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THE RELATIONSHIP BETWEEN GLOBAL AND REGIONAL DISTRIBUTION DIMINISHES AMONG PHYLOGENETICALLY BASAL SPECIES

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Abstract.—Phylogenetic legacy and phylogenetic trends affect the ecology of species—except, apparently, for the width of their distribution. As a result, ''macroecological'' patterns of species distributions emerge constantly in phylogenetically very distinct species assemblages. The width of the global distribution of species, for instance, constantly correlates positively to the width of their regional distribution. However, such patterns primarily reflect the phylogenetically derived species that dominate most assemblages. Basal species, in contrast, might show different macroecological patterns. We tested the hypothesis that the correlation between global and regional distributions of species diminishes among the phylogenetically basal species. We considered central European higher plants and defined global distribution as the occupancy of global floristic zones, regional distribution as the grid occupancy in Eastern Germany, and phylogenetic position as the rank distance to tree base. We also took into account a number of confounding variables. We found that, across all lineages, the global/regional correlation diminished among basal species. We then reanalyzed 19 lineages separately and always found the same pattern. The pattern reflected both increases in global distributions and decreases in regional distributions among basal species. The results indicate that many basal species face a risk of global or at least regional extinction, but have escaped the downward spiral of mutually reinforcing extinction risks at multiple scales. We suggest that many basal species had much time to expand their global ranges but are presently displaced locally by more derived species. Overall, the study shows that macroecological patterns may not be static and universal, but may undergo macroevolutionary trends. Analyses of macroecological patterns across a phylogeny may thus provide insights into macroevolutionary processes.

Key words.—Extinction, macroecology, macroevolution, occupancy, phylogeny, range size, speciation.

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''Nothing in biology makes sense, except in the light of evolution''—Dobzhansky's (1973) classic words have recently been further corroborated by studies demonstrating that evolution also strongly determines the biogeographic and ecological distribution of species. Species in different phylogenetic lineages are differently distributed across the globe and across major environmental gradients (e.g., Prinzing et al. 2001; Pärtel 2002). Moreover, phylogenetically basal species are overrepresented in certain regions and habitats (Vermeij 1987; Pärtel 2002; ''basal'' species branch off deep in a phylogeny, which indicates low speciation rates and high extinction of their respective lineages). Such phylogenetic inertia and trends are the prerequisites for coevolution among species and lineages (Futuyma 1983; Farrell and Mitter 1993). However, phylogeny seems to have no effect on the widths of species distributions such as range size or ecological amplitude, which vary greatly even among closely related species (Gaston 1998; Webb and Gaston 2003). Indeed, certain patterns of species distributions emerge constantly in species assemblages of very different phylogenetic composition: the width of the regional distribution is positively correlated to the local abundance (Willis 1922; Brown 1984; Harte et al. 2001), and mostly also to the width, of the global distribution (Hengeveld 1990; Jablonski and Valentine 1990; Brown 1995; Gregory and Blackburn 1998). Species narrowly distributed within a region are thus also narrowly distributed across the globe. They are hence prone to extinction and deserve special conservation efforts (Gaston et al. 2000). This global/regional relationship runs counter to several evolutionary theories stating that global and regional distributions are determined by different processes or that species with wide distributions at multiple scales only exist in certain lineages or environments (Vermeij 1978; Hubbell 2001). Overall, the global/regional relationship has important implications. A whole new discipline, macroecology, is now devoted to the discovery of such ''universal'' patterns, which appear to be independent of the species' phylogeny, and to the discovery of the underlying universal processes (Brown 1995; Brown et al. 2003).

However, macroecological patterns, such as the relationship between global and regional distribution, primarily portray the phylogenetically derived members of a given taxon, which mostly outnumber the basal species; the ''living fossils'' (Stanley 1979). This effect cannot be eliminated by statistical procedures that take into account phylogeny (e.g., Felsenstein 1985), because derived species still contribute more datapoints than basal species. Hence, the question arises whether macroecological patterns are really independent of the phylogenetic composition of species assemblages, or whether they change from phylogenetically derived to increasingly basal species.

Phylogenetically basal species may be special because they have fewer close relatives than derived species (Vermeij

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TABLE 1. Characteristics of basal species and hypothesized mechanisms affecting regional distribution and global distribution, and the correlation between both.

Basal characteristics	Consequences	Regional distribution	Global distribution	Regional/global correlation
Few close relatives	little competition	many large ranges	—	declines
Low speciation rate	long period of range expansion of species	—	many large ranges	declines
	slow occupation of new niches	many small ranges	—	declines
	accumulation of natural enemies	many small ranges	—	declines
High extinction rate	filters out species with narrow distribution	many large ranges	many large ranges	declines

1987; Table 1). Given that closely related species are often ecologically similar (Webb et al. 2002), basal species may suffer little competition, resulting in a wide regional distribution (Valentine 1967). For example, among birds, basal species are marginally distributed ecologically or geographically, and may thus suffer little competition from more actively diversifying clades (Ricklefs 2003). The low number of close relatives reflects either low speciation or high extinction rates (Sims and McConway 2003; Magallon and Sanderson 2001; Ricklefs and Renner 1994), which may themselves affect the distribution of species, even though there is little consensus on the mechanisms involved. A low speciation rate might result in a high age of many species and a long period of global range expansion from the locality of origin (Vermeij 1978; Levin 2000). It may also result in a long period of accumulation of natural enemies and hence a decline of regional distribution (Ricklefs and Bermingham 2002). Finally, assuming that speciation is a major trigger of evolutionary change (Kemp 1999), a low speciation rate may result in a slow colonization of new environmental niches (Latham and Ricklefs 1993; Farrell and Mitter 1993; DiMichele 1994; Prinzing et al. 2001). Basal species might thus be locally displaced by more derived species and regional distribution may decline (DiMichele and Bateman 1996; Bennett 1997; Benton 1998). Finally, a high extinction rate may filter out species with narrow global or regional distributions (Jablonski 1994; Johnson 1998; Gaston 1998; Janssen and Dynesius 2002). Each of these mechanisms results in an expansion or contraction of either global or regional distribution of basal species. Hence, the correlation between the two might diminish.

