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RESEARCH PAPER

Environmental correlates of body size distributions of European springtails (Hexapoda: Collembola)

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ABSTRACT

Aim Species–body size distributions (SBDs) are plots of species richness across body size classes. They have been linked to energetic constraints, speciation–extinction dynamics and to evolutionary trends. However, little is known about the spatial variation of size distributions. Here we study SBDs of European springtails (Collembola) at a continental scale and test whether minimum, average and maximum body size and the shapes of size distributions change across latitudinal and longitudinal gradients and whether SBDs of islands and mainlands differ. We also test whether the island rule and the positive body size–range size relationship of vertebrates also holds for Collembola.

Location Europe.

Methods We use a unique data set on the spatial distributions of 2102 species of European springtails across 52 countries and larger islands together with associated data on body size, area, climate variables, longitude and latitude. Differences in the central moments of SBDs are inferred from simultaneous spatial autoregression models.

Results The SBD of the European Collembola and its largest suborder Entomobryomorpha is unimodal and symmetrical. Average, minimum and maximum body weight and the skewness of the mainland/island SBDs peaked at intermediate latitudes. We could not find simple latitudinal gradients in minimum and maximum body weight. Average and maximum body size increased with country/island area in accordance with the island rule in vertebrates, while minimum body size did not significantly differ between islands and mainlands. Finally, we found a weak but statistically significant positive correlation of range size and body size.

Main conclusions We provide evidence for differences in body size distributions between islands and mainlands that are in part in line with the island rule in invertebrates. We also find evidence for an interspecific body size–range size relationship similar to that of vertebrates although the vertebrate pattern is much stronger than the springtail pattern. Our results on latitudinal gradients of maximum and average body size imply the need to account for species richness and area effects in the study of latitudinal gradients in body size. We recommend implementing sample size and area effects in the study of body size distributions on islands and mainlands.

Keywords

Body size distributions, Collembola, island rule, latitudinal gradient, longitudinal gradient, macroecology, spatial autoregression.

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INTRODUCTION

The study of animal body sizes has a long tradition in ecology (Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996) and is still one of the major drivers in recent macroecological theories. Empirical (Damuth, 1987) and theoretical work documented how body size is related to evolutionary traits and life history (Calder, 1996), mass-specific metabolic rates (Brown *et al.*, 2004), population biomass and abundance (Damuth, 1987; Savage *et al.*, 2004). Particular interest is centred on species–body size distributions (SBDs) of whole communities which have been linked to energetic constraints (May, 1978; Brown & Nicoletto, 1991), speciation–extinction dynamics (Dial & Marzluff, 1988; Allen *et al.*, 1999; Knouft & Page, 2003; Etienne & Olff, 2004) and to evolutionary trends towards larger or smaller body sizes (Orme *et al.*, 2002; Smith *et al.*, 2004).

Recent work from local (Gaston *et al.*, 2002) to global scales (Orme *et al.*, 2002; Smith *et al.*, 2004; Ulrich, 2006, 2007; Clauset & Erwin, 2008; Ulrich & Szpila, 2008) has clarified many patterns around SBDs. Most appeared to be unimodal across animal taxa, predominantly right skewed in vertebrates (Kozłowski & Gawelczyk, 2002; Smith *et al.*, 2004; Clauset & Erwin, 2008) and symmetrical or moderately right skewed in larger insect taxa (Chislenko, 1981; Ulrich, 2006, 2007; Ulrich & Szpila, 2008). Differences in SBD shapes at both ends of the body size spectrum (Ulrich & Szpila, 2008) pointed to size-dependent extinction and speciation rates in insects in line with current theory about taxon-specific upper and lower size boundaries (Maurer *et al.*, 1992; Alroy, 2000; Makarieva *et al.*, 2005; Clauset & Erwin, 2008). However, these studies (particularly Orme *et al.*, 2002) do not confirm hypotheses about universal relationships between body size and speciation rate that predict peaks in speciation rate and species richness at low body size (May, 1978; Morse *et al.*, 1985; Currie & Fritz, 1993).

Body size distributions are generally constructed from pooled data within a certain region. However, little is known about the spatial (and temporal) variation of size distributions. Knouft (2004) reported a trend towards left-skewed SBDs for North American freshwater fishes at higher latitudes. In birds and mammals right-skewed regional SBDs become symmetrical at local scales (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Cardillo, 2002). Comparable studies for invertebrates are largely lacking. In particular nothing is known about possible latitudinal and longitudinal gradients of SBD shapes. Nevertheless, recent macroecological and evolutionary theories imply the existence of distinct gradients.

1. Maximum body size within invertebrate taxa seems to increase towards lower latitudes, probably due to temperature constraints (Makarieva *et al.*, 2005; but see Meiri & Thomas, 2007). This model implies either an associated latitudinal shift of the whole SBD if the variance is constant or a larger variance in body size at lower latitudes if the average body size is latitude invariant.

2. The possible latitudinal gradient in minimum body size has so far received little attention. Implicitly energetic constraint models treat minimum body size as being independent of latitude (Makarieva *et al.*, 2008). If this were true the observed shift of maximum body size should generate a gradient towards more right-skewed size distributions and larger size spectra at lower latitudes.

3. Several studies on vertebrates proposed a trend towards smaller body size in large species and larger body size in small species on islands (the island rule; Lomolino, 2005; but see Meiri *et al.*, 2006, 2008). There is no systematic study of this rule for invertebrates, although some corroborating examples exist (Palmer, 2002). The rule implies a smaller range of island body sizes, a lower SBD variance and possibly an excess of small-bodied species on islands and an associated shift of SBDs towards a smaller mean and a negative skewness.

4. In vertebrates a positive relationship between body weight and range size is well documented at the individual (Harestad & Bunnell, 1979; Kelt & van Vuren, 2001) and species level (Brown & Maurer, 1989; Gaston & Blackburn, 1996). Plots of interspecific range size versus body size can further be described by a polygonal constraint envelope defined by lines for the minimum body sizes–maximum range size constraints (Diniz-Filho *et al.*, 2005). Far less is known in invertebrates, although some work on body size and area requirements also points to a positive relationship (Biedermann, 2003; Greenleaf *et al.*, 2007). Population size N generally decreases with body weight W by an allometric function (NW^{-z}). The abundance–range size relationship (Loder, 1997) predicts larger range sizes R of locally and regionally abundant species [$Rf(N)$]. Although abundance refers in both models in part to different scales, we might combine both equations (Biedermann, 2003) and speculate that at some spatial scales range size might even decrease with increasing body weight ($RW^{-h(x)}$) as found in some New World carnivores (Diniz-Filho *et al.*, 2005). These contrasting predictions might give rise to more complicated relationships between home range and body size in arthropods and deserve a detailed study.

