



Spatial patterns in the distribution of European springtails (Hexapoda: Collembola)

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Using a large database on the spatial distribution of European springtails (Collembola) we investigated how range sizes and range distribution across European countries and major islands vary. Irrespective of ecological guild, islands tended to contain more endemic species than mainland countries. Nestedness and species co-occurrence analysis based on country species lists revealed latitudinal and longitudinal gradients of species occurrences across Europe. Species range sizes were much more coherent and had fewer isolated occurrences than expected from a null model based on random colonization. We did not detect clear postglacial colonization trajectories that shaped the faunal composition across Europe. Our results are consistent with a multiregional postglacial colonization. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **105**, 498–506.

ADDITIONAL KEYWORDS: coherence – endemics – latitudinal gradient – longitudinal gradient – macroecology – range size – widespread species.

INTRODUCTION

Multivariate modelling of species richness and range sizes of terrestrial and aquatic organisms (Rangel, Diniz-Filho & Bini, 2010; Thieltges *et al.*, 2011) have improved our understanding of how evolutionary and ecological history and environmental factors constrain species richness at different spatial and temporal scales. In particular, these models showed how area, climate variables, and the physical structure of the landscape work together as drivers of animal and plant species richness and spatial distribution (Keil & Konvicka, 2005; Svenning & Skov, 2007; Ulrich, Sachanowicz & Michalak, 2007; Baselga, 2008; Keil, Dziock & Storch, 2008; Keil, Simona & Hawkins, 2008; Ulrich & Fiera, 2009; Bąkowski, Ulrich & Laštůvka, 2010).

Species range sizes appear to be positively correlated with regional abundance (Huston, 1999), dispersal ability (Rundle, Bilton & Foggo, 2007; Thieltges *et al.*, 2011), ecological niche width (Gaston & Spicer, 2001), and evolutionary lineage age (Webb & Gaston, 2000; McGaughran *et al.*, 2010). Recent work on European Sesiidae (Ulrich, Bąkowski & Laštůvka, 2011) has also shown how differences in postglacial dispersion from glacial refuges have influenced today's pattern of distribution and range size.

In bioconservation, species of restricted range size (hereafter rare species) are of ecological interest (Kunin & Gaston, 1997). They are most vulnerable to extinction after habitat changes (Gaston, 2003; Fagan *et al.*, 2005). Improved understanding of the factors that restrict range sizes and sufficiently precise models to foresee changes in the spatial distribution of rare species are therefore indispensable tools in biodiversity forecasting and conservation management.

Most work on range size distributions has focused on vertebrates, especially on mammals and birds (Orme *et al.*, 2006; Anderson *et al.*, 2009; Araújo *et al.*, 2011) and a few comparably well-studied arthropod taxa, particularly butterflies (Ulrich & Buszko, 2003;

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Barros & Benito, 2010), diving beetles (Calosi *et al.*, 2010), and ground beetles (Jiménez-Valverde & Ortuňo, 2007). Comparative studies on ranges size for all species of larger invertebrate taxa are still scarce (Thieltges *et al.*, 2011). Other species of well-studied taxa are generally winged and highly dispersive. Thus, the observed spatial patterns in these taxa might not be generally applicable. Particularly poorly studied are range size distributions of species associated with the soil subsystem (Gaston & Spicer, 2001; Maraun, Schatz & Scheu, 2007). These are mostly wingless species of comparatively low dispersal ability.

In the present study we use an updated compilation (Ulrich & Fiera, 2009, 2010) of the spatial distribution of European springtails (Collembola) and tested several hypotheses concerning the postglacial colonization of Europe from glacial refuges. Springtails are among the most abundant soil-dwelling arthropods with densities up to several hundred thousand individuals per square metre in forest soils. Although mostly associated with the soil and leaf litter subsystems, many species live in the vegetation, in littoral and neustonic habitats, caves, or even glaciers. The current geographical distribution of species reflects not only the ability of a given species to survive specific environmental conditions but also the ability to have successfully colonized a habitat once the appropriate niche became available (Ávila-Jiménez & Coulson, 2011). Thus, we should see geographical range sizes in terms of colonization and persistence.

