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Potential effects of climate change on the distribution of Scarabaeidae dung beetles in Western Europe

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Abstract Dung beetles are indispensable in pasturelands, especially when poor efficiency of earthworms and irregular rainfall (e.g. under a Mediterranean climate) limit pad decomposition. Although observed and projected species range shifts and extinctions due to climate change have been documented for plants and animals, little effort has focused on the response of keystone species such as the scarab beetles of dung beetle decomposers. Our study aims to forecast the distribution of 37 common Scarabaeidae dung beetle species in France, Portugal and Spain (i.e. more than half of the western European Scarabaeidae fauna) in relation to two climate change scenarios (A2 and B1) for the period leading to 2080. On average, 21 % of the species should change in each 50-km UTM grid cell. The highest faunistic turnover rate and a significant increase in species richness are expected in the north of the study area while a marked impoverishment is expected in the south, with little difference between scenarios. The potential enrichment of northern regions depends on the achievement of the northward shift of thermophilous species, and climate change is generally likely to reduce the current distribution of the majority of species. Under these conditions, the distribution of resource—i.e. the extent and distribution of pastures—will be a key factor limiting species' responses to climate change. The dramatic abandonment of extensive grazing across many low mountains of southern Europe may thus represent a serious threat to dung beetle distribution changes.

Keywords Dung beetles · Scarabaeidae · Climate change · Land use change · Europe

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Introduction

Although sudden disruptions to biogeochemical cycles and land use changes have severe impacts on biodiversity, an increasing number of studies show that climatic change has already affected many species and ecosystems during the last century (McCarty 2001; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006). The latitudinal and altitudinal distributions of terrestrial biota prove that temperature may play an important role in the response of many organisms. Changes in species distributions modify interspecific interactions and could lead to the extinction of more specialized species (Hughes 2000; McCarty 2001; Parmesan 2006), whereas generalist, thermophilous or invasive species could expand in new habitats (Thuiller 2007). Marked species turnover could strongly affect ecosystem functioning. In this way, the disruption of regulation processes provided by species (e.g. carbon storage) will exacerbate the anthropogenic global warming by

positive retroaction (Friedlingstein 2008; Heimann and Reichstein 2008).

In terrestrial ecosystems, where C and N are stored in perennial vegetation and in the soil, mineralisation by decomposers (microorganisms and fungi) is the last step of a complex decomposition process carried out by detritivores (invertebrates). Among detritivores, some keystone species have a strong impact on decomposition (Hättenschwiler et al. 2005). In grazed ecosystems, for example, dung beetles (Scarabaeoidea: Scarabaeidae, Aphodiidae, Geotrupidae) play an essential role in tearing up faeces, burying, and sowing them with microorganisms (Hanski and Cambefort 1991). Their absence can cause major problems and, in Australia, the introduction about twenty Scarabaeidae species from the Mediterranean basin and South Africa was required to bury the dung of the domestic stock, and thereby benefit pasture production and reduce the numbers of pest flies (Doube et al. 1991).

In Europe, both species richness and endemism of Scarabaeidae are concentrated around the Mediterranean basin (Lumaret and Lobo 1996; Lobo and Martín-Piera 2002; Lobo et al. 2002) and one may expect that climate warming could induce a global northward shift of the distribution of most of these species. Nevertheless, during the twentieth century, a significant rarefaction of Scarabaeidae was observed in Europe (Lumaret 1990; Biström et al. 1991; Barbero et al. 1999; Roslin 1999; Lobo 2001; Lobo et al. 2001; Carpaneto et al. 2007). This worrying trend should be attributed to the drastic changes observed in land use and farm practices.

Consequently, the magnitude of potential changes in species distribution driven by climate change needs to be evaluated both at medium latitudes where the burying activity of Scarabaeidae could become crucial if aridity prevents the activity of mesophilous dung beetles (Aphodiidae, Geotrupidae) and earthworms, and in the southernmost extremities of the continent (Iberian, Italian and Balkan peninsula) where the rapid replacement of European species by a more thermophilous fauna is questionable. Our ultimate goal is actually not to precisely map the future distribution of species (an unreachable goal considering the complexity of biotic and abiotic interactions; Duncan et al. 2009) but to examine the probable effect of climatic change on the current species distribution in order to evaluate the possible variations in species richness and regional faunas. By comparing the consequences of extreme A2 and B1 scenarios developed by the IPCC for the twenty-first century (Nakicenovic and Swart 2000), we would also determine if the differences in climatic conditions related to these alternative economic scenarios could have very different consequences for this family of beetles.

Methods

Distribution data

The study area extends from 36°N to 51°N across the Iberian Peninsula and France, i.e. the main centre of species richness for European dung beetles and contiguous temperate extension. Data were extracted from the French Scarabaeoidea Laparosticti database (Lumaret 1990; Lobo et al. 1997a; http://inpn.mnhn.fr) and the Iberian Scarabaeidae database (Lobo and Martín-Piera 1991; BANDA-SCA free on www.biogeografia.org). The French database includes more than 42,000 records (compiled from 1762 to 2006) for nearly 190 species (49 Scarabaeidae) observed in mainland France and on Corsica. The Iberian database includes more than 15,900 records (from 1872 to 2001) for 55 Scarabaeidae species observed in the Iberian Peninsula and Balearic islands. The 61 Scarabaeidae species with records later than 1950 (in the French or Iberian database) were selected. For each species, we extracted and mapped the records from 1950 with ArcGis 9.1 (ESRI Corp., Redlands, California).

