

The niche of higher plants: evidence for phylogenetic conservatism

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A species' ecological niche depends on the species' adaptations to its present habitat, but also on the legacy from its ancestors. Most authors argue that such a phylogenetic niche conservatism is of minor importance, although no quantitative analyses across a major taxon is available. Higher plants from central Europe offer a unique opportunity for such an exercise, as the niche positions along various environmental gradients are available for most species. We quantified niche conservatism by two approaches. First, we used a phylogenetic tree and quantified the degree of retention of niches across the tree. Depending on the gradient, the values ranged from 0.43 to 0.22. This was significantly greater than the null expectation. Second, we used a taxonomy and quantified the amount of variance among species that could be explained at higher taxonomic levels. The values ranged from 25 to 72%. Again, this was significantly higher than the null expectation. Thus, both approaches indicated a clear niche conservatism. The distribution of conservatism across taxonomic levels differed considerably among environmental gradients. The differences among environmental gradients could be correlated with the palaeoenvironmental conditions during the radiation of the phylogenetic lineages. Thus, niche conservatism among extant plant species may reflect the opportunities of their ancestors during their diversification.

Keywords: ecology; evolution; palaeoecology; phylogenetic inertia; quantitative convergence index; variance component analysis

1. INTRODUCTION

The variation in traits across species has two non-random components. First, traits are influenced by the convergent adaptations of species to their present habitats. Second, traits are a legacy from their ancestors. This second component is called phylogenetic conservatism, phylogenetic inertia or historical constraint. Such conservatism is important in morphological and physiological traits (Peat & Fitter 1994; Ackerly & Reich 1999) and, consequently, morphological traits can be used for retrieving phylogeny. Phylogenetic conservatism has also been found for biogeographical traits, i.e. for the species' geographical range (Good 1974). Is conservatism also important in the ecological niche of species? The ecological niche has been defined in several ways (review in Wiens 1989). Here we refer to the ecological niche in the sense of Grinnell (1917) as the natural environmental conditions under which a species can reproduce. Until now, all assessments of niche conservatism have been based on only a few examples. Most authors have referred to single examples from systematics, phylogeny, ecophysiology or quaternary ecology and concluded that niche conservatism is of minor importance (Stebbins 1975; Cronquist 1988; Walter & Breckle 1991; Bennett 1997). On the other hand, some authors have assumed a major conservatism of niches, either based on examples from pre-quaternary ecology (e.g. Boucot 1990) or recent distributions of species (Riedl 1966; Hodgson 1986). However, the amount and pattern of niche conservatism has never been quantified across a major taxon.

The higher plant species (pteridophytes, gymnosperms and angiosperms) from central Europe provide a unique opportunity for quantifying niche conservatism. Based on Ellenberg's (1979) 'indicator values' we can rank the niches of species along various environmental gradients. These ranks are estimates of the niche position of the plants (Wiens 1989). We estimated niche conservatism from the degree to which a plant species' niche position along a gradient is determined by its phylogeny (Harvey & Pagel 1991). We used two complementary approaches for describing a species' phylogeny: a phylogenetic tree and a taxonomy (Knox 1998). While the phylogenetic approach gives an optimal description of the phylogenetic genealogy, the taxonomic approach additionally takes into account the degree of phylogenetic modification. More modified lineages are assigned to higher taxonomic ranks (Knox 1998). In the phylogenetic approach, niche conservatism among extant species can be measured as the degree of retention or non-convergence of their niche positions across their phylogeny. In the taxonomic approach, niche conservatism can be measured as the percentage of variance among extant species that can be explained at higher taxonomic levels. In the case of no conservatism, all variance should occur at the species level.

2. METHODS

(a) Data

The indicator values of Ellenberg (1979; taken from Frank & Klotz 1990) are available for six environmental gradients: light, temperature, continentality, soil moisture, soil reaction and soil nitrogen. These indicator values divide each gradient into 9 to 12 sections of approximately equal size and species are assigned to these sections. With a sample size of more than 100 species the indicator values behave as continuous variables (Ter Braak

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Table 1. Analysis of niche conservatism along six environmental gradients by the quantitative convergence index.

