



# Species richness and turnover patterns in European tenebrionid beetles

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**Abstract.** 1. We used a hyperdiverse invertebrate group, tenebrionid beetles, to test competing hypotheses about the factors correlated with the spatial variation in species richness and composition across Europe.

2. We considered the following hypotheses for explaining variation in species richness, (i) spatial heterogeneity, (ii) environmental energy, and (iii) dispersal limitation and post-glacial recolonisation, and the following hypotheses for variation in species composition, (i) current climate, (ii) Pleistocene glaciations, and (iii) neutral dynamics.

3. We used inventories of 36 European territories, built from a database containing the distributions of 1010 species or subspecies. Area, spatial position, and topographical and climatic variables were used as predictors in regression (richness) and constrained analysis of principal coordinates (composition) analyses.

4. The latitudinal richness gradient found in European tenebrionids was mostly explained by the joint effect of environmental and spatial variables, supporting the climate and incomplete recolonisation hypotheses.

5. A parabolic relationship of endemism with longitude points to the presence of centres of endemism in the Iberian Peninsula and the Balkans. Current climatic conditions alone were not sufficient to explain spatial turnover patterns of European tenebrionids, which are largely influenced by spatial factors.

6. Both the Pleistocene glaciations and neutral hypotheses were supported, but the fact that turnover is not uniform across Europe suggests that the historical effects of Pleistocene glaciations had a deeper impact on tenebrionid assemblages than neutral dynamics. Thus, variation in species richness seems more directly controlled by climatic factors, whereas geographical constraints related to dispersal limitation or stochastic colonisation events influenced species composition.

**Key words.** Endemics, latitudinal gradient, Pleistocene refugia, species–area relationship.

## Introduction

A prominent pattern in species richness in Europe is its steep downward gradient from the Mediterranean Basin to the Pole (Hawkins & Porter, 2003; Svenning & Skov, 2007a; Whittaker

*et al.*, 2007; Baselga, 2008; Schuldt & Assmann, 2009). This trend falls within the well-known latitudinal gradient, that is, the increase in the number of plant and animal species from high-to-low latitudes, particularly in the northern hemisphere (Pianka, 1966; Stevens, 1989; Rohde, 1999). Although some authors attempted to explain this gradient in terms of ‘geometric constraints’ that limit the geographical ranges of species (i.e. the mid-domain effect) (Colwell & Lees, 2000; Willig *et al.*, 2003), recent work suggests that this model explains very little variation in species richness at macroscale (Whittaker *et al.*, 2001;

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Hawkins & Diniz-Filho, 2002; Zapata *et al.*, 2003), and statistical associations between species richness and latitude are typically considered as a result of hidden covariances between latitude and present or past environmental (notably climatic) variables (Rosenzweig, 1995; Turner *et al.*, 1996; Hawkins *et al.*, 2003, 2006; Hewitt, 2004; Svenning & Skov, 2007a,b; Whittaker *et al.*, 2007).

While alternative explanations have been tested for the better-known taxonomic groups (e.g. birds, butterflies, vascular plants) (Hawkins & Porter, 2003; Svenning & Skov, 2007a,b; Whittaker *et al.*, 2007), little is known about large-scale spatial biodiversity patterns for most groups of organisms, and the occurrence of numerous exceptions and incongruities among groups cautions us against any generalisation. Moreover, most research on large-scale diversity patterns focused on species richness. Little is known about factors regulating spatial turnover (i.e. the variation in species composition independent of richness gradients; see Baselga, 2010), although it is already known that both can show markedly different patterns (Baselga, 2008; Gañán *et al.*, 2008). Patterns of spatial turnover are the result of the complex interaction of species traits (e.g. dispersal capacity and niche width) and characteristics of the physical landscape (e.g. environmental dissimilarity, topographic complexity, and isolation) over time (Shmida & Wilson, 1985; Nekola & White, 1999; Williams *et al.*, 1999; Fattorini, 2006, 2009a,b).

In this study, we used European tenebrionid beetles (Coleoptera: Tenebrionidae), a hyperdiverse insect group, to test competing hypotheses about the factors correlated with the latitudinal richness gradient and to assess whether they are able to explain the variation in species composition (spatial turnover).

Competing hypotheses on species distribution generally are not mutually exclusive and may operate together, either sequentially or concurrently, to determine distributional patterns (Gaston, 2000; Whittaker *et al.*, 2001). Therefore, we considered multiple environmental and spatial variables that can be plausibly linked with several postulated mechanisms (Hawkins & Diniz-Filho, 2004). This way, we took advantage from the additional power provided by testing multiple hypotheses simultaneously (Hilborn & Mangel, 1997; Hawkins & Diniz-Filho, 2004).

On the basis of biogeographical and ecological principles, we developed some basic predictions for the strength and direction of relationships between tenebrionid species richness and climatic, topographic, and spatial variables in Europe at continental scale. Species with restricted distributions (endemics) may be influenced by environmental factors that operate on a local or regional scale more distinctly than widespread species (Brown & Maurer, 1989; Brown, 1995; Jetz & Rahbek, 2002). Thus, in addition to analyses dealing with overall richness, we performed specific analyses for endemic taxa.

Large-scale analyses of insect distribution patterns are still rare (Diniz-Filho *et al.*, 2010). However, comparisons among taxa are needed for an assessment of which factors determine differences in species richness and whether and how their importance differs in organisms with different ecology. For this purpose, we also compared our results with those previously

achieved with similar methods for another hyperdiverse group of insects, the cerambycid beetles (Baselga, 2008). These two groups differ considerably in dispersal power (cerambycids are typically winged, whereas tenebrionids are generally flightless) and feeding habits (cerambycids are more or less specialised phytophagous insects, whereas tenebrionids are generally detritivorous).

## Hypotheses

### *Species richness*

Our hypotheses about latitudinal variation in species richness were formulated as follows.

### *Spatial heterogeneity*

The habitat heterogeneity hypothesis proposes that regions that are topographically and environmentally more diverse have higher species richness because the limiting resources can be more readily subdivided in complex habitats (Pianka, 1966; Wilson, 1974; Currie, 1991; Kerr & Packer, 1997; Kerr, 2001; Rahbek & Graves, 2001). This promotes greater specialisation and the coexistence of a great number of species (see Simpson, 1964; Pianka, 1966; MacArthur, 1972; McCoy & Connor, 1980; Rohde, 1992; Kerr & Packer, 1997; Brown & Lomolino, 1998).

### *Environmental energy*

The number of species is limited by the available energy (Connell & Orians, 1964), with high-energy availability promoting the persistence of more species (Wright, 1983; Brown, 1988; Currie, 1991; Gaston & Blackburn, 2000; Brown & Lomolino, 2005). In particular, according to the ambient-energy hypothesis, the animal species richness of a region is directly controlled by the total or average energy available, because higher temperatures promote faster growth of individuals and populations and this greater biomass, in turn, promotes greater species richness (Brown, 1988; Blackburn & Gaston, 1996b; Turner *et al.*, 1996; Hawkins *et al.*, 2003).

