Scaling local abundance determinants in mediterranean dung beetles

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Abstract. 1. We study the factors that contribute to the variation in the local abundance of dung beetle species inhabiting Cabañeros National Park, a Mediterranean reserve in Central Spain. The relative roles of five different groups of explanatory variables (climatic, local-scale vegetation, landscape-scale vegetation, landscape connectivity and trophic resources) were assessed for 27 sampling sites established by a nested hierarchical sampling design that considered three regional landscapes (woodland, scrubland, grassland) and three local habitat types (forest, scrub, pasture) within each landscape.

2. Connectivity variables related to the spatial configuration of closed vegetation and distance to patches of open or closed vegetation were the best predictors of the species abundance. Precipitation was the most important climatic variable, whereas grassland area at the local- or landscape-scale and woodland area at the landscape-scale were the most important vegetation variables. Dung resources variables had the lowest explanatory ability.

3. More than 60% of the models explained more than 70% of the total variability. Observed and predicted abundance were highly and positively correlated and the mean percentage of absolute predictive errors was approximately 50%. Low-abundance observations had higher predictive errors and model accuracies seemed to be lower for species with narrow distributional ranges and presence in a high number of sampling localities.

4. Mediterranean ecosystems contain a diverse assemblage of dung beetle species whose composition and abundance are influenced by a variety of factors operating across different spatial scales. The most important variables are the spatial configuration and the habitat connectivity around each locality.

Key words. Abundance models, Cabañeros National Park, landscape connectivity, landscape scale, Scarabaeoidea, species traits.

Introduction

Species abundances and distributions result from the combined action of historical, species-specific and ecological factors that influence individual survival and reproductive success (Ricklefs, 2006). These patterns are sensitive to the spatio-temporal scale (Wiens, 1989). At the local scale, biotic interactions and population dynamics can influence species extinction processes with no effect on regional occurrence, due to recolonization from neighbouring localities connected by immigration processes (Wegner & Merriam, 1990; Hanski, 1998). Thus, information on the relative role played by local and regional factors in the abundance of a species might be essential for understanding species persistence and for designing reliable conservation strategies (Potts & Elith, 2006). Recently, interest in modelling species abundance has been increasing (Iverson & Prasad, 1998; Welsh *et al.*, 2000; Pearce & Ferrier, 2001; Bahn & McGill, 2007). In general, abundance varies across a species' range (Brown, 1984; Murphy *et al.*, 2006), so its variability may allow us to identify

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spatial variation in *habitat quality* using parameters such as reproductive success, longevity or carrying capacity.

Some studies about the determinants of distribution and abundance of animal species have emphasised the usefulness of multiscale approaches to explain existing patch occupancy patterns (Roslin & Koivunen, 2001; Swihart *et al.*, 2006). In this sense, variation in patch quality, patch connectivity and general landscape characteristics are all highly relevant factors for explaining local population dynamics and the manner in which they are connected (Wiens *et al.*, 1997) as well as the scale at which individuals perceive the factors that are relevant to their survival (Wiens & Milne, 1989).

Many diverse factors may influence the presence and abundance of dung beetles. At the local scale, habitat type, vegetation structure and habitat quality are important predictors of species diversity (Lumaret & Kirk, 1987; Hanski & Cambefort, 1991). Habitat quality can be evaluated using characteristics of patch structure and configuration, such as patch size, shape and degree of connection with other habitat patches as well as by studying the diversity, quality and availability of trophic resources. As a general pattern, larger habitat patches sustain larger and more species-rich dung beetle populations (Nichols *et al.*, 2007). Similarly, dung type (Martín-Piera & Lobo, 1996) and dung density (Kadiri *et al.*, 1997; Lobo *et al.*, 2006) can influence the presence and relative abundance of dung beetles. However, the importance of the landscape matrix in which different habitat patches are embedded is increasingly recognised as a factor influencing the distribution and abundance of dung beetle species (Numa *et al.*, 2009).

Despite the important role of dung beetles in ecosystem functioning, we lack knowledge about the factors influencing local dung beetle abundance (but see Roslin & Koivunen, 2001) and the factors that are important in Mediterranean conditions because previous studies have concentrated solely on individual factors such as habitat type, grazing intensity or abiotic gradients (Lobo *et al.*, 2006; Verdú *et al.*, 2007b; Zamora *et al.*, 2007; Jay-Robert *et al.*, 2008). Here, we jointly studied the role played by different local and regional factors in explaining variation in dung beetle abundances within a Mediterranean reserve (Cabañeros National Park; Spain) assessing (i) how spatial variation in local species abundance is influenced by habitat and landscape structures, (ii) the relative influence of climatic, landscape structure and trophic factors in explaining variation in local species abundances; (iii) the efficiency of abundance model predictions based on these factors; and (iv) species-specific differences in the accuracy of the abundance predictions.

Methods

Study area

The study was carried out in Cabañeros National Park, in the centre of the Iberian Peninsula (0°35′W; 39°24′N). The area is within the Mediterranean region and has a climate characterised by a dry summer period, annual rainfall from 500 to 750 mm and mean annual variation in temperature from 18 to 21 °C, with a maximum temperature of 40 °C and minimum tempera-tures reaching −12 °C. With an area of nearly 41 000 ha, the park is primarily covered by a mesomediterranean-type vegetation (*sensu* Rivas-Martínez, 1987), that includes the following: Mediterranean mixed forests growing on siliceous soils and characterised by *Quercus ilex ballota*, *Quercus suber*, *Quercus faginea broteroi* and *Myrthus edulis*; scrublands with tall and dense cover of *Cistus ladanifer* and *Arbutus unedo*; and grasslands with various graminoids and leguminous herbs accompanied by scattered *Q. ilex ballota* and *Q. suber* trees.

