Original article

# Latitudinal trends in body length distributions of European darkling beetles (Tenebrionidae)

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ABSTRACT

The largest species of many invertebrate taxa occur in tropical regions. Nevertheless systematic studies on temperature and latitudinal trends in body size distributions of specific taxa have given inconclusive results and did not unequivocally corroborate existing models of body size evolution. We studied regional body size distributions of tenebrionid beetles across Europe to infer climate dependent trends that could be linked to the postglacial colonization of Europe. Even after correction for sample size effects and phylogenetic relatedness we found an increase in average and maximum body length towards southern Europe. Body size distributions were right skewed and skewness and the width of the distribution decreased significantly with temperature, indicating a more homogeneous species composition with respect to body size at lower latitudes. Our study supports the view that maximum size of heterothermic arthropods is limited by ambient temperature, which triggers the rate of metabolism. Our results contradict models that predict an increase in body size at higher latitudes.

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## 1. Introduction

The study of animal body sizes has a long tradition in biogeographical and evolutionary research (Peters, 1983; Calder, 1996; Watt et al., 2010; Meiri, 2011). Bergmann (1847) noticed that the body size of closely related endothermic vertebrates increases at higher latitudes and explained this trend by the lower surface/volume ratio of large animals, which helps endotherms to conserve heat and therefore to live in cold climates. The rule outlined by Bergmann has been repeatedly confirmed for endothermic vertebrates (Lomolino et al., 2010). Attempts to apply this rule to ectothermic vertebrates (Meiri and Thomas, 2007; Olalla-Tárraga and Rodriguez, 2007; Pincheira-Donoso et al., 2008; Shelomi, 2012), however, gave inconclusive results.

Theoretically, the geometric heat conservation arguments behind Bergmann's rule apply to insects too, although in general the effect should be small because of the much lower heat production. On the other hand, the (semi-)passive oxygen dissipation that is ubiquitous in insects involves a more effective respiration and cell functioning at higher temperatures (Speight et al., 2008), which would allow species to attain larger body sizes at higher ambient temperature (Kaiser et al., 2007). This implies a positive interspecific temperature – body size relationship (TBR) contrary to Bergmann's pattern as the rule for invertebrates (Makarieva et al., 2005; but see Heinrich, 1977). However, studies on temperature and latitudinal trends in arthropod body size distributions have given inconclusive results (e.g., Cushman et al., 1993; Barlow, 1994; Hawkins and Lawton, 1995; Brehm and Fiedler, 2004; Huston and Wolverton, 2011; Shelomi, 2012) and pointed to taxon and life history specific factors that constrain body size, such as taxon specific desiccation resistance (Remmert, 1981; predicting a positive TBR), resource storage and starvation resistance (Cushman et al., 1993; positive TBR), resource limitation (Turner and Lennon, 1989; negative TBR), food availability (Peat et al., 2005; positive TBR), freezing resistance (Lee and Costanzo, 1998; positive TBR), net primary productivity (Huston and Wolverton, 2011; often negative TBR), seasonality (Peat et al., 2005; positive TBR), and metabolic constraints (Mousseau, 1997; Walters and Hassall, 2006; positive TBR). The strongest point in favour of a positive TBR in terrestrial arthropods made so far was provided in a study by Entling et al. (2010), who found a linear increase in average European spider

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body length with decreasing latitude and increasing temperature at different spatial resolutions. Further, the compilation of Makarieva et al. (2005) reported for major invertebrate taxa, particularly for arthropods, largest body sizes in low latitudinal tropical areas. On the other hand, Ulrich and Fiera (2010) observed a peak in average and maximum body size of regional European springtail faunas at intermediate latitudes.