### *Dispersal limitation and post-glacial recolonisation*

The number of species is limited by the capacity of populations to arrive at a given area since last deglaciation (Svenning & Skov, 2007a). Spatial variables (longitude and latitude) account for the spatial pattern that would be generated by dispersal limitation, as many species would have not yet reached northern areas. Patterns purely explained by spatial variables, independent of environmental variables, could be attributed to this historical process (Lobo *et al.*, 2001). Patterns jointly explained by climatic and spatial variables could not be attributed unequivocally to any of these processes.

### *Species turnover*

Regarding spatial turnover, we considered the following three hypotheses.

#### *Current climate*

This hypothesis predicts the existence of strong latitudinal turnover as climate exhibits a particularly strong latitudinal gradient. Thus, turnover would reflect ecological sorting (Whittaker, 1960; Nekola & White, 1999), as species with different physiological tolerances are sorted along environmental gradients, replacing one to each other and making species similarity to decrease with environmental dissimilarity.

#### *Pleistocene glaciations*

This hypothesis predicts particularly strong turnover in southern Europe (compared with northern Europe), where the glacial impacts were mild enough to allow numerous refugia as well as local evolutionary differentiation and diversification. Thus, southern European assemblages are the result of long-term persistence of isolated populations affected by dispersal limitation, as suggested in the context of species distribution modelling studies (Svenning & Skov, 2004) and supported later by phylogeographical data (Petit *et al.*, 2005). Turnover should exhibit spatial patterns beyond what can be explained by climate alone.

#### *Neutral dynamics*

This hypothesis implies that spatial patterns are entirely driven by stochastic population dynamics and spatially constrained dispersal (Hubbell, 2001). These stochastic processes predict a distance decay of similarity, but turnover should be uniform in all regions, as it is not linked to the specific local conditions but to random processes. Again, turnover should exhibit spatial patterns beyond what can be explained by climate alone. Table 1 summarises these hypotheses along with the attached variables and the relative predictions and justifications.

## Methods

### *Biological data*

*Taxonomic treatment.* An impressive number of European tenebrionids are classified as subspecies. In fact, the current taxonomic dividing line between species and subspecies, as applied to the tenebrionids of Europe, is arguably arbitrary. 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).

In consideration of the highly derivative and specialised characters of Alleculinae (formerly considered a separate family of winged and flower-visiting beetles), we did not consider them in our database. Moreover, distributional data for alleculines are less reliable than those obtained for the other Tenebrionidae.

We also excluded (i) synanthropic species associated with human food, which became cosmopolitan or subcosmopolitan (e.g. various species belonging to the genera *Tenebrio*, *Tribolium*, *Alphitobius*, *Alphitophagus*, and *Lathetycus*); (ii) alien species introduced into Europe; (iii) species occurrences in certain European countries because of recent and documented introductions from other European countries (e.g. Mediterranean species introduced into central and north European countries); (iv) doubtful occurrences because of uncertain identification or possible wrong locality records.

*Geographical units.* The study area included continental Europe. Thirty-six inventories of tenebrionids were obtained from literature records (see Appendix S1). In general, these inventories refer to European countries, but some countries were split or aggregated on the basis of biogeographical criteria and data availability (see Baselga, 2008). For simplicity, all these territorial units are hereafter referred to as 'countries'. Islands were excluded from this study to avoid insularity effects that could confound general patterns of diversity. The final matrix of 1010 species or subspecies of tenebrionids from the 36 countries included in this study (hereafter referred to as 'species' for simplicity) is reported in Appendix S2. Each inventory ranged from 10 (Moldova) to 557 taxa (Spain), with a mean of  $75.6 \pm 95.1$  SD, and between 0 and 333 endemics (country-based endemism), with a mean of  $14 \pm 55.7$  SD.

It is difficult to evaluate the completeness of these inventories. We used a very conservative approach and omitted all countries for which no recent checklists were available or which were considered not adequately sampled by expert taxonomists (see Acknowledgements).

As for most arthropod groups, fine-grained distribution data are unavailable. However, previous works on butterflies (Ulrich & Buszko, 2003; Konvicka *et al.*, 2006), longhorn beetles (Baselga, 2008), carabid beetles (Schuldt & Assmann, 2009), springtails (Ulrich & Fiera, 2009), clearwing moths (Bąkowski *et al.*, 2010), and bats (Ulrich *et al.*, 2007) showed that even coarse-grained data (whole country species occurrences and climate variables) are able to identify major environmental predictors of animal species distribution (see also Hortal, 2008) and are of particular importance for conservation implications (Fattorini, 2009c; Schuldt & Assmann, 2010). Finally, Keil and Hawkins (2009) tested whether broad-scale patterns of species richness are robust to the violation of constant grain size and found that using country models can yield weaker associations between species richness and environmental predictors. However, for the groups analysed by these authors, the variables entering the models and their respective parameters are very similar between grid and country models. Therefore, in our opinion, models fitted with country inventories are an acceptable tool for describing broad-scale diversity patterns when more precise data are lacking.

**Table 1.** Summary of hypotheses on spatial variation in species richness and turnover for the European tenebrionid beetles. For the acronyms of variables, see Methods.

Hypothesis	Associated variables	Predictions	Justifications	Supported
Species richness				
Spatial heterogeneity	Alt, Alt <sub>ran</sub> , T <sub>ran</sub>	(a) Direct but weak relationship with Alt or Alt <sub>ran</sub> . Significant fraction of variation purely explained by Alt or Alt <sub>ran</sub> .  (b) Direct and stronger relationship with T <sub>ran</sub> . Significant fraction of variation purely explained by T <sub>ran</sub>	(a) Larger range in elevation → larger habitat diversity, but most regions have high peaks.  (b) larger range in temperature → presence in the same area of thermophilous, mesophilous and cryophilous species	Partially. Overall richness is related to Alt <sub>ran</sub> , but this variable does not remain significant in the final model  No
Environmental energy	T <sub>ann</sub> , T <sub>max</sub> , T <sub>min</sub> , P <sub>ann</sub> , P <sub>ran</sub> , P <sub>dri</sub> , P <sub>dri</sub>	(a) Positive relationship with T <sub>ann</sub> , T <sub>min</sub> , T <sub>max</sub> . Significant fraction of variation purely explained by T variables  (b) Positive relationship with P <sub>ann</sub> , P <sub>ran</sub> , P <sub>dri</sub> , and P <sub>dri</sub> . Significant fraction of variation purely explained by P variables	(a) High temperature → warmer winters → longer food availability, because tenebrionids are mostly thermophilous insects feeding on decaying matter  (b) High precipitation → high primary productivity	Yes (T <sub>max</sub> )  Yes (P <sub>dri</sub> ) However, the independent effect of climate is weak, being most of the variation explained both by climate and by spatial position.
Dispersal limitation and post-glacial recolonisation	Long, Long <sub>min</sub> , Long <sub>max</sub> , Lat, Lat <sub>min</sub> , Lat <sub>max</sub>	(a) Negative relationship with Lat, Lat <sub>min</sub> , Lat <sub>max</sub> . Significant fraction of variation purely explained by Lat variables  (b) Quadratic relationship with Long, Long <sub>min</sub> , Long <sub>max</sub> . Significant fraction of variation purely explained by Long variables	Post-Pleistocene recolonisation of frozen areas from southern refugia  Post-Pleistocene recolonisation from two main refugial centres: the Iberian Peninsula and the Balkans	Yes  Yes, but mostly for endemics, being the effect on overall richness weak and not included in the final model
Species turnover				
Current climate	T <sub>ann</sub> , T <sub>max</sub> , T <sub>min</sub> , P <sub>ann</sub> , P <sub>dri</sub>	Relationship of species composition with T <sub>ann</sub> , T <sub>max</sub> , T <sub>min</sub> , P <sub>ann</sub> , P <sub>dri</sub> . Significant fraction of variation purely explained by climatic variables	Species distributions controlled by niche filtering; therefore, composition is explained by climate	Yes, but weak explanatory power

