

Body size–climate relationships of European spiders

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ABSTRACT

Aim Geographic body size patterns of mammals and birds can be partly understood under the framework of Bergmann’s rule. Climatic influences on body size of invertebrates, however, appear highly variable and lack a comparable, generally applicable theoretical framework. We derived predictions for body size–climate relationships for spiders from the literature and tested them using three datasets of variable spatial extent and grain.

Location Europe.

Methods To distinguish climate from space, we compared clines in body size within three datasets with different degrees of co-variation between latitude and climate. These datasets were: (1) regional spider faunas from 40 European countries and large islands; (2) local spider assemblages from standardized samples in 32 habitats across Europe; and (3) local spider assemblages from Central European habitats. In the latter dataset climatic conditions were determined more by habitat type than by geographic position, and therefore this dataset provided a non-spatial gradient of various microclimates. Spider body size was studied in relation to latitude, temperature and water availability.

Results In all three datasets the mean body size of spider assemblages increased from cool/moist to warm/dry environments. This increase could be accounted for by turnover from small-bodied to large-bodied spider families. Body size–climate relationships within families were inconsistent.

Main conclusions Starvation resistance and accelerated maturation can be ruled out as explanations for the body size clines recorded, because they predict the inverse of the observed relationship between spider body size and temperature. The relationship between body size and climate was partly independent of geographic position. Thus, the restriction of large-bodied spiders to their glacial refugia owing to dispersal limitations can be excluded. Our results are consistent with mechanisms invoking metabolic rate, desiccation resistance and community interactions to predict a decrease in body size from warm and dry to cool and moist conditions.

Keywords

Araneae, Bergmann’s rule, Europe, family sorting, latitude, moisture, precipitation, temperature.

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INTRODUCTION

Many life-history traits of animals, such as life span, clutch size and growth rate, are correlated with body size (Peters, 1983). For this reason, body size represents an important surrogate

for other ecological attributes across species and environments (Blackburn & Gaston, 1994; Chown *et al.*, 2002). The most commonly used framework for large-scale patterns in body size is Bergmann’s rule, which predicts an increase in body size towards cold environments (Bergmann, 1847). However, the

Table 1 Potential mechanisms and their predictions for body size clines in spider assemblages.

Mechanism	Taxonomic resolution	Applicability	Prediction	References
Starvation resistance increases with body size, and is more important under cold, seasonal climates	Inter- and intraspecific	Animals	Body size decreases with temperature	Cushman <i>et al.</i> , 1993
Accelerated maturation leads to smaller adult size at high temperatures	Mostly intraspecific	Ectotherms	Body size decreases with temperature	Atkinson, 1995; Kaspari, 2005
Metabolic rate and season length increase with temperature, allowing larger growth under warm climate	Inter- and intraspecific	Ectotherms	Body size increases with temperature	Mousseau, 1997
Desiccation resistance increases with body size owing to stronger cuticle and smaller surface-area-to-volume ratio	Inter- and intraspecific	Animals	Body size increases with aridity	Remmert, 1981
Dispersal is more far-ranging in small spider species owing to their increased ballooning ability	Interspecific	Spiders	Body size increases with time since glaciation (which correlates with temperature, but only on large spatial scales)	adapted from Cushman <i>et al.</i> , 1993
Prey body size determines body size of their predators, and can itself be influenced by climate	Inter- and intraspecific	Predators	Body size increases with prey size	Nentwig & Wissel, 1986
Competition and predation pressure are higher in warm environments, favouring large-bodied organisms	Interspecific	Animals	Body size increases with temperature	Blackburn <i>et al.</i> , 1999

predictions by Bergmann are specific to geographic patterns of body size among closely related species of birds and mammals. Thus, Bergmann's rule does not make predictions either for animal assemblages or for ectotherms (Blackburn *et al.*, 1999).

Spiders are important predators in terrestrial habitats (Wise, 1993) and show considerable variation in body size. To understand possible relationships of spider body size with climate, we compiled predictions of body size patterns from the literature that may apply to assemblages of spiders as well as to other ectotherm predators (Table 1). We make no claim for completeness, but we regard the selected mechanisms to be the most relevant for spiders. Of the mechanisms considered (Table 1), starvation resistance, metabolic rate and desiccation resistance invoke climatic influences on the physiology of the organisms. Dispersal is a characteristic of the species, whereas the body size of potential prey species, competition and predation refer to biotic interactions (Table 1).

