Geographic variability of ecological niches of plant species: are competition and stress relevant?

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A species' niche position may differ strongly between geographic regions, for instance due to the effect of competitors or ecophysiological stress. However, it is unclear whether such strong geographic niche variation is the rule or the exception. We compared the niche positions of plant species between central England and eastern central Europe (as available from the literature), using phylogenetically independent contrasts. We found that most species occupied similar niche positions in both regions. More importantly, we found that niche variation was not higher in species susceptible to competitive displacement. Nor was niche variation higher in species that reach the edge of their range and thus suffer ecophysiological stress. We suggest that although these species might be easily displaced in their position along a niche axis, they may only be displaced over a short distance. Overall, ecological mechanisms that cause niche variation at the local scale may be much less relevant at the geographic scale.

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One of the basic concepts in ecology is the ecological niche, which can be defined as the position and breadth of a species' distribution along various niche axes (Schoener 1989). The physiology of a species determines its "physiological niche" (Ellenberg 1953) or "fundamental niche" (Hutchinson 1957), i.e. its niche in monoculture under laboratory conditions. The impacts of other species then shape the "ecological" or "realised" niche: they reduce the niche breadth and may shift the niche position (Ellenberg 1953, Hutchinson 1957) or at least change the physiological performance of individuals along niche axes (Austin 1982). For the rest of the paper we will focus on the realised (ecological) niche of species.

Most authors stress that both the position and the breadth of a species' realised niche are highly variable (Begon et al. 1990). Pianka (1988), for instance, states that "realised niches of most organisms change both in time and from place to place as physical and biotic environments vary". Such authors often consider a species' realised niche position as a merely regional phenomenon (Walter and Breckle 1991). This notion is based on two lines of evidence. First, in a number of species drastic variation of niche positions between regions has been observed (for plants: Walter and Breckle 1991). However, it has only rarely been tested whether such drastic variation is the rule or the exception (see below). Second, a number of mechanisms are known that favour variation of niche positions between regions. Two mechanisms are mentioned frequently. The first is competitive displacement – a competitively inferior species is displaced to different niche positions in different regions by competitively superior species (Parrish and Bazzaz 1976, Austin and Austin 1980,

Walter and Breckle 1991). Only among highly competitive species the effect of competition on niche positions may be small (Parrish and Bazzaz 1982). Competitive displacement is only one form of displacement by antagonistic species; displacement by grazers or parasites are other forms (Francis and Read 1994, Zobel 1997). The second mechanism that is frequently mentioned is compensation of ecophysiological stress – a species compensates the deterioration of physiological living conditions at the edge of its range by a change in the niche position (Brown 1984, Brussard 1984, Walter and Breckle 1991). Physiological living conditions include the climate and soil but also the effect of mutualistic species such as mycorrhizal fungi (Walter and Breckle 1991). Overall, species which are susceptible to competitive displacement or to ecophysiological stress should therefore show stronger niche variation between geographic regions than other species. However, this expectation has never been tested.

Thompson et al. (1993) tested whether drastic variation of niche positions between regions is the rule or the exception. They compared the niche positions occupied by plant species in central England (Sheffield region) and central Europe. This central England/central Europe comparison had three unique advantages. First, most species from central England also occurred in central Europe. So Thompson et al. could study the niche variation for the vast majority (97%) of the species of a region. At the same time, the two regions harboured different vegetation types, dominated by different species (Rodwell 1991–1998, Dierschke 1994, Ellenberg 1996). Second, niche positions in both regions were assessed independently and on a solid basis. For central England the assessment was based on a large quantitative ecological survey (Hodgson et al. 1995). For central Europe, no such survey had been available but instead Ellenberg's "Indicator Values" could be used (Ellenberg 1979). Various validations have shown that these values are a very good surrogate for standardised surveys or even measurements (Ellenberg 1992, Ertsen et al. 1998, Schaffers and Sýkora 2000), particularly in stable plant communities (Dzwonko 2001), and hence it can be assumed that the "Indicator Values" indeed indicate the central European niche positions of plant species. In their analysis, Thompson et al. (1993) found that most species occupied similar niche positions in central England and central Europe. Drastic variation was the exception. Hill et al. (2000) also used Ellenberg's assessments of niche positions of plant species in central Europe, but compared them to the species' niche positions across the whole of Britain. The authors inferred the British niche positions indirectly from the species' community membership. Just like Thompson et al. (1993), Hill et al. found that most species occupied similar niche positions in central Europe and in Britain. Diekmann and Falkengren-Grerup (1998) came to a similar result in a

comparison of 80 species between central Europe and Sweden.