The effect of phylogeny on the relationship between macroecological variables has not been adequately investigated thus far. Nee et al. (1991) showed that basal and derived bird species differ in their abundance/body-size relationships. But their dataset did not allow them to test whether this effect is a general phenomenon that occurs independently in multiple lineages. At a biogeographic scale, Johnson (1998) showed that among Australian marsupials basal species show a negative abundance/range-size relationship, contrary to derived species. However, this study considered a taxon with a very unusual macroecology (Murray and Dickman 2000), and did not address a number of uncertainties: it treated phylogenetic position as a binary variable; did not test whether the effect of phylogeny occurs independently in multiple lineages; and did not correct for confounding variables such as the species' distribution across vegetation types, their adaptation to anthropogenic impact, or their competitiveness (Good 1974; Brown 1984; Hodgson 1986; Walter 1990; DiMichele and Bateman 1996; see Materials and Methods). The information needed to resolve these uncertainties was simply not available for the marsupials of Australia, or for other taxa elsewhere. However, recently published databases have markedly improved the situation in some taxa, in particular in the central European flora (Benkert et al. 1998; Durka 2002).

In the present study we investigated the central European flora. We first tested the hypothesis that the positive relationship between the widths of global and regional distributions of species diminishes among phylogenetically basal species. We accounted for the above-mentioned confounding variables and tested whether the effect of phylogeny occurs independently in multiple lineages. Second, we tested the separate effects of phylogeny on global and on regional distributions of species. We then explored how these separate effects contribute to the observed impact of phylogeny on the relationship between global and regional distribution.

MATERIAL AND METHODS

Data

Our analyses examined all Spermatophyte species native to central Europe ($N = 1514$; Schubert et al. 1990). For each species, we defined the width of its global distribution in two ways. First, we counted the number of floristic zones occupied by the species' native range (arctic; boreal; northern temperate; southern temperate; submeridional [summergreen dry forests and steppes]; meridional [evergreen forests and steppes, deserts]; subtropical; tropical; and austral/antarctic; Schubert et al. 1990; Meusel and Jäger 1992). These zones are defined according to the homogeneity of their flora, their life-form composition, and their taxonomic structure. They thus represent biogeographic units (Good 1974; Walter 1990; Meusel and Jäger 1992). Similar measures of global distribution have been repeatedly used in macroecological studies (e.g., Reichard and Hamilton 1997; Cowley et al. 2001). They primarily characterize the global ecological distribution of species, not the geographical range size. For example, no distinction is made between species with paleotropical and pantropical distributions. Second, we very roughly assessed the global range size of species based on Kühn and Klotz (2002; based on Schubert et al. 1990). These authors assign species to 25 different sections of continents. We classified the area of these sections on a three-rank scale (a more precise classification of areas was not adequate because most species did not occupy the total area of the sections in which they occurred). The range size of a given

species was then estimated as the sum of the areas of the occupied sections of continents. This approximation of a species' range size was very crude, but it was still much finer than the occupancy of global floristic zones on a one-to-nine rank scale. Nevertheless, we found that the occupancy of global floristic zones was much more strongly correlated to the regional distribution of species than the global range size (Pearson's $r = 0.34$ vs. Pearson's $r = 0.13$). The probable reason is that the occupancy of floristic zones measures the width of the global distribution independent of the extensions of the floristic zones. The extensions of these zones have changed dramatically across time periods of a few thousand years (Lang 1994) and strongly depend on the current shape of continents (compare, for instance, boreal to Mediterranean zones). We therefore considered the occupancy of global floristic zones as our measure of the width of global distribution in all further analyses.

We defined the regional distribution of species as the grid occupancy in eastern Germany (Benkert et al. 1998; grid size $= 31$ km^2). The grid occupancy of a species reflects the extension and number of localities occupied (the ''ubiquity''; MacNally 1995) as well as the overall extension of the occupied region along various geographic and ecological gradients (for eastern Germany, Benkert et al. 1998). Eastern Germany as a region is in the core of central Europe. It includes almost all central European vegetation types (Ellenberg 1996) and the distribution of plant species has been investigated in more detail than in any other region of comparable size in central Europe and possibly worldwide (Benkert et al. 1998). Note that in our analyses we used the untransformed estimates of regional and global distributions. Some authors additionally use log-transformed estimates (Brown 1995). In our case, however, transformation of either or both range estimates weakened the global/regional relationship and led to highly skewed residuals in the further analysis.

Finally, we defined the phylogenetic position of species as the clade rank; that is, the number of phylogenetic nodes between the species and the root of the phylogeny (Norell 1995; Benton 1998). The underlying phylogeny encompassed the 1514 species of the central European flora and was compiled from 50 sources listed in Prinzing et al. (2001). Basically, we took the topological relationships among lower groups of vascular plants from Doyle (1998) and the familial level relationships from Pryer et al. (1995) for ferns; Chase et al. (1993) for gymnosperms; Graham and Olmstead (2000) for basal angiosperms; Savolainen et al. (2000) for dicots; Kubitzki (1998) for monocots excluding Potamogetonales; Haynes et al. (1998) for Potamogetonales; and Olmstead and Reeves (1995), Wolfe and dePamphilis (1998), Oxelman et al. (1999), and Olmstead et al. (2001) for Scrophulariales. The phylogeny did not include microspecies (subspecific segregates without clear taxonomic rank mostly formed by apomicts). Such microspecies would severely inflate the number of nodes in a few, taxonomically very well-investigated taxa (Wisskirchen and Haeupler 1998). The phylogeny was 70% resolved; that is, some of the phylogenetic radiations were represented as a single or a few polytomies rather than many dichotomies. This correctly reflected the fact that the different species in a radiation are of similar phylogenetic position even though they may be separated by many dichotomous phylogenetic nodes. The clade rank of species was strongly determined by their rank within the families to which they belonged, as well as the rank of these families within the overall Angiosperm family tree. In fact, the rank distance between the root of the family tree and a given family was usually (in >90% of the families) at least as large as the rank distance between the base of this family and its most derived species.

