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Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian *Copris* species

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Abstract

Dung beetle populations, in decline, play a critical ecological role in extensive pasture ecosystems by recycling organic matter; thus the importance of their conservation status. Presence data available for *Copris hispanus* (L.) and *Copris lunaris* (L.) (Coleoptera, Scarabaeidae) in Comunidad de Madrid (CM), and BIOMAPPER, a GIS-based tool, was used to model their environmental niches. The so derived potential distributions of both species were used to exemplify the utility of this kind of methodologies in conservation assessment, as well as its capacity to describe the potential sympatry between two or more species. Both species, distributed along a Dry-Mediterranean to Wet-Alpine environmental conditions gradient, overlap in areas of moderate temperatures and mean annual precipitations in the north of CM. *Copris* are poorly conserved in the existing protected sites network, but protection provided by new sites included in the future Natura 2000 Network will improve the general conservation status of these species in CM. © 2004 Published by Elsevier Ltd.

Keywords: Copris; Iberian Peninsula; Dung beetle conservation; GIS predictive niche-modelling; Species distribution

1. Introduction

Research has become increasingly focused on the extrapolation of species distribution from incomplete data to obtain reliable distribution maps most efficiently (Mitchell, 1991; Pereira and Itami, 1991; Buckland and Elston, 1993; Iverson and Prasad, 1998; Manel et al., 1999a,b; Parker, 1999; Peterson et al., 1999; Pearce and Ferrier, 2000; Vayssières et al., 2000; Hirzel et al., 2001; Guisan et al., 2002; Hortal and Lobo, 2002; Ferrier et al., 2002). By processing environmental information and presence/absence data, several statistical methods can provide estimates of the probability of occurrence of a given species (Guisan and Zimmermann,

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2000). However, since the absence of a species from a locality is difficult to demonstrate, and since faunistic atlases do not usually cover localities where sampling has failed to produce a capture, false absences can decrease the reliability of predictive models. As an alternative, species distribution prediction based on presence-only data has been developed (Busby, 1991; Mitchell, 1991; Walker and Cocks, 1991; Carpenter et al., 1993; Scott et al., 1993; Stockwell and Peters, 1999; Peterson et al., 1999; Hirzel et al., 2001, 2002; Robertson et al., 2001). Generally, these alternative methods delimit the environmental niche of species within a geographical area and with a given resolution by comparing the environmental distribution of all the cells with that of cells where the species has been observed.

Pinpointing the areas where appropriate environmental conditions exist to sustain species is vital for biogeographical and conservation studies. It allows identifying

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environmentally suitable regions still not colonized, or where the species has become extinct; then the contribution of unique historical or geographical factors to the shaping of the current distribution of a species can be judged. With regard to conservation, potential distribution area identification can help locate sites suitable for reintroduction programs, or faunistic corridors, favouring success in regional conservation planning. Following this line of thought, niche-based modelling of potential distributions has been used recently to examine different ecological and evolutionary aspects, such as competition between phylogenetically related species (Anderson et al., 2002) or variation in species' niche requirements through evolutionary time (Peterson et al., 1999; Peterson and Holt, 2003).

To exemplify the use of these techniques for conservation and ecological purposes, the Ecological-Niche Factor Analysis method (ENFA; Hirzel et al., 2001, 2002) was used to delimit the potential distributional areas for two Copris species (Coleoptera, Sacarabaeoidea) in central Spain. This genus is made up of around 70 large-size dung beetle species, three of them present in the Western Palaearctic region (Baraud, 1992), being two of them, Copris lunaris and Copris hispanus, present in the Iberian Peninsula (Martín-Piera, 2000). C. lunaris, widely distributed throughout the Palaearctic region, inhabits mainly northern and temperate Iberian localities below 1000 m. in altitude, although it does reach 1700 m. in the south (Fig. 1). On the contrary, C. hispanus, a western Mediterranean species, frequents the southern half of the Iberian Peninsula at a slightly lower altitude. Both species occur together rarely, as they do in the Comunidad de Madrid (CM), in the centre of the Iberian Peninsula.

Dung beetles play a key role in Mediterranean cattlegrazed traditional landscapes. They are responsible for most organic matter recycling (Martín-Piera and Lobo, 1995) and control dipterous populations (Hanski, 1991). However, Western European dung-beetle assemblages present several conservation problems related to intensive management of agriculture and farming activities (Martín-Piera and Lobo, 1995; Barbero et al., 1999; Hutton and Giller, 2003). Their sensitivity to landscape transformation (e.g., Verdú et al., 2000; Verdú and Galante, 2002) and several cattle antibiotic treatments (e.g., ivermectins; Lumaret et al., 1993; Hutton and Giller, 2003), has leaded to the proposal of making use of them as indicators for conservation evaluation (Halffter, 1998; Davis et al., 2001; Andresen, 2003). Among them, largesize dung beetles, such as Copris species, seem to be the most affected. Their European populations are declining, and even becoming extinct (e.g., rollers, see Lobo, 2001). This is the case for C. lunaris, that has been declared critically endangered or extinct in the countries located at its northern range margins (see, e.g., Skidmore, 1991; Rassi et al., 1992; http://www2.dmu.dk/ 1_Om_DMU/2_Tvaer-funk/3_fdc_bio/projekter/redlist/

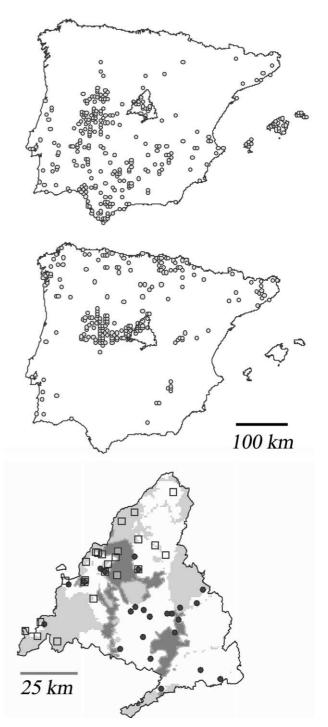


Fig. 1. Presence of *Copris hispanus* (upper) and *C. lunaris* (centre) in the Iberian Peninsula and distribution of both species in the Comunidad de Madrid (lower). Squares represent *Copris lunaris* presences, and dark circles do for *Copris hispanus* ones. Dark shadow represents existing Protected Natural Sites, light shadow future Nature 2000 network sites

redlist_en.asp or http://www.daba.lu.lv/ldf/CORINE/Insect.html).