The oxygen dissipation and other models do not make predictions about minimum size in invertebrates. The smallest terrestrial arthropods of the Hymenopteran family Mymaridae and of eriophyid mites with body length below 0.2 mm are known from the majority of climatic regions (Huber and Noyes, 2013; Mohanasudaram, 1987). However, there is no meta-analytical study on climatic gradients of minimum arthropod size. If minimum body size were independent of ambient temperature, the increase in maximum body size towards lower latitudes would imply a higher number of large bodied species in regional faunas. This bias would then directly translate into a less right-skewed faunal body size distribution (*BSD*) at lower latitudes (Fig. 1). However, in contrast with this expectation, Entling et al. (2010) reported a decrease in the skewness of European spider size distributions towards lower latitude, whereas Ulrich and Fiera (2010) did not find any clear latitudinal skewness gradient in European springtails. These contrasting results do not point to any simplistic climatic or physiological explanation for the spatial variation in arthropod body size distributions. Apparently, manifold other factors have to be considered to explain large scale spatial body size variation. In particular, speciation − extinction dynamics (Dial and Marzluff, 1988; Allen et al., 1999; Clauset and Erwin, 2008), length of growth season (Blackenhorn and Demont, 2004), evolutionary constraints (Verdú and Lobo, 2008), and colonization history (Etienne and Olff, 2004) might leave their signature in observed body size distributions at large spatial scales.

In Europe, postglacial colonization from glacial refuges determined the faunal composition of middle and northern European countries (Hewitt, 1999, 2000; Husemann et al., 2013) and may have played an important role in determining current patterns in the spatial variation of body sizes. However, while genetic (Gassert et al., 2013) and phylogenetic (Ulrich and Fattorini, 2013) gradients, as well as species spatial distributions (Ulrich and Fiera, 2010) along postglacial colonization trajectories, have received considerable interest, respective gradients in body size distributions are still not well understood (cf. Ulrich and Fiera, 2010; Huston and Wolverton, 2011).

If central and northern European faunas contained mainly species coming from southern glacial refuges, they might be rega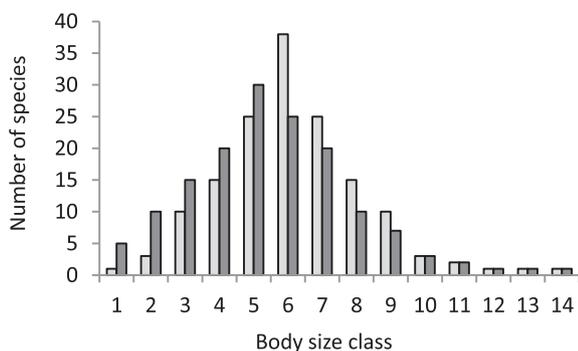rded as subsamples of these southern faunas. Under the assumption of random colonization, body size distributions of these subsamples should have the same central tendencies (mean, variance, and skewness) as the respective refuges. In reality, a manifold of environmental factors may distort these distributions. Thus a comparison of observed regional BSDs with that of the largest glacial refuge might indicate the degree of filtering during colonization.

In the case of warm blooded animals, average, minimum, and maximum body size should increase with latitude according to Bergmann's rule, while the width and the skewness of the *BSD*s should remain stable. According to the oxygen limitation hypothesis, for heterothermic insects we expect that mean and maximum body size, but not necessarily minimum size, decrease with latitude. This pattern is sometimes called the "converse Bergmann's rule" (Shelomi, 2012). However, these simple hypotheses are complicated by additional factors that might even cause U or bell shaped *TBR*s. For instance, Peat et al. (2005) found bumble bee body size to be lowest in temporal habitats, while increasing towards northern latitudes in line with Bergmann's rule and towards the tropics in line with the food availability hypothesis.

Here we investigate how the distribution of body length of European darkling beetles (Tenebrionidae) varies with latitude and associated climatic variables to answer to the following questions:

(1) do mean and maximum body size increase with temperatures (positive *TBR*) as expected by the oxygen limitation hypothesis?
(2) do *BSD* variance and skewness vary along the presumed postglacial colonization trajectories as predicted if lower temperatures filter against larger species?
(3) did colonization from other source areas than the Mediterranean basin glacial refuges influence body size distributions?