Estimation of adequately surveyed areas

Adequately surveyed cells were discriminated to increase the reliability of the used absence data. The study area (France and the Iberian Peninsula), was divided into 10×10 km UTM grid cells, to give a total of 11,995 cells. Because the number of species per cell depends on environmental conditions, the main biogeographic regions were defined according to the classification proposed by the European Topic Centre on Biological Diversity (http://biodiversity.eionet.europa.eu/) for France and by Lobo and Martín-Piera (2002) for the Iberian Peninsula. Each 100 km^2 UTM grid cell was attributed to a bioclimatic subregion (Figs. 1, 2). For each bioclimatic subregion, well surveyed cells were identified. The adequacy of sampling in each cell was determined by a negative exponential function relating the number of species (Sr) to the number of records from 1950 (r) (Soberón and Llorente 1993):

$$Sr = Smax(1 - \exp(-br)) \\ = a(1 - \exp(-br))/b \text{ with } Smax = a/b$$

where $Smax$, the asymptote, was the estimated total number of species per cell, a corresponded to the increase rate at the beginning of the inventory ($r = 0$) and b characterized the shape of the curve. Because the value of the asymptote depended on the subregion, the function was fitted for each subregion by the Quasi-Newton method (Jiménez-Valverde and Hortal 2003). Then, we calculated the number of

Fig. 1 Distribution of the five biogeographic climatic areas of France (*A* Alpine, *B* Atlantic, *C* Continental, *D* Corsica, *E* Mediterranean)
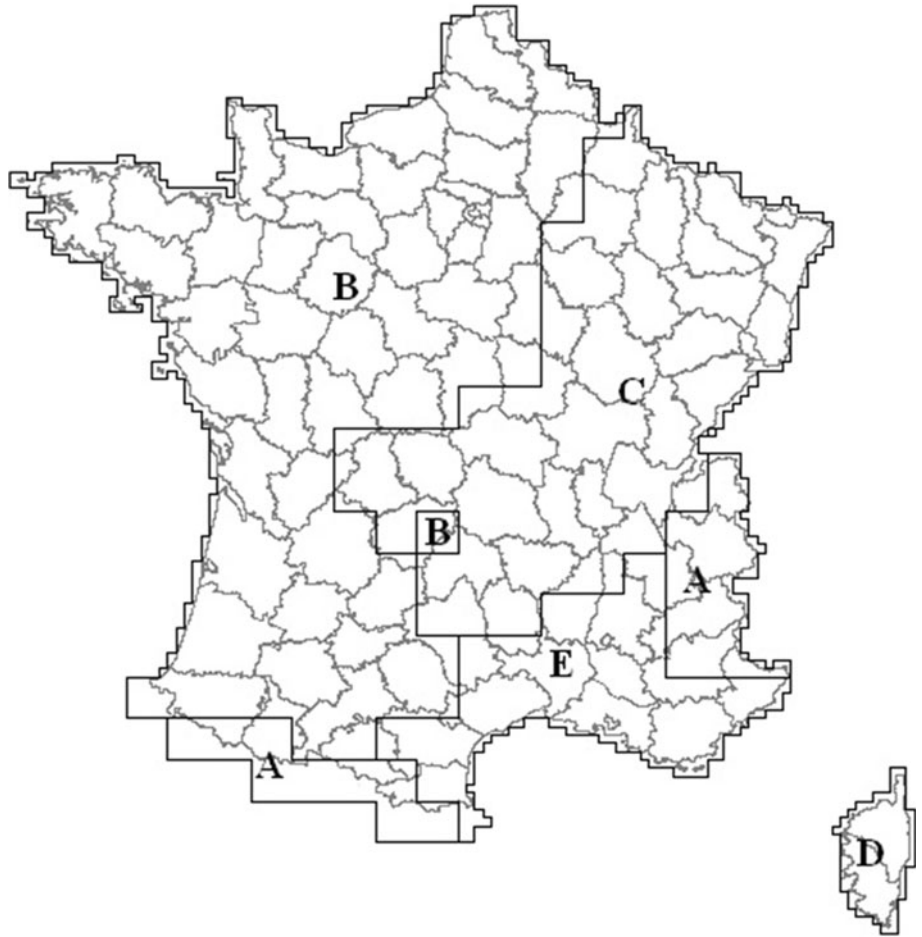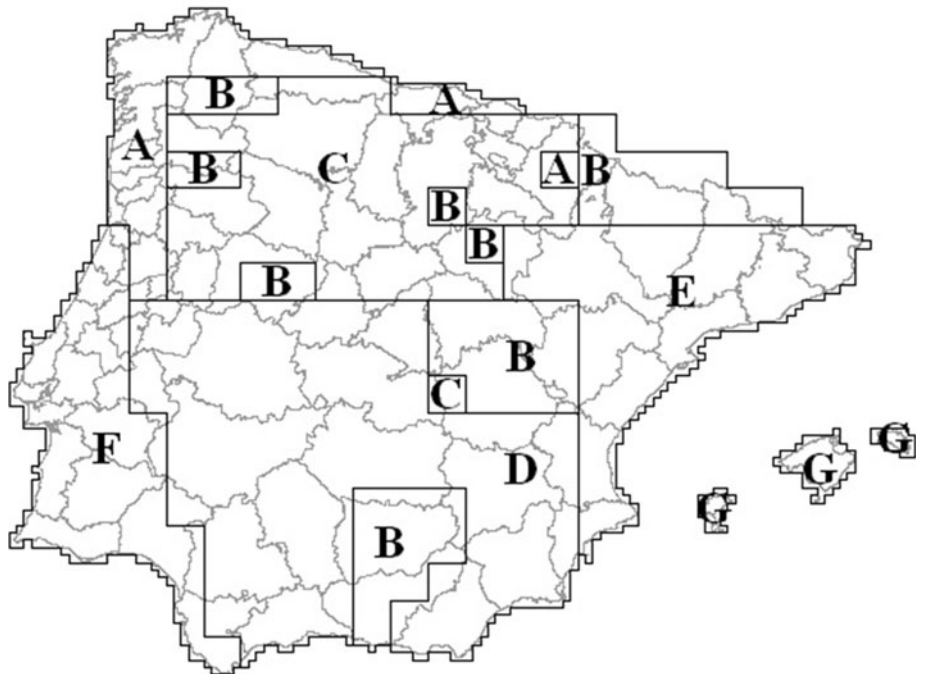

