



# Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche

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## ABSTRACT

**Aim** Niche theory emphasizes the importance of environmental conditions for the distribution and abundance of species. Using a macroecological approach our study aimed at identifying the important environmental gradients for spiders. We generated numerical values of niche position and niche width. We also investigated relationships between these niche properties as well as the degree of phylogenetic conservatism in order to draw conclusions about the evolution of the habitat niche.

**Location** Central Europe: lowlands of Austria, Belgium, Germany, Luxembourg, the Netherlands and Switzerland.

**Methods** We analysed 244 published spider communities from 70 habitat types by correspondence analysis. The resulting community scores were used to test for correlations with habitat characteristics. Species scores were used to derive niche position (mean scores) and niche width (standard deviation of scores). To test for niche conservatism we estimated variance components across the taxonomic hierarchy.

**Results** The first two axes of the correspondence analysis were correlated with shading and moisture, respectively. Niche width had a hump-shaped relationship to both environmental gradients.  $\beta$ -diversity was strikingly higher in open habitats than in forests. Habitat niche conservatism was lower than phylogenetic conservatism in body size.

**Main conclusions** Environmental factors are important drivers for the  $\beta$ -diversity of spiders, especially across open habitats. This underlines the importance of preserving the whole range of moisture conditions in open habitats. Narrow niches of species occurring at the ends of both environmental gradients indicate that adaptations to extreme habitats lead to constraints in ecological flexibility. Nevertheless, the habitat niche of species seems to evolve much faster than morphological or physiological traits.

## Keywords

Araneae, correspondence analysis, environmental gradients, habitat specialization, habitat types, indirect gradient analysis, niche position, niche width, spiders.

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## INTRODUCTION

Within the framework of the niche theory, differences between species and environmental factors drive the distribution of species and ultimately the composition and diversity of communities (Hutchinson, 1958; Schoener, 1989; Tokeshi, 1999). The theory of island biogeography was the first attempt to predict certain patterns in nature without considering the niche of species (MacArthur & Wilson, 1963, 1967). In his neutral theory of

biodiversity and biogeography, Hubbell recently revived the view that the niche is of limited importance for predicting characteristics of communities (Hubbell, 1997, 2001). Although controversial, the neutral theory successfully predicts species-abundance distributions, species–area relationships and changes in  $\beta$ -diversity from a process called ecological drift. Although niche differences between species were ignored, the predictions often fit the patterns in natural communities very well (Hubbell, 2005). Nevertheless, few field ecologists will

question the fact that species differ in their niche. Hence, the main discussion currently centres on the issue of whether major patterns in nature can be understood without considering the niche in detail.

Although a simple and straightforward concept, the measurement of niche properties is fraught with a series of problems (Colwell & Futuyma, 1971). First, the niche has two aspects: niche position and niche width. Many studies concentrate on only one of these two properties (but see Gregory & Gaston, 2000). Second, niche position and niche width of a species are contingent on co-occurring individuals of the same species, co-occurring species in the same community and environmental conditions (realized niche). Hence, studies that describe the niche properties of a species by analysing one specific community may be biased or even misleading. By analysing many species across many environments, idiosyncrasies become less important and general patterns may appear (Brown, 1999; Lawton, 1999). So far, such macroecological studies have concentrated on well-studied groups of organisms (e.g. birds, plants, beetles; Gregory & Gaston, 2000; Peterson & Holt, 2003; Coudun & Gégout, 2005; Eyre *et al.*, 2005). However, for the majority of arthropod groups, and thus for the bulk of the world's biodiversity, analyses of niche characteristics on regional or continental scales are still rare.

Spiders are dominant predators in most terrestrial ecosystems (Wise, 1993). They are a species-rich group, in which species occurrence is frequently related to factors such as vegetation structure, soil moisture, disturbance and management regime (Rushton & Eyre, 1992; Marc *et al.*, 1999; Bonte *et al.*, 2002). Reviewing the literature, Wise (1993) suggested that the distribution and abundance of spiders depends on three niche axes: wind, moisture and temperature. However, other studies failed to find convincing correlations between the environment and the occurrence of spiders (Mallis & Hurd, 2005). These authors claimed that spider communities are stochastic assemblages and habitat conditions as well as niche properties have little influence on their structure and dynamics. This is essentially a neutral view on spider communities. These conflicting interpretations are likely to be due to the fact that Mallis & Hurd (2005) investigated spider communities on a relatively small spatial scale (six communities from an area of about 10 ha). The importance of stochastic processes (environmental and demographic) decreases as the size of the study area increases (Bonsall & Hastings, 2004). Therefore their results are likely to be contingent on local conditions. A macroecological approach may help in clarifying whether niche characteristics structure spider communities.

