

LOCAL AND REGIONAL PATTERNS OF SPECIES RICHNESS IN CENTRAL EUROPEAN VEGETATION TYPES ALONG THE pH/CALCIUM GRADIENT

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Abstract: We investigated the relationship between soil pH/calcium content and species richness of vascular plants in seven broadly defined Central European vegetation types, using Ellenberg indicator values for soil reaction and a phytosociological data set of 11,041 vegetation sample plots from the Czech Republic. The vegetation types included (A) broad-leaved deciduous forests, (B) meadows, (C) dry grasslands, (D) reed-bed and tall-sedge vegetation, (E) fens and transitional mires, (F) perennial synanthropic vegetation and (G) annual synanthropic vegetation. Relationships between local species richness (alpha diversity) and pH/calcium were positive for vegetation types A and C, negative for D and G, unimodal for E, and insignificant for B and F. Ellenberg soil reaction values explained 37% of variation in local species richness for vegetation type E, 24% for A, 13% for D, but only less than 4% for the others. Species pool size, i.e., the number of species that can potentially occur in a given habitat, was calculated for each plot using Beals index of sociological favourability applied to a large phytosociological database. For most vegetation types, the relationships between species pool size and pH/calcium were similar to the relationships between local species richness and pH/calcium, with the exception of meadows (weak unimodal) and perennial synanthropic vegetation (weak negative).

These patterns suggest that for those types of Central European vegetation that developed independently of human influence in the Pleistocene or early Holocene (dry grasslands, deciduous forests), there are larger pools of calcicole than calcifuge species. This pattern is also found at the level of local species richness, where it is, however, less clearly pronounced, possibly due to the predominance of a few widespread and generalist calcifuges in acidic habitats. The unimodal pattern found in mires may result from similar underlying mechanisms, but in high pH environments mineral-rich spring waters probably decrease species richness by having toxic effects on plant growth. By contrast, vegetation types developed under direct human influence (meadows, synanthropic vegetation) show weak negative or no relationships of local species richness or species pool to pH/calcium gradient. These results support the hypothesis of PÄRTEL (*Ecology* 83: 2361–2366, 2002) and EWALD (*Folia Geobot.* 38: 357–366, 2003), that the modern calcicole/calcifuge disparity in the species pool of Central European flora has resulted from historical and evolutionary processes that took place on high pH soils. In the Pleistocene, calcareous soils dominated both the dry continental landscapes of Central Europe and glacial refugia of temperate flora, which were mostly situated in southern European mountain ranges with abundant limestone and dolomite. The negative pattern of species richness along the pH/calcium gradient found in reed-bed and tall-sedge vegetation, however, is not consistent with this historical explanation.

Keywords: Calcareous, Calcicole, Calcifuge, Ellenberg indicator values, Historical and evolutionary processes, Soil acidity, Species pool, Vascular plants

INTRODUCTION

Soil pH and calcium content are among the most important factors controlling species composition and diversity in plant communities. A possible explanation for patterns of local species richness (alpha diversity) along the pH/calcium gradient is the disparity existing in

regional floras between calcicoles and calcifuges, i.e., species adapted respectively to high or low pH soils. This disparity has been suggested to result from evolutionary and historical processes operating on a regional scale (GRIME 1973, 1979, GRUBB 1987, PÄRTEL 2002, EWALD 2003). Such an explanation follows the species pool concept (TAYLOR et al. 1990, ZOBEL 1992, 1997, ERIKSSON 1993, PÄRTEL et al. 1996), which stresses the role of the regional species pool as the major determinant of local species richness, while it ascribes less importance to local interspecific interactions (see also CORNELL & LAWTON 1992, RICKLEFS & SCHLUTER 1993, CALEY & SCHLUTER 1997).

Using a global review of plant ecological literature, PÄRTEL (2002) demonstrated that positive relationships between local species richness and pH are more frequent at higher latitudes, where the Pleistocene evolutionary centres were in areas with rejuvenated calcareous soils. For the Central European forest flora, EWALD (2003) pointed out that its pool of calcicoles by far exceeds the pool of calcifuges, which is in sharp contrast to the predominance of acidic soils in modern Central European landscapes. He also hypothesized that this pattern is a result of evolutionary and historical processes.

Different habitats in modern landscape harbour specific species pools that vary in their evolutionary and migration histories. New insights into the relationships between local species richness, species pool and soil pH or calcium content can therefore be gained by analyses performed separately in different vegetation types. The analyses presented in this paper make use of a large phytosociological data set and Ellenberg indicator values. They aim at identifying vascular plant diversity patterns in major vegetation types of Central Europe along the pH/calcium gradient, with focus on to local species richness and species pool.