To address these questions we compiled tenebrionid body size distributions of 49 European countries and major islands using an updated version of the faunistic and phylogenetic tenebrionid data sets of Fattorini and Ulrich (2012a) and Ulrich and Fattorini (2013). In Fattorini and Ulrich (2012a, b), we have already reconstructed the tenebrionid postglacial colonization of Northern Europe and detected multiple Mediterranean glacial refuges with Spain being the major glacial refugium. Thus, we used the *BSD* of Spain as a standard to infer the strength of potential body size filters in other regional European faunas.

## 2. Material and methods

We considered the faunal composition of 49 faunistically well known European mainland areas (hereafter simply "mainlands") and larger islands colonized by a total of 1395 tenebrionid species or subspecies (including the former family Lagriidae, but excluding the ecologically specialised and possibly phylogenetically derived Alleculidae, cf. Ulrich and Fattorini, 2013), using an updated version of the European tenebrionid database given in Fattorini and Ulrich (2012b). This revised database is contained in the electronic Supplement A. Details of the main sources used to compile country and island lists were already given in Fattorini and Ulrich (2012a). For each species we compiled data on the minimum and maximum body length from more than 360 literature sources and personal measurements, and used the average values to calculate for each country/island the corresponding size distributions (*BSD*s). Below we concentrate on average body size, the width of the *BSD* measured by the coefficient of variation CV, and the skewness $\gamma$. We use the parametric standard error $SE(\gamma) = (6/n)^{1/2}$ (Tabachnick and Fidell, 1996) to test for significant *BSD* skewness.



**Fig. 1.** Hypothetical body size distributions (appropriately modified normal distributions) of two taxa both including 150 species. The light bars show a slightly right skewed distribution ($\delta = 0.74$) with average and modal size in the sixth class. The dark bars show the distribution with the average in the fifth weight class. The distribution has a higher right skew ($\delta = 1.20$).

Because the current taxonomic division into species and subspecies, as applied to the tenebrionids of Europe, is arguably arbitrary (cf. Ulrich and Fattorini, 2013 for a detailed discussion) we based our analysis on subspecies as the basic 'evolutionarily significant units' (*sensu* Ryder, 1986). Species and subspecies will be referred to as 'species' for simplicity. We excluded various synanthropic species, which have become cosmopolitan (e.g., various species belonging to the genera *Tenebrio*, *Tribolium*, *Alphitobius*, *Alphitophagus*, *Lathetycus*, etc.). 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.

Recently, Shelomi (2012) discussed Bergmann's rule in insects in connection with life history and pointed to voltinism (univoltine vs. bivoltine species) as a factor that might influence intraspecific gradients in body size. Because the level of voltinism is known to change with temperature (Kivelä et al., 2011) this might also cause body size clines at the interspecific level. Although only for a minority of tenebrionid species full life history data are available, there is no example of a bivoltine or multivoltine life cycle among species living in the Western Palaearctic. All investigated tenebrionid species appear to be univoltine or even semivoltine; only synantropic species (not considered in this paper) may have two or more generations within a year under artificial conditions (reviews in Butler, 1949; Allsopp, 1980; Fattorini, 2008). Therefore the problem of voltinism does not arise in our study.

As for most arthropod groups, fine grained tenebrionid distribution data are unavailable for large areas. However, previous work showed that even coarse grained data (whole country species richness and climate variables) are able to identify major environmental correlates of animal species distribution (e.g., Baselga, 2008; Hortal, 2008; Keil and Hawkins, 2009). Keil and Hawkins (2009) compared biogeographical regional checklist and grid based models of environmental correlates. Although they found grid based models to be superior checklist models returned qualitatively similar results albeit with weaker statistical support in the case of poor checklist quality.

