RESEARCH
SIGNPOST

8

The relationship between forecasted rarity and species richness values for Scarabaeidae and Aphodiinae species in France (Coleoptera, Scarabaeoidea)

Jorge M. Lobo[1], Pierre Jay-Robert[2] and Jean-Pierre Lumaret[2]
[1]Departamento de Biodiversidad y Biologia Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), C/ José Gutiérrez Abascal 2, 28006 Madrid, Spain
[2]UMR 5175, Département Dynamique des Systèmes Écologiques, Laboratoire de Zoogéographie, Université Montpellier 3, route de Mende, 34199 Montpellier cedex 5, France

Abstract

The distribution of rarity was predicted for Scarabaeidae and Aphodiinae in France using Generalized Linear Models and environmental variables as predictors. The entire French territory

Correspondence/Reprint request: Dr. Jorge Miguel Lobo, Departamento de Biodiversidad y Biologia Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), C/ José Gutiérrez Abascal 2, 28006 Madrid, Spain
E-mail: mcnj117@mncn.csic.es

was studied, divided into 301 0.72 × 0.36 degree grid squares, and models were developed using 66 grid squares previously identified as well-sampled. The first factor of a Principal Component Analysis conducted on the matrix of squares described by three rarity indices (number of rare species, sum of rarity scores, and mean of rarity scores) was used as a synthetic rarity value. Final models accounted for 67.3% and 69.2% of total deviance but with high mean jack-knife predictive errors of 77.6% and 45.8% for Scarabaeidae and Aphodiinae, respectively. For Scarabaeidae, rarity hotspots corresponded to diversity hotspots. In contrast, rarity and species richness were uncorrelated for Aphodiinae. We argue that different types of processes have contributed to create and maintain the current distribution of rare species in the two dung beetle groups. Warm-adapted Scarabaeidae and Aphodiinae rare species that have experienced a recent range expansion from southern refuges would be explained by current climatic factors. Contrariwise, those cold-adapted Aphodiinae rare species that recently suffered a range contraction would be less predictable by contemporary environmental variables.

Introduction

Conservation strategies and human-induced environmental changes motivate scientists to know and survey both population dynamics and the locations of those rare species that have restricted distribution because this type of species may be threatened and rapidly disappear [1-3]. Although regions with a higher number of species also usually contain many rare species [4-7], rarity and species richness often provide independent and complementary measures of biological diversity [5, 8-14]. The discrepancies in the geographical distribution of species richness and rarity are probably due to differences in the rates of extinction and speciation experienced by each group in every region [6, 15, 16]. Thus, to recognize the distribution of the areas with more rare species and to examine the relationship with species richness is a task of high concern for both biogeographical and conservation reasons.

Using range size as a criterion of rarity, the survey of rare species is frequently documented at the country level [17] in attempts: i) to locate the areas where these species are numerous, and ii) to identify the causes of these restricted distributions [10, 18-20]. Unfortunately, even in countries with a long tradition of naturalist studies, knowledge is not uniform across regions and taxa, and the patterns of distribution are frequently influenced by sampling effort bias since the information about rare species is quite insufficient [21, 22]. A strategy to overcome this lack of distributional information consists of the estimation of the probability of species occurrence using predictive model techniques running with presence-only data or presence/absence data [23-28]. Thus, to infer the distribution of a biodiversity attribute like rarity, it is necessary to overlap the

predicted individual distributions. Unfortunately, as rare species often are characterized by scarce geographical information, it is impossible to elaborate reliable individual models. But it is possible to estimate the distribution of rarity using synthetic indices applied to homogeneous taxonomical group levels (see Hortal and Lobo [29]). This procedure firstly needs to identify well-inventoried areas and subsequently examine if they represent the environmental heterogeneity of the considered region [30-33]. Finally, this biodiversity attribute can be extrapolated to the neighbouring poorly-inventoried regions using environmental predictors and modelling techniques [25, 26, 31, 34-41]. This strategy would yield results more quickly, while additional fieldwork could empirically validate the proposed models of distribution.

Thanks to a long-standing naturalist tradition, the taxonomy of Scarabaeidae and Aphodiinae has been studied for a long time in France [42, 43], and the distribution of species is relatively well known [44-46]. However, in a previous analysis [30] we showed that 78% of the French territory divided into 301 0.72 × 0.36 degree grid squares should be considered poorly surveyed. Using the previously recognized well-surveyed squares, the species richness distribution for both taxonomic groups has been estimated using environmental surrogates and generalized linear modelling techniques [40, 41]. In this paper, we do not aim to estimate the most relevant factors related to the distribution of species rarity, but only to forecast the rarity scores of Scarabaeidae and Aphodiinae for the whole territory of France. The so derived rarity distributions will be subsequently related with former species richness predictions to estimate the degree of spatial congruence among these two synecological variables for the studied taxonomical groups, discussing the probable causal processes behind obtained relationships.