In our study we analysed a large data set on Central European spider communities (Hänggi *et al.*, 1995), using correspondence analysis (CA) to characterize niche positions and niche widths along indirect environmental gradients. Once niche properties have been extracted, further issues arise. First, the evolution of the niche may be constrained by trade-offs. Leaving aside the methodological problem that extreme environments are rare, inhabitants of extreme environments may require a higher degree of specialization due to the harsher environmental conditions and therefore may not readily be able to deal with a broad range of conditions. Few studies consider these issues from a

macroecological perspective (but see Thuiller *et al.*, 2004). Secondly, at least from a broad taxonomic view, species within phylogenetically defined lineages should have similar niche properties. As noted by Wiens & Graham (2005): 'few tropical rainforest species have a sister species in undersea vents'. Although to some extent niche properties are always constrained by phylogenetic legacy, sister species have by definition different niches. Hence the more important question is: to what extent we can predict the niche position or niche width of a species from phylogenetically related species?

In our paper we investigate three important questions. (1) Do Central European spider communities show relationships to environmental gradients and thereby support niche theory? (2) What are their niche properties and are there trade-offs in the evolution of niches? (3) Do niche properties show phylogenetic conservatism?

## MATERIALS AND METHODS

### Data set

We analysed the data base of Central European spider communities (Hänggi *et al.*, 1995). This data base comprises 1382 communities originating from 223 publications. In the data base each community is attributed to one of 85 habitat types. [Habitat is the physical area occupied by an animal and the abiotic and biotic resources contained in that space (Morrison & Hall, 2002). Therefore, the term habitat is originally characterized from the perspective of a given species or species group that uses the same resources in the same ways. However, often the naming of habitats is mainly based upon vegetation types (e.g. Brometalia) or physical and geographical properties of the environment (e.g. coastal dunes), for example in the habitat types classification of the European Nature Information System of the European Environment Agency (<http://eunis.eea.europa.eu>), on which our study is based. Therefore, the classification of the habitats into 'habitat types' is used in this sense throughout the paper.] To minimize variation caused by climate, biogeography and sampling method, we selected communities from this data base according to the following criteria. (1) We considered only communities sampled in Austria, Belgium, Germany, Luxembourg, the Netherlands and Switzerland. Hence, our analysis is based on a geographically well-defined pool of species. (2) We restricted our analysis to sampling locations below 800 m above sea level (planar/colline regions). (3) We selected only spider communities sampled with pitfall traps. Hence our data set is based on standardized sampling at the soil surface. (4) To minimize the influence of individual studies, we included only one spider community per habitat type and publication. However, if a publication reported data from different habitat types these communities were included in our selection. Overall this procedure selected 244 communities representing 70 habitat types from the original list of 85 habitat types.

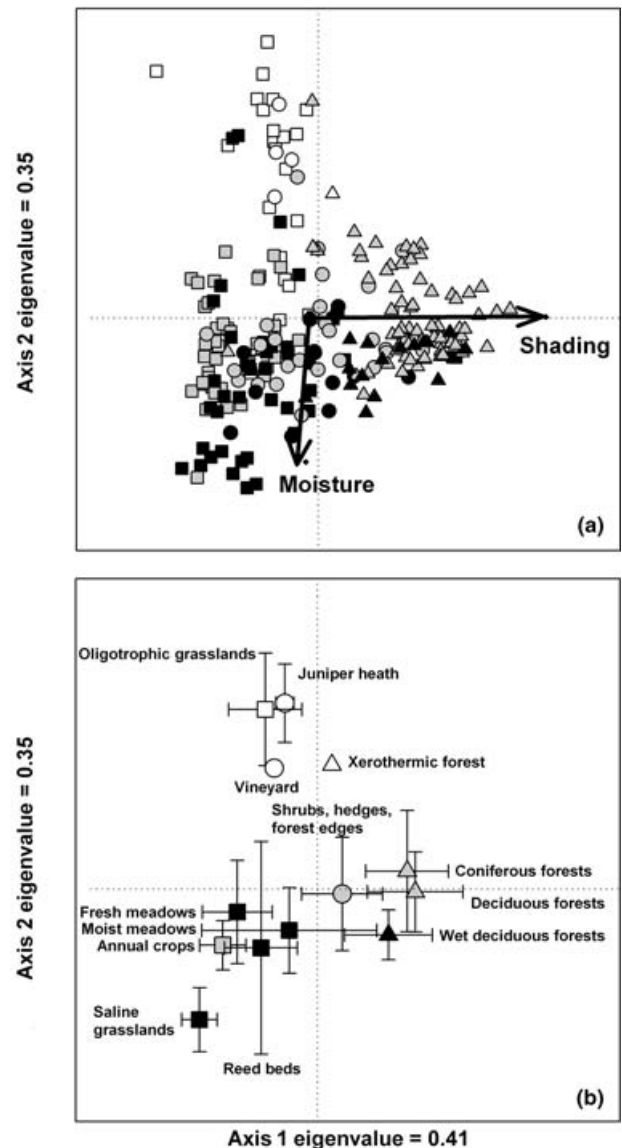
For our investigations the basic environmental unit was the habitat, defined as an area with homogeneous environmental conditions. Note that many macroecological studies rely on grid-based data. However, environmental conditions can vary