Here we use a unique data set on the spatial distributions of 2102 species of European springtails across 52 countries and larger islands together with associated data on body size, area and climate to address the aforementioned hypotheses. We indeed detect latitudinal gradients in body size distributions and find evidence for the island rule.

MATERIALS AND METHODS

We compiled data on the geographical distribution and body length of European springtails (as faunistically defined in Fauna Europaea; Deharveng, 2007) from major catalogues (Gisin, 1960; Jordana *et al.*, 1997; Fjellberg, 1998, 2007; Pomorski, 1998; Bretfeld, 1999; Potapov, 2001; Thibaud *et al.*, 2004) and recently described species (Appendices S1 & S2 in Supporting Information). We did not include Russia and some smaller islands (Cyclades, Aegean and Channel Islands) and countries (Liechtenstein, Monaco, San Marino, Vatican) and the European part of Turkey due to incomplete recording. In total the database contains 2102 species in 239 genera, 22 families and 12 superfamilies of Collembola, which occur in 52 countries and larger islands mentioned in Fauna Europaea (Appendix S3). These species represent 84% of the estimated 2500 described European springtails (Hopkin, 1997). We did not include subspecies. For 1850 species of Collembola sufficiently precise body length data were available. The classification of species into families and superfamilies follows Bellinger *et al.* (1996–2009). Because missing species might possibly be predominately small (May, 1986), we compared the average body size of all genera with that of those genera that included species without body size data (74 genera). To our surprise, the average body weight of the latter group was slightly (but statistically not significantly: $P > 0.5$) larger (0.42 mg) than the average of all genera (0.40 mg). Therefore the missing species should not bias our results.

Based upon our previous results on environmental variables that influence springtail species richness (Ulrich & Fiera, 2009) we evaluated the influence of six geographical variables on springtail body sizes. For each European country and larger island (Appendix S4), we determined the area in km^2 and the latitude and longitude of its capital or (in the case of islands) its main city (data from World Atlas, http://www.worldatlas.com/aatlas/world.htm). We used Weatherbase (http://www.weatherbase.com) to compile data on mean temperatures in January (T_{January}) and July (T_{July}) and to estimate yearly temperature differences ($\Delta T = T_{\mathrm{July}} - T_{\mathrm{January}}$). Next, we estimated the mean length of the winter from the mean number of days below 0 °C ($N_{T<0}$) (Appendix S3). We did not use averaged climate data for each country because in many cases high mountain areas biased the data. Further, different country sizes inflated the temperature ranges for larger countries.

To correct for spatial autocorrelation we used the simultaneous autoregression model (Liechstein *et al.*, 2002; Bini *et al.*, 2009) with a generalized least squares estimation that is implemented in the Spatial Analysis in Macroecology 3.0 (SAM) package of Rangel *et al.* (2006). This model uses an additive linear estimation model that is corrected for spatial autocorrelation of data (in this case the effect of distance between the countries). Species richness and area entered as ln-transformed data. To account for possible peaks of body weight at intermediate latitudes we also used the quadratic term of latitude in our regression analysis. Spatial autocorrelation was quantified using Moran's I (Rangel *et al.*, 2006). We applied the Akaike information criterion (AIC) for model choice as implemented in SAM. Errors refer to standard errors.

We also used a random sampling model to infer a latitudinal gradient of maximum body size. For all countries north of 50° N, 55° N and 60° N and south of 35° N, 40° N and 45° N we compared the observed number of species of the upper and lower 0.3, 0.6, 0.9, 1.2 and 1.5 percentiles of body size (the largest and smallest 5, 10, 15, 20 and 25 species) with those expected from the species–area relationship of European springtails (Ulrich & Fiera, 2009: $S = 1.6A^{0.4}$ where S denotes species richness and A is area in km^{-2}) under the null assumption of an equal distribution of body sizes within any given area.

To ensure comparability with previous work on insect and vertebrate body size distributions (Kozłowski & Gawelczyk, 2002; Smith *et al.*, 2004; Ulrich, 2006, 2007) the present work is based on mean species dry weight W (mg) calculated from the arithmetic mean L (mm) of available data on minimum and maximum body length using the regression equation of Ganihar (1997)

$$W = 0.153L^{2.3} \tag{1}$$

Of course, in the majority of species the literature-based mean lengths will only be rough estimates. However, these inaccuracies are counterbalanced by the large number of data points used for the analysis. Body weight distributions (in the following the term SBD always refers to the species–body weight distribution) were calculated for the fauna of the whole of Europe and for each country/island separately and were always based on ln-transformed weights to eliminate the effect of the scaling exponent. Skewness γ was computed as in Ulrich (2006, 2007):

$$\gamma = \frac{n}{(n-1)(n-2)} \sum_{i=1}^{n} \left(\frac{w_i - \bar{w}}{\sigma_w} \right)^3 \tag{2}$$

where w_i is the ln-transformed body weight of species i and n is the number of species. We calculated the standard error of γ according to Tabachnick & Fidell (1996): SE $(\gamma) = (6/n)^{1/2}$.

Because discontinuous range sizes are common among the European Collembola we used the number of occurrences across countries and islands, the total area of all countries/islands occupied and the latitudinal and longitudinal range as independent variables in multiple regression to study the dependence of species body weight on range size (occupancy). Following the approach of Diniz-Filho *et al.* (2005), we used the macroecology randomization procedures of ECOSIM 7.72 (Gotelli & Entsminger, 2005) to test whether the occupancy–body size relationship can be described by a constraint envelope. As the test criterion we used the number of species that were outside the triangular or pyramidal shapes defined by ECOSIM and compared this number with the distribution of expected numbers obtained from 5000 randomizations.

