



# Spatial distributions of European Tenebrionidae point to multiple postglacial colonization trajectories

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Many studies have found that species richness in the Western Palaearctic follows a latitudinal trend, yet the importance of geographical and ecological factors in shaping species ranges remains obscure. In this article, we present geographical patterns of darkling beetles (Tenebrionidae), a species-rich group of arthropods. We relate the spatial distributions of species, instead of simply species richness, to spatial and climatic gradients, and test the effects of area (by species–area relationships), latitude (by various climatic gradients) and environmental diversity (by elevation) using simultaneous autoregressive models to identify major correlates of species richness. We then use nestedness and co-occurrence analyses to identify glacial refugial centres and postglacial dispersal trajectories responsible for current species ranges. Our results indicate the presence of two refugial centres (in the Iberian and Balkan peninsulas) that appear to have been particularly important in shaping extant tenebrionid ranges. Northern countries were selectively colonized by more tolerant and, possibly, more mobile species, which survived in southern refugia during the Pleistocene glacial maxima, whereas the low dispersal capabilities of many species that evolved in these southern isolated areas prevented their spread northwards. High levels of endemism recorded in Spain and Sardinia suggest that the faunas of these regions originated during the Tertiary period and have remained substantially isolated. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **105**, 318–329.

**ADDITIONAL KEYWORDS:** endemics – latitudinal gradient – Pleistocene refugia – spatial autoregression – species–area relationship.

## INTRODUCTION

Many studies have identified latitudinal trends in the species richness of animals and plants in Europe, with the highest richness at lower latitudes (e.g. Schuldt & Assmann, 2009; Ulrich & Fiera, 2009; Bąkowski, Ulrich & Laštůvka, 2010). However, latitude is not the controlling factor in itself, but a proxy for a number of variables that include both climatic gradients and the effect of historical factors, for instance glaciations (Willig, Kaufman & Stevens, 2003; Mittelbach *et al.*, 2007; Lomolino *et al.*, 2010). Rosenzweig (1995) and Lomolino *et al.* (2010) pointed

to area and climate as major predictors of large-scale variation in the species richness of animals and plants, with latitude being a surrogate of diverse climatic variables. Recent studies (Currie *et al.*, 2004; Hawkins *et al.*, 2007; Ulrich & Fiera, 2009; Bąkowski *et al.*, 2010) have identified, in particular, temperature and precipitation gradients as major drivers of species richness. However, most research dealing with the latitudinal diversity gradient has focused on plants and vertebrates (Lomolino *et al.*, 2010), and large-scale analyses of insect distribution patterns are still rare (Diniz-Filho, De Marco & Hawkins, 2010). Studies dealing with latitudinal gradients typically have been based on species richness patterns, without regard to species identity (cf. Kreft, Sommer

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& Barthlott, 2006). Thus, the importance of climatic, geographical and ecological factors in shaping the ranges of individual species remains obscure (cf. Ulrich, Bąkowski & Laštůvka, 2011). Previous work has shown that species range sizes are positively correlated with regional abundance (Huston, 1999) and dispersal potential (Rundle, Bilton & Foggo, 2007; but see Thieltses *et al.*, 2011). Because species abundance and dispersal are linked to environmental variables, particularly to climatic ones, we might expect a link between the spatial distributions of individual species and environmental gradients.

The other important factor that influences spatial distribution is ecological history. The last glaciation events and the subsequent recolonization routes have had important impacts in determining large-scale species range size distributions in Europe. European Pleistocene refugia, such as the Iberian, Italian and Balkan peninsulas with their surrounding islands, were both centres of speciation and sources of recolonization (e.g. Hewitt, 1999; Ribera & Vogler, 2004; Dapporto *et al.*, 2009, 2011). Both processes should have had a major impact on the current spatial distributions of plant and animal species across Europe and should have introduced observable gradients in species richness. However, because of the southern location of these Pleistocene refugia, their importance cannot be disentangled from current ecological factors associated with latitude in a simple manner.

In this article, we present a study of the geographical patterns of European tenebrionid beetles (Coleoptera: Tenebrionidae), a species-rich group of arthropods, based on high-quality species lists of European countries and major islands.

Tenebrionids occur in a great variety of habitats in all biogeographical regions, and are ideal objects for large-scale studies of ecological biogeography (Fattorini, 2008). They are primarily saprophagous beetles, with striking adaptations to water collecting and retention, and they are also speciose and abundant in isolated and hostile environments, such as deserts and islands, where other insect groups may be rare (Fattorini, 2008). Most Tenebrionidae are also characterized by flightlessness. As the vagility of flightless beetles is greatly reduced by their inability to fly, tenebrionids are a group of great interest in historical biogeography (Fattorini, 2000).