However, all these studies suffered from a methodological problem: species had been treated as independent data points. Such a procedure ignores the phylogenetic non-independence among species and leads to pseudoreplication within lineages, or "phylogenetic bias" (Harvey and Pagel 1991, Hendriks et al. 1999). This may be of special importance since in central Europe some taxa, e.g. *Carex*, are species rich and ecologically quite similar and thus might overproportionally influence an analysis.

In the present study we first simply re-analysed the relationship between niche positions of plant species in central England and central Europe, applying techniques that avoid phylogenetic bias ("phylogenetically independent contrasts"; Harvey and Pagel 1991). Then, we inspected the mechanisms that may cause niche variation. We asked: do plant species which are susceptible to competitive displacement or to ecophysiological stress occupy more disparate niche positions in both regions than other species? We inferred a species' susceptibility to competitive displacement from its potential competitiveness as defined by Grime et al. (1988). And we inferred a species' susceptibility to ecophysiological stress from the location of its range. Species which reach the edge of their range in a region generally suffer a higher burden of stress than the other species in the same region (Brown 1984).

Methods

Niche positions

Niche positions in central England (3000 km² in the surrounding of Sheffield) were taken from Hodgson et al. (1995), based on a survey in 1967 (Grime et al. 1988). Niche positions in central Europe (mainly Germany) were from Ellenberg (1979). We included the modifications by Frank and Klotz (1990) for eastern central Europe in order to increase the geographic contrast to central England. For instance, the climate of eastern central Europe is distinctly more continental than the climate of central Europe in total, which increases the contrast to the oceanic climate of central England (Walter 1990, Ellenberg 1996). We expected that this large geographic contrast corresponds to a high degree of geographic niche variation (see Ellenberg 1996 for niche shifts that occur already between eastern and western central Europe). Regrettably, the most recent edition of Ellenberg's Indicator Values (Ellenberg 1992) has not yet been modified for eastern central Europe, and thus we refrained from using this recent edition. However, we checked the consistency between both sets of indicator values (Frank and Klotz 1990, Ellenberg 1992) and found a very high correlation

($R_p > 0.97$). Moreover, we found that both sets yielded very similar results in our analysis. R_p values in Table 1, for instance, change for only 0.003, 0.009 and 0.015, respectively.

Both Hodgson et al. (1995) and Ellenberg (1979) consider the niche axes light, soil moisture and soil pH. Hodgson et al. characterise a species' position along the niche axes light and soil-moisture in central England by its relative frequency in forests, or in wetlands, respectively (Thompson et al. 1993). Ellenberg only assigns those species that show a clear niche position within central Europe. Depending on niche axis these are 59% (for soil pH), 88% (for soil moisture), or 96% (for light) of the 484 species that also occur in central England. In fact, only such species with a clear within-region niche position are suitable for our comparisons between regions.

To directly compare the species' niche position between central Europe and central England we had to adapt the 9- or 12-rank-scale used by Ellenberg (1979) for light or soil moisture to the five-rank-scale used by Hodgson et al. (1995). Following the definitions of Ellenberg we defined five re-scaled ranks for light, equivalent to the following original ranks: 1–2; 3–4; 5; 6–7; 8–9. Moreover, we defined five re-scaled ranks for soil moisture, equivalent to original ranks 1–3; 4–5; 6–7; 8–9; 10–12. Re-scaling the original Ellenberg ranks linearised the relationship between the niche positions in central England and central Europe. In contrast, without re-scaling, the relationship would be sigmoidal because Ellenberg differentiated the extremes of the niche axes more finely than did Hodgson et al. (1995). It was not necessary to re-scale Ellenberg's ranking of soil pH, because his definitions of ranks were very similar to those of Hodgson et al. Correspondingly, both rankings were linearly related. (But note that they need not be linearly related to the true pH of the soil [Schaffers and Sýkora 2000]).