considerably within grids (Gregory & Gaston, 2000; Pasinelli *et al.*, 2001; Eyre *et al.*, 2005). Therefore, concentrating on habitats is more appropriate for studying species–environment relationships than species inventories within grids.

### Data analysis

We subjected the presence–absence matrix of species across the 244 communities to CA to extract the major patterns of variation (Canoco for Windows, version 4.5; ter Braak & Šmilauer, 2002). The spread of the communities along the extracted axes is an estimate of their  $\beta$ -diversity (Legendre *et al.*, 2005). However, since CA is sensitive to rare species (Jongmann *et al.*, 1995), we considered only species that occurred in more than five communities (296 out of 590 species). The remaining 294 species were included as passive species. These passive species had no influence during the extraction of axes, but their niche properties could still be calculated. The arch effect can be a problem during CA analyses (Jongman *et al.*, 1995). However, visual inspection of the ordinations provided no evidence that this artefact biases our analyses (see Fig. 1).

As CA is an indirect gradient analysis, the interpretation of axes relies on additional *post hoc* information on environmental conditions at the sampling sites. Nevertheless, this approach has two advantages. First, the solutions are not influenced by a priori selected environmental factors (ter Braak & Prentice, 1988). Second, even non-quantitative information on the environmental conditions of communities can be used to interpret the axes extracted by indirect gradient analyses. Based on three arguments, we selected shading and moisture as environmental gradients. First, these variables are thought to be the most important environmental factors for spiders (Rushton & Eyre, 1992; Wise, 1993). Second, shading and moisture are related to factors such as habitat structure or temperature, which may have important effects on spider communities. Although we named the two gradients ‘shading’ and ‘moisture’ the underlying factors may be more complex than our labels suggest. Third, shading and moisture are important environmental gradients for plants. Vegetation scientists routinely use the Ellenberg indicator values to characterize plant communities and thereby habitats (light value, L, and moisture value, F; Ellenberg, 1974; Ellenberg *et al.*, 1992). One can easily rank habitats along these two gradients using the general description of the vegetation. Therefore we ranked each of the 70 habitat types along a shading and moisture gradient according to the general description of the vegetation and habitat in the original data base (see Appendix S1 in Supplementary Material; ranks: low, medium, high). A posteriori, we used correlation analysis (Pearson) to test for relationships between the scores of communities on the axes extracted by the indirect gradient analysis and the ranking of habitats along the two gradients. In CA as well as other ordination techniques, the first or second axis often represents a gradient of species richness. Therefore we also tested for correlations between first- and second-axis scores of communities and their species richness. Finally, to check the robustness of our results, we also analysed our data with canonical correspondence analysis (CCA). The results and



**Figure 1** Differentiation of Central European spider communities along the first two axes extracted by a correspondence analysis. The percentage of explained variance is 6% for axis 1 and 5.2% for axis 2. CA scores of (a) all 244 communities and (b) mean scores ( $\pm$  SD) of selected habitat units (for a detailed listing of included habitat types see Appendix S3 in Supplementary Material). Environmental factors are displayed as arrows. The levels for the environmental factors are coded as squares (open habitats), circles (semi-open habitats), triangles (forests), white (dry habitats), grey (mesic habitats) and black (moist habitats). Sample size for mean in (b): 16 annual crops, 21 coniferous forests, 50 deciduous forests, 21 fresh meadows, two juniper heath lands, 16 moist meadows, 14 oligotrophic grasslands, nine reed beds, three saline grasslands, 18 shrub lands, hedges and forests edges, one vineyard, 16 wet deciduous forests and one xerothermic forest.

interpretations, however, were qualitatively very similar to the indirect gradient analyses and we decided to present only the CA.