(Large values indicate low niche conservatism. We report the means, minima and maxima from an analysis of 100 phylogenies, each representing a randomly dichotomized version of our original phylogeny which was not fully resolved. We also report the results of a randomization (1000 randomizations for each dichotomized phylogeny). Convergence indices were always significantly ($p < 0.001$) larger for randomized niches than for the real niches.)

gradient	quantitative convergence index					
	niches			randomized niches		
	mean	minimum	maximum	mean	minimum	maximum
light	0.71	0.70	0.72	0.88	0.87	0.88
temperature	0.73	0.72	0.74	0.85	0.85	0.85
continentality	0.78	0.76	0.79	0.84	0.84	0.84
soil moisture	0.57	0.56	0.58	0.85	0.85	0.85
soil reaction	0.73	0.72	0.74	0.87	0.87	0.88
soil nitrogen	0.59	0.58	0.60	0.81	0.81	0.81

& Barendregt 1986). The indicator values have been validated several times (e.g. Degórski 1984; Ertsen *et al.* 1998; Schaffers & Sýkora 2000). Out of the 2208 central European species listed in Frank & Klotz (1990) 76% have been ranked along at least one gradient. Only 50% of the species have been ranked along the soil-reaction gradient, but 74% have been ranked along the light gradient. Species with no rank along a gradient show such a wide and continuous distribution along this gradient that no position can be given (Crawley 1997). Thus, depending on the gradient, our analyses are based on different sets of species. However, our results appeared to be robust against such differences (see § 3).

We compiled a phylogeny from the 52 sources listed in electronic Appendix A (available on The Royal Society's Publications Web site) for the phylogenetic approach. Only 69% of the nodes were dichotomies. In order to generate a fully dichotomous phylogeny, we randomly dichotomized polytomies using TREEEDIT v. 1.0 (Rambaut & Charleston 2000). We generated 100 fully resolved phylogenies, which all lead to very similar results (Ackerly & Reich 1999) (table 1).

For the taxonomic approach we compiled a taxonomy from divisions down to genus from the following sources.

- (i) The divisions were taken from Schubert *et al.* (1990) and Moore *et al.* (1998). We pooled the division and subdivision levels and differentiated pteridophytes, angiosperms and gymnosperms. Lycopside and sphenopsids were pooled into a single 'division' with pteridophytes, as the two taxa contain only few species and no indicator values are available for several species.
- (ii) The families and higher taxa of angiosperms were taken from the Angiosperm Phylogeny Group (1998). Non-classified families (or orders) were arbitrarily classified into monotypic suprafamilies (or supraorders) (K. Bremer, personal communication). Because the diversification at the highest monocot level approximately took place during the diversification at the second highest dicot level (Wing 2001), we treated these two levels as equivalent. We also applied alternative classification systems (Dahlgren 1980; Cronquist 1988; Thorne 1992), which, however, basically generated the same results.
- (iii) The families and higher taxa of non-angiosperms are from Schubert *et al.* (1990). We set the class and ordinal level equivalent to the two highest levels in the angiosperm

classification. However, different treatments lead basically to the same results.

- (iv) The genera are from Schubert *et al.* (1990).

Contrary to recent ideas (DiMichele & Bateman 1996), for several reasons we treated gymnosperms, angiosperms and pteridophytes as taxonomically equivalent. First, the alternative classification, i.e. angiosperms and gymnosperms as subdivisions of the spermatophytes, would inflate the number of classification levels. Second, pooling angiosperms and gymnosperms would pool lineages that diversified during different periods. This would interfere with the palaeoecological interpretation of our results (tables 2 and 3). Nevertheless, we explored how our decision to include angiosperms, gymnosperms and pteridophytes as equivalent 'divisions' affected the results of the variance component analysis (VCA) (see § 2b). For this purpose we omitted all non-angiosperms and then reanalysed the data (omitting all angiosperms was impracticable). We found that the variance components correlated very closely with those calculated from the complete species pool. Depending on the environmental gradient, the correlation between both sets of variance components ranged between 0.81 and 1.0 (average 0.97).