Tenebrionid species richness and body length were significantly spatially autocorrelated (Moran's $I$ at the first distance class: $P_{I=0} < 0.05$). Therefore, we performed simultaneous spatial autoregressive modelling (Lichstein et al., 2002; Beale et al., 2010) as implemented in the SAR module of the SAM v. 4.0 package of Rangel et al. (2010) to relate body length to the raw and the squared terms of country/island centroid longitude and latitude and country/island wide annual average temperature and precipitation, and average winter length as estimated by the number of days below 0 °C, as contained in Fattorini and Ulrich (2012a,b) and Ulrich and Fattorini (2013). In general, space explained less than 10% of variance in the dependent variables (Tables 1 and 2) and ordinary least squares (OLS) and SAR regressions gave qualitatively very similar results (OLS results, not shown). We used log transformed country/island area and species richness as a covariate to account for sample size effects that might influence regional body length distributions. Statistical significance of regression analysis might also be influenced by non-independence of data due to phylogenetic autocorrelation (Felsenstein, 1985). Therefore we used as an additional covariate the data on the 49 country/island net relatedness indices (*NRI*) provided by Ulrich and Fattorini (2013). *NRI* returns the standardized form of the mean phylogenetic distance (Webb et al., 2002) and increases with increasing phylogenetic clustering. The raw database for the SAR analysis is contained in the electronic Supplement B.

Spain was probably the major glacial refugium of European Tenebrionidae and contains 575 of the 1395 species (41.2%)

**Table 1**
Slopes of simultaneous autoregression (SAR) of minimum, mean, maximum tenebrionid body length of 49 countries/islands, and the coefficient of variation (CV) and the skewness of the respective country/island body size distribution in dependence of log transformed area and species richness (ln A, ln S), net relatedness index (NRI), simple and squared average temperature, winter length as estimated by the number of days below 0 °C $N (t < 0)$, average precipitation, and distance from Spain. Additionally given are the total explained variance ($r^2$) and the part of variance explained by the predictor variables only. All models are significant at $P < 0.01$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

| Variable | Minimum length | Mean length | Maximum length | CV | Skewness |
|---|---|---|---|---|---|
| Constant | 2.730** | 2.769 | 39.911*** | 1.370*** | 6.113*** |
| ln A | −0.020 | −0.162 | −0.600 | <0.001 | 0.007 |
| ln S | −0.332*** | 0.056 | 4.965*** | −0.016 | 0.108 |
| NRI | −0.002 | −0.038 | 0.080 | 0.008 | 0.008 |
| Temperature | 0.030 | 1.319*** | −2.597* | −0.108*** | −0.797*** |
| Temperature$^2$ | <0.001 | −0.041** | 0.091* | 0.004** | 0.026*** |
| $N (t < 0)$ | <0.001 | 0.011 | −0.062 | <0.001 | −0.009** |
| Precipitation | <0.001 | −0.001 | 0.094*** | <0.001 | 0.008* |
| Distance from Spain | −0.010 | −0.023 | −0.100 | −0.002* | −0.288* |
| $r^2$ | 0.42 | 0.64 | 0.73 | 0.41 | 0.60 |
| $r^2$ (predictors only) | 0.34 | 0.59 | 0.71 | 0.37 | 0.51 |

occurring in Europe. Thus we used the distance from Spain as an additional covariate in the SAR analyses. Islands and mainland areas might differ in body size patterns and geographical gradients as reported by Entling et al. (2010) and Ulrich and Fiera (2010). We first analysed latitudinal and temperature gradients of the island and mainland size distributions separately but did not find major qualitative differences (cf. electronic Supplement C for the respective SAR analyses). Therefore, we decided to treat islands and mainlands together.

## 3. Results

Average body size across the tenebrionid species recorded in each geographical unit linearly increased with environmental temperature (Fig. 2A, $P < 0.001$). Average body size was largest in Portugal, Spain, and Macedonia (Fig. 2A, electronic Supplement D). Lowest average body size occurred in Norway, Denmark, Finland, and Belarus (electronic Supplement D). We also observed a weak though insignificant increase in minimum body size ($P > 0.10$, Fig. 2B, electronic Supplement E) and a pronounced increase in maximum body size ($P < 0.001$, Fig, 2C, electronic Supplement F). Neither Spain nor other potential glacial refugia contained the