Table 1. Similarity of niche positions occupied in central England and in central Europe by the same species. PICs, phylogenetically independent contrasts (for explanation of "CAIC-Crunch" and "Burt" see Methods). R_p, Pearson correlation coefficient; Beta, standardised regression coefficient; $+/-$, number of positive/negative contrasts. All similarities are significant at $p < 0.001$ (t-test or sign test).

Niche axis	Species	Data points "CAIC-Crunch-PICs"	"Burt-PICs"
	R_p ($n \geq 276$)	Beta ($n = 201$)	$+/-$
Light	0.608	0.628	48/7
Soil moisture	0.832	0.793	63/6
Soil pH	0.703	0.621	44/4

Niche variation

We calculated a species' niche variation between central England and central Europe using two approaches. First, we simply calculated the absolute difference between niche positions in both regions. Second, we calculated a linear regression of niche positions in central England against niche positions in central Europe and recorded the absolute residual for each species. We then calculated the reverse regression and again recorded the absolute residuals. The mean of both absolute residuals was then used as a measure of a species' niche variation. In the analysis, both approaches lead to qualitatively identical results. So we only present the results of the latter approach because it permitted to measure niche variation on a finer scale than the former approach.

Competitive displacement and ecophysiological stress

We inferred a species' susceptibility to competitive displacement from its potential competitiveness as defined by Grime et al. (1988) ranging from C (competitive) to either S (stress tolerant) or R (ruderal) on a rank scale (0, 1, 2, 3, 4).

We inferred a species' susceptibility to ecophysiological stress from the position of its range relative to central England and central Europe: species that reach the edge of their range in either of the two regions were assessed as "ecophysiologically stressed". Information on range edges in central England was taken from Hodgson et al. (1995). These authors classify species which are completely absent from northern Britain and species which are largely absent from the north and completely absent outside the Atlantic seaboard. Central England is thus very close to the northern or north-eastern range edge of these species, albeit the edge only rarely passes directly through the small area of central England. Five of these species are also absent from Ireland and thus central England is also close to the western range-edge of these species (Grime et al. 1988). None of the non-classified species is absent from, or very rare in, Ireland or Wales (Grime et al. 1988). Information on range edges in eastern central Europe was taken from grid maps in Benkert et al. (1998), with additional reference to Haeupler and Schoenfelder (1989). A species' range was approximated as the continuous outer limit of the occupied grid cells. Species whose range covered less than approximately two thirds of the total area were assessed as being "at the edge of their range". We found that our assessment of the central European range of species was highly correlated to the continentality classification by Ellenberg (1979) which was based on a different source (global distribution maps in Meusel et al. 1965): 94% of our "range-

edge species'' had been classified as "euoceanic" or "oceanic" by Ellenberg (1979), 93% of the remaining species had been classified as less oceanic. This agreement with Ellenberg's classification made us confident in our assessment. Nonetheless, the criteria for assessing range-edge species were inevitably somewhat arbitrary. But it is unlikely that different criteria would have led to different conclusions, given the very large sample size on which our analysis was based and given that the effect of range edge turned out to be distinctly non-significant in the vast majority of tests ($p > 0.29$ in 13 out of 15 cases, $p > 0.14$ in another case; Table 3).

We did not differentiate between species that reach the edge of their range in central England and those that reach the edge in central Europe because 85% of the range-edge species reached the edge of their range in both regions. This suggests that most species that are constrained by the short growing period in the north of England are also constrained by the winter frost in the east of central Europe (Walter 1990). The remaining species can presumably tolerate both.

Analysis

In our analysis we first treated species as independent data points. We analysed these data points by correlation analysis, Mann-Whitney U-test or linear regression analysis (Sokal and Rohlf 1981). Such an analysis ignores that traits of different species are not independent but connected by the species' phylogeny (Harvey and Pagel 1991; Introduction).

Then, we analysed the data using phylogenetically independent contrasts (PICs) as data points to account for the phylogenetic relationships among species (Harvey and Pagel 1991). The basic philosophy of PICs is to separate groups of species which do not overlap phylogenetically. For each group the change of one trait is compared to the changes of other traits. Finally, the coincidence between changes of different traits is tested across all groups (Harvey and Pagel 1991). Two basic classes of methods to calculate PICs are available, conservative ones which make no assumptions but treat the data inefficiently, and less conservative ones which treat the data more efficiently but make several assumptions (Harvey and Pagel 1991 and see below). In our analysis we applied both types of methods to check the robustness of our results across methods.