Table 1. (Continued)

Hypothesis	Associated variables	Predictions	Justifications	Supported
Pleistocene glaciations	Long, Long <sub>min</sub> , Long <sub>max</sub> , Lat, Lat <sub>min</sub> , Lat <sub>max</sub>	Relationship of species composition with Long, Long <sub>min</sub> , Long <sub>max</sub> , Lat, Lat <sub>min</sub> , Lat <sub>max</sub> , and higher turnover in the south. Significant fraction of variation purely explained by spatial variables	Different extinction rates between north and south and dispersal limitation; therefore, composition is explained by spatial variables	Yes
Neutral dynamics	Long, Long <sub>min</sub> , Long <sub>max</sub> , Lat, Lat <sub>min</sub> , Lat <sub>max</sub>	Relationship of species composition with Long, Long <sub>min</sub> , Long <sub>max</sub> , Lat, Lat <sub>min</sub> , Lat <sub>max</sub> , and turnover constant across the continent. Significant fraction of variation purely explained by spatial variables	Random (but limited) dispersal and stochastic extinction control species distributions; thus, composition is explained by spatial variables and turnover is uniform across zones	Yes (but not as unique explanation)

### Predictor variables

Three sets of variables were obtained for each country: (i) area (A); (ii) spatial position: mean, minimum, and maximum longitude (Long, Long<sub>min</sub>, Long<sub>max</sub>) and mean, minimum, and maximum latitude (Lat, Lat<sub>min</sub>, Lat<sub>max</sub>); and (iii) environmental factors: mean altitude (Alt); altitudinal range (Alt<sub>ran</sub>); annual mean temperature ( $T_{ann}$ ); spatial range of  $T_{ann}$  ( $T_{ran}$ ), which is the difference in the mean temperature of  $T_{ann}$  between the two localities with the most extreme values within a country; maximum temperature of the warmest month ( $T_{max}$ ); minimum temperature of the coldest month ( $T_{min}$ ); annual precipitation ( $P_{ann}$ ); spatial range of  $P_{ann}$  ( $P_{ran}$ ); precipitation of driest quarter ( $P_{dri}$ ); and spatial range of  $P_{dri}$  ( $P_{dri}$ ) (see Table 1). Topographic and climatic variables were obtained from Worldclim 1.4 layers (Hijmans *et al.*, 2005). Thereafter, mean or range values for each country were extracted from a European GIS database (0.08° resolution) using IDRISI (CLARK LABS, 2000), together with their respective areas (km<sup>2</sup>) and geographical coordinates (lat-long).

### Analytical methods

The relationship between the aforementioned predictors and richness, endemism, and turnover of European Tenebrionidae was assessed as follows (Table 1):

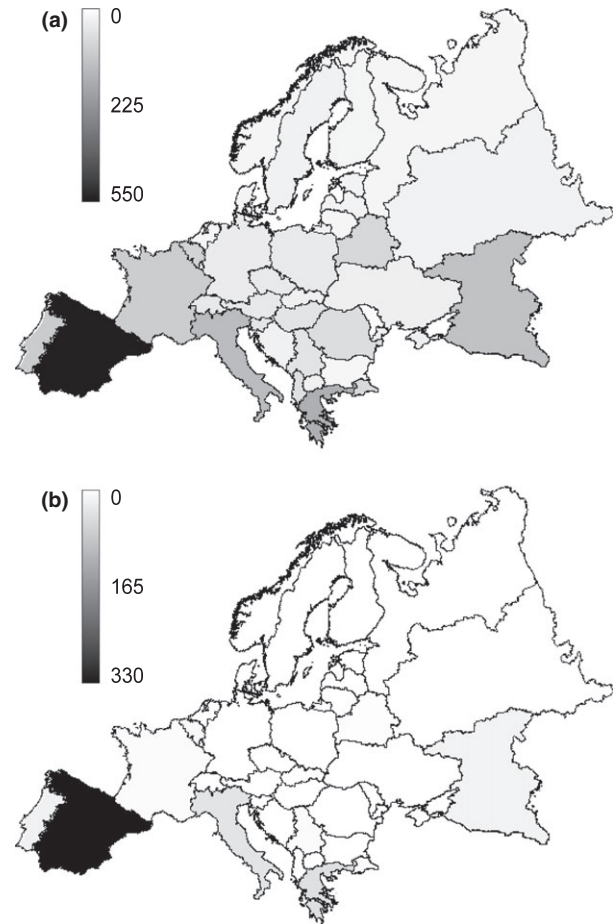
**Richness.** Multiple relationships between species richness and the explanatory variables were analysed using OLS regression modelling (Legendre & Legendre, 1998) performed with Statistica 7.0 (StatSoft, 2004). Richness was log transformed to normalise model residuals. As a previous step, linear and quadratic functions of the predictors were independently regressed against each response variable to determine significant relationships. This was done

to identify potentially relevant predictors that were thereafter included in the multiple regressions. Significant terms for each set (area, environment, and spatial variables) were selected by means of a backward stepwise procedure, to avoid a high level of co-linearity within each set of predictors. Finally, variation partitioning among sets of predictors was used to quantify the relative importance of the pure effects of area (A), environment (E), and spatial variables (S) and their respective shared influences (Legendre & Legendre, 1998). Such an approach allows non-independent explanatory variables to be dealt with, as it is explicitly designed to identify the portions of explained variability that are shared by different sets of variables and those that are independent (Borcard *et al.*, 1992). Area is also included in the analyses to control for the effect of differences in area among sampling units.