MATERIALS AND METHODS

Data set

We used vegetation-plot data (relevés) from the Czech National Phytosociological Database (CHYTRÝ & RAFAJOVÁ 2003) for seven broadly delimited vegetation types, defined by phytosociological classes according to MORAVEC et al. (1995): (A) broad-leaved deciduous forests (class *Quercus-Fagetum*), (B) meadows (*Molinio-Arrhenathereteum*), (C) dry grasslands (*Festuco-Brometeum*), (D) reed-bed and tall-sedge vegetation (*Phragmito-Magnocariceteum*), (E) fens and transitional mires (*Scheuchzerio-Cariceteum fuscae*), (F) perennial synanthropic vegetation (*Artemisietum vulgaris*, *Galio-Urticeteum*, *Agropyreteum repentis*, *Plantagineteum majoris*), and (G) annual synanthropic vegetation (*Chenopodietum*, *Secalietum*). Main characteristics of these vegetation types in the Czech Republic are summarized in Table 1. Only relevés from plots of 100–400 m² for forests and 9–25 m² for herbaceous vegetation were used. As the geographical coverage of the relevé sites was not uniform across the country, we made a geographical stratification of the data set, taking only one relevé per each phytosociological association in each cell of a grid dividing the Czech Republic into quadrats of 1.25 longitudinal × 0.75 latitudinal minute (ca. 1.5 × 1.4 km). Traditional phytosociological associations as indicated by the relevé authors were used for this stratification. We excluded all cryptogam records and merged multiple species records in different layers of the same relevé. Resulting relevé numbers per vegetation type ranged between 393–3331 (Table 2).

Table 1. Characteristics of distribution, altitudinal belts, degree of naturalness and period of origin of the studied vegetation types in the Czech Republic.

| Vegetation type | Distribution | Altitudes | Naturalness | Origin |
|--|--------------|---------------------|---------------------|----------------|
| (A) Broad-leaved deciduous forests | common | lowland - montane | natural | early Holocene |
| (B) Meadows | common | lowland - montane | managed | mid Holocene |
| (C) Dry grasslands | scattered | lowland - colline | managed, natural | Pleistocene |
| (D) Reed-bed and tall-sedge vegetation | scattered | lowland - montane | natural | Pleistocene |
| (E) Fens and transitional mires | scattered | lowland - subalpine | managed, natural | Pleistocene |
| (F) Perennial synanthropic vegetation | common | lowland - montane | intensively managed | mid Holocene |
| (G) Annual synanthropic vegetation | common | lowland - montane | intensively managed | mid Holocene |

Estimating soil reaction

For each relevé, we calculated the average Ellenberg indicator value for “soil reaction” (ELLENBERG et al. 1992), using the JUICE program (TICHÝ 2002). As suggested by SCHAFFERS & SÝKORA (2000), Ellenberg soil reaction value best corresponds to a combined gradient of soil pH and calcium content. When calculating Ellenberg values, it was important to avoid the effect of an uneven number of species assigned to different indicator values by ELLENBERG et al. (1992; see also EWALD 2003). Since the pool of calcicoles as defined by ELLENBERG et al. (1992) is larger than the pool of calcifuges, one may suppose accidental occurrences of calcicoles in acidic sites to be more frequent than accidental occurrences of calcifuges in basic sites. If so, average indicator values calculated for acidic sites would be biased towards the basic end of the gradient, especially in species-rich vegetation with many accidental species. To remove this element of circularity from the analysis, we used the procedure proposed by SCHAFFERS & SÝKORA (2000) and calculated average indicator values for relevés using negative weighting by the number of species assigned to particular values on Ellenberg scale. The weights were determined separately in each of the vegetation types A–G, considering only species occurring in particular data sets. In such a way, our calculations of mean values for relevés were only based on species ranking along the soil reaction gradient and were not influenced by the putative higher pool of calcicoles in Central European flora presumed by ELLENBERG et al. (1992). Nevertheless, our pilot analyses showed that calculations based on weighted and unweighted averages gave roughly similar results.