In this article, we investigate the tenebrionid distribution in Europe, focusing on the following questions: (1) what did the present-day pattern in tenebrionid biodiversity in Europe cause?; (2) where did Tenebrionidae survive during Quaternary glaciations?; and (3) what colonization routes did they use to expand their distribution in the Western Palaearctic?

To answer these questions, we first related species spatial distributions with area and climatic gradients.

We then undertook species-specific analyses of range size distributions to uncover the basic processes that have shaped continental-wide spatial distributions. In particular, we tested the following three predictions:

1. If glaciated areas were recolonized from southern refugia, we should see a gradient in species richness in which northern countries are increasingly species poor and where the species composition of northern countries forms subsets of the composition of southern countries. Such a pattern is called nested (Atmar & Patterson, 1993), and nestedness analysis has been proven to be a tool for the analysis of gradients in colonization and extinction (cf. Ulrich, Almeida-Neto & Gotelli, 2009). A nested pattern of species range sizes also implies that southern European species might either be widespread throughout Europe or restricted to southern Europe. Northern European species should have wide range sizes in the vast majority.
2. Continuous colonization from postglacial refugia should also result in coherent range sizes centred in southern European countries. Gaps in the spatial distribution might indicate postglacial regional extinction (Ulrich *et al.*, 2009). Occurrences outside the major range size, in turn, point to long-distance dispersal or the existence of glacial refugia in these places.
3. Species with restricted ranges are probably more influenced by environmental factors that operate on a local or regional scale, whereas widespread species should be less affected by such regional factors (e.g. Brown, 1995; Jetz & Rahbek, 2002). Thus, we predict that northern countries should be colonized by ecologically more tolerant species with wider ecological ranges.

## MATERIAL AND METHODS

### BIOLOGICAL AND DISTRIBUTIONAL DATA

We considered the faunal composition of 1491 species and subspecies of Tenebrionidae from 63 European countries and larger islands as defined in the Fauna Europaea project (<http://www.faunaeur.org>). Although there are obvious faunal links between the South European and North African countries, we did not include North African countries in our analyses because their faunas are still poorly known.

Offshore islands (such as the small islands surrounding Sicily, the Tuscan Islands, etc.), which are aggregated to adjacent mainlands or major islands in the Fauna Europaea, and hence their faunas, were also not considered in this study. A list of main references used to compile a matrix of occurrence of each species/subspecies in each country/island is given in Appendix S1 (see Supporting Information).

The final matrix of 1478 native species/subspecies (13 cosmopolitan species excluded, see below) is given as Appendix S2 (see Supporting Information).

It is difficult to evaluate the completeness of these taxonomic inventories. We used a very conservative approach and omitted all countries for which no recent checklists were available or which were considered not to be adequately sampled by expert taxonomists (see Acknowledgements). In particular, data for Andorra, the Faroe Islands, the Channel Islands, Gibraltar, Northern Ireland, Iceland, Liechtenstein, Monaco, Svalbard & Jan Mayen, Franz-Josef Land, the Kaliningrad region, Novaya Zemlya, San Marino and Vatican City were considered to be more or less incomplete or unreliable. We excluded these countries/islands from our environmental modelling. In turn, we included some non-European areas, notably the Macaronesian Islands (Canary Islands, Azores and Madeira). These archipelagos certainly pertain to the Western Palaearctic and have strong biogeographical similarities with Europe. In total, we retained 49 countries and major islands (Appendix S3, see Supporting Information).

As for most arthropod groups, fine-grained distribution data are unavailable for tenebrionids. However, previous work (e.g. Ulrich & Buszko, 2003; Baselga, 2008; Ulrich & Fiera, 2009; Bąkowski *et al.*, 2010) has shown that even coarse-grained data (whole-country species richness and climate variables) are able to identify major environmental correlates of animal species richness (see also Hortal, 2008). Keil & Hawkins (2009) tested whether broad-scale patterns of species richness are robust to the violation of constant grain size, and found that country-based models might yield weaker associations between species richness and environmental predictors. For the groups analysed by these authors, the variables entering the models and their respective parameters were very similar between grid and country models. Therefore, models fitted with country inventories are an acceptable tool for describing broad-scale diversity patterns when more precise data are lacking.

An impressive number of European tenebrionids are classified as subspecies. Indeed, the current taxonomic dividing line between species and subspecies, as applied to the tenebrionids of Europe, is arguably arbitrary, and the exclusion of subspecies could result in a significant underestimation of endemic tenebrionid diversity (cf. Fattorini, 2006, 2007, 2008, 2009). Thus, we considered both species and subspecies as 'evolutionarily significant units' (Ryder, 1986) and counted terminal taxonomic units irrespective of their taxonomic rank (species or subspecies). Species and subspecies are referred to as 'species' for simplicity.

Tenebrionid systematics has changed radically since the 1970s, with the inclusion of several lineages previously assigned to other families or even regarded as families in their own right (see Fattorini, 2002). The present article includes the former family Lagriidae as a subfamily within the Tenebrionidae. However, we did not include Alleculinae (formerly considered as a separate family of winged and flower-visiting beetles) because distributional data for alleculines are definitively less reliable than those obtained for the other Tenebrionidae.