When we compared two continuous variables we applied 1) PICs calculated by the "conservative" method of Burt (1989), "Burt-PICs" in the rest of the paper). Basically, this method calculates the correlation between two traits across extant species within a phylogenetic dichotomy or polytomy. A sign test is then used to check whether across the whole phylogeny the proportion of positive, or negative, correlations is significant. 2) PICs calculated by the "non-conservative"

method of Felsenstein (1985) and Pagel (1992). These PICs represent standardised trait differences between endpoints of dichotomies, which are either extant species or ancestral states of extant species. Polytomies are splitted into dichotomies. The calculated differences can then be compared among traits by regression analysis with an intercept of zero (Harvey and Pagel 1991). This method uses the available information efficiently but makes the assumption that traits evolve in a random walk pattern, and that the number of evolutionary steps is proportional to the length of the phylogenetic branches (Harvey and Pagel 1991). Moreover, the method assumes that polytomies can be splitted into dichotomies based on the traits analysed, which only makes sense if the traits are phylogenetically conservative (Pagel 1992, Purvis and Rambaut 1995). In our study such a trait conservatism was clearly given for the niche position of species along the soil-moisture gradient (Prinzing et al. 2001), and thus we selected this trait to split the polytomies. To calculate these PICs we used the CAIC software by Purvis and Rambaut (1995), option Crunch (hereafter "Crunch-PICs").

When we compared a continuous and a binary variable we applied 1) PICs calculated by the conservative method of Burt (1989) as above, and 2) PICs calculated by the less conservative method suggested by Purvis and Rambaut (1995). The latter PICs represent differences between extant species connected by a phylogenetic dichotomy. If there is no variation of the considered variable within a dichotomy the dichotomy is pooled with other dichotomies. Again, polytomies are splitted into dichotomies, based on the above-mentioned assumptions. At each dichotomy the sign of the difference between the two species (or groups of species) is recorded for each trait. Then, the signs are compared between traits by a sign test. To calculate these PICs we again used the CAIC software (Purvis and Rambaut 1995), option Brunch (hereafter "Brunch-PICs").

We treated niche positions, niche variation and competitiveness as continuous variables, which is appropriate with a sample as large as ours (Ter Braak and Barendregt 1986). We treated edge of range as a binary variable in univariate analysis. However, when we tested its multivariate effect in combination with competitiveness we treated edge of range as a continuous variable as suggested by Purvis and Rambaut (1995). Treating a binary variable as a continuous variable may introduce some error into the multivariate analysis. But the results were unambiguous (p was either < 0.05 or > 0.50) and generally agreed with the results of the univariate analysis. So we were confident in the results of the multivariate analysis.

There is no hypothesised phylogeny available which covers all our species. Thus, we compiled a supertree from phylogenies suggested in the literature for single lineages (we used a total of 52 publications, references

Table 2. List of species with lowest and highest variation of niche positions between central England and central Europe averaged across the three niche axis considered. We arbitrarily selected species with a niche variation <0.28 or >1.8, respectively. Note that the two groups of species do not share a single family.

Species	Family	Niche variation
Species with lowest niche variation		
Ranunculus acris	Ranunculaceae	0.10
Dactylorhiza fuchsii	Orchidaceae	0.10
Dactylis glomerata	Poaceae	0.16
Elytrigia repens	Poaceae	0.16
Veronica chamaedrys	Scrophulariaceae	0.16
Holcus lanatus	Poaceae	0.20
Urtica dioica	Urticaceae	0.20
Chenopodium album	Chenopodiaceae	0.22
Stachys palustris	Lamiaceae	0.22
Brachypodium pinnatum	Poaceae	0.27
Clinopodium vulgare	Lamiaceae	0.27
Species with highest niche variation		
Conium maculatum	Apiaceae	1.82
Salix purpurea	Salicaceae	1.85
Lysimachia nummularia	Primulaeceae	1.85
Salix repens	Salicaceae	1.92
Carduus acanthoides	Asteraceae	2.00
Betula pendula	Betulaceae	2.25
Corylus avellana	Corylaceae	2.25
Quercus robur	Fagaceaeo	2.25
Prunus spinosa	Rosaceae	2.25
Reynoutria japonica	Polygonaceae	2.29
Cardamine pratensis	Brassicaceae	2.57