Estimating species pool

The species pool was estimated by the probabilistic method proposed by EWALD (2002). This method makes use of the Beals index of sociological favourability (BEALS 1984, MCCUNE 1994), which estimates the probability of encountering species in a relevé from

actual species composition of the relevé and the pattern of species co-occurrence in a large database:

$$b_{ij} = \frac{1}{S_i} \cdot \sum_k \frac{M_{jk}}{N_k}$$

where b_{ij} is the estimated probability of species j to occur in relevé i , S_i the number of species in relevé i , M_{jk} the number of joint occurrences of species j and k in the whole database and N_k the number of occurrences of species k in the whole database. We used a database of 21,794 geographically stratified phytosociological relevés that included all major vegetation types of the Czech Republic. For each relevé used in this study, we calculated the probability of occurrence for each species present in the database, using the JUICE program (TICHÝ 2002). Then we estimated the size of the species pool for each relevé as the number of species whose probability of occurrence in the given relevé exceeded the value of $b_{ij} = 0.1$. Mean values of estimated species pool size for particular vegetation types are given in Table 3.

Statistical analysis of the relationship between species richness and soil reaction

Local species richness (alpha diversity, number of species per relevé) of vascular plants and the estimated size of species pool per relevé were regressed against the Ellenberg soil reaction values for relevés. In both cases, species numbers were square-rooted in order to get an appropriate transformation for counts (SOKAL & ROHLF 1995). The fact that the relevés came from plots of unequal size could influence the analysis of local species richness. Therefore we removed the area effect by calculating linear regressions of the local species richness on log-transformed plot size. Logarithmic transformation was used in order to fit the empirical species-area relationship (ROSENZWEIG 1995). Then we used standardized residuals from these regression and regressed them against Ellenberg soil reaction values. In the analysis of species pool, controlling for the area effect was not necessary, however, we standardized the values of estimated species pool to zero mean and unit variance so as to make them directly comparable with the standardized residuals of local species richness. In each regression, we first fitted the linear term and then we possibly added the quadratic term, provided the following two conditions were simultaneously fulfilled: (1) quadratic term explained, in addition to the linear term, a significant portion of the residual sum of squares (F -test, $P < 0.01$); (2) the fitted quadratic curve attained its maximum within the studied range of soil reaction values, suggesting a unimodal relationship. Equality of regression slopes for local species richness and for species pool was tested for each of the vegetation types A–G, using factor and interaction term in a general linear model. Regression analyses were calculated in the STATISTICA program (STATSOFT INC. 2001).

RESULTS

The relationships between local species richness and Ellenberg soil reaction values (Table 2) were positive for broad-leaved deciduous forests and dry grasslands (Fig. 1A, C), unimodal for fens and transitional mires (Fig. 1E), and negative for reed-bed and tall-sedge vegetation and annual synanthropic vegetation (Fig. 1D, G). There were no significant

Table 2. Regressions of local species richness on Ellenberg soil reaction values for relevés. Dependent variable was standardized residuals from regressions of local species richness on log-transformed relevé area. n – number of relevés, mean \pm SD – mean and standard deviation of the local species richness, R^2 – coefficient of determination. Regression coefficients and coefficients of determination reported are significant at $P < 0.01$. Asterisks in brackets (**) are given where quadratic term explained significant variation in addition to the variation explained by linear term, but it was not included into the model because the quadratic curve peaked outside the range of the soil reaction values studied. n.s. – not significant.

| Vegetation type | n | mean \pm SD | Regression coefficients | | R^2 |
|--|------|-----------------|-------------------------|-----------|-------|
| | | | linear | quadratic | |
| (A) Broad-leaved deciduous forests | 2473 | 26.8 \pm 11.9 | 1.166 | (**) | 0.241 |
| (B) Meadows | 3334 | 31.2 \pm 11.0 | n.s. | n.s. | n.s. |
| (C) Dry grasslands | 1709 | 28.3 \pm 12.6 | 0.071 | (**) | 0.003 |
| (D) Reed-bed and tall-sedge vegetation | 1502 | 9.2 \pm 6.4 | -0.261 | n.s. | 0.132 |
| (E) Fens and transitional mires | 396 | 21.7 \pm 11.3 | 0.240 | -0.195 | 0.373 |
| (F) Perennial synanthropic vegetation | 876 | 18.0 \pm 7.7 | n.s. | n.s. | n.s. |
| (G) Annual synanthropic vegetation | 751 | 24.0 \pm 9.4 | -0.147 | n.s. | 0.034 |

Table 3. Regressions of species pool size on Ellenberg soil reaction values for relevés. Dependent variable, number of species in the species pool, was standardized to zero mean and unit standard deviation. n – number of relevés, mean \pm SD – mean and standard deviation of the estimated number of species in the species pool, R^2 – coefficient of determination. Regression coefficients and coefficients of determination reported are significant at $P < 0.01$. Asterisks in brackets (**) are given where quadratic term explained significant variation in addition to the variation explained by linear term, but it was not included in the model because the quadratic curve peaked outside the range of the soil reaction values studied. n.s. – not significant.