Sampling design

We established a nested hierarchical sampling design considering three regional landscapes (woodland, scrubland and grassland) and three local habitat types nested within each landscape (forest, scrub and pasture). In each landscape we selected three sampling sites of the same habitat type separated by around 300 m from one another. Thus, a total of 27 sampling sites were surveyed to examine the influence of local vegetation cover according to the landscape characteristics of the region (Fig. 1 and Table S1 in the supplementary material). Dung beetles were sampled following a standardised protocol (Lobo *et al.*, 1988; Verdú *et al.*, 2000). Two pitfall traps spaced 50 m apart were installed at each sampling site. Each trap was baited with *ca.* 100 g of sheep dung and 70% ethylene glycol as a preserving fluid. Traps were baited with sheep dung because this type of dung is similar in form, odour and composition to deer pellets, the most available food resource within the reserve. Sampling was carried out in 2004 over six 20-day periods in which traps remained active (March, April, May, July, October and November). The average number of pitfall traps per sampling site was 11.5, and the total number of pitfall traps was 310 (14 traps were damaged by wild animals) (see Table S1).

Survey completeness was assessed at different spatial scales (the entire study area, landscapes, habitats and sampling sites) by calculating the percentage of observed species out of the total number of species predicted by ACE, ICE and Chao1 species richness estimators using EstimateS 8.0 (Colwell, 2005). Previous results (Numa *et al.*, 2009) showed that *ca.* 90% of total predicted species in the entire area would have been collected by this survey; being these proportions 90%, 75% and 71% for landscapes, habitats and sampling sites, respectively. Total species abundance from the six collecting periods at each sampling site was used as the dependent variable in all analyses.

Explanatory variables

We estimated the relative effects of five groups of explanatory variables (Table 1) on dung beetle abundance: climate, local-scale vegetation, landscape-scale vegetation, landscape connectivity and trophic resources.

Climate variables included total annual precipitation and yearly mean temperature and were calculated for each sampling site by interpolating values from 87 weather stations located in a buffer zone of 100 km around of the study area, from which climatic data were available for at least the last 10 years. A
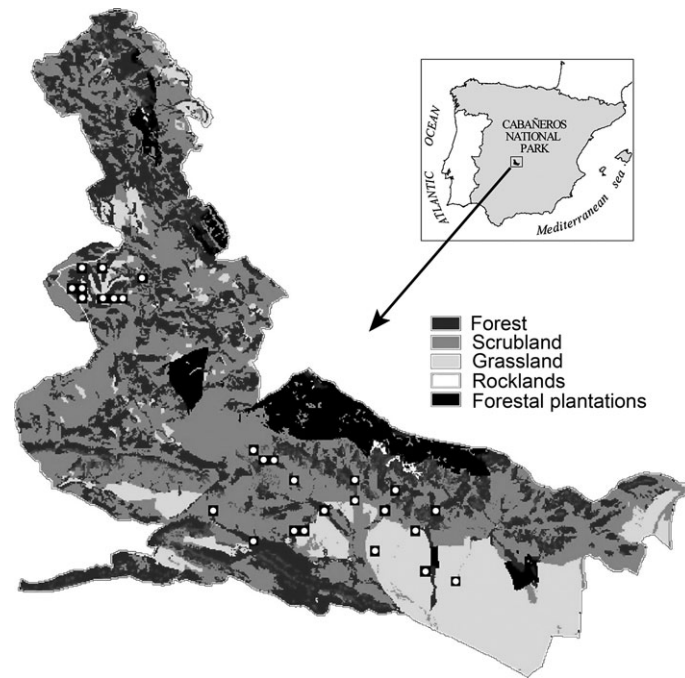
Fig. 1. Vegetation map of Cabañeros National Park showing all sampling localities (at 500 m resolution).

Table 1. Explanatory variables used in the study, mean percentage of total variability in species abundances that were explained by them (%EV) and the 95% confidence interval (±95% CI) of this explanatory capacity across dung beetle species.

Type	Variables	Description	% EV	95% CI
Climatic	TEMP	Annual mean temperature in °C	28.67	6.27
	PP	Annual mean precipitation in mm	50.54	7.38
Landscape connectivity	DGRASS	Nearest neighbour distance among grasslands	49.06	4.96
	DSCRUB	Nearest neighbour distance among scrublands	30.07	3.79
	DFOR	Nearest neighbour distance among forests	45.76	7.46
	HELIOCOST	Movement cost for heliophilous species	42.11	6.88
	FORCOST	Movement cost for forest species	52.40	6.26
Local scale-vegetation	GRASSAREA	Grassland area	46.27	7.45
	SCRUBAREA	Scrubland area	34.74	3.36
	FORESTAREA	Forest area	31.20	4.93
Landscape scale vegetation	LGRASSAREA	Grassland area	46.20	6.04
	LSCRUBAREA	Scrubland area	30.41	5.11
	LFORESTAREA	Forest area	41.38	6.06
Trophic resources	SPRINGDUNG	Mean number of faecal pellets in 30 m^2 squares during the spring	23.60	3.35
	WINTERDUNG	Deer abundance in winter (ratio of the number of observed animals to the distance travelled by the observer along a set of transects)	27.40	5.74

cokriging procedure using a Digital Elevation Model as a covariable was used for this interpolation (ClarkLabs, 2000). This procedure allowed us to obtain climatic values at a grid-based resolution of 100 m^2.