Fig. 2 Map of the six principal physioclimatic subregions of the Iberian Peninsula determined by Lob and Martín-Piera (2002) (*A* Eurosiberian, *B* Montane, *C* North Plateau, *D* South Plateau, *E* East Mediterranean, *F* West Mediterranean, *G* Balearic Islands)

records required for a rate of species increment ≤0.01 (less than one added species for each 100 database records):

$$r0.01 = 1/b \ln(1 + b/0.01)$$

The cells for which the number of records r was higher than $r0.01$ were considered well surveyed and kept for the species distribution modelling part. This analysis showed that 188,100 km^2 cells out of 11,995 can be considered well surveyed (1.57 %; Table 1; Fig. 3). These cells were widely distributed along the latitudinal gradient and most of them were located in hilly subregions (Mediterranean, South Plateau, Continental and Alpine) characterized by a high climatic and edaphic heterogeneity. France was slightly more prospected than Spain. For Corsica, well inventoried cells were deduced from the results ($r0.01$) obtained for the Mediterranean subregion. All calculations were performed with STATISTICA 6.0 (Stat Soft 2001).

Explanatory variables

Nine climatic variables were used as predictors: annual spring rainfall (mm; RAINSP), annual summer rainfall (mm; RAINSU), annual winter rainfall (mm; RAINW), annual autumnal rainfall (mm; RAINA), annual mean temperature (°C; T), minimum and maximum monthly mean temperature (°C; TMIN and TMAX respectively), annual mean net radiation (MJ m^{-2}; RAD) and mean annual real evapotranspiration/potential evapotranspiration ratio (EVA). Considering that Scarabaeidae species are soil-digger beetles with a complete endogenous larval development, we also used 7 edaphic variables: 4 variables reflecting the texture of soil (fine, medium fine, medium, coarse) and 3

variables reflecting the soil water regime (soil very dry, dry, or wet). The inclusion of these non-climatic variables in the modelling process may help to determine the true independent contribution of climatic variables, thus enhancing the reliability of future projected distributions (Luoto and Heikkinen 2008; Real et al. 2010; Aragón et al. 2010). The edaphic data came from the Soil Geographical Database of Eurasia provided by the European Commission (http://eusoils.jrc.ec.europa.eu/). We considered that soil characteristics remain constant for the studied period.

The climatic data were obtained from the Climate Research Unit (CRU data center). The current values corresponded to 1961–1990 averages. The forecasted values corresponded to 2070–2099 averages (Hadley Climate Model) established according to both extreme scenarios (A2 and B1) developed by the IPCC Special Report (Nakicenovic and Swart 2000). Scenario A2 considers a very heterogeneous world with a strong population growth, slow economic and technological developments and a reinforcement of current regional inequalities. Scenario B1 assumes a converging world with global solutions oriented at durability, the decline in inequality between regions, the decrease in population from 2050. Thus, 3.4 and 1.8 °C worldwide increase in temperature are forecasted for A2 and B1 scenarios, respectively. For each variable, the mean current and forecasted values were calculated for each 100 km^2 UTM cell (performed with ArcGis 9.1).

Forecasting models

To summarize the relationship between the presence/absence of species in UTM-cells (response variable) and all

Table 1 Asymptotic relationship between number of species and sampling effort for the biogeographic areas and physioclimatic subregions

	Number of records	Total UTM-cells	R^2	Smax	a	b	r0.01	Well surveyed cells
France								
Alpine	4,159	464	0.909	35.47	1.206	0.034	43.577	22 (4.74 %)
Atlantic	3,571	3,031	0.968	55.45	1.109	0.020	54.931	4 (0.13 %)
Continental	8,121	1,775	0.936	40.20	1.206	0.03	46.21	33 (1.86 %)
Mediterranean	11,892	634	0.901	53.60	1.340	0.025	50.11	63 (9.94 %)
Corsica	1,477	126	0.943	37.60	1.504	0.04	40.236	5 (3.97 %)
Total	29,220	6,030						127 (2.11 %)
Iberian peninsula								
Eurosiberian	337	487	0.958	23.092	1.247	0.054	34.376	0
Montane	1,832	1,005	0.953	34.125	1.365	0.04	40.236	12 (1.19 %)
North Plateau	2,376	1,200	0.954	29.104	1.397	0.048	36.622	10 (0.83 %)
South Plateau	6,039	1,946	0.930	36.459	1.349	0.037	41.826	34 (1.75 %)
East Mediterranean	199	841	0.984	37.933	1.138	0.03	46.21	0
West Mediterranean	994	703	0.947	30.909	1.360	0.044	38.327	5 (0.71 %)
Balearic Islands	120	95	0.974	22.222	1.200	0.054	34.376	0
Total	11,897	6,277						61 (0.9 %)