are available from the authors upon request). There were no branch lengths available for our tree, so we set all branch lengths to the same arbitrary value. Simulations (e.g. Martins and Garland 1991), and practical tests (e.g. Blackburn et al. 1996, Ackerly 2000, Dunn et al. 2001) have shown that this is a valid method. For technical reasons, the approach of Burt (1989) was based on a taxonomy which we compiled from Schubert et al. (1990) and Thorne (1992). The choice of taxonomy was not crucial. The application of alternative taxonomies (e.g. Cronquist 1988) generated very similar results.

Results

Most species occupied similar niche positions in central England and in central Europe, i.e. the geographic niche variation was low (Table 1). Niche position was particularly conserved along the soil moisture axis, whereas along the light and soil pH axes more variation was observed. Table 2 lists the species with lowest and highest niche variation. The two groups of species did not share a single family. This was not simply a chance effect, as in a null model (n = 300 randomisations) we found that such a situation occurs in only 3.3% of the cases. Thus, niche variation was not independent of phylogeny. Nevertheless, even when we corrected our analysis for phylogenetic relatedness, we only found

little niche variation between central England and central Europe (Table 1).

We then analysed whether poor competitors or species that reach the edge of their range show increased niche variation. In univariate analyses (Table 3) low competitiveness significantly increased niche variation only along the niche axis soil pH, but not along the soil-moisture axis and the light axis. This result was consistent across all types of univariate analysis. Edge of range did not increase niche variation along either of the niche axes. Again, this result was consistent across all types of univariate analysis. In the multivariate analysis (Table 3) we also found that low competitiveness increased niche variation along the soil pH axis. This was clear from both, analyses based on species as data points as well as analyses based on PICs. In the latter analyses we also found that edge of range significantly increased a species' niche variation along the soil-moisture axis, albeit the beta value was comparatively small.

Discussion

We compared niche positions occupied by the plant species that occur in central England to the niche positions occupied by the same species in eastern central Europe. We found that most species occupied similar niche positions in both regions. "Similar" is a subjective assessment. But at least, our results contradict the idea that niche positions are a merely regional phenomenon. Thompson et al. (1993) and Hill et al. (2000) came to the same conclusion. Our results show that this conclusion holds even if one avoids phylogenetic bias. The conclusion, however, is scale-specific. We considered a between-region scale and analysed only species that display a clear within-region niche position, i.e. species that have been assigned by Ellenberg (1979). Depending on the niche axis these are 59, 88 or 96% of all species occurring in central England. Our observations at the species level can explain earlier observations at the community level (Diekmann 1995, Hill and Carey 1997, Diekmann and Falkengren-Grerup 1998): the average of central European niche-positions across a community correlates to the local abiotic conditions, even if the community is located outside central Europe.

Most importantly, we found that a species' susceptibility to competitive displacement or to ecophysiological stress only rarely increased the species' geographic niche-variation (Table 3). There was only one clear exception. Susceptibility to competitive displacement increased niche variation along the soil-pH axis. Hence, a part of the flora did show a distinct between-region variability of the niche positions along the soil pH axis (for a similar observation in The Netherlands see Schaffers and Sýkora 2000). This between-region variability

Table 3. Factors determining niche variation between central England and central Europe. We tested the hypothesis that niche variation is higher in poor competitors and in species that reach the edge of their range. We used either species or phylogenetically independent contrasts ("PICs") as data points. For explanation of "CAIC", "Crunch", "Brunch", and "Burt" see Methods. Beta, standardised regression coefficient; Z, Z-value in a Mann-Whitney U-test; +/−, number of positive/negative contrasts; p, one-tailed probability.