There are various tenebrionid species that are synanthropic, being associated with human food, and which have become cosmopolitan or subcosmopolitan (e.g. various species belonging to the genera *Tenebrio*, *Tribolium*, *Alphitobius*, *Alphitophagus*, *Latheticus*, etc.). Therefore, it can be assumed that their distribution in Europe is strongly dependent on human activities. Therefore, we excluded these species from our analyses because they can artificially inflate the values of species richness. Likewise, we did not consider citations of certain species as a result of recent and documented introductions. Finally, we excluded doubtful data because of taxonomic problems, misidentifications or ancient unconfirmed records.

## STATISTICAL ANALYSES

### *Correlates of species richness*

Apart from country/island area, we considered average annual precipitation ( $P_{\text{mean}}$ ), average annual temperature ( $T_{\text{mean}}$ ), yearly temperature difference ( $\Delta T = T_{\text{July}} - T_{\text{January}}$ , where  $T_{\text{July}}$  is the mean temperature in July and  $T_{\text{January}}$  is the mean temperature in January) and average number of days with temperatures below zero ( $N_{T<0}$ , an estimate of winter length) (see Ulrich & Fiera, 2009). Finally, we also considered the quotient of highest elevation through country/island area as a rough measure of topographical and environmental diversity (Ricklefs, Qian & White, 2004; Ulrich & Fiera, 2009). To assess which variables best correlated with tenebrionid richness, we used spatial autoregressive models (Lichstein *et al.*, 2002; Rangel, Diniz-Filho & Bini, 2006; Beale *et al.*, 2010). To account for spatial autocorrelation, we calculated, for each country, the latitude and longitude of its geographical centroid. Centroids were estimated from multiple longest diagonals using Google Earth. Tenebrionid species richness and climate data were significantly spatially autocorrelated (Moran's  $I$  for  $S$ ,  $N_{T<0}$  and  $\Delta T$  at the first distance class:  $P_{I=0} < 0.05$ ). Most studies that have investigated competing hypotheses to predict species richness over broad spatial scales have used ordinary least-squares (OLS) regressions (e.g. Kerr, Southwood & Cihlar, 2001; Rahbek & Graves, 2001; Ribera, Foster & Vogler,

2003; Patten, 2004). However, failure to incorporate the spatial structure of the data into a model may affect the efficiency of OLS regression estimates, leading to misleading fitting measures and incorrect assessment of the relative importance of the variables used as predictors (Legendre *et al.*, 2002). In particular, the effects of covariates, which are themselves autocorrelated, tend to be exaggerated (Lichstein *et al.*, 2002; Tognelli & Kelt, 2004). Therefore, we applied a generalized least-squares estimation for autoregressive models as implemented in the Spatial Autocorrelation Model (SAM v. 3.0) package of Rangel *et al.* (2006). To estimate the relative influence of each variable, we used squared semi-partial correlations between the variables and applied the corrected Akaike information criterion (AICc) to select the best-fitting model. Species richness and area were log transformed to accommodate for a power function relationship (Rosenzweig, 1995; Drakare, Lennon & Hillebrand, 2006).

#### *Range size analyses*

We used different types of analysis to test our three predictions.

*Prediction 1.* We used nestedness and co-occurrence analyses to assess whether the species occurrences in northern areas are subsets of species occurrences of the southern areas assumed to have acted as refugial/recolonization centres. To assess the degree of nestedness, we used the temperature metric *MT* (Atmar & Patterson, 1993) because the weighed distance concept that is inherent in this metric seems to be particularly able to deal with large-scale spatial datasets (Ulrich *et al.*, 2009). *MT* has recently been criticized for having unfavourable type I error probabilities (Almeida-Neto *et al.*, 2008). However, in biogeographical gradient analyses, where the same matrix is sorted according to different environmental gradients, probability levels are of minor importance and do not outweigh the advantages of *MT* (cf. Santos *et al.*, 2010). We further used species co-occurrence analysis to infer whether range sizes are randomly distributed or whether they are segregated. Segregation was inferred using the *C* score (Stone & Roberts, 1990) which counts the matrix-wide number of checkerboards ( $\{1,0\},\{0,1\}$  submatrices). Significance levels for nestedness and co-occurrence analysis were obtained from a conservative null model that preserves occurrence and richness totals (the fixed-fixed model) and has been shown to best account for biases introduced by differences in occurrence (Ulrich & Gotelli, 2007). In biogeography, this model tests for the null hypothesis of random association under the assumption that both species incidences and species richness have achieved equilibrium and can be

assumed to be dynamically constant. We used 30 000 independent swaps for each random matrix (cf. Gotelli & Ulrich, 2011).