Using clade rank of species across the central European flora ($n = 1514$ species) as a parameter of their phylogenetic position suffers from an obvious problem (Norell 1995; Webb et al. 2002): some lineages are only poorly represented in central Europe but have strongly diversified in other parts of the world (e.g., Piperales and Cucurbitales). Across a purely central European phylogeny, species from such lineages will be ranked too low; too basal. Moreover, clade rank may be strongly biased toward species from only a few species-rich lineages (Sims and McConway 2003; Magallon and Sanderson 2001); hence clade rank becomes indiscernible from clade membership. Overall, clade rank may be a biased parameter of the phylogenetic position of species. We responded to this problem in three ways. First, we assessed the magnitude of the bias in clade rank. We checked to what extent clade rank deviates from branch lengths as revealed by molecular phylogenetic analyses. We considered four parts of the phylogeny for which branch lengths were readily available. We found that clade rank was always highly correlated to the total length of the branches connecting a taxon to the root of the respective part of the phylogeny (dicot families [Savolainen et al. 2000]: $n = 96$, $r = 0.626$, $P < 0.0001$; Poaceae species [Catalan et al. 1997]: $n = 20$, $r = 0.792$, $P < 0.0001$; Rosaceae species [Morgan et al. 1994]: $n = 15$, $r = 0.671$, $P = 0.006$; Apiaceae species [Downie et al. 2000]: $n = 25$, $r = 0.563$, $P = 0.0034$). Hence, the bias of clade rank was relatively small. It is important to note that we could not simply use branch lengths instead of clade rank as a parameter of phylogenetic position in the first place. Branch lengths are unavailable for the vast majority of species and are often incompatible across species from different lineages, as they have been quantified based on different molecular markers. Second, we controlled our analysis for the bias of clade rank in certain poorly represented lineages. We introduced a factor, lineage, into the multivariate analysis, and we analyzed different lineages separately (Norell 1995; details are given below). Third, we tested whether the bias of clade rank in lineages poorly represented in central Europe affects our results. In the cross-lineage analysis we tested whether the residual variation is higher in lineages poorly represented in central Europe. In the within-lineage analyses we tested whether within-lineage effects of clade rank depend on the representation of lineages in central Europe (details are given below).

Analysis

Effects of phylogeny on the relationship between global and regional distribution

In the first step of our analysis, we analyzed the effect of phylogenetic position on the relationship between global and

regional distribution by multiple regression analysis (Statsoft Inc. 1999, module GLR). The width of the regional distribution was the dependent variable; the width of the global distribution, the phylogenetic position, and the interaction between both were the independent variables. This interaction term was the crucial term in the analysis.

In a multivariate analysis we included the following additional independent variables that may be confounded with the distribution, or the phylogenetic position, of species.

Lineage.—Defined as the suprafamilial groups in the classification system of the Angiosperm Phylogeny Group (1998; Bremer et al. 2003; $n = 46$ taxa), a robust consensus of many phylogenetic analyses. These lineages explained a significant part of the errors in the above univariate analysis ($P = 0.004$).

Vegetation type.—The distribution of species across major vegetation types obviously affects their regional distribution. Forest species, for instance, are more widely distributed in central Europe than seashore species. Vegetation type may also affect the global distribution of species as many species from aquatic or alpine vegetation are widely distributed across the globe (Walter 1990). Finally, vegetation type may also affect the rate of speciation (Vermeij 1987), and thereby the phylogenetic position of the species. We classified the species into eight vegetation types according to Frank and Klotz (1990, based on Schubert et al. 1990), for example, seashore vegetation, deciduous forests, alpine boulders, and meadows. We did not differentiate below the vegetation type level into classes. This would have introduced more than 50 additional categories into the analysis (Schubert et al. 2001). In addition, many classes are defined based on the presence of individual plant species; hence, the distribution of classes is partly a function of the distribution of species and not the reverse.

Occurrence in anthropogenic vegetation.—Most species that can use anthropogenic vegetation are widely distributed throughout central Europe (Ellenberg 1996); moreover, many of them are phylogenetically derived (Hodgson 1986). We ranked the occurrence of species in anthropogenic vegetation according to the Hemerobie system of Frank and Klotz (1990, based on Kunick 1974 and Klotz 1984): (1) oligohemerobous species occur only in vegetation types with little anthropogenic influence (e.g., forests with no or selective logging); (2) mesohemerobous species also occur in vegetation types with rare and strong or with continuous and moderate anthropogenic influence (e.g., forests with clear-cuts, or meadows with yearly mowing); and (3) polyhemerobous species even exist in vegetation types with continuous and strong anthropogenic influence (e.g. agricultural fields). These Hemerobie rankings of Frank and Klotz have been validated repeatedly (e.g. Dierschke 1994; Grabherr et al. 1995; Prinzing et al. 2002).

Potential competitiveness of species.—Most species of high potential competitiveness are widely distributed throughout central Europe (Ellenberg 1996), and many of them seem to be phylogenetically peripheral (Vermeij 1987). We ranked the potential competitiveness of species from 0 (stress tolerant strategy or ruderal strategy, without elements of competitive strategy) to 3 (pure competitive strategy) according to Frank and Klotz (1990). These authors largely applied the criteria of Grime et al. (1988), such as stature, longevity, and phenology of flowering or seed dormancy. The predictive value of the Frank and Klotz assignments has been repeatedly validated (e.g., Pyšek et al. 1995; Prinzing et al. 2002). Moreover, there is a correlation between assignments by Frank and Klotz (1990) and by Grime et al. (1988), despite the different scaling of both assignments: Pearson's $r = 0.62$ ($P < 0.0001$, $n = 418$). Competitiveness does not equal vegetation type as highly stress (i.e., shade) tolerant species can coexist with highly competitive species (Grime et al. 1988).

Latitudinal position of the global range.—Species with a southern global distribution may be narrowly distributed throughout central Europe because since the retreat of the glaciers these species may not have managed to re-establish in all suitable parts of central Europe (Lang 1994). Moreover, many species of such southern distribution are phylogenetically basal (Good 1974; Schuster 1976). We thus quantified the latitudinal position of a species' global distribution by calculating the mean across the floristic zones occupied (from 1 = boreal to 9 = austral).

Distance of a species' latitudinal position from Central Europe.—Species with a latitudinal position that is far from central Europe are mostly restricted to very special localities within central Europe (Hengeveld 1990; Ellenberg 1996). Species with a boreal range position, for instance, are likely to occupy only the coldest localities within central Europe. This results in a narrow regional distribution in central Europe. We thus quantified the distance between a species' range position and central Europe as the absolute difference between the species' latitudinal range position (see above) and position 3, the latitudinal position of central Europe (Meusel and Jäger 1992).