(b) Analysis

In our phylogenetic approach we adopted the concept of the quantitative convergence index (QVI) (Ackerly & Donoghue 1998; Ackerly & Reich 1999; implemented in Schwikl 2000) (Ackerly and co-workers abbreviate convergence as V in order to avoid confusion with Maddison & Maddison's (1992) consistency index (CI)). The QVI ranges from zero (no convergence) to unity (maximal convergence). For instance, the QVI is 0.5 when the difference between the observed and the smallest possible amounts of evolutionary change is half the difference between the largest and the smallest possible amounts of change. The QVI is based on Farris' (1989) 'retention index', but Ackerly & Donoghue (1998) demonstrated the suitability of this index for analysis of phylogenetic conservatism. We calculated the QVI with all branch lengths set to unity, as the true length for most branches is unknown. However, when large numbers of species are used, branch lengths do not bias calculation of the QVI (Ackerly & Reich 1999). We compared the observed QVIs with those expected if niches of extant species were independent of their phylogeny (as in Ackerly & Reich 1999). These null expectations were calculated by a null model with 1000

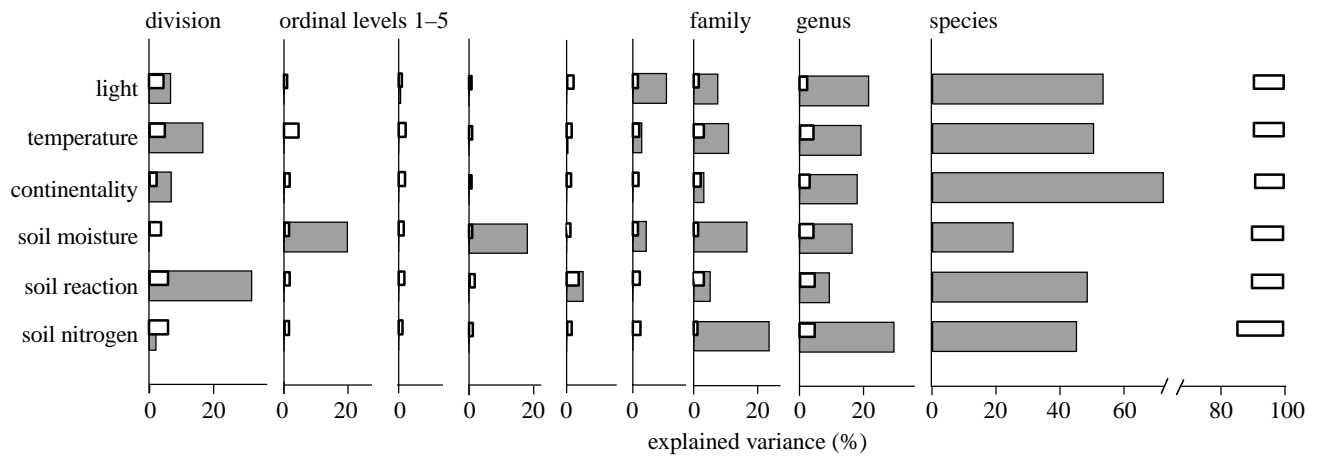


Figure 1. Percentage of the variance in species' niche positions that can be explained at different taxonomic levels. Niche positions along six environmental gradients are analysed ($n = 1108$ – 1633 species). Grey bars indicate the variance explained at the respective taxonomic level. White bars indicate the 99% range of a null model which describes how much variance would be explained when niche positions were randomly distributed across a taxonomy.