RESULTS

Basic patterns

The European springtails range from less than 0.001 mg (*Folsomides lawrencei*) to more than 13 mg (*Tetrodontophora bielanensis* and *Orchesella chiantica*) and therefore span more than 10 orders of magnitude in body size. The SBD of the European Collembola and its largest suborder Entomobryomorpha was unimodal and symmetrical (Fig. 1). Poduromorpha had slightly negatively skewed and the mainly small-bodied Symphypleona slightly positively skewed distributions (both $P(\gamma = 0) < 0.05$). Intermediate-sized genera were in all cases most species rich (Fig. 2). The species number–body size plot was best fitted by a second-order polynomial function with a highly significant ($P < 0.001$) negative quadratic term in comparison to higher-order polynomials.

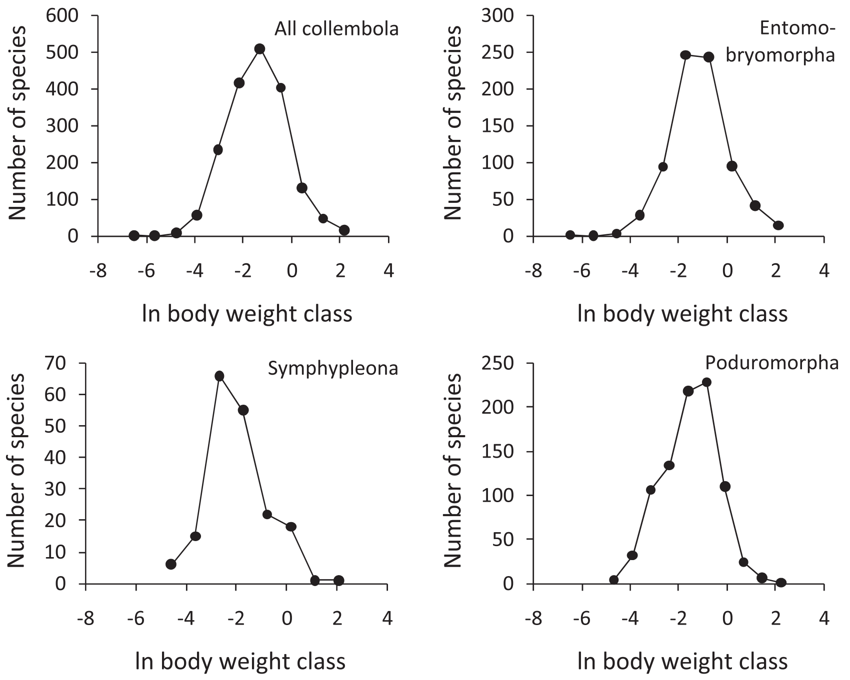

Figure 1 Body weight (mg) distributions of European Collembola (all species and suborders). Skewness: all Collembola: $\gamma = 0.02$, n.s.; Entomobryomorpha: $\gamma = 0.08$, n.s.; Symphypleona: $\gamma = 0.45$, $P(\gamma = 0) < 0.05$; Poduromorpha: $\gamma = -0.18$, $P(\gamma = 0) < 0.05$. Neelipleona are not shown, as they have only 10 European species.

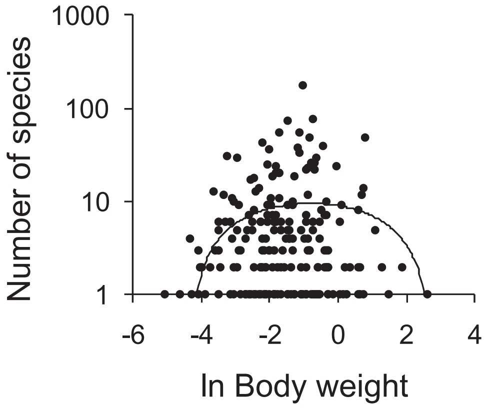

Figure 2 Species richness of springtail genera peaks at intermediate genus body weight (mg). Body weights are average weights per genus. Second-order polynomial regression: P(quadratic term) < 0.001.

Latitudinal and longitudinal gradients

Average and maximum body size peaked at intermediate latitudes (Fig. 3). The largest species *Tetrodontophora bielanensis* and *Orchesella chiantica* occur in central European countries (Fig. 3b). The highest average body size occurred at 40–50°N (Fig. 3c) with peaks in Andorra, Slovenia, Macedonia and the Kaliningrad region. The quadratic terms of second- and third-order polynomial regressions in Fig. 3(b,c) were highly significant ($P < 0.01$). Minimum body size did not significantly depend on latitude (Fig. 3a). The smallest species *Folsomides lawrencei* occurs on the Canary Islands while the second smallest, *Mackenziella psocoides*, is from Scandinavia.

Spatial autoregression modelling revealed significant negative quadratic latitudinal terms of mean, minimum and maximum body weight per country/island (Table 1). Hence, our analysis did not detect simple latitudinal gradients in body size. Because SBDs potentially depend on species richness S, $\ln(S)$ served always as covariate and appeared in all cases to be of importance ($P < 0.001$). Neither area nor longitude nor any of the climate variables entered our regressions at the 5% error benchmark.

The random sample model (Table 2) revealed a significant although weak trend towards lower numbers of very large and very small species at higher latitudes. This trend was visible for all latitudes north of 50° N. In contrast, the model did not identify clear trends at the lower range of latitudes studied (Table 2). Below 40° N numbers of the largest and smallest springtail species did not significantly differ from expectation.

Of the higher-order moments of the SBDs (variance, skewness and kurtosis) only skewness was significantly correlated to latitude (Table 1). In accordance with the difference in the trends for minimum, average and maximum body weight there was a trend towards right-skewed distributions at intermediate latitudes (Fig. 3d). Neither higher moment correlated significantly to area, longitude or climate variables (not shown).

