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Original article

Drivers of species richness in European Tenebrionidae (Coleoptera)

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ABSTRACT

The species-area relationship (SAR) and the latitudinal gradient in species richness are the most widespread and best-documented patterns in ecology, yet few studies have explored how the two patterns are interrelated. We used tenebrionid beetles as a species rich invertebrate group to investigate how area, habitat heterogeneity, climate, and ecological history act together in shaping species richness across Europe. We tested the effects of various climatic gradients on tenebrionid richness, with separate analyses for endemics and non-endemics. To take into account differences in area size among geographical units, we included species-area relationships using simultaneous autoregressive models. Although area had a significant effect on richness, the signal associated with temperature is so strong that it is still evident as a major driver. Also, the effect of area was only apparent when the effect of spatial coordinates had been accounted for, which has important implications for the use of SARs to locate diversity hotspots. The influence of latitude was mainly explained by a temperature gradient. Our findings support a postglacial European colonisation mainly from glacial southern refuges. Large Mediterranean islands were also important refugial areas.

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1. Introduction

The species-area relationship (SAR) and the latitudinal richness gradient are the two most widespread and best-documented patterns in ecology (see Rosenzweig, 1995; Lomolino et al., 2010 for reviews). There are two major groups of explanations for the increase in species richness with area. A first group of explanations assumes an effect of area *per se* based on sampling effects (larger areas contain more individuals and hence more species, and/or are larger targets for dispersing individuals), a second group considers increasing habitat heterogeneity over larger areas as the main reason for the SAR (Rosenzweig, 1995; Fattorini, 2007a; Lomolino et al., 2010). Both mechanisms are not exclusive and it is likely that they work, but with different intensity dependent on spatial scale, to cause the observed patterns (Kallimanis et al., 2008).

The latitudinal gradient in species richness has been mainly explained as a consequence of climatic gradients (Lomolino et al., 2010), although some alternative explanations have been proposed, especially for latitudinal gradients at smaller scales

(Currie et al., 2004; Hawkins et al., 2007; Lomolino et al., 2010 for a review).

Differences in climatic factors at local scales are typically moderate, which makes it difficult to appreciate their role in determining species richness. By contrast, an area is easy to measure at all scales, from square millimetres to the entire surface of the Earth (Dengler, 2009). This is the reason why SARs have been studied at many scales, while studies in latitudinal variations in species richness are typically performed at global or continental scales (e.g., Kocher and Williams, 2000; Patten, 2004; Ulrich and Fiera, 2009).

At continental scales, both area and climatic variables can emerge as important correlates of species richness. Most studies have focussed on taxa for which large databases are available, such as vertebrates and plants, whereas insects have been traditionally neglected (see Diniz-Filho et al., 2010). However, independent spatial models for many taxa are needed for an assessment of which factors are tightly correlated with large-scale differences in species richness and whether and how their importance differs in organisms with different ecologies.

In this paper, we used tenebrionid beetles (Coleoptera: Tenebrionidae) as a species rich invertebrate group to investigate how climate and ecological history act together in shaping species richness patterns across Europe controlling for differences in size of geographical units and spatial autocorrelation. We considered

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multiple environmental variables that can plausibly explain the latitudinal gradient (Hawkins and Diniz-Filho, 2004). This way, we took advantage of the additional power provided by testing multiple hypotheses simultaneously (Hawkins and Diniz-Filho, 2004). In particular, we tested the following predictions about variation in species richness:

Prediction 0. The number of species should increase with area (species-area relationship, SAR). Area has been proven to be an important predictor of species richness of mammals and birds at different scales (Rosenzweig, 1995; Ricklefs and Lovette, 1999) and holds for tenebrionids at small to regional scales (Fattorini, 2002, 2007a, 2009a,b,c). Thus, area should be an important correlate of tenebrionid species richness in Europe. However, several studies (reviewed in Lomolino and Weiser, 2001) argued that the SAR does not hold for small islands (but see Tjørve and Tjørve, 2011), and others argued that a SAR can be still found in small islands, but with a different pattern from that of larger islands (Gentile and Argano, 2005). If Tjørve and Tjørve (2011) critique of the small island effect is correct, we expected not to see any small island effect for European Tenebrionidae, with a single SAR adequately fitting also areas which are much smaller than others.