*Prediction 2.* Coherence in range size (expected if continuous colonization occurred from southern refugial areas northwards) was evaluated using two complementary approaches: nestedness idiosyncrasies and outlier distributions. We used nestedness analysis to identify which species and areas deviate from an overall pattern of occurrences (idiosyncrasies). Significant idiosyncrasy scores were used to identify: (1) which species have a less coherent range size than expected; and (2) which areas deviate from the nested patterns because of too high or too low numbers of unexpected occurrences. To detect species occurrences outside the major range size (outlier distributions), we counted, for each species with at least three occurrences, the number of isolated occurrences in the countries/islands with no connection (no border) with any other country/island of occurrence. In the case of islands, we counted all nearest mainland countries as having a direct borderline. We compared the numbers of isolates with a random sample model in which we reshuffled species occurrences among countries. The null distribution  $\mu$  of the expected numbers of isolates or holes and the respective standard deviation  $\sigma$  were obtained from 1000 replicates. We also calculated standardized effect sizes  $Z = (x - \mu)/\sigma$ . *Z* scores that are approximately normally distributed indicate statistical significance at the 5% error level below  $-2.0$  or above  $2.0$  (two-tailed test).

*Prediction 3.* To evaluate spatial variations in species ranges, we considered two aspects: the 'extent of occurrence' and the 'area of occupancy'. As a measure of the extent of occurrence, we calculated, for each species, the average Euclidean distance between the centroids of the countries/islands in which a given species occurred. We obtained the null expectation of distance from a random sample model (1000 replicates) in which we reshuffled latitude and longitude among the countries/islands. The 95% confidence limits of the null distribution and *Z* scores were calculated as above. As a measure of area of occupancy, we considered the number of occurrences. We then correlated the mean distances with latitude and longitude to assess whether species range sizes have a geographical trend. We would expect that the species ranges would increase northwards if the faunas of northern countries are composed of ecologically tolerant species originating from southern refugia. Longitudinal trends are expected if recolonization occurred from western (Iberian) or eastern (Balkan) centres. We also correlated the numbers of occurrences and mean latitude of occurrence to assess whether species with more northern distributions are also those with a wider area of occupancy.

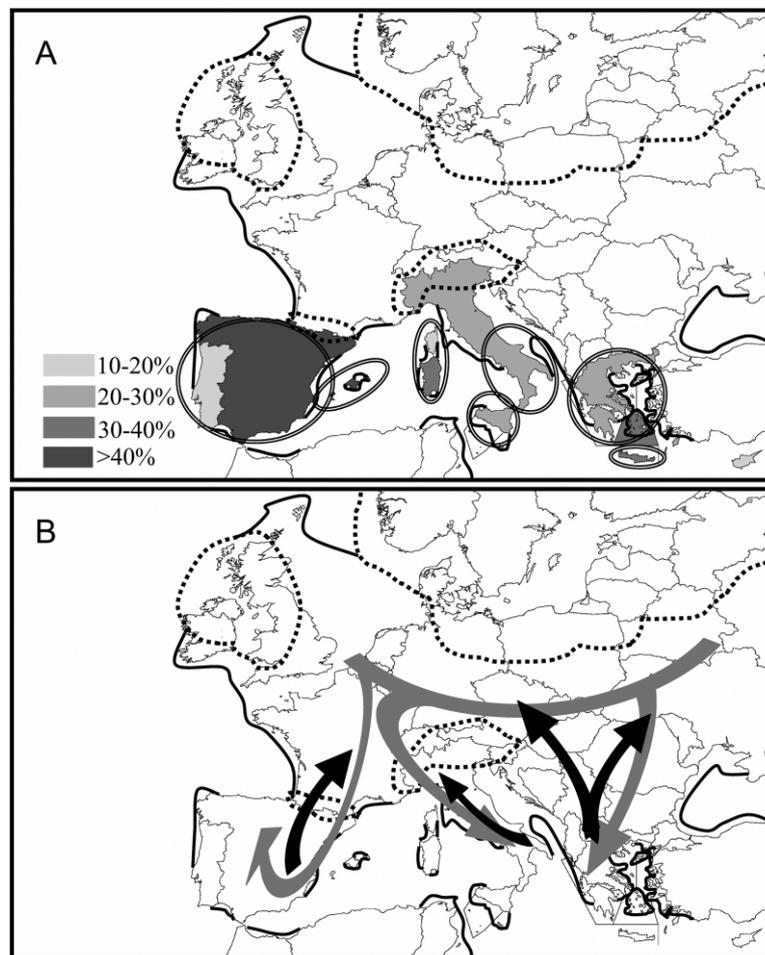
## RESULTS

Tenebrionid species richness differed widely between the 49 European countries and major islands included in the present study. The total number of species in all countries for which reliable data were available was 1375. Spain appeared to be the most species rich (557 species), followed by Greece (205) and mainland Italy (172). Spain also contained the largest number of endemic species (328; 59.8%), followed by the Canary Islands (118; 79%) and Sardinia (45; 50.6%). These results identified Mediterranean countries, and the Iberian and Balkan peninsulas in particular, as possible refugial areas (Fig. 1A).