Island rule

Minimum body size decreased (Fig. 4a) and maximum body size increased (Fig. 4b) with country/island area ($P < 0.001$). Because islands are mostly of small size this pattern implies that minimum body size of springtails on islands was comparably larger and maximum body size smaller than on mainlands (not shown). To account for the possible effect of area and species richness on body size we used analysis of covariance (Table 3)

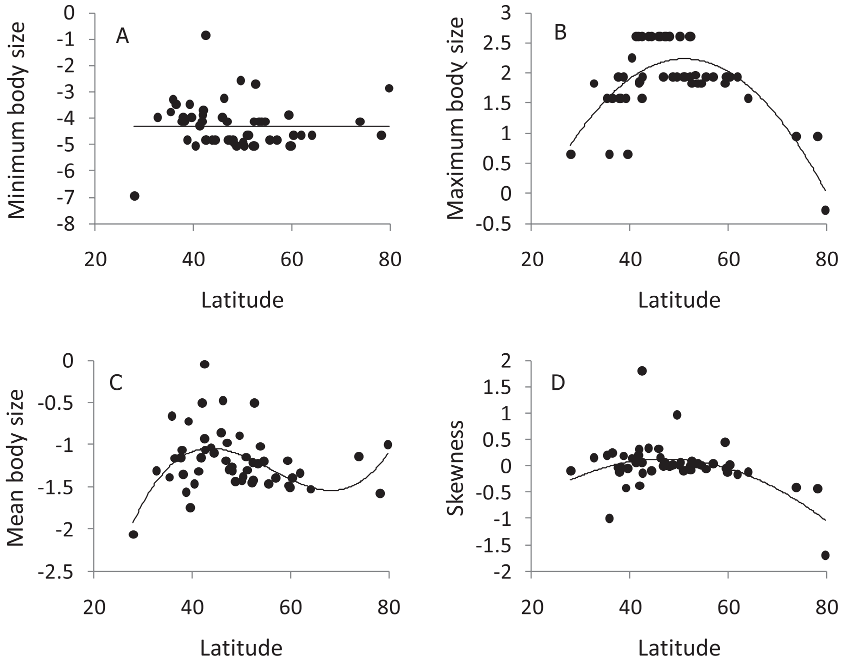

Figure 3 Minimum (a) and maximum (b) body weight (mg) as well as mean and skewness of 52 species–body size distributions (SBDs) of European springtails do not show clear latitudinal gradients but tend to peak at intermediate latitudes. Second- (a, b, d), and third-order (c) polynomial regressions: quadratic terms (a) $P > 0.5$; (b) $P < 0.001$; (c) $P < 0.01$; (d) $P < 0.001$.

Table 1 Spatial autoregression models of springtail body size distributions.

Variable	Coefficient	SE	*t*	*P*
Mean body weight				
Constant	−2.268	0.056	−4.06	< 0.001
ln *S*	−0.229	0.032	−7.03	< 0.001
Latitude	0.089	0.023	3.90	< 0.001
Latitude^2	−0.001	< 0.001	−4.10	< 0.001
Maximum body weight***				
Constant	−4.332	0.834	−5.19	< 0.001
ln *S*	0.197	0.042	4.62	< 0.001
Latitude	0.216	0.034	6.40	< 0.001
Latitude^2	−0.002	< 0.001	−6.81	< 0.001
Minimum body weight***				
Constant	−4.793	1.159	−4.06	< 0.001
ln *S*	−0.694	0.071	−9.79	< 0.001
Latitude	0.151	0.048	3.16	< 0.01
Latitude^2	−0.001	0.001	−3.24	< 0.01
Skewness***				
Constant	−2.49	0.810	−3.09	< 0.01
ln *S*	−0.116	0.045	−2.57	0.01
Latitude	0.133	0.033	4.07	< 0.001
Latitude^2	−0.001	< 0.001	−4.55	< 0.001

$n = 52$. Mean body weight: $R^2 = 0.50$; $P = < 0.001$. Maximum body weight: $R^2 = 0.73$; $P < 0.001$. Minimum body weight: $R^2 = 0.66$; $P < 0.001$. Skewness: $R^2 = 0.39$; $P = < 0.001$. *S*, species richness; Latitude^2, squared values of latitude. Given are the best performing models as inferred from Akaike information criterion model selection.

and still found significant differences between islands and mainland countries with regard to average and maximum body size. Body size of the largest species was higher on mainlands ($P < 0.001$). None of the four largest species (*Orchesella chiantica*, *Disparrhopalites tergestinus*, *Orchesella dallaii*, *Seira pini*) occurred on any island but did occur on two mainlands close to many of these islands: Spain (*Seira pini*) and Italy (*Orchesella chiantica*, *Disparrhopalites tergestinus*, *Orchesella dallaii*).

Contrary to the classical formulation of the island rule we found a weak tendency towards smaller sizes ($P = 0.06$; Table 3). The two smallest species (*Acherongia minima*, *Folsomides lawrencei*) occur on islands with *F. lawrencei* (the smallest European springtail) being endemic in the Canary Islands. Average body size was significantly higher on mainlands ($P = 0.001$; Table 3). We also found a significant difference in skewness between island and mainland SBDs ($P = 0.002$). Islands tended to have left-skewed and mainlands right-skewed distributions (Table 3). Again we did not find any significant difference in SBD variance and kurtosis between islands and mainlands (not shown).

Body size and occupancy

Despite the large variability in occurrence we found a trend towards larger range size of large-bodied springtails (Fig. 5a). After reducing the noise in the data using average range sizes within $\log_2$ body weight classes (Fig. 5b), this trend was even more pronounced. Multiple regression and partial correlation analysis (Table 4) found numbers of occurrences ($P < 0.01$) and the longitudinal difference in occurrence ($P = 0.015$) as being significantly positively correlated and the latitudinal difference

Table 2 Expected and observed numbers of smallest and largest species of European springtails in dependence of latitude.