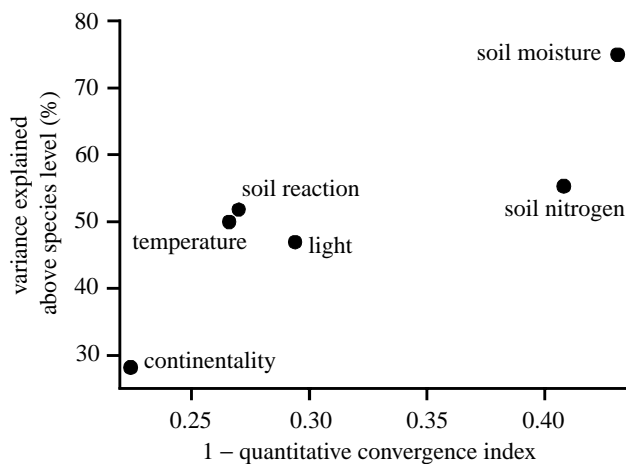


Figure 2. Relationship between the variance explained above the species level versus one minus the QVI for six environmental gradients. The latter was chosen in order to obtain an index of conservatism. The two measures of conservatism are significantly correlated with $r = 0.85$ (one-tailed, $p = 0.033$).

randomizations of the species across the tree. Note that it does not matter whether one randomizes the species or the tree (Ackerly & Donoghue 1998).

In our taxonomic approach we applied VCA (Harvey & Mace 1982) using a restricted maximum likelihood (SAS PROC VARCOMP) (SAS Institute 1998). VCA quantifies how much of the variance in a trait can be explained by the species' position across a taxonomy. We give variance components at different taxonomic levels as the percentage of the total variance. We assessed the reliability of our results in three ways. First, we generated null models in order to assess how much variance would be explained at the different taxonomic levels without any conservatism. The null model was based on 1000 randomizations of the species across the taxonomy. Second, we inspected the covariance between variance components. Large values, relative to the within-level covariance, would indicate non-independence between different taxonomic levels. Third, we conducted a cross-validation. We randomly divided the species pool into two halves, analysed each half separately and

correlated the two sets of variance components. We repeated this protocol 10 times.

QVI analysis and VCA represent two extremes from a pool of techniques for quantification of the 'phylogenetic signal' in the variation of a trait (Harvey & Pagel 1991). The advantage of the QVI and VCA is that they give directly comparable results and that other authors have already applied them to trait variation in higher plants.

3. RESULTS

(a) Degree of niche conservatism

The QVIs ranged from 0.57 (for soil moisture) up to 0.78 (for continentality) and were significantly less than the QVIs from the null model for all gradients (table 1). The amount of variance explained at taxonomic levels above species level ranged from 28% (for continentality) to 75% (for soil moisture). This was significantly more than expected from our null models (figure 1). Both results show that the niche position of an extant species was significantly determined by the species' phylogenetic position. Overall, the percentages of variance explained above species level were significantly correlated with the corresponding QVI values (figure 2). The higher the explained variance above species level the lower the degree of convergence, i.e. the QVI.

(b) Taxonomic pattern of niche conservatism

The variance explained at a given taxonomic level varied considerably among gradients (figure 1). For example, consider the soil-nitrogen and soil-reaction gradients. Some 55% of the variance was explained above species level for both gradients. However, most of this variance was explained at the family and genus level for the soil-nitrogen gradient, while that for the soil-reaction gradient was explained above family level (figure 1). Note that such a difference also affects the above QVI analysis. The QVI is influenced more by the many phylogenetic bifurcations at the family and genus levels than by the few bifurcations at higher levels. Indeed, the QVI analysis indicated a much lower niche convergence along the soil-nitrogen gradient than along the soil-reaction