The large number of European species (> 2000: Ulrich & Fiera, 2010; Deharveng, 2011) and the fact that previous studies showed how collembolan distribution can be determined both by broad zoogeographical factors and local ecological conditions (Ávila-Jiménez & Coulson, 2011) make them an ideal candidate group for studies on range sizes and postglacial dispersal. We focused on three hypotheses on the European distribution of springtails.

1. Jetz & Rahbek (2002), Kreft, Sommer & Barthlott (2006), and Szabo, Algar & Kerr (2009) found species richness patterns of widespread species at the continental scale to be more affected by climatic factors than richness of species with restricted range size. Species with restricted ranges are considered to be influenced by environmental factors that operate on a local or regional scale, whereas widespread species should be less affected by such regional factors (e.g. Brown, 1984; Jetz & Rahbek, 2002). Under this premise we expected to see significant differences in range size patterns between widespread and endemic species independent of latitude and longitude.

- 2. Many insect and plant taxa colonized Europe postglacially from three main refuges (or hotspots) – Spain, Turkey, and possibly middle Asia (Hewitt, 1999; Médail & Quézel, 1999; Myers, Mittermeier & Mittermeier, 2000). Thus, we expect the highest number of species with restricted range size to be in southern Europe and therefore a latitudinal gradient in range size. Immigrants from the middle Asian refuge, in turn, should have comparably large range sizes (eastern, northern, and middle European countries).
- 3. Nestedness describes a situation where the species composition of species-poorer sites forms a true subset of the composition of species-richer sites (Patterson & Atmar, 1986; Ulrich, Almeida-Neto & Gotelli, 2009). A postglacial colonization pattern from southern Europe implies such a nested pattern of occurrence with an ordered loss of species towards northern European countries (Cutler, 1991; Patterson & Atmar, 2000; Ulrich *et al.*, 2009). Nestedness analysis might therefore be a tool to identify single postglacial colonization directories.

MATERIAL AND METHODS

We compiled data on the geographical distribution of European springtails (Supporting Information, Tables S1 and S2) as faunistically defined in Fauna Europaea (Deharveng, 2011) from major catalogues (Gisin, 1960; Jordana et al., 1997; Fjellberg, 1998, 2007; Pomorski, 1998; Bretfeld, 1999; Potapov, 2001; Thibaud, Schulz & da Gama Assalino, 2004; Dunger & Schlitt, 2011), and recently described species (cf. Ulrich & Fiera, 2010). We did not include Russia, some islands and group of islands (Cyprus, Cyclades, Aegean, Channel Islands), countries (Liechtenstein, Monaco, San Marino, Vatican), and the European part of Turkey due to incomplete recording. In total, the database contains 2069 species in 235 genera, 22 families and 12 superfamilies of Collembola, which occur in 53 countries and larger islands mentioned in Fauna Europaea (Tables S1 and S2). Apart from total species richness per country/island we determined the numbers of species, which had been reported only in a given country or island (country/island endemics, hereafter endemics).

The classification of Rusek (2007) allows us to group nearly all European springtails into ecologically meaningful guilds. We classified them into epigeic species (mostly dispersive above-ground dwellers), euedaphic (low dispersive soil dwellers), and hemieuedaphic (mostly dispersive species of the leaf litter and the upper humus layer) species, neustonic species (dispersive species associated with water films), and dispersive plant dwellers (mostly phytophagous species) (Table 1). In total, 133 species could not be classified according to dispersion and microhabitat.

For each European country and larger island (Table 1), we determined the area (km²) and the latitude and longitude of its geographical centroid (estimated from multiple longest diagonals using Google Earth). To assess coherence or scatter of range sizes we calculated for each species the average Euclidean distance between the centroids of the countries/ islands where a given species occurred. We obtained the null expectation of distance and the upper and lower 95% confidence limits from a random sample model (1000 replicates) where we reshuffled latitude and longitude among the countries/islands. Additionally, we calculated for each species with at least two occurrences:

- 1. the number of isolated occurrences where the country/island with occurrence was not directly connected (had no borderline with) to any other country/island of occurrence and
- 2. the number of gaps where the country/island without occurrence was completely surrounded by countries/islands with occurrences.