Fig. 3 Map of 1,199,510 km
UTM-cells (adequately sampled
cells in *black*)
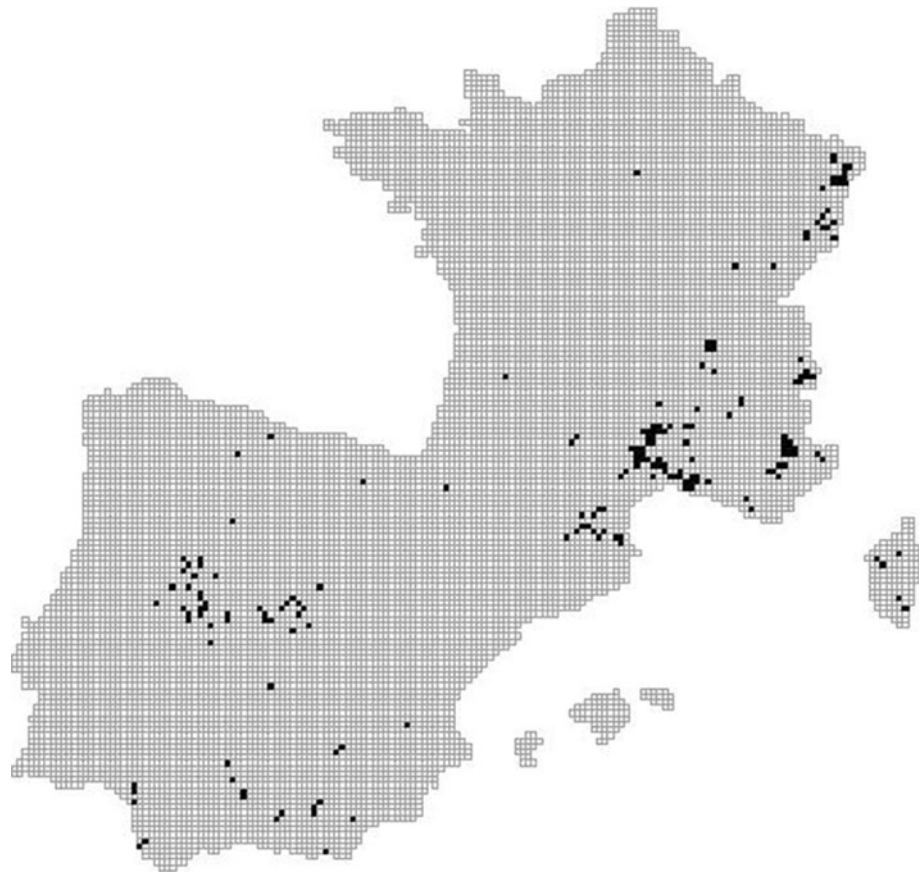
the formerly mentioned explanatory variables, we used three kind of modelling techniques implemented into the BIOMOD library (Thuiller 2003; Thuiller et al. 2009) under the R software: Generalised Linear Model (GLM), Generalised Additive Model (GAM) and Boosted Regression Trees (BRT). GLMs were fitted using linear and quadratic functions. GAMs were fitted using 4 degree of smoothing. We used a forward stepwise selection for variable selection into the GLM and GAM using the AIC criteria. We used 100-fold cross-validation to select the optimal number of trees for the BRT with an interaction-depth of 2.

The models were run for each species, using all available presence data but only absences coming from cells previously considered as well surveyed. By using these absences in both calibration and evaluation processes we try to minimize the effects of false absences. We assume that the estimated parameters of the so obtained predictive functions are capable of reflecting the effect of climate on current distributions, and that these effects remain similar under the future climatic conditions. The obtained continuous probabilities were converted into binary presence/absence data, selecting the recommended threshold that maximized the percentage of presences and absences correctly predicted (see Jiménez-Valverde and Lobo 2007).

The models were finally performed for 40 species (35 species common to France and Iberian Peninsula, 1 species strictly French and 4 species strictly Iberian) observed in at least 40 presence cells and 40 absence cells considered as well surveyed. To be reliable, predictions must be validated using independent data but such data did not exist in our case. We thus randomly divided the original dataset into two subsets: the calibration data (70 % of total presence/absence data) used to calibrate the models and the evaluation data (30 %) used to examine the reliability of the predictions.

The best model among the outputs of the three modelling techniques was determined, for each species, by using the area under the Receiver Operating Characteristic curve (AUC Hanley and McNeil 1982) on the evaluation data. This curve represents the fraction of presences correctly predicted (sensitivity) as a function of commission errors (1-specificity) for a range of thresholds, being used as a standard discrimination measure. AUC method cannot be used when the comparisons differ in the relative occurrence area (the ratio between the species extent and the whole extent of the region of study), as occur in the case of distributional models carried out at the same extent for species differing in range size (Lobo et al. 2008). That was not the case here as AUC was used to compare models built with the same species data. Furthermore, we assume that the use

of absence data selected from well surveyed cells should increase the capacity of minimizing both commission and omission errors in the evaluation process. We overlaid both observed individual species maps and predicted estimations in order to obtain two species richness maps at a 10×10 km cell resolution, calculating the correlation between observed and predicted species richness in the well surveyed cells as a measure of the general accuracy of predictions.

Changes in species' distribution

The number of species by 50×50 km UTM grid cells (pools of 25,100 km^2 UTM grid cells) was calculated for the twentieth century and for the twenty-first century according to A2 and B1 scenarios. To do that we overlap each one of the individual predictions being the species considered present in a 50×50 km cell if it is predicted as present in any one of their constituent 10×10 km cells. The use of 50×50 km UTM grid cells should allow to reduce the bias induced by the relative lack of precision of forecasted species distributions. β-diversity was used to evaluate the species turnover between the end of the twentieth century and the end of the twenty-first century. The temporal turnover was estimated with the Wilson and Shmida's β-diversity index (1984) rescaled at a 0–100 range:

$$\beta = 100 * (S_g + S_l)/(S_{20} + S_{21})$$

where S_g is the number of species gained between the dates, S_l the number of species lost, S_{20} the predicted number of species for the twentieth century and S_{21} the predicted number of species for the twenty-first century. $\beta = 0$ if fauna does not change between the dates, $\beta = 50$ if there is as many gained and lost species as shared species, $\beta = 100$ if fauna completely changes.

Results

Choice of models

The mean of the obtained AUC values is 0.898 ± 0.017 (± 95 % confidence interval; minimum $= 0.783$, maximum $= 0.997$; see Table 2) which may be considered a high value when compared to those obtained in similar studies (Elith et al. 2006). The Pearson correlation value between observed and predicted species richness in the well surveyed 10×10 km cells is positive and statistically significant ($r = 0.66$, n $= 188$, $p < 0.001$). In spite of high AUC values, three species (*O. stylocerus, S. semipunctatus* and *S. typhon*) were excluded from the analysis because of too peculiar forecasted distributions. The present work finally concerned 37 Scarabaeidae species (maps in Annex).