**Endemism.** Species with single country distribution may be more likely 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 & Maurer, 1989; Brown, 1995; Jetz & Rahbek, 2002). Thus, we analysed whether determinants of overall species richness patterns are also representative for endemics. There are two basic approaches to define levels of endemism. In spatially based quantitative measures of endemism, known as threshold endemism, weighted endemism, and corrected weighted endemism (see Fattorini, 2007), 'endemism' is considered as a measure of the size of the distribution range of a species. By contrast, as currently interpreted by most biogeographers, endemism refers to the exclusive occurrence of a species in a given area, regardless of the range size (Fattorini, 2007). In this paper, we used both concepts. A measure of the uniqueness of the fauna of each country was computed as the number of species living exclusively in each country (country-based endemism). A second measure (range-based

endemism) was computed as the number of species with a distribution range smaller than  $6 \times 10^5 \text{ km}^2$  (category IV by Lumaret & Lobo, 1996). Because available data note the presence of a species in each country, the areas of all countries where a species was recorded were combined to estimate its distribution range. Scores of endemism (country- and range-based measures) were log transformed to normalise model residuals and regressed against the predictors following the same procedure as described for richness. *Turnover*. Variation in species composition among countries was analysed with pairwise Simpson's dissimilarity index ( $\beta_{\text{sim}}$ ). This index was preferred to other alternatives because it is independent of species richness gradients (Koleff *et al.*, 2003; Baselga, 2007), thus  $\beta_{\text{sim}}$  accounts only for spatial turnover (species replacement) and excludes the effect of dissimilarity owing to nestedness (Baselga *et al.*, 2007; Baselga, 2010). Simpson's dissimilarities were computed in R (R Development Core Team 2006) using the function provided by Baselga (2010). This dissimilarity matrix was then used to aggregate countries into different clusters using the R cluster package (Maechler *et al.*, 2005). Clusters were built with the average linkage method. After visual inspection of the dendrogram, an arbitrary cut-off of five clusters was set using the maptree package (White, 2007) to map the spatial patterns of species composition. The significance of these five groups was assessed by means of ANOSIM tests (Clarke, 1993) using the vegan package (Oksanen *et al.*, 2010).

Thereafter, the variables determining the described patterns were explored. A constrained analysis of principal coordinates (CAP) was computed in R using the vegan package (Oksanen *et al.*, 2010) to examine the relationship between variability in the table of species occurrences and the three sets of predictor variables. CAP was selected instead of alternative methods as canonical correspondence analysis (CCA) or redundancy analysis (RDA) because CAP can be computed with any dissimilarity index with ecological significance, and therefore,  $\beta_{\text{sim}}$  dissimilarity was preserved in the constrained ordination. Area, the ten aforementioned environmental variables, and spatial variables (the nine terms of a third degree polynomial of mean latitude and longitude; Trend Surface Analysis, see Legendre & Legendre, 1998) were used as predictors to perform constrained ordinations yielding, respectively, A, E, and S models. Because the order of inclusion in the model affects the significance computed by the permutation tests (Oksanen *et al.*, 2010), the amount by which the explained variation was reduced because of the elimination of a single variable (compared with the complete model) was tested prior to the final analysis. This allowed the individual variables to be ranked in order of their independent contribution to the total variation in the response variable (from greatest to least), and the variables were included in the significance test in this order. The test statistic is pseudo- $F$ , which is the ratio of constrained and unconstrained total inertia ( $\beta_{\text{sim}}$  in our analysis), each divided by their respective ranks (Oksanen *et al.*, 2010). Only significant variables were retained ( $P < 0.05$ ) to avoid overfitting owing to the inclusion of non-significant terms. Finally, to partition the variation among A, E, and S sets of predictors, partial CAPs were



**Fig. 1.** Study area and scores of (a) species richness and (b) endemism of tenebrionid beetles in the territories considered as sampling units.

performed, eliminating the effects of each variable (covariable) on the others, yielding estimates of pure effects.

*Cross-taxon congruence of diversity patterns.* Richness, endemism, and turnover patterns of European tenebrionids were compared with those of European cerambycids (Baselga, 2007, 2008) by computing Pearson correlation between richness, endemism, and dissimilarity matrices of both beetle families. Because of the lack of independence between dissimilarities between pairs of countries within matrices (Legendre *et al.*, 1994), significance of correlation between dissimilarity matrices was computed through a Mantel test, using the vegan package (Oksanen *et al.*, 2010) in R.

## Results

### Richness

Species richness formed a clear latitudinal gradient (Fig. 1a), significantly related to a number of variables

**Table 2.** Relationships between predictors and species richness and models for each group of variables. The sign of the relationships and percentage of explained variance ( $R^2$ ) are shown. S and E are the spatial and environmental models, respectively. For the acronyms of variables, see Methods.

Variable	Function (sign)	$R^2$	$F$	d.f.	$P$
Log of Area	NS	0.07	2.40	1, 34	0.131
Long	NS	0.09	3.18	1, 34	0.083
Long <sub>min</sub>	Quadratic (-, +)	0.26	5.76	2, 33	0.007
Long <sub>max</sub>	NS	0.07	2.43	1, 34	0.128
Lat	Linear (-)	0.30	14.29	1, 34	0.001
Lat <sub>min</sub>	Linear (-)	0.37	20.24	1, 34	<0.001
Lat <sub>max</sub>	Linear (-)	0.21	8.98	1, 34	0.005
Alt	NS	0.07	2.49	1, 34	0.124
Alt <sub>ran</sub>	Linear (+)	0.17	7.09	1, 34	0.012
$T_{ann}$	Linear (+)	0.30	14.85	1, 34	<0.001
$T_{ran}$	Linear (+)	0.17	6.86	1, 34	0.013
$T_{max}$	Linear (+)	0.30	14.50	1, 34	0.001
$T_{min}$	Linear (+)	0.23	10.06	1, 34	0.003
$P_{ann}$	NS	0.00	0.14	1, 34	0.708
$P_{ran}$	Linear (+)	0.19	7.92	1, 34	0.008
$P_{dri}$	NS	0.02	0.64	1, 34	0.429
$P_{drn}$	Linear (+)	0.23	10.31	1, 34	0.003
Model for E	$T_{max} + P_{drn}$	0.46	14.24	2, 33	<0.001
Model for S	Lat + Lat <sub>max</sub>	0.57	22.18	2, 33	<0.001
Model E + S	$T_{max} + P_{drn} +$ Lat + Lat <sub>max</sub>	0.58	10.68	4, 31	<0.001

(Table 2). Country area was neither linearly nor logarithmically related to richness. Altitudinal range, range of precipitation, and temperature variables showed positive relationships; latitudinal variables were negatively related to richness; and minimum longitude presented a quadratic relationship, with the highest richness at both extremes. The models of environmental (E) and spatial (S) variables were comprised, respectively, of  $T_{max}$  and  $P_{drn}$ , and Lat and Lat<sub>max</sub> (Table 2). The independent effects of the E and S models were small and negligible, respectively, but they shared important portions of the explained variance (Fig. 2a).

