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Environmental correlates of species richness of European springtails (Hexapoda: Collembola)

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ABSTRACT

Our knowledge about environmental correlates of the spatial distribution of animal species stems mostly from the study of well known vertebrate and a few invertebrate taxa. The poor spatial resolution of faunistic data and undersampling prohibit detailed spatial modeling for the vast majority of arthropods. However, many such models are necessary for a comparative approach to the impact of environmental factors on the spatial distribution of species of different taxa. Here we use recent compilations of species richness of 35 European countries and larger islands and linear spatial autocorrelation modeling to infer the influence of area and environmental variables on the number of springtail (Collembola) species in Europe. We show that area, winter length and annual temperature difference are major predictors of species richness. We also detected a significant negative longitudinal gradient in the number of springtail species towards Eastern Europe that might be caused by postglacial colonization. In turn, environmental heterogeneity and vascular plant species richness did not significantly contribute to model performance. Contrary to theoretical expectations, climate and longitude corrected species–area relationships of Collembola did not significantly differ between islands and mainlands.

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1. Introduction

Understanding the factors that regulate spatial variation in species richness has been one of the fundamental questions in ecology for decades (Rosenzweig, 1995; Hawkins and Diniz-Filho, 2004; Brown and Lomolino, 2005). Major predictors of large scale variation in species richness of animals and plants are area, latitude and climate (cf. Rosenzweig, 1995; Maurer, 1999; Brown and Lomolino, 2005).

Species richness usually increases with area (Rosenzweig, 1995; Lomolino, 2000; Scheiner, 2003). This species–area relationship (SAR) has mainly been attributed to area per se (the

increase in species richness with increasing sample size in larger areas) and to increasing habitat heterogeneity in larger areas that allows for additional species to occur, which differ in their niches (Rosenzweig, 1995; Scheiner, 2003). SARs often follow an allometric function of the form:

$$S = S_0 A^z \tag{1}$$

where S denotes the number of species in a given area A. S_0 and z are the parameters of the model with S_0 being an estimate of the mean number of species per unit area (the species density). Shmida and Wilson (1985) and Rosenzweig (1995) pointed to the triphasic shape of SARs with higher slopes

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(often z > 0.3) at local and intercontinental scales and lower slopes (z < 0.2) at regional to continental scales.

A second major predictor of large scale species richness is latitude (Hillebrand, 2004). With few exceptions (sawflies, Ichneumonidae, aphids) species richness of a given taxon peaks at lower latitudes (Rhode, 1992; Hillebrand, 2004). However, latitude per se does not control species richness. Latitude is an aggregate variable that integrates over many distinct factors. Of these factors, temperature and precipitation gradients are major predictors of global patterns of vegetation structure, productivity and plant and animal species richness (Gitay et al., 2002; Hawkins et al., 2007; Currie et al., 2004).

Recently, ecological and evolutionary history has come into the focus of interest as a descriptor of continental wide patterns of species richness (Hewitt, 1999; Hawkins et al., 2007; Svenning and Skov, 2007a,b). Particularly, postglacial colonization trajectories from glacial refuges in combination with dispersal limitation have been identified to influence present day differences in species richness of European bats (Horáček et al., 2000) and trees (Svenning and Skov, 2007b). Whether this also holds for arthropods is largely unknown (Storch et al., 2003).

Despite recent critiques (Dormann, 2007), the use of species distribution models has become a standard tool in macroecology and the development of easy to use software (Rangel et al., 2006) for spatial autocorrelation models will surely boost this trend. However, most models focused on vertebrates (Willig et al., 2003; Rodriguez and Arita, 2004; Qian et al., 2007; Ulrich et al., 2007) vascular plants (particularly trees, Qian et al., 2005) and a few invertebrate taxa like butterflies (Dennis et al., 1998; Ulrich and Buszko, 2003a), dung beetles (Lumaret and Lobo, 1996) and longhorn beetles (Baselga, 2008). This concentration on a few taxa implies that major generalizations on environmental determinants of large scale species richness are based on a few taxa for which appropriate data are available. The lack of appropriate data means that for the vast majority of invertebrates, particularly for major arthropod taxa, spatial modeling is missing. However, the Fauna Europaea project (Fauna Europaea, 2004) and recent advances in faunistic surveys of the arthropod faunas of many European countries allows for more detailed modeling at least of species richness patterns. These approaches should contribute to our understanding of the determinants of large scale patterns of species distribution. What is necessary is independent spatial modeling for many invertebrate taxa. A comparison of these independent models allows then for an assessment of which factors determine large scale differences in species richness and how they work together.

