, H., 1997. Passive dispersal on mountain slopes: shell shape-related differences in downhill rolling in the land snails *Arianta arbustorum* and *Arianta chamaeleon* (Helicidae). Veliger 40, 84–86.

Cowie, R.H., 1990. Climatic selection on body colour in the land snail *Theba pisana* (Pulmonata: Helicidae). Heredity 65, 123–126.

Cowie, R.H., Jones, J.S., 1985. Climatic selection on body colour in *Cepaea*. Heredity 55, 261–267.

Cox, C.B., Moore, P.D., 2005. Biogeography. An Ecological and Evolutionary Approach, seventh ed. Blackwell Publishing, Malden.

Cunningham, A.A., Daszak, P., 1998. Extinction of a species of land snail due to infection with a microsporidian parasite. Conserv. Biol. 12, 1139–1141.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Method to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609–628.

Dutilleul, P., 1993. Modifying the t-test for assessing the correlation between two spatial processes. Biometrics 49, 305–314.

Fechter, R., Falkner, G., 1993. Moluscos. Blume, Barcelona.

García San Nicolás, E., 1957. Estudio sobre la biología, la anatomía y la sistemática del género *Iberus* Montfort 1810. Boletín la Real Soc. Española Hist. Nat. 55, 199–390.

Giokas, S., Panayiotis, P., Valakos, E., 2005. Ecological and physiological adaptations of the land snail *Albinaria caerulea* (Pulmonata: Clausiliidae). J. Molluscan Stud. 71, 15–23.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdoff, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84, 3105–3117.

Humphreys, J., 1976. Field observations on *Theba pisana* (Müller) (Gastropoda: Helicidae) at St. Ives, Cornwall. J. Conchol. 29, 93–106.

Johnson, M.S., 2011. Thirty-four years of climatic selection in the land snail *Theba pisana*. Heredity 106, 741–748.

Körner, C., 2007. The use of "altitude" in ecological research. Trends Ecol. Evol. 22, 569–574.

Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74, 1659–1673.

Lichstein, J.W., Simons, T.R., Shriner, S.A., Franzreb, K.E., 2002. Spatial autocorrelation and autoregressive models in ecology. Ecol. Monogr. 72, 445–463.

Luchtel, D.L., Deyrup-Olsen, I., 2001. Body wall: form and function. In: Barker, G.M. (Ed.), The Biology of Terrestrial Molluscs. CAB International, Wallingford, pp. 147–178.

Martin, K., Sommer, M., 2004. Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. J. Biogeogr. 31, 531–545.

Moreno-Rueda, G., 2002. Selección de hábitat por *Iberus gualtierianus, Rumina decollata* y *Sphincterochila candidissima* (Gastropoda: Pulmonata) en una sierra del sureste español. Iberus 20, 55–62.

Moreno-Rueda, G., 2006a. Habitat use by the arid-dwelling land snail *Iberus g. gualtieranus*. J. Arid Environ. 67, 336–342.

Moreno-Rueda, G., 2006b. Selección de hábitat por dos subespecies de *Iberus gualtieranus* (Gastropoda, Helicidae) en Sierra Elvira (SE de España). Zool. Baetica 17, 47–58.

Moreno-Rueda, G., 2006c. Selección de hábitat y conservación del caracol en peligro de extinción *Iberus gualtieranus gualtieranus*. Acta Granatense 5, 45–56.

Moreno-Rueda, G., 2007. Refuge selection by two sympatric species of arid-dwelling land snails: different adaptive strategies to achieve the same objective. J. Arid Environ. 68, 588–598.

Moreno-Rueda, G., 2008. The colour white diminishes weight loss during aestivation in the arid-dwelling land snail *Sphincterochila (Albea) candidissima*. Iberus 26, 47–51.

Moreno-Rueda, G., 2009. Disruptive selection by predation offsets stabilizing selection on shell morphology in the land snail *Iberus g. gualtieranus*. Evol. Ecol. 23, 463–471.