### Endemism

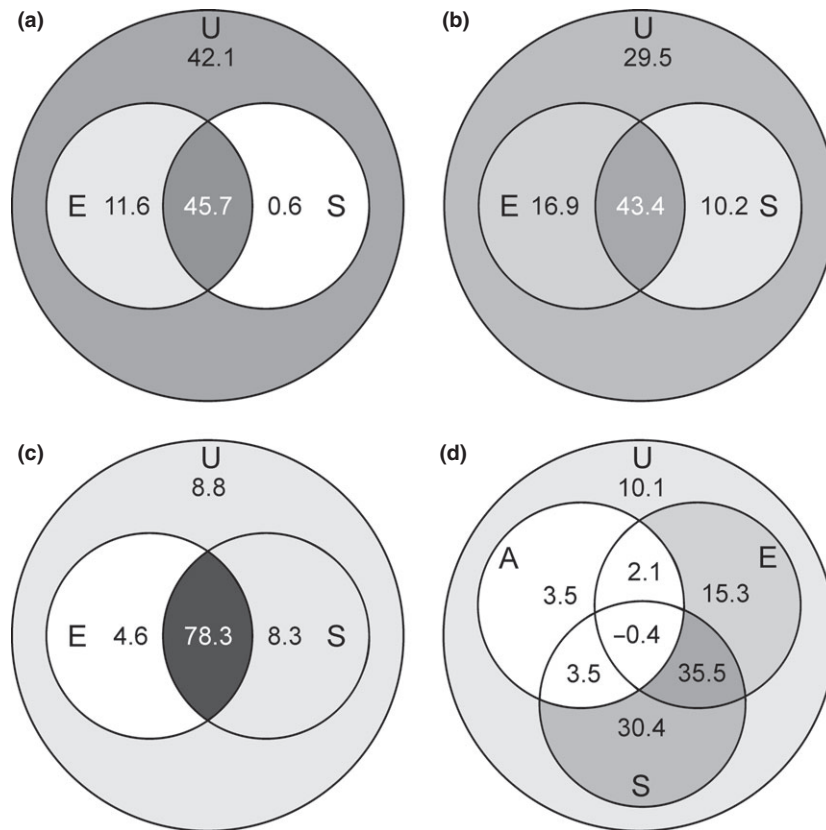
Country endemics were concentrated in southern Europe (Fig. 1b). A high positive Pearson correlation was found between log-transformed endemism and species richness ( $r = 0.88$ ,  $t = 11.07$ ,  $P < 0.001$ ). Therefore, similar spatial and environmental variables were found to be significantly related to endemism (Table 3a). Temperature variables and range of precipitation showed a positive linear relationship, and latitudinal variables presented a negative relationship with country-based endemism. Longitudinal variables showed a quadratic relationship, with the highest scores at low and high values of longitude. Environmental (E) and spatial (S) models were comprised of  $T_{ann}$ ,  $T_{min}$ ,  $T_{max}$ , and  $P_{drn}$ , and Lat and the quadratic function of Long<sub>min</sub>, respectively (Table 3a). The pure effects of environmental and spatial variables were small, being the great-

est part of the variance explained by the joint effect of both sets of variables (Fig. 2b).

The distribution of range-based endemism was similar to that of country-based endemism but not identical, as showed by the correlation between log-transformed scores ( $r = 0.67$ ,  $t = 5.19$ ,  $P < 0.001$ ). Differences between measures are because of the fact that small countries have lower numbers of exclusive country endemics, but higher numbers of narrow-ranged species living in a given country and the neighbours. Because of these differences, range-based endemism tends to be related to different predictors (Table 3b). Range-based endemism was positively related to temperature variables and to the altitudinal range, negatively related to latitude and presented a cubic relationship with longitude, with highest values to the west. Environmental (E) and spatial (S) models were comprised of Alt<sub>ran</sub>,  $T_{ann}$ , and  $T_{ran}$ , and Lat, Lat<sub>max</sub> and the cubic function of Long<sub>min</sub>, respectively (Table 3b). The pure effects of environmental and spatial variables were small, being the greatest part of the variance explained by the joint effect of both sets of variables (Fig. 2c).

### Spatial turnover

The dendrogram based on the  $\beta_{sim}$  dissimilarity matrix revealed the presence of five major faunal regions among continental European countries (Fig. 3a): (i) the Greek peninsula and the Balkan countries; (ii) European Turkey; (iii) Romania and Moldova; (iv) the Iberian Peninsula; and (v) the rest of Europe including Italy (ANOSIM  $R = 0.81$ ,  $P < 0.001$ ). Faunal composition showed no significant relationship with species richness (pseudo- $F = 1.67$ ,  $P = 0.148$ ) or the logarithm of species richness (pseudo- $F = 1.16$ ,  $P = 0.292$ ), but in contrast, 9% of the variation in composition was explained by endemism (log-transformed scores) (pseudo- $F = 2.11$ ,  $P < 0.041$ ). The assessment of the predictors explaining spatial turnover yielded significant contributions of the three sets of variables considered (A, E, and S models). If variables are considered individually, area, annual, minimum, and maximum temperature, and all terms of the third-degree polynomial of mean longitude and latitude (with exception of Long<sup>3</sup>) turned out to be significantly related to spatial turnover (Table 4). When included together in the models, Alt also turned out to be significantly related to spatial turnover. Among the spatial variables, only the four terms (Lat, Lat<sup>2</sup>, Long, and Long<sup>2</sup>) explaining a greater portion of variance were selected, to avoid spurious interpretations because of unbalanced comparison of models built with different numbers of predictors. Partitioning of the variation showed that the pure effect of A was non-significant (pseudo- $F = 1.46$ ,  $P = 0.152$ ), leaving the greatest part of the variation attributed to area in the fractions shared with E and S (Fig. 2d). In contrast, pure effects of E (pseudo- $F = 1.58$ ,  $P = 0.018$ ) and S (pseudo- $F = 2.58$ ,  $P < 0.001$ ) were significant and moderately important, especially the pure spatial fraction, that accounted for 30% of the variation in species composition. The joint effect of environmental and geographical sets of variables explained 35% of the variation. The variables that remained significant in the conditional models and thus were responsible for the pure effect of each set of predictors were Long, Lat<sup>2</sup> among the spatial variables, and



**Fig. 2.** Partitioning of the variation (%) in (a) richness, (b) country-based endemism, (c) range-based endemism, and (d) faunal composition of tenebrionid beetles, among groups of explanatory variables, A, area; E, environment; and S, spatial variables. U is the unexplained fraction. Grey tones are proportional to the amount of explained variation.

$T_{\text{ann}}$  among the environmental variables. Table 1 summarises main results according to the hypotheses tested.

#### Cross-taxon congruence of diversity patterns

Richness patterns of European tenebrionids and cerambycids were only moderately related ( $r = 0.47$ ,  $t = 3.11$ ,  $P = 0.004$ ), whereas correlation was higher for country-based endemism ( $r = 0.68$ ,  $t = 5.43$ ,  $P < 0.001$ ). However, it was the relationship between country species composition of both families that reached the highest value, as correlation between dissimilarity matrices was  $r = 0.72$  ( $P < 0.001$ ). As shown by the intercepts and slopes of these relationships, country richness and country-based endemism are in general lower for tenebrionids than for cerambycids, but spatial turnover is greater for tenebrionids than for cerambycids (Fig. 4).