Spatial autoregressive models pointed to area and average annual temperature as being highly sig-

nificant correlates of tenebrionid species richness (Table 1), accounting for more than one-half of the richness variance. Temperature difference, winter length and geographical heterogeneity appeared to be of minor importance. Latitude as a surrogate variable for temperature remained significant when we used only geographical variables for modelling (Table 1).

We used the full model of Table 1 to predict the expected species richness for the six major islands in the Mediterranean (Balearics, Corsica, Sardinia, Sicily, Crete and Cyprus). The model underestimated the observed species richness for all of these major islands and the differences between the observed and expected values were significant (Wilcoxon matched pairs test,  $P = 0.028$ ). If only mainland areas were used to construct a model similar to that of Table 1,



**Figure 1.** Schematic diagram to illustrate the effects of the last Pleistocene glacial maximum on the European tenebrionid fauna. A, Localization of main refugial areas (ellipses) corresponding to countries with high percentages of endemic taxa (levels of endemism are represented by grey tones keyed in the inset). B, Main directions of range expansion of cold-adapted species during Pleistocene temperature lowering (grey arrows) and post-glaciation (Holocene) recolonization pathways (black arrows). Significant extensions of the coastline during glaciation are shown by thick full lines. Ice shields are identified with broken lines. Physical conditions during the last glacial maximum according to Dennis (1993) and Reimann *et al.* (2002).

**Table 1.** Parameter values, standard errors and associated probability levels of spatial autoregressive (SR) models for natural log-transformed total tenebrionid species richness with climate and area ( $N = 49$ ,  $R^2 = 0.53$ ;  $P < 0.001$ ) and with area and spatial variables only ( $N = 49$ ,  $R^2 = 0.60$ ,  $P < 0.001$ )

Full model			
Variable	SR coefficient	Standard error	$P(t)$
Constant	-2.001	1.264	0.121
ln(area)	0.291	0.067	< 0.001
Elevation/area	0.089	0.303	0.77
Precipitation	-0.006	0.004	0.146
$D_{T < 0}$	0.003	0.004	0.484
$T_{\text{mean}}$	0.175	0.047	< 0.001
$\Delta T$	0.005	0.035	0.880
Spatial model			
Variable	SR coefficient	Standard error	$P(t)$
Constant	4.278	0.623	< 0.001
ln(area)	0.331	0.049	< 0.001
Latitude	-0.095	0.014	< 0.001
Longitude	0.003	0.044	0.709

the values of species richness predicted for the six major islands were similar to the observed values ( $P = 0.753$ ). These results suggest that the tenebrionid faunas of these islands are not significantly impoverished.

Species spatial distributions were significantly segregated even under the conservative fixed-fixed null model (Table 2). Separate analyses for all species and subsets of species with more than three (241 species), 10 (74 species) and 15 (47 species) occurrences resulted in higher significance levels (as quantified by  $Z$ -transformed  $C$  scores), and therefore increased levels of species segregation for more widespread species.

The European distribution of tenebrionid species was significantly nested when columns were sorted to species richness and important environmental gradients (Table 3). Of course, sorting according to species richness resulted in the highest degree of nestedness, followed by average annual temperature, and area. However, contrary to Prediction 1, sorting according to the distance from the supposed main European centres of postglacial colonization, Spain and Greece, resulted in matrices that were not significantly nested (Table 3). Subsequent idio-

syncrasy analysis showed that only the middle European countries, Hungary, Slovakia, Austria, Poland and the Madeira Islands, appeared to be more nested (aggregated) than expected from the null distribution after Bonferroni correction for multiple testing (not shown). Moreover, none of the countries/islands and none of the species appeared to be more scattered at the 5% error level than expected (not shown).

Of the 241 species with at least three occurrences, 178 (74%) had no occurrences outside the major range. This means that these species showed completely coherent distribution ranges. Forty-six species had one outlying country/island (19%), and only 17 species (7.5%) had at least two outliers. *Cheirodes brevicollis* occurred on three archipelagos (Canary Islands, Corsica, Malta) and Spain showed the highest degree of scatter, although even this species can be treated as a typical south-western European one. Thus, we did not find evidence for postglacial extinctions that produced scattered species ranges across Europe.

A spatial regression analysis to assess the factors that influenced the numbers of outliers ( $N_{\text{out}}$ ) returned the following best-fitting model:

$$N_{\text{out}} = (8.71 \pm 2.72) + (0.03 \pm 0.005)S - (0.16 \pm 0.05)\text{Lat} \quad (1)$$

This model implies that the numbers of outliers per country increase with total species richness  $S$  and decrease with latitude (Lat) ( $R^2 = 0.54$ ,  $P < 0.001$ ). Residuals of the plot of the expected vs. observed numbers of outliers (Fig. 2) pointed particularly to Ukraine, Sicily, Cyprus and the Canary Islands as being outliers too often, and to Portugal and Italy as being outliers too seldom.