Dependent variable Independent variable	Univariate analysis Species (n≥275) Beta	Z	p	Multivariate analysis "CAIC-PICs" "Crunch" (n≥276) Beta	p	"Brunch" +/−	p	"Burt-PICs" +/−	p	Species (n≥275) Beta	p	"CAIC-Crunch-PICs" (n≥211) Beta	p
Niche variation along light gradient													
Low competitiveness	−0.16		>0.5	−0.09	>0.5			29/36	>0.5	−0.11	>0.5	−0.08	>0.5
Edge of range		−0.52	>0.5			42/63	>0.5	22/38	>0.5	−0.01	>0.5	−0.03	>0.5
Niche variation along soil-moisture gradient													
Low competitiveness	−0.12		>0.5	−0.06	>0.5			28/39	>0.5	−0.80	>0.5	−0.06	>0.5
Edge of range		0.53	0.299			49/47	0.46	34/25	0.148	0.02	0.33	0.10	0.049
Niche variation along soil pH gradient													
Low competitiveness	0.15		0.006	0.17	0.007			35/17	0.049	0.09	0.06	0.17	0.006
Edge of range		−1.30	>0.5			36/43	>0.5	21/27	>0.5	−0.04	>0.5	−0.01	>0.5

of pH niches corresponds to the variability within-region. For instance, within central Europe 41% of the species in our data set are so variable that Ellenberg (1979) could not assign them to a soil pH category. The between-region variability along the soil pH axis also corresponds the phylogenetic variability (Prinzing et al. 2001). So niche positions along the soil pH axis seem to be less fixed than along the other two axes, and a higher susceptibility to regional differences in competition pressure should be expected.

One reason for the high variability along the soil pH axis may be that the effect of soil pH can be overridden by the effect of soil microclimate. Most calcareous soils heat up quickly, and in a cool region this microclimatic property of calcareous soils may be more important for plant growth than the soil pH (Ellenberg 1996, Schaffers and Sýkora 2000). Another reason may be that in some regions plants have to use high-pH soils in order to ensure a sufficient supply of calcium (Schaffers and Sýkora 2000). Finally, the pH of many soils has dramatically changed during the recent decades due to "acid rain" and in some regions the distribution of plants may not have fully adopted to these changes by now (see Dzwonko [2001] for similar observations on the long term dynamics of plant niches in woodlands).

The comparatively high variability of non-competitive species along the soil pH axis does not necessarily mean that they have been displaced by more competitive species. The high variability might also be explained on a physiological basis. First, highly competitive species usually have a high nutrient demand, and may thus be simply incapable of growing in low-pH soils with their low nutrient availability (Ellenberg 1996, Crawley 1997). Second, competitive species usually produce a large amount of litter and can thereby strongly influence the microflora and chemistry of their own soil substrate (Crawley 1997). Hence, if for instance the microflora of calcareous soils differs between central England and central Europe this would affect competitive species less than non-competitive species. Both of these physiological processes would fix the niche positions of competitive species rather than vary the niche positions of non-competitive species. Therefore, across all species, the niche variation along the pH axis should be lower than along the moisture axis or the light axis. However, this was not the case (Table 1). Thus, the two physiological processes cannot fully explain our results. We therefore suggest that competitive displacement is part of the explanation for the high variability of non-competitive species along the soil pH axis.

Why did the species occupy similar niche positions in central England and central Europe? We see four possible, mutually non-exclusive reasons.

Firstly, the regions are geographically similar, i.e. climate, soils and land use are similar. Obviously, there are regions that are geographically more disparate than

central England and the east of central Europe. But such disparate regions only share a small portion of their floras. Hence, it is not possible to assess the between-region similarity of niches for most species. Another important point is that even central England and central Europe may be quite disparate from the point of view of two groups of plant species: 1) competitively inferior species; and 2) species that reach the edge of their range in either of the two regions. Nevertheless, even these two groups of species usually occupied similar niche positions in both regions. Overall, the geographic similarity between central England and central Europe cannot fully explain the similarity of the species' niche positions in both regions.

Secondly, variable species might have "disappeared" by breaking up into sister species which are restricted to either central England or central Europe (Brown 1984). However, only 3% of the species in central England are absent from central Europe. So, the proposed reason cannot explain the similarity of niche positions between central England and central Europe.

Thirdly, plants may respond to a change of the regional environment in terms of physiology, rather than niche shift. Take for example a region with little rainfall. If a plant species reduces stomatal water loss in that region, the scarcity of rainfall need not affect the saturation of the plant tissues with water (Larcher 1995). So, the plant need not shift its niche towards moister soils. A plant may also respond to a change of the regional environment in terms of reproductive strategy, rather than niche shift (Rapoport 1982). For instance, in a cold mountainous region a species may reproduce only during occasional warm years, rather than shift its distribution towards warmer altitudes.