Habitats Directive, the European Community initiative for a continental-scale network of protected areas (Natura 2000 Network), uses different kinds of habitats

as conservation goals. In Spain, the selection and management of these areas has been led to the Autonomous Communities, which constitute administrative divisions with full environmental jurisdictional autonomy. In this paper, we explore how this habitat-based selection may be useful to preserve the populations of two sympatric dung beetle species in an area where their respective northern and southern range margins overlap. We have chosen these species as indicators of the conservation status of traditionally managed landscapes, one of the targets of Natura 2000 Network. In addition, we explore how these two species respond to a strong environmental gradient at the edge of their respective distributions.

Using all distributional information available for C. hispanus and C. lunaris, the environmental niche occupied by each species in CM was modelled and used to extrapolate their respective potential distributions. Environmental requirements of both species are reviewed to identify differences and similarities. From the maps soobtained, most probable areas of joint occurrence are identified. Specific environmental conditions and habitat heterogeneity are considered as possible causes for cooccurrence, while taking into account the probability that competitive interactions may play a significant role in shaping local species distribution in these areas. The efficacy of existing protected natural sites (PNS) of Madrid, and also that of the complete set of sites included in the Spanish proposal for Natura 2000 Network in the preservation of populations of both species is assessed. Finally, we identify key Copris population sites in Madrid.

2. Materials and methods

2.1. Study site

CM, an autonomous Spanish region with full jurisdiction over local environmental policy, also complies with Spanish and European policy (see Fig. 1). Its northern peak, Somosierra (latitude 41°8'N) is 140 km from the most southern point (the Tajo valley, latitude 39°52′N). Although its mean altitude is around 800 m, CM climate and topography vary, along with elevations, from 434 m in the Alberche valley, to the 2430 m of the Peñalara peak, in the Central System mountain range. Its geologic history, also very eventful, gave rise to considerable lithologic diversity, with acidic rocks in the mountains; alluvial deposits on mountain slopes, terraces and valleys; and calcareous rocks and clays, and even gypsum soils, in the southeast. Its diversity, together with strategic positioning in the centre of the Iberian Peninsula, has made of CM a region of transition between Mediterranean and Eurosiberian faunas (see Fernández-Galiano and Ramos-Fernández, 1987), an

ideal region for small-scale pilot studies, as it is home to a synthesis of all inland Iberia.

2.2. Data sources

Biological data came from BANDASCA database, a compilation of all the information available in the bibliography and collections of natural history on the 53 Iberian species of the Scarabaeidae family (see structure in Lobo and Martín-Piera, 1991), as well as from a number of standardized surveys. The most recent of these sampling campaigns was environmentally and spatially designed explicitly to account for the spatial patterns of biodiversity variations in the region (see Hortal, 2004 and Hortal and Lobo, in press). After its results, it can be assumed that current presence records cover the main environmental and spatial patterns in both *Copris* species' distributions (for a detailed assessment of sampling effort and success see Hortal, 2004).

In this kind of geographically explicit analyses, the spatial resolution (grain size) constitutes a key decision for the accuracy and reliability of the obtained results. If cell size is larger than the area required to support a population, then the model will have very poor resolution. On the other hand, if it is too much small, then the model would present a high false prediction rate. Western Palaearctic temperate dung beetle populations have been estimated to have an approximate size of 1 km² (Roslin, 2000, 2001a,b; Roslin and Koivunen, 2001). Although no results have been yet published, a small scale study carried out in a semi-arid area of Central Spain gives support to a similar population size for Mediterranean species (J. M. Lobo, J. Hortal and F. J. Cabrero-Sañudo, unpublished). Thus, we have chosen 1 km² as the most appropriate spatial scale to carry out our analysis.

From the 72 database records available for C. hispanus and 111 for C. lunaris in the CM, only 24 reliable presence points could be obtained for each of the two species (see Fig. 1). The spatial resolution of most BANDASCA records, referred to the UTM 1×1 km grid, was also 1 km², so most of this biological information extracted from the database was directly used for the analyses. However, ten presence records for C. lunaris and seven for C. hispanus were limited to 10×10 km squares. We explored database information for each of these records (coming from museum specimen labels or from the literature). We thus assigned, where possible, their geographical position to the 1 km² pixel placed nearest to the centroid of the 10×10 km grid square, that complies with the altitude and/or geographical information in the database. If, e.g., a record was referred to have an altitude of 750 m.a.s.l, and to pertain to the San Lorenzo de El Escorial territory in the 30TVK09 UTM 10 km cell, we located a presence in one of the pixels that comply with both characteristics,

using the rule of thumb of selecting the closest to the centroid of the UTM cell. We assume that the error thus introduced is negligible, since both species are excellent flyers, as are almost all dung beetles.

Environmental data comes from CM-SIG, an environmental GIS database of CM (J. Hortal, unpublished; see Hortal, 2004), which contains the information of several variables relevant to the distribution of Scarabaeidae species. The richness and variation of Scarabaeidae assemblages in Western Europe has been formerly related with topography (Lobo et al., 2002; Hortal et al., 2003), climate (Lobo and Martín-Piera, 2002; Hortal et al., 2001, 2003; Lobo et al., 2002; Verdú and Galante, 2002), and soil composition (Hortal et al., 2001, 2003). Thus, we have selected five variables to account for these factors, on the assumption that they constitute the most important environmental determinants of the distribution of *Copris* species in the studied region. Landscape structure variables are known to effect the microdistribution of dung beetles (i.e., at spatial scales smaller than 1 km²), but were not considered for the environmental niche modelling procedure because such present-day land use variables are not adequate to model presence records from a large temporal resolution. However, land use information has been used to characterize the habitat heterogeneity of the areas potentially adequate for both species (see below).