We found two interspecific mechanisms that predict an increase in body size towards cold environments. Starvation resistance is expected to increase with body size, and should be more important in cold, seasonal environments (Cushman *et al.*, 1993). Accelerated maturation is a pattern rather than a mechanism. In fact, it may have multiple causes (Angilletta *et al.*, 2004; Kaspari, 2005). However, because of the generality of smaller adult size in warm environments, at least within species (Atkinson, 1995), we agree with Kaspari (2005) that it should also be considered to explain interspecific body size clines. The remaining mechanisms predict an increase in body size towards warm and/or dry environments. However,

depending on the mechanism, the increase in body size is inferred to be due either to water or to energy availability. With respect to the spatial structure of the pattern, the dispersal mechanism predicts that body size clines are restricted to broad-scale spatial gradients. In contrast, all other mechanisms can explain body size differences in non-spatial gradients such as habitat climate.

Most studies on large-scale patterns of body size have investigated latitudinal or elevational gradients (Blackburn & Hawkins, 2004; Brehm & Fiedler, 2004; Rodríguez-Jimenez & Sarmiento, 2008). Although latitude *per se* is not a meaningful predictor of body size (Hawkins & Diniz-Filho, 2004), we use it as a proxy for the general climatic variation across Europe. In a second step, we test which temperature- or water-related climatic factors can explain body size clines. To distinguish climate from space, we compared clines in body size within three datasets with variable degrees of co-variation between latitude and climate. These datasets were: (1) regional spider faunas from 40 European countries and large islands; (2) local spider assemblages from standardized samples in 32 habitats across Europe; and (3) local spider assemblages from Central European habitats. The latter dataset is crucial for our analysis as it provides a spatially interspersed dataset with habitat conditions that vary from cool/moist to warm/dry. These habitat conditions are largely independent of broad-scale climatic clines and geographic location. Therefore, the third dataset provides a non-spatial habitat gradient. In accordance with the majority of predictions in Table 1, we expect the mean body size of spider assemblages to increase with temperature and aridity. To distinguish between dispersal

and the remaining mechanisms, we tested whether the body size–climate relationships were consistent across the three datasets: a significant non-spatial body size gradient among Central European habitats would mean that mechanisms other than dispersal must be active. Finally, to distinguish between family sorting and rapid adaptation of body size to climatic conditions, we were interested in the degree to which body size patterns change within or between spider families.

MATERIALS AND METHODS

We investigated the body size–climate relationships of spiders in three datasets. Based on the database of the European Spider Determination key (Nentwig *et al.*, 2003), which now includes 3659 spider species, we extracted body sizes (total length) for 2191 species from the taxonomic literature. As the results of the analyses did not differ between females and males, we present only the results for females. To address the overall right skew in the spider body size distributions, body sizes were \log_{10} -transformed prior to all calculations and analyses.

For the first dataset, based on species lists of European countries and large islands (van Helsdingen, 2007), we calculated the mean log body size across the spider species recorded within the borders of 40 European countries and large islands (Fig. 1a). We excluded biogeographical extremes that are far from the mainland and/or lie in different bioclimatic zones (Canary Islands, Cyprus, Turkey, Azores, Faroe Islands, Madeira, Salvage Islands, Franz Josef Land, Novaya Zemlya, Svalbard and Jan Mayen). Countries and islands smaller than 500 km² were also excluded (all Greek islands except Crete, and Monaco, Gibraltar, Liechtenstein, Channel Islands, Malta, Andorra). To assess whether the spider fauna of each country was sufficiently well known, deviation from a log (species richness)-to-log (area) relationship was examined. All points outside the 90% confidence prediction band were excluded (Luxemburg, Albania and Bosnia-Herzegovina). Species numbers ranged from 115 species on the Balearic Islands to 1490 species in France. Overall, 3447 spider species occurred in the 40 considered countries, and body sizes were available for 2091 of them. As the corresponding latitude we took the midpoint of the countries/islands (calculated with ARCMAP version 9.1, ESRI Inc., Redlands, CA, USA).