## Discussion

### Richness and endemism

The latitudinal trend in species richness found in the European tenebrionids is consistent with the pattern reported for

most groups of species (Pianka, 1966; Rohde, 1992; Hawkins & Porter, 2003; Svenning & Skov, 2007a,b; Whittaker *et al.*, 2007; Baselga, 2008; Schuldt & Assmann, 2009).

Various hypotheses identified both current ecological factors (i.e. climate and geographical heterogeneity) and historical contingency (i.e. glaciation effects, differences in dispersal, and speciation rates) as important explanations for the latitudinal gradient (Gaston, 2000; Kerr, 2001; Whittaker *et al.*, 2001; Hawkins *et al.*, 2003; Svenning & Skov, 2007a). Topographic heterogeneity, levels of precipitation, and energy have been evoked to explain the increase in species richness from the pole to the equator in both hemispheres (Pianka, 1966; Rosenzweig, 1995; Kerr, 2001; Whittaker *et al.*, 2001; Blackburn & Gaston, 2003).

As for other organisms, the latitudinal trend found in European tenebrionids is mostly associated both with environmental and with spatial variables. Spatial heterogeneity does not seem to have a clear effect on total species richness, and the independent effect of climate is weak, being most of the variation explained by both climate and spatial position. Thus, any factor causing a spatial gradient in richness (as postulated by the hypothesis of an incomplete recolonisation process after glaciations) would cause richness to be correlated with climate, even if climate is not the causal factor. The number of endemics, being a component of the total number of species, was significantly



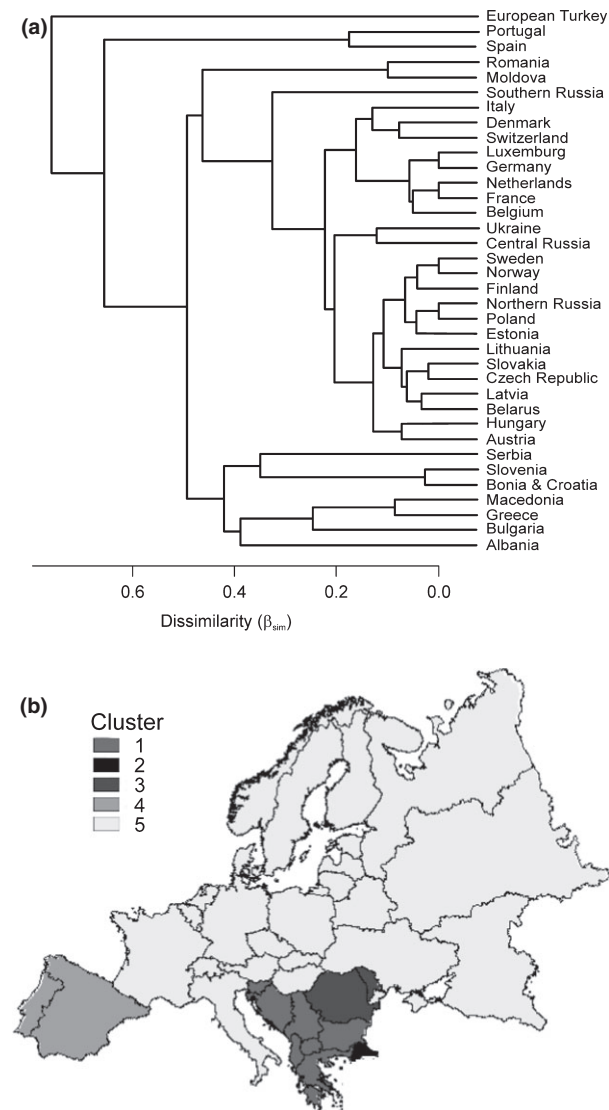
**Table 3.** Relationships between predictors and endemism and models for each group of variables. The sign of the relationships and percentage of explained variance ( $R^2$ ) are shown. A, S, and E are the area, spatial, and environmental models, respectively.  $f^2$  and  $f^3$  are the quadratic and cubic functions of the variable considered. For the acronyms of variables, see Methods.

Variable	Function (sign)	$R^2$	$F$	d.f.	$P$
(a) Country-based endemism					
Area	NS	0.04	1.27	1, 33	0.267
Long	Quadratic (-, +)	0.25	5.47	2, 33	0.009
Long <sub>min</sub>	Quadratic (-, +)	0.39	10.64	2, 33	0.000
Long <sub>max</sub>	NS	0.07	2.55	1, 34	0.120
Lat	Linear (-)	0.26	12.24	1, 34	0.001
Lat <sub>min</sub>	Linear (-)	0.36	19.41	1, 34	<0.001
Lat <sub>max</sub>	Linear (-)	0.18	7.36	1, 34	0.010
Alt	NS	0.03	0.88	1, 34	0.356
Alt <sub>ran</sub>	NS	0.09	3.44	1, 34	0.072
$T_{ann}$	Linear (+)	0.34	17.72	1, 34	0.000
$T_{ran}$	Linear (+)	0.13	5.07	1, 34	0.031
$T_{max}$	Linear (+)	0.33	16.91	1, 34	0.000
$T_{min}$	Linear (+)	0.27	12.69	1, 34	0.001
$P_{ann}$	NS	0.00	0.06	1, 34	0.802
$P_{ran}$	Linear (+)	0.15	5.80	1, 34	0.022
$P_{dri}$	NS	0.06	1.98	1, 34	0.168
$P_{drn}$	Linear (+)	0.15	6.14	1, 34	0.018
Model for E	$T_{ann} + T_{min} + T_{max} + P_{drn}$	0.54	12.30	4, 31	<0.001
Model for S	$f^2$ Long <sub>min</sub> + Lat	0.60	11.79	2, 33	<0.001
Model for E + S	$T_{ann} + T_{min} + T_{max} + P_{drn} + f^2$ Long <sub>min</sub> + Lat	0.71	9.56	6, 29	<0.001
(b) Area-based endemism					
Area	NS	0.00	0.01	1, 33	0.932
Long	Cubic (-, +, -)	0.28	4.13	3, 32	0.014
Long <sub>min</sub>	Cubic (-, +, -)	0.36	6.10	3, 32	0.002
Long <sub>max</sub>	NS	0.08	3.07	1, 34	0.089
Lat	Linear (-)	0.61	53.40	1, 34	<0.001
Lat <sub>min</sub>	Linear (-)	0.67	69.24	1, 34	<0.001
Lat <sub>max</sub>	Linear (-)	0.50	33.58	1, 34	<0.001
Alt	Quadratic (+, -)	0.34	8.37	2, 33	0.001
Alt <sub>ran</sub>	Linear (+)	0.15	5.97	1, 34	0.020
$T_{ann}$	Linear (+)	0.55	40.76	1, 34	<0.001
$T_{ran}$	Linear (+)	0.20	8.53	1, 34	0.006
$T_{max}$	Linear (+)	0.52	36.89	1, 34	<0.001
$T_{min}$	Linear (+)	0.40	23.08	1, 34	<0.001
$P_{ann}$	NS	0.01	0.50	1, 34	0.485
$P_{ran}$	NS	0.08	3.12	1, 34	0.087
$P_{dri}$	NS	0.02	0.79	1, 34	0.380
$P_{drn}$	NS	0.07	2.53	1, 34	0.121
Model for E	Alt <sub>ran</sub> + $T_{ann}$ + $T_{ran}$	0.87	38.92	3, 32	<0.001
Model for S	$f^3$ Long <sub>min</sub> + Lat + Lat <sub>max</sub>	0.83	51.70	5, 30	<0.001
Model for E + S	Alt <sub>ran</sub> + $T_{ann}$ + $T_{ran}$ + $f^3$ Long <sub>min</sub> + Lat + Lat <sub>max</sub>	0.91	35.05	8, 27	<0.001