A Digital Elevation Model (DEM; map of elevations) was extracted from a global DEM with 1 km spatial resolution (Clark Labs, 2000a). Mean annual precipitation and mean annual temperature scores for 41 stations of Central Iberia (30-year monthly data) were obtained from an agroclimatic atlas (Ministerio de Agricultura, Pesca y Alimentación, 1986). We interpolated data from these points onto 1-km-spatial-resolution maps using a moving-average procedure (using a six-point search radius; see Clark Labs, 2000b). Maps of solar radiation and lithology (11-categories) were digitized from a CM Atlas (ITGE, 1988). Categories in the lithology map were reclassified into areas with stony acidic soils; with calcareous soils or deposits; and with acidic deposits. As ENFA does not work with multinomial data, we derived three maps of the proportion of each kind of soil category in the $5 \times 5 \text{ km}^2$ window surrounding each pixel, using Idrisi32 Pattern module (Clark Labs, 2000b). Only the first two lithological variables were used, as the information from the third was redundant.

To ascertain if areas highly suitable for both species were more heterogeneous than the rest of the region, we also extracted five heterogeneity variables, three of them to take into account habitat heterogeneity. As steeper slopes are correlated with higher environmental variability, a slope map was calculated from the DEM using the GIS (Clark Labs, 2000b). A nine-categories aspect map was also derived from the DEM, and a land use map of 14-categories, obtained by reclassifying and

enlarging the 250 m European Land Use/Land Cover map provided by the CORINE programme (European Environment Agency, 1996). For both maps, the Shannon diversity index of the cells within a 5 × 5 km window was calculated to obtain an aspect-diversity map and a land-use diversity map (Clark Labs, 2000b). Annual variation (i.e. temporal heterogeneity) in monthly precipitation and temperature were also calculated for each climatic station as the mean of the differences between monthly extreme values within each year, and then interpolated using the procedure referred to above.

Finally, we obtained additional vectorial cartography of CM administrative limits from the digital version of the CM 1:200.000 map (Servicio Cartográfico de la Comunidad de Madrid, 1996). Protected natural sites (PNS) and future Natura 2000 network sites were obtained from the "Banco de Datos de la Naturaleza" of the Spanish "Dirección General de Conservación de la Naturaleza" (see http://www.mma.es/bd_nat/menu.htm).

2.3. Data analysis

2.3.1. Potential distribution maps

Ecological-niche factor analysis (ENFA) was done using BIOMAPPER 2.1 software (Hirzel et al., 2000; see http://www.unil.ch/biomapper). ENFA uses diverse environmental information to characterize the ecological distribution of the species. It computes a group of uncorrelated factors, summarizing the main environmental gradients in the region considered, similarly to common ordination techniques such as Principal Component Analysis. However, ENFA derives these factors using data only from known species presences (and absences, when available), thus providing factors with biological meaning. The first axis (marginality factor) is chosen to describe the marginality of the niche with respect to the regional environmental conditions, by maximizing the difference between the environmental mean value of the species' presences, and the global mean environmental value of all the studied region. The following axes (specialization factors), sorted according to their decreasing amounts of explained variance, are used to represent the species' degree of specialization in the rest of the (orthogonal) environmental gradients identified in the study area. Habitat suitability is modelled using the so-selected factors by estimating the ecogeographic degree of similarity between each grid square and the environmental preferences of the species, that is, the probability that a given grid square belongs to the environmental domain of the presence observations. Thus, starting from a species presence map a potential distribution map takes on the form of a habitat suitability map (HSM) of values that vary from 0 (minimum habitat quality) to 100 (maximum). The distribution models obtained were validated by a Jackknife procedure, whereby each HSM was computed 24 times (the number of presence points of each species), leaving out one point of presence with each iteration. By this procedure one independent habitat suitability score for each presence point was obtained and the observed and estimated scores compared. For a more extensive explanation of the method see Hirzel et al. (2002).

2.3.2. Environmental and spatial characterization of realized niche

The HSM maps obtained were reclassified as of: very low habitat suitability (0-25); low habitat suitability (26-50); high habitat suitability (51-75) or very high habitat suitability (76–100). These new maps were cross-tabulated in the GIS environment to pinpoint zones of spatial coincidence (very high/very high and very low/very low habitat suitability) and also of difference (very high for one species and very low for the other) for both species. By means of a Mann-Whitney U test (StatSoft, 1999), we extract those environmental variables that characterize each of these four zones, because of being significantly different to the conditions in the rest of CM. In order to compare the environmental variability between the cells with a very high suitability value for both species and the remaining cells, another Mann-Whitney U test was carried out, taking into account the five heterogeneity variables described above.

2.3.3. Conservation status

The degree of protection of *C. hispanus* and *C. lunaris*, achieved by existing PNS, and to be achieved by future Natura 2000 network sites in CM, was evaluated by extracting minimum, maximum, mean and standard deviation of the suitability values for both species in each protected site. The area of the zones with very high suitability values for each species (HS > 75) and for both together was also located. To assess conservation status of each species we have used two different criteria: the mean suitability scores, and the area with very high suitability scores (HS > 75) per PNS.

3. Results

3.1. Potential distributional maps

The six environmental variables considered were reduced to two factors for each species that explained a similar percentage of the variance: 96.7% for C. hispanus and 95.9% for C. lunaris, respectively. The first selected axis, which maximizes the absolute difference between global environmental mean and the species mean (the marginality factor), explains 74% of the specialization for C. hispanus and 72% for C. lunaris (see Hirzel et al., 2002), (i.e. the ratio of the standard deviation between the global distribution and that of the species). These high percentages of specialization point out that the high importance of these first factors to explain both marginality and niche breadth of each one of the two species. The next factors (specialization factors) explain 19% and 18% respectively. Solar radiation and calcareous soils are the variables with higher marginality coefficients for Copris hispanus, showing that the scores of these variables in the presence cells differ from the mean values in the region (Table 1). As these coefficients are positive, this species is shown to prefer sunny areas and basic soils. Mean annual precipitation has the higher coefficient of the specialization factor, showing that the distribution of C. hispanus in CM is specially restricted by this variable. In the case of C. lunaris, acid soils and mean annual precipitation are the variables related to the marginality factor, meaning a higher probability of presence in siliceous and rainy cells. The specialization of this species is mainly conditioned by the presence of calcareous soils, mid-to-high altitudes and high solar radiation scores.