Vegetation cover is one of the most important structural characteristics that might influence habitat preferences in dung beetles and consequently their distribution patterns in Mediterranean ecosystems (Lumaret & Kirk, 1987; Verdú *et al.*, 2000;

Numa *et al.*, 2009). For this reason, we extracted connectivity and vegetation variables using a raster map with five categories: natural forest, pine plantations, scrublands, grasslands and rocky areas. This map was digitised at a resolution of 10 m from a map provided by the park administration (1:5000 resolution). We calculated the area of forest, scrubland and pastures for each 100 m^2 cell in which a sampling site was located (local-scale vegetation variables) and for the 500 m buffer zone around each

sampling site (landscape-scale vegetation variables). The vegetation map described above was also used to estimate five landscape connectivity variables. The three variables measured were the distance to the nearest forest, scrub or pasture cell; these variables were selected to test the possible influence of the distance to each habitat type on local species abundance. The other two connectivity variables were selected to represent the colonisation cost for heliophilous- or forest-specialist species. To do this, we used the cost operator of the IDRISI GIS software package (Eastman, 2006), which generates a proximity or cost surface where distance is measured as the least effort required to move over a friction map. Two different friction maps were built to represent the difficulty of crossing the different habitat types according to the specialisation of the species (heliophilous vs. forest specialist). For heliophilous species, friction values were lower for grasslands but higher for pine plantation cells (friction values: pastures $= 1$, rocklands $= 3$, scrublands and forests $= 4$, pine plantations $= 5$); for forest specialists friction values were higher in open habitats (friction values: forests $= 1$, scrublands and pine plantations $= 3$, pastures and rocklands $= 5$). Finally, displacement costs were calculated as the mean values for the 500 m buffer zones around each sampling site.

Trophic variables were based on dung density measures during the spring (supplementary material in Numa *et al.*, 2009) and a map provided by the park administration representing the deer census during the winter of 2004. All variables were standardised to a mean of zero and a standard deviation of one to avoid bias due to differences in the scale of measurement among variables.

Model building

All collected species were grouped in quartiles according to their abundance and occurrence (number of sampling sites). Only those species whose values were greater than the first quartile (the most abundant and most widely distributed species in the region) were analysed. Species abundance was modelled using Generalised Linear Models (Crawley, 1993), with a Poisson distribution for the dependent variable and a logarithmic link function (Vincent & Haworth, 1983). First, the individual explanatory capacity of each variable was estimated by examining the statistical significance of linear and quadratic functions to detect possible curvilinear relationships. Using this procedure, we identified the most relevant explanatory variables. Then, a forward stepwise procedure was used to enter the variables into the model (Austin & Meyers, 1996). The variable that accounted for the greatest reduction in deviance was selected first. Next, the remaining variables were added to the model one at time according to their order of importance. After each significant inclusion, the new model was subject to a backwards selection procedure to eliminate those terms that had become non-significant $(P > 0.05)$. This procedure was repeated iteratively until no more statistically significant changes remained. When two or more competing models were identified by this procedure, we used the Akaike information criterion (AIC) to select the final model (Akaike, 1973). All models were checked for overdispersion (when the observed variance is greater than the variance of a theoretical model) and parameter estimates and related statistics were computed taking this overdispersion into account.

Explanatory variables are frequently correlated with one another, hindering an accurate estimation of their true causal effects (Mac Nally, 2000). To estimate the relevance of each explanatory variable in such a situation, we applied a hierarchical partitioning procedure (Chevan & Sutherland, 1991; Mac Nally, 2000) in which the amount of variation attributed exclusively to each variable is measured by calculating the average effect of its inclusion. Thus, we first calculated the percentage of the deviance explained by each type of variable (climate, local-scale vegetation, landscape-scale vegetation, landscape connectivity, and trophic resources) and the variability explained by all possible variable combinations in which each type of variable participates. Subsequently, we calculated the average effect of the inclusion of each type of variable in all models for which that type of variable was relevant. The STATISTICA 6.0 package (StatSoft, 2001) was used for all statistical computations.

Model error assessment

A Jackknife procedure was used to examine model reliability. In this procedure, each final model is recalculated leaving out one observation at a time and the resulting model is applied to the excluded observation. The Jackknife and original values for each species were used to calculate the mean predictive error (MPE), which was estimated as the average of the absolute differences between observed and predicted values ([observed-expected]/observed $\times$ 100) using log base 2 of abundance data so that the relative increase in abundance corresponds to a doubling of population size. The error levels thus obtained and the percentages of variability explained for each species were subsequently regressed (using Generalised Linear Models) against nine categorical or continuous variables representing biological, ecological, taxonomic and biogeographical species traits. The aim of this last analysis was to discover the primary species traits that were related to the accuracy of the species abundance models. These same species traits were also regressed against the five types of explanatory variables to identify whether the relevance of the predictors used depends on species attributes.

Nine different species traits were considered, four categorical traits (behaviour, taxonomic family, habitat preference and seasonal activity), two categorical traits that were transformed into continuous traits (dung preference and geographic distribution) and three continuous traits (occurrence, abundance and body size). Dung beetle species were divided into three main functional groups according to their nesting and trophic behaviour: dwellers, tunnellers and rollers (see Doube, 1990). Dweller species live in dung pats, and their larvae have a free life style, where they mainly pupate in the ground. In contrast, environmental conditions have a reduced chance of affecting tunneller species because they live underneath the dung and their larvae inhabit brood balls made with dung prepared by their parents. Roller dung beetle species may be considered to represent an intermediate position between dwellers and