Methods
Rarity index

The French database of Coleoptera Scarabaeoidea Laparosticti (191 species) is composed of 37,300 records distributed all over the French territory [44]. The French mainland and Corsica Island were divided into 301 [0.72 × 0.36] degree grid squares (about 2,229 km^2 each) (Fig. 1). An analysis of the asymptotic relationship between the number of species and the number of database records in the squares of each one of French biogeographic provinces (Atlantic, Continental, Mediterranean, Mountains, Corsica Island) allowed for the discrimination of 66 well inventoried squares (22% of 301; see Lobo et al. [30]). All the Scarabaeidae and Aphodiinae species listed in Lumaret [44] were used for calculations, except the chimera *Aphodius* (*Bodilus*) *arvernicus* Hoffman 1928 (Aphodiidae) [47]. In total, 48 Scarabaeidae species and 112 Aphodiinae were concerned.
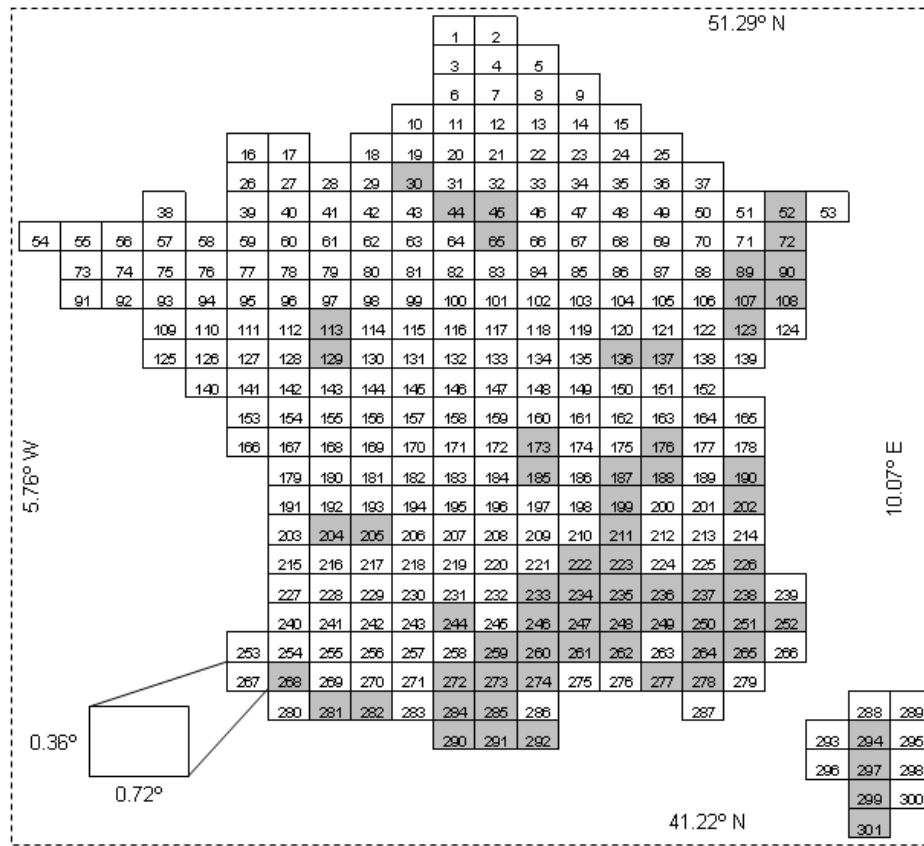
Figure 1. France mainland and Corsica Island divided into 301 squares of 0.72 × 0.36 degrees. Shaded squares are the 66 well-sampled grid squares [30].

Our aim was to identify the squares where most of the rarely observed species were concentrated (considering Scarabaeidae and Aphodiinae separately). For each square, a rarity value (*R*) was calculated (see Kier and Barthlott [48]) as:

$$R = \sum_{j=1}^{n} \frac{1}{Gi}$$

where *Gi* was the range size of species *i* and *n* the total number of species observed in the square; the value 1/*Gi* expressed the rarity score of each species *i*. In the present study, the species range size was the number of squares where the species was observed (from 1 to 301), while species rarity scores ranged from 1 to 0.003. As the rarity value *R* depends on the number of species in each square, we also calculated the mean rarity score of the species present in each square (*RM* = *R*/*n*). Lastly, as a similar *RM* score can be obtained with different proportions of restricted and widespread species [1], the number of rare species

has been also estimated (*RS*). For that, the species belonging to the first quartile of the distribution of rarity scores (1/*Gi*) were considered as rare and their number calculated for each square. In order to characterize each square by a unique rarity value pooling all the advantages of the three previous indices, a Principal Component Analysis was conducted on the matrix of the 66 well inventoried squares and the three formerly described indices. PCA is a powerful ordination method able to summarize in a few dimensions most of the variability of a matrix of quantitative descriptors [49]. The first factor was used as a synthetic index (*RI*) of the rarity value for each square.

Selected environmental variables

As the available biological data come from an extensive temporal period (more than 100 years) those explanatory variables related with land uses were avoided. Thus, for each grid square, six climate, two topographic, and two spatial variables were used. All variables were continuous and were standardised to a mean of zero and a standard deviation of one in order to eliminate the effect of differences in measurement scale. The sources and the method of obtaining this environmental and spatial information have been described in Lobo et al. [40]. The variables used here were: mean annual temperature (TM), annual temperature variation (TV), maximum monthly mean temperature i.e. temperature of July (T), minimum monthly mean temperature i.e. temperature of January (t), mean annual precipitation (P), annual precipitation variation (PV), mean elevation (E), altitude range (AR), central latitude (LAT), and central longitude (LON).

Model building

Generalized Linear models (GLMs) have been used to summarize the relationships between the rarity index (*RI*) and the above-mentioned explanatory variables [35, 50-53]. GLMs are an extension of linear models that allow for non-linearity in the data and also a wide range of model specification distributions other than the normal distribution of the random component [54]. In our case, the assumed relationship between the rarity value and the explanatory variables is logarithmic (the link function), with a Poisson error distribution for the rarity value. The rarity value in the 66 well-surveyed grid squares [30] was firstly related separately to each environmental variable, selecting either a linear, a quadratic, or a cubic function of each environmental variable in order to consider possible curvilinear relationships [55]. The goodness-of-fit for the competing functions was measured by the deviance statistic and the change in deviance tested by an F-ratio test [56, 57] with a 5% significance level. The obtained reduction in deviance was compared with a null model in which no explanatory variables were included in order to estimate

the reduction in deviance accounted by each model (a measure of the explained percentage of variability; see Dobson [57]).

A forward-stepwise procedure was used subsequently to enter the variables into the model [35, 51]. Firstly, the linear, quadratic, or cubic function of the variable that accounts for the most important change in deviance was selected for inclusion. Next, all the remaining variables were tested for significance, adding them sequentially, one by one. The procedure was iteratively repeated until no more statistically significant explanatory variables remained ($p < 0.05$). After each inclusion, the significance of the terms previously selected was also tested, submitting the new model to a backward selection procedure in order to exclude the terms that had become non-significant. The significance of all pairwise interaction terms between the explanatory variables (44 interaction terms) were also tested [34], adding them one by one to the model previously obtained and selecting they by a similar forward-backward procedure. This procedure was iteratively repeated until no more significant interaction terms remained. Lastly, the third-degree polynomial equation of the central latitude (Lat) and longitude (Lon) of each square was included in the model (Trend Surface Analysis [58]) because spatial structures can incorporate the effects caused by other historical, biotic, or environmental variables not otherwise taken into consideration [49]. Latitude and longitude were in UTM coordinates and centred on their respective means. We performed a backward stepwise regression with the nine terms of the equation as predictor variables and the rarity index (*RI*) as the dependent variable in order to remove the non-significant spatial terms. The significant spatial terms ($p < 0.05$) were retained and included in the previous model if they remain statistically significant. STATISTICA package [59] was used for all statistical computations.