Lineage and vegetation type were treated as factors. The other variables were treated as continuous variables, even though some of them were on a rank scale. Treating ranks as continuous variables introduces some error into the statistical analysis. However, given our very large sample size, the high levels of significance and the consistency of our results across different lineages, it is unlikely that this error affected our conclusions (Sokal and Rohlf 1981).

Several further variables may also be related to the width of distribution of plant species. First, temperature requirements may be important. Highly frost-sensitive species, for instance, cannot persist in most places in central Europe. However, temperature requirements are not known for several hundred central European species (Ellenberg 1996), particularly for those with a wide regional distribution. Hence, inclusion of temperature requirements would have further reduced the degrees of freedom, which was particularly problematic in the within-lineage analyses (see below). It would also have biased the species set toward species with narrow regional distributions. Thus, we omitted temperature requirements from our analysis. We did, however, test whether the residuals of our analysis correlated to the known temperature requirements, and found that this was not the case ($R^2 = 0.01$). Hence, our analysis did not suffer from a temperature bias. Second, it has been asserted that polyploidy increases the width of distribution (Löve and Löve 1949). However, this assertion has been refuted repeatedly (e.g., Stebbins 1985; Stebbins and Dawe 1987), and paleoploidy, a very common form of polyploidy, has not been interpreted at all

(Durka 2002). Moreover, in many species the ploidy level is not constant but varies strongly among populations (Durka 2002). For most species, neither the range nor the commonness of ploidy levels is known within central Europe or worldwide (Grime et al. 1988; Durka 2002). Therefore, inclusion of ploidy levels was neither adequate nor practicable. Third, it has been suggested that the capability to disperse by wind or with the help of vertebrates might increase the width of distribution of plant species (Thompson et al. 1999; Richardson et al. 2000). We therefore included these two variables (defined on a rank scale as in Prinzing et al. 2002) in a preliminary analysis. However, neither of them had a direct effect on the distribution of species ($P > 0.84$; see also Thompson et al. 1999; Prinzing et al. 2002), nor does either of them modify the effect of phylogenetic position on the correlation between global and regional distribution ($\Delta P < 0.00001$). We therefore omitted both variables from further analyses to improve the ratio between the number of independent variables and the sample size, which was particularly important when we restricted the analysis to individual lineages (see below).

We first analyzed the complete species pool using a generalized linear model ($n = 1340$ species for which all traits were known). We tested whether the bias of phylogenetic position (= clade rank) in lineages poorly represented in central Europe affects our results. For this purpose we recorded the partial residuals for the phylogenetic position × global distribution interaction term for each species and averaged them across suprafamilial lineages (Angiosperm Phylogeny Group 1998; Bremer et al. 2003; $n = 32$). We then correlated these average partial residuals against the representation of the lineages within central Europe. Representation was quantified as the percentage of the global species richness represented in our database, with information on the global species richness taken from Stevens (2001) and Earle (2003). The representation of the different lineages ranged from less than 0.05% (for Piperales and Cucurbitales) to more than 3% (for Dipsacales and Pinales).

Next, we analyzed several independent lineages. Only if phylogenetic position shows a consistent effect within the majority of lineages can the effect be considered statistically significant. We considered the Pteridophytes as well as the lineages classified at the suprafamilial rank in the Angiosperm Phylogeny Group's system (Angiosperm Phylogeny Group 1998; Bremer et al. 2003). We excluded all lineages with less than 15 species because the sample size would obviously be too small to correctly estimate the sign of the effect of global distribution × phylogenetic position. Even among the remaining 19 larger lineages, the analyses showed a strong multicollinearity among independent variables with tolerance values for the global distribution × phylogenetic position interaction term below 0.01 in 16 lineages. That is, more than 99% of the variance in the interaction term was redundant with other variables. We thus decided to apply ridge regression analysis (Neter et al. 1985; Statsoft Inc. 1999). Ridge regression analysis strongly reduces multicollinearity by adding a small constant λ to the diagonal of the correlation matrix, which is then restandardized. This reduces the diagonal values in the inverted matrix and hence the variance of the estimators of the regression coefficients, which are calculated from it. The estimates of regression coefficients are thus much more stable, albeit slightly biased (Neter et al. 1985; Statsoft Inc. 1999). We used a λ of 0.05 and found that tolerances increased to at least 0.09. The choice of λ, however, did not affect our results. Lower λ values of 0.01 to 0.03 yielded regression coefficients with the same sign. And so did a drastically high λ value of 0.5. With such a high λ, multicollinearity was minimal (tolerances >0.69), but the R^2 values strongly declined due to the bias arising from the inclusion of λ itself. Because ridge regression cannot handle categorical variables, we excluded both vegetation type and lineage from the analyses of separate lineages. This was a harmless modification. The original analysis across the complete species set had shown that inclusion of neither of the categorical variables affected the *P*-value of the global distribution × phylogenetic position interaction term ($\Delta P = 0.000007$).

We summarized the results of these within-lineage analyses adopting the concept of ''effect sizes,'' which is widely used in meta-analyses (Rosenthal 1984). Effect sizes permit a comparison of effects across different analyses without bias due to differences in the underlying sample sizes (Rosenthal 1984). First, we quantified the size of the effect of phylogenetic position × global distribution on the regional distribution for each lineage. We used the Fisher *Z*-transformed effect-size parameter *r* (Rosenthal 1984), which we calculated from the *t*-value of the corresponding regression parameter (Rosenthal 1984). Then, we tested the one-tailed hypothesis that, across all lineages, the effect of phylogenetic position × global distribution is positive; that is, that in most lineages the positive relationship between the width of global distribution and the width of the regional distribution is strong among derived species but diminishes among basal species. We used a Wilcoxon-rank test as well as a *t*-test against an expectation of zero. The advantage of the Wilcoxon rank test was that it does not depend on the normality assumption (Sokal and Rohlf 1981). The advantage of the *t*-test was that the datapoints could be weighted by the sizes of the underlying lineages (Gurevitch and Hedges 1991), even though weighting hardly modified the results ($\Delta P < 0.0001$).

We again tested whether the bias of phylogenetic position (= clade rank) in lineages poorly represented in central Europe affected the results. For this purpose we correlated the effect sizes of phylogenetic position × global distribution in different lineages against their representation within central Europe (quantified as above) using the parametric Pearson and the nonparametric Spearman coefficient.