The present study uses such new data and investigates whether and how European springtail (Collembola) species richness can be explained by the aforementioned three important environmental variables. We use recent and reliable faunal surveys (Table 1) to infer the geographical distribution of approx. 2500 European springtail species (Hopkin, 1997).

The large scale patterns of collembolan species richness are insufficiently known (Koh et al., 2002; Deharveng, 2007). The fact that springtails colonize extreme habitats like deserts, high mountain soils and even the Antarctic soils (Hopkin, 1997) indicates that climate might play a more minor role for species richness than in other arthropods. In turn, Collembola seem to follow the general rule that diversity peaks at low latitudes. In tropical rain forests, more than 130 species have been found in soil, leaf litter and aboveground vegetation (Deharveng et al., 1989). In temperate forests, diversity is lower, but it is not unusual to find more than 40

Table 1 – Species numbers of European countries and larger island included in the present study with major references. Additionally we used recent descriptions of single species from these countries and islands (the complete literature list can be requested from the authors)

Country	Species richness	Authors
Albania	108	Deharveng, 2007; Traser and Kontschan, 2004
Austria	485	Querner, in press
Azores	95	Gama, 2005a,b
Balearic Islands	42	Deharveng, 2007; Jordana et al., 2005
Belgium	210	Janssens, 1996–2007
Canary Islands	103	Deharveng, 2007; Gama, 2005b
Crete	93	Ellis, 1976
Czech Republic	534	Rusek, 1977, 2003, (Rusek unpubl. data)
Denmark	226	Fjellberg, 2007
Dodecanese Islands	40	Deharveng, 2007
Faeroe Islands	86	Fjellberg, 2007
Finland	225	Fjellberg, 2007
France	619	Deharveng, 2007; Beruete et al., 2002; Potapov and Deharveng, 2005; Deharveng et al., 2005; Jordana and Baquero, 2005; Thibaud, 2006
Franz-Josef Land	14	Babenko and Fjellberg, 2006
Germany	430	Schulz, personal communication
Great Britain	383	Hopkin, 2002; Skarzynski and Smolis, 2006
Hungary	412	Danyi and Traser, unpublished
Iceland	162	Fjellberg, personal communication
Italy	420	Dallai et al., 1995; Fanciulli et al., 2005
Jan Mayen	28	Babenko and Fjellberg, 2006
Latvia	200	Jucevica E., personal communication
Moldavia	170	Busmachiu G., personal communication
Netherlands	204	Berg, 2002
Norway	316	Fjellberg, 2007
Novaya Zemlya	53	Babenko and Fjellberg, 2006
Poland	468	Sterzyńska et al., 2007
Portugal	236	Deharveng, 2007; Gama, 2004
Romania	388	Fiera, 2007
Sicily	105	Dallai et al., 1995; Fanciulli et al., 2006
Slovakia	400	Rashmanova N., personal communication
Spain	730	Arbea J., personal communication
Svalbard	62	Fjellberg, personal communication
Sweden	285	Fjellberg, 2007
Switzerland	320	Deharveng, 2007; Potapov and Deharveng, 2005
Ukraine	527	Kaprus et al., 2004

species in deciduous woodland (Wolters, 1985; Lauga-Reyrel and De Conchat, 1999).

We test six major predictions about geographical factors that should influence large scale patterns of species richness.