In the case of islands, we counted all nearest mainland countries as having a direct borderline. Again we compared the number of isolates and gaps with a random sample model (1000 replicates) where we reshuffled species occurrences among countries/ islands. The degree of coherence and scatter was calculated using standardized effect sizes $[Z = (x - \mu)/\sigma$, where μ is the expected number and σ the standard deviation of expectation].

Nestedness analysis (Ulrich *et al.*, 2009) is a tool to identify countries/islands with too high or too low numbers of unexpected occurrences (idiosyncrasies). To assess the degree of nestedness and idiosyncrasy we sorted the ordinary species (in rows) × countries/ islands (in columns) presence-absence matrix and used the temperature metric T (Atmar & Patterson, 1993). Temperature is based on a distance concept and is therefore particularly suited to study biogeographical patterns (Ulrich *et al.*, 2009). The spatial segregation of species range sizes was inferred using the *C*-score (Stone & Roberts, 1990), which counts the matrix-wide number of checkerboards (Ulrich & Gotelli, 2007).

Seriation is a tool to visualize the spatial species turnover across countries/islands. It sorts rows and columns of the presence-absence matrix in a way to maximize the number of presences along the matrix diagonal (Leibold & Mikkelson, 2002). We quantified species spatial turnover from the coefficient of determination R^2 between row (species) and column (countries/islands) ranks of all matrix entries of the

Guild	Temperature (sorted according to richness)	Temperature (sorted according to distance from Spain)	Temperature (sorted according to distance from Turkey)	C-score	Nearest neighbour distance	Embedded absences	R^2
All species	-6.67	-44.71	-47.94	-7.76	-1.53	-2.13	+0.26
Epigeic	-8.38	-67.47	+64.77	-12.36	+1.73	-2.08	-0.08
Euedaphic	-5.93	+56.44	+60.70	-8.10	-2.27	-2.65	-0.05
Hemiedaphic	-5.98	-45.30	+44.80	-6.19	-2.45	-1.62	-0.21
Neustonic	-8.45	+96.98	+96.18	-14.18	-1.48	-1.37	-0.15
Plant dwellers	-5.86	+37.18	+42.89	-4.20	-2.47	-1.97	0.45
High dispersal	-7.40	-45.95	-47.47	-8.39	-1.63	-2.25	0.18
Low dispersal	-5.91	+56.43	+60.71	-8.10	+2.38	-2.42	-0.01
Values are raw sco after Bonferroni co	es of five metrics. Bold type prection for multiple testi	e indicates significant score ng. To indicate positive or	s (inferred from the fixed negative deviations from	column – equipro null model expe	bable row null m ctations, raw sco	odel distributions: <i>P</i> ores are given as pos	< 0.001) sitive or
negative values.							

Table 1. Species co-occurrences analysis of European springtail guilds



Figure 1. A, proportion of European endemic species on islands (grey bars) and mainlands (black bars) for dispersal and five microhabitat types. B, proportions of dispersal and microhabitat type on islands (grey bars) and mainlands (black bars). Significant differences $[P(\chi^2) < 0.05]$ are marked by an asterisk.

seriated matrix. Matrix-wide species aggregation was inferred from the quadratic nearest neighbour distance, NDD, according to Clark & Evans (1954) applied to the seriated matrix. Presley, Higgins & Willig (2010) proposed a count of the number of embedded absences, EmbAbs, between the first and the last occurrence of each species in the seriated matrix as a metric of coherence of species range size. Significance levels for the C-score, T, R^2, NND , and *EmbAbs* were obtained from a null model that fixes site richness totals but treats species totals as being equiprobable. This null model seems appropriate because it accounts for differences in site suitability but assumes that all species have the same probability of colonizing each country/island irrespective of observed range sizes. Thus, the null model does not assume a priori constraints on the colonization abilities of species. Calculations were made using the NODF (Almeida-Neto & Ulrich, 2010) and Turnover (Ulrich, 2011) software.