Because the SAR may obscure other relationships, we have controlled for the effect of area in all other predictions relating species richness with other environmental variables.

Prediction 1. Species richness and latitude should correlate negatively (Hawkins and Diniz-Filho, 2004; Hillebrand, 2004). Accordingly, species richness should peak in Mediterranean countries and decrease continuously towards Great Britain, Scandinavia, and other northern countries. Latitude is not an ecological factor in itself, but a proxy for a number of things, which include climatic gradients. If a correlation between species richness and latitude is a reflection of change in climatic parameters, significant correlations are expected with temperature.

Prediction 2. According to Hawkins and Pausas (2004) the observed association between plant richness and animal richness is not directly causal, but determined by a shared response of plants and animals to the same environmental (namely climatic) variables and to area. Although many tenebrionid species are poly-saprophagous, several groups are arboreal, associated with particular tree species or vegetation types. So we predict a positive correlation between vegetational richness and tenebrionid species richness.

Prediction 3. Islands and mainlands should differ in species numbers even after correcting for other factors, such as area and climate, because of a number of effects related to isolation. In particular, islands should have impoverished faunas because they are hardly colonised by species with reduced dispersal ability (Dapporto and Dennis, 2009, 2010). Also, classical island biogeography and recent models on island colonisation predict island SARs to have lower intercepts and higher z-values, possibly because species spatial turnover among islands tends to be higher than among mainland areas (Rosenzweig, 1995; Ulrich and Fiera, 2009).

2. Material and methods

2.1. Biological data

We considered the faunal composition of 1478 native species and subspecies of Tenebrionidae of 63 European countries and larger islands (Fig. 1) as given in Fattorini and Ulrich (2012). To compile country and island lists, we checked and integrated data reported by Löbl and Smetana (2008) using the most recent comprehensive work(s) available for each country, updated with successive literature if any. We referred to older works if they contained important information not considered in the most recent

works, or in case of inconsistencies among authors. A list of scrutinised papers are reported in Fattorini and Ulrich (2012).

It is difficult to evaluate the completeness of these inventories. In general, we applied a very conservative approach and used in this study only countries which were investigated with high sampling intensity and for which species lists were considered fairly complete. For this, we restricted the analysis to countries for which recent checklists were available and which were considered adequately sampled by expert taxonomists and local entomologists with faunistic experience (see Acknowledgements). This led to the exclusion of the following countries: Andorra, the Faroe Islands, the Channel Islands, Gibraltar, Northern Ireland, Iceland, Liechtenstein, Monaco, Svalbard and Jan Mayen, Franz-Josef Land, the Kaliningrad region, Novaya Zemlya, San Marino, and Vatican City. We included some Macaronesian Islands (Canary Islands, Azores, and Madeira) as they certainly pertain to the Western Palearctic and have strong biogeographical similarities with Europe. In total we retained 49 countries and major islands.

As for most arthropod groups, fine-grained distribution data are unavailable. However, previous work (e.g., Ulrich and Buszko, 2003; Baselga, 2008; Ulrich and Fiera, 2009; Bąkowski et al., 2010) showed 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; Kiel and Hawkins, 2009; Fattorini and Baselga, 2012 for a discussion). In particular, Kiel and 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.

Because the current taxonomic dividing line between species and subspecies, as applied to the tenebrionids of Europe, is arguably arbitrary, 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) (see also Fattorini and Ulrich, 2012). Species and subspecies will be referred to as 'species' for simplicity. Furthermore, the present paper includes the former family Lagriidae as a subfamily within the Tenebrionidae. 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 definitively less reliable than those obtained for the other Tenebrionidae.

We performed separate analyses for endemic and non-endemic species. In spatially based quantitative measures of endemism, known as threshold endemism, weighted endemism, and corrected weighted endemism (see Fattorini, 2007b), 'endemism' is considered as a measure of the size of the distribution range of a species. However, 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, 2007b). In this paper we used this second concept of endemism. Thus, we computed the number of species living exclusively in each country/island as a measure of the uniqueness of the fauna of each area (country-based endemism). This approach is the same used in other studies about the distribution of animals and plants in Europe (e.g., Ulrich and Buszko, 2003, 2005; Fattorini, 2007c) and is particularly important because most conservation programmes are performed at the national level (see Fattorini, 2009d).