1. According to the SAR, area should explain a major part of the variability in species richness. In mammals and birds, area frequently explains more than 50% of variability in species richness (Rosenzweig, 1995).
2. Species richness and latitude should correlate negatively (Hillebrand, 2004). Accordingly, species richness should peak in Mediterranean countries and decrease monotonically towards Great Britain, Scandinavia and other northern countries.
3. Regions that are topographically more diverse should have enhanced numbers of species because of greater habitat heterogeneity (Wilson, 1974).
4. Temperature should influence species richness. Collembola might be sensitive to two aspects of temperature: yearly temperature range and absolute length of the winter. Particularly the length of the winter should influence springtail reproductive cycles and possibly species richness.
5. Islands and mainlands should differ in species numbers after correcting for area, heterogeneity, temperature and latitude. Classical island biogeography (MacArthur and Wilson, 1967) and recent models about island colonization (Lomolino and Weiser, 2001; Rosenzweig, 2001) predict islands to have lower intercepts (expected species densities) and steeper slopes of SARs when fitted by the power function model.
6. A postglacial colonization of central and Western Europe from Eastern Asia should be visible as a positive longitudinal gradient. Hence, Western European countries should have fewer species than expected from models that lack longitude as a predictor variable.

2. Materials and methods

We used recent taxonomic revisions and faunal surveys to update the faunal composition of 66 countries (mainlands and larger islands regardless of national affiliation) mentioned in Fauna Europaea (Deharveng, 2007). For 35 countries and larger islands reliable recent faunistic surveys were available (Table 1).

According to the six hypotheses mentioned above, we evaluated the influence of six geographical variables on springtail species richness. For each European country and larger island (Table 1), 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/atlas/world.htm). We compiled mean temperatures in January $T_{January}$ and July T_{July} from data in Weatherbase (http://www.weatherbase.com) and estimated the yearly temperature difference ΔT of a country or island from $\Delta T = T_{July} - T_{January}$. Next, we estimated the mean length of the winter from the mean number of days below $0\,^{\circ}C$ ($N_{T < 0}$). 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 temperature ranges for larger countries.

Further, we compiled data of the number of vascular plants (S_{plants}) from data in EarthTrends: The Environmental Information Portal (http://earthtrends.wri.org) and used these as a second estimate of habitat heterogeneity. However, because reliable data were available for only two islands and 22 countries, we did not include plant species numbers in our basic model. As an estimate of topographical heterogeneity H we used the quotient of highest elevation through country or island area (Ricklefs et al., 2004). Because this is a very crude measure, we use H mainly to have an additional variable to control for possible heterogeneity effects. We did not use mean precipitation due to the large variability within most countries that often exceeded 200%.

Geographical and environmental data of the present type are susceptible to spatial autocorrelation that might inflate type I error probabilities (Legendre, 1993; Bahn et al., 2006). To correct for spatial autocorrelation we used the simultaneous autoregression model (Liechstein et al., 2002) with generalized least squares estimation that is implemented in the spatial autocorrelation model (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. Spatial autocorrelation was quantified using Moran's I (Rangel et al., 2006). To estimate the relative influence of each of the predictors, we used squared semipartial correlations between these predictors (ln-transformed in the case of area and species richness). We applied the Akaike information criterion for model choice using R^2 as the measure of goodness of fit. Errors refer to standard errors.

3. Results

Springtail species richness differed widely between the 35 European countries and major islands included in the present study. Of the countries for which reliable data were available (Table 1), Spain appeared to be most species rich (730 species) followed by France (619) and Ukraine (527).

Species richness and climate data were significantly spatially autocorrelated (Moran's I for S, $N_{t < 0}$ and ΔT at the first distance class: $P_{I = 0} < 0.05$). Therefore, we used spatial autoregression models (Rangel et al., 2006) to infer the parameters of linear additive species richness models (general least squares). Within this approach the SAR of the European springtails (including the estimate for the whole of Europe) was best described by a power function according to Eq. (1) ($r^2 = 0.73$, $p < 0.00001$) with a slope $z = 0.42 \pm 0.07$ and a species density $S_0 = 2 \pm 1$ species $* km^{-2}$ (Fig. 1A). For comparison, we also tested the logarithmic SAR model ($S = S_0 + z \ln(A)$) and found its fit worse ($r^2 = 0.43$, $p < 0.0001$). It predicted a negative number of species per unit area ($S_0 = -457 \pm 158$).