Autocorrelation, residuals, and model validation

As most environmental variables are spatially autocorrelated on a geographical scale, broad scale spatial structure becomes an important source of information that must be taken into account to improve the predictive power of models [49, 60, 61]. When autocorrelated variables are used, it is critical to examine the spatial independence of errors [62, 63], so if residuals are spatially autocorrelated the model should probably be enlarged to include some spatially structured variables not otherwise taken into account by the model [61-63]. Thus, the autocorrelation of the residuals of the final model was checked by calculating Moran's *I* spatial autocorrelation statistic (lag distance of 80 km) with a Bonferroni-corrected significance level [62, 64].

The adequacy of the final model was improved by detecting the outliers that disproportionately influence the fit of the model, examining the standard errors of coefficients, plotting the residuals vs. the fitted predicted values,

plotting the residuals in a normal probability plot, and by examining the leverage of the observations (a measure of the distance of each observation from the centroid of the multi-dimensional space defined by the variables included in the model [35, 57]).

A jack-knife procedure was applied in order to validate the final model, so from the dataset of the 66 well-sampled grid squares, the model was recalculated 66 times leaving out one square in turn. Each one of the regression models based on the n-1 grid squares was then applied to that excluded square in order to predict rarity values for each one of the squares. The predictive power of the model was checked both by examining the correlation between the recorded and the jack-knife-predicted species richness, and by estimating the percentage error for each observation. The mean of the 66 estimates of error provides a measure of the prediction error associated with the model and data used.

A more extensive discussion of the statistical considerations contemplated for the construction of this model can be found in Lobo et al. [40, 41].

Results
Calculation of the rarity indices

The mean rarity scores for Scarabaeidae and Aphodiinae species were not significantly different (Table 1). Twelve Scarabaeidae species (first quartile of 48) with rarity scores higher than 0.07 and 29 Aphodiinae species (28 species from the first quartile of 112, plus the 29th whose value was identical to the 28th) with rarity scores higher than 0.11, were considered as rare species (Fig. 2).

Table 1. Mean rarity scores (± SD) for Scarabaeidae and Aphodiinae (Z values of Wilcoxon Matched Pairs Test with p associated values). R_{sp} is the mean rarity of the species of each taxonomic group in which the rarity score of each species was estimated as the inverse of number of 0.72×0.36 degree grid squares where the species was observed. R is the total rarity of the squares according to the index of [48], RM is mean rarity score of the species present in each square, and RS the number of rare species per square (those species belonging to the first quartile of the distribution of rarity scores).

	Species	Grid squares (n= 66)		
	R_{sp}	R	RM	RS
Scarabaeidae (n=48)	0.135 ± 0.040	0.463 ± 0.053	0.021 ± 0.002	0.818 ± 0.152
Aphodiinae (n=112)	0.127 ± 0.022	0.962 ± 0.074	0.026 ± 0.002	1.364 ± 0.241
Z	0.25	5.87	3.41	2.37
p	ns	<0.001	<0.001	0.02

The three rarity measurements calculated for the 66 well-surveyed grid squares were significantly higher for Aphodiinae than for Scarabaeidae species (Table 1). As expected, the three measurements were highly correlated in both taxonomic groups (Pearson correlation coefficients between 0.84 and 0.89 in the case of Scarabaeidae, and between 0.66 and 0.80 for Aphodiinae). The first PCA factor represented 91.5% and 81.5% of the variability of the three rarity measures for Scarabaeidae and Aphodiinae, respectively. The three rarity indices have high factor loadings both in the case of Scarabaeidae (between 0.95 and 0.97) and Aphodiinae (between 0.87 and 0.93).
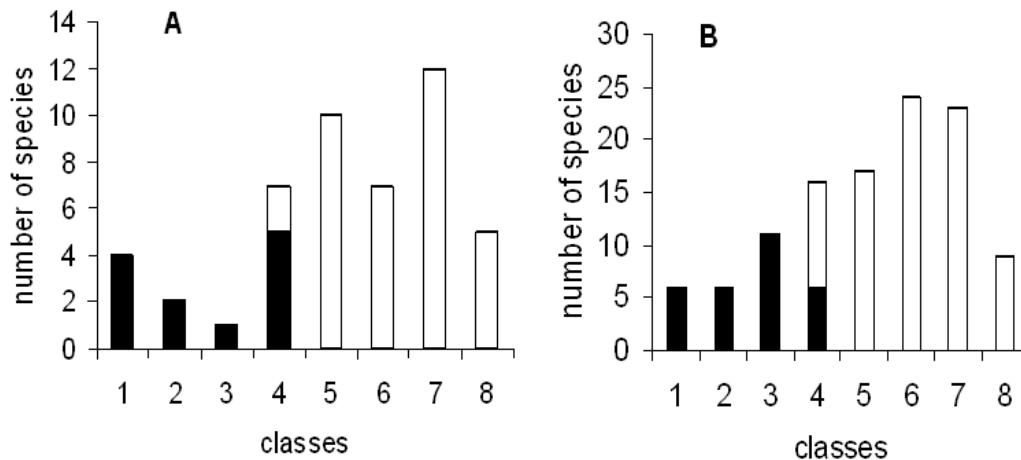

Figure 2. Distribution of Scarabaeidae (A) and Aphodiinae (B) species among decreasing geometric classes of rarity scores (1: rarity scores between 0.50-1.00; 2: 0.49-0.25; 3: 0.24-0.13; 4: 0.12-0.06; 5: 0.05-0.03; 6: 0.02-0.015; 7: 0.015-0.008; 8: < 0.008). The considered rare species are indicated in black.

The predictive model for Scarabaeidae

Among the environmental variables, only maximum monthly mean temperature (T; 54.5% of total deviance) and the annual precipitation variation (PV; 5.7% of total deviance) remained statistically significant in a stepwise procedure as predictors of the synthetic index *RI*. When environmental variables and all pairwise interaction terms between environmental and spatial variables were considered at the same time, a backward stepwise procedure selected a function with only three variables: maximum monthly mean temperature, the interaction between this variable and longitude (T × LON), and the interaction between annual precipitation variation and longitude (PV × LON). This model accounted for 67.30% of variation in the Scarabaeidae rarity synthetic index ($F_{(3, 62)} = 42.6$; $p < 0.001$). The addition of the nine terms of a third polynomial degree function of latitude and longitude allowed for a slight increase in the predictive capacity

of this model (to 69.91%), adding the longitude as significant variable ($F_{(4, 61)}$ = 35.4; $p < 0.001$).