Table 1

Parameter values (SR coefficients), standard errors and associated probability levels of complete (a, b, and c), and best-fit (d, e, and f) spatial autoregressive models.

Variable	SR coefficient	Standard error	$P(t)$	Variable	SR coefficient	Standard error	$P(t)$	Variable	SR coefficient	Standard error	$P(t)$
(a) Total species richness				(b) Mainland species richness				(c) Island species richness			
Constant	−1.781	1.210	0.150	Constant	−2.591	1.386	0.073	Constant	0.641	2.947	0.830
ln area	0.285	0.064	<0.001	ln area	0.508	0.099	<0.001	ln area	0.045	0.128	0.740
Elevation/area	0.082	0.292	0.780	Elevation/area	5.603	2.477	0.032	Elevation/area	−0.150	0.316	0.650
Precipitation	−0.006	0.004	0.140	Precipitation	−0.002	0.004	0.579	Precipitation	−0.018	0.010	0.120
$N_{T<0}$	0.003	0.004	0.510	$N_{T<0}$	−0.005	0.004	0.289	$N_{T<0}$	0.02	0.011	0.130
T_{mean}	0.168	0.044	<0.001	T_{mean}	0.092	0.046	0.056	T_{mean}	0.178	0.096	0.110
ΔT	0.006	0.030	0.870	ΔT	0.013	0.040	0.813	ΔT	−0.027	0.042	0.550
(d) Total species richness				(e) Mainland species richness				(f) Island species richness			
Constant	−2.328	0.649	<0.001	Constant	−3.372	1.319	0.016	Constant	−2.867	1.865	0.153
ln area	0.29	0.005	<0.001	ln area	0.485	0.097	<0.001	ln area	0.277	0.112	0.031
T_{mean}	0.188	0.043	<0.001	Elevation/area	4.274	2.433	0.090	T_{mean}	0.263	0.065	0.002
ΔT	0.004	0.003	0.280	T_{mean}	0.129	0.028	<0.001				

Tenebrionid species richness (response variable) was always $\ln(S + 1)$ transformed. Complete autoregressive models were developed for total species richness (a: $n = 49$, $R^2 = 0.54$; $P < 0.001$; AICc: 85.6), mainland species richness (b: $n = 34$, $R^2 = 0.66$; $P < 0.001$; AICc: 70.99), and island species richness (c: $n = 15$, $R^2 = 0.52$; $P > 0.05$; AICc: 59.61). Best-fit models were also developed for total species richness (d: $n = 49$, $R^2 = 0.53$, $P < 0.001$; AICc: 79.1), mainland species richness (e: $n = 34$, $R^2 = 0.62$; $P < 0.001$; AICc: 62.15), and island species richness (f: $n = 15$, $R^2 = 0.52$; $P < 0.001$; AICc: 25.85). $N_{T<0}$ is the average number of days with temperatures below zero, T_{mean} is average annual temperature and ΔT is the yearly temperature difference. AICc values of the best-fit models were always substantially (Burnham and Anderson, 2002) lower than those of the full models.

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

2.2. Statistical analyses

We evaluated the importance of nine geographical and climate variables as correlates of tenebrionid species richness to test the aforementioned predictions (values of geographical and climatic variables were taken from Fattorini and Ulrich, 2012; latitudinal and longitudinal ranges were taken from Google Earth). We tested climate and other gradients while correcting for area of the units under study (countries/islands) by introducing area as a covariate in all models.

Prediction 0. For each European country and larger island, we determined the area in square kilometres and the latitude and longitude of its geographical centroid. We used a linearised power function to investigate the SAR with spatial autocorrelative models.

Prediction 1. In Europe, climate tends to vary both latitudinally (from boreal to Mediterranean conditions) and longitudinally (reflecting a gradient from maritime to continental conditions). To investigate how the latitudinal and longitudinal patterns in species richness are related to climatic gradients we used average annual precipitation (P_{mean}), average annual temperature (T_{mean}), yearly temperature difference ($\Delta T = T_{July} - T_{January}$, where T_{July} is mean temperature in July and $T_{January}$ is mean temperature in January), and average number of days with temperatures below zero ($N_{T<0}$) as an estimate of winter length. In addition to centroids, we also included latitudinal and longitudinal ranges as the difference of the respective maximum and minimum values to take into account the different latitudinal extent of the areas under study. For example, Italy has a centroid latitude similar to that of Yugoslavia, Bulgaria,

Macedonia, and Albania, but Italy has a larger latitudinal range that can explain a higher richness. Because climates tend to vary not only according to latitude and longitude, but also with elevation, we have also considered the quotient of highest elevation through country/island area as a possible measure reflecting elevational variation in temperature (Ricklefs et al., 2004).

