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RESEARCH ARTICLE

Plant species richness of nature reserves: the interplay of area, climate and habitat in a central European landscape

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ABSTRACT

Aim To detect regional patterns of plant species richness in temperate nature reserves and determine the unbiased effects of environmental variables by mutual correlation with operating factors.

Location The Czech Republic.

Methods Plant species richness in 302 nature reserves was studied by using 14 explanatory variables reflecting the reserve area, altitude, climate, habitat diversity and prevailing vegetation type. Backward elimination of explanatory variables was used to analyse the data, taking into account their interactive nature, until the model contained only significant terms.

Results A minimal adequate model with reserve area, mean altitude, prevailing vegetation type and habitat diversity (expressed as the number of major habitat types in the reserve) accounted for 53.9% of the variance in species number. After removing the area effect, habitat diversity explained 15.6% of variance, while prevailing vegetation type explained 29.6%. After removing the effect of both area and vegetation type, the resulting model explained 10.3% of the variance, indicating that species richness further increased with habitat diversity, and most obviously towards warm districts. After removing the effects of area, habitat diversity and climatic district, the model still explained 9.4% of the variance, and showed that species richness (i) significantly decreased with increasing mean altitude and annual precipitation, and with decreasing January temperature in the region of the mountain flora, and (ii) increased with altitudinal range in regions of temperate and thermophilous flora.

Main conclusions We described, in quantitative terms, the effects of the main factors that might be considered to be determining plant species richness in temperate nature reserves, and evaluated their relative importance. The direct habitat effect on species richness was roughly equal to the direct area effect, but the total direct and indirect effects of area slightly exceeded that of habitat. It was shown that the overall effect of composite variables such as altitude or climatic district can be separated into particular climatic variables, which influence the richness of flora in a context-specific manner. The statistical explanation of richness variation at the level of families yielded similar results to that for species, indicating that the system of nature conservation provides similar degrees of protection at different taxonomic levels.

Key words altitude, central Europe, climate, habitat diversity, nature reserves, species–area relationship, taxonomic level, temperate flora.

INTRODUCTION

Diversity remains one of the central topics in contemporary ecology (e.g. Magurran, 1988; Huston, 1994; Rosenzweig, 1971, 1995; Klötzli & van der Maarel, 1996) and the object of studies at various levels, from community to landscape (Ricklefs & Schluter, 1993; Boyle & Boyle, 1994; Palmer, 1994; Frankel *et al.*, 1995; Cook & Jain, 1996) and in all types of ecosystems (Schulze & Mooney, 1994; Mooney *et al.*, 1996). In nature protection, biodiversity is considered a suitable measure of the quality of environment (Usher, 1986; Pickett *et al.*, 1997).

At the regional level, diversity has been related to various factors such as area (for a detailed analysis of species–area relations see Rosenzweig, 1995), altitude (Rahbek, 