Marginality scores characterize how much each species habitat' differs from the conditions available in the study area (from 0, close to the mean, to 1, when it prefers habitats extreme in the region). Overall marginality value was higher than 0.65 for both species, evidencing a high separation of both species from the central part of the strong environmental gradient present in CM. *C. lunaris*, adapted to cold mountain environments (see

Table 1
Specialisation explained by the two factors extracted by ENFA, and coefficient values of the six environmental variables used in the analysis

Copris hispanus		Copris lunaris	
Marginality factor (74%)	Specialization factor (19%)	Marginality factor (72%)	Specialization factor (18%)
Solar radiation (0.80)	Precipitation (0.89)	Acid soil (0.69)	Calcareous soil (0.64)
Calcareous soil (0.45)	Acid soil (0.32)	Precipitation (0.51)	Altitude (0.50)
Acid soil (0.29)	Temperature (0.27)	Temperature (-0.34)	Solar radiation (0.50)
Altitude (-0.24)	Solar radiation (0.12)	Solar radiation (0.28)	Precipitation (0.22)
Temperature (0.11)	Altitude (0.11)	Altitude (0.26)	Temperature (0.15)
Precipitation (-0.06)	Calcareous soil (0.01)	Calcareous soil (-0.05)	Acid soil (0.12)

Positive values on the marginality factor mean that the species prefers localities with higher values regarding to the CM mean score. Variables with higher specialisation coefficients restrict more the distribution range of the species.

below), which are more rare in the region, presented a very high marginality (0.91), whilst *C. hispanus*, more adapted to the intermediate environments of the marginal slopes of the mountains, presented lower values (0.68). On the other hand, the global tolerance values (the opposite of specialization ones) were 0.43 for *C. lumaris* and 0.17 for *C. hispanus*. The score for this species (close to 0) suggests that *C. hispanus* tends to live near mean regional conditions, and tolerates an smaller environmental range than does *C. lunaris*, which is adapted to conditions that are more extreme at CM.

Habitat suitability maps so obtained (Fig. 2) show a high probability of appearance for *C. lunaris* in north-western CM, while highest habitat suitability values for *C. hispanus*, distributed patchily across the region, are basically limited to the centre and southeast. Jackknife validation results for these HSMs indicate that the *C. hispanus* potential map is more

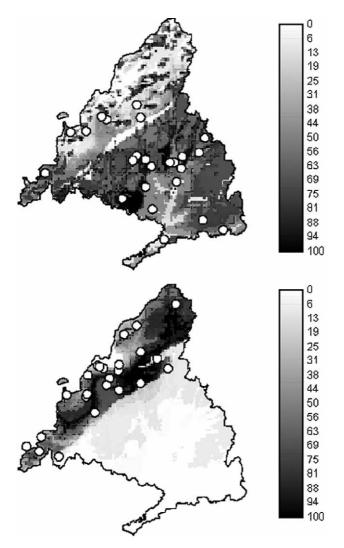


Fig. 2. Habitat suitability maps for *C. hispanus* (upper) and *C. lunaris* (lower). The scale on the right shows the habitat suitability values (0 = low suitability; 100 = high suitability).

reliable than the one for *C. lunaris*. A habitat suitability value greater than 50 was found in 87.5% of 24 1 km² grid squares in the case of *C. hispanus* (SD=33.1%), while in the case of *C. lunaris* such a suitability value was found in just 66.7% of the 24 1 km² cells with presence (SD=47.1%).

3.2. Environmental and spatial characterization of realized niche

Reclassified and cross-tabulated habitat suitability maps show the areas of spatial coincidence and difference between both species (Fig. 3). The very highly suitable areas for both species are located in the north of CM, in the spurs of the "Sierra de Guadarrama" (Fig. 3(a)). These zones differ significantly from the rest of CM because of their higher altitudes (Mann-Whitney U test; Z = 14.7, p < 0.001), higher mean annual precipitations (Z = 11.9, p < 0.001), greater presence of stony acid soils (Z = 13.83, p < 0.001) and lower mean annual temperatures (Z = 9.97, p < 0.001). Three of the five variables considered as environmental heterogeneity surrogates also differ significantly between these coincidence areas and the rest of CM, which present higher values of annual range of precipitation (Z = 12.69, p < 0.01) and slope (Z = 12.56, p < 0.01), and lower values of annual range of temperature (Z = 12.37, p < 0.01). On the contrary, landscape heterogeneity (aspect and land use

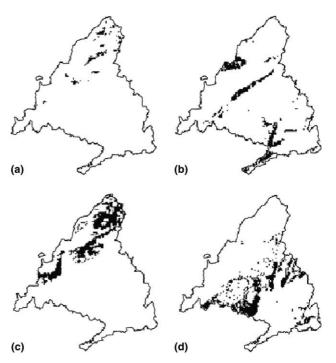


Fig. 3. Maps of areas that are: (a) very highly suitable for both species; (b) very poor for both species; (c) very poor suitability for *C. hispanus* and very high for *C. hunaris*; (d) very highly suitable for *C. hispanus* and very poorly for *C. lunaris*.

diversity variables) was not significantly different between these areas and the rest of CM.

The zones with very poor suitability scores for both species are, on the one hand, Cotos, Navacerrada and "Sierra de Cuerda Larga", mountainous areas with altitudes higher than 1300 m; and on the other, low altitude quaternary terraces (around 600 m) of the rivers Jarama, Manzanares, Tajo and Tajuña; and also transition zones between stony acid soils of the sierra and acid deposits of the "ramp" (the southern slope of the Guadarrama mountains; see Fig. 3(b)). Very low suitability areas also differ from the rest of CM in altitude (Z = 6.9, p < 0.001), the presence of stony acid soils (Z = 4.9, p < 0.001) and mean annual temperature (Z = 3.6, p < 0.001).