Prediction 2. We compiled data of the number of vascular plants (S_{plants}) from data in EarthTrends: The Environmental Information Portal (http://earthtrends.wri.org and additional online sources). However, reliable estimates of plant species richness were not available for all islands and countries. Thus, we did not considered plant species numbers in our basic models which included all countries/islands, but developed separate analyses for the subset of geographical units for which plant data were available.

Prediction 3. We analysed mainland and island areas separately and compared the respective SARs.

Calculation of Moran's index I for ten equally sized distance classes (Rangel et al., 2010) showed that tenebrionid species richness and climate data were significantly spatially autocorrelated at the first two classes (Moran's I for S, $N_{T<0}$ and ΔT: $P_{I=0} < 0.05$). Therefore, to test the aforementioned predictions, we used spatial autoregressive models to account for spatial autocorrelation (Liechstein et al., 2002; Beale et al., 2010; see also Fattorini and Ulrich, 2012; Hawkins, 2012). We applied a generalised least squares estimation for autoregressive models as implemented in SAM (Spatial Analyses in Macroecology) v. 4.0 software (Rangel et al., 2010). Tenebrionid and plant species richness and area entered always as ln-transformed data. To estimate the relative influence of each variable, we used squared semi-partial correlations between the variables (Legendre and Legendre, 1998). We used the corrected Akaike information criterion (AICc) for model choice by comparing all variable combinations and selected models with the lowest AICc values. These values were in all cases substantially (Burnham and Anderson, 2002) lower than all competing models. Errors refer to standard errors.

3. Results

A simple power function for the SAR applied to the whole data set by OLS regression of ln-transformed variables is not significant ($\ln(S + 1) = (0.08 \pm 0.06) \ln A + (3.1 \pm 0.7)$; $R^2 = 0.03$, significance of constant: $P = 0.01$; significance of slope: $P = 0.21$; model: $F = 1.613$,

Table 2
Parameter values (SR coefficients), standard errors, and associated probability levels of the complete spatial autoregressive (SR) models for $\ln(S + 1)$ transformed tenebrionid species richness with area and spatial variables.

Variable	SR coefficient	Standard error	$P(t)$	Variable	SR coefficient	Standard error	$P(t)$	Variable	SR coefficient	Standard error	$P(t)$
(a) Total species richness				(b) Mainland species richness				(c) Island species richness			
Constant	5.020	0.713	<0.001	Constant	4.477	1.177	<0.001	Constant	6.544	1.142	<0.001
ln area	0.241	0.067	<0.001	ln area	0.344	0.093	<0.001	ln area	0.320	0.090	0.007
Latitude	−0.099	0.013	<0.001	Latitude	−0.086	0.012	<0.001	Latitude	−0.163	0.030	<0.001
ΔLatitude	0.004	0.046	0.940	ΔLatitude	−0.049	0.038	0.210	ΔLatitude	0.308	0.127	0.050
Longitude	0.003	0.007	0.650	Longitude	−0.021	0.006	0.003	Longitude	0.014	0.010	0.240
ΔLongitude	0.046	0.028	0.120	ΔLongitude	0.047	0.024	0.064	ΔLongitude	−0.239	0.115	0.070

Separate models were developed for total species richness (a: $n = 49$, $R^2 = 0.62$; $P < 0.001$), mainland species richness (b: $n = 34$, $R^2 = 0.81$; $P < 0.001$), and island species richness (c: $n = 15$, $R^2 = 0.70$; $P = 0.03$). ΔLatitude and ΔLongitude are latitudinal and longitudinal ranges, respectively.