Although our interpretation of CA axes is based on ranked environmental variables, the habitat and species scores generated

by the CA are continuous and allow for a fine-tuned ranking of habitats and species. Species scores indicate the centre of the species' distribution in a unimodal model. Therefore, species scores represent the niche position (optimum) of species along the extracted axes (ter Braak & Šmilauer, 2002). The standard deviations of species scores quantify the niche width. If the ordination axes are correlated with environmental gradients, the scores and the associated standard deviations can be used to characterize the niche properties of each species with respect to that gradient. To estimate niche conservatism we calculated variance components using a restricted maximum likelihood across the taxonomic hierarchy. The percentage of variation in species traits that could be explained at the level of families and genera was used as an index of niche conservatism. This index was calculated as 1 minus the percentage of variation between species within genera.

For the statistical analyses we use the appropriate procedures of STATISTICA (Kernel version 5.5 A; StatSoft Inc., <http://www.statsoft.com>) or R (version 2.3.0; R Development Core Team, 2005). We used the package *vegan* for R (Oksanen *et al.*, 2005) to estimate the reliability of our CA solutions and the reliability of our interpretations of the extracted axes by randomizing species across habitats as well as by sampling a specified number of communities from the original data set to explore the impact of sample size.

## RESULTS

Spider communities were clearly arranged according to their habitat type along the first two axes extracted by CA (Fig. 1). The first axis represented a shading gradient (Table 1). In Fig. 1(a) spider communities from open habitats had negative values on axis 1, those from forests had positive values. Communities from habitats with scattered woody plants fell in between. The second axis represented a moisture gradient (Table 1), whereby in Fig. 1(a) communities from moist habitats had negative scores and communities from dry habitats had positive scores. The species richness of communities was not correlated with the scores of communities on the first or second axis (Table 1).

The first and second axes extracted by CA explained only 6.0% and 5.2%, respectively, of the variance in species occurrences across habitats. However, the eigenvalues of these axes were clearly

larger than expected by chance. To show this we randomized species across habitats. The eigenvalues extracted by subsequent CAs were much lower than the eigenvalues extracted from the original data set (Fig. 2a,b). When we sampled increasing numbers of communities from our data set, the mean eigenvalues of axis 1 decreased whereas the total inertia increased with the number of sampled communities. Through this sampling, the variance extracted by axis 1 decreased from almost 20% ( $n = 10$ ) to 6% ( $n = 244$ ) (Fig. 2c,d). The patterns of axis 2 correspond to those of axis 1 (results not shown). Furthermore, even for a small number of randomly sampled communities we found fairly high correlations of the community scores of axis 1 with shading (Fig. 2e,f). Hence, the interpretation of axes did not depend on sample size. The comparatively low proportion of variance summarized by the first two axes of the CA is a result of the large number of communities ( $n = 244$ ) used in our analyses. Overall this suggests that the interpretation of axes is robust.

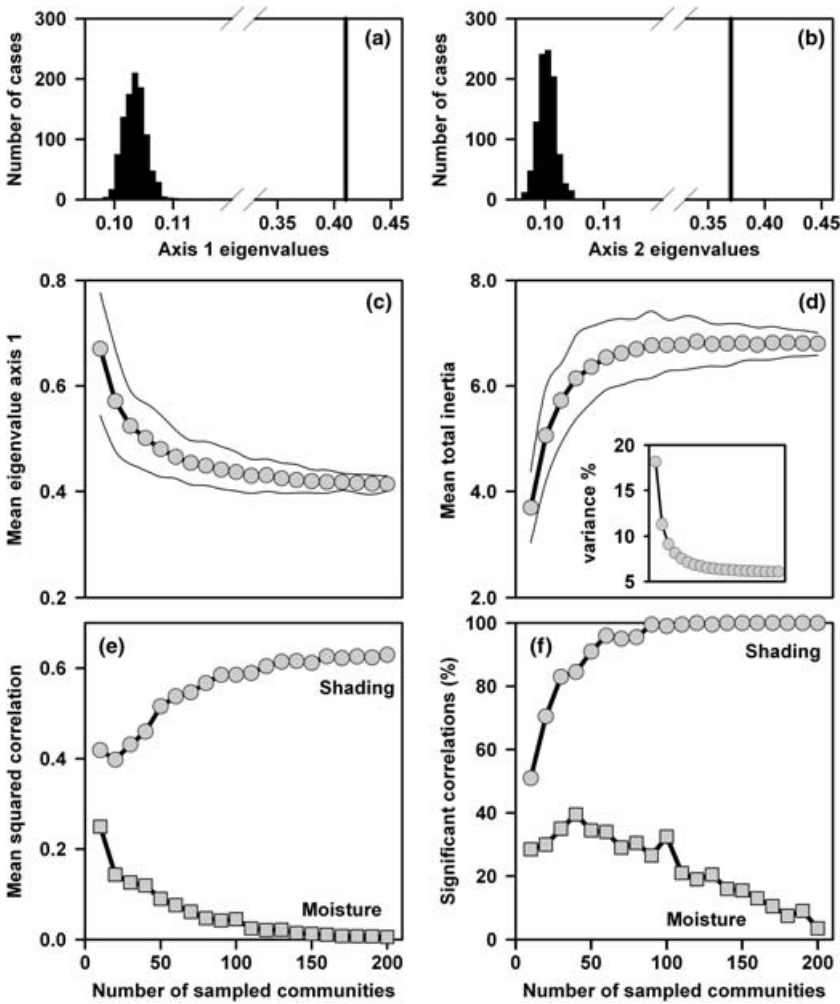
The variation of communities along the second axis differed between habitat types. The scores of open habitats (in Fig. 1a communities with scores on axis 1 < 0) varied six times more than the scores of forests (communities with scores on axis 1 > 0; test for homogeneity of variances: Levene statistic = 54.8,  $P < 0.0001$ ). Thus,  $\beta$ -diversity of spiders was higher between communities of open habitats than between communities of forests (Fig. 1a).