The mean jack-knife error was relatively high (mean= 77.6%) but observed and jack-knife-predicted values were highly correlated (Pearson's correlation coefficient $r = 0.73$, $p < 0.0001$). The model did show neither special outliers nor peculiar structure in the distribution of residuals or in the relationship between residuals and fitted values. Residuals seemed not to be spatially autocorrelated as none of the Moran's I values in the different lag classes were significant at a 0.05 significance level with the Bonferroni correction. Thus, we can assume that no spatially structured variable remained to be included in the model. The predictive function generated a rarity geographical pattern in which the areas with highest rarity would be located in the southeastern French fringe under Mediterranean and alpine conditions and, to a lesser extent, along the northwestern and northeastern borders (Fig. 3A).

The predictive model for Aphodiinae

Among the selected explanatory variables, only the maximum monthly mean temperature (T; 22.5% of total deviance) remained statistically significant. Two significant interaction terms were added to this single variable: the product of annual precipitation variation and minimum monthly mean temperature (PV $\times$ t), and the interaction between altitude range and maximum monthly mean temperature (AR $\times$ T). This model accounted for 29.47% of total variability. However, two clear outliers greatly influenced this model. Grid squares 202 and 261, located in the Alps and the Mediterranean region, respectively, with positive standard residuals higher than 1.5 (2.70 and 3.28, respectively) and low leverage values (0.06 and 0.03) were excluded and the model was rebuilt (n=64).

In the new model, mean annual temperature (TM; 30.7% of total deviance) and the cubic function of annual temperature variation (TV; 15.9% of total deviance) were the only significant terms that remained significant in the stepwise procedure. The inclusion of interaction terms allowed the building of a model with five terms in which three interaction terms (LON $\times$ TM, LAT $\times$ TV, and E $\times$ TM) were added to the formerly selected variables increasing the explained variance to 69.22%. Lastly, the inclusion of the nine spatial terms of a third polynomial degree of latitude and longitude allowed the addition of the quadratic function of latitude (LAT +LAT^2) to the former model increasing the explained variability to 75.19%.

The mean jack-knife error of this model was 45.8% but again a high correlation between observed and jack-knife-predicted values appeared ($r = 0.81$, $p < 0.0001$). This model showed neither aberrant structure in the distribution of

residuals nor in the relationship between residuals and fitted values. Also, the residuals were not spatially autocorrelated. Thus, we assumed that no spatially structured variable remained to be included in the model. The predictive function generated a complex pattern in which the main high rarity regions were located the south-eastern Mediterranean region, the southern Atlantic and north-western borders, but also in the central mountainous regions (Fig. 3B).
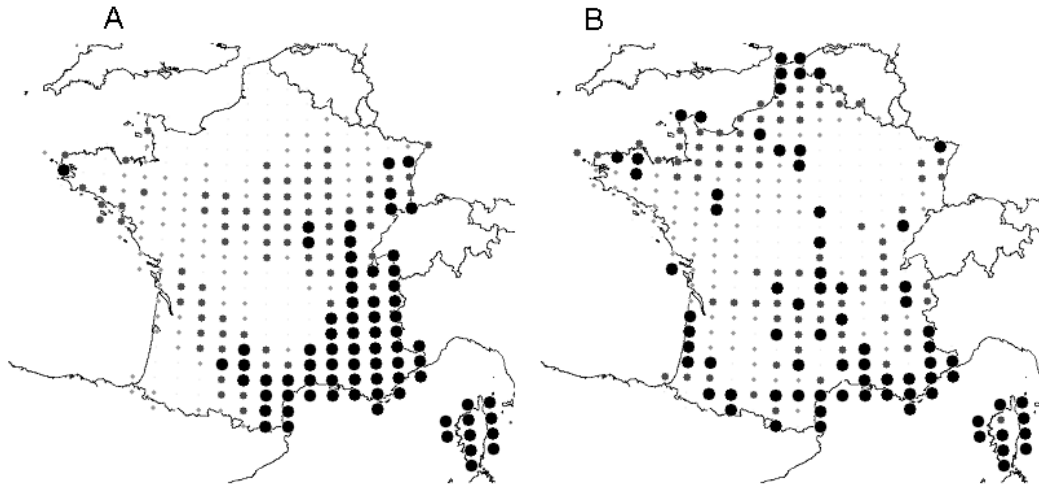

Figure 3. Predicted rarity values for Scarabaeidae (A) and Aphodiinae (B) in France and Corsica. Rarity scores were divided in four quartiles which differ in its size and grey tone (higher rarity scores are represented by bigger dark circles).
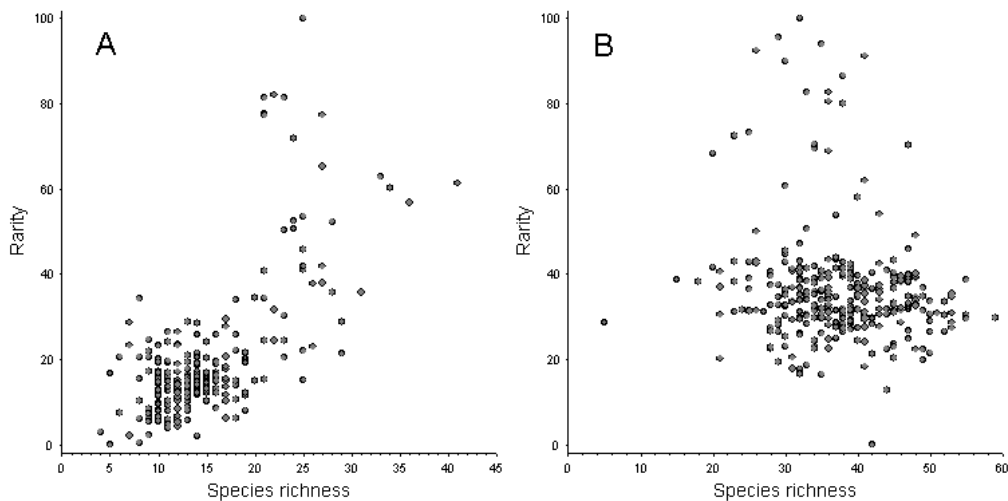

Figure 4. Relationships between Scarabaeidae (A) and Aphodiinae (B) predicted species richness and rarity scores for the 301 squares of 0.72×0.36 degrees of France. Rarity scores were rescaled at a 0-100 interval.