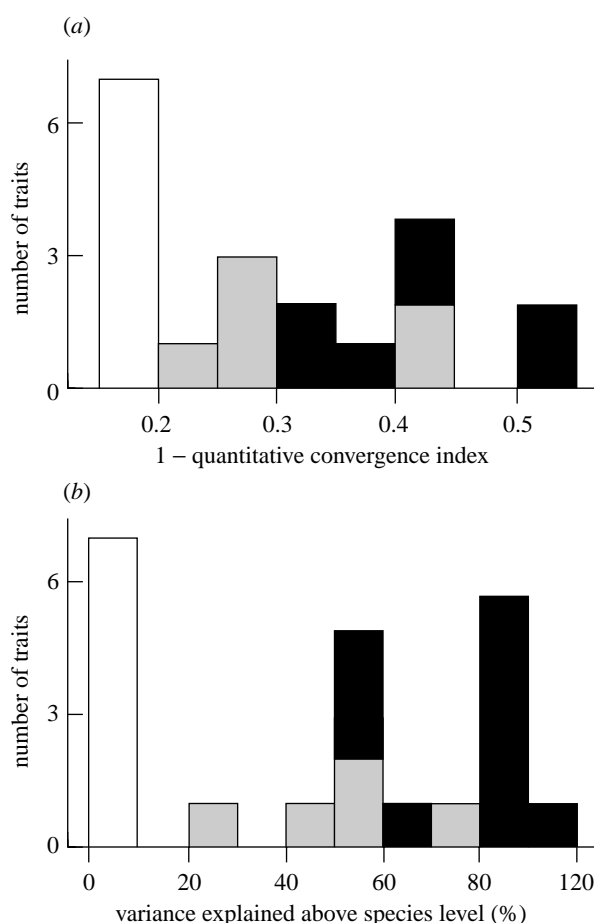


Figure 3. Conservatism of different traits measured by (a) one minus the QVI and (b) by the variance explained above species level. Grey bars: conservatism of niches along environmental gradients (present study). Black bars: conservatism of morphological and physiological traits (from (a) Ackerly & Reich (1999) and (b) Peat & Fitter (1994)). White bars: the result of our null models, which simulate the expected values of conservatism for traits without conservatism.

gradient (table 1). We found that the taxonomic patterns of niche conservatism were not biased. First, the interactions between taxonomic levels were only weak. The covariances between levels were small relative to the within-level covariances (less than one-third in 90% of cases). Second, the patterns did not depend on the species set considered. The 10 cross-validations always gave similar sets of variance components for the two halves of the species pool. The mean correlations between the two sets of variance components were 0.86 (s.d. = 0.063 and $n = 10$) for the light gradient, 0.87 (0.060) for the temperature gradient, 0.97 (0.034) for the continentality gradient, 0.82 (0.169) for the soil-moisture gradient, 0.87 (0.129) for the soil-reaction gradient and 0.97 (0.023) for the soil-nitrogen gradient.

4. DISCUSSION

Our analyses generated two important results. First, contrary to general belief, we found considerable phylogenetic conservatism in the niche positions of plants with the two techniques. However, the degree of conservatism was still smaller than in many morphological and physiological traits (figure 3). Second, the niche conservatism

differed strongly between environmental gradients, both in its general degree as well as its taxonomic pattern.

We see three possible, mutually non-exclusive reasons that explain the differences between gradients.

First, gradients differ in their spatial scales. Light, for example, varies even within a habitat, whereas continentality only differs between landscapes. Eldredge (1996) suggested that large-scale patterns should lead to phylogenetic conservatism. However, the niche conservatism along the two large-scale gradients temperature and continentality (Ellenberg 1979) was no larger than along the small-scale gradient light.

Second, complex adaptations are necessary in order to colonize extreme niche positions along some particular gradients. Such complex adaptations may require a deep reorganization of the genome (Price 1996) and, thus, only evolve in a few lineages. Subsequently, these lineages colonize environmental extremes and are able to diversify in a competition-free environment. This hypothesis predicts that niche conservatism is largest for the soil-reaction and soil-moisture gradients. Along these gradients complex physiological adaptations are always necessary in order to colonize not only the lower but also the higher extremes within central Europe (Ellenberg 1979; Crawley 1997). This prediction is clearly wrong for the soil-reaction gradient. Moreover, this hypothesis cannot explain why, for a given gradient, niche conservatism could be high at both the division and family levels, but low in-between. Overall, complex adaptations to extreme niche positions might be better understood as a result of niche conservatism and not as its cause (see below).