Body size	North of 60°			North of 55°			North of 50°		
Percentile	Expected *S*	Observed largest species	Observed smallest species	Expected *S*	Observed largest species	Observed smallest species	Expected *S*	Observed largest species	Observed smallest species
0.3	2 ± 1	0	0	3 ± 1	0	1	4 ± 1	1	2
0.6	4 ± 1	1	1	6 ± 1	1	3	8 ± 1	4	5
0.9	6 ± 1	2	1	9 ± 1	3	4	12 ± 2	6	8
1.2	8 ± 2	3	3	11 ± 2	4	6	16 ± 2	10	11
1.5	10 ± 2	5	3	14 ± 2	7	7	20 ± 3	14	13

Body size	South of 35°			South of 40°			South of 45°		
Percentile	Expected *S*	Observed largest species	Observed smallest species	Expected *S*	Observed largest species	Observed smallest species	Expected *S*	Observed largest species	Observed smallest species
0.3	1 ± 1	0	2	2 ± 1	0	2	3 ± 1	5	3
0.6	1 ± 1	0	3	3 ± 1	1	4	6 ± 1	8	6
0.9	2 ± 1	0	5	5 ± 1	2	6	9 ± 2	11	10
1.2	2 ± 1	1	6	6 ± 2	3	8	12 ± 2	15	14
1.5	3 ± 2	3	6	8 ± 2	6	8	15 ± 3	20	16

S, species richness. Expected numbers come from the equiprobable random sample model. Given are predicted numbers ± 1 standard deviation for the 5 (0.3 percentile) to the 25 (1.5 percentile) smallest and largest European springtail species.

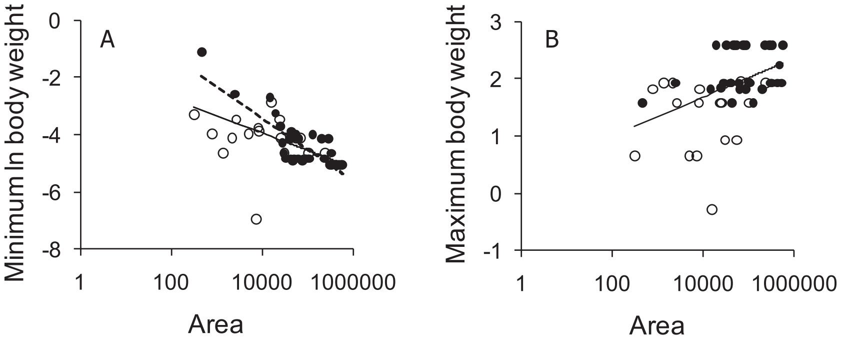

Figure 4 Minimum (a) and maximum (b) body weight (mg) of European springtails dependent on mainland (full dots) and island (open circles) area. All islands (full regression lines): minimum weight: Pearson $r = -0.55$, $P(r = 0) < 0.001$; maximum weight: Pearson $r = 0.45$, $P(r = 0) < 0.001$. In (a) the regression for mainlands only is statistically significant (broken line: Pearson $r = 0.82$, $P(r = 0) < 0.01$).

in occurrence ($P < 0.001$) as being significantly negatively correlated with body weight. However, the whole regression model is statistically significant ($P < 0.001$), mainly due to the large number of data points, and the predictors explained only 1% of variance in body weight.

A *U*-test that compared the 744 endemic species (those occurring only once) with those that occurred on at least half of the 52 studied European countries/islands ($n = 79$) revealed a highly significant difference ($P < 0.001$) in body size, again with the larger species having larger range sizes. We did not find strong evidence for a constraint envelope of the body size–occupancy relationship. An inverse triangular polygon fitted best ($P < 0.01$), although even in this case more than 600 species (38%) ranged outside the envelope.

Table 3 Covariance analysis to detect differences between islands ($n = 17$) and mainlands ($n = 35$) with respect to minimum, maximum and average of springtail body size and to the skewness of the body size distribution.

	Mean			
	Islands	Mainlands	*F*	*P*
Minimum body weight	−0.205	0.099	3.44	0.06
Maximum body weight	−0.047	0.587	27.9	< 0.001
Mean body weight	−0.174	0.085	11.76	0.001
Skewness	−0.254	0.124	10.39	0.002

Due to the differences in mainland/island areas and species richness the ln-transformed area *A* and species richness *S* served as a covariates.

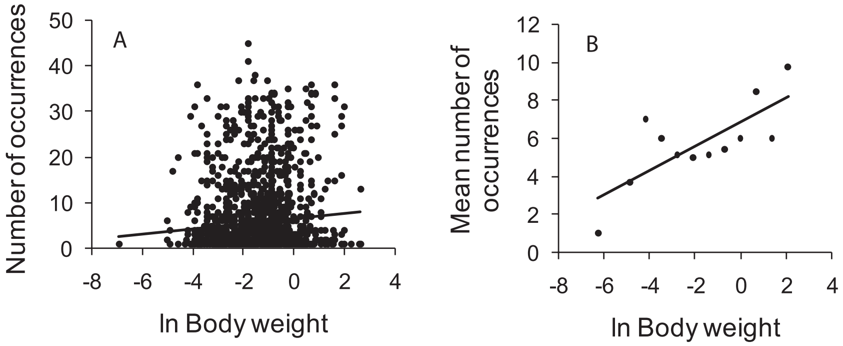

Figure 5 Range size of European springtails (estimated from the number of occurrences) increases with body weight (mg): (a) all species: $r = 0.09$, $P(r = 0) < 0.001$; (b) average number of occurrences per $\log_2$ body weight class; Pearson $r = 0.79$, $P(r = 0) < 0.001$.

Table 4 Multiple regression and partial correlation results ($n = 1817$) to infer the dependence of springtail body weight (ln-transformed prior to analysis) on four measures of European range size.

Variable	Coefficient	Std error	*t*	*P*	Partial correlation	*P*
Constant	−1.685	0.319	−5.279	< 0.0001		
Area	0.019	0.026	0.727	0.47	0.02	0.47
ΔLat	−0.017	0.005	−3.510	< 0.001	−0.008	< 0.001
ΔLong	0.009	0.004	2.433	0.02	0.06	0.02
Occ	0.011	0.004	2.689	< 0.01	0.004	< 0.01

Area, ln-transformed sum of all country/island areas of occurrence; Occ, number of occurrences; ΔLat, ΔLong, maximum latitudinal and longitudinal range of occurrence. $P(R^2 = 0) < 0.001$.