It is important to note that in the within-lineage analyses our goal was to test whether the effect of phylogeny is consistent across lineages. Our goal was not to correct for phylogeny. Procedures to correct for phylogeny would include sister-taxon comparisons (Felsenstein 1985), which compare only clades of equal phylogenetic position, or numerous techniques that remove a phylogenetic component (e.g., Harvey and Pagel 1991). Both approaches would of course delete the component of interest from our analysis. Only Pagel (1997) has described a method that permits testing the effect of phylogenetic position directly, that is, without separately analyzing different lineages. However, his method was not applicable because it does not permit inclusion of multiple in-

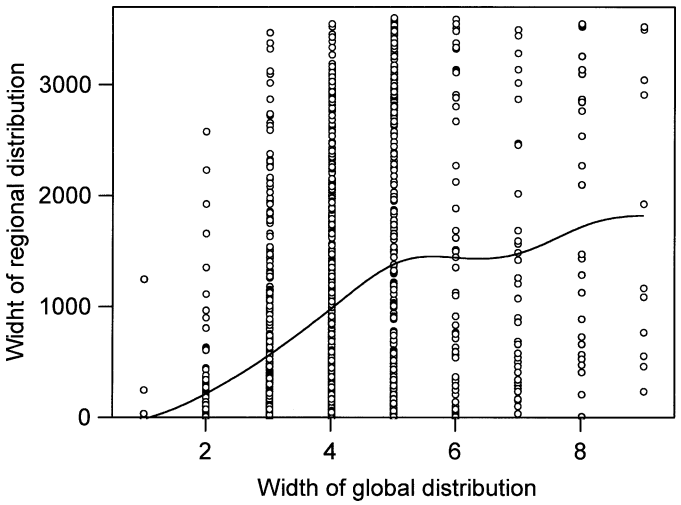

FIG. 1. Relationship between the widths of distributions of central European plant species at global and regional scales. Global distribution is measured as occupancy of global floristic zones, regional distribution as the grid occupancy across eastern Germany. The smoothing (by distance weighted least squares) reflects the clustering of points, including those hidden by overlying points. A linear model yields: $R^2 = 0.12$ and $P < 0.00001$.

dependent variables. We also decided not to apply a phylogenetic correction for the various confounding variables (e.g., competitiveness). Any such phylogenetic correction would have been based on the phylogenetic position of species, and hence the confounding variables would have become numerically nonindependent of the phylogenetic position.

Separate effects of phylogeny on global and regional distribution

In the second stage of our analysis, we tested the separate effects of phylogeny on the global and on the regional distributions of species. As before, we used ridge regression analysis, and analyzed the complete species set as well as individual lineages. For each lineage, we described the effect size of phylogeny on species distribution, and summarized the results across lineages by meta-analyses (see above). Finally, we used partial correlation analyses (Statsoft Inc. 1999) to explore how the within-lineage effects of phylogeny on the global and on the regional distribution of species contribute to the effect of phylogeny on the relationship between global and regional distribution.

RESULTS

Effects of Phylogeny on the Relationship between Global and Regional Distribution

As expected, the flora of central Europe showed a significantly positive relationship between the width of their global and regional distributions ($R^2 = 0.12$; $P < 0.00001$; Fig. 1).

The relationship between the widths of the global distribution and of the regional distribution of species changed during phylogeny: an interaction phylogenetic position × global distribution had a highly significant positive effect on the regional distribution of species (Table 2A); that is, the positive relationship between global and regional distribution of species was strongest among phylogenetically derived species and diminished among phylogenetically basal species. Figure 2 shows that this effect involved both a decline of the slope of the global/regional relationship, and an increase in

TABLE 2. (A) Multiple regression analysis relating the width of the regional distribution of species to the width of their global distribution, their phylogenetic position (basal to derived), and the interactions between phylogenetic position and global distribution. Potentially confounding variables have additionally been taken into account in (B). Estimates of regression parameters, beta values (standardized regression parameters), and the associated *t*-, *F*- and *P*-values are given. For the two categorical variables, lineage and vegetation type, the overall *F*- and *P*-values are given; parameter estimates of the individual categories are not presented. *P*-values are one-tailed for phylogenetic position × width of global distribution and two-tailed for the other variables. Sample size is 1514 species for (A) and 1340 species for (B).

	Effect on the width of the regional distribution of species				
	Parameter	Beta	*F*	*t*	*P*
(A)					
Constant	478.26				
Width of global distribution	−86.67	−0.11	1.56	−1.25	0.2124
Phylogenetic position	−45.79	−0.26	10.18	−3.19	0.0014
Phylogenetic position × width of global distribution	19.56	0.60	35.73	5.98	<0.0001
			$R^2 = 0.18$		
(B)					
Constant	−15.71		<0.01	−0.04	0.9715
Lineage			1.00		0.4662
Vegetation type			8.89		<0.0001
Occurrence in anthropogenic vegetation	659.77	0.34	171.64	13.10	<0.0001
Competitiveness	516.67	0.15	37.12	6.09	<0.0001
Latitudinal position of range	−222.61	−0.13	15.84	−3.98	0.0001
Distance of range position from central Europe	−201.83	−0.08	3.14	−1.77	0.0765
Width of global distribution	18.17	0.02	0.04	0.21	0.8380
Phylogenetic position	−62.28	0.30	11.95	−3.46	0.0006
Phylogenetic position × width of global distribution	16.92	0.50	19.14	4.38	<0.0001
			$R^2 = 0.40$		