$P = 0.21$). If an autoregressive model is applied, the SAR is still insignificant ($F = 0.407$; $P = 0.527$) but the importance of area becomes apparent ($\ln(S + 1) = (0.151 \pm 0.06) \ln A + (2.0 \pm 0.7)$; $R^2 = 0.08$, significance of constant: $P = 0.007$; significance of slope: $P = 0.013$). When other variables are included in a more general model, species richness consistently increased with area (Prediction 0; Tables 1–3). However the area effect for the islands was statistically insignificant after Bonferroni correction (Table 1; corrected $P > 0.1$) and slope values were below 0.3 (Table 1). Latitudinal and longitudinal ranges of countries and islands did not significantly enter the models that include the geographical variables (Table 2). Separate analyses for endemic and non-endemic species supported these findings (Appendix A, Tables S1–S3).

Latitude and longitude corrected tenebrionid SAR slopes and intercepts (predicting species densities) (Table 2) did not significantly ($P > 0.1$) differ between mainlands ($z = 0.44 \pm 0.07$, ln intercept $= -0.56 \pm 0.34$) and islands ($z = 0.27 \pm 0.11$, ln intercept $= 0.17 \pm 0.44$) (Fig. 2). These results do not point to differences between island and mainland species-area relationships (Prediction 3). Our models predict between one and two tenebrionid species per square kilometre on islands and mainlands. Our data do also not point to any small island effect. Species richness on the two smallest islands below 1000 km² (Malta and Madeira) did not deviate from the overall SAR (Fig. 2). The fact that mainland and island SAR slopes did not significantly differ is equivalent to the statement that there may be no flattening of the SAR at smaller (island) areas (Fig. 2) contrary to the pattern predicted by the small island effect.

We used the best-fit autoregressive models of Table 1 to predict the expected species richness for the six major islands in the Mediterranean (Corsica, Sardinia, Sicily, Crete, Cyprus, and the Baleares; the Baleares were considered a single island because species distribution on each Balearic island is not well known). If the mainland best-fit model (Table 1e) is used to predict island species richness, there is no significant difference between the observed values of species richness and those predicted by the mainland model (Wilcoxon matched pairs test, $T = 3$, $Z = 1.572$,

$P = 0.116$). A similar result is obtained if the island best-fit model (Table 1f) is used to predict the species richness of the aforementioned Mediterranean islands ($T = 6$, $Z = 0.943$, $P = 0.345$). Both results suggest that the tenebrionid faunas of Mediterranean major islands may not be impoverished in comparison with the mainland faunas or the general island trend.

Species richness and latitude correlated negatively (Prediction 1, Table 2; Appendix A, Tables S1 and S2). However, significant correlations between species richness and temperature suggest that the correlation between species richness and latitude is at least in part a reflection of the change in climatic parameters (Table 2; Appendix A, Tables S1–S3).

Vascular plant species richness appeared to be a highly significant correlate of tenebrionid species richness (Prediction 2). AICc best-fit models for total and non-endemic species richness (Table 3) identified annual temperature and plant richness as being highly significant correlates, while discarding other climate and structure variables as well as area. Endemic species richness however was not significantly correlated with plant species richness (Table 3c). We did not run separate analyses for islands and mainlands due to the low number of islands with reliable plant estimates.

A separate analysis for cosmopolitan species, which were not included in the prior analyses, revealed that their species richness was only weakly correlated with area ($S = 0.66A^{013}$; $R^2 = 0.1$; $P = 0.02$), with no any other environmental or geographical variable being significant (all regression parameters $P > 0.1$, not shown). This indicates that these species are not strictly correlated with environmental factors, but only respond to area, with larger countries being probably more prone to be colonised.

4. Discussion

Recent studies on European bats (Ulrich et al., 2007) and a few invertebrate taxa, such as butterflies (Dennis et al., 1998; Ulrich and Buszko, 2003, 2005; Fattorini, 2007c), clearwing moths (Bąkowski et al., 2010), aquatic beetles (Ribera et al., 2001), longhorn beetles (Baselga, 2008), hoverflies and dragonflies (Keil et al., 2008a,b), and

Table 3
Parameter values (SR coefficients), standard errors, and associated probability levels of the best-fit spatial autoregressive (SR) models (lowest AICc, all scores are substantially (Burnham and Anderson, 2002) lower than those of the full models) for $\ln(S + 1)$ transformed values of total number of tenebrionid species (a: $n = 41$, $R^2 = 0.44$; $P < 0.001$), number of non-endemic species (b: $n = 41$, $R^2 = 0.56$; $P < 0.001$), and number of endemics (c: $n = 41$, $R^2 = 0.59$; $P < 0.001$).