Niche width, estimated as the number of habitat types in which a species occurred, showed a highly significant curvilinear relationship to the number of communities in which a species was recorded ( $r^2 = 0.94$ ,  $P < 0.0001$ ; Fig. 3a). Therefore, this definition of niche width is strongly influenced by the commonness or rarity of species. For example, rare species with a wide niche are not possible according to this definition (indicated by the (upper grey area in Fig. 3a). However, there is no a priori biological reason for a rare species to have a narrow niche, and analyses using the above definition of niche width are prone to finding a spurious correlation between niche width and occurrence. In contrast, when we used the standard deviation of species scores from CA, the relationship between the number of communities in which a species occurred and niche width along both axes approached a central niche width value (Fig. 3b,c). Thus, combinations of low frequency and broad niche are common and the niche widths extracted from CA are less dependent on the rarity of species. Nevertheless, this measurement of niche width correlated significantly with the number of communities in which a species occurred (niche width axis 1:  $r^2 = 0.20$ ,  $P < 0.0001$ ; niche width axis 2:  $r^2 = 0.02$ ,  $P = 0.01$ ), but this may be more of a biological rule than an artefact, as it seems intuitively true that common species also have a wide niche.

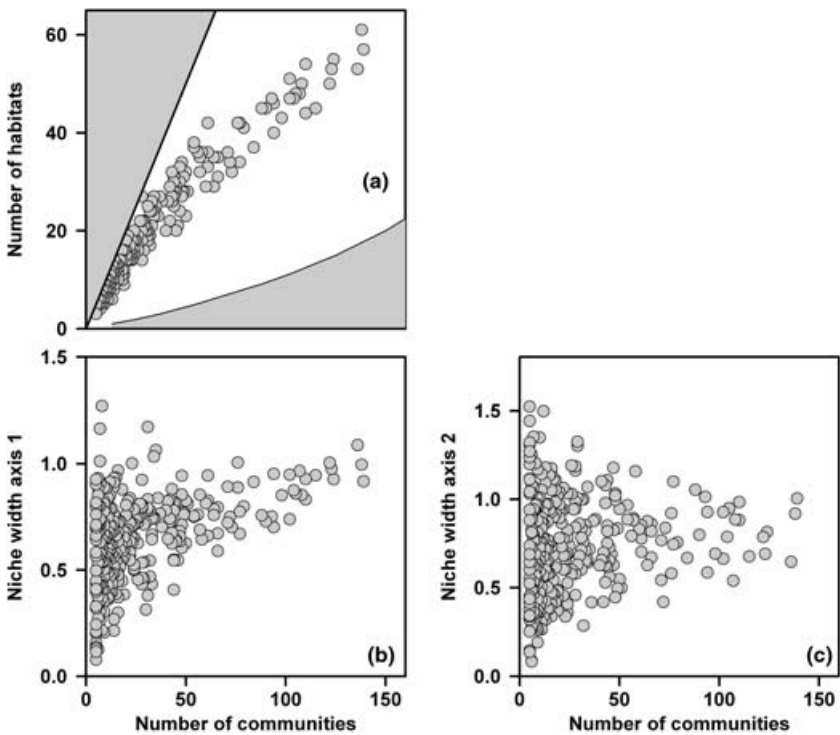
The distribution of species along the first two ordination axes was significantly skewed with a tail in the direction of forests and dry habitats (Fig. 4a,b; axis 1: skew  $0.329 \pm 0.142$ , excess  $-0.968 \pm 0.282$ ; axis 2: skew  $0.879 \pm 0.142$ , excess  $-0.697 \pm 0.282$ ). Niche characteristics were interrelated in a number of ways (Fig. 4c-f). Most importantly, the relationship between niche position and niche width appeared to be hump-shaped along both axes (significant quadratic terms in second-order regressions). Hence for shading as well as for moisture, species living at the extreme