We first inferred the internal structure of our predictor variables from a principal component analysis (Table 2). The PCA identified three factors that explained 78% of total variance. The first factor captured the temperature differences with latitude. The second factor loaded particularly with longitude, difference in temperature and area. It depicts the
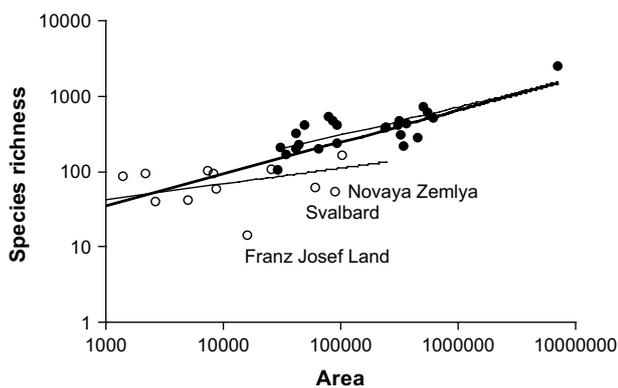
Fig. 1 – The simple SAR of the European Collembola (bold regression line) is well fitted by a power function model of the form $S = (2 \pm 1)A^{0.40 \pm 0.06}$; $R^2 = 0.61$; $p < 0.0001$. Separate SARs for islands (open dots) and mainlands (full dots): Island SAR: $S = (9.9 \pm 3.0)A^{0.21 \pm 0.11}$ $R^2 = 0.44$; $p = 0.07$. Mainland SAR: $S = (4.3 \pm 0.9)A^{0.37 \pm 0.06}$ $R^2 = 0.41$; $p < 0.001$.

increasing continental climate towards Eastern European countries and their comparably larger areas. The third factor loaded with precipitation and heterogeneity.

Area corrected plots of species richness versus latitude (Fig. 2A) and longitude (Fig. 2B) pointed to a decrease in species richness towards higher latitudes. This trend was more pronounced for islands. Fig. 2B also points to a longitudinal trend in species richness with a decrease in species richness towards Eastern Europe.

To evaluate these patterns in detail we used an additive spatial autoregression model that assumed smooth latitudinal and longitudinal gradients. This model pointed to significant correlations of species richness with area, latitude and longitude (all $p < 0.015$).

$$\ln(S) = (0.44 \pm 0.04)\ln(A) - (0.02 \pm 0.007)\,Latitude$$
$$- (0.02 \pm 0.005)\,Longitude + (1.5 \pm 0.56) \qquad (2)$$

The model explains 76% of the variance in species richness and identifies a group of central European counties as having more springtail species than expected: Hungary (412 observed, 209 expected), Austria (485, 215), the Czech Republic (534, 198), and Slovakia (418, 156). In turn, particularly Portugal (236, 383) and Iceland (162, 292) appear to be depauperate.

We next included the other environmental variables that might influence collembolan species richness S. Stepwise variable reduction using AIC resulted in a final model with four predictive variables that explained 83% of variance in species richness:

$$\ln(S) = (0.36 \pm 0.05)\ln(A) - (0.03 \pm 0.007)\,Longitude$$
$$- (0.004 \pm 0.001)\,N_{T<0} + (0.09 \pm 0.03)\,\Delta T \qquad (3)$$

All predictors entered the model with $p < 0.001$. This model basically contains the first two principal factors of Table 2. Area and longitude still appeared to be significant predictors of species richness. Latitude, as a surrogate variable, was replaced by $N_{T<0}$ and ΔT. Indeed, particularly $N_{T<0}$ correlated strongly with latitude ($r = 0.91$, $p < 0.001$). This high co

linearity and the unknown error terms of the predictor variables prohibited further separation of the singles effects of latitude and climate variables (cf. Heikkinen et al., 2004). The model predicts that species richness decreases with winter length and increases with annual temperature range. Squared semipartial correlation coefficients pointed to area ($r^2_{semipar} = 0.61$) as the most important predictor in this model followed by $N_{T<0}$ ($r^2_{semipar} = 0.35$), Longitude ($r^2_{semipar} = 0.32$), and ΔT ($r^2_{semipar} = 0.24$). Eq. (3) does not contain precipitation, yearly mean temperature, heterogeneity and the number of vascular plants. In none of the modeling steps did these variables significantly contribute to model performance.