tunnellers because although their larvae live in buried brood balls as tunnellers, adults roll spherical dung pieces in the soil and are therefore somewhat affected by external environmental conditions. The abundance of roller species may be limited in those habitats with closed vegetation because this hinders movement. By examining the variation in model errors between these three behaviour categories, we aimed to assess if the supposed differences in the sensitivity to environmental conditions affects the accuracy of abundance models. We also considered the high-level taxonomic status of species (e.g., taxonomic family: Aphodiidae, Geotrupidae and Scarabaeidae) as a species trait because it is closely related with other morphological, ecophysiological or functional traits, such as body size, thermoregulatory capacity or nesting behaviour capable of influencing population abundance. For example, Aphodiidae species are generally small-sized, ectothermic dwellers with low movement ability (Roslin, 2000) so their abundances could be more influenced than other groups by local factors and environmental temperatures. In contrast, Scarabaeidae species have diverse body sizes and flight abilities, even showing some endothermic behaviour that implies diverse strategies of thermoregulation (Verdú & Lobo, 2008). Many Mediterranean Geotrupidae species are apterous and their movements could also be strongly conditioned by vegetation structure or micro-environmental factors. The general trophic preference of species based on the hydric content of the dung (low = 1, medium = 2 and high water content = 3) has been included because the type, distribution and quantity of the available dung resources may influence both species abundances and the ability to predict them. Habitat preference is a binary species trait representing the ability of inhabiting both closed and open biomes (generalist) or, alternatively, the specialisation on one of the two biomes (specialist species). This trait was considered because it is probable that the abundance of the species inhabiting a wider spectrum of habitat conditions would be more difficult to predict. Seasonal activity classifies the species into four categories (spring, autumn, summer or bimodal) and was included in order to examine whether abundance predictability is affected by seasonal occurrence because this characteristic seems to be related to the habitat tolerance of a species (Galante *et al.*, 1993). The last variable considered was the geographic distribution of species based on 12 biogeographical categories according to Pawlowski (1967), Stebnicka (1976a,b) and Horion (1958), which were converted to continuous values depending of the range from narrowly = 1 to widely = 12 distributed; see Table S2 in the supplementary material). The geographic distribution of species could be an important trait affecting model performance due to the well-known relationship between distribution and abundance (Gaston, 2003), as well as because the large-scale distribution of a species could be influencing the environmental conditions at which a species is abundant locally. Continuous traits such as occurrence (the number of sampling localities at which the species is present), abundance (the total number of individuals collected) and body size (body length) may affect model performance because these traits are frequently associated (Gaston, 2003) and the abundance of stenotopic and rare species seem to be difficult to predict (Carrascal *et al.*, 2006).

Results

A total of 51 dung beetle species and 74 953 individuals were collected (Table S2). Of them, 35 species were considered to be sufficiently abundant and well distributed according to the selected criteria (observed values greater than the first quartile) to be considered in the modelling process.

Explanatory ability of individual variables

Connectivity variables had the highest ability to explain the abundance of the species considered (Table 1 and Table S3 in the supplementary material). The displacement cost for a hypothetical forest species was able to explain the greatest average percentage (mean ± 95% CI; 52.4 ± 6.3) of the variation in species abundances. Other connectivity variables, such as the distance to pasture and the distance to forest, were also highly explanatory (49.1 ± 5.0 and 47.7 ± 6.8, respectively). Precipitation was the climatic variable with the greatest explanatory capacity (50.5 ± 7.4). Grassland area at the local and landscape scales and woodland at the landscape scale were the most important vegetation variables for explaining dung beetle abundance (>40%). In contrast, variables related to dung resource availability had the lowest explanatory ability. The estimation of the average effect of each type of variable (Table 2) again suggested that landscape connectivity variables are, on average, the most relevant ones in explaining species abundances (≈21%), followed by local-scale vegetation variables (≈17%), climatic variables (≈15%) and landscape-scale vegetation (≈14%).

Final abundance models

The majority of models (n = 22; 63% of total) explained more than 70% of the variance (Table 2 and Table S3). A climate variable (precipitation) and a local vegetation variable (grassland area) were the most frequently retained in the individual species' models (for 18 and 14 species, respectively). Other variables frequently included in species' models were those related to vegetation at the local and landscape scales; scrub area at the local scale and grassland area at the landscape scale were retained in eight models (Table 2).

A negative relationship with precipitation was observed for 18 species, eight of which had positive relationships with grassland area. Seven species showed positive relationships with precipitation, and two of these also showed positive relationships with forest area. Scrubland area was negatively associated with species abundance in all models where this variable was retained. In contrast, the majority of species' models retaining grassland area at the landscape scale showed positive relationships for this variable (Table S3).

Predictive errors

A positive and significant correlation was found between observed and Jackknife predicted abundance values (Pearson

Table 2. Mean percentages of explained variability for the five considered groups of predictors included in the species abundance models estimated by using the hierarchical partitioning procedure (Chevan & Sutherland, 1991; Mac Nally, 2000). Acronyms as in Table 1.