**Table 1** Squared correlation coefficients between the first and second axis of the correspondence analysis (CA) across 244 spider communities of Central Europe (296 species of spiders with more than five records) with the environmental factors 'shading' and 'moisture' as well as with the species richness of spider communities

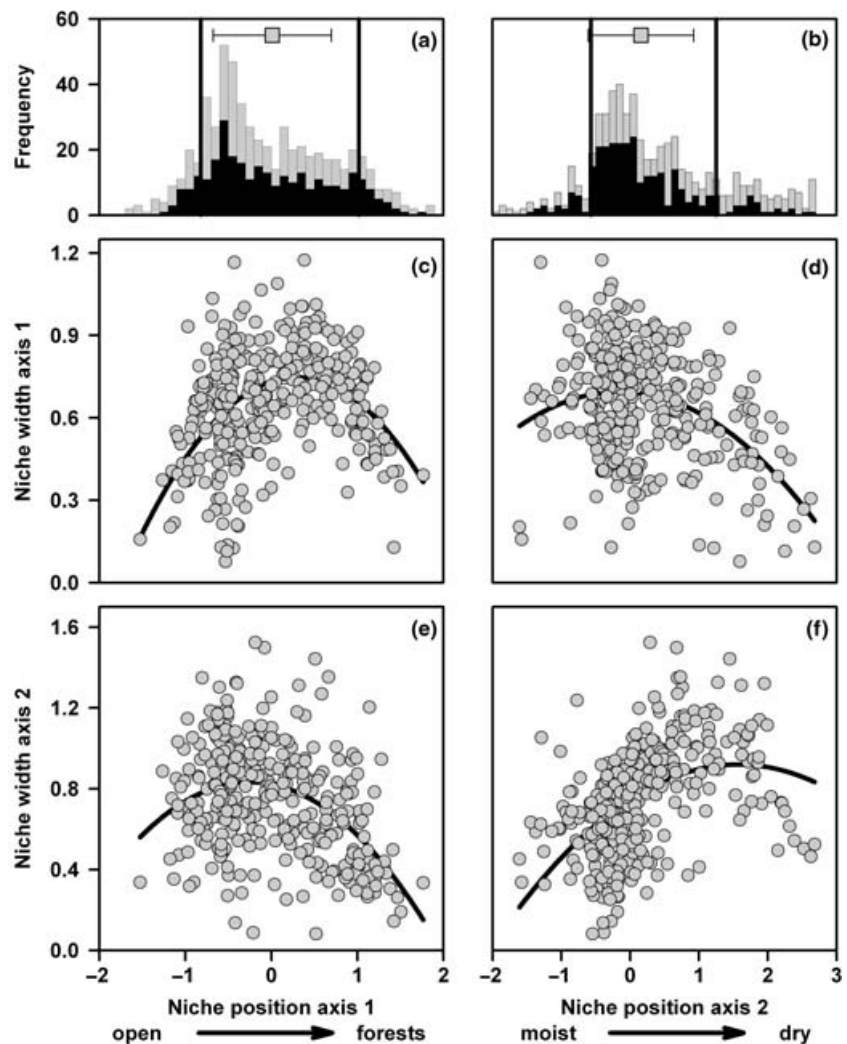
	CA axis 1		CA axis 2	
	$r^2$	$P$	$r^2$	$P$
Shading	0.63	< 0.0001	< 0.0001	> 0.8
Moisture	0.0016	0.53	0.35	< 0.0001
Species richness	0.01	0.23	0.02	0.06



**Figure 2** Tests of the reliability of the ordination shown in Fig. 1. Parts (a) and (b) show the results of 1000 runs during which we randomized the distribution of species across communities. Note that for axis 1 and axis 2, the eigenvalues extracted from these 1000 randomized data sets were much lower than the eigenvalues of the original data set (heavy vertical line). For parts (c)–(f) we randomly selected an increasing number of communities from the original data and performed a CA on each selected data set (each point based on 200 random draws). Note that the eigenvalues of axis 1 decrease with the number of sampled communities (c) (we show mean and 95% confidence limits). Simultaneously the total inertia increased (d) and the percentage of total variance represented by axis 1 declined (inset in d). Parts (e) and (f) show correlations of the axis 1 scores of the communities to the environmental factors. Note that, even with a small number of communities, axis 1 was often significantly correlated to the factor shading (f).