| Vegetation type | n | mean \pm SD | Regression coefficients | | R^2 |
|--|------|-----------------|-------------------------|-----------|-------|
| | | | linear | quadratic | |
| (A) Broad-leaved deciduous forests | 2473 | 87.5 \pm 12.0 | 0.675 | (**) | 0.527 |
| (B) Meadows | 3334 | 83.1 \pm 4.5 | 0.571 | -0.047 | 0.010 |
| (C) Dry grasslands | 1709 | 83.4 \pm 10.1 | 0.182 | (**) | 0.062 |
| (D) Reed-bed and tall-sedge vegetation | 1502 | 48.8 \pm 21.9 | -0.309 | (**) | 0.182 |
| (E) Fens and transitional mires | 396 | 78.2 \pm 11.8 | 2.270 | -0.209 | 0.520 |
| (F) Perennial synanthropic vegetation | 876 | 71.4 \pm 11.2 | -0.131 | n.s. | 0.025 |
| (G) Annual synanthropic vegetation | 751 | 75.8 \pm 8.2 | -0.301 | n.s. | 0.140 |

relationships for meadows and perennial synanthropic vegetation (Fig. 1B, F). The proportion of variation in local species richness explained by Ellenberg soil reaction values (Table 2) was 24% for broad-leaved deciduous forests, 37% for fens and transitional mires and 13% for reed-bed and tall-sedge vegetation. For the other vegetation types, the explained variation was very low (< 3.5 %).

For most of the studied vegetation types, the relationships between species pool and Ellenberg soil reaction values (Table 3) were similar to the relationships detected for local species richness. For broad-leaved deciduous forests and dry grasslands, the relationships remained positive but with a significantly steeper slope (F -test, $P < 0.01$) (Fig. 2A, C). For fens and transitional mires and reed-bed and tall-sedge vegetation, there were no significant changes in the parameters of the regression relationships as compared with the relationships