Moreno-Rueda, G., 2011. Revisión del estatus de conservación del caracol amenazado *Iberus gualtieranus gualtieranus*. Zool. Baetica 22, 69–85.

Moreno-Rueda, G., 2012. The importance of moisture in the activity patterns of the arid-dwelling land snail *Iberus gualterianus*. In: Hämäläinen, E.M., Järvinen, S. (Eds.), Snails: Biology, Ecology and Conservation. Nova Science Publishers, New York, pp. 137–149.

Moreno-Rueda, G., Collantes-Martín, E., 2007. Ciclo anual de actividad del caracol *Sphincterochila (Albea) candidissima* (Draparnaud, 1801) en un medio semiárido. Iberus 25, 49–56.

Moreno-Rueda, G., Díaz-Fernández, D.F., 2003. Notas sobre la alimentación de *Iberus gualtierianus gualtierianus* (Linnaeus, 1758) (Gastropoda: Helicidae). Acta Granatense 2, 89–92.

Moreno-Rueda, G., Pizarro, M., 2007. Census method for estimating the population size of the endemic and threatened land snail *Iberus gualtieranus gualtieranus*. Anim. Biodivers. Conserv. 30, 1–5.

Moreno-Rueda, G., Pizarro, M., 2009. Relative influence of habitat heterogeneity, climate, human disturbance and spatial structure on vertebrate species richness in Spain. Ecol. Res. 24, 335–344.

Moreno-Rueda, G., Ruiz-Ruiz, A., Collantes-Martín, E., Arrébola, J.R., 2009. Relative importance of humidity and temperature on microhabitat use by land-snails in arid versus humid environments. In: Fernández-Bernal, A., De la Rosa, M.A. (Eds.), Arid Environments and Wind Erosion. Nova Science Publishers, New York, pp. 331–343.

Moyer, B.R., Drown, D.M., Clayton, D.H., 2002. Low humidity reduces ectoparasite pressure: implications for host life history evolution. Oikos 97, 223–228.

Murray, J., Murray, E., Johnson, M.S., Clarke, B., 1988. The extinction of *Partula* on Moorea. Pac. Sci. 42, 150–153.

Pianka, E.R., 2000. Evolutionary Ecology, sixth ed. Benjamin/Cumming, San Francisco.

Prior, D.J., 1985. Water-regulatory behaviour in terrestrial gastropods. Biol. Rev. 60, 403–424.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists, first ed. Cambridge University Press, Cambridge.

Rangel, T.F., Diniz-Filho, J.A.F., Bini, L.M., 2010. SAM: a comprehensive application for spatial analysis in macroecology. Ecography 33, 46–50.

Rosin, Z.M., Olborska, P., Surmacki, A., Tryjanowski, P., 2011. Differences in predatory pressure on snails by birds and mammals. J. Biosci. 36, 691–699.

Rosin, Z.M., Kobak, J., Lesicki, A., Tryjanowski, P., 2013. Differential shell strength of *Cepaea nemoralis* colour morphs — implications for their anti-predator defence. Naturwissenschaften 100, 843–851.

Ruiz Ruiz, A., Cárcaba Pozo, A., Porras Crevillen, A.I., Arrébola, J.R., 2006. Guía de los caracoles terrestres de Andalucía. Fundación Gypaetus, Seville.

Shachak, M., 1981. Comparative study of the water economy of two sympatric species of desert snails (*Sphincterochila zonata* and *S. prophetarum*). J. Arid Environ. 4, 115–121.

Sih, A., Crowley, P., McPeek, M., Petranka, J., Strohmeier, K., 1985. Predation, competition, and prey communities: a review of field experiments. Annu. Rev. Ecol. Syst. 16, 269–311.

Tryjanowski, P., Koralewska-Batura, E., 2000. Inter-habitat shell morphometric differentiation of the snail *Helix lutescens* Rossm. (Gastropoda: Pulmonata). Ekol. Bratisl. 19, 111–116.

Yom-Tov, Y., 1971. Body temperature and light reflectance in two desert snails. J. Molluscan Stud. 39, 907–911.