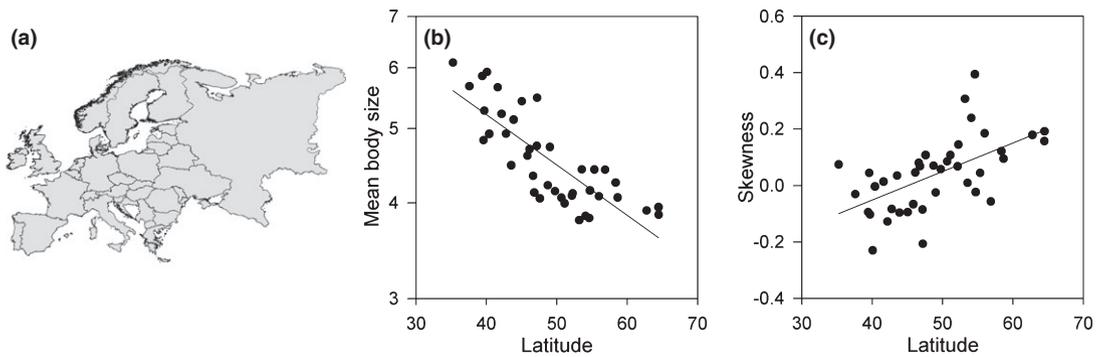
The second dataset was based on spiders captured with pitfall traps in the field-site network of the EU-project ALARM (Settele *et al.*, 2005; Kumschick *et al.*, in press). We calculated mean log body sizes of spiders occurring within 32 habitats in 16 geographic locations across Europe (Fig. 1d). All locations lay below 800 m a.s.l., so that climate was driven mostly by latitude. In each location, two habitats (one disturbed and one natural habitat) were sampled using a standardized effort by pitfall traps. Species numbers ranged from 14 species in the natural habitat in Garraf (Spain) to 55 species in the natural habitat in Berkshire (UK). We calculated the mean body size for each habitat using the above-mentioned body size data. Overall, 347 species were captured in these habitats, and body size was available for all of them.

For the third dataset we calculated the mean log body size of spiders from pitfall traps in 135 open habitats in Central Europe (Fig. 1g; Hänggi *et al.*, 1995). These habitats formed a gradient in local climate from cool/moist to warm/dry. Examples for cool and moist habitats were salt marshes, reed beds and fens, whereas vineyards, dry grasslands and juniper heath were warm and dry. Cool/moist and warm/dry habitats were geographically interspersed and showed only weak spatial autocorrelation (Entling *et al.*, 2007). All samples lay below 800 m a.s.l. Therefore, dataset three provides a climatic gradient that is largely independent of latitude and elevation. Although direct measures of climate were not available for the habitats, a broad classification of habitat types with respect to climate revealed a highly significant differentiation from cool/moist to warm/dry habitats on the second axis of a correspondence analysis (Entling *et al.*, 2007). We used axis scores along this second ordination axis as an indirect measure of the microclimate of the habitat. Species numbers in the habitats ranged from 3 species in a dry/semi-dry grassland in Bavaria to 112 species in a raised bog in Belgium. Overall species number in the Central European habitats was 590 and body size was known for all of them.

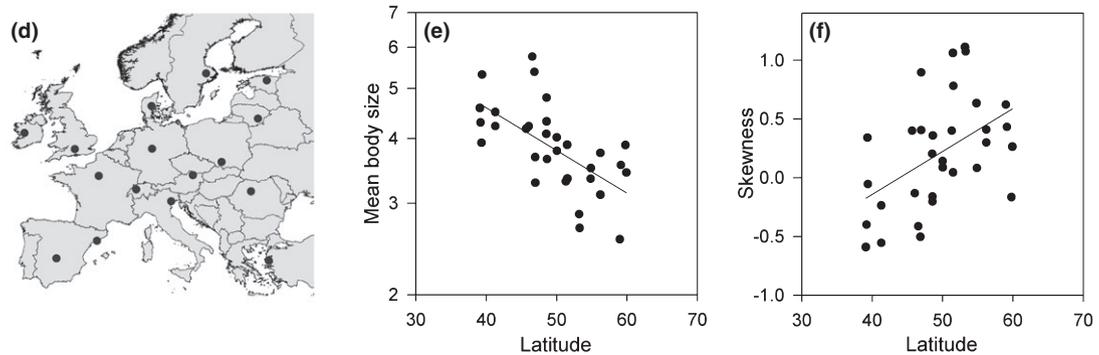
To investigate body size–climate relationships within families and to test the influence of body size differences among families on the overall pattern, we applied general linear models using the program SPSS version 14.0 with default settings unless specified (SPSS Inc., Chicago, IL, USA). We used mean log body size as the dependent variable, and spider family, climatic position and their interaction as independent variables. Climatic position is the latitude of the country/habitat in the first and the second dataset and position of the habitats along a temperature/moisture gradient in the third dataset. Mean log body size was calculated for each family within: (1) countries and islands, (2) habitats across Europe, and (3) Central European habitats for families that accounted for more than 1% of all occurrences.