Third, different environmental gradients dominated the plants' environment during different geological epochs. During most geological epochs the terrestrial environments on the earth were differentiated mainly along certain 'dominant' gradients. The present strong differentiation along all six environmental gradients is exceptional in the history of the earth (Vakhrameev *et al.* 1978; Stanley 1999). Species specialized in extreme positions along a dominant gradient could colonize more areas and a larger total area than species specialized in extremes along other gradients. The increased total area may have triggered speciation (DiMichele & Aronson 1992; Rosenzweig 1995; Bennett 1997). For example, take an epoch with steep gradients in moisture. During such an epoch, species specialized in extreme moisture conditions were able to colonize large (dry or moist) areas, which increased their chance of speciation. This burst of speciation was the origin of new lineages with each lineage being adapted to certain moisture conditions. This original adaptation of the lineages may have become conserved by the 'incumbent advantage', i.e. the advantage of a taxon in its original environment over taxa immigrating from outside (Rosenzweig & McCord 1991). As a result, the niches of extant species would show phylogenetic conservatism.

Most extant plant lineages diversified during the Cretaceous epoch (Magallón *et al.* 1999; Wing 2001). This epoch was characterized by strong differentiation of the soil moisture gradient (table 3). The continentality gradient, on the other hand, was hardly differentiated until the second half of the Tertiary epoch (table 3). Overall, if niche conservatism is influenced by

Table 2. Literature review of the epochs of the evolution of the main taxonomic levels in plants.

(The available data did not allow separation between different ordinal levels or localization of time-gaps between epochs of evolution. Only angiosperms are considered at the family, genus and species level because they represent the majority of taxa in our analysis. Myr, million years.)

taxonomic level	main epoch(s) of evolution	references
division	Carboniferous (gymnosperms and modern pteridophytes), Jurassic and possibly Late Triassic (angiosperms)	Vakhrameev <i>et al.</i> (1978), Behrensmeyer <i>et al.</i> (1992), DiMichele & Aronson (1992), Sytsma & Baum (1996) and Krassilov (1997)
ordinal levels	Permian, Triassic (modern gymnosperm taxa and Pteridophyte taxa) and Cretaceous (angiosperm taxa)	Vakhrameev <i>et al.</i> (1978), Behrensmeyer <i>et al.</i> (1992), DiMichele & Aronson (1992), Sytsma & Baum (1996), Krassilov (1997), Magallón <i>et al.</i> (1999) and Wing (2001)
family	first half of Tertiary (60–35 Myr before present), then <i>ca.</i> 50% of the extant angiosperm families appeared in the fossil record	Benton (1993) and Wolfe (1997)
genus	second half of Tertiary (35–10 Myr before present)	Behrensmeyer <i>et al.</i> (1992) and Wolfe (1997)
species	since 10 Myr before present	Behrensmeyer <i>et al.</i> (1992)

Table 3. Literature review of the importance of environmental gradients during the evolution of different taxonomic levels (table 2).

(Double plus signs, a single plus sign and zero represent dominant, intermediate and minor importance, respectively. We only consider the European palaeoenvironments at the genus and species level as many of our genera and species originated in Europe. The bottom row gives the Spearman's rank correlation coefficient between the relative importance of gradients and the variance components for these gradients (figure 1). All correlations are positive, giving a significant overall pattern (one-tailed sign test, $p < 0.05$ and $n = 5$ levels).