Species richness rarity relationships

Scarabaeidae species richness and rarity values were positively and significantly correlated both within the 66 well-surveyed squares ($r = 0.54$, $p < 0.0001$) and considering all predicted values ($r = 0.69$, $p < 0.0001$). Thus, richest squares generally comprised higher rarity scores (Fig. 4A). By contrast, rarity and species richness values were uncorrelated or negatively correlated in Aphodiinae (well-surveyed squares: $r = -0.20$, $p = 0.10$. All predicted squares: $r = -0.15$, $p = 0.01$). In this case, there were no correlation between species richness and rarity (Fig. 4B).

Discussion

Rarity may be related to a restricted geographic distribution, to peculiar habitat specificities, to small population sizes, or to a combination of these features [18]. Geographical rarity is always a relative concept because depends on the considered geographical extent (ultimately all the species are endemic of the Earth). On a wide geographical scale, the rarity measurement used in the present study can be considered as a measure of endemism richness [48, 65]. Hence, as the ranges of species are not considered in their whole, the estimated rarity calculated considering French distribution may not correspond with their complete geographical range size. A previous study established the geographic range size of Palaearctic dung beetles in six categories according to the percentage of the total western Palaearctic region area covered by the distribution range of each species [66]. The relationship between the species rarity in France and their complete geographic range size clearly shows that rarity at this small scale is correlated with the rarity estimated at a larger scale (Spearman rank correlation text, $rs = -0.43$, $p < 0.0001$). However, although all common French species have widely distributional ranges French rare species can have wide distribution range sizes (Fig. 5); 63% of species with rarity values higher than 0.80 belong to the sixth geographic range-size category of Lumaret and Lobo [66] (i.e. distribution areas over than 10% total area of the western Palaearctic region). How the extent dependence of rarity scores can affect our detected patterns? Some French squares with high rarity scores would have lower ones if species rarity was measured at a Palaearctic extent. Thus, the extent bias can affect the detected positive relationship between rarity and species richness in Scarabaeidae but not the lack of correlation in Aphodiinae.

Many Scarabaeidae and Aphodiinae species have probably high dispersal capacities (necessary to exploit ephemeral dung pat microhabitats), high tolerance to environmental variables and, consequently, wide macrohabitat requirements [67-70]. Broadly (and without any consideration for food availability), the local dung beetle assemblages are affected by both the

structure of the vegetation cover and by the soil type, each parameter acting in a similar way for a large majority of species: i) in Europe, forests are poor in dung beetles and most of the species observed in woodlands are common in pastures [68, 71-73]; ii) the poorly drained soils are unfavourable for many tunnelers and rollers (Scarabaeidae in the present study), which are burying species [72]. As the large size of grid squares (approximately 60 km $\times$ 30 km) might allow various environmental conditions (forest vs. pasture, well vs. poorly-drained soils etc.) to be represented in each square, one can assume that neither vegetation cover nor soil type were relevant variables in the present study.

If there was no relationship between rarity and endemism nor between rarity and habitat specificity, one can assume that French rarity was linked to: i) the species rarely observed in the local inventories because of small population sizes (life history traits) or because of sampling biases and/or, ii)
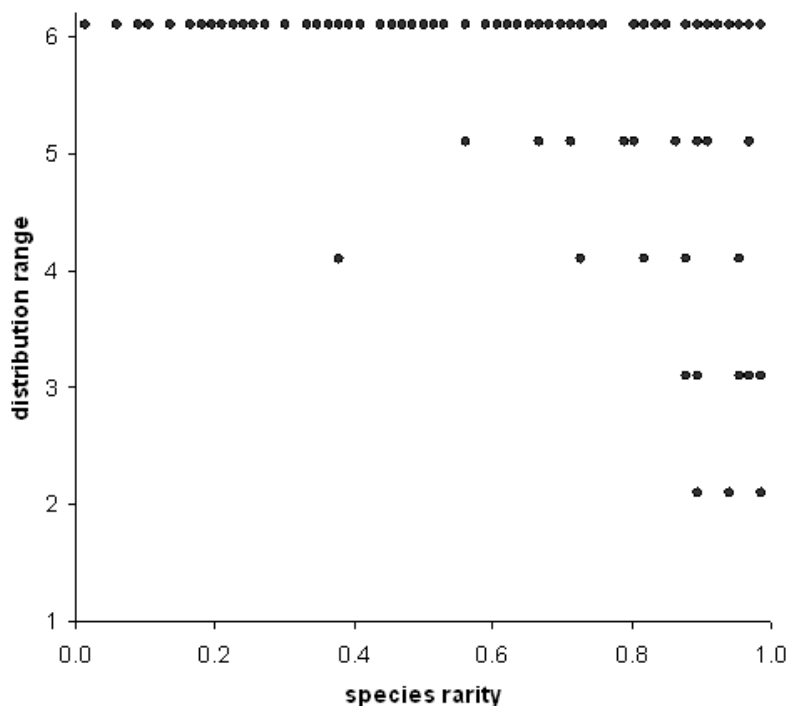

Figure 5. Relationship between the rarity scores of each French dung beetle species and their geographical range size. Rarity was estimated as the inverse of the relative frequency of each species according to the squares where they was observed over total French squares. Geographic range size correspond to six classes according to the percentage of the total western Palaearctic region area covered by the distribution range of each species (i.e. 1: species with a distribution area less or equal to 0.1% of the total area of the western Palaearctic. 6: species with a distribution area over than 10% total area of the western Palaearctic region; see Lumaret and Lobo [66]).

the species at the border of their geographic distribution, abundance and patch occupancy being widely believed to decline towards the edge of the geographical range of species ([74] and references therein). Some dung beetles are rare because they have specific ecological requirements, such as preferences for particular trophic resources. For example, *Onthophagus* (*Parentius*) *emarginatus* (Mulsant, 1842) feeds on dry pellets whereas *O.* (*Palaeonthophagus*) *vitulus* (Fabricius, 1766) only exploits hamster (*Cricetus cricetus* (Linnaeus, 1758)) pellets. Likewise, dung beetles may be located in very special places: *O.* (*Palaeonthophagus*) *semicornis* (Panzer, 1798) lives in rodent holes, *O.* (*Trichonthophagus*) *maki* (Illiger, 1803) exhibits kleptoparasitism behaviour in the brood balls of *Scarabaeus* species, and *Aphodius* (*Sigorus*) *porcus* (Fabricius, 1792) uses dung reserves buried by Geotrupidae. Some species also have very restricted periods of activity (e.g. the alpine species *Acrossus laticollis* (Baudi, 1870) is active only one month a year). These unique behaviours could systematically diminish the detectability of some species and could have biased samples [75, 76] because the survey of dung beetles is generally based on standardized trapping or on searching in natural pats deposited by animals. Rare species would require more intensive and diversified sampling to be conducted through direct observation instead of trapping, surveying year-round in a variety of microhabitats, and taking into account different kinds of trophic resources. Thus, rarity is always a difficult attribute to measure.