In addition to the arithmetic mean we also considered the skewness of body size distributions in all three datasets and tested for correlations between skewness and climatic gradients. The arithmetic mean of body size derived from habitat samples is often influenced by the species richness in the habitat, even after \log_{10} -transformation of the raw data (Meiri & Thomas, 2007). To control for this problem, we included species richness in our analyses and randomized the sampling of body sizes from the regional species pools for each dataset (Greve *et al.*, 2008). We then checked the correlations of the corresponding mean/skewness with latitude (see Appendix S1 in Supporting Information). As the presence of a given species in more than one country or habitat violates the assumption of independence required by parametric statistics, we used a second method to check if the pattern was consistent when each species was included only once ('species approach'; Hawkins & Lawton, 1995; Hawkins & DeVries, 1996; Brehm & Fiedler, 2004). For that we calculated the centroid of all occurrences of each species with respect to climatic position in the three datasets and tested for correlations of this

European countries and islands



Habitats across Europe



Central European habitats

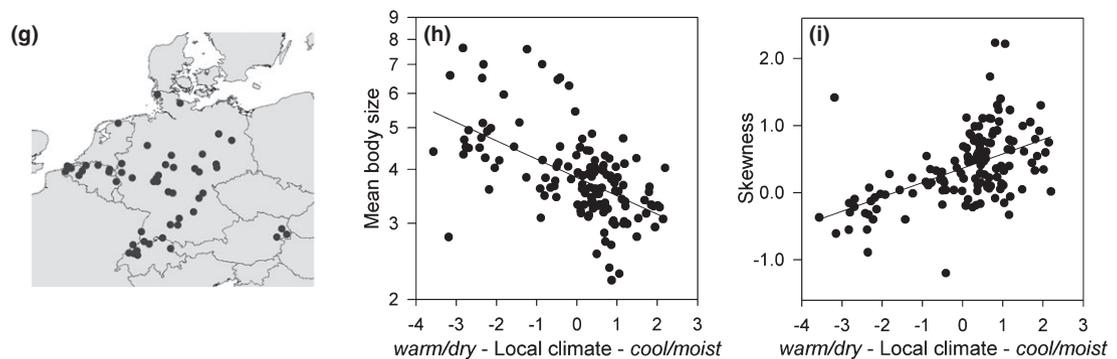


Figure 1 Spider body size patterns of (a–c) regional faunas of European countries and islands (dataset 1), (d–f) local spider assemblages at 32 habitats across Europe (dataset 2), and (g–i) local spider assemblages in a non-spatial habitat gradient (dataset 3). The mean body size (mm) of spider assemblages is negatively correlated with latitude in (b) 40 European countries and islands ($n = 40$, $r^2 = 0.65$, $P < 0.0001$) and (e) habitats across Europe ($n = 32$, $r^2 = 0.39$, $P < 0.0001$). (h) Along a non-spatial habitat gradient the mean spider body size is negatively correlated with the niche position of these habitats along a temperature/moisture gradient ($n = 135$, $r^2 = 0.32$, $P < 0.0001$). Simultaneously, the skewness of the body size distributions is positively correlated with latitude in (c) 40 European countries and islands ($n = 40$, $r^2 = 0.34$, $P < 0.0001$) and (f) habitats across Europe ($n = 32$, $r^2 = 0.23$, $P = 0.006$) and with the niche position of (i) Central European habitats along a temperature/moisture gradient ($n = 135$, $r^2 = 0.27$, $P < 0.0001$).

measurement with the species' body size. However, as the two sets of results were similar, we display only the analysis of the means across species in assemblages.