Variable	SR coefficient	Standard error	$P(t)$	Variable	SR coefficient	Standard error	$P(t)$	Variable	SR coefficient	Standard error	$P(t)$
(a) Number of species				(b) Number of non-endemics				(c) Number of endemics			
Constant	−1.801	1.215	0.15	Constant	−2.603	0.943	0.009	Constant	−5.778	1.559	<0.001
T_{mean}	0.094	0.026	<0.001	ln area	0.169	0.067	0.020	ln area	0.319	0.106	0.005
S_{Plant}	0.607	0.151	<0.001	T_{mean}	0.087	0.023	<0.001	T_{mean}	0.319	0.047	<0.001
				S_{Plant}	0.461	0.147	0.003				

The models include only those countries/islands, for which reliable estimates of the number of vascular plants (S_{Plant}) were available. T_{mean} is average annual temperature. Area did not significantly enter the model for total number of species.
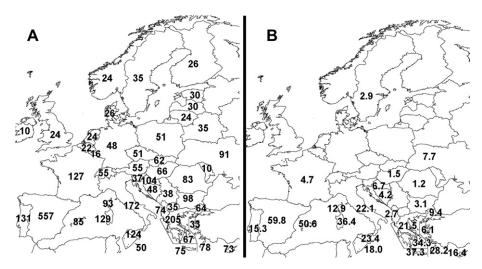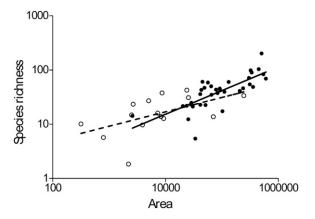
Fig. 1. Number of tenebrionid taxa (species and subspecies) in European countries (A) and percentage of endemics (B; countries in blank do not have any endemic species). Atlantic islands are not shown.

springtails (Ulrich and Fiera, 2009), found that area is significantly correlated with species richness. Our results are in line with these findings (Prediction 0): area appeared to be the most important predictor of tenebrionid richness (Table 1). Although our use of arbitrarily defined geographical units makes it difficult to attach a particular biological interpretation to this result, it is important in removing the effect of area to disclose the effects of other variables, such as the mean annual temperature and latitude.

On the other hand, a comparison of separate SAR models (e.g., for island and mainland areas), constructed using the same criteria, may reveal non-obvious patterns. Contrary to most studies (Rosenzweig, 1995; Dennis et al., 2008; Ulrich and Fiera, 2009), our island SAR slopes were not higher than the respective mainland ones (Table 2, Fig. 2), which is in contrast with Prediction 3, and for island endemics even insignificant (Appendix A). Crawley and Harral (2001) attributed this slope difference to the difference in mainland and island areas used to calculate the SAR. Because SARs from regional to global scales are known to be triphasic (Preston, 1960; Shmida and Wilson, 1985) with continental wide SARs

Fig. 2. Latitude (Table 2a model) corrected SARs of European Tenebrionidae for 15 islands (open circles) and 34 mainlands. Mainland OLS regression (solid line): $S = 0.27A^{0.44}$; $R^2 = 0.56$; $P(t) < 0.001$. Island OLS regression (dotted line): $S = 1.47A^{0.27}$; $R^2 = 0.29$; $P(t) < 0.01$. Areas in square kilometres. Axes are log-transformed. The two equations were obtained regressing latitude corrected species richness values (CSR) against mainland and island areas separately. To obtain CSR values of species richness we calculated expected richness values from the constant and latitude coefficient of the complete model of Table 2a (ESR) and then subtracted these ESR values from species richness values.

having the steepest slopes, island SARs might have shallower slopes than mainland SARs. Although we used arbitrarily defined geographical units, we think this could not be invoked as a bias to explain our results, because in the present case island and mainland areas overlap to a large degree (Fig. 2). Another important result of our study is that the tenebrionid faunas of major islands in the Mediterranean were not impoverished. This strongly contrasts with what is known for lepidopterans, which show clearly impoverished faunas on Mediterranean islands such as Sardinia and Corsica (Dapporto and Dennis, 2009, 2010). Most probably, these islands, not affected by glaciations, have largely retained their Tertiary tenebrionid faunas. Moreover, because of the long-time isolation and poor dispersal ability of most tenebrionids, these islands evolved high numbers of endemic taxa, which further increased their diversity (see Fattorini and Ulrich, 2012). It is also important to note that tenebrionid species peaked at about 40°N (Spain, Greece, and Italy). Hence, the general distribution of tenebrionid richness and endemism is in accordance with the hypotheses that the main centres of glacial refugia and postglacial invasions of arthropods and plants were placed in countries in southern Europe (Médail and Quézel, 1997; Svenning and Skov, 2007). The 'anomalous' occurrence of an endemic taxon (*Blaps sinuaticollis suecica*) in Sweden might be explained by the presence of cryptic refugia in snowless regions of the Scandinavian sheets (see Lomolino et al., 2010).