Species	PP	TEMP	FORESTAREA	SCRUBAREA	GRASSAREA	FORCOST	HELIOCOST	DFOR	DSCRUB	DGRASS	LFORESTAREA	LSCRUBAREA	LGRASSAREA	SPRINGDUNG	WINTERDUNG	Climatic	Landscape-scale vegetation	Landscape connectivity	Local-scale vegetation	Trophic resources	N	P	N var	% EV.	AIC	MPE
Aphodiidae																										
Aphodius (Acrossus) luridus	X		X													14.0	12.8	18.1	13.5	2.0	863	19	2	95.8	156.0	98.9
A.(Ammoecius) lusitanicus	X		X												X	31.6	5.8	16.4	14.6	12.6	2254	22	3	75.0	894.0	355.6
A. (Aphodius) fimetarius				X											X	3.5	16.4	15.4	45.8	6.9	137	18	2	58.0	147.0	113.8
A.(Aphodius) foetidus				X												3.0	19.4	31.2	29.3	4.7	428	24	1	48.4	400.0	281.0
A.(Chilothorax) cervorum	X	X						X							X	30.2	6.6	20.3	11.4	9.4	159	11	4	90.2	98.0	84.6
A. (Chilothorax) lineolatus				X												10.0	12.5	19.8	28.5	4.3	181	25	1	44.5	147.0	105.6
A. (Colobopterus) erraticus				X											X	4.9	12.0	23.0	18.6	16.1	49	11	2	78.3	67.0	39.3
A. (Eudolus) quadriguttatus	X		X								X					12.5	15.5	16.9	19.5	3.6	682	18	3	87.8	263.0	160.0
A. (Euorodalus) coenosus				X				X	X						X	12.0	21.2	31.7	9.5	7.0	804	20	4	86.5	363.0	465.2
A. (Euorodalus) tersus	X		X						X						X	15.3	11.1	26.5	11.6	1.7	258	24	4	79.7	168.0	134.1
A. (Melinopterus) consputus	X			X											X	17.9	11.1	23.9	10.0	5.4	956	16	3	95.6	235.0	167.1
A. (Melinopterus) sphacelatus	X	X	X					X						X		13.3	12.8	20.2	7.9	6.6	1254	23	5	90.7	341.0	274.7
A. (Nimbus) affinis	X	X						X								15.1	20.0	22.6	16.4	10.9	29254	27	3	77.7	9509.0	310.5
A. (Pseudoacrossus) sharpi	X	X														18.0	15.9	21.4	10.6	8.3	278	22	2	47.9	234.0	174.3
Scarabaeidae																										
Bubas bison	X		X				X									17.6	9.2	19.5	21.8	2.9	43	11	3	84.5	52.0	37.2
Caccobius schreberi				X												13.1	11.8	27.0	10.8	1.9	73	12	1	84.9	72.0	84.5
Copris hispanus		X		X												16.3	14.3	16.9	12.4	2.9	659	18	2	82.6	340.0	201.3
Euonthophagus amyntas	X		X												X	17.7	13.0	23.4	11.6	22.0	79	13	3	79.0	88.0	100.9
Gymnopleurus flagellatus	X			X	X			X								23.6	8.8	28.6	7.1	1.7	1406	17	4	98.9	125.0	125.6
O. (P.) vacca				X	X			X								8.8	12.5	18.2	14.2	4.2	165	16	3	89.2	110.0	79.7
O. (P.) fracticornis	X	X						X						X		21.8	11.5	15.3	9.2	12.1	834	15	4	95.2	218.0	221.5
O. (Furconthophagus) furcatus				X												5.7	22.4	15.8	45.5	4.8	4229	26	1	48.4	3932.0	402.2
O. (Palaeonthophagus) lemur														X	X	4.2	8.1	11.8	5.2	38.9	2459	27	2	66.6	529.0	68.1
O. (Trichonthophagus) maki	X		X									X	X			13.5	16.2	15.5	13.4	3.6	3287	26	4	82.3	947.0	374.9
O. (P.) opacicollis				X										X		5.2	13.4	10.0	34.4	18.0	6597	27	2	68.5	1825.0	105.0
O. (Parentius) punctatus	X															27.5	10.0	28.2	9.9	2.3	637	25	1	54.1	524.0	276.8
O. (Onthophagus) taurus	X		X	X		X										19.8	9.8	37.8	7.4	5.2	101	17	4	76.0	117.0	108.2
Scarabaeus laticollis									X							9.7	23.9	24.5	9.9	5.0	11151	27	1	22.9	5307.0	120.3
Scarabaeus sacer	X		X													16.3	10.4	21.2	17.5	0.9	28	10	2	70.8	52.0	55.8
Sisyphus schaefferi		X	X						X							23.8	14.0	14.2	5.5	6.5	316	11	3	95.6	112.0	461.8
Geotrupidae																										
Jekelius nitidus						X					X					7.2	33.9	27.5	3.3	7.4	2122	27	2	57.3	1619.0	801.8
Sericotrupes niger		X													X	9.8	10.0	15.9	33.3	13.9	177	18	2	54.3	173.0	145.4
Thorectes baraudi		X	X			X			X							13.7	10.6	22.6	18.6	8.0	673	14	4	77.5	487.0	319.9
Typhoeus typhoeus	X															46.9	3.9	20.6	9.1	3.3	1364	27	1	54.1	515.0	198.2
Trogidae																										
Trox hispanicus				X	X	X	X									2.8	10.6	23.6	32.1	1.9	206	22	4	66.2	144.0	66.3
Mean																15.0	13.5	21.3	16.6	7.6	2118.9	19.6	2.6	73.3	866.0	203.5
95% Interval of confidence																3.2	2.0	2.1	3.7	2.5	1724.9	1.9	0.4	6.1	615.8	52.9

%EV = percentage of total variability explained in a final model including all of the significant variables. Total abundance (N), presence at sampling localities (P), number of variables retained in the final models (Nvar), explained variability (% EV), Akaike coefficients (AIC) and mean predictive error (MPE) using the jackknife procedure (data not log transformed).
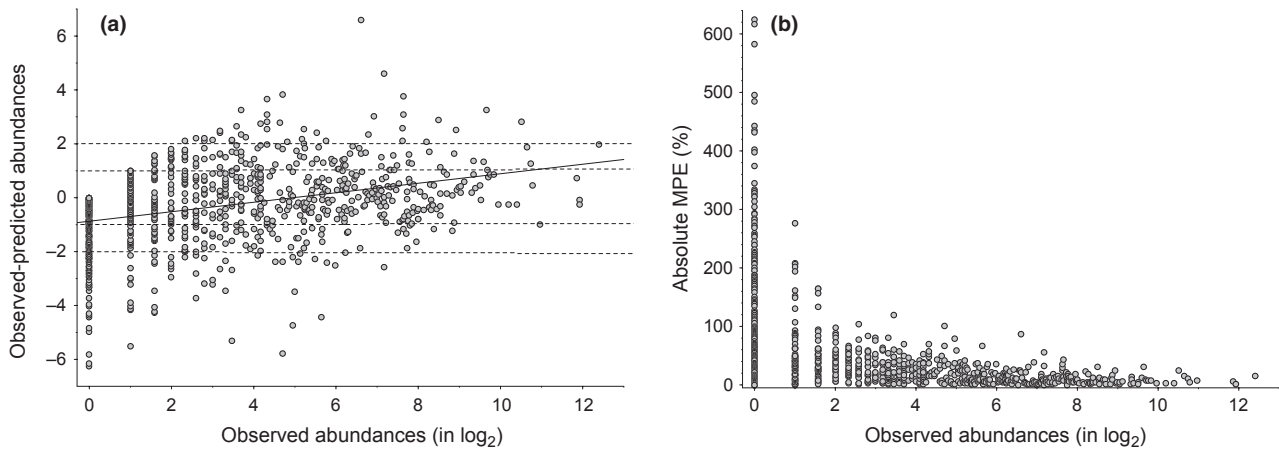
Fig. 2. (a) Relationship between observed abundances and predicted deviations (the difference between observed and Jackknife predicted abundances) for all the considered species ($n = 35$) and sampling sites ($n = 27$) in a log base 2 scale, showing the linear fit (continuous line) and the lines delimiting predicted deviations higher or lower than two and four times the observed values (broken lines). (b) Relationship between observed abundances and mean predictive error (MPE) estimated as the percentage of predicted deviations out of observed values $\times 100$.