Table 2 AUC values obtained in the evaluation data (30 % of total data) for all the considered species

Species	GAM	BRT	GLM
Bubas bison	0.962	0.972	0.964
Bubas bubalus	0.959	0.935	0.942
Caccobius schreberi	0.836	0.866	0.798
Cheironitis hungaricus	0.851	0.777	0.630
Copris hispanus	0.947	0.958	0.954
Copris lunaris	0.840	0.878	0.841
Euoniticellus fulvus	0.832	0.846	0.837
Euoniticellus pallipes	0.966	0.911	0.941
Euonthophagus amyntas	0.899	0.912	0.903
Euonthophagus gibbosus	0.831	0.828	0.755
Gymnopleurus flagellatus	0.871	0.891	0.869
Gymnopleurus sturmi	0.687	0.783	0.606
Onitis belial	0.947	0.945	0.927
Onitis ion	0.902	0.902	0.879
Onthophagus baraudi	0.976	0.985	0.824
Onthophagus coenobita	0.835	0.871	0.840
Onthophagus emarginatus	0.842	0.891	0.837
Onthophagus fracticornis	0.917	0.943	0.898
Onthophagus furcatus	0.821	0.845	0.821
Onthophagus grossepunctatus	0.791	0.816	0.782
Onthophagus illyricus	0.741	0.818	0.799
Onthophagus joannae	0.883	0.873	0.838
Onthophagus latigena	0.944	0.973	0.956
Onthophagus lemur	0.863	0.892	0.852
Onthophagus maki	0.829	0.888	0.792
Onthophagus nuchicornis	0.864	0.938	0.912
Onthophagus opacicollis	0.898	0.889	0.901
Onthophagus ovatus	0.915	0.862	0.911
Onthophagus punctatus	0.927	0.897	0.882
Onthophagus ruficapillus	0.767	0.819	0.792
Onthophagus similis	0.850	0.838	0.861
Onthophagus stylocerus	0.919	0.941	0.861
Onthophagus taurus	0.875	0.870	0.808
Onthophagus vacca	0.814	0.956	0.914
Onthophagus verticicornis	0.853	0.890	0.872
Scarabaeus laticollis	0.846	0.850	0.842
Scarabaeus sacer	0.958	0.963	0.946
Scarabaeus semipunctatus	0.995	0.997	0.869
Scarabaeus typhon	0.850	0.851	0.712
Sisyphus schaefferi	0.808	0.871	0.785

Future forecasted distributions

Important changes in distribution appeared for both scenarios: the mean change (sum of gain and loss) reached 70 % for A2 and 63 % for B1 (Table 3) and only four species did show a change in distribution lower than 30 %

Table 3 Estimated changes in the distribution of species according to the A2 and B1 IPCC scenarii

Species	Model	Estimated current range size (nb cells)	Scenario A2				Scenario B1			
			Loss (%)	Gain (%)	ΔLon	ΔLat	Loss (%)	Gain (%)	ΔLon	ΔLat
Bubas bison	BRT	3,658	0	110.69	1.4	2.74	0.14	81.25	0.99	2.06
Bubas bubalus	GAM	3,789	9.77	83.5	0.62	1.03	12.83	78.65	0.35	0.89
Caccobius schreberi	BRT	8,556	32.82	20.47	−0.03	0.51	26.05	23.19	0.39	0.72
Cheironitis hungaricus	GAM	3,178	76.49	12.24	−0.41	1.73	51.1	4.37	0.57	1.05
Copris hispanus	BRT	3,844	0.05	103.46	1.12	2.3	0.03	71.96	0.79	1.66
Copris lunaris	BRT	6,676	84.17	14.92	1.94	3.1	71.39	18.05	1.79	2.5
Euoniticellus fulvus	BRT	8,560	6.99	25.34	0.58	0.39	15.02	26.13	0.61	0.36
Euoniticellus pallipes	GAM	3,115	0	137.98	1.51	2.64	0.51	95.76	1.13	1.98
Euonthophagus amyntas	GAM	5,086	75.01	56.04	3.15	5.44	73.48	60.48	2.87	4.8
Euonthophagus gibbosus	GAM	2,943	23.82	96.47	−3.08	−0.87	6.56	140.47	−1.65	−0.06
Gymnopleurus flagellatus	BRT	4,369	29.96	28.66	1	1.37	22.98	28.36	0.92	1.21
Gymnopleurus sturmi	BRT	3,592	0.22	149.33	1.95	2.94	0.33	118.62	1.95	2.58
Onitis belial	BRT	3,447	3.16	42.3	0.66	0.39	12.01	40.59	0.75	0.2
Onitis ion	BRT	2,818	0.71	44.18	0.75	0.51	2.66	40.92	0.9	0.44
Onthophagus baraudi	BRT	310	74.52	0	1.96	0.54	62.58	0	1.48	0.28
Onthophagus coenobita	BRT	6,074	64.82	11.46	0.88	0.79	43.48	10.9	0.87	0.86
Onthophagus emarginatus	BRT	6,147	19.44	32.44	0.66	0.79	18.32	31.02	0.55	0.87
Onthophagus fracticornis	BRT	7,833	75.32	0.79	0.94	−0.2	56.49	0.84	1.08	−0.76
Onthophagus furcatus	BRT	5,975	1.82	31.62	0.89	1.19	1.77	29.84	0.84	1.1
Onthophagus grossepunctatus	BRT	5,294	27.92	31.6	1.01	1.05	26.14	30.9	1.01	1.19
Onthophagus illyricus	BRT	6,344	14.52	7.52	0.49	0.49	14.56	7.22	0.43	0.43
Onthophagus joannae	BRT	6,204	56.88	5.14	0.93	−0.2	48	5.08	0.55	−0.41
Onthophagus latigena	BRT	1,675	18.57	64.96	1.12	1.06	16.96	72	1.1	1.09
Onthophagus lemur	BRT	6,298	55.83	12.38	1.54	0.77	48.89	12.67	1.1	0.55
Onthophagus maki	BRT	4,519	19.36	48.59	0.51	1.11	21.04	53.44	0.87	1.59
Onthophagus nuchicornis	BRT	5,694	16.05	15.1	−0.13	0.17	18	13.12	−0.08	0.25
Onthophagus opacicollis	GLM	5,575	0.04	69.29	1.25	1.12	1.42	49.69	0.89	0.68
Onthophagus ovatus	GAM	6,688	15.68	12.87	0.42	0.43	9.46	18.53	0.02	0.18
Onthophagus punctatus	BRT	4,912	4.05	19.89	0.98	0.92	3.14	25.47	1.07	1.13
Onthophagus ruficapillus	GLM	6,503	3.48	42.98	1.43	1.12	4.81	43.4	1.29	1.13
Onthophagus similis	GLM	7,859	43.87	10.89	1.25	1.96	41.9	13.3	1.94	1.96
Onthophagus taurus	GAM	8,521	0	34.26	1.38	1.22	0.04	32.75	1.35	1.12
Onthophagus vacca	BRT	10,136	0.01	14.7	0.67	0.59	0.21	13.21	0.62	0.56
Onthophagus verticicornis	BRT	5,708	61.63	13.58	1.26	0.42	53.01	13.89	0.97	0.49
Scarabaeus laticollis	BRT	4,322	23.3	43.48	0.32	1.18	22.61	38.89	0.25	0.94
Scarabaeus sacer	BRT	3,792	13.16	72.49	1.25	1.43	14.06	58.18	1.05	1.12
Sisyphus schaefferi	BRT	2,936	85.49	13.28	0.65	0.75	74.9	18.15	0.43	0.76