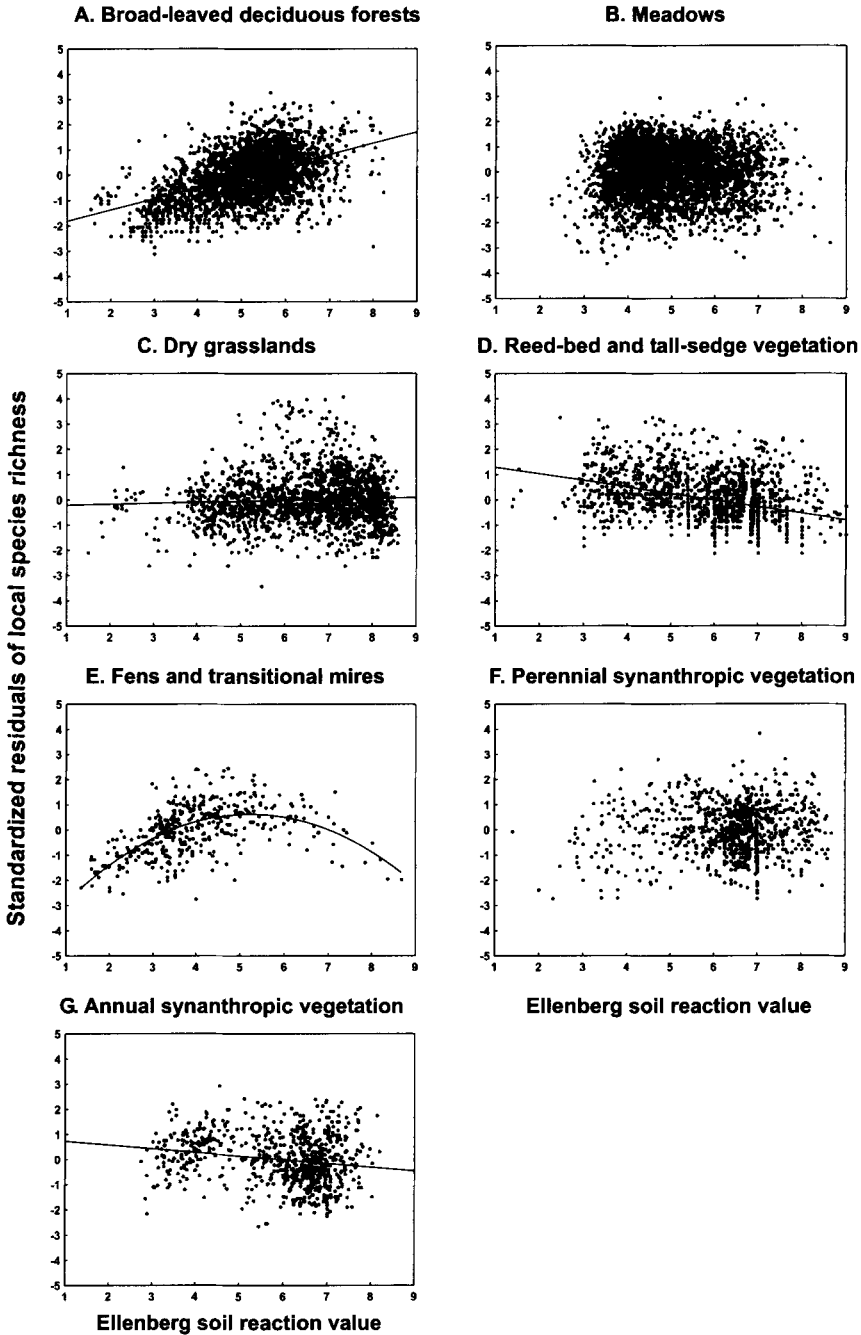


Fig. 1. Relationships between local species richness and pH/calcium gradient, with the area effect removed. Standardized residuals from the linear regressions of local species richness on log-transformed size of relevé plots are plotted against Ellenberg soil reaction values for relevés. Curves are not fitted in cases where regression coefficients are not significant. See Table 2 for regression parameters.