The mean distance between centroids of species ranges decreased with longitude and increased with latitude (Fig. 3A, B). Distances also increased with the number of occurrences (Fig. 3C).  $Z$  scores that are estimates of the degree of difference of the observed distance from the null expectation decreased with the number of occurrences (Fig. 3D). Thus, widespread species were less segregated than expected from a null model of equal occupancy probability and had therefore significantly more coherent range sizes than expected by chance alone.

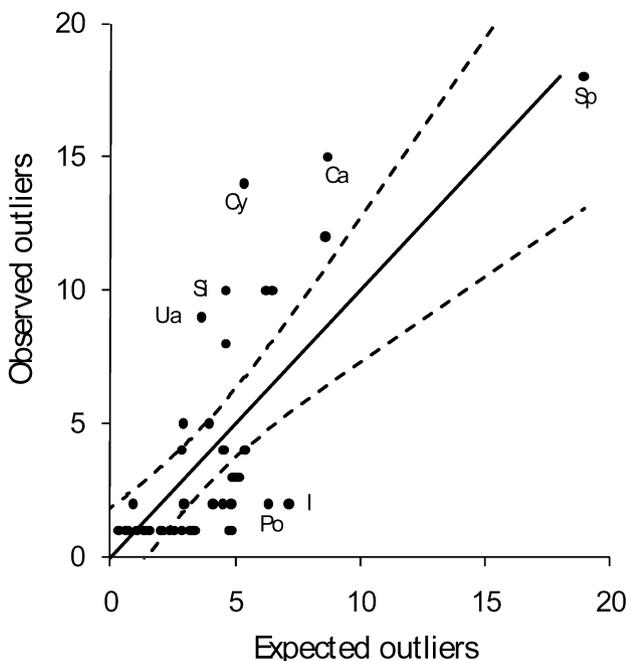
The numbers of occurrences per species increased significantly with latitude (Fig. 4). Therefore, European species increased range sizes (measured as the number of countries of occurrence) with increasing latitude. Overall, these patterns indicate that middle and northern European countries/islands contained relatively more widespread species than southern European countries/islands.

**Table 2.** Co-occurrence ( $C$  scores) analysis of species  $\times$  country/island matrices of European Tenebrionidae. Analysis was performed with all species and with subsets containing species with at least three, 10 and 15 occurrences. Expected scores and probability levels obtained from 1000 random matrices. Significance levels are Bonferroni corrected

Subset	Observed	Expected	Z score	P
All species	3.53	$3.29 \pm 0.03$	8	< 0.001
> 3 occurrences	29.2	$26.7 \pm 0.1$	25	< 0.001
> 10 occurrences	70	$62.7 \pm 0.4$	18.25	< 0.001
> 15 occurrences	70.7	$60.6 \pm 0.4$	25.25	< 0.001

**Table 3.** Nestedness ( $MT$  values) analysis of species  $\times$  country/island matrices of European Tenebrionidae. Columns were sorted according to five ecologically important gradients. Rows were always sorted according to species richness. Expected scores and probability levels obtained from 1000 random matrices. Significance levels are Bonferroni corrected

Sorting	Observed	Expected	Z score	P
Richness	4.76	$5.20 \pm 0.1$	-4.4	< 0.001
Distance from Spain	28.51	$28.67 \pm 0.2$	-0.8	> 0.10
Distance from Greece	18.64	$18.88 \pm 0.1$	-2.4	> 0.05
Area	13.84	$13.49 \pm 0.1$	3.5	< 0.001
$T_{\text{mean}}$	8.21	$8.97 \pm 0.1$	-7.6	< 0.001