rank correlation coefficient; $r = 0.803$; $P < 0.0001$, $n = 945$), indicating a generally good fit between excluded observations and model predictions. The mean absolute difference between observed and predicted values was 1.08 ± 0.06 (mean $\pm 95\%$ CI). Low abundances or zero data are frequently overpredicted, whereas high abundances are underpredicted (Fig. 2a). However, the error level of more than 60% of predicted abundances does not exceeded or decreased more than two times the observed abundances and almost 85% of total predictions were not exceed or decreased in four times the observed abundances (Fig. 2a). The mean percentage of absolute predictive errors (MPE) was $50.10 \pm 4.97\%$ and was caused for the most part by

inaccuracies in low-abundance observations (Fig. 2b). MPE values were not correlated with the variability explained by the final models (Table 3) ($rs = -0.07$, $n = 35$; ns) nor with the number of variables retained in the final models ($rs = 0.09$, ns).

The variation in the percentage of variability explained by the models can be mainly related with the occurrence of each species, but also with their abundances and geographical distributions. Thus, more explanatory models can apparently be obtained when the species are present in a low number of sampling localities, have intermediate population sizes and are widely distributed (Table 3). MPE values are related to the occurrence of species, their geographical distribution or dung preferences

Table 3. Explanatory ability of the species traits ($n = 35$; Generalised Linear Models) for the variation in the amount of variability accounted for by the final models (%EV), mean predictive error using the jackknife procedure (MPE), and the explanatory power of each group of predictors considered.

Species traits	% EV	MPE	Climatic	Landscape scale-vegetation	Landscape connectivity	Trophic resources	Local scale-vegetation
Behaviour	0.10	0.66	0.9	0.5	1.6	**9.4**	1.4
Taxonomic family	3.40	5.40	2.3	0	0.4	0.6	1.0
Occurrence	**31.0 (−)**	**12.9 (+)**	1.7	**15.9 (+)**	0.3	1.8	0.9
Abundance	**15.8 (− +)**	2.10	0.8	**10.4 (+)**	0.2	1.6	0.2
Body size	2.50	0.40	0.3	0	0.2	3.1	0.3
Dung preference	3.50	**11.1 (−)**	1.8	1.8	1.6	0.9	2.6
Habitat preference	0	11.68	1.4	2.6	0.4	**18.5**	1.8
Seasonal activity	4.40	5.35	0.1	0.8	1.3	1.9	0.8
Geographic distribution	**11.5 (+)**	**11.6 (−)**	4.0	1.0	0.1	0.5	2.1

Variables with statistically significant relationships are in bold. Signs of each term of linear or quadratic functions are shown. Species traits included behaviour (categorical: dweller, tunneller and roller), taxonomic family (categorical: Aphodiidae, Geotrupidae and Scarabaeidae), occurrence (continuous: number of sampling localities at which the species is present), Abundance (continuous: total number of individuals collected), body size (continuous: length), dung preference (categorical: low, medium and high water content), habitat preference (categorical: generalist, specialised to open and closed biomes), seasonal activity (categorical: spring, autumn, summer or bimodal), and geographic distribution (see Table S2).

Table 4. Explanatory ability of the variables considered (% EV; $n = 27$) from the jackknife predictive mean error procedure of each locality (MPE).

Variable	% EV	
PP	0.3	+
TEMP	**13.8**	−
FORESTAREA	**19.2**	+ −
SCRUBAREACRUBAREA	1.0	+
GRASSAREA	2.9	−
SPRINGDUNG	0.1	+
WINTERDUNG	0.9	−
FORCOST	4.0	−
HELIOCOST	**16.7**	+ −
DFOR	4.7	−
DSCRUB	0.2	−
DGRASS	**18.0**	+ −
LFORESTAREA	9.2	+
LSCRUBAREA	2.4	−
LGRASSAREA	2.5	−

Variables with significant relationships are shown in bold. Signs of the linear and quadratic function terms are shown. Acronyms as in Table 1.

(Table 3), so model accuracies seem to be lower when the species have narrow distribution ranges, are present in a high number of sampling localities and/or prefer the dung with low water content. Finally, only four environmental variables showed statistically significant relationships with the variation in the MPE of sampling localities (Table 4). Sampling localities with higher annual temperatures, medium forest areas and higher or lower distances to grasslands appeared to have small error levels.

Intrinsic species traits are generally not associated with the relevance of the different types of variables, except in the case of landscape-scale vegetation and trophic variables. The relevance of landscape-scale vegetation variables is positively related to the occurrence and abundance of species (Table 3); the landscape configuration around each locality seems to be especially influential for the more abundant and ubiquitous species in the study area. Similarly, the habitat preferences of species were related to the explanatory capacity of trophic variables; the abundances of habitat generalist species were better explained by trophic variables (Table 3).

Discussion

The most influential factors explaining dung beetle abundances

Our results suggest that Mediterranean ecosystems contain a diverse assemblage of dung beetle species whose composition and abundance appears to be influenced by a variety of factors operating across different spatial scales. The climatic and vegetation conditions prevailing at each locality are relevant, but so are the spatial configuration and the connectivity of the landscape around each locality. As Hortal *et al.* (2010) suggest, occupancy

dynamics, biotic interactions and climatic conditions are probably the most important factors affecting species distributions at the scale of our study. However, in the specific case of Mediterranean dung beetles the demography of their populations seems to be especially influenced by the concurrence of small-distance dispersal processes and the resistance to connectivity determined by landscape vegetation heterogeneity.