DISCUSSION

The SBDs of the European springtails follow the typical insect pattern of symmetrical or nearly symmetrical unimodal distributions (Fig. 1; Ulrich, 2006, 2007; Ulrich & Szpila, 2008). Hence there are roughly as many large- as small-bodied species. This contrasts with the vertebrates with their marked right-skewed distributions and an excess of relatively small-bodied species (Kozłowski & Gawelczyk, 2002; Smith *et al.*, 2004). Our findings further corroborate the observation that taxa of intermediate body size are the most species rich (Fig. 2; Knouft, 2004; Smith *et al.*, 2004; Ulrich, 2006). To date the only exception to this rule are European Diptera where small-bodied genera appeared to be more species rich than larger-bodied genera (Ulrich & Szpila, 2008). These findings have implications for models of body size-dependent speciation and extinction and largely corroborate the diffusion model where speciation and extinction is seen as a random walk along the body size axis (McKinney, 1990). The existence and strength of upper and lower boundaries of body size for a given taxon decide then whether SBDs become symmetrical, left- or right-skewed and whether intermediate- or small-bodied taxa are most species rich.

Latitudinal gradients in maximum body size were reported for a variety of terrestrial taxa including vertebrates (Smith *et al.*, 2004), earthworms, spiders and many insect orders (Makarieva *et al.*, 2005). Our study differs from previous ones while accounting for possible covariates. In particular species richness appeared to be an influence. Maximum body size increased with species richness irrespective of latitude. This is expected as a sample artefact under a simple random sampling model where a larger sample size covers a wider spectrum of sizes (Marquet & Taper 1998). However, we did not find a simple pattern of increasing body size at lower latitudes. Instead springtail maximum and average body size appeared to peak at intermediate latitudes (Fig. 3) as also inferred from the negative quadratic latitude term in Table 1. This is corroborated by the results of the random sample model where we failed to detect higher numbers of very large species at lower and higher latitudes (Table 2). These findings demand caution when studying simple size gradients and might account for some of the gradients of Makarieva *et al.* (2005). However, our result appears to be robust within a multiple regression framework that used species richness as covariate (Table 1).

Minimum body size also did not show a simple latitudinal gradient but appeared to peak at intermediate latitudes (Tables 1 & 2) although this trend was weak (Fig. 3a). Again minimum body size was correlated with species richness in the way expected from a random sample model (Table 1). Together with the trend towards larger maximum size in species-rich countries/islands our findings are partly explained from passive sampling out of the whole European species pool. The larger the sample is, the higher the probability of finding very large and very small species.

Spatial distributions and latitudinal trends in higher-order moments of invertebrate SBDs have so far not been studied. From the trends in maximum and average body size we expected to see a shift towards right-skewed distributions at intermediate latitudes. This was indeed the case (Table 1, Fig. 3), although skewness was generally low and ranged between −0.5 and 0.5.

This trend differs from the negative correlation of skewness and latitude reported by Knouft (2004) for freshwater fishes. Nevertheless even a slight latitudinal trend in SBD skewness might account for reported differences in SBD shapes between different species-rich taxa that were based on pooled data sets from different geographical regions (Smith *et al.*, 2004; Ulrich, 2006, 2007).

Skewness, variance and kurtosis were not correlated to area (Table 1). Our results imply therefore that, at least in springtails, SBDs are largely invariant across spatial scales. In vertebrates several studies have reported a trend towards symmetrical size distributions at local scales while regional distributions tend to be right skewed (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Cardillo, 2002). Given the differences in SBDs between vertebrates and some larger insect taxa (Chislenko, 1981; Smith *et al.*, 2004; Ulrich, 2006, 2007; Ulrich & Szpila, 2008) and a random walk of body size evolution we might speculate that SBD shape is taxon specific and its shape constrained by upper and lower body weight boundaries. Further spatially explicit studies of SBDs of other taxa are needed to confirm this hypothesis.

We were surprised to see that none of our climate variables entered the regression analysis for latitudinal trends (Table 1). Previous studies on European vertebrates (Ulrich *et al.*, 2007) and invertebrates (Baselga, 2008, Keil *et al.*, 2008a,b) that used similar coarse-grained environmental and climate data found significant correlations of bats, longhorn beetles, butterflies, hoverflies and dragonflies with temperature and evapotranspiration and geographical heterogeneity. In particular, Ulrich & Fiera (2009) found winter length and average temperature to be major predictors of species richness in European springtails. However, the latter work also showed how climate variables can be linked with latitude and longitude within a factor analysis. Latitude mainly integrates over temperature-connected variables like average, minimum, maximum temperature and winter length, while longitude is connected with absolute temperature differences (Ulrich & Fiera 2009), which means the gradient from maritime to continental climate. The fact that longitude and the annual temperature difference did not enter our regressions implies that the latter gradient is of less importance for springtail body size distributions.

Our study is the first to clearly demonstrate a trend to smaller body sizes on islands for a larger invertebrate taxon (Fig. 4, Table 3). None of the four largest springtail species occurs on any European island. Previously Palmer (2002) found some evidence for larger body sizes of the tenebrionid beetle *Asida planipennis* on mainlands and *Ornithoctonus aureotibialis* spiders were found to decrease in size on a offshore Thai island (http://biology.uta.edu/mlogan/Current%20Projects.htm). These findings corroborate the part of the island rule (Lomolino, 2005) that deals with maximum body weight. However, our results call for a rethinking of possible explanations for the observed trend. In vertebrates insular dwarfism has particularly been linked to resource limitation. Collembola are at least four orders smaller than the smallest land vertebrates and we can't see how size differences between islands and mainlands might influence resource availability. Tentatively we prefer an ecological filtering mechanism. Even in small invertebrates larger species tend to have smaller population sizes (Stork & Blackburn, 1993) and might be, at least over longer time periods, more prone to local extinction. Even a small bias in extinction probability might therefore generate a trend towards a loss of larger species on islands. In this view the island rule in Collembola is not seen as an evolutionary tendency towards smaller size but as a pattern that stems from selective extinction. However, further studies will have to show whether islands size really influences the extinction/colonization trade-off in small-sized invertebrates like Collembola.

A simple bivariate comparison also pointed to an increase in minimum body size on islands in line with the island rule for minimum size (Fig. 4a). However, our covariance analysis (Table 3) that corrected for differences in species richness and area rather pointed to a decrease of minimum size on islands, although this trend was statistically not significant ($P = 0.06$). The smallest European species *F. lawrencei* is an island endemic. Hence, studies on the island rule have to account for important covariates such as species richness and area.