**Table 2**
Slopes of simultaneous autoregression (SAR) of minimum, mean, maximum tenebrionid body length of 49 countries/islands, and the coefficient of variation (CV) and the skewness of the respective country/island body size distribution in dependence of log transformed area and species richness (ln S), net relatedness index (NRI), and simple and squared centroid latitude and longitude. Additionally given are the total explained variance ($r^2$) and the part of variance explained by the predictor variables only. All models are significant at $P < 0.01$.*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

| Variable | Minimum length | Mean length | Maximum length | CV | Skewness |
|---|---|---|---|---|---|
| Constant | 6.729** | 5.787 | 28.580 | 0.661 | 4.385* |
| ln A | 0.039 | −0.038 | −1.553** | −0.020 | −0.097 |
| ln S | −0.44** | 0.099 | 6.232*** | 0.023 | 0.180 |
| NRI | 0.008 | 0.036 | −0.227 | 0.003 | −0.042 |
| Longitude | −0.008 | −0.054* | −0.198 | −0.003 | <0.001 |
| Longitude$^2$ | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| Latitude | −0.135 | 0.278 | −0.159 | −0.009 | −0.164 |
| Latitude$^2$ | <0.001 | −0.004 | 0.004 | <0.001 | 0.002* |
| $r^2$ | 0.51 | 0.69 | 0.68 | 0.49 | 0.63 |
| $r^2$ (predictors only) | 0.34 | 0.66 | 0.68 | 0.38 | 0.53 |
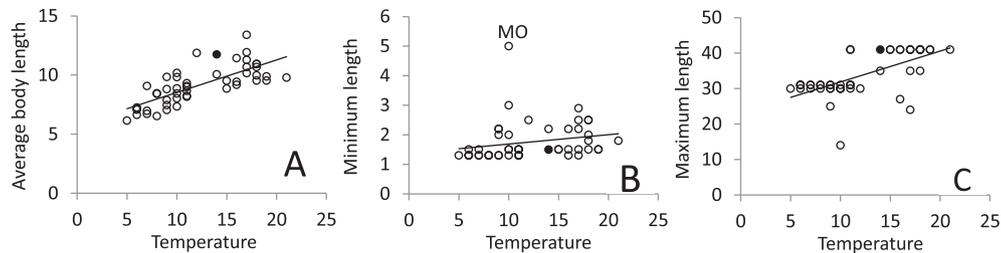
**Fig. 2.** Average (A), minimum (B), and maximum (C) body length of the Tenebrionidae of 49 European country/islands in dependence on average country/island temperature. A: $r^2 = 0.56$ ($P < 0.001$); B: $r^2 = 0.04$ ($P > 0.10$); C: $r^2 = 0.41$ ($P < 0.001$). MO refers to the outlying Moldavia. The black point refers to Spain.

smallest Tenebrionidae *Myrmechixenus subterraneus* (length < 1.5 mm), a typical middle and northern European species.

The largest species (*B. lusitanica* and *B. walti*, length 34–41 mm) occur on the Spanish mainland and Balearic islands only, while the slightly smaller *B. gigas* (length 26–41 mm) is widespread in southern Europe and the Balkans. No species with average body size (and hence with maximum body size) >30 mm occurs north of the Alps (Fig. 3C, electronic Supplement F).

Body size distributions of European Tenebrionidae, particularly those of middle and northern European countries/islands, were unimodal and significantly right skewed (Figs. 3 and 4, electronic Supplement G). Skewness was lowest at intermediate average temperatures and increased particularly towards colder and slightly also towards hotter temperature (Fig. 4, electronic Supplement G). Moldavia appeared to be an interesting exception (Fig. 4, electronic Supplement G), being the only country with a left skewed size distribution (Fig. 4A). The width of the body size distributions as measured by the coefficient of variation decreased significantly ($P < 0.001$) with temperature (Fig. 4B), again with Moldavia being an exception.

Simultaneous autoregression modelling that allowed for a closer look at the influencing factors did not recover the temperature effect on minimum body length but identified species richness as the only decisive predictor (Table 1). Minimum size decreased with species richness. The opposite effect occurred for maximum body length (Table 1), which increased with species richness. A strong signal was made by the positive correlation of maximum body length with average precipitation (Table 1).