The model still identified Austria (485, 305), Slovakia (418, 266), and particularly the Czech Republic (534, 235) as having more species than expected (Fig. 3B). In turn, Sweden (285 observed, 393 expected), Finland (225, 371), Norway (316, 487), Portugal (236, 299) and Iceland (162, 309) seem to be too species poor. In the case of Portugal this might stem from undersampling.

In the next step, we looked at whether islands and mainlands differ in patterns of species richness. According to current theory (Rosenzweig, 1995, 2001) islands should have steeper SAR slopes than mainlands. A spatial autocorrelation model that contained area, latitude and longitude to islands and mainlands separately gave a latitude and longitude corrected island SAR slope of $z = 0.32 \pm 0.06$ and a respective mainland slope of $z = 0.30 \pm 0.07$. The respective intercepts are $S_0 = 2.1 \pm 0.6$ species $* \, km^{-2}$ (islands) and $S_0 = 3.3 \pm 0.9$ species $* \, km^{-2}$ (mainlands). Slopes and intercepts do not significantly differ at the 5% error benchmark. Further, the model of Eq. (3) equally applies to islands and mainlands (Fig. 3).

4. Discussion

Our knowledge about the spatial distribution of European arthropods comes mainly from a few well studied taxa like butterflies (Dennis et al., 1998; Ulrich and Buszko, 2003a; Ulrich, 2005) ground (Kotze et al., 2003) and longhorn beetles (Baselga, 2008). These few studies largely corroborated

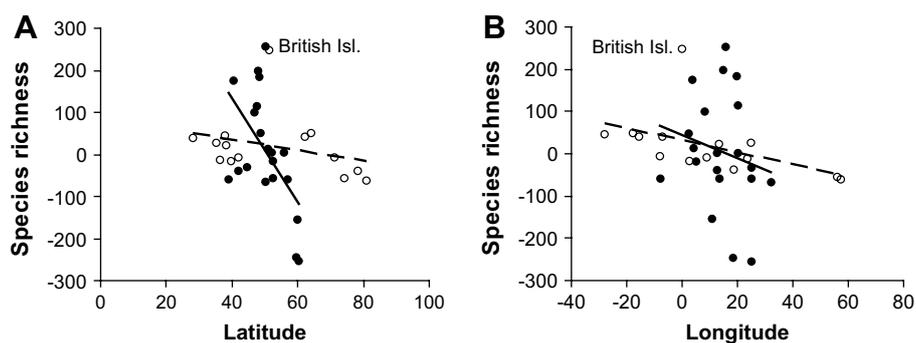| Table 2 – Principal component analysis of the predictor variable included in the present study			
Variable	Factor loadings		
	1	2	3
Latitude	**0.95**	0.06	0.12
Longitude	0.43	**0.70**	0.15
ln(A)	−0.01	**0.78**	−0.16
T_{mean}	**−0.96**	−0.17	−0.04
ΔT	0.38	**0.88**	0.14
$N_{T<0}$	**0.95**	0.26	−0.07
Precipitation	−0.42	−0.07	**0.62**
S_{plants}	−0.40	**0.65**	−0.25
Heterogeneity	−0.44	0.14	**−0.72**
Eigenvalue	3.57	2.42	1.05
Variance	0.40	0.27	0.12

Fig. 2 – Area corrected (separate for islands and mainlands according to Fig. 1) species richness of European Collembola in relation to latitude (A) and longitude (B). Regressions A: mainlands: $r = -0.47$, $p = 0.03$; islands: $r = -0.57$, $p = 0.04$; B: mainlands: $r = -0.21$, n.s.; islands: $r = -0.82$, $p < 0.01$. The British Isles, which behave like a mainland, are not included in the island regressions.

theoretical expectations about the influence of climatic variables, area, and ecological history.