Lastly, we found a weak but highly significant positive body weight–occupancy relationship (Table 4, Fig. 5) when occupancy was measured as number of occurrences and longitudinal range. Latitudinal range in turn seems to negatively influence occupancy (Table 4). Although interspecific body weight–occupancy relationships are well documented for vertebrates (Brown & Maurer, 1989; Gaston & Blackburn, 1996), only a few papers from local to regional scales indicated a similar rule in invertebrates (Biedermann, 2003). Particularly in brachypterous ground beetles (Gutiérrez & Menéndez, 1997), stoneflies and mayflies (Malmqvist, 2000) a positive relationship between body size and regional occupancy has been observed. Our data on springtails are apparently the first to demonstrate a body size–occupancy relationship at a continental scale. However, as for the latitudinal gradient in body sizes our data do not point to a simple positive relationship independent of how occupancy is estimated. Our results rather point to qualitative differences for latitudinal and longitudinal range. Further, our springtail regression analysis explained only 1% of variance and is statistically significant only due to the large number of species involved (Table 4). This contrasts sharply with the vertebrate pattern where body size generally accounts for more than 30% of the variance in range size. Hence our data tentatively indicate a much weaker relationship between range size and body size in invertebrates than found in vertebrates. Further studies in other taxa have to confirm these hypotheses.

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REFERENCES

Allen, C.R., Forys, E.A. & Holling, C.S. (1999) Body mass patterns predict invasions and extinctions in transforming landscapes. *Ecosystems*, **2**, 114–121.

Alroy, J. (2000) Understanding the dynamics of trends within evolving lineages. *Paleobiology*, **26**, 319–329.

Bakker, V.J. & Kelt, D.A. (2000) Scale-dependent patterns in body size distributions of Neotropical mammals. *Ecology*, **81**, 3530–3547.

Baselga, A. (2008) Determinants of species richness, endemism and turnover in European longhorn beetles. *Ecography*, **31**, 263–271.

Bellinger, P.F., Christiansen, K.A. & Janssens, F. (1996–2009) Checklist of the Collembola of the world. Available at: http://www.collembola.org (accessed 13 January 2010).

Biedermann, R. (2003) Body size and area–incidence relationships: is there a general pattern? *Global Ecology and Biogeography*, **12**, 381–387.

Bini, L.M. *et al.* (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography*, **32**, 193–204.

Bretfeld, G. (1999) Synopses on Palaearctic Collembola: Symphypleona. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **71**, 1–318.

Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243**, 1145–1150.

Brown, J.H. & Nicoletto, P.F. (1991) Spatial scaling of the species composition–body masses of North-American land mammals. *The American Naturalist*, **138**, 1478–1512.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Towards a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Calder, W.A. (1996) *Size, function, and life history*. Dover Press, New York.

Cardillo, M. (2002) Body size and latitudinal gradients in regional diversity of new World birds. *Global Ecology and Biogeography*, **11**, 59–65.

Chislenko, L.L. (1981) *Structure of fauna and flora as dependent on organismal body size*. University Press, Moscow.

Clauset, A. & Erwin, D.H. (2008) The evolution and distribution of species body size. *Science*, **321**, 399–401.

Currie, D.J. & Fritz, J.T. (1993) Global patterns of animal abundance and species energy use. *Oikos*, **67**, 56–68.

Damuth, J. (1987) Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biological Journal of the Linnaean Society*, **31**, 193–246.

Deharveng, L. (2007) Collembola. *Fauna Europaea version 1.3*. Available at: http://www.faunaeur.org (accessed 13 January 2010).

Dial, K.P. & Marzluff, J.M. (1988) Are the smallest organisms the most diverse? *Ecology*, **69**, 1620–1624.

Diniz-Filho, J.A.F., Carvalho, P., Bini, L.M. & Tôrres, N.M. (2005) Macroecology, geographic range-size body size relationship and minimum viable population analysis for New World carnivora. *Acta Oecologica*, **27**, 25–30.

Etienne, R.S. & Olff, H. (2004) How dispersal limitation shapes species–body size distributions in local communities. *American Naturalist*, **163**, 69–83.

Fjellberg, A. (1998) Collembola of Fennoscandinavia and Denmark. Part I: Poduromorpha. *Fauna Entomologica Scandinavica*, **35**, 1–184.

Fjellberg, A. (2007) The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona. *Fauna Entomologica Scandinavica*, **42**, 1–252.

Ganihar, S.R. (1997) Biomass estimates of terrestrial arthropods based on body length. *Journal of Biosciences*, **22**, 219–224.

Gaston, K.J. & Blackburn, T.M. (1996) Conservation implications of geographic range size–body size relationships. *Conservation Biology*, **10**, 638–646.

Gaston, K.J., Chown, S.L. & Mercer, R.D. (2002) The animal species–body size distribution of Marion Island. *Proceedings of the National Academy of Sciences USA*, **98**, 14493–14496.

Gisin, H. (1960) *Collembolenfauna Europas*. Museum d'Histoire Naturelle, Geneva.

Gotelli, N.J. & Entsminger, G.L. (2005) *ECOSIM: null models software for ecology*. Version 7.72. Acquired Intelligence Inc. and Kesey-Bear, Jericho, VT.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.

Gutiérrez, D. & Menéndez, R. (1997) Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: Caraboidea) in relation to dispersal ability. *Journal of Biogeography*, **24**, 903–914.

Harestad, A.S. & Bunnell, F.L. (1979) Home range and body weight – a reevaluation. *Ecology*, **60**, 389–402.

Hopkin, S.P. (1997) *Biology of the springtails (Insecta: Collembola)*. Oxford University Press.

Jordana, R., Arbea, J.I., Benito, S.C. & Luciáñez, M.J. (1997) Collembola, Poduromorpha. *Fauna Ibérica*, vol. 8 (ed. by M.A. Ramos, J.A. Tecedor, J.B. Ros, J.G. Noguera, A.G. Sierra, E.M. Mayol, F.M. Piera, J.S. Marino and J.T. Gonzales), pp. 1–807. Museo Nacional de Ciencias Naturales, Madrid.

Keil, P., Dziock, F. & Storch, D. (2008a) Geographical patterns of hoverfly (Diptera, Syrphidae) functional groups in Europe: inconsistency in environmental correlates and latitudinal trends. *Ecological Entomology*, **33**, 748–757.