Mean length was independent of species richness, but positively dependent on temperature ($P < 0.001$), with intermediate temperature allowing for the largest average body sizes as inferred from the negative sign of the quadratic term (Table 1). Distance from Spain did not influence average faunal body size (Table 1). The model predicted the coefficient of variation of the *BSD*s to decrease with increasing temperature (Fig. 4B, electronic Supplement H), but pointed also to a minimum at an intermediate average temperature (Table 1). Skewness of the size distributions increased towards northern European countries with lower average temperature (Fig. 4A) and longer winters and was lowest at an intermediate temperature of about 14 °C, the average annual temperature of Spain (Table 1). Skewness decreased with distance from Spain (Table 1). Country/island area and phylogenetic relatedness did not significantly enter any of the regressions (Table 1).

Because previous work on large scale invertebrate body size distributions was mainly based on latitude as a surrogate variable for climatic gradients, we performed also a SAR modelling using latitude instead of temperature (Table 2). This analysis recovered the species richness dependence of minimum and maximum body length, but gave inconclusive results for latitude. We found only a weak negative correlation of maximum body length with latitude ($P < 0.05$), including a weak positive quadratic latitudinal term (Table 2). Latitude did not significantly enter the regression for minimum and mean body length and for the width of the BSD.

## 4. Discussion

Body size gradients can be studied in different ways. A focus on the possible ranges of body size values generally involves metabolic constraints either towards maximum or towards minimum size (Makarieva et al., 2005). For endothermic vertebrates heat loss might be decisive with respect to both minimum and maximum size. In ectothermic arthropods, minimum size seems only constrained by the number of cells necessary for organismal functioning (Björkman et al., 2009) and can be as low as 0.1 mm in a number of mites (Mohanasudaram, 1987) and parasitic Hymenoptera (Mockford, 1997). Maximum possible arthropod size in turn is apparently limited by metabolic constraints (Kaiser et al., 2007; Björkman et al., 2009; Harrison, 2009) and thus generally increases towards tropical regions (Makarieva et al., 2005).

European Tenebrionidae are always longer than one mm and thus are far above the arthropod or even coleopteran minimum. Theoretically minimum possible size should not be limited by temperature (Makarieva et al., 2008). Therefore we did not expect to see a temperature gradient for minimum size. Indeed our SAR modelling did not return temperature to be significantly correlated with minimum body length across Europe. The moderate and statistically insignificant increase in minimum size with temperature in the bivariate plot of Fig. 2 vanished when accounting for regional species richness. In the only comparable study on minimal sizes, Ulrich and Fiera (2010) also did not find any temperature dependence in European springtails.

Tenebrionidae of European faunas are at most 41 mm long, and far below the upper length boundary for beetles. The largest beetles (*Dynastes hercules*) might reach more than 180 mm (Encyclopedia of Life, http://eol.org/pages/1026724/details, retrieved 09.05.2013). Nevertheless maximum regional size might be constrained by, for instance, resource availability, winter temperature or humidity. In the present case we did not find a significant increase in maximum length with temperature (Table 1) after accounting for species richness effects and distance from the presumed major glacial refuges. However, both factors apparently mask the temperature dependency. The simple plot of maximum size and temperature as well as the spatial distribution of maximum size across Europe (Table 2 and electronic Supplement F) point to a strong latitudinal effect. Indeed, Tenebrionidae are mostly thermophilic species and often adapted to arid environments (Doyen, 1993; Fattorini, 2008). Laboratory and field experiments conducted on several Mediterranean species (reviewed in Fattorini, 2008) indicate that, in general, temperatures below 15–20 °C not only tend to make adults inactive, but have also severe negative effects on ovarian maturation, egg viability, incubation time, and larval development, whereas adult activity correlates positively with increasing
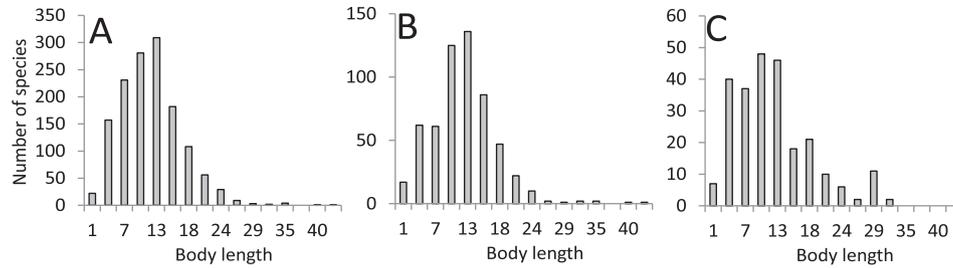
**Fig. 3.** Body size (mm) distributions of European (A), Spain (B), and Middle and Northern European (C, Latitude > 45°) Tenebrionidae. A: mean body length: 11.05 mm, Skewness: 0.93 ± 0.14 (mean ± 1 standard error); B: mean body length: 11.75 mm, Skewness: 1.05 ± 0.24; C: mean body length: 9.6 mm, Skewness: 1.27 ± 0.19.