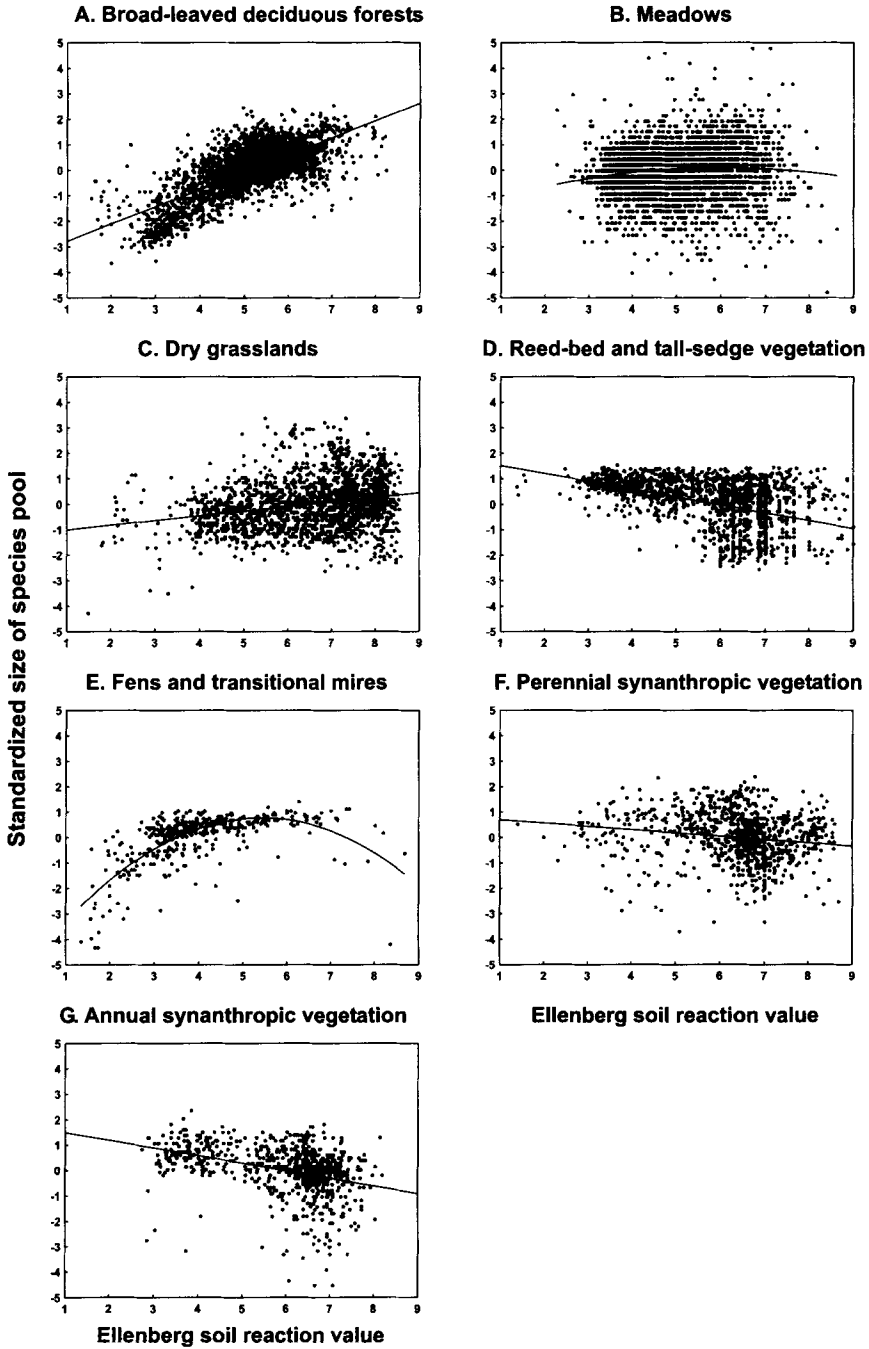


Fig. 2. Relationships between estimated number of species in species pool for particular relevés and pH/calcium gradient. Dependent variable is standardized to zero mean and unit standard deviation and plotted against the Ellenberg soil reaction values for relevés. See Table 3 for regression parameters.

of local species richness (Fig. 2D, E). For annual synanthropic vegetation, the relationship remained negative but with a significantly steeper slope (F -test, $P < 0.01$) (Fig. 2G). Unlike in the regression for local species richness, regression for species pool detected significant relationships for meadows (unimodal, Fig. 2B) and for perennial synanthropic vegetation (negative, Fig. 2F). The proportion of variation in species pool explained by the regressions (Table 3) was generally higher than in case of local species richness due to the effect of data smoothing by Beals function. However, except for broad-leaved deciduous forests and fens and transitional mires, less than 20% of the total variation was explained.

DISCUSSION

Local species richness along the pH/calcium gradient

Our results show that among the broadly defined vegetation types of Central Europe, there is no single form of the relationship between local species richness and pH/calcium content (Table 2, Fig. 1). A pronounced positive relationship was detected for broad-leaved deciduous forests, a pronounced unimodal relationship for fens and transitional mires, and a negative relationship for reed-bed and tall-sedge vegetation. In the other vegetation types, pH/calcium gradient explained only a very low proportion of variation in local species richness.

Some of these patterns correspond to the patterns already reported from temperate or boreal vegetation types. For deciduous forests, local species richness was found to have positive relationships to pH or exchangeable cation concentrations, e.g. in southern Sweden (BRUNET et al. 1997), Belgium (DUMORTIER et al. 2002), North Carolina (PEET & CHRISTENSEN 1980) and Wisconsin (BROSOFKSKE et al. 2001). Positive relationships were also reported from coniferous forests, e.g. in British Columbia (REY BENAYAS 1995), Wisconsin (BROSOFKSKE et al. 2001) and the Austrian Alps (EXNER et al. 2002). Unimodal patterns were also found in deciduous forests (see DUPRÉ et al. 2002 for a review of local studies from northern and Central Europe). Occasionally reported negative relationships between forest species richness and pH can be explained by sampling performed along short gradients, situated in the basic part of the entire pH/calcium gradient, a small number of study plots or confounding effects of other factors (DUPRÉ et al. 2002).

The evidence for a unimodal relationship between local species richness of vascular plants and pH/calcium gradient in mires is supported by the study of GLASER et al. (1990) from Minnesota. The results of other studies showing positive relationships in bogs and poor fens (GUNNARSSON et al. 2000 – central Sweden; HÁJKOVÁ & HÁJEK 2003 – Western Carpathians) are not contradictory to the unimodal pattern presumably existing over the entire range of different mire types. In our data set, a decrease in species richness in high pH fens was due to species-poor communities dominated by *Juncus subnodulosus*, *Schoenus ferrugineus* and *S. nigricans*. In the extremely high pH habitats, e.g. under the influence of mineral-rich springs or brackish water, species richness may be reduced due to high concentration of toxic compounds, as reported from saline meadows or coastal marshes (REY BENAYAS & SCHEINER 1993, GOUGH et al. 1994). Evidence for the unimodal pattern of species richness along the pH/calcium gradient in mires was provided also for bryophytes (VITT et al. 1995, HÁJKOVÁ & HÁJEK 2003).

For the other herbaceous vegetation types analyzed in this study, pH/calcium gradient explained a very low proportion of variation in local species richness (13% for reed-bed and tall-sedge vegetation and less than 4% for the other vegetation types). These weak relationships were either negative, positive or insignificant. It is possible that the species richness of these vegetation types mainly depends on other factors than pH/calcium, in particular on the disturbance regime (management) and productivity (GRIME 1979, HUSTON 1994, GRACE 1999). Nevertheless, several observational and experimental studies from temperate grasslands report a positive relationship between species richness and soil pH (SILVERTOWN 1980, TILMAN & OLFF 1991, OLDE VENTERINK et al. 2001).