Although the obtained models have higher predictive errors than those previously obtained to estimate the distribution of Scarabaeidae and Aphodiidae species richness in France [40, 41], our methodological approximation highlights that it is possible to obtain reliable general pictures of the distribution of this synecological variable. Thus, in spite of methodological difficulties and statistical biases, the estimated distribution of rarity shows a very clear spatial pattern both for Scarabaeidae and for Aphodiinae. Scarabaeidae have their highest rarity scores at the southernmost border of the mainland and on Corsica Island, i.e. in the French part of the Mediterranean biodiversity hotspot [77, 78], but also in the western boundary with the Alps. As species richness and rarity scores are highly and positively correlated, this distributional pattern of rarity is very similar to the one depicted by the Scarabaeidae species richness [40]; the species richest areas generally also harbour more rare species. In this case, the increase in species richness is partially due to the addition of some narrowly distributed species to the general pool of widely distributed species. Scarabaeidae are generally warm-adapted species [72, 79-82] and the Mediterranean French region has the highest Scarabaeidae diversity due to the presence of rare thermophilous species at the northern border of their

range. Within this region, some territories such as Corsica and the western Mediterranean Alps have higher comparative rarity scores (Fig. 6A), probably due to their capacity to serve as refuges for species or to differentiate new taxa (endemism).

In contrast, rarity and species richness were not similarly distributed for Aphodiinae. The highest rarity scores for this group are also located in the Mediterranean region, but also in some Atlantic and mountainous zones located in the inner part of France. However, Aphodiinae species richness hotspots are located in the western head, in the southwestern and in the northeastern part of the territory [41]. The weak but negative relationship between Aphodiinae species richness and rarity highlights that the richest areas do not necessarily contain more rare species, making it possible to find poor species squares with high rarity scores probably by historical reasons or because these rare species have specific environmental tolerances with regard to the general environmental adaptations of Aphodiinae. This subfamily is an essentially Holarctic group composed of cool-adapted species which dominate the communities of north temperate regions [71, 83-85]. However, the comparative highest French Aphodiinae rarity scores are mainly distributed across the Mediterranean regions (Fig. 6B), showing that this territory constitutes the area in which one can find the main pool of rare species belonging to some warm temperate lineages [86-89].
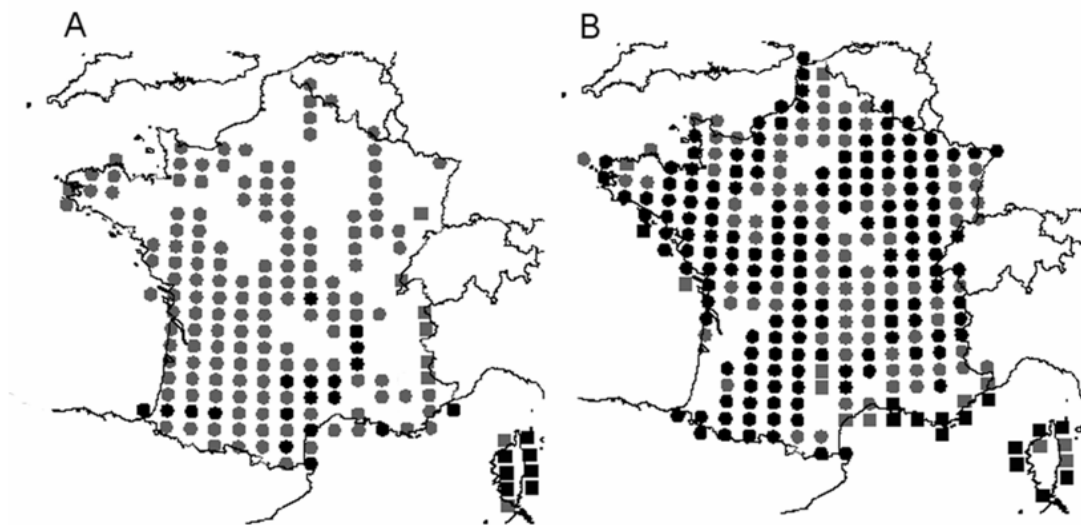

Figure 6. Cells in which species richness scores dominate over rarity ones (black circles = ≥25%, grey circles = 10%-25%) and cells in which rarity dominates over species richness (black squares = ≥25%, grey squares = 10%-25%). Both species richness and rarity scores are rescaled at a 0-100 range. A = Scarabaeidae, B = Aphodiinae.

Our study supports previous evidence [5, 8-11, 13, 14] emphasizing that species richness and rarity are not universally correlated depending on the phylogenetic similarity between the species of the taxonomical group, their main adaptations, the general environmental conditions of the considered territory and its extent. The correlation between these two important synecological variables does not imply that a selection of richness priority areas allows for the correct representation of rare species [14, 15]. As has been frequently stated, conservation decisions should be based on the complementary principle which considers the identity of each one of the species. However, although knowing the geographical distribution of species richness and rarity hotspots is not very useful for conservation purposes, this is an outstanding biogeographical task.

Species richness is the consequence of the coincidence in the geographic ranges of species, and the agreement between species richness and rarity geographical patterns imply that the processes that create and maintain the distribution of rare species are probably similar to the processes implied for most of the species. This happens, although rich places with many narrow-ranged species can possess particular conditions such as high altitudinal heterogeneity [12, 90]. Many different factors have been proposed to explain the current distribution of species richness (see Whittaker et al. [91] and references therein) and we argue that different types of processes have created and maintained the current distribution of rare species in the two studied dung beetle groups, probably as consequence of differences in their dispersal ability and sensitivity to different key factors.

Water, energy or temperature factors are especially relevant to explain species distributions [92, 93]. Warm-adapted Scarabaeidae species would mainly be conditioned by the existence of favourable temperature condition variables [31, 40] and the strength of this restriction seems to condition equally all the species of this group. On the contrary, Aphodiinae species constitute a group in which most basal lineages are probably originated in northern Mesozoic territories under relatively cold conditions, while some others would have originated during the Tertiary under warmer environmental conditions [88, 89]. In this case, the explanation of the current distribution of rare species depends on several complex factors, e.g. the capacity of some areas to serve as refuges during the glacial-interglacial cycles both to warm- and cold-adapted species. The first ones would currently attain their northern distribution limits in the French areas under Mediterranean climatic conditions and their distribution can probably also be partially explained by temperature or energy related factors (see Lobo et al. [41], and Cabrero-Sañudo and Lobo [90, 94]). However, the current distribution of the Aphodiinae rare species adapted to cold conditions would

be the consequence of the contraction of their distribution area after the coming of warmer environmental conditions. For example, the rare alpine species *Amidorus immaturus* (Mulsant, 1842) is present in the last 100 meters under the summit of the Mont Ventoux (1900 m elevation). The mixture of both patterns within the same taxonomic group would cause the lack of correlation between species richness and rarity.