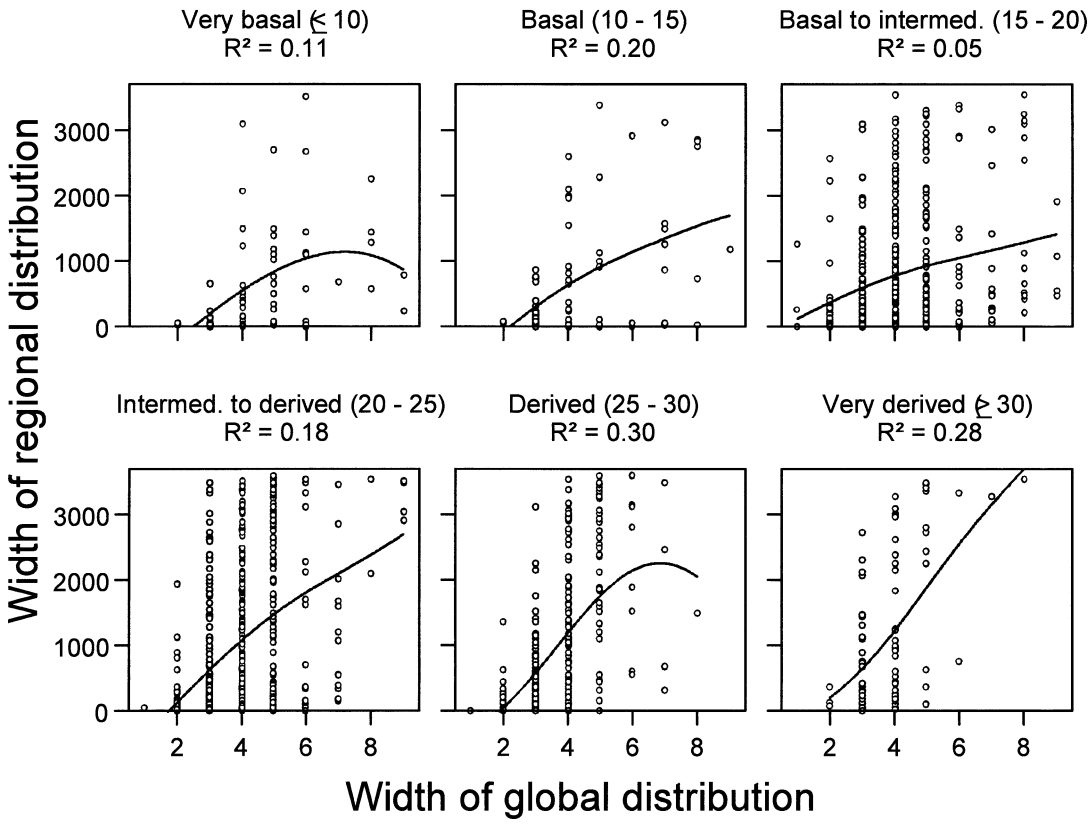

FIG. 2. Relationship between the width of the global distribution (occupancy of global floristic zones; x-axes) and the width of the regional distribution (grid occupancy in eastern Germany; y-axes) among species of different phylogenetic position. Phylogenetic positions (basal to derived) are given in brackets as the clade ranks of species. Smoothing is by distance-weighted least squares.

the scatter around the general relationship. In particular, the combination of wide global with wide regional distribution disappeared among basal species. This phylogenetic trend of the global/regional relationship was much stronger than the general relationship per se (Table 2). When we included several potentially confounding variables into the analysis, the effect of phylogenetic position × global distribution on the regional distribution of species remained highly significantly positive (Table 2B).

The observed effect of phylogenetic position on the global/regional relationship was not confounded by cases of very wide global distributions as we found them in several basal species (Fig. 2). A restriction of the analysis to species with a distribution of only five or fewer floristic zones yielded the same result: the correlation between regional and global distribution diminished among basal species (df = 909; $t = -4.09$; $P = 0.000046$; compared to df = 1288, $t = 4.38$; $P = 0.000013$ in the original analysis). The effect of phylogenetic position was also not confounded by the bias in phylogenetic position, particularly in species from lineages that are poorly represented in central Europe. Partial residuals of the phylogenetic position × global distribution interaction, averaged across lineages, did not correlate to the representation of the lineages in central Europe ($n = 32$ suprafamilial lineages; Pearson's $r = -0.159$, $P = 0.5277$, Spearman's $r = 0.052$; $P = 0.779$).

Multiple regression analyses across separate independent lineages always yielded a positive effect of phylogenetic position × global distribution on the regional distribution of species (effect sizes: mean = 0.10; 95% conf. interval: 0.07–0.13; Table 3). The meta-analysis showed that, across all lineages, the effect of phylogenetic position × global distribution on regional distribution was highly significantly positive (Table 3). In other words, the correlation between global and regional distribution of species diminished among phylogenetically basal species independently within all lineages. Interestingly, the within-lineage relationship was about as strong as the above across-lineage relationship (effect size = 0.12).

Again, the results were not confounded by the bias of phylogenetic position in lineages poorly represented in central Europe. We correlated the within-lineage effect size of phylogenetic position × global distribution to the representation of the lineages in central Europe. We found that representation was not generally correlated to the effect size ($n = 19$; Pearson's $r = 0.34$; $P = 0.092$, Spearman's $r = 0.022$; $P = 0.929$). If anything, there was a particularly large effect size in two particularly well represented lineages for which phylogenetic position was thus only very slightly biased (Pinales and Dipsacales). This increased the parametric Pearson's r coefficient.

Separate Effects of Phylogeny on Global and Regional Distribution

We then tested the separate effects of phylogenetic position on the regional and on the global distributions of species.

TABLE 3. Separate analyses of phylogenetic lineages. For each lineage, the width of the regional distribution of species was related to the width of the global distribution, the phylogenetic position (basal to derived), and the interaction between both. Moreover, a set of control variables was included (see Materials and Methods). For each lineage, the taxa involved, degrees of freedom (df), *t*-value of the interaction term phylogenetic position × global distribution, and effect size Z_r of the interaction are given. The last row gives a meta-analysis of the effect sizes. As predicted, the interaction phylogenetic position × global distribution is consistently positive; that is, the positive correlation between the width of distribution at global and regional scales is strongest among derived species and diminishes among basal species.