The areas in which the niches of both species do not coincide are markedly different. Areas of very high suitability for C. lunaris and very low for C. hispanus are found in the "Sierra de Guadarrama" (Fig. 3(c)), where all environmental variables considered are significantly different from the rest of CM (p < 0.001). Stony acid soil is predominant, altitude (1061.8) m ± 191.6 m) and mean annual precipitation (716.9 mm \pm 50.5 mm) are higher than median values of CM, while solar radiation (4 kwh/m²/día) and mean annual temperature (11.8 °C \pm 0.8 °C) are lower. On the contrary, C. hispanus finds very-high suitability and C. lunaris very-poor suitability areas in the "ramp" of acid deposits, and also in a calcareous soil area between the rivers Tajo and Tajuña (Fig. 3(d)). In these areas, all the environmental variables considered differ significantly from the rest of CM (p < 0.001). Stony acid soil is less frequent in these areas, mean annual temperatures (13.9 °C \pm 0.5 °C) and the solar radiation are higher, while altitude $(636.5 \text{ m} \pm 87.6 \text{ m})$ and mean annual precipitation (459.5 mm \pm 58.7 mm) are lower than in the rest of the CM.

3.3. Conservation status

At present, there are only two PNS where *C. hispanus* has considerable areas with habitat suitability scores higher than 75 (PNS 2 and 8). On the other hand, *C. lunaris* is well represented in just one site (PNS 2), the broadest park with mountainous territory, and the only one with sites highly suitable for both species (Table 2). The mean suitability scores for both species in the PNS are lower than 30%. Future Natura 2000 network sites will protect a more extensive area (Table 2), and consequently, will improve the protection of *Copris* species, facilitating greater interconnectivity among populations. The area with high suitability scores increases eight times for *C. hispanus* and three for *C. lunaris*.

Table 2 Habitat suitability values for *C. hispanus* and *C. lunaris*, and co-occurrence zones in each protected natural site and Natura 2000 network sites

			,									
Protected natural sites (PNS)	Area (km^2)	Copris	hispanu	s habitat	suitabili	ty values	Copris	lunaris habita	nabitat su	iitability	/ values	Co-occurrence
		Min.	Max.	Mean	SD	HS > 75 area	Min.	Max.	Mean	SD	HS > 75 area	HS > 75 area
1. Peñalara	7	0	8	2.3	3.9	0	0	42	22.3	14.2	0	0
2. Cuenca Alta del Manzanares	458	0	100	34.7	27.6	32	0	100	50.9	38.7	183	15
3. Parque Regional del Sureste	315	0	86	40.5	20.2	7	0	∞	0.2	1.3	0	0
4. Refugio de la Laguna de San Juan y Torcal de Valmayor	1	11	11	11.0	0.0	0	0	0	0.0	0.0	0	0
5. Sitio Natural de Interés Nacional del Hayedo de Montejo	3	0	7	2.3	4.0	0	61	77	71.3	9.0	2	0
6. Regajal y Mar de Ontígola	9	10	75	45.7	23.5	0	0	0	0.0	0.0	0	0
7. Paraje Pintoresco del Pinar de Abantos y Zona de Herrería	17	0	86	41.1	33.4	3	33	61	43.2	8.9	0	0
8. Parque Regional del Curso Medio del RÍo Guadarrama	183	0	86	57.9	25.7	29	0	75	17.0	21.0	0	0
9. M. N. I. N. del Collado del Arcipreste de Hita	1	0	0	0.0	0.0	0	53	53	53.0	0.0	0	0
Total	991					61					185	15
New Natura 2000 network sites	3457	0	100	45.0	25.9	487	0	100	31.8	33.3	598	50

HS > 75 area: zones with a suitability value greater than 75, expressed in km

4. Discussion

4.1. The niches of Iberian Copris species

The study area, representative of central Iberia, is a zone of confluence of Mediterranean and Eurosiberian-like climate regions. We find that both Copris species are distributed along a gradient from the Tajo basin (warmer, dryer, with strong annual weather variations) where C. hispanus is found, towards the mountain slopes of the Sistema Central (colder and rainier) where C. *lunaris* predominates. Interestingly, both species present nearly equal marginality factors (and also specialization factors), these axes being so highly correlated that they may be considered identical (Pearson correlation coefficients higher than 0.99). Thus, it can be assumed that Copris species are responding to the same main environmental variations in Madrid. However, as can be seen in Table 1, the factors driving each one's distribution seem to be opposite, evidencing different environmental responses with respect to the average conditions of the region. To ascertain the way they confront the environmental determinants described by these axes, we have represented the means and deviations of the habitat suitability values for each species along them (see Fig. 4). Both species seem to show opposite environmental adaptations: whilst the niche of *C. hispanus* is mainly restricted to calcareous bedrock areas with intense solar radiation, *C. lunaris* prefers sites with acid bedrock and more abundant precipitation. Thus, the principal environmental adaptations of both species respond to the same environmental variations in the studied area, but in a different way (see Fig. 4).

Copris dung beetles, tunnelling nesters, construct a tunnel under cattle droppings, burying several dung balls (up to 250 gr., unpublished data) where they lay their eggs. So, environmental factors that affect temperature extremes and water content in the soil throughout the year are likely, in the main, to shape their distribution in Madrid. Probably C. hispanus' physiological adaptations to warm environments with long dry spells, and avoidance of freezing, allow it to nest in highly water-stressed soils, such as sunny calcareous ones. C. lunaris, on the contrary, may not be able to nest in such dry areas, but its tolerance of freezing allows it to nest in soils with greater water availability but lower temperatures. Hence, our data show that the environmental niche of both species is biased towards two extreme

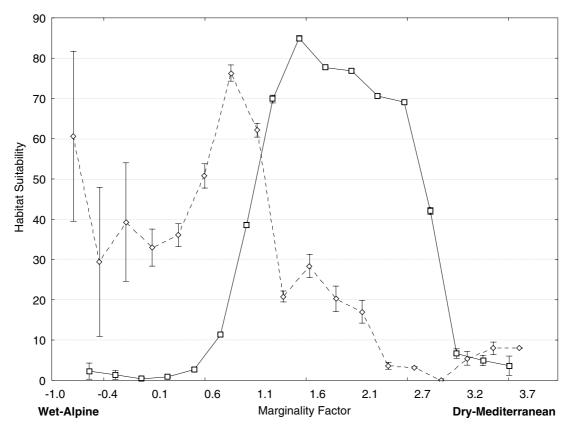


Fig. 4. Variation of mean habitat suitability scores along the Marginality Factor (ranging from Wet-Alpine to Dry-Mediterranean environmental conditions). The factor was divided into 20 intervals, and mean values are shown. *Copris hispanus* is represented by squares and solid lines, and *C. lunaris* by rhombus and broken lines. Vertical lines delimit 95% confidence interval. As marginality factors for both species were highly correlated, the one used for representation was that of *C. hispanus* (see text).