temperatures. Even widely distributed species in Central and Northern European countries, like *Blaps mucronata*, have a thermal optimum above 4 °C (Crovetti et al., 1982), whereas the flight period of *Bolitophagus reticulatus* in Sweden coincides with the first days when the maximum temperature exceeds 22 °C (Jonsell et al., 2003). Thermophily might therefore explain why species richness sharply declines towards northern and cooler latitudes in Europe (Fattorini and Ulrich, 2012a).

In contrast to minimum and maximum size, we found a significant positive correlation of average regional body size with temperature (Fig. 2). Therefore, our results do not corroborate the applicability of Bergmann's rule to these ectothermic invertebrates but are in line with a positive temperature–size relationship.

The phylogenetic relationship did not enter any of our regression models (Tables 1 and 2). Therefore, we conclude that on average phylogenetic constraints are of minor importance in tenebrionid body size distributions. This does not mean that phylogeny is without importance. The largest European Tenebrionidae with maximum length above 30 mm are all from the two genera *Blaps* (Blaptini) and *Morica* (Akidini). However, the 30 *Blaps* species present in Europe are widespread even across northern countries (electronic Supplement A). Nevertheless even within this smaller lineage a significant positive correlation of body size and average temperature occurred ($r = 0.37$, $P = 0.01$).

A shift of the average of a statistical distribution without respective shifts of the distribution margins is only possible if the shape of the distribution changes too (Fig. 1). This was indeed the case for the present size distributions. *BSD* width and skewness generally decreased with increasing temperature (Fig. 4) with minima at a relatively higher environmental temperature (Table 2). The two single comparable studies (Entling et al., 2010; Ulrich and Fiera, 2010) reported contrasting patterns for European spiders and springtails, respectively. While Entling et al. (2010) found a significant increase in skewness with latitude, Ulrich and Fiera (2010) indicated a peak of skewness at intermediate latitudes. In general our study is in line with the spider pattern. We found a clear

increase in skewness at higher latitudes (lower temperatures, Table 1, Fig. 4, electronic Supplement G). However, the high *BSD* skewness on the low latitudinal eastern Mediterranean islands, Turkey, and Albania (electronic Supplement G) caused the U-shaped signal of Tables 1 and 2 and Fig. 4 in contrast to the peaked pattern found in European springtails (Ulrich and Fiera, 2010). Since these are south-eastern European regions, it is possible that additional longitudinal effects cause taxon specific patterns in the spatial distribution of *BSD* shapes.

In this respect it is important to note that the Tenebrionidae deviate from other larger arthropod taxa in having significantly right skewed *BSD*s (Fig. 3). Previous studies reported nearly symmetric *BSD*s in European Hymenoptera (Ulrich, 2006), Coleoptera (Ulrich, 2007), Diptera (Ulrich and Szpila, 2008), and Araneae (Entling et al., 2010). Collembola even have left skewed distributions (Ulrich and Fiera, 2010). Right skewed distributions found in vertebrates reflect evolutionary constraints (Kozłowski and Gawelczyk, 2002; Knouft, 2004; Clauset and Erwin, 2008), particularly lower size boundaries (McKinney, 1990) and asymmetric speciation and extinction dynamics (Clauset and Erwin, 2008). With respect to colonization trajectories even slightly higher dispersal abilities of smaller species might cause a decrease in average size, but also a tendency towards right skewed *BSD*s along this trajectory. Our study might therefore be an indication of increased dispersal rates in smaller tenebrionid species. It has been suggested that small body size may increase the dispersal abilities of insect populations (Gaston and Lawton, 1988; Basset and Kitching, 1991) and our research seems to support this hypothesis.