correlated with total richness (see also Fattorini, 2007); thus, it is not surprising that endemic richness showed a similar latitudinal pattern. The positive influence of temperature on species richness would be a consequence of the thermophilic preferences of most tenebrionid species, but as the tenebrionids are also strongly dispersal limited, it is difficult to define which are the relative contributions of spatial gradients linked to dispersal limitation (Svenning & Skov, 2007a) and of the effects of energy gradients (Hawkins *et al.*, 2003). The influence of the spatial

range of precipitation of driest quarter makes tenebrionids quite different from cerambycids, which are correlated with energy, but neither with water availability or its spatial range. This difference might be related to the tenebrionids having smaller ranges, so species tend to be associated with specific raining regimes, what would cause the relationship between richness and precipitations heterogeneity.

The combined effect of  $T_{max}$  and  $P_{drn}$  suggests the relation between tenebrionids and productivity is not unimodal but



**Fig. 3.** Classification tree of the European countries based on tenebrionid species composition ( $\beta_{sim}$  dissimilarity and average linkage method) (a), and cluster groupings subject to ANOSIM tests (b).

direct within our study area. Although different mechanisms have been proposed to explain the influence of productivity on richness (see Tilman, 1982; Abrams, 1995), the direct productivity–diversity relationship observed in the European tenebrionids might be explained simply by a lack of very high temperatures in Europe. This lack of very high temperatures prevents a wide range of productivity that goes from moderate-to-extremely high, and this might cause the absence of an inverse slope in the relationship between species richness and productivity.

The effect of energetic constraints – as expressed by the minimum temperature of the coldest month – is more clearly detectable for endemics. Because tenebrionids are typically thermophilic insects (Fattorini, 2008), a direct relationship between richness and minimum temperature is not surprising.

However, the fact that pure effects of environmental and spatial variables were largely inferior to the joint effect of both sets of variables suggests that the correlation between endemism and climate could reflect a pattern caused by any spatially structured factor. Thus, high number of endemics in South Europe is probably a result of the joined effect of historical factors and temperature. The special history of southern regions, which were not glaciated, gave place to a greater long-term stability and thus more time for speciation and especially a lower number of extinctions, allowing communities to differentiate between regions and sub-regions.

Past climates in Europe have oscillated greatly from the Eocene to post-Pleistocene. During cold periods, such as Pleistocene glacials, species adapted to warm-temperate climates retreated into southern refugia, while cold-adapted species were favoured in expanding their range in central and southern Europe. By contrast, during warm periods, species adapted to warm-temperate climatic conditions expanded over large distances to central and even northern Europe, whereas cold-adapted species were driven away to the high north and to the high altitudes (see Çiplak, 2008 for references and discussion). Populations of glaciated territories that shifted their range southwards contributed to the biodiversity of these refugial areas and evolved as new populations or taxa in subsequent periods. Subsequent increases in temperature in warm periods led these populations to return northwards. Thus, communities in previously glaciated areas were re-established by these populations that begun to re-expand their range from the northern borders of their refuges. Therefore, Pleistocene refugia were both centres of speciation and sources of recolonisation (Hewitt, 1999; Ribera & Vogler, 2004).

Various lines of evidence support the existence of a main centre of post-glacial invasions of arthropods and plants in the southern part of Balkans and Turkey (Médail & Quézel, 1997; Bąkowski *et al.*, 2010), but an additional post-glacial centre on the Iberian Peninsula has been hypothesised for bats (Ulrich *et al.*, 2007) and possibly for collembolans (Ulrich & Fiera, 2009).

The parabolic relationship of endemics with longitude points to the presence of centres of endemism in the Iberian Peninsula (60% of taxa are endemic, with an impressive cladogenesis in the genus *Asida*) and the Balkans (22%), while the longitudinal trend in total species richness suggests that both these areas were also important centres of post-glacial dispersal. A further additional centre of endemism for the European tenebrionids is the Italian peninsula (22% of taxa are endemic). However, Italy does not show a really differentiated fauna. A homogenisation of the Italian fauna with those of central and northern countries can be explained by a twofold pumping mechanism. On the one hand, Italian coastal sites could have played an important role of refugial areas for thermophilous species with ‘Mediterranean’ ranges during Pleistocene glaciations because of their more favourable climate (Fattorini, 2008). On the other hand, the occurrence in Italy of some species with ‘northern’ distribution, which likely colonised Italy from central European regions, can be related to the presence of high altitude areas with colder climate and relicts of mesophilous phytocoenoses even in certain coastal sites (Fattorini, 2008).

**Table 4.** Relationships between predictors and variation in species composition (spatial turnover) and models for each group of variables. Percentages of variation explained (*inertia*) are shown. A, S, and E are the area, spatial, and environmental models, respectively. For the acronyms of variables, see Methods.