environments at each of the edges of the gradient: (1) Dry-Mediterranean, with high temperatures and intense solar radiation, calcareous soils and low altitudes and precipitation, and (2) Wet-Alpine, with high altitudes and precipitation, acid soils and low temperatures and weaker solar radiation (Fig. 4). Whilst C. hispanus does not find suitable areas near the semi-arid first extreme, C. lunaris is able to reach the Alpine limit of the gradient. Both species find suitable sites in between the extremes, due to their respective tolerance to mediumto-low temperatures with high-to-moderate precipitations and acid stony and sandy soils. In these sites, the greater water content of the soil and the infrequency of freezing temperatures throughout the year probably constitute highly suitable environmental conditions for nesting success of both Copris species.

4.2. Competition remarks

Both species seem to co-occur in some areas located in the mid-slopes of the sierra, where competition might take place as a result of their large-size and high capability of nutrient removal (a couple is able to bury up to 250 gr. of dung). However, the presence of competition between both species is possible just in the case they live in the same habitat, appearing at the same time and pasture. Environmental heterogeneity may allow both species to coexist in the same area but in different habitats; or they may occur in the same locality but at different dates, due to seasonal weather variation; for that reason, competition may not exist. Present results do not clearly support the hypothesis of a higher heterogeneity in the co-occurrence areas, as only two of the five environmental diversity variables tested presented higher values in these zones. However, competitive interactions have been proven for large Afrotropical dung beetles (see Hanski and Cambefort, 1991, and references therein), but information is lacking about interspecific competition in Mediterranean Scarabaeidae (see Finn and Gittings, 2003). Although unpublished data (Veiga, 1982) suggest that specimens of the two species could inhabit the same dung pat, no extensive data is available, so no evaluation of competitive exclusion can yet be made. Further small-scale studies in the sympatric area are necessary to clarify how populations from both species coexist.

4.3. Conservation status assessment

Biodiversity conservation of insects, a challenge difficult to respond to due to the lack of information, requires predictive models, as both the most efficient way to obtain reliable maps of insect distributions, and also to evaluate the ability of proposed and existing sites to further conservation. Comunidad de Madrid, an autonomous region with complete jurisdictions over environmental policies, needs an evaluation of both the effectiveness of its PNS and of the potential gains from new ones

As we commented before, populations of *Copris lunaris* and *Copris hispanus*, as well as those of other dung beetles, are in decline in the Iberian Peninsula, probably because of the use of ivermectines (Lumaret et al., 1993) and the diminution of traditional cattle herding (Lobo, 2001; Roslin and Koivunen, 2001). These species play an important role in extensive pasture ecosystems by recycling organic matter (Andrzejewska and Gyllenberg, 1980) that, otherwise could cause major damage through accumulation (as occurred in Australia; see Bornemissza, 1976). For this reason, it is important to control and reverse any decline in their populations.

To evaluate the conservation status of *Copris* species, we have taken into account the size of protected sites as well as the values of habitat suitability in each PNS and future Nature 2000 network sites. Only one protected site (Hayedo de Montejo; PNS 5) presented an average habitat suitability higher than 70 for one of the species, C. lunaris. However, this site is an ancient beech forest, only 3 km² in extent, and so not very effective in preserving populations of this species. Mean suitability values alone are not enough to guarantee protection for a species in protected areas. It is also necessary to take into account the size of the area highly suitable for the species in each protected site. Using the area with habitat suitability greater than 75 for this task, important differences between the two species appear. Whilst for C. hispanus only two PNS (2 and 8) measured around 30 km² (for a total area of 61 km²), for *C. lunaris* a single area (PNS 2) measured 183 km².

The rarity in PNS of areas highly suitable for both species at the same time highlights two main deficiencies in the CM conservation network. One of them is the area of replacement between basin and mountain assemblages, a gradient zone called "ramp" ("rampa" in Spanish), protected in part by PNS 2, that has been identified as an important dung beetle diversity hotspot (Martín-Piera, 2001); another is the Sierra of Guadarrama, scarcely protected by the already-mentioned PNS 5. Areas of faunistic replacement and range-margins are of great importance for the survival of most species (Spector, 2002) where important processes occur (Thomas et al., 2001), specially when faced with climate change (Hill et al., 2002). Using data from additional, extant groups, these areas should be identified, studied, and protected effectively. Connectivity is another weak point of CM protected sites (Sastre et al., 2002). This may be of secondary importance for many dung beetles, such as *Copris* species, as they are presumably good fliers. But less vagile species would need dispersal corridors to be able to disperse as climate change occurs.

In the future, Nature 2000 network will improve the general conservation status of CM because the area and connectivity of protected sites will be increased substantially. Nature 2000 Network annexes habitats for protection that favour Copris species presence such as "dehesas" (forests of Quercus sp. used for grazing), and natural pastures of Festuca indigesta. In Europe, protected sites' agriculture and cattle uses are restricted to traditional ones. Intensive agriculture or monocultures are not let while traditional cattle herding is promoted and conserved so Copris species will be favoured by this new protection programme wherever traditional cattle herding is promoted and conserved (Barbero et al., 1999; Verdú et al., 2000; Lobo, 2001; Roslin and Koivunen, 2001). Transhumance, pasture conservation and avoidance of the use of cattle antibiotics such as ivermectins are vital conditions for the conservation of *Copris* populations.