To identify the important ecological factors behind body size we correlated the mean body size of the assemblages with variables characterizing temperature and moisture. For the first

dataset we calculated annual mean temperature and annual precipitation per country/island from grid data from the WorldClim database (long-term averages from 1950 to 2000; <http://www.worldclim.org>; Hijmans *et al.*, 2005). For the second dataset we used annual mean temperature, annual precipitation and soil water content. Long-term temperature

averages were derived from existing published data (1990–2002; Mitchell & Jones, 2005), supplemented with additional measurements from 2003 to 2006. Soil water content was modelled from climate, geology and vegetation and expressed as the fraction of available water-holding capacity in the first soil layer (0–0.5 m; see Sitch *et al.*, 2003). As the temperature/moisture gradient of the third dataset was indirectly derived from assemblage composition, additional environmental factors were not available.

Finally, we partitioned body size variation into components explained by space, by climate, and by spatially structured climate (joint effects of space and climate). This was done using trend surface analysis and partial regression in the open source program SAM (version 3.1; Rangel *et al.*, 2006). Space was represented by first-order spatial coordinates (longitude and latitude), and climate by the most strongly correlated climatic variable for each dataset. As it was necessary to reduce the habitats to one per coordinate, we randomly selected $n = 78$ habitats with different coordinates for the spatial analyses of the third dataset.

RESULTS

Mean spider body size in European countries and islands decreased with latitude (Fig. 1b). Across countries, mean body size ranged from 3.8 ± 1.9 mm in the cool and moist country of Ireland to 5.9 ± 1.7 mm in the warm and dry climate of Greece. A similar correlation was found for the habitats across Europe (Fig. 1e). Here, the mean body size of the assemblages ranged from 2.6 ± 1.5 mm in a forest near Tartu (Estonia) to 5.8 ± 1.7 mm in a scrubland near Cluj (Romania). Across the Central European habitats, the mean body size of spider assemblages also increased from cool/moist to warm/dry habitats (Fig. 1h). Mean body size ranged from 2.3 ± 1.1 mm in a moist grassland to 7.6 ± 1.5 mm in a dry grassland. These patterns were independent of species richness, because mean log body size did not correlate significantly with species richness in any of the three datasets: (1) European countries and islands: $n = 40$, $r^2 = 0.04$, $P = 0.24$; (2) habitats across Europe: $n = 32$, $r^2 < 0.001$; $P = 0.97$; (3) Central European habitats: $n = 135$; $r^2 = 0.009$, $P = 0.26$.

We found positive as well as negative values in the skewness of log body size within spider assemblages. A positive (right) skew reflects a higher frequency of small compared to large species, and a negative (left) skew reflects a prevalence of large species when compared to a log-normal distribution. Skewness of the body size distributions within spider assemblages increased towards cool/moist environments in all three datasets (Fig. 1c, f, i). Thus, there was a turnover from large to small species towards cool/moist environments in all three datasets. Random sampling showed that neither mean log body size–latitude nor skewness–latitude patterns could be produced by random placement of species (see Appendix S1).

Across all three datasets, mean log species body size differed more strongly among families than among climatic positions (i.e. latitude of the country/habitat in the first and the second dataset and position of the habitat along a temperature/moisture gradient in the third dataset) (Table 2). We found no consistent relationship of body size to climatic position within families (significant interactions between family and climate in all three datasets). Thus, the general relationship between body size and climate was mostly attributable to the prevalence of families with larger species in warmer/drier environments and to the prevalence of families with smaller species in cool/moist environments.

When using climatic variables instead of latitude in the first two datasets, mean log body size was correlated positively with temperature and negatively with precipitation and soil water content (Table 3). This relationship between body size and the most closely correlated environmental factors remained significant in all three datasets after taking spatial autocorrelation into account (Fig. 2). However, the degree of co-variation between space and climate differed considerably among the three datasets. In European countries, most of the body size variation explained by temperature was spatially structured, mostly resulting from a decrease in temperature with latitude ($r = -0.90$). Among the habitats across Europe, both soil water content and space had considerable independent effects on spider body size in spite of an increase in soil water content towards the north ($r = 0.25$). As expected, the climatic influence within the Central European habitats showed only little dependence on spatial location.