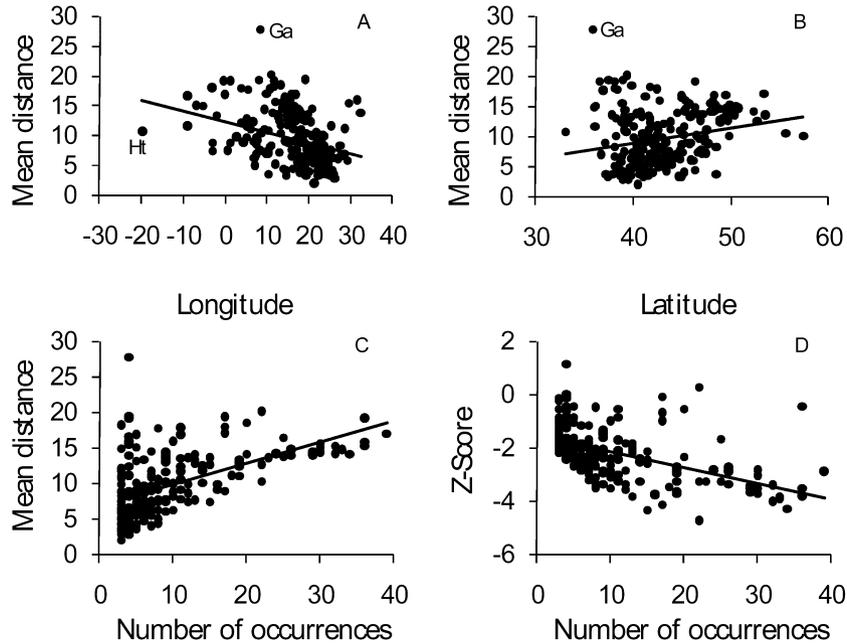
**Figure 2.** Outliers: observed vs. expected numbers. Expected numbers were calculated from Eqn. (1). Full line, 1 : 1 regression line; broken lines, 99% confidence limits. Ca, Canary Islands; Cy, Cyprus; I, Italy; Po, Portugal; Si, Sicily; Sp, Spain; Ua, Ukraine.

## DISCUSSION

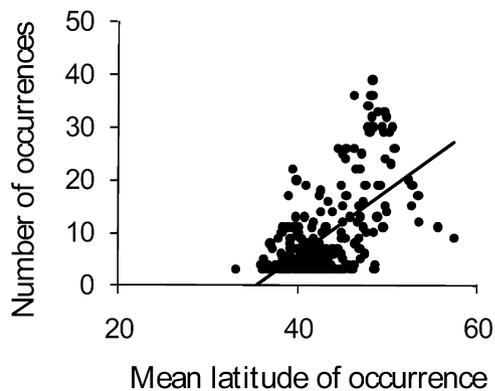
Under the hypothesis of a northern European post-glacial colonization from either south-eastern or

south-western Europe (Prediction 1), we expect to see clear gradients in the nestedness analysis and analysis of idiosyncratic countries. Postglacial colonization trajectories from glacial refugia, in combination with dispersal limitations, have been identified to influence present-day differences in species richness of European bats (Horáček, Hanák & Gaisler, 2000) and trees (Svenning & Skov, 2007). However, the results of our analyses are only partly in line with simplistic biogeographical predictions based on the role of Spain and Greece as refugial areas. Under postglacial colonization from Spain or Greece, we expected a significant degree of nestedness after sorting the matrix according to distance from these countries. This was not the case. Nestedness followed the temperature and area gradients, but not the gradients of distance. Further, our co-occurrence analysis pointed to significant degrees of species segregation, a pattern expected if different habitat requirements and spatial species turnover obscure the primary colonization gradients. Our results are rather in accordance with a multiregional colonization concept with several glacial refugia (Taberlet *et al.*, 1998; Dapporto *et al.*, 2009, 2011; Dapporto, 2010).

The numbers of occurrences per species, and therefore species range sizes, increased with latitude (Fig. 4). This pattern suggests that northern countries were selectively colonized by more tolerant and, possibly, more mobile species, thus supporting Prediction 3. The low dispersal capabilities of most tenebrionid species, which evolved in the southern isolated areas during the Pleistocene glacial maxima



**Figure 3.** Relationships between the mean distance between centroids of countries/islands and the mean longitude of occurrence (A), mean latitude of occurrence (B) and the total number of occurrences (C). In all cases, only species with at least three occurrences in European countries/islands were analysed, for a total of 241 species. A,  $R^2 = 0.13$ ;  $P(R^2 = 0) < 0.001$ . B,  $R^2 = 0.05$ ;  $P(R^2 = 0) < 0.001$ ; C,  $R^2 = 0.32$ ;  $P(R^2 = 0) < 0.001$ . Ga, *Gonocephalum affine*; Ht, *Hegeter tristis*. D, The Z scores of these species [(observed distance – expected. distance)/standard deviation<sub>expectation</sub>] decrease with the number of occurrences [ $R^2 = 0.29$ ;  $P(R^2 = 0) < 0.001$ ].



**Figure 4.** Relationship between number of occurrences of 241 tenebrionid species and the mean latitude of occurrence (only species present in at least three countries/islands were considered).  $R^2 = 0.34$ ;  $P(R^2 = 0) < 0.001$ .

(Fattorini & Baselga, 2011), prevented their successive spreading northwards. Such a process should also generate some degree of species spatial turnover that was indeed visible in the significant degree of segregation (Table 2). At this time, it should be noted that Europe, as defined in this study and in former work (Ulrich & Fiera, 2009; Bąkowski *et al.*, 2010; Fattorini & Baselga, 2011; Ulrich *et al.*, 2011), is an

inherently inhomogeneous assemblage of countries/islands whose faunas differ dramatically by their biogeographical composition.