It is important to remark that, although this study has been developed on a small working scale, the studied region has full jurisdiction over local environmental policy. Thus, it has a direct application to the conservation of these species. However, the same methodology can be applied to similar studies on different working scales. In our opinion, accurate estimates of the potential distribution of species are obtainable without recourse to exhaustive data. Habitat suitability maps elaborated with this or similar methods have proven to be quite reliable, insofar as they provide a reasonable approximation to the species niche, even without very many presence points. Together with GIS, habitat suitability maps delimit quite well areas highly suitable for each species and for both species (sympatric areas). A greater sampling effort in these areas would validate them as sympatric and would confirm their actual presences.

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References

- Anderson, R.P., Peterson, A.T., Gómez-Laverde, M., 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos 98, 3–16.
- Andresen, E., 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. Ecography 26, 87–97.
- Andrzejewska, L., Gyllenberg, G., 1980. Small herbivore subsystem. In: Breymeyer, A.I., van Dyne, G.M. (Eds.), Grasslands Systems Analysis and Man. Cambridge University Press, Cambridge, pp. 201–267.
- Baraud, J., 1992. Coléoptères Scarabaeoidea d'Europe, Faune de France 78. Fédération Française des Sociétés de Sciences Naturelles, Société Linnéenne de Lyon, Lyon.
- Barbero, E., Palestrini, C., Rolando, A., 1999. Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeidae). Journal of Insect Conservation 3, 75–84.
- Bornemissza, G.F., 1976. The Australian dung beetles project 1965–1975. Australian Meat Research Commission Review 30, 1–30.
- Buckland, S.T., Elston, D.A., 1993. Empirical models for the spatial distribution of wildlife. Journal of Applied Ecology 30, 478–495.
- Busby, J.R., 1991. BIOCLIM a bioclimate analysis and prediction system. In: Margules, C.R., Austin, M.P. (Eds.), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Melbourne.
- Carpenter, G., Gillison, A.N., Winter, J., 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. Biodiversity and Conservation 2, 667–680.
- Clark Labs, 2000a. Global Change Data Archive, vol., 3. 1 km Global Elevation Model. CD-Rom, Clark University.
- Clark Labs, 2000b. Idrisi 32.02. GIS software package, Clark University.
- Davis, A.J., Holloway, J.D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A.H., Sutton, S.L., 2001. Dung beetles as indicators of change in the forests of northern Borneo. Journal of Applied Ecology 38, 593–616.
- European Environment Agency, 1996. Natural Resources CD-Rom. European Environment Agency.
- Fernández-Galiano, E., Ramos-Fernández, A., 1987. La Naturaleza de Madrid. Comunidad de Madrid. Consejería de Agricultura y Ganadería, Madrid.
- Ferrier, S., Watson, G., Pearce, J., Drielsma, M., 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. Biodiversity and Conservation 11, 2275–2307.
- Finn, J.A., Gittings, T., 2003. A review of competition in north temperate dung beetle communities. Ecological Entomology 28, 1–13.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147–186.
- Guisan, A., Edwards, T.C., Hastie, J.T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157, 89–100.
- Halffter, G., 1998. A strategy for measuring landscape biodiversity. Biology International 36, 3–17.
- Hanski, I., 1991. The dung insect community. In: Hanski, I., Cambefort, Y. (Eds.), Dung Beetle Ecology. Princeton University Press, New Jersey, pp. 5–21.
- Hanski, I., Cambefort, Y., 1991. Competition in dung beetles. In: Hanski, I., Cambefort, Y. (Eds.), Dung Beetle Ecology. Princeton University Press, New Jersey, pp. 305–329.
- Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J., Huntley, B., 2002. Responses of butterflies to twentieth century

- climate warming: implications for future ranges. Proceedings of the Royal Society of London B 269, 2163–2171.
- Hirzel, A.H., Hausser, J., Perrin, N., 2000. Biomapper 2.0. Laboratory for Conserv. Biol., University of Lausanne.
- Hirzel, A.H., Helfer, V., Metral, F., 2001. Assessing habitat-suitability models with a virtual species. Ecological Modelling 145, 111–121.
- Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecologicalniche factor analysis: how to compute habitat-suitability maps without absence data?. Ecology 83, 2027–2036.
- Hortal, J., 2004. Selección y Diseño de Áreas Prioritarias de Conservación de la Biodiversidad mediante Sinecología. Inventario y modelización predictiva de la distribución de los escarabeidos coprófagos (Coleoptera, Scarabaeoidea) de Madrid. Unpublished PhD Thesis. Departamento de Biología, Facultad de Ciencias. Universidad Autónoma de Madrid, pp. 333.
- Hortal, J., Lobo, J.M., 2002. Una metodología para predecir la distribución espacial de la diversidad biológica. Ecología (n.s.) 16, 151–178 + 14 plates.
- Hortal, J., Lobo, J.M., in press. An ED-based protocol for the optimal sampling of biodiversity. Biodiversity and Conservation.
- Hortal, J., Lobo, J.M., Martín-Piera, F., 2001. Forecasting insect species richness scores in poorly surveyed territories: the case of the Portuguese dung beetles (Col. Scarabaeinae). Biodiversity and Conservation 10, 1343–1367.
- Hortal, J., Lobo, J.M., Martín-Piera, F., 2003. Una estrategia para obtener regionalizaciones bióticas fiables a partir de datos incompletos: el caso de los Escarabeidos (Coleoptera) Ibérico-Baleares. Graellsia 59, 331–344.
- Hutton, S.A., Giller, P.S., 2003. The effects of intensification of agriculture on northern temperate dung beetle communities. Journal of Applied Ecology 40, 994–1007.
- ITGE, 1988. Atlas Geocientífico y del Medio Natural de la Comunidad de Madrid. Serie: Medio Ambiente. Instituto Tecnológico GeoMinero de España, Madrid.
- Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68, 465–485.
- Lobo, J.M., 2001. Decline of roller dung beetle (Scarabaeinae) populations in the Iberian Peninsula during the 20th century. Biological Conservation 97, 43–50.
- Lobo, J.M., Martín-Piera, F., 1991. La creación de un banco de datos zoológico sobre los Scarabaeidae (Coleoptera: Scarabaeoidea) íbero-baleares: una experiencia piloto. ELYTRON 5, 31–38.
- Lobo, J.M., Martín-Piera, F., 2002. Searching for a predictive model for species richness of Iberian dung beetle based on spatial and environmental variables. Conservation Biology 16, 158–173.
- Lobo, J.M., Lumaret, J.P., Jay-Robert, P., 2002. Modelling the species richness of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. Global Ecology and Biogeography 11, 265–277.
- Lumaret, J.P., Galante, E., Lumbreras, C., Mena, J., Bertrand, M., Bernal, J.L., Cooper, J.F., Kadiri, N., Crowe, D., 1993. Field effects of ivermectin residues on dung beetles. Journal of Applied Ecology 30, 428–436.
- Manel, S., Dias, J.M., Buckton, S.T., Ormerod, S.J., 1999a.
 Alternative methods for predicting species distribution: an illustration with Himalaya river birds. Journal of Applied Ecology 36, 734–747.
- Manel, S., Dias, J.M., Ormerod, S.J., 1999b. Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. Ecological Modelling 120, 337–347.
- Martín-Piera, F., 2000. Familia Scarabaeidae. In: Martín-Piera, F.,
 López-Colón, J.I. (Eds.), Fauna Ibérica 14. Coleoptera, Scarabaeoidea I. Museo Nacional de Ciencias Naturales. Consejo Superior de Investigaciones Científicas, Madrid.