Latitude and longitude corrected tenebrionid SAR slopes for mainland regressions ($z > 0.34$, Table 2, Fig. 2) were higher than reported for many other arthropod taxa (Rosenzweig, 1995; Drakare et al., 2006). This fast increase in species richness with area points to a comparably higher regional species turnover for tenebrionids. This high species turnover is also best explained by the low dispersal ability of these beetles (Fattorini, 2008). Moreover, our SAR slopes were similar to the SARs calculated for the tenebrionids of Mediterranean archipelagos (Fattorini, 2007a, 2009b).

Latitude is typically a major predictor of variation in species richness at the continental scale (Hawkins et al., 2004) and reflects the influence of climatic variables (Currie et al., 2004; Hawkins et al., 2007) (Prediction 1). Our results are also in line with these findings, showing that temperature plays a dominant role even after using a single measure for each country and controlling for the confounding area effect. In particular, average temperature proved to be the most important variable (after the obvious effect of area) in determining richness of tenebrionids, which are typically

thermophilous insects (Fattorini, 2008). Winter length and annual maximum temperature difference have been proved to be of importance for European bats and springtails (Ulrich et al., 2007; Ulrich and Fiera, 2009), whereas they appeared not relevant for tenebrionid richness. Most tenebrionids are active only in spring and summer, passing the winter as larvae or as hibernating adults (Fattorini, 2008) and are therefore not directly exposed to the effects of winter length. This pattern of life history might explain the tolerance to winter length and very low winter temperatures.

The coefficient for temperature in Table 3 can be interpreted as the effect of temperature on tenebrionid richness after correcting for plant richness, thus suggesting that temperature has an effect on tenebrionid richness independently of plant richness. On the other hand, the significant coefficient for plant richness in Table 3 shows that temperature is not the only variable that affects tenebrionid richness, and that there is an effect of plant richness independently of climate. Thus, our study did not offer a full support to Hawkins and Pausas (2004) hypothesis (Prediction 2) (Table 3) about the importance of plant richness. According to Hassan et al. (2005), one of the ecosystem functions provided by diverse plant communities is the maintenance of rich animal communities. Thus, the number of animal species in an area might be expected to be influenced by the number of plant species (Siemann et al., 1998), which is supported by our findings. Tenebrionids are typically detritivores, thus an increase in tenebrionid richness with plant richness cannot be simply explained as a reflection of a broader food diversity. Non-trophic factors responsible for this correlation may include shelter, oviposition sites, resting sites, overwintering places, refuges from predators, etc. (cf. Fattorini, 2008). The lack of significance for the influence of plant richness on endemic diversity suggests that tenebrionid cladogenesis is not driven by coevolution with plants, and that these insects are mostly generalists whose evolution is mainly influenced by 'geodetic' (*sensu* Cook, 2008) processes.

Finally, it is important to note that although area is the strongest predictor of species richness in our models, the influence of area is not evident when a SAR is fitted with a simple species–area function. This insignificance is largely a consequence of the effects of spatial autocorrelation due to the spatial non-independence of the geographical units used in our study. Moreover, the importance of area appears more distinctly when other variables are included in multiple models. This incongruence has important implications for the identification of hotspots based on simple SARs. Hotspots are frequently identified as those areas that have more species than expected on the basis of a SAR (Fattorini, 2006). Our results strongly call for the application of spatially explicit SAR modelling, when geographical units are spatially structured, a common situation when units based on political/administrative borders are used in hotspot analyses (see Ulrich and Buszko, 2005). Inadequately modelled SARs might identify areas of minor importance and/or miss important hotspots.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.actao.2012.05.003.

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