First, area appeared to be the major predictor of European springtail species richness. The simple uncorrected SAR explained 60% of the variance in species richness (Fig. 1). Similar values had been obtained in previous studies on European arthropod SARs (Ulrich and Buszko, 2003a; Baselga, 2008; Michalak, 2008). Current theory (Rosenzweig, 1995; Lomolino, 2000) and recent meta-analysis (Michalak, 2008) found island slopes as being steeper than mainland slopes. The latter were frequently best fitted by a power function with slope $z < 0.2$. Island SAR slopes, in turn, were found to have $z > 0.2$ (Rosenzweig, 1995; Scheiner, 2003). The Collembola of the present study deviate while having mainland and island slopes at the continental scale of $z > 0.3$ even after correcting for climate variables. This fast increase in species richness with area points to a comparably high regional species turnover of springtails and therefore to low average regional species range sizes.

We were surprised to find that islands are not species poorer than mainlands as predicted by current theories on island biogeography (Lomolino and Weiser, 2001; Scheiner, 2003). Island and mainland SAR slopes and intercepts did not significantly differ. Therefore, Collembola have either relatively low extinction or high immigration rates on islands, which counterbalances island isolation. Rosenzweig (2001)

concluded that mainland habitat fragmentation causes a shift from mainland to island SAR patterns. The effect would be lower local α-diversities (expressed by the SAR intercept) and in the long run also lower regional β- and γ-diversities. Our finding about similar island and mainland species densities implies that Collembola might be more resistant against species loss in fragmented mainland habitats than other taxa that differ in island and mainland SARs.

Our results also show that it is dangerous to compare large scale island and mainland SARs directly without correcting for environmental correlates. The uncorrected SARs differ significantly in slope and intercept (Fig. 1) and imply a much higher species accumulation (β-diversity) and a lower α-diversity of mainlands. After correcting for climate and longitude these differences vanished. This effect might have influenced to a certain degree previous meta-analytical comparisons of island and mainland SARs (Connor and McCoy, 1979; Rosenzweig, 1995). Our results call for a spatial modeling approach for the comparison of SAR slopes and intercepts.

Our analysis confirmed the latitudinal gradient in species richness of European springtails (Eq. (2)). This gradient appeared to be caused by climatic differences as had been advocated by Hawkins et al. (2007). Eq. (3) points to winter length ($N_{T < 0}$) as a main factor that is responsible for this trend while average annual temperature appeared to be of
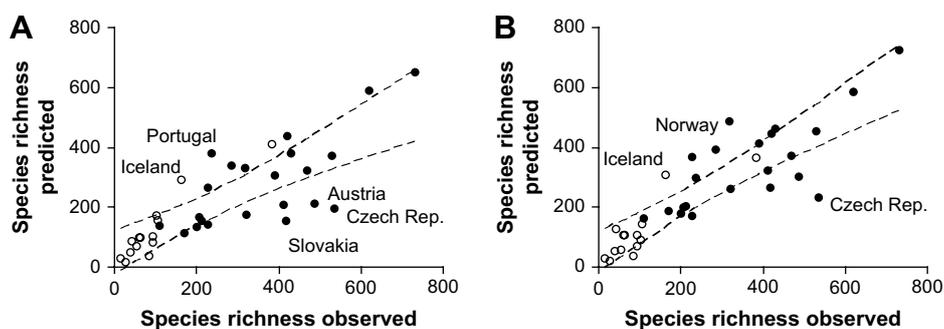