Table 2 Influence of family, climatic position and their interaction with mean log body size of spiders in the three datasets analysed: (1) European countries and islands, (2) habitats across Europe, and (3) Central European habitats. Climatic position is the latitude of the country/habitat in the first and the second dataset, and the niche position of the habitats along a temperature/moisture gradient in the third dataset.

	(1) European countries and islands			(2) Habitats across Europe			(3) Central European habitats		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Climatic position	1	25.4	<0.0001	1	1.5	0.22	1	1.7	0.20
Family	16	27.1	<0.0001	10	5.7	<0.0001	8	545.6	<0.0001
Climatic position × Family	16	9.4	<0.0001	10	2.6	0.005	8	17.6	<0.0001
Error	631			178			804		

Table 3 Correlations between climatic variables and mean log body size of spiders in the first two datasets analysed: (1) European countries and islands ($n = 40$), and (2) habitats across Europe ($n = 32$).

Dataset	Climatic variable	r	P
(1) European countries and islands	Annual mean temperature	0.74	<0.0001
	Annual precipitation	-0.30	0.061
(2) Habitats across Europe	Annual mean temperature	0.46	0.009
	Annual precipitation	-0.47	0.007
	Soil water content	-0.63	<0.0001

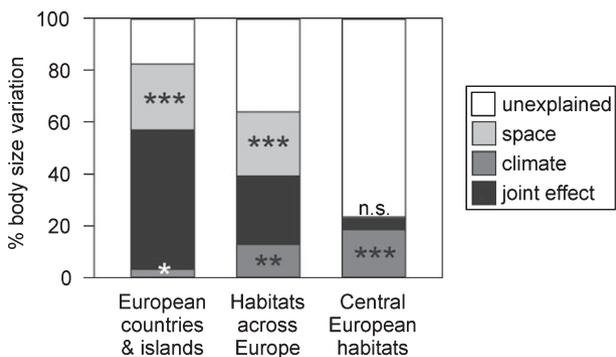


Figure 2 Partitioning of spider body size variation by partial regression (using the program SAM) into components explained by space, by climate, and by spatially structured climate (=joint effect of space and climate) for each of the three datasets analysed. Space was represented by first-order spatial coordinates (longitude and latitude), and climate by the most strongly correlated climatic variable for each dataset (annual mean temperature, soil water content, and local climate; see also Table 3). Asterisks denote significance levels of independent (conditional) effects: n.s., not significant, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

DISCUSSION

As predicted by most mechanisms listed in Table 1, spider body size decreased towards high latitudes in spider faunas of European countries and islands as well as in assemblages of local habitats. Body size decreased from warm/dry to cool/moist environments, both at a continental scale across Europe and at a smaller scale within Central Europe. This pattern was consistent and robust even after accounting for spatial autocorrelation. The partial independence of body size clines from geographic position demonstrates that dispersal alone cannot explain the observed patterns. Dispersal limitation of large-bodied spiders would result in a spatially structured decline of body size from glacial refugia in southern Europe towards the north. Clearly, the body size differences among spider assemblages in Central European habitats cannot be explained by different lengths of time available for colonization since the last ice age. Thus, body size differences among European spider assemblages result either from physiological constraints or from community interactions.

Physiology

Starvation resistance and accelerated maturation can be excluded as main drivers of spider body size across Europe, because they predict the inverse of the observed relationship of spider body size to temperature (Table 1). The remaining two mechanisms based on physiological arguments are consistent with the observed decrease in body size towards cool/moist environments. Mousseau (1997) suggested that the evolution of larger species in warm environments results from the length of seasons during which species can grow, and from higher growth rates under warm temperatures. R Emmert (1981) proposed water availability as a key driving factor of body size variation in insects and spiders. Large arthropods should be more resistant to desiccation because of their more compact and waterproof cuticle and their lower ratio of surface area to volume. Consistent with both mechanisms, spiders in warm/dry environments were on average larger than spiders in cool/moist environments (Table 2). The relationship between precipitation and body size was not significant in the European countries and islands, but variation in climatic factors within countries and islands is enormous, so patterns may be blurred. Moreover, moisture in an environment does not depend solely on precipitation. For example, the same amount of precipitation can create humid conditions in a cool environment but arid conditions in a warm environment. On a habitat scale, soil water content had the strongest correlation with mean log body size (Table 3). Soil water content reflects the actual water availability of a habitat better than precipitation and may be more important for ground-dwelling spiders. In conclusion, our results are consistent with both temperature-related and moisture-related mechanisms. We are unable to distinguish between the two mechanisms because of the negative relationship between water availability and temperature in most of Europe.