gradient	taxonomic level				
	division	ordinal levels	family	genus	species
light	++ ^a	++ ^a	++ ^a	++ ^{a, h}	++ ^j
temperature	+ ^b	+ ^b	+ ^b	++ ⁱ	++ ^j
continentality	0 ^c	0 ^c	0 ^c	++ ⁱ	++ ^h
soil moisture	+ ^d	++ ^g	0 ^d	+/ ⁰ not ^g	+/ ⁰ not ^g
soil reaction	++ ^e	0 ^{not e nor j}	++ ^e	+/ ⁰ not ^{e nor j}	++ ^j
soil nitrogen	+ ^f	0 ^{not f nor h}	++ ^f	++ ^h	++ ^j
correlation	0.25	0.81	0.15	0.83	0.65

^aThere was a light/shade mosaic below the open canopy of forests. Moreover, there was darkness during polar winters which were often sufficiently warm to permit plant growth (Behrensmeyer *et al.* 1992; Mai 1995; Stanley 1999).

^bThe global differentiation of temperature was low, except during the Permian epoch (Mai 1995; Wolfe 1997; Stanley 1999).

^cContinental climates with strong seasonal temperature fluctuations were absent (Behrensmeyer *et al.* 1992; Mai 1995; Stanley 1999).

^dVegetation was largely restricted to wetlands (note that our measure of niche position does not differentiate between seasonal and permanent wetlands) with the exception of aridization during the origin of angiosperms (Ellenberg 1979; Behrensmeyer *et al.* 1992; DiMichele & Aronson 1992; Mai 1995; Stanley 1999).

^eSoil pH was strongly differentiated due to local peat formation or degradation or due to different kinds of plant litter (from pteridophytes, gymnosperms or angiosperms) (Behrensmeyer *et al.* 1992; Mai 1995).

^fAvailability of soil nitrogen was strongly differentiated for the reasons given in ^e; this differentiation of nitrogen availability became crucial when most plants were deciduous, i.e. starting with the diversification of families, because deciduousness increases a plant's yearly nitrogen demand (Behrensmeyer *et al.* 1992; Mai 1995).

^gClimate was warm and arid, so local differences of soil moisture were crucial for plants. The very wet places (riparian corridors) and very dry places (burnt areas) may have been particularly important for early angiosperm diversification (Vakhrameev *et al.* 1978; Behrensmeyer *et al.* 1992; DiMichele & Aronson 1992; Krassilov 1997; Wing & Boucher 1998).

^hThere was frost during winter. During spring, plants had to build up large amounts of leaf biomass, so local differences in light and nitrogen availability were crucial. Flush and shedding of leaves in turn created a mosaic of light and nitrogen availability (Tilman 1986; Behrensmeyer *et al.* 1992; Lang 1994).

ⁱExtensive areas with highly continental climates occurred, such as the Eurasian continent (Behrensmeyer *et al.* 1992; Lang 1994; Mai 1995; Wolfe 1997).

^jThere was an extreme cooling (glaciation) interrupted by warming. With increasing distance from glaciation in space and time the conditions changed from cold, light, bare bedrock to warm, dark forests with a nitrogen-rich, comparatively acid soil (Behrensmeyer *et al.* 1992; Lang 1994; Stanley 1999).

environmental conditions during earlier geological epochs, one would expect that the degree of niche conservatism will be highest along the soil-moisture gradient and lowest along the continentality gradient. This is exactly what we observed.

The environmental changes between geological epochs may also have affected the pattern of variance components across taxonomic levels, because most taxa at different taxonomic levels evolved during different geological epochs (table 2). We conducted a preliminary test of this hypothesis. In a first step, we assigned each of the major taxonomic levels to one or two geological epochs. The exact dating is not crucial as we used rather broad time-periods. In a second step we reviewed the literature in order to assess the ranking of importance of different environmental gradients during these epochs (table 3). In a third step, we correlated this ranking of gradients to the ranking of variance components. We found that, for each of the major taxonomic levels, our ranking of gradients shows a positive correlation to the corresponding variance components (table 3). Thus, the environmental changes between geological epochs may explain not only the different degrees of niche conservatism along different environmental gradients, but also the detailed pattern. We suggest that the niche conservatism among extant plant species may reflect the environmental opportunities of their ancestors during their diversification.

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