		Effect of phylogenetic position × global distribution on regional distribution of species	
Lineage	df	*t*	Z_r
Pinales	17	0.776	0.187
Liliales	25	0.199	0.040
Asparagales	45	0.784	0.117
Poales	247	2.459	0.156
Ranunculales	43	0.392	0.060
Saxifragales	10	0.084	0.027
Caryophyllales	110	0.900	0.086
Rosales	64	0.047	0.006
Fabales	62	0.883	0.113
Malpighiales	47	0.822	0.120
Myrtales	13	0.340	0.094
Brassicales	50	0.413	0.058
Ericales	25	0.116	0.023
Gentianales	25	1.037	0.206
Solanales	22	0.232	0.050
Lamiales	85	1.249	0.135
Apiales	47	0.621	0.090
Dipsacales	17	1.067	0.256
Asterales	163	0.743	0.058
		Overall effect (n = 19)	
		Weighted *t*-test: t = 8,170; $P < 0.0001$	
		Wilcoxon rank test: Z = 3.823; P = 0.0001	

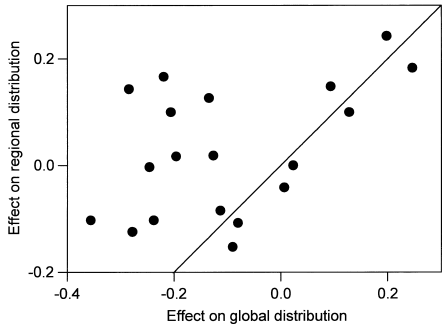

FIG. 3. Effect of the phylogenetic position (basal to derived) on the global distribution and on the regional distribution of species in 19 lineages. Effects are given as *Z*-transformed effects sizes (see Materials and Methods). The line indicates x = y; that is, identical phylogenetic trends of global and regional distribution. Note that positive trends in global distribution always coincide with equivalent trends in regional distribution.

We found a very weak albeit still significant decrease of the global distribution from basal to derived species (R^2 = 0.034; $P < 0.01$). The regional distribution, in contrast, increased very slightly (R^2 = 0.012; $P < 0.01$). When we explored the 19 lineages separately we again found a decline of the global distribution from basal to derived species in 13 lineages (sign test, P = 0.17), a pattern that was significant in a meta-analysis across all lineages (weighted *t*-test: $t = -3.32$, P = 0.0038; Wilcoxon rank test: Z = 2.17, P = 0.0298). For the regional distribution we found a very low consistency of phylogenetic trends across lineages (sign test, P = 0.646) and a clearly nonsignificant overall pattern across lineages (weighted *t*-test: t = 1.49, P = 0.1523; Wilcoxon rank test: P = 0.3341). Note, however, that the relationship between phylogenetic position and regional distribution becomes stronger once the interaction between phylogenetic position and global distribution is also taken into account (see above multiple regression analysis; Table 2).

The within-lineage effects of phylogeny on global distributions and on regional distributions of species showed an interesting interaction. In the few lineages in which the global distribution increased among derived species (Pinales, Liliales, Ranunculales, Fabales, Ericales, Asterales) we also found an increase of regional distribution among derived species. The two trends were strongly correlated (n = 6; Pearson's r = 0.90; P = 0.016). In contrast, in the numerous lineages in which the global distribution increased among basal species, we found no correlated trend in the species' regional distribution at all (n = 13; Pearson's $r = -0.012$; P = 0.704; Fig. 3). These results were confirmed in randomization tests in which global and regional values were randomized with respect to each other (P = 0.032 vs. P = 0.689; 1000 randomizations).

Finally, we explored how the within-lineage effects of phylogeny on global distribution and on regional distribution contributed to the diminishing global/regional relationship among basal species. We found that increases of global distributions among basal species, but also decreases of regional distributions, had a significant effect (n = 19; partial $r = -0.48$ and 0.60, $t = -2.19$ and 3.00, P = 0.0441 and 0.0086, respectively). Together, these two effects explained 37% of the variation. Hence, both regional and global factors contributed independently to the observed decline of the global/regional relationship among basal species. This explains why univariate relationships between phylogeny and either global or regional distribution are generally weak, whereas the combined relationship to both in multiple regression analysis is strong (Table 2).

DISCUSSION

The results confirm the hypothesis that the positive relationship between the width of the global distribution and the width of the regional distribution diminishes among phylogenetically basal species. This phylogenetic trend occurs consistently across all lineages tested. We also found a rather consistent, albeit weak, increase of global distributions among basal species (see also Taylor and Gotelli 1994; Gaston and Blackburn 1997). Finally, we found that the phylogenetic trend of the global/regional relationship depends on the phylogenetic trends of both the global and regional distributions. Note that the prerequisite to all these analyses was a definition of the width of global distribution that was unaffected by quaternary shifts in the extension of vegetation zones, or by the shape of the continents; namely, the occu-

pancy of global floristic zones. The occupancy of sections of continents, indicating the absolute global range size, was hardly correlated to the regional distribution of species (see Materials and Methods).

In our analyses we restricted ourselves to the central European flora. This is clearly a limited basis, and such geographic sampling may introduce two major types of errors. First, geographic sampling biases the assessment of phylogenetic position of species; that is, their clade rank across the central European flora. Species from lineages poorly represented in central Europe will be ranked as too basal because many of their related clades are absent from central Europe. However, by comparison to molecular data we had found that the magnitude of this bias is only low (see Materials and Methods). Moreover, we had accounted for this bias in our analyses by testing for consistency across lineages. Finally, we had found that the bias in phylogenetic position did not affect the results of our analyses. The results did not differ among poorly and strongly represented lineages. Second, the geographic sampling may bias the assessment of the regional distribution of species. Species in lineages that have diversified outside central Europe might have their distributions centered in other parts of the world or within vegetation types that are exceptional for central Europe. This would result in an atypical, constrained regional distribution within central Europe. However, we had accounted for this possible bias in regional distribution by including global range-position and vegetation type in our analyses (Materials and Methods). This did not change the results. Moreover, we had assured that the results of our analyses do not depend on the lineage investigated. Hence, our restriction to central European species did not affect the results of our analysis. We thus believe that the patterns observed are not an idiosyncratic result of the region we analyzed.

Geographic sampling is not only methodologically inevitable and, as we found, harmless to the results of our analysis, but may even be adequate. Most of the mechanisms by which phylogeny may influence the global/regional relationship (see introduction) are at least as relevant within a geographic subset of a taxon as across the whole taxon. Competition from closely related species, for instance, is clearly a local or regional process, and only the number of close relatives that co-occur within the same geographic region is relevant. Also, the accumulation of natural enemies, the use of present-day ecological niches, and the extinction of species with a narrow regional distribution are regional processes; thus, the phylogenetic position at a regional scale may be at least as relevant as the phylogenetic position at a global scale.