Assuming that the last Pleistocene events are the main contributing forces able to explain current European biodiversity patterns [95-97], we should concur that extinction has probably been more outstanding than speciation in generating current biodiversity patterns. In this scenario, the species with comparatively larger distributions and wider environmental adaptations - as Scarabaeidae species - should have more possibilities to persist [98], being their distributions explained by current environmental factors that are able to limit their range expansion. In the case of dung beetles, we suggest that those warm-adapted rare species that have experienced a recent range expansion from southern refuges from the last glacial period can also be explained by these climatic factors. Contrariwise, the cold-adapted rare species that recently suffered a range contraction would be less predictable by contemporary environment variables, making it necessary to invoke contingent geographical and historical factors to explain their current distribution.

Acknowledgments

References

1. Gaston, K.J. 1994, Rarity. Chapman and Hall, Great Britain, London
2. Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., and Williams, S.E. 2004, Nature, 427, 145.
3. Gaston, K.J., and Spicer, J.I. 2001, Global Ecol. Biogeogr., 10, 179..
4. Blackburn, T.M., and Gaston, K.J. 1996, Phil. Trans. R. Soc. Lond. B, 351, 897.
5. Kerr, J. T. 1997, Conserv. Biol., 11, 1094.
6. Domínguez-Lozano, F., and Schwartz, M.W. 2005, Biol. Conserv., 126, 146.
7. Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W., and Shugart, H.H. 2005, Nature, 440, 212.
8. Prendergast, J.R., Wood, S.N., Lawton, J.H., and Eversham, B.C. 1993, Biodiv. Letters, 1, 39.

9. Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C., and Pressey, R. 1996, Conserv. Biol., 10, 155.
10. Arita, H., Figueroa, F., Frisch, A. Rodríguez, P., and Santos-del-Prado, K. 1997, Conserv. Biol., 11, 92.
11. Hughes, T.P., Bellwood, D.R., and Connolly, S.R. 2002, Ecology Letters, 5, 775.
12. Jetz, W., Rahbek, C., and Colwell, R.K. 2004, Ecology Letters, 7, 1180.
13. Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J., and Owens, I.P.F. 2005, Nature, 436, 1016.
14. Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgley, R.S., Rasmusen, P.C., Ding, T.S., Bennetts, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L., and Owens, I.P.F. 2006, *Nature*, 444, 93.
15. Ricketts, T. H. 2001, Anim. Biodiv. Conserv., 24, 91.
16. Schwartz, M.W., and Simberloff, D. 2001, Taxon size predicts rates of rarity in vascular plants. Ecol. Lett., 4, 464.
17. Venevsky, S., and Venevskaia, I. 2005, Biol. Conserv., 124, 235.
18. Rabinowitz, D., Cairns, S., and Dillon, T. 1986, Conservation Biology: the science of scarcity and diversity, M. E. Soulé, (Ed, Sinauer Associates, Massachusetts, Sunderland, 182.
19. Gregory, R.D., and Gaston, K.J. 2000, Oikos, 88, 515.
20. Lowry, E., and Lester, S.E. 2006, J. Biogeogr., 33, 1975.
21. Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C., and Gibbons, D. W. 1993, Nature, 365, 335.
22. Gaston, K.J. 1996, Biodiversity. A Biology of Numbers and Difference, K.J. Gaston, (Ed.), Blackwell Science, Great Britain, Oxford, 77.
23. Mitchell, N.D. 1991, J. Roy. Soc. New Zeal., 21, 13.
24. Pereira, J. M. C., and Itami, R. M. 1991, Photogramm. Eng. Rem. S., 57, 1475.
25. Buckland, S.T., and Elston, D.A. 1993, J. Appl. Ecol., 30, 478..
26. Iverson, L.R., and Prasad, A. 1998, Divers. Distrib., 4, 49.
27. Parker, V. 1999, S. Afr. J. Zool., 34, 39.
28. Peterson, A.T., Soberón, J., and Sánchez-Cordero, V. 1999, Science, 285, 1265.
29. Hortal, J., and Lobo, J.M. 2006, Biodiversity Informatics, 3, 16.
30. Lobo, J.M., Lumaret, J.P., and Jay-Robert, P. 1997, Ann. Soc. Entomol. Fr., 33, 129.
31. Lobo, J.M., and Martín-Piera, F. 2002, Conserv. Biol., 16, 158.
32. Hortal, J., and Lobo, J.M. 2005, Biodiv. Conserv., 14, 2913.
33. Romo, H., García-Barros, E., and Lobo, J.M. 2006, Ecography, 29, 873.
34. Margules, C.R., Nicholls, A.O., and Austin, M.P. 1987, Oecologia, 71, 229.
35. Nicholls, A.O. 1989, Biol. Conserv., 50, 51.
36. Walker, P.A. 1990, J. Biogeogr., 17, 279.
37. Carpenter, G., Gillison, A.N., and Winter, J. 1993, Biodiv. Conserv., 2, 667.
38. Hortal, J., Lobo, J.M., and Martín-Piera, F. 2001, Biodiv. Conserv., 10, 1343.
39. Pearce, J., and Ferrier, S. 2001, Biol. Conserv., 98, 33.