RESULTS

Among the 2069 European springtail species, 861 were single island/country endemics (Table S1). Most widespread were *Parisotoma notabilis* (45 occurrences), *Isotomiella minor* (42), *Isotomurus palustris* (39), *Folsomia quadrioculata*, *Xenylla maritima*, and *Friesea mirabilis* (38). All of these widespread species occur from Ireland in the west to Ukraine in the east and from Norway and Sweden in the north to Italy and Spain in the south. The distribution of occurrences was well fitted by a Pareto model ($S = 754class^{-0.63}$; $R^2 = 0.84$).

The southern European mainland countries Spain (198 species, 28%), France (141, 22%), and Italy (62, 15%) had the highest number of endemics. Only the Baltic countries and Sweden did not have endemic species. Among islands, the Canary Islands (36, 32%),

Crete (15, 14%), and Novaya Zemlya (12, 3%) were most species-rich in endemics. Only 14 mainly smaller countries/islands did not have endemics. Spatial autocorrelation modelling that controlled for country/island area and spatial distances corroborated this pattern and pointed to a significant decrease in the number of endemic species at higher latitudes (P < 0.01) but not to any latitudinal gradient. The proportion of endemic species in a given country/island did not change with latitude or longitude.

Guild-specific comparisons of European islands and mainland countries (raw data in Table S2) revealed generally higher proportions of endemics on islands although only for weak dispersers, and euedaphic and epigeic species this difference was statistically significant (Fig. 1A; $P(\chi^2) < 0.05$). Islands and mainland did not differ with respect to the proportions of species of different guilds and dispersal ability (Fig. 1B).

COHERENCE OF RANGE SIZES

On average, springtail range sizes appeared to be significantly more coherent than expected from our random sample model. Of the 1212 species which occurred at least twice, 290 (24%) had a significantly (P < 0.05) more coherent range size than predicted from our random sample model. Plots of Z-scores for mean centroid distance (Fig. 2A) and Z-scores for the number of isolated occurrences (Fig. 2B) revealed a relative increase in range size coherence (lower Z-scores) and a relative decrease in the number of isolated occurrences (higher Z-scores) with the total number of occurrences. Neither the number of isolated occurrences per species nor the number of gaps depended on the total number of occurrences, mean latitude, and mean longitude of occurrence (OLS regression N = 1212 species, $R^2 = 0.003$; P > 0.3). The EmbAbs metric also pointed to a prevalence of coherent range sizes (Table 1).



Figure 2. *Z*-scores of the random sample model for mean distances between countries/islands of occurrence (A) and numbers of isolated occurrences (B) depending on the total number of occurrences for 1212 species which occurred at least twice. Logarithmic trend in A: $R^2 = 0.33$; $P(R^2 = 0) < 0.001$. Logistic trend in B: $R^2 = 0.08$; $P(R^2 = 0) < 0.001$.

Table 2. OLS regression for the Z-transformed number of gaps of 1212 springtail species with at least two occurrences against the number of occurrences per species and mean latitude and longitude of the respective range size ($R^2 = 0.09$; F = 37.8; P < 0.001), and best-fit spatial autoregression model to detect dependencies of the numbers of gaps per country/island depending on environmental correlates and species richness (N = 53; $R^2 = 0.53$, F = 15.7; P < 0.001)

Variable	Coefficient	SE	t	Р
Z-scores for the number of gaps per species				
Constant	-1.99	0.341	5.84	< 0.001
Occurrences	0.047	0.0046	10.12	< 0.001
Latitude	-0.012	0.008	-1.56	0.12
Longitude	0.016	0.005	2.99	0.003
Number of gaps per country/island				
Constant	247.5	37.5	6.6	< 0.001
ln S	-33.61	5.95	-5.65	< 0.001
Longitude	-1.69	0.59	-2.87	0.006

S, species richness.