These physiological or reproductive responses of plants to the regional environment should be least efficient for species that occupy extreme niche positions, because such species may be pressed to their absolute physiological limits by a change of the regional environment (Økland 1990, Huston 1994, Larcher 1995). So, the geographic niche variation should be larger for species occupying the extremes of a niche axis than for other species. This expectation, however, is not supported by the data (Fig. 1). So, physiological or reproductive responses of a plant species to changes of the regional environment can not explain why species occupied similar niche positions in central England and central Europe.

Fourthly, the breadth of niche variation may have been constrained. In other words, a niche may only be displaced over a short distance along a niche axis. It is obvious that the variation of the fundamental niche of a species is constrained, given that the species' physiology, which determines the fundamental niche, is constrained by the species' phylogenetic roots (Larcher 1995). For instance, most descendants of species with a C_3 metabolism again display a C_3 metabolism. How-
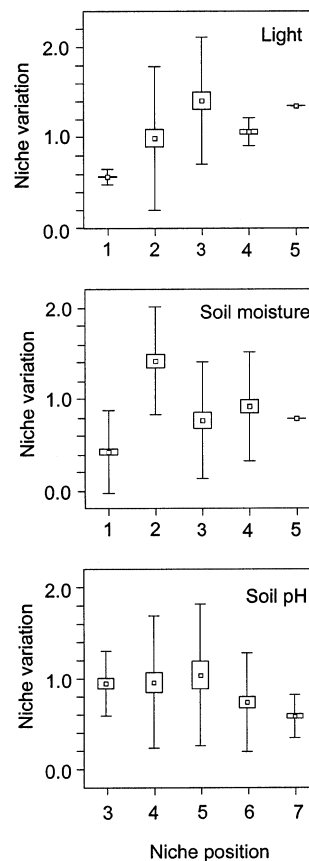

Fig. 1. Niche variation between central England and central Europe in plants growing along different positions of a niche axis. Niche axes are light and soil-moisture (both on an arbitrary 1–5 scale) and soil pH. Niche positions are averaged across central England and central Europe. Dots are means; boxes are standard errors; whiskers are standard deviations.

ever, it has recently been demonstrated that also the variation of the realised niche, the topic of the present study, is phylogenetically constrained (Ricklefs and Latham 1992, Prinzing et al. 2001; theoretical framework in Brown 1984). Interestingly, the variation of realised niches along the soil-moisture axis is phylogenetically more constrained than the variation along the light or the soil pH axes (Prinzing et al. 2001). This fits to our observation that the geographic niche-variation is lowest along the soil-moisture axis. Hence, phylogenetic constraints on the breadth of niche variation may explain the low geographical variation of niches.

The phylogenetic constraint of niche variation may be strongest in species of low competitiveness or species that reach the edge of their range: a) species of low competitiveness often utilise abiotically extreme environments or ruderal environments. Abiotically extreme environments constrain the breadth of niche variation because, on an evolutionary time scale, the living conditions in these environments are rather constant (Schmalhausen 1986, Vermeij 1987). Living conditions

in hot deserts or on cold mountain tops, for instance, changed less during the recent millions of years than living conditions in forests (Behrensmeyer et al. 1992). Some authors suggest that also ruderal environments constrain the breadth of niche variation (Valentine 1973, Vermeij 1987), and indeed many ruderal species respond to environmental variation primarily by an increase or decrease in population size, not by a niche shift (Valentine 1973, Vermeij 1987). b) Species that reach the edge of their range often have a low genetic recombination rate (Good 1974, Levin 1975) which may constrain their niche variation. Overall, constraints on the breadth of niche variation may explain why the geographic variation of niches was low even in species of low competitiveness and species that reach the edge of their range.

In summary, most species occupied similar niche positions in central England and eastern central Europe. Contrary to our expectation, the geographic niche variation did usually not increase in species susceptible to competitive displacement or ecophysiological stress. We suggest that although such species may be displaced easily along a niche axis, they can only be displaced over a short distance. This may explain why for most species the niche position was more than a regional phenomenon.

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