40. Lobo, J.M., Lumaret, J.P., and Jay-Robert, P. 2002, Global Ecol. Biogeogr., 11, 265.
41. Lobo, J.M., Jay-Robert, P., and Lumaret, J.P. 2004, Ecography, 27, 145.
42. Paulian, R., and Baraud, J. 1982, Faune des Coléoptères de France. II. Lucanoidea et Scarabaeoidea. Lechevalier, France, Paris
43. Baraud, J. 1992, Coléoptères Scarabaeoidea d'Europe, Faune de France 78. Fédération Française des Sociétés de Sciences Naturelles, France, Paris, and Société Linnéenne de Lyon, France, Lyon
44. Lumaret, J.P. 1990, Atlas des Scarabéides Laparosticti de France. Secrétariat Faune - Flore / MNHN, Paris.
45. Lumaret, J.P., Lobo, J.M., and Jay-Robert, P. 1996, Catalogue et Atlas des Scarabéides Laparosticti endémiques de France. Service du Patrimoine Naturel / IEGB / MNHN – OPIE, Paris.
46. Cabrero-Sañudo, F.J., and Lobo, J.M. 2003, Biodiv. Conserv., 12, 147.
47. Bordat, P. 1999, B. Soc. Entomol. Fr., 104, 343.
48. Kier, G., and Barthlott, W. 2001, Biodiv. Conserv., 10, 1513.
49. Legendre, P., and Legendre, L. 1998, Numerical Ecology. Elsevier, The Netherlands, Amsterdam.
50. Austin, M.P., Nicholls, A.O., and Margules, C.R. 1990, *Ecol. Monogr.*, 60, 161.
51. Austin, M.P., Pausas, J.G., and Nicholls, A.O. 1996, Austr. J. Ecol., 21, 154.
52. Heikkinen, R.K., and Neuvonen, S. 1997, Biodiv. Conserv., 6, 1181.
53. Guisan, A., Edwards, T.C., and Hastie, J.T. 2002, Ecol. Model., 157, 89.
54. Crawley, M.J. 1993, GLIM for Ecologists. Blackwell Scientific Publications, Great Britain, Oxford.
55. Austin, M.P.1980, Vegetatio, 42, 11.
56. McCullagh, P., and Nelder, J.A. 1989, Generalized Linear Models. Chapman & Hall, Great Britain, London
57. Dobson, A.J. 1990, An introduction to Generalized Linear Models. Chapman & Hall, Great Britain, London.
58. Legendre, P. 1993, Ecology, 74, 1659.
59. StatSoft Inc. 1999, STATISTICA for Windows. Computer program manual. OK, Tulsa
60. Smith, P.A. 1994, Global Ecol. Biogeogr., 4, 47.
61. Wagner, H.H., and Fortin, M.J. 2005, Ecology, 86, 1975.
62. Cliff, A.D., and Ord, J.K. 1981, Spatial processes. Models and Applications. Pion, Great Britain, London
63. Odland, J. 1988, Spatial Autocorrelation. Sage Publications, CA, Newbury Park.
64. Sawada, M. 1999, B. Ecol. Soc. Am., 80, 231.
65. Freitag, S., and Van Jaarsveld, A. S. 1997, Biodiv. Conserv., 6, 211.
66. Lumaret, J.P., and Lobo, J.M. 1996, Biodiv. Lett., 3, 192.
67. Hanski, I., and Cambefort, Y. 1991, Dung Beetle Ecology, I. Hanski and Y. Cambefort, (Eds.), Princeton University Press, New Jersey, Princeton, 330.
68. Wassmer, T. 1995, Acta Oecol., 16, 461.
69. Lobo, J.M., Sanmartín, I., and Martín-Piera, F. 1997, Elytron, 11, 71.
70. Lobo, J.M., and Martín-Piera, F. 1999, Acta Oecol., 20, 587.

71. Hanski, I. 1991, Dung Beetle Ecology, I. Hanski and Y. Cambefort, (Eds.), Princeton University Press, New Jersey, Princeton, 75.
72. Lumaret, J.P., and Kirk, A.A. 1991, Dung Beetle Ecology, I. Hanski and Y. Cambefort, (Eds.), Princeton University Press, New Jersey, Princeton, 97.
73. Kadiri, N., Lobo, J.M., and Lumaret, J.P. 1997, Acta Oecol., 18, 107.
74. Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M., and Lawton, J.H. 2000, J. App. Ecol., 37, 39.
75. Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E., and Pollock, K.H. 1998, Ecology, 79, 1018.
76. Yoccoz, N.G., Nichols, J.D., and Boulinier, T. 2001, Trends Ecol. Evol., 16, 446.
77. Blondel, J., and Aronson, J. 1999, Biology and Wildlife of the Mediterranean Region. Oxford University Press, Great Britain, Oxford.
78. Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., and Kent, J. 2000, Nature, 403, 853.
79. Halffter, G. 1976, Folia Entomol. Mex., 35, 1.
80. Cambefort, Y. 1991, Dung Beetle Ecology, I. Hanski and Y. Cambefort, (Eds.), Princeton University Press, New Jersey, Princeton, 51.
81. Lobo, J.M., and Halffter, G. 2000, Ann. Entomol. Soc. Am., 93, 115.
82. Errouissi, F., Jay-Robert, P., Lumaret, J.P., and Piau, O. 2004, Ann. Entomol. Soc. Am., 97, 701.
83. Jay-Robert, P., Lobo, J.M., and Lumaret, J.P. 1997, Arct. Antarct. Alp. Res., 29, 196.
84. Lobo, J.M., and Davis, A.L.V. 1999, Divers. Distrib., 5, 91.
85. Lobo, J.M. 2000, Can. Entomol., 132, 307.
86. Dellacasa, G., Bordat, P., and Dellacasa, M. 2001, Mem. Soc. Entomol. It., 79, 1.
87. Krell, F.T., Krell-Westerwalbesloh, S., Weiss, I., Eggleton, P., and Linsenmair, K.E. 2003, Ecography, 26, 210.
88. Cabrero-Sañudo, F.J., and Zardoya, R. 2004, Mol. Phyl. Evol., 31, 1084.
89. Cabrero-Sañudo, F.J. 2007, Syst. Entomol., 32, 156.
90. Cabrero-Sañudo, F.J., and Lobo, J.M. 2006, J. Biogeogr., 33, 1021.
91. Whittaker, R.J., Nogués-Bravo, D., and Araújo, M.B. 2007, Global Ecol. Biogeogr., 16, 76.
92. Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., and Turner, J.R. 2003, Ecology, 84, 3105.
93. Kaspari, M., Ward, P.S., and Yuan, M. 2004, Oecologia, 140, 407.
94. Cabrero-Sañudo, F.J., and Lobo, J.M. 2003, Graellsia, 59, 166.
95. Bennet, K.D., Tzedakis, P.C., and Willis, K.J. 1991, J. Biogeogr., 18, 103.
96. Brewer, S., Cheddadi, R., De Beaulieu, J.L., Reille, M., and Data Contributors. 2002, Forest Ecol. Manag., 156, 27.
97. Hewitt, G. 2000, Nature, 405, 907.
98. Gaston, K.J. 1998, Philos. T. Roy. Soc. B, 353, 219.