Fig. 3 – Predicted versus observed species richness of European Collembola as inferred from Eq. (2) (A) and Eq. (3) (B). Given are also the 99% confidence limits of the regression.
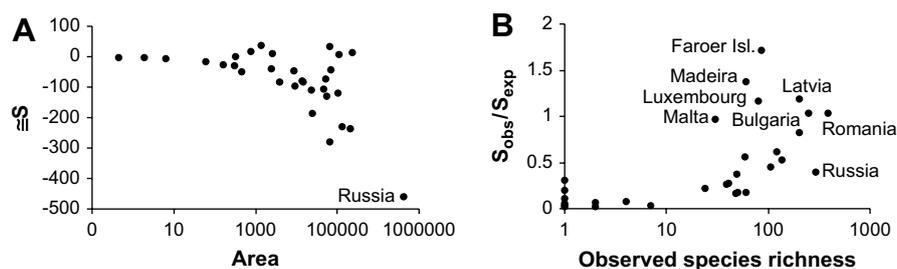
Fig. 4 – The difference of observed and predicted (Eq. (3)) species numbers (ΔS) versus area for all European countries/islands mentioned in Fauna Europaea that are not included in the present study. B: Observed/expected species numbers of these countries/islands in dependence on observed species richness. Negative values in A and values < 1 in B point to undersampling of species.

minor importance. Winter length was also found by Ulrich et al. (2007) as a main predictor of European bat species richness. However, its relative impact was much more severe for bats than for the springtails of the present study. Even Svalbard (62 species) and Franz Josef Land (14) have a comparably diverse springtail fauna that is covered by Eqs. (2) and (3). Collembola are adapted to cold and drought periods and survive sub-zero temperatures by supercooling and a form of anhydrobiosis (Block, 1990; Holmstrup, 2002). They rapidly increase metabolism at temperatures above zero.

The European Collembola exhibited a clear longitudinal trend in species richness even after correcting for area and climatic variables. Species richness decreased with increasing longitude. Hence Eastern European countries have comparably fewer species than Western European countries and islands after correcting for climate variables. This trend is contrary to the trend found by Rokas et al. (2003) for European gall wasps. Eq. (3) also points to an antagonistic behavior of longitude and the annual temperature range ΔT despite the fact that both variables correlate positively ($r = 0.8$, $p < 0.001$, Table 2), which reflects the transition from the maritime to the continental climate with increasing longitude. Obviously other variables influence the longitudinal trend in springtails. One candidate might be a postglacial colonization from a South–Western European center of colonization (Atkinson et al., 2007). However, without better resolved spatial data we cannot test this hypothesis. On critical point in this respect regards undersampling (see below). Many countries excluded from analysis due to insufficient data are in eastern and South–Eastern Europe. This bias might have influence on the effect of longitude in Eq. (3).

One shortcoming of the present approach is surely its coarse grain. The explanatory power of input variables depends on the spatial resolution (Rahbek and Graves, 2001) and spatially better resolved data would surely allow for a precise identification of predictor variables. In the best case of species based distribution data these models would even be suited for predictions of future species home ranges under climate and land use change (Dormann, 2007). However, fine grained distribution data are currently unavailable for larger arthropod taxa. Nevertheless, the present modeling corroborates previous work on butterflies (Ulrich and Buszko, 2003a,b; Ulrich, 2005), bats (Ulrich et al., 2007) and Cerambycidae (Baselga, 2008), which showed that even a coarse grain approach is able to identify major environmental predictors of insect species richness. These results encourage the use of newer faunal data of other larger taxa for a similar modeling and to compare the results. This would surely contribute to our understanding of the environmental correlates of large scale arthropod species richness.

The present approach allows for the identification of undersampled areas (Fig. 4). Absolute undersampling (ΔS) increases with country/island area while relative undersampling (S_{obs}/S_{exp}) increases with decreasing species richness. Highly undersampled are particularly Eastern European Russia (−460 species), Lithuania (−279), and Belarus (−238), but also Greece (−228), Macedonia (−187), and Croatia (−130). Further, a ranking of countries according to their residual species richness ($\Delta S = S_{observed} - S_{expected}$) identified the Northern European countries Norway ($\Delta S = -171$), Iceland (−147), Finland (−147), and Sweden (−108) as being comparably species poor. Whether this is caused by undersampling or by additional environmental factors remains unclear. In turn, of the well studied countries (Table 1) the Central European Czech Republic (+299), Austria (+180), Slovakia +152, Hungary (+89), and Poland (+93) seem to be rather species rich.

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