Loss and Gain are expressed in % of estimated current range size

ΔLon and ΔLat (decimal degrees) = difference in central location of each species' longitude and latitude between the current and the forecast estimated distributions (positive = shift toward East/North; negative = shift toward West/South)

of their current distribution (*O. vacca*, *O. illyricus*, *O. punctatus* and *O. ovatus*). This change in distribution mainly corresponded to a northward shift: on average 1.16° for A2 and 1.01° for B1 (max. ~5° for *E. amyntas*). Results obtained for the two scenarios were not very different (slightly higher changes for A2). The geographical

boundaries of our study might lead to an underestimation of the latitudinal shift. Moreover, an altitudinal shift (difficult to detect with 10-km UTM grid cells) was also observed (e.g. *O. ovatus*, *O. verticicornis*).

Two parameters were important to distinguish: (1) the loss of present favourable cells and (2) the net balance
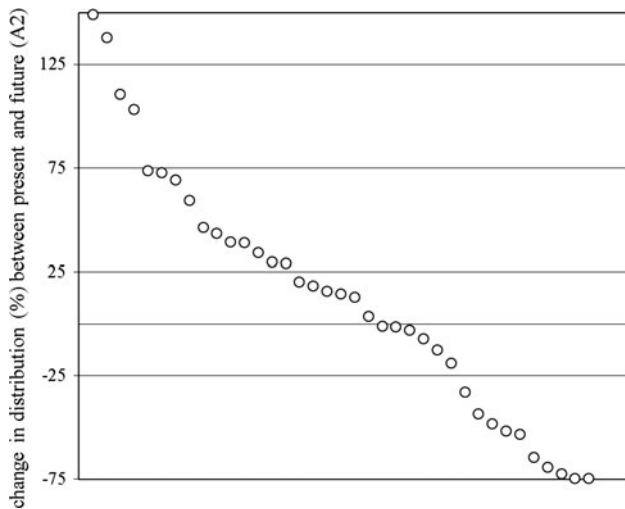
Fig. 4 Change in distribution between present and future (A2 scenario). Each *circle* represents a species (positive values for gain, negative values for loss)

between gain and loss of cells. The loss of current favourable areas could lead to the disappearance of populations and, consequently, could weaken the capacity of species to face global warming by reaching new favourable territories. The net gain of favourable territories should be

considered with caution because the actual presence of species in such new territories depends on many factors (landscape structure, population dynamics, etc.).

Three categories of species can be distinguished (values for A2 scenario; Table 3; Fig. 4):

(1) Species with no clear trend: twelve species could lose or gain no more than 20 % of their predicted distribution (*C. schreberi*, *E. fulvus*, *E. amyntas*, *G. flagellatus*, *O. emarginatus*, *O. grossepunctatus*, *O. illyricus*, *O. nuchicornis*, *O. ovatus*, *O. punctatus*, *O. vacca*, *S. laticollis*). This relatively low change was associated with a reduced loss of present favourable surfaces, except for *E. amyntas* (75 %).

(2) Looser species: ten species could lose at least one third of their distribution in the studied area. This global decrease corresponded to a loss of current favourable cells comprised between 44 % (*O. similis*) and 86 % (*S. schaefferi*). For seven of these species (*C. lunaris*, *O. coenobita*, *O. fracticornis*, *O. joannae*, *O. lemur*, *O. similis*, *O. verticicornis*), an expansion north of the studied area is possible while for *C. hungaricus*, *S. schaefferi* (Mediterranean) and *O. baraudi* (alpine endemic) the disappearance of present favourable sectors could not be compensated and

Fig. 5 The distribution of estimated dung beetle species richness at the present time (**a**), and at the end of the twenty-first century according to the two climatic scenarii A2 (**b**) and B1 (**c**)
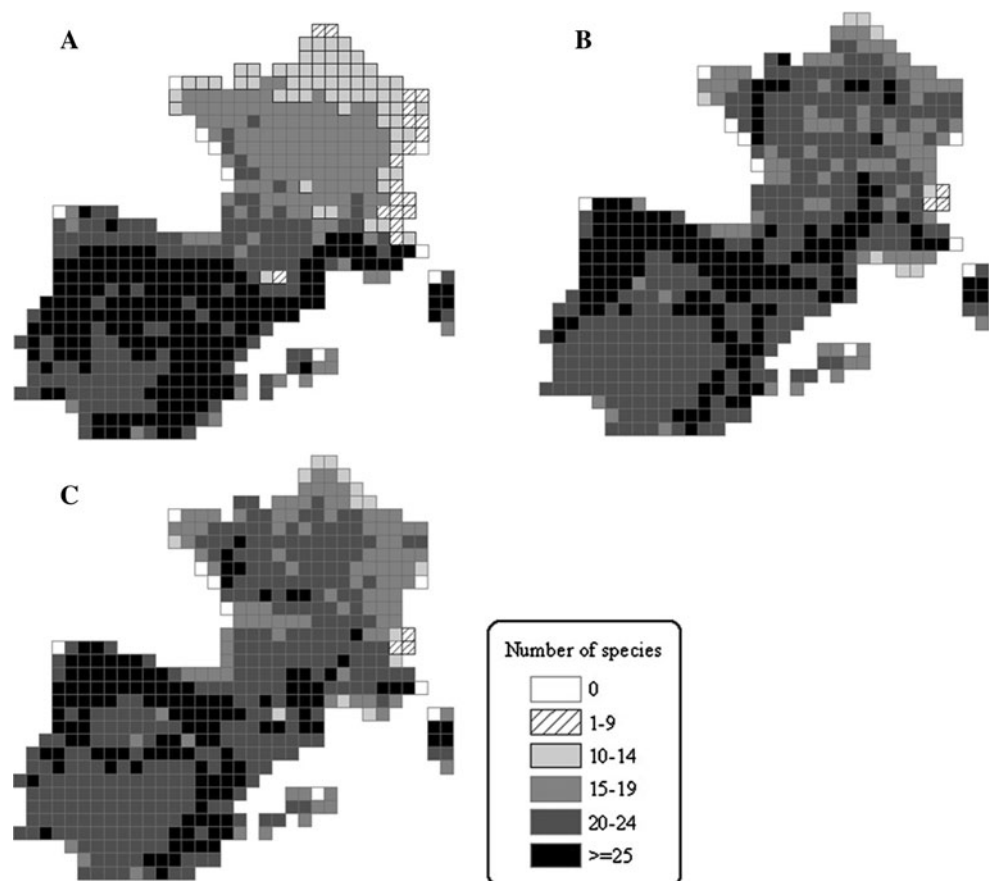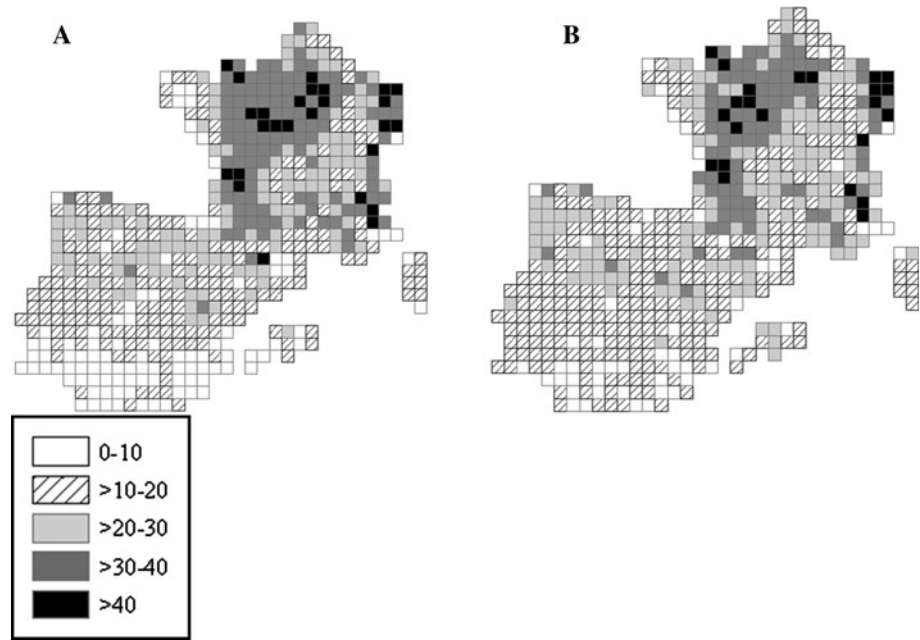
Fig. 6 The spatial distribution of estimated dung beetle species turnover for the end of the twenty-first century according to the A2 (**a**) and B1 (**b**) climatic scenarii

the species could lose more than 2/3 of their current distribution.

(3) Winner species: fifteen species could increase their current predicted distribution in the area by more than 29 % (*B. bison*, *B. bubalus*, *C. hispanus*, *E. gibbosus*, *E. pallipes*, *G. sturmi*, *O. belial*, *O. ion*, *O. furcatus*, *O. latigena*, *O. maki*, *O. opacicollis*, *O. ruficapillus*, *O. taurus*, *S. sacer*). For *E. gibbosus*, *O. latigena* and *O. maki* this increase was accompanied by a loss of more than 15 % of present favourable cells, whereas, at the opposite, the net gain exceeded 100 % for *B. bison*, *C. hispanus*, *E. pallipes* and *G. sturmi*.

Changes in biodiversity

The map of current predicted species richness deriving from the overlay of individual distribution maps (Fig. 5a) showed a similar spatial pattern that the estimations of species richness distribution previously obtained by another way (Lobo and Martín-Piera 2002; Lobo et al. 2002). By comparison with the present, the species richness maps corresponding to the scenarios A2 and B1 showed a general increase in diversity in France, and a significant decrease in the centre of the Iberian Peninsula for the end of the twenty-first century (Fig. 5b, c). A very similar regional species turnover was expected under both scenarios (Fig. 6a, b): on average 21 % of the fauna could change in each 50 × 50 km UTM grid cell (20.8 % with A2; 20.9 % with B1; $t = -0.22$, $df = 1,116$, $p = 0.82$) with highest values along the eastern French boundary and in the north-western half of this country (up to 68 % for A2 and 55 % for B1).

Discussion

In the Western Palaearctic region, the Scarabaeidae fauna contains 162 species split into 12 genera (Cabrero-Sañudo and Lobo 2003). The present study focused on 37 of the 61 species from the Iberian Peninsula and France. These species represent eleven genera, are all widely distributed in the studied area (Lumaret and Lobo 1996) and one can assume that the 15° latitudinal gradient/4,000 m altitudinal gradient covered by our study captured a well part of their environmental niche. The choice of these species, primarily imposed by the necessity to have a large number of observations, allowed us to avoid the problems related to microendemism and historical contingencies (Guisan 2003; Araújo et al. 2008). The widespread distribution of the 37 studied species proved that they have been able to disperse and, consequently, one may expect that they should be able to respond to future climate change by modifications in their distribution. Because local abundance and distribution range are generally correlated in dung beetles (Lobo 1993), one may consider that our work dealt mainly with core species that constitute the bulk of local assemblages (Hanski 1991).

Our results forecast a general northward shift of Scarabaeidae with a related increase in species richness at intermediate and northernmost latitudes. In parallel, an altitudinal increase—hard to depict with 100 km² UTM-cells—may operate for some species. The static nature of our modelling, as well as the scale and resolution considered, does not allow to derive more detailed conclusions, especially about the effect of climate change on the modalities of species coexistence (Guisan and Thuiller 2005; Duncan et al. 2009).

This shift was expected because Scarabaeidae constitute the main thermophilous group of dung beetles (Lumaret and Kirk 1991; Lobo and Martín-Piera 2002; Lobo et al. 2002), and some recent empirical evidences support it. *Onitis belial*, a species formerly restricted to some places of the Mediterranean seashore in France (Paulian and Baraud 1982), was recently observed at an altitude of 900 m at the eastern end of the Pyrenees (Jay-Robert unpubl.).

The mean northward shift in the predicted distributions reached ca. 13 km per decade under the A2 scenario and, for some species, the northern range boundary could move around 75 km per decade. An extensive analysis of recent changes in European butterfly communities suggests that these predictions are conservative (Devictor et al. 2012). Nevertheless, differences between A2 and B1 scenarios were slight and, for both scenarios, the mean change in regional compositions (50 × 50 km UTM grid cells) could exceed 20 % of species. Several core species—that can constitute more than 75 % of local dung beetle assemblages (Lumaret and Kirk 1991; Errouissi et al. 2004; Jay-Robert et al. 2008a)—would lose a large part of their current distribution (e.g. *O. fracticornis*, *O. joannae*, *O. lemur* or *O. similis*). Even if little is known about the respective functional efficiency of species in dung removal (Rosenlew and Roslin 2008), one may fear that the local disappearance of such very common species may induce a depletion of ecosystem functioning (Cardinale et al. 2006).

At intermediate latitude the northward shift of mesophilous species might be compensated by the arrival of more thermophilous ones. This replacement requires a very rapid response of populations (Parmesan and Yohe 2003), one that is questionable for low-fecundity taxa like *Bubas* sp., *Copris* sp. or *Gymnopleurus* sp. For most species, the potential gain of new territories would be concomitant to a significant loss of present habitats, and population dynamics could be weakened by this rapid turnover of favourable areas (Keith et al. 2008). Additionally, the migration towards these new favourable areas would require a good connectivity among pastured habitats (especially along the French Atlantic coast and the Rhone valley). The significance of the connectivity will depend on species characteristics. In Aphodiidae—the dominant group of dung beetles in northern Europe (Cabrero-Sañudo and Lobo 2003)—pasture specialist species had lower migration abilities than generalist species (Roslin 2000; Roslin and Koivunen 2001). Unfortunately, available scenarios forecast the continuation of the polarisation of cattle breeding during the twenty-first century, with intensification in favourable areas versus abandonment in harsh regions like southern mountain ranges (Schröter et al. 2005). This polarisation and several concomitant changes in practices (the stalling of cattle, the increasing using of parasiticides toxic for beetles…), that begun in the middle

of the twentieth century, were invoked to explain the decrease in dung beetle diversity which was already observed from northern latitudes to the Mediterranean region (Lumaret 1990; Biström et al. 1991; Barbero et al. 1999; Roslin 1999; Lobo 2001; Lobo et al. 2001; Carpaneto et al. 2007). Although Scarabaeidae appear to be less sensitive to habitat heterogeneity than Aphodiidae or Geotrupidae in southern Europe (Lobo et al. 1997b; Lobo and Martín-Piera 1999), the expansion of ungrazed wooded habitats could also severely limit the movements of beetles (Kadiri et al. 1997; Jay-Robert et al. 2008c) and exacerbate the role of barrier naturally played by longitudinal European mountain ranges (Jay-Robert et al. 1997).

In the Iberian Peninsula, separated from North Africa by the Strait of Gibraltar, the settling of a more thermophilous fauna would be probably more difficult and the shift in the distribution of mesophilous species should induce a significant drop in species richness. An early emergence in spring could allow insects to maintain local populations and limit the decline in species richness (Stefanescu et al. 2003), but nowadays adult Scarabaeidae have a typical spring-summer period of activity everywhere in Europe (Wassmer 1994; Jay-Robert et al. 2008a, b).

The extent of the faunistic changes forecasted in our study (and the insignificance of differences between A2 and B1 scenarios) should force breeding industry and conservationists to collaborate on a win–win strategy which associates grazing network (e.g. Natura2000 areas) and agroecological guidelines (which still remain to be designed). In that case, Scarabaeidae should succeed in adjusting their distribution to climate change and compensate for the local risk of rarefaction of mesophilous Aphodiidae and Geotrupidae species.

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