How can we explain the observed decline of the global/regional relationship among basal species? We can largely rule out the possibility that this pattern is the result of a pseudocorrelation with confounding variables, such as taxonomic position, vegetation type, absolute and relative position of the global distribution of species, competitiveness of species, or their adaptation to anthropogenic impacts. We took all these variables into account. In doing so, we also accounted for the possibility that basal species are marginally distributed across ecological or geographic gradients (Vermeij 1987; Ricklefs 2003).

Many other explanations, however, cannot be ruled out so clearly. These explanations are related to the fact that basal species have fewer close relatives than derived species, and that their lineages have undergone either little speciation or much extinction (see introduction). The small number of close relatives is evident from an analysis of species numbers and species-to-genus ratios across families. Both parameters are smaller in families composed of basal species than in families composed of derived species ($n = 144$; $r = 0.34$ and 0.19; $P < 0.001$ and 0.021, respectively). The small number of close relatives may translate into a small number of competitors (Webb et al. 2002) and finally result in a wide regional distribution (Valentine 1967). Also, the low speciation rates or high extinction rates might have consequences, although the exact nature of these consequences is subject to much debate. Low speciation rates, for instance, correspond (almost by definition) to a larger number of old species (Vermeij 1978). If we assume that speciation is mostly local (for plants see Levin 2000) this means that these old species within the basal lineages could expand their global distribution over long periods of time. The resulting large global distributions may then have reduced the speciation rates even further (Jablonski et al 2003). Moreover, old species have passed through many global climatic oscillations that may also have increased their global distribution (Jansson and Dynesius 2002). However, low speciation rates may also foster the accumulation of natural enemies (Ricklefs and Bermingham 2002), resulting in a decline of the regional distribution. Low speciation rates might finally reflect high gene flow within species and low diversifying selection. Both may slow down the pace of evolutionary change (Cockburn 1991; Kemp 1999). Basal species may thus stick to their original, ancient niches (Farrell and Mitter 1993) and only slowly occupy new niches, for instance those resulting from the increasingly cool climate since the mid-Tertiary (Behrensmeyer et al. 1992). Derived species, in contrast, may be much more efficient in occupying new niches and may thereby gradually displace the basal species across a given region. (From a punctualistic point of view this process would be outright inevitable; Stanley 1979.) At the same time the global distribution may remain constant because species persist for a long time in their global outpost. The high extinction rate, on the other hand, may filter out species with narrow global or regional distributions (Jablonski 1994).

These possible explanations can to some degree be assessed based on our results. First, we found that in most lineages basal species showed a distinctly wider global distribution than derived species. This is partial confirmation of the notion of global range expansion in basal species. The global expansion did not affect the regional range of species, and hence the global/regional relationship diminished. Second, we found no consistent changes of regional distributions among basal species in different lineages. This seems to contradict the notions of reduced competition pressure, accumulation of natural enemies, or slow occupation of new niches in basal species. Nevertheless, these processes may still operate within some of the lineages. In fact, our final analysis has shown that the global/regional relationship diminishes not only with increasing global distribution of basal species, but also with decreasing regional distribution. Hence, such decreases not only occur within some lineages, for instance

due to accumulation of natural enemies or slow occupation of new niches, but also contribute to the diminishing global/regional relationship among basal species.

In six lineages, we found that among basal species the global distribution declined. None of the above-mentioned explanations predict such a global decline. Two of them, however, predict declines of regional distributions that may take place across the whole globe, and may thus amount to a decline of the global distribution: basal species may accumulate natural enemies, and they may slowly occupy new niches. Hence, these six lineages may be in a stage in which global distribution is largely determined by regional processes. Indeed, global declines of basal species within these lineages were always accompanied by regional declines. We find it remarkable that even in these lineages the correlation between global and regional distribution diminished among basal species.

The effect of phylogeny on the global/regional relationship might, finally, be triggered by the narrow global distributions of many derived species and the resulting range dynamics. Due to their narrow global distributions, many derived species might be more receptive to global climatic oscillations than basal species (Bennett 1997; Jansson and Dynesius 2002). Imagine, for instance, a derived species that has originated and established a narrow global distribution at the northern edge of a climatically suitable part of the globe. This species will strongly profit from a northward shift of global climatic zones and will densely occupy many of the now available regions, resulting in an increase of both regional and global distributions. In contrast, a derived species that established its narrow range at the southern edge of the originally suitable part of the globe would face the opposite fate: regional and global distributions would decline. As a result, global and regional distributions would be strongly correlated across derived species, as we have observed. However, at the same time, the variation of global and of regional distributions would be particularly high among derived species. This was not the case ($n = 19$ lineages, $t_{19} = 1.05$, and -0.18; $P = 0.155$ and 0.5, respectively; results not shown). Hence, range dynamics resulting from narrow global distributions of derived species may contribute little to the observed effect of phylogeny on the global/regional relationship.

Our results have a number of implications for conservation biology. The fact that most basal species are narrowly distributed either globally or, mostly, regionally implies that they may face a risk of extinction due to factors operating at either of these scales. Basal species thus deserve special attention in conservation planning. Moreover, assessment of the risk of extinction in a basal species requires information on their regional as well as their global distribution. Extrapolation from regional to global distribution or vice versa is not possible. However, the fact that global and regional distributions are decoupled among basal species implies that many of them have succeeded in escaping the downward spiral of mutually reinforcing declines at multiple scales (Gaston et al. 2000). There are even many basal species that are narrowly distributed at both regional and global scales and have nevertheless not gone extinct (contrary to Johnson 1998). We need to understand the mechanisms that permit such species to escape the double jeopardy of correlated declines at multiple scales to effectively protect them.

In conclusion, the negative message from the present investigation is that the relationship between global and regional distribution of species may be less general than was previously thought (Lawton 1999). It may hardly apply to phylogenetically basal species. There is a risk that other macroecological patterns are ''biased'' in a similar way. The patterns may be less universal than previously thought, and so may be the underlying processes. The positive message, however, is that the analysis of macroecological patterns across a phylogeny may provide new insights into macroevolutionary processes. The present analysis was only a first step. It was restricted to extant species, and therefore could not tease apart, with certainty, the effects of extinction, speciation, and evolutionary modification of species. In the future we will need in situ analyses of macroecological patterns across phylogenies (Jablonski et al 2004), that is, analyses of fossil floras and faunas.

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