Above we used the *BSD* of the major postglacial refuge, Spain, as a standard to which we compared the *BSD*s of other countries and islands. We found significant trends in *CV* and skewness with respect to distance from Spain even after accounting for species richness and phylogenetic effects (Table 1). Clearly, these trends can be linked to a filtering effect of lower temperature against large species. Interestingly skewness significantly ($P < 0.01$, Table 1) decreased with distance from Spain after accounting for species richness and temperature effects. This effect is contrary to what is seen in the raw data (Fig. 4, electronic Supplement G), where Spain has one of lowest degrees of skewness and where skewness increased towards north-eastern Europe. These diverging results imply that the main trigger of *BSD* skewness across Europe is temperature, while after temperature correction (Table 1) other factors step in that decrease skewness with distance from the major glacial refuge. A parsimonious explanation for this effect is a certain degree of homogenization of faunal composition in the Mediterranean region due to immigration from eastern postglacial refuges such as the Near East. Such an explanation would be in line with the longitudinal effects on *BSD* shapes mentioned above. The trade-off of these colonization routes would cause a tendency towards symmetric *BSD* shapes in the eastern Mediterranean basin.
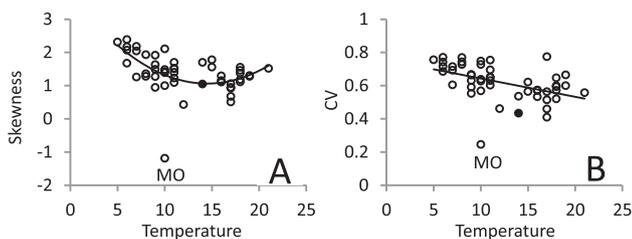


**Fig. 4.** Skewness (A) and the coefficient of variation (CV) (B) of the tenebrionid body size distributions of 49 European country/islands in dependence of average country/island temperature. A: $r^2 = 0.26$, P (quadratic term) < 0.001; B: $r^2 = 0.21$, P < 0.001. MO refers to the outlying Moldavia. The black point refers to Spain.

Previous studies that used latitude as a surrogate variable for temperature (e.g., Hawkins and Lawton, 1995; Entling et al., 2010; Ulrich and Fiera, 2010) reported taxon specific gradients in body size. Above we compared the results obtained by temperature and by latitude. Latitude explained much less of the body size variability across Europe than temperature (Tables 1 and 2, electronic Supplement D). This is interesting insofar as our temperature data are country/island averages (Fattorini and Ulrich, 2012a, b) and thus very coarse grained. Therefore, we conclude that prior inconclusive results about the temperature − size relationship in invertebrates might be at least partly due to the additional variability introduced by the surrogate variable latitude that masked the temperature effect.

Country based data on faunal composition and environmental correlates are not able to provide precise quantitative models. Spatial autocorrelation, differences in country size, shape and physical heterogeneity, and the fact that the whole environmental variation of each country is reduced to a single central tendency necessarily reduces the explanatory power of this type of biogeographic models (see Olalla-Tárraga et al., 2010 for a discussion). However, after correcting for important covariates they are able to generate reproducible qualitative hypotheses. Moreover we note that variation in climate parameters within a country is surely much lower than that between countries, at which we focused here. Thus, we are confident that our main findings depict the true patterns. However, our approach did not include other potentially important sources of variation in tenebrionid faunal composition, like host plant diversity, food availability, starvation and desiccation resistance, or human impact (cf. Chown and Gaston, 2010). Further research has to assess the possible contribution of these factors to tenebrionid body size variation in Europe.

## Acknowledgements

## Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2013.09.006.

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