Biotic interactions

It is also possible that in contrast to its being a direct effect of climate, spider body size is indirectly determined by biotic interactions. First, spiders are generalist predators. Their body size may depend on prey availability and/or size, which in turn may be influenced by climate (Nentwig & Wissel, 1986). Second, spiders have numerous enemies (e.g. wasps, parasites, parasitoids, birds, lizards and spiders; Wise, 1993). If large spiders are less susceptible to natural enemies, the observed body size distributions in spiders may be determined by predation pressure. However, the effect of predation pressure on prey body sizes is contingent on additional factors such as food availability for prey (Abrams & Rowe, 1996). In contrast, interference competition clearly favours large-bodied species (e.g. Eichenberger *et al.*, 2009). Increased abundances of spider enemies or competitors towards warm/dry environments can be found in at least some of the important groups. For example, ants are more abundant and species-rich in warm/dry than in cool/moist environments (Cushman *et al.*, 1993). Sanders & Platner (2007) showed experimentally that higher

ant densities negatively affected spider densities. This increased intraguild interference may select for spiders with a larger body size. Interference in general is hypothesized to increase with temperature, because cold stress excludes numerous taxa from local communities (Chown *et al.*, 2002) and thereby reduces the number of potentially interacting species. Accordingly, predation and competition could contribute to the observed pattern.

Phylogeny

If interspecific relationships between body size and climate have a common ecological origin, it can be expected that patterns within families will resemble the overall pattern across families (Hawkins & Lawton, 1995; Brehm & Fiedler, 2004; Meiri & Thomas, 2007). However, body size is a phylogenetically conservative trait. This means that species have only a limited potential to change body size compared with other ecological traits such as habitat preference (Entling *et al.*, 2007). In spiders, more than 80% of the variability in body size occurred between families, a finding that is also true for other animal groups (e.g. birds, Brändle *et al.*, 2002; see also Diniz-Filho *et al.*, 2007). The phylogenetic conservatism of spider body size is reflected in the prevalent influence of the family compared with the climatic position in all three datasets (Table 2). Moreover, positive and negative trends within families were not consistent among the datasets; that is, some families that had a positive relationship between body size and climate at one scale showed a negative relationship at other scales (results not shown). The variable body size–climate relationships within families suggest that multiple factors affect body size clines, and that some of these factors are mediated by family-specific attributes of life history. However, the variable body size–climate relationships within families were minor compared to the overall clines in body size resulting from family turnover. This overall increase in body size towards warmer/drier conditions is a complex joint response attributable to species within multiple families. As an alternative to an ecological explanation, it has been argued that small- and large-bodied families could be unevenly distributed across Europe owing to historical patterns of speciation (Hawkins & Lawton, 1995). However, body size increased as environmental conditions became warm/dry in the dispersed habitat climate gradient that was characterized by the minimum degree of spatial autocorrelation (third dataset). We therefore conclude that the distribution of large- and small-bodied families among habitats and also across latitude results from family sorting according to environmental conditions.

Wider context

Given the clear and consistent body size pattern of European spiders, it is surprising that body size–climate relationships of terrestrial arthropods are variable: the body size of ants has been shown to decrease with temperature (Cushman *et al.*, 1993; Heinze *et al.*, 2003; Kaspari, 2005), whereas bees, butterflies and moths show a variety of body size–climate patterns (Hawkins,

1995; 1996; Brehm & Fiedler, 2004). Different body size patterns have been attributed to historical patterns of speciation, as in the case of bees and butterflies (Hawkins, 1995; Hawkins & Lawton, 1995). European spider families also show a variety of relationships of body size to climate. However, this variation appeared to be unified through strong family sorting. At the assemblage level, mean body size increased uniformly towards warm/dry environments at the contrasting spatial grains of countries and habitats. This suggests that the study of geographic body size patterns across larger taxonomic groups would be useful.

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SUPPORTING INFORMATION

Appendix S1 Randomized effects of spider species richness on sample means and skewness.