Species pool along the pH/calcium gradient

Additional insights into species richness patterns can be obtained by comparing local species richness with the species pool size (Fig. 2). We endorse the statement that the correlation between local species richness and species pool size does not necessarily imply that the former is determined by the latter, as the two are interdependent: not only can the species pool influence local species richness, but also local processes can affect the formation of the species pool (HERBEN 2000, GRACE 2001, LEPŠ 2001, WILSON & ANDERSON 2001). In our case, patterns of species pool size along the pH/calcium gradient do not differ from the patterns of local species richness for reed-bed and tall-sedge vegetation and for fens and transitional mires (Figs. 1D, E, 2D, E, Tables 1, 2). However, particularly interesting and worth studying can be those cases where local and regional species richness follow different patterns.

In broad-leaved deciduous forests and dry grasslands, both the local species richness and the species pool increased with increasing soil reaction, but the increase in species pool size was steeper (Figs. 1A, C, 2A, C, Tables 1, 2). These results suggest that species adapted to these habitats are mainly calcicoles, but on more acidic soils local species richness is higher than would be expected from the species pool, possibly due to the comparatively high proportion of a restricted number of widespread calcifuges occurring in local communities.

For annual synanthropic vegetation, both local species richness and species pool were negatively related to the pH/calcium gradient, but the decrease was steeper for the species pool (Figs. 1G, 2G, Tables 1, 2). Annual synanthropic vegetation is mainly typical of arable fields and the patterns detected in this study probably reflect disproportional effects of intensive agricultural management on acidic and basic soils. In the Czech Republic, basic soils are generally found at lower altitudes. Due to more favourable climate at low altitudes, these soils were rather early subjected to intensive agricultural management and effective methods of weed control, which resulted in a decrease in species richness (PYŠEK et al., unpubl. data). By contrast, intensification was delayed on more acidic soils at higher altitudes, where arable fields could host more species, including some perennial herbs from adjacent meadows and pastures.

Regression of species pool size on the pH/calcium gradient for meadows and perennial synanthropic vegetation (Figs. 2B, F, Tables 2) explained a very low proportion of the total variation (< 3%). These weak relationships can be presumably due to large heterogeneity of these vegetation types, which is caused by other factors than pH/calcium.

Historical interpretations

One possible explanation of the modern predominance of calcicoles over calcifuges in some temperate ecosystems is based on the historical predominance of calcareous soils, on which the evolution and formation of modern floras took place (GRUBB 1987, PÄRTEL 2002, EWALD 2003). During the Pleistocene, several rather long periods of cold and dry climate alternated with much shorter periods of warm and humid climate (LANG 1994, BERGLUND et al. 1996, ROBERTS 1998). The cold and dry climate, which has been rather typical of the past 1–2 million years, supported the development of calcareous soils by such processes as cryoturbation, erosion, loess deposition and decreased leaching (WALKER et al. 2001). In the modern arctic landscape, which may be considered as a partial analogue of the Central European Ice Age tundra or cold steppe, soil pH was repeatedly reported to be strongly positively correlated with species richness (GOUGH et al. 2000, WALKER et al. 2001, PÄRTEL 2002), although this relationship can be modified by the effects of other factors (e.g. GOULD & WALKER 1999 reported unimodal relationship in sites where high pH was maintained by soil disturbances).

Both palaeoecological data and modern analogies from high-latitude ecosystems suggest that evolution of modern species, which started ca. 10 million years before present (BEHRENSMEYER et al. 1992), took place in the epoch with rather strong pH gradients developed on large spatial and temporal scales. In the analysis of phylogenetic conservatism of species niche for Central European flora, PRINZING et al. (2001) demonstrated that more than 40% of variance in species niche positions along the pH gradient can be explained at the level of species, while less than 10% at the levels of genera or families. This analysis supports the hypothesis that the remarkable calcicole/calcifuge differentiation existing among extant species of Central European flora is the result of rather young evolutionary processes, which took place on high pH soils in periglacial areas. The higher extinction of calcifuge than calcicole species in Pleistocene environments, proposed by EWALD (2003), may also have played a role.

Our results seem to be consistent with the above considerations at least for two vegetation types whose origin can be traced back to the Ice Age, i.e., dry grasslands, which at least partly correspond to species-rich, cold and dry Pleistocene steppes (WALKER et al. 2001), and fens and transitional mires, which correspond to wet depressions of Pleistocene tundra with draining impeded by underlying permafrost.