The highest numbers of isolated occurrences were noted for *Deuterosminthurus pallipes*, *Hypogastrura papillata*, and *Protaphorura meridiata* (five isolates). *Desoria antennalis*, *Lepidocyrtus weidneri*, *Mesaphorura simoni*, *Sminthurinus domesticus*, *Orthonychiurus stachianus*, and *Isotomurus balteatus* had four isolates. These are central and northern European species with isolates at their southern range borders. In total, 602 species (29% of all European springtails) had isolated occurrences in one or more of the European countries/islands under study.

The number of gaps was strongly dependent on country area, the total number of occurrences, and on edge effects (not shown). Therefore, we used only the Z-transformed values from our random sample model (where these effects are already accounted for by the null model) to compare the distribution of gaps with respect to latitude and longitude of occurrences and total number of occurrences per species (Table 2). The number of gaps appeared to be positively dependent on the total number of occurrences (P < 0.001) and negatively on longitude (P = 0.003) with eastern European countries being less often a gap than western

European countries/islands. In accordance with this trend, spatial autocoregression modelling pointed to a significant negative correlation of the number of gaps per island/mainland with longitude (P = 0.006: Table 2) but also with species richness (P < 0.001). Hence north-western European islands/countries appeared to be more often a gap in the distribution range of species than expected by chance.

LARGE-SCALE PATTERNS OF SPECIES CO-OCCURRENCES

Species co-occurrences were significantly (P < 0.001)aggregated and accordingly more nested than expected from our null assumption (Table 1). Nevertheless spatial turnover (measured by R^2) explained 26% of the variance in the seriated matrix. These results are an indication of a clustered matrix substructure and spatial segregation of these clusters. Accordingly, the seriation analysis identified a strong latitudinal and a weak longitudinal gradient in species turnover (Fig. 3). Both gradients were more pronounced for mainland countries than for islands.



Figure 3. Country/island ranks of the seriated species × sites matrix of European springtails depending on latitude (A) and longitude (B). Ca, Canary Islands; Si, Sicily; Gr, Greece; Ae, Aeolian Islands; Ba, Balearic Islands; L, Luxembourg; NZ, Novaya Zemlya; FJL, Franz-Josef Land; SV, Svalbard; P, Portugal; An, Andorra; F, France; S, Spain. Full dots: mainland countries: regression in A: $R^2 = 0.33$, $P(R^2 = 0) < 0.001$; regression in B omitting the outliers P, F, An, S: $R^2 = 0.09$ $P(R^2 = 0) = 0.08$; open dots: islands: regression in A: $R^2 = 0.32$, $P(R^2 = 0) = 0.01$.

Epigeic and euedaphic species had significantly less spatial species turnover than expected from our null model (Table 1) while the other guilds appeared to be random. Similarly, weak dispersers had less turnover (and were more nested) than good dispersers.

Only 24 species (1%) were identified as being significantly idiosyncratic. In turn, as many as 2037 species (98.5%) were less idiosyncratic (more nested) than expected. To detect gradients in the degree of idiosyncrasy from hypothesized centres of postglacial colonization, we correlated the degree of idiosyncrasy of countries/islands with the geographical distance from Spain and from Turkey. In both cases idiosyncrasy did not depend on geographical position (both coefficients of correlation, P > 0.1). Furthermore, all matrices were much less nested when the countries/islands were sorted according to the distance from Spain (T > 35) and Turkey (T > 40) compared with a sorting according to species richness (T < 10) (Table 1).

DISCUSSION

Recent macroecological work on large-scale distributions of species range sizes highlighted the influence of climatic (Jetz & Rahbek, 2002; Szabo et al., 2009) and ecological history (Hewitt, 1999; Svenning & Skov, 2007). Climatic variables appeared to have a higher influence on the richness of widespread species than that of species with restricted range size (cf. Szabo et al., 2009 for a review). Our study corroborates this view only partly. Although we found an increase in the number of widespread species at higher latitudes, the proportion of endemics within countries/islands remained constant. Range size coherence increased only with longitude (Table 2). In Europe longitude can be seen as a surrogate variable for the gradient from maritime to continental climate regimes. We did not find any significant change of range size coherence with latitude and therefore with temperature regimes (Table 2).