In general, we found coherent range sizes centred in southern European countries, supporting Prediction 2. Exceptions to the main patterns were the faunas of Cyprus (dominated by Middle Eastern species with few European species), the Canary Islands (characterized by a high incidence of endemic and African species), Sicily (with a number of species mainly distributed in northern Africa) and Ukraine (with many typical Mediterranean species) (cf. Löbl & Smetana, 2008). Portugal has fewer outlier species than expected because its fauna is mostly a subset of the Spanish fauna, and this is even exaggerated by the fact that faunal data for Portugal are probably less complete than for Spain. The position of Italy can be explained by the fact that this country is in the centre of the Mediterranean basin and received immigrants from different trajectories (western and eastern) in different ways (see Dapporto *et al.*, 2009, 2011 for details).

The two species that mostly deviate from the main longitude–range size pattern (Fig. 3) have distinctive distributions: *Hegeter tristis* is a species with a reduced range, but at a very western location because it is distributed on the Macaronesian Islands, with

some records on the adjacent Saharan coast, whereas *Gonocephalum affine* is a species occurring in many southern European locations, but with a range centred in northern Africa (Löbl & Smetana, 2008), which explains its position at intermediate latitude.

The complex interaction between current and historical factors made it difficult to detect regular patterns of postglacial colonization. The Holocene and late Pleistocene biogeography of Europe cannot be summarized as a recolonization of northern countries by cold-tolerant species from refugia primarily in the south. Our data strongly indicate that current patterns of spatial species range size result from complex interactions of geographical isolation, current climate and past events that cannot be reduced to a single explanation.

The three main peninsulas (Iberian, Italian and Balkan) contributed differently to the postglacial recolonization of Europe, resulting in different main 'paradigms'. First, some subspecies, species or lineages, mainly belonging to eastern areas, have moved very far in terms of both latitude and longitude, whereas other subspecies/species/lineages belonging to other refugia were blocked by huge geographical structures, such as the Alps and Pyrenees (Fig. 1B). This could have resulted in a nested order from south to north (associated with temperature) without a strong signal of longitudinal ordering. Second, cold-adapted species, associated with mesophilic woodlands or high-altitude habitats, could have dispersed from central Europe to southern European areas during Pleistocene glaciations, thus producing a certain faunal homogenization (see Fattorini & Baselga, 2011). Third, there are species/subspecies/lineages which moved from their occupied area and met/replaced the species/subspecies/lineages from other refugia well after postglacial recolonization. Such relatively recent (a few hundred to thousand years ago) movements could well have hidden the original postglacial pattern of recolonization.

Our study was focused on postglacial recolonization, thus assuming that the most important historical factors determining current distributions were the effects of Pleistocene and Holocene climate changes. We adopted this point of view because the last Pleistocene glaciation was the last palaeoecological event having large-scale effects on species distribution, largely erasing the effects of previous palaeogeographical and palaeoecological events. However, some pre-Pleistocene patterns still seem to be evident in the European tenebrionids. For example, phylogenetic reconstructions of Mediterranean *Tentyria* (Palmer & Cambefort, 2000) and *Blaps* (Condamine *et al.*, 2011) species indicate an ancient colonization of southern European areas from North Africa across the Gibraltar Strait during an episode in which the

strait was closed. A striking pattern found in our study is that the tenebrionid faunas of major islands in the Mediterranean were not significantly impoverished. This strongly contrasts with what is known for lepidopterans, which clearly show impoverished faunas on Mediterranean islands, such as Sardinia and Corsica (Dapporto & Dennis, 2009, 2010). Most probably, these islands, not affected by glaciations, have largely retained their tenebrionid Tertiary faunas which, because of the long period of isolation, have evolved large numbers of endemic taxa. A case study of the genus *Tentyria* based on cladistic reconstructions confirms that the Balearic Islands, Corsica and Sardinia evolved endemic taxa by vicariance as a result of microplate isolations (Palmer, 1998).

More generally, the global distributions of several species or lineages indicate their Tertiary origin in Europe. For example, the distributions of the genera *Dilamus* and *Boromorphus*, and that of the tribe Scaurini, with two genera in the Mediterranean and two in southern Africa, suggest an old (possibly pre-Tertiary) faunal exchange between these two areas through the Drakensberg system–eastern Rhodesia–eastern Zaïre highlands and Ethiopia (Endrödy-Younga, 1978). However, the lack of reliable phylogenetic reconstructions for most tenebrionid groups makes it very difficult to speculate about the origin of single species or lineages. We hope that in the future more phylogenetic reconstructions of tenebrionid beetles will be available to test the patterns outlined in this study.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Main references used to assess tenebrionid distribution in European countries/islands.

**Appendix S2.** Occurrence of each species/subspecies in each country/island.

**Appendix S3.** Geographical and climatic variables used in autoregressive models.

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