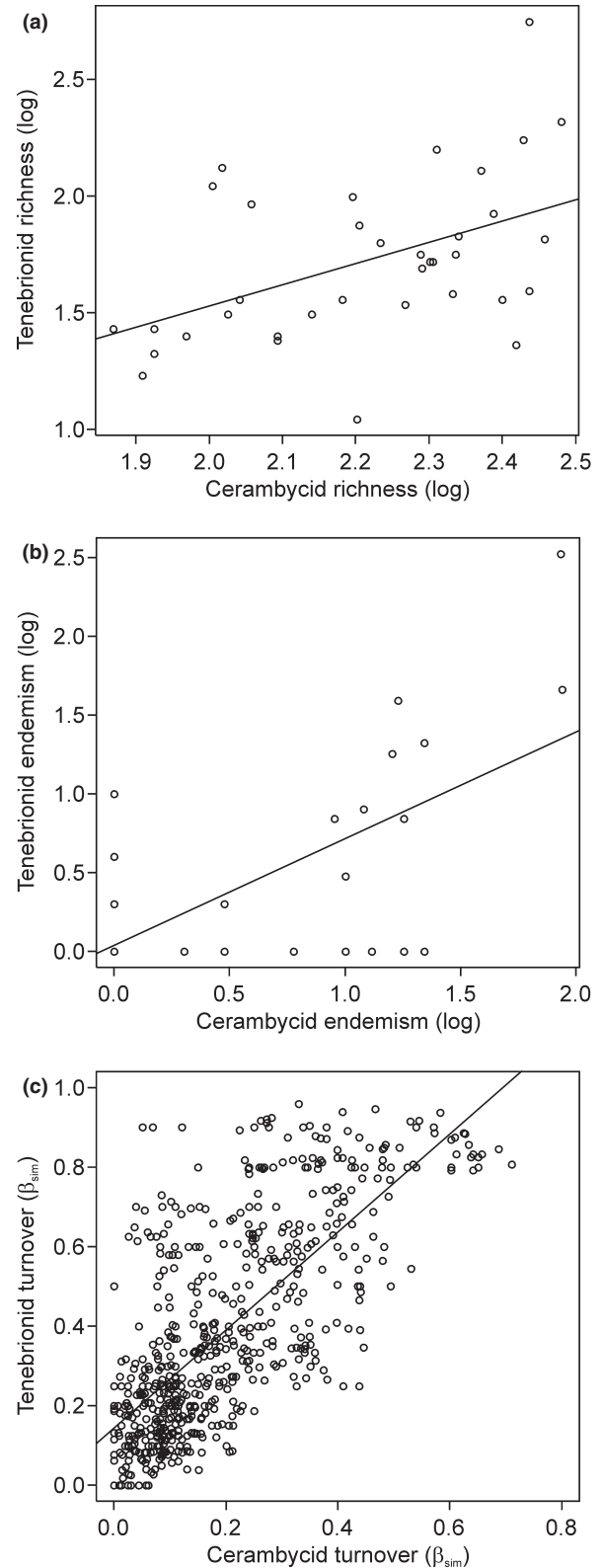
Variable	Variation (%)	Pseudo- <i>F</i>	<i>P</i>
Area	8.7	2.05	0.046
Long	18.0	4.56	< 0.001
Long <sup>2</sup>	10.5	2.51	0.037
Long <sup>3</sup>	8.2	1.94	0.090
Lat	24.2	6.41	< 0.001
Lat <sup>2</sup>	22.9	6.02	< 0.001
Lat <sup>3</sup>	21.5	5.60	< 0.001
Long*Lat	14.7	3.64	0.003
Long <sup>2</sup> *Lat	9.4	2.24	0.046
Long*Lat <sup>2</sup>	13.3	3.25	0.003
Alt	6.5	1.52	0.145
Alt <sub>ran</sub>	6.5	1.52	0.151
<i>T</i> <sub>ann</sub>	21.0	5.42	< 0.001
<i>T</i> <sub>ran</sub>	3.8	0.86	0.534
<i>T</i> <sub>max</sub>	20.6	5.30	< 0.001
<i>T</i> <sub>min</sub>	18.6	4.73	< 0.001
<i>P</i> <sub>ann</sub>	7.1	1.66	0.099
<i>P</i> <sub>ran</sub>	2.9	0.66	0.682
<i>P</i> <sub>dri</sub>	6.1	1.41	0.181
<i>P</i> <sub>dri</sub>	4.5	1.04	0.388
Model for A	8.7	2.05	0.046
Model for E	52.4	3.72	< 0.001
Model for S	68.9	5.32	< 0.001
Model A + E + S	89.9	4.13	< 0.001

Almost half of the variation in species richness remained unexplained. This may be due to unexpected absences determined by man-induced local extinction or other confounding factors, such as the different quality of the inventories or the possible occurrence of unrecognised sibling species.

#### Spatial turnover

In this study on tenebrionids, we found that turnover patterns are independent from richness gradients, i.e. variation in species richness is not correlated with variation in species composition because of spatial turnover, as previously found in the European cerambycids using the same methods (Baselga, 2008). Such independence may be because northern, less diverse faunas are the consequence of post-glacial recolonisation from the southern refugia. Thus, northern assemblages are subsets of southern ones. Faunas of northern countries are mainly composed of widespread species that reached more or less northern latitudes from southern refugia, whereas southern countries have these same widespread species plus the ones that have not left their refugia. These endemics are responsible for a relevant part of turnover, and thus the scores of endemism covary with composition.

Generally, the variation in tenebrionid species composition appeared regulated by the same environmental factors mostly responsible for variation in species richness, notably tempera-



**Fig. 4.** Correlations between richness (a), country-based endemism (b), and turnover (c) patterns of European tenebrionids and cerambycids.

tures. However, geographical position also had an important independent effect, as was previously found for Iberian leaf beetles (Baselga & Jiménez-Valverde, 2007) and European cerambycids (Baselga, 2008). Species composition varies distinctly not only with latitude but with longitude as well. In contrast with results obtained for cerambycids, where this longitudinal turnover does not generate (or covary with) the richness gradients, longitude had an important effect also on tenebrionid richness (especially for endemics), although less distinctly than it does on turnover.

The large purely spatial fraction indicates that current climatic conditions alone, although important, are not sufficient to explain geographical turnover patterns of European tenebrionids. Because of the high number of climatic factors used in this study, it is unlikely that unmeasured climatic variables possibly contained in the pure geographical fraction are responsible for the purely spatial fraction. Thus, pure geographical constraints, independent from climatic gradients but reflecting dispersal limitation or stochastic colonisation events, seem to have exerted an important role in determining both species richness gradients and species composition. Therefore, both the Pleistocene glaciations and neutral hypotheses are supported, but the fact that turnover is not uniform across Europe suggests the historical effects of Pleistocene glaciations had a deeper impact on tenebrionid assemblages than neutral dynamics. Indeed, species turnover is greater in Southern Europe, as evidenced by the higher number of clusters compared with the uniformity of northern assemblages (Fig. 3b).

#### *Comparison with cerambycids*

As a rule, tenebrionid turnover patterns were similar to those found in cerambycids. This suggests that, at continental scale, major macroecological factors determine similar turnover patterns even in groups, which differ considerably in dispersal ability and feeding habits. On the other hand, we found some important differences between these groups. Country richness and endemism seem in general lower for tenebrionids than for cerambycids, but this is mainly a result of the higher concentration of tenebrionid richness and endemics in certain countries. In other words, tenebrionid species distribution across Europe is much more uneven than in cerambycids, especially for the high concentration on endemic forms in certain southern countries, such as Greece, Italy, and notably Spain. This is consistent with the lower dispersal ability of tenebrionids, which are mostly flightless insects (Fattorini, 2006), while most cerambycids are winged insects capable of flying (Villiers, 1978; Bílý & Mehl, 1989).

#### **Conclusions**

Patterns of biodiversity are the product of a long history of evolution, diversification, and extinction interacting with local ecological processes, which are influenced by intrinsic characteristics of organisms and by a complex and changing geographical/ecological setting. Large-scale latitudinal diversity

gradients and interregional differences have obvious implications for assessing biodiversity for conservation purposes (Rex *et al.*, 1993), yet the mechanisms generating these patterns are not fully documented nor understood. Our study of geographical patterns of tenebrionid diversity in Europe provides new insights into invertebrate diversity patterns, using a general interpretative framework aiming to put biodiversity studies based on broad data in their appropriate context to be helpful for establishing comprehensive conservation policies.

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#### **Supporting Information**

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2011.00164.x:

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

**Appendix S2.** Tenebrionid distribution in European countries.

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