Keil, P., Simova, I. & Hawkins, B.A. (2008b) Water-energy and the geographical species richness pattern of European and North African dragonflies (Odonata). *Insect Conservation and Diversity*, **1**, 142–150.

Kelt, D.A. & van Vuren, D. (2001) The ecology and macroecology of mammalian home range area. *The American Naturalist*, **157**, 637–645.

Knouft, J.H. (2004) Latitudinal variation in the shape of the species body size distribution: an analysis using freshwater fishes. *Oecologia*, **139**, 408–417.

Knouft, J.H. & Page, L.M. (2003) The evolution of body size in extant groups of North American freshwater fishes: speciation, size distributions, and Cope's rule. *The American Naturalist*, **161**, 413–421.

Kozłowski, J. & Gawelczyk, A.T. (2002) Why are species' body size distributions usually skewed to the right? *Functional Ecology*, **16**, 419–432.

Liechstein, J.W., Simons, T.R., Shriner, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autoregressive models ecology. *Ecological Monographs*, **72**, 445–463.

Loder, N. (1997) *Insect species – body size distributions*. PhD Thesis, Unversity of Sheffield, UK.

Lomolino, M. (2005) Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*, **32**, 1683–1699.

Makarieva, A.M., Gorshkov, V.G. & Li, B.-L. (2005) Temperature associated upper limits to body size in terrestrial poikilotherms. *Oikos*, **111**, 425–436.

Makarieva, A.M., Gorshkov, V.G., Li, B.-L., Chown, S.L., Reich, P.B. & Gavrilov, V.M. (2008) Mean mass-specific metabolic rates are strikingly similar across life's major domains: evidence for life's metabolic optimum. *Proceedings of the National Academy of Sciences USA*, **105**, 16994–16999.

Malmqvist, B. (2000) How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? *Biological Conservation*, **93**, 271–276.

Marquet, P.A. & Taper, M.L. (1998) On size and area: patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology*, **12**, 127–139.

Maurer, B.A., Brown, J.H. & Rusler, R.D. (1992) The micro and macro in body size evolution. *Evolution*, **46**, 939–953.

May, R.M. (1978) The dynamics and diversity of insect faunas. *Diversity of insect faunas* (ed. by L.A. Mound and N. Waloff), pp. 188–204. Oxford University Press, Oxford.

May, R.M. (1986) The search for patterns in the balance of nature: advances and retreats. *Ecology*, **67**, 1115–1126.

McKinney, M.L. (1990) Trends in body size evolution. *Evolutionary trends* (ed. by K.C. McNamara), pp. 75–118. University Arizona Press, Tucson.

Meiri, S. & Thomas, G.H. (2007) The geography of body size – challenges of the interspecific approach. *Global Ecology and Biogeography*, **16**, 689–693.

Meiri, S., Dayan, T. & Simberloff, D. (2006) The generality of the island rule reexamined. *Journal of Biogeography*, **33**, 1571–1577.

Meiri, S., Cooper, N. & Purvis, A. (2008) The island rule: made to be broken? *Proceedings of the Royal Society B: Biological Sciences*, **275**, 141–148.

Morse, D.R., Lawton, J.H., Dodson, M.M. & Williamson, M.H. (1985) Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature*, **314**, 731–733.

Orme, C.D.L., Quicke, D.L.J., Cook, J.M. & Purvis, A. (2002) Body size does not predict species richness among the metazoan. *Journal of Evolutionary Biology*, **15**, 235–247.

Palmer, M. (2002) Testing the 'island rule' for a tenebrionid beetle (Coleoptera, Tenebrionidae). *Acta Oecologica*, **23**, 103–107.

Peters, R.H. (1983) *The ecological implications of body size*. University Press, Cambridge.

Pomorski, J. (1998) *Onychiurinae of Poland (Collembola: Onychiuridae)*. Polish Taxonomical Society, Wroclaw.

Potapov, M. (2001) Synopses on Palaearctic Collembola: Isotomidae. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **73**, 1–603.

Rangel, T.F.L., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321–327.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004) Effects of body size and temperature on population growth. *The American Naturalist*, **163**, 429–441.

Schmidt-Nielsen, K. (1984) *Scaling: why is animal size so important?*. Cambridge University Press, Cambridge.

Smith, F.A., Brown, J.H., Haskell, J.P., Lyons, S.K., Alroy, J., Charnov, E.L., Dayan, T., Enquist, B.J., Ernest, S.K.M., Hadley, E.A., Jones, K.E., Kaufman, D.M., Marquet, P.A., Maurer, B.A., Niklas, K.J., Porter, W.P., Tiffney, B. & Willig, M.R. (2004) Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *The American Naturalist*, **163**, 672–691.

Stork, N.I. & Blackburn, T.M. (1993) Abundance, body size and biomass of arthropods in tropical forest. *Oikos*, **67**, 483–489.

Tabachnick, B.G. & Fidell, L.S. (1996) *Using multivariate statistics*, 3rd edn. Harper Collins, New York.

Thibaud, J.M., Schulz, H.J. & Da Gama Assalino, M.M. (2004) Synopses on Palaearctic Collembola: Hypogastruridae. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **75**, 1–287.

Ulrich, W. (2006) Body weight distribution of European Hymenoptera. *Oikos*, **114**, 518–528.

Ulrich, W. (2007) Body weight distributions of central European Coleoptera. *European Journal of Entomology*, **104**, 769–776.

Ulrich, W. & Fiera, C. (2009) Environmental correlates of species richness of European springtails (Hexapoda: Collembola). *Acta Oecologica*, **35**, 45–52.

Ulrich, W. & Szpila, K. (2008) Body size distributions of eastern European Diptera. *Polish Journal of Ecology*, **56**, 557–568.

Ulrich, W., Sachanowicz, K. & Michalak, M. (2007) Environmental correlates of species richness of European bats (Mammalia: Chiroptera). *Acta Chiropterologica*, **9**, 347–360.

SUPPORTING INFORMATION

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

Appendix S1 List of European Collembola species and body size data.

Appendix S2 Literature used to compile Appendices S1, S3 and S4.

Appendix S3 Basic entries of the collembolan database. Numbers of superfamilies, families and species included in the analysis of 22 European families of Collembola with references.
Appendix S4 Basic environmental data and species richness of European countries and islands used in the present study.

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