For historical interpretations of modern species pools in Central Europe, not just the historical predominance of calcareous soils *in situ* must be taken into account, but also soil conditions in the presumed glacial refugia of temperate flora. Many species of modern Central European flora had their glacial refugia in southern European mountain ranges (HUNTLEY & BIRKS 1983, LANG 1994, BERGLUND et al. 1996), which are mostly formed from limestone or dolomite. Some refugia may have also been on calcareous bedrocks of the Outer Alps (NIKLFELD 1972). Limestone is a suitable bedrock for refugia as it creates more rugged topography than siliceous bedrocks, thus with more habitats which are able to host more species. Limestone predominance in the glacial refugia may have been the reason why the species pool of forest flora that immigrated to Central Europe after the retreat of the last

glaciation is rich in calcicoles, as shown by EWALD (2003) and confirmed by the present study.

The hypothesis that the modern predominance of calcicoles in some vegetation types of Central Europe results from Pleistocene evolutionary and migration processes is further supported by the absence of clear patterns in those vegetation types that originated relatively recently under human impact, since the mid-Holocene. In our analysis, meadows and synanthropic vegetation types showed only weak, negative or no relationships of their local species richness or species pool to the pH/calcium gradient. These vegetation types are composed partly of native species assembled from different natural habitats, partly of naturalized aliens (PYŠEK et al. 2002), but have no direct relationships to the Pleistocene vegetation of Central Europe.

From the historical perspectives outlined above, however, it is difficult to explain the negative relationship of reed-bed and tall-sedge vegetation to the pH/calcium gradient. This species-poor vegetation did presumably occur in Pleistocene landscapes, but its species richness is possibly influenced by overriding effects of other factors, such as competition.

Methodological aspects

Making use of large phytosociological databases (EWALD 2001, HENNEKENS & SCHAMINÉE 2001) is an attractive option for analyzing local species richness and species pools over wide ranges of habitats and large areas. Such analyses provide more general results than small-scale studies describing diversity patterns in a restricted ecological or geographical space. However, there are difficulties with estimating both species richness and base status of the soils from phytosociological data.

Relevés in phytosociological databases are biased towards high species richness, as phytosociologists tend either to avoid species-poor stands or to sample species-poor stands in larger plots in order to obtain species-richer relevés (CHYTRÝ 2001). This fact, however, does not so much concern the analyses done in the present paper, as we only used relative comparisons and such biases presumably affect relevés from both acidic and base-rich soils to a similar extent. In addition, we used only relevés from a rather narrow range of plot sizes.

A more severe problem is that relevés in the databases are rarely furnished with soil pH measurements, and if they are, then the values given by different authors may not be directly comparable. In Central Europe, Ellenberg indicator values (ELLENBERG et al. 1992) for "soil reaction" are sometimes used as a substitute for direct soil pH measurements. These values proved to be sufficiently robust in several studies (HILL & CAREY 1997, DIEKMANN & LAWESSON 1999, SCHAFFERS & SÝKORA 2000), though using them instead of direct soil pH measurement has some disadvantages.

Ellenberg indicator values are based on field-experienced species relationships to particular ecological factors and species co-occurrence patterns, i.e., on the realized rather than fundamental niches. Thus, they are not independent of local processes. Moreover, there is no precise information on the scaling of Ellenberg ordinal scale: a higher number of calcicoles might merely result from an artifact created by an expert judgement, i.e., intervals for individual values at the basic end of the scale might be set broader than at the acidic end. If this is true, a high proportion of species with a high Ellenberg indicator value for soil reaction,

accepted by EWALD (2003) as evidence for the predominance of calcicoles in the Central European flora, might simply be a projection of this eventual artifact. Such scaling inconsistencies of Ellenberg indicator values were revealed by WAMELINK et al. (2002) who compared average Ellenberg indicator values for relevés with measured pH. They showed that Ellenberg indicator values were biased towards either higher or lower pH for different vegetation types, but performed well within individual vegetation types.

Fortunately, the issue of possibly unequal ranges for individual values on the Ellenberg ordinal scale can be fixed by the procedure proposed by SCHAFFERS & SÝKORA (2000), as used in the current study. This procedure includes calculating site averages of Ellenberg indicator values with negative weighting by the number of species assigned to particular values. Then the only information used from the Ellenberg indicator values is species ranking along the gradient that seems to be more or less reliable, provided the analyses are done separately within individual vegetation types (WAMELINK et al. 2002), which was also the case of the current study. Therefore we believe that the results obtained in our study are rather robust, in particular due to using large relevé data sets, which covered an extensive area and a broad range of different habitats.

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