- Martín-Piera, F., 2001. Area networks for conserving Iberian insects: a case study of dung beetles (col., Scarabaeoidea). Journal of Insect Conservation 5, 233–252.
- Martín-Piera, F., Lobo, J.M., 1995. Diversity and ecological role of dung beetles in Iberian grassland biomes. In: McCracken, D.I., Bignal, E.M., Wenlock, S.E. (Eds.), Farming on the Edge: the Nature of Traditional Farmland in Europe. Joint Nature Conservation Committee, pp. 147–153.
- Ministerio de Agricultura, Pesca y Alimentación, 1986. Atlas Agroclimático Nacional de España, second ed. Dirección General de la Producción Agraria, Madrid.
- Mitchell, N.D., 1991. The derivation of climate surfaces for New Zealand, and their application to the bioclimatic analysis of the distribution of kauri (*Agathis australis*). Journal of the Royal Society of New Zealand 21, 13–24.
- Parker, V., 1999. The use of logistic regression in modelling the distributions of bird species in Swaziland. South African Journal of Zoology 34, 39–47.
- Pearce, J., Ferrier, S., 2000. An evaluation of alternative algorithm for fitting species distribution models using logistic regression. Ecological Modelling 128, 127–147.
- Pereira, J.M.C., Itami, R.M., 1991. GIS-based habitat modelling using logistic multiple regression: a study of the Mt. Graham Red Squirrel. Photogrammetric Engineering and Remote Sensing 57, 1475–1486
- Peterson, A.T., Holt, R.D., 2003. Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation. Ecology Letters 6, 774–782.
- Peterson, A.T., Soberón, J., Sánchez-Cordero, V., 1999. Conservatism of ecological niches in evolutionary time. Science 285, 1265–1267.
- Rassi, P., Kaipainen, H., Mannerkoski, I., and Ståhls, G., 1992. Report on the Monitoring of Threatened Animals and Plants in Finland. Committee Report 1991, 30. Ministry of the Environment, Helsinki, Finland.
- Robertson, M.P., Caithness, N., Villet, M.H., 2001. A PCA-based modelling technique for predicting environmental suitability for organisms from presence records. Diversity and Distributions 7, 15–27
- Roslin, T., 2000. Dung beetle movement at two spatial scales. Oikos 91, 323–335.
- Roslin, T., 2001a. Large-scale spatial ecology of dung beetles. Ecography 24, 511–524.
- Roslin, T., 2001b. Spatial population structure in a patchily distributed beetle. Molecular Ecology 10, 823–837.
- Roslin, T., Koivunen, A., 2001. Distribution and abundance of dung beetles in fragmented landscapes. Oecologia 127, 69–77.
- Sastre, P., de Lucio, J.V., Martínez, C., 2002. Modelos de conectividad del paisaje a distintas escalas. Ejemplos de aplicación en la Comunidad de Madrid. Ecosistemas, 2002/2. Available from: http://www.aeet.org/ecosistemas/022/investigacion5.htm.
- Scott, J.M., Davis, F.W., Csuti, B., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards, T.C., Ulliman, J., Wright, R.G., 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123, 1–41.
- Servicio Cartográfico de la Comunidad de Madrid, 1996. Mapa de la Comunidad de Madrid. Escala 1:200.000. Consejería de Ordenación Territorial, Comunidad de Madrid, Madrid.
- Skidmore, P., 1991. Insects of the British Cow Dung Community. Field Studies Council, Monfort Bridge, 166 pp.
- Spector, S., 2002. Biogeographic crossroads as priority areas for conservation. Conservation Biology 16, 1480–1487.
- StatSoft, 1999. STATISTICA for Windows, Computer program manual. StatSoft, Inc., Tulsa, OK.
- Stockwell, D., Peters, D., 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science 13, 143–158.

- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., Conradt, L., 2001. Ecological and evolutionary processes at expanding range margins. Nature 411, 577–581.
- Vayssières, M.P., Plant, R.E., Allen-Diaz, B.H., 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11, 679–694.
- Veiga, C.M., 1982. Los Scarabaeoidea (Col.) coprófagos de Colmenar Viejo (Madrid). Perfiles autoecológicos. Licenciature Thesis. Universidad Complutense de Madrid, Madrid.
- Verdú, J.R., Galante, E., 2002. Climatic stress, food availability and human activity as determinants of endemism patterns in the
- Mediterranean region: the case of dung beetles (Coleoptera, Scarabaeoidea) in the Iberian Peninsula. Diversity and Distributions 8, 259–274.
- Verdú, J.R., Crespo, M.B., Galante, E., 2000. Conservation of a nature reserve in Mediterranean ecosystems: the effects of protection from grazing on biodiversity. Biodiversity and Conservation 9, 1707–1721.
- Walker, P.A., Cocks, P.A., 1991. HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. Global Ecology and Biogeography Letters 1, 108–118.