Despite the small differences in environmental values among sampling localities (maximum difference in mean temperature: 0.7 °C; in total precipitation: 155 mm; in elevation: 160 m), local environmental variables had a relatively high ability for explaining variation in dung beetle abundance. Micro-thermohygrometric conditions can influence the colonisation of dung (Koskela & Hanski, 1977); for example, in more humid zones dung desiccation may be delayed or soil texture may be softer than in non-humid zones. Indeed, this climatic factor can also explain dung beetle species movements from open to closed areas during the hottest months (Galante *et al.*, 1993). In our case, this might explain why precipitation and temperature were the most important climate variables for eight and eleven species, respectively. These observations are also consistent with those of Lumaret and Kirk (1987), who pointed out that temperature differences of 0.3 °C among sampling localities separated by 10 km may affect the distribution of thermophilous species and therefore local species composition.

With regard to vegetation variables, grasslands are the most frequently preferred habitats of Iberian dung beetles (Lumaret & Kirk, 1987; Romero-Alcaraz & Ávila, 2000; Zamora *et al.*, 2007). Accordingly, we observed that grassland area was the variable with the highest explanatory ability. Abundances for a large number of species were positively related to grassland area at both local and landscape scales. These species could be considered heliophilous. Grassland preferences for 15 of the 35 species analysed coincided with preferences reported in previous studies (Lumaret & Kirk, 1987; Martín-Piera *et al.*, 1992; Roslin & Koivunen, 2001). However, a few species previously considered heliophilous, such as *A. foetidus* (Martín-Piera *et al.*, 1992), had a positive correlation with grasslands at the local level (100 m) and a negative trend at the landscape level (500 m). Therefore, in our study, this species was more abundant in grasslands surrounded by forest or scrubland. In contrast, the abundance of *G. flagellatus* was positively related with grassland area only at the landscape level because it was found in various habitats but was abundant only in those surrounded by a grassland landscape. From an ecophysiological viewpoint, this species can be considered a typical endothermic heliophilous species (Verdú & Lobo, 2008) characterised by a pattern of flight that is very rapid but prolonged in time, requiring extensive grassland areas for dispersal and thermoregulation (J. R. Verdú, unpubl. data).

Only a few species showed preferences for either forest (*Sisyphus schaefferi*, *Aphodius cervorum*, and *Thorectes baraudi*) or scrubland (*Trox hispanicus*). These results are consistent with those of previous studies (Lumaret, 1990; Romero-Samper & Lobo, 2006), supporting the general absence of dung beetle ensembles specific for woodlands in the Euromediterranean region due to biogeographical and historical factors (Cambefort & Walter, 1991; Martín-Piera & Lobo, 1996). In our study region, these species were more abundant in sites with a large

area of forest at the landscape scale. However, the abundance of *S. schaefferi* was related to pasture and forest clearings, whereas the abundances of *A. cervorum* and *T. hispanicus* were related to localities dominated by a landscape of woodland and scrubland. Although there is little information about *T. baraudi*, the genus *Thorectes* is known to be associated with open and semi-open scrubland areas grazed by rabbits and lambs (Martín-Piera & López-Colón, 2000). In our study, this species was abundant in highly connected forests. The recent discovery that a closely related species, *Thorectes lusitanicus*, consumes acorns in *Quercus* forests (Pérez-Ramos *et al.*, 2007), and the recent observation of the same behaviour in *T. baraudi* (Verdú *et al.*, 2011), might explain the high abundance of *T. baraudi* in forest habitats of the woodland landscape where various species of *Quercus* occur. The abundance of other species, such as *Onthophagus fracticornis*, was positively related to forest area at both the local and the landscape scale. This species was abundant in forest and open areas surrounded by a forested landscape. However, in other zones of Europe (Wassmer, 1995) and the Iberian Peninsula (Martín-Piera *et al.*, 1992), this species has been reported as abundant in open areas. Many factors might help to explain the high variability in the habitat preferences of species across regions; however, this is difficult to evaluate because studies of dung beetle ecology generally ignore the relevance of landscape variables to describe species habitat preferences. Thus, more data representing different scales are necessary to better identify the factors that influence dung beetle species occurrence and abundance among localities.

The negative relationship between species abundance and scrubland area might be due to structural features of this habitat type. As discussed above, the tall, dense and relatively homogeneous structure of scrublands may explain the lack of a particular ensemble of species in this habitat. Nevertheless, this result contrasts with other scrubland types that support an ensemble of dung beetle species in the Iberian Peninsula (Verdú *et al.*, 2000). These scrublands have a more open structure as a consequence of intense rabbit and sheep grazing, a process that has historically been related to high endemicity values of dung beetles in the Iberian Peninsula (Verdú & Galante, 2002). Grazing systems that combine cattle with smaller herbivores such as sheep, deer or rabbits can suppress scrubland and forest growth more effectively (Bokdam & Gleichman, 2000). An increase in other types of herbivores, such as rabbits (a rare species in the study area), would likely generate more structurally diversified scrublands, facilitating dung beetle movements and dung colonisation, especially for species adapted to rabbit dung pellets (Verdú & Galante, 2004).

In addition to climatic and vegetation variables, dung availability has frequently been considered to be a factor explaining the habitat selection of dung beetles and therefore the differences in local species richness (Cambefort & Walter, 1991; Kadiri *et al.*, 1997; Lobo *et al.*, 2006). In our case, we observed that variables related to the amount of trophic resources had low explanatory power, probably as a consequence of the relatively homogeneous distribution of deer dung across the studied region (Numa *et al.*, 2009).