Under the hypotheses of a northern European postglacial colonization either from south-eastern or south-western Europe (hypotheses 2) we expected to see clear gradients in our co-occurrence and nestedness analyses and the analysis of idiosyncratic countries. Indeed, we found a significant spatial turnover across European mainlands (Fig. 3) along a latitudinal and a longitudinal gradient and accordingly a segregated pattern of species spatial co-occurrence. Such gradients are not in accordance with strong colonization trajectories but rather reflect an ordered pattern of change in faunal composition across Europe. Thus, the analysis recovered specific assemblages of species that correspond to different European geographical and therefore climatic regions (Fig. 3) and we reject our hypothesis. Interestingly, south-western Europe deviated from the longitudinal gradient and (to a weaker degree) south-eastern Europe from the latitudinal gradient. In both cases faunal elements from outside Europe (northern Africa, Turkey, and Middle East) are probably of importance. Accordingly, our nestedness analysis did not recover colonization gradients but showed a strongly nested pattern when countries/islands were sorted according to species richness. Therefore, country size, as the most important determinant of richness (Ulrich & Fiera, 2009), accounted for a major part of the observed level of nestedness but not the ordered pattern of colonization and extinction (Table 1).

Patterson & Atmar (2000) favoured gradients in colonization and extinction as the main causes of nestedness. Our results do not corroborate this view. However, nestedness analysis is only able to identify a single gradient (Ulrich *et al.*, 2009). Our results are therefore in accordance with a multiregional colonization concept with several glacial refuges as reported for various species by Taberlet *et al.* (1998),

for clearwing moths by Ulrich *et al.* (2011), and for Antarctic Collembola by Stevens *et al.* (2007). Furthermore, several species of Collembola are parthenogenetic and it would only require a single surviving female for successful colonization to take place (Coulson *et al.*, 2002).

In line with the theoretical expectation within the framework of island biogeography (Chen & He, 2009; Rosindell & Phillimore, 2011) European islands contained comparably more species with restricted range size than mainland countries (Fig. 1, Table S2). This finding is in line with a recent global assessment of island endemism rates (Kier *et al.*, 2009) although this meta-analysis did not deal with European invertebrates. It should be noted that the number of single-island endemics in Europe in Tables S1 and S2 is very probably an underestimation. In particular, Mediterranean regions are rich in endemics, many of them undescribed (Deharveng, D'Haese & Bedos, 2008). However, future corrections would even strengthen the pattern reported here.

Theoretically the analysis of richness patterns should be based on gridded data with equal cell sizes (Hurlbert & Jetz, 2007; Hawkins, Rueda & Rodriguez, 2008; Keil & Hawkins, 2009) to be consistent with the assumption of constant grain size (Whittaker, Willis & Field, 2001) on which most regression analyses are based. Spatially better resolved gridded data would surely allow for a precise identification of predictor variables. Ideally these analyses would even be suited for predictions of future species home-ranges under climate and land-use change (Dormann, 2007). Unfortunately, fine-grained distribution data are currently unavailable for larger arthropod taxa. However, Keil & Hawkins (2009) showed that at least in species-rich taxa country-based species list data effectively recover true ecological gradients and do not necessarily perform worse than gridded data. The present modelling corroborates this work and previous analyses on butterflies (Ulrich & Buszko, 2003), 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 species richness. These results encourage the use of species list data for large-scale modelling of species richness and spatial distribution patterns.

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SUPPORTING INFORMATION

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

Table S1. Countries/islands considered in the present study: area, latitude and longitude of the capitals/largest cities, total species richness, number of country/island endemics, and numbers of species S in six logarithmic occurrence classes.

Table S2. Numbers of European species of five microhabitats and low and high dispersal ability.

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