**Figure 3** Correlation of the niche width of 296 Central European spider species with the number of communities in which the species were recorded. (a) The niche width was estimated by the number of different habitat types in which the species was recorded using the original habitat classification by Hänggi *et al.* (1995; overall 70 habitat types). All species have to fall outside the shaded area, because the number of habitat types cannot exceed the number of communities (upper limit) and the frequency with which a habitat type appeared was given by the data set (lower limit). In (b) and (c) the niche width was derived from the correspondence analysis (standard deviation of species scores).



**Figure 4** (a,b) The frequency distribution of species along the two axes (black bars, species with at least six records; grey bars, species with fewer than six records). The heavy lines indicate the 80th percentiles, and the squares with error bars the mean with the standard deviation calculated across the species with at least six records. Parts (c)–(f) show the relationships among niche width and niche position of 296 Central European spider species. We also plot second-order regressions (c:  $r^2 = 0.21$ ,  $P < 0.0001$ ; d:  $r^2 = 0.13$ ,  $P < 0.0001$ ; e:  $r^2 = 0.18$ ,  $P < 0.0001$ ; f:  $r^2 = 0.26$ ,  $P < 0.0001$ ; all  $n = 296$ ). In all four regressions the quadratic term was significant.

ends of a gradient had narrower niches than species at intermediate niche positions.

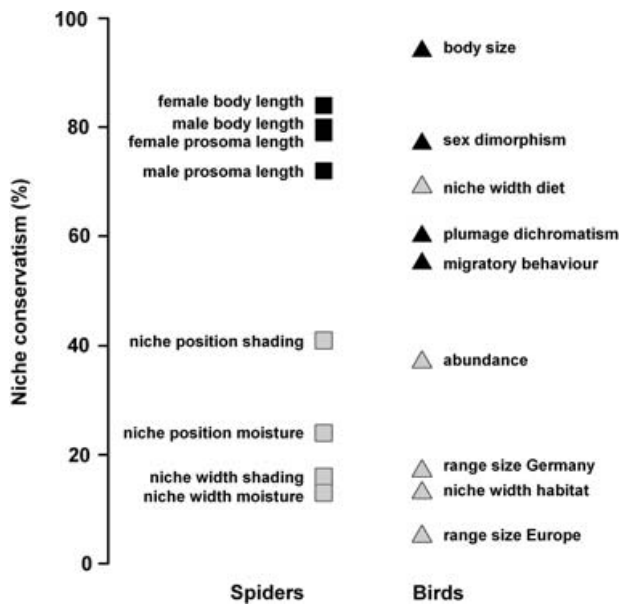
By using variance components we found that for all four niche characteristics most variation was between species within genera. Hence niche conservatism was low (< 40%) when compared with morphological traits such as body size (> 60%; Fig. 5) indicating that during speciation species are more easily able to change their niche than their body size. This result is not unusual. In Fig. 5 we compare the values of niche conservatism found during our study with similar estimates for birds (extracted from Brändle *et al.*, 2002). In both birds and spiders, conservatism of niche parameters is lower than conservatism of morphological and life-history traits (Fig. 5).

## DISCUSSION

Our results demonstrate that there is a strong relationship between community composition and environmental gradients. Based on unimodal response models for 296 species, we characterized the distribution of spider species in Central Europe along two environmental gradients that we labelled 'shading' and

'moisture'. While environmental factors were shown to influence the niches and composition of communities of various taxa on local or national scales (ostracod species from Iberian water bodies, Mezquita *et al.*, 2005; ground beetle species in Britain, Eyre *et al.*, 2005; butterflies in the Netherlands, Oostermeijer & Van Swaay, 1998), our study is the first to demonstrate the importance of environmental factors for an arthropod group on the Central European scale. The large spatial scale of our study and the extensive number of spider species, sites and habitat types included in the analysis suggest that the basic patterns revealed in our study are robust.

Our results show that niche differences play an important role in structuring spider communities. According to neutral theory, the distribution and abundance of species would be mainly based on stochasticity, meaning that differences between habitats would be of little importance for the composition of communities (Hubbell, 2005). Only the number and size of habitats would be relevant. Our results on spiders point to the opposite. Spider communities are related to the type of habitat, and the composition of spider communities depends on the shading as well as the moisture of habitats. Thus, for spiders, these two gradients are



**Figure 5** Niche conservatism of spiders and birds as the percentage of total variation explained at higher taxonomic levels (genera and families in the case of spiders). Dietary, morphological and life-history traits are given as black symbols, whereas ecological traits are given as grey symbols for the two groups. Spider body size was measured for males and females using either body size or prosoma length (W. Entling, unpublished data). The data for birds were extracted from Brändle *et al.* (2002; Germany).

major drivers of  $\beta$ -diversity between habitats, in accordance with MacArthur (1965) and Whittaker (1967).

During our study we quantified niche position (mean species scores) and niche width (standard deviation of species scores) along a shading and moisture gradient for 296 species of spiders (see Appendix S2 in Supplementary Material). Compared with the existing information our approach has a number of advantages. Some Red Lists and field guides also give habitat preferences for spider species (= niche position) as well as their degree of specialization (= niche width; Platen, 1984; Heimer & Nentwig, 1991; Roberts, 1995). While large numbers of species are covered by Red Lists and field guides, classifications with respect to habitat and rarity therein are based on qualitative expert knowledge. The few quantitative analyses using an objective methodology are usually restricted to specific habitat types (e.g. dunes, Bonte *et al.*, 2003a; dry grassland, Pozzi & Borcard, 2001; agricultural habitats, Schmidt & Tschardtke, 2005). In contrast, we derive an ecological classification system for spider species in a quantitative way using information from most of the habitats occurring in Central Europe. Furthermore, previous quantitative studies of spiders estimated the niche width by counting the number of habitat types in which a species has been recorded (Bonte *et al.*, 2003b). However, as we have shown, such measures depend on the rarity of species: species occurring in few samples are constrained to have a small niche width (Fig. 3a, see also Hanski *et al.*, 1993). In addition, the number of habitat types in

which a species was recorded does not necessarily account for the range of environmental conditions across these habitats. We have overcome these problems by deriving the niche width from correspondence analysis, which is less dependent on species' commonness and includes the similarity of habitats in its calculation. Finally, as noted above, the procedure used to extract the gradients (CA) ensures their independence (see also Table 1). Therefore these gradients can be used as independent variables in subsequent analyses.

The niche properties generated during our study can be used to approach general evolutionary and ecological issues and provide new insights for decision-making.

First, our results have implications for the evolution of the niche: species that have their optima at the extreme ends of an environmental gradient have narrow realized niches (Fig. 4). Thuiller *et al.* (2004) found a similar pattern in three bioclimatic gradients for 88 *Leucadendron* taxa, evergreen woody plants which occur in the Cape Floristic region. Apparently, adaptations to extreme conditions lead to inherent constraints in niche width. However, niche properties extracted by gradient analysis are niche properties valid only for the study region. Clearly, across the whole of Europe more extreme habitats and environmental conditions occur and it is possible that the spider species occurring at the ends of our gradient also live under more extreme conditions outside our study area. Therefore, one could argue that niche width may be constrained by the availability of habitats at the extreme ends of the gradients. However, this argument may apply to the dry end of our moisture gradient but not to the wet end of this gradient as well as the extremes of the shading gradient, as the three latter extremes are well represented in Central European habitats.

Second, while the evolution of the niche seems to be constrained under extreme habitat conditions (at least at three ends of the gradients), the phylogenetic constraints of the niche were low. Compared with body size (Fig. 5), most of the variability in niche position and niche width occurred between species within genera. Thus, the niche properties of closely related species may differ considerably. A similar pattern was also found in birds: diet, morphological and life-history traits in a regional bird community showed much more phylogenetic conservatism than ecological traits (Böhning-Gaese & Oberrath, 1999; see also Fig. 5). Prinzing *et al.* (2001) likewise found a smaller degree of conservatism in the niche positions of plants than in many morphological and physiological traits. In general, the habitat niche of species seems to evolve faster than morphological or physiological traits. Thus, it may be misleading to predict niche properties of a species from the properties of a related species.

Third, our data on niche properties can be used to classify habitats and species. Our analysis showed that in both environmental gradients niche width depends on niche position in a hump-shaped manner: species having their optima at the extreme positions of the gradients are habitat specialists with a narrow niche. Therefore, one can consider all species that fall outside the 80th percentile of the distribution of niche positions as specialists (vertical lines in Fig. 4a,b). Consequently one can use the percentage of specialists in a habitat to rank habitats according to

their priority for conservation. For a stricter classification one can use 95th percentiles or any other quantitative criterion. Such a procedure would push the use of spiders for decision-making beyond Red Lists.

Finally, our data can be used to identify especially endangered habitats. Along the moisture gradient, the  $\beta$ -diversity of open habitats is more pronounced than the  $\beta$ -diversity of closed habitats (Fig. 1). The two ends of the moisture gradient host a considerable number of species (see Fig. 4b) but cover only a small fraction of the actual landscape. Furthermore, such habitats (e.g. oligotrophic grasslands or reed beds) have decreased massively over the last century (Kaule, 1991). Hence, our analysis provides quantitative arguments for the particular protection of dry and moist habitats with low stratification of the vegetation.

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## BIOSKETCH

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Classification of Central European habitats according to shading and moisture

**Appendix S2** Values for niche properties of Central European spiders

**Appendix S3** Habitat units displayed in Fig. 1(b)

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