In terms of individual species' models, a large number of species ($n = 25$) showed a positive correlation with vegetation area at the local level, especially with grasslands ($n = 17$). Fourteen species showed a strong positive correlation with vegetation area at the landscape level, five of them were positively correlated with vegetation area at both the local and landscape levels. Similar results have been found in temperate cattle farms (Roslin & Koivunen, 2001), suggesting that in this type of landscape, the abundances of many species are influenced by processes operating at different spatial scales. The effects of patch area on dung beetle abundance were analysed recently in tropical ecosystems from a fragmentation perspective (Nichols *et al.*, 2007; Radtke *et al.*, 2008). However, in vegetation mosaics such as Mediterranean landscapes, species do not seem to perceive habitat patches as discrete units, but rather show a gradual range of affinity for different habitats or combinations of habitats (Dunning *et al.*, 1992; Brotons *et al.*, 2005). This might explain the high variability in species habitat preferences observed in Mediterranean dung beetle assemblages (Lumaret & Kirk, 1987; Menéndez & Gutiérrez, 1996; Barbero *et al.*, 1999). Interestingly, our models showed that both connectivity variables, such as the distance between similar vegetation patches, and landscape vegetation variables are factors that explain the variation in abundance of dung beetle species. The landscape variation in friction values for a forest species type and the distance to patches of open or closed vegetation were the most important variables for explaining local abundances. The relevance of the amount of vegetation cover to species distributions has been highlighted in several studies of Palaearctic dung beetles (Lumaret & Kirk, 1987; Galante *et al.*, 1993; Menéndez & Gutiérrez, 1996). In short, studies about habitat preferences in dung beetles in Mediterranean conditions have shown that closed vegetation characterised by dense scrubland or brushwood cover can impede the movements of individual dung beetles (Lumaret & Kirk, 1987; Zamora *et al.*, 2007) and the dispersion of odour cues (Romero-Alcaraz & Ávila, 2000), consequently hindering the colonisation of dung resources. Our evidence corroborates the suggestion that the particular structure of dense scrublands is a key factor that determines both the presence and the abundance of dung beetle species in heterogeneous Mediterranean landscapes. Our study provides the first results on the relationship between local Mediterranean dung beetle abundances and the spatial configuration of the landscape. In our opinion, this relationship suggests that dispersal restrictions caused by landscape heterogeneity and configuration have strong effects on local populations (Hanski, 1980). Local abundances can be influenced by intrinsic population processes, but also by changes in immigration and emigration rates, which are in turn conditioned by the landscape structure (Hanski, 1986). Thus, regional variation in Mediterranean dung beetle abundances may be viewed as a consequence of the impact of vegetation filters on a group of species mainly adapted to the consumption of herbivorous faeces in open biomes.

Modelling abundances

Our results demonstrate that variation in dung beetle abundance can be predicted moderately well when the data come from a standardised and complete multi-scale survey. More than

62% of the final models showed good explanatory ability with percentages of explained deviances higher than 70%. However, the reliability of these models should be cautiously considered. Jackknife results indicated that of the high number and diversity of the used predictors, 74% of species models had more than a 100% error level, and 37% had at least a 200% level of error when transferred to localities not considered in the training process without log transforming the abundance data. If we consider that the mismatch between observed and predicted abundances is high when predictions are at least four times higher or lower than observed abundances, the obtained models may be considered unreliable only for 15% of the observations, especially for those with less than 10 individuals.

Other unconsidered variables such as soil types (Vessby & Wiktelius, 2003) or biotic interactions (Comita *et al.*, 2010) could help to increase the predictive ability of these abundance models. However, the most probable factors hindering accurate predictions are those related to the difficulty of measuring a variable that is subject to temporal and/or chance variations. Different species and even individuals of the same species may differ in their detectability, which, in turn, may vary according to the environmental conditions (Hwang & Huggins, 2005). Furthermore, species abundance is a variable whose oscillations can originate from random or demographically intrinsic effects that are unrelated to environmental characteristics of their localities and surroundings (Lande *et al.*, 2003). In our study, model errors were larger at cold sites, sites with medium values for forest area and/or sites with medium values for distance and movement costs to grassland patches. In general, this means that our abundance models were less reliable in some habitat patches that were surrounded by contrasting habitat matrices. Diverse species responses to the matrix surrounding a habitat patch can influence patch species composition, increasing turnover among similar habitats (Roslin & Koivunen, 2001; Numa *et al.*, 2009). In addition to physical barriers to flight through dense vegetation, some species might have dispersal limitations due to their thermoregulatory capacity (Verdú *et al.*, 2007a). This might explain why predicting species abundance in habitat patches that have lower mean temperatures or that are surrounded by a different matrix is more difficult.

Understanding species-specific idiosyncrasies is essential for understanding the regional distribution, local abundance and spatial dynamics of dung beetles (Roslin & Koivunen, 2001). Contrary to our expectations, we found that the relevance of the different types of variables was not related to intrinsic species characteristics such as body size, nesting behaviour or phenological period. However, some environmental and biological factors seem to influence the error rate and variability accounted for by the models. Species attributes such as total abundance, local and geographic species patterns and trophic preferences seem to be related to the error level of the models. Thus, we obtained less reliable abundance models for generalist species. The abundances of species with low population sizes, broad regional occurrences, without marked trophic or habitat preferences and with reduced geographic distributions (Iberian, Iberian-Maghrebian or Mediterranean) seemed to be more poorly predicted. On the other hand, variables related to the landscape matrix had a stronger influence on species with high abundances and wide distributions within the reserve. These results suggest that the abundance of species with Mediterranean distributions and generalist adaptations is difficult to predict at the local scale and that the abundance of these generalist species may be conditioned primarily by the dispersal limits imposed by the landscape (Chust *et al.*, 2003, 2004).

Acknowledgements

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2011.00137.x:

Table S1. Sampling effort (number of pitfall traps; PT), landscape type, habitat type and percentages of each habitat in 100 m and 500 m buffer zones around each sampling site.

Table S2. List of species captured in Cabañeros National Park and a comparison of dung beetles abundances according to different species traits: habitat type, season, preference for hydric content of dung and geographic distribution.

Table S3. Individual explanatory percentages of total variability accounted for by the different variables used to model dung beetle species abundance (see Table 1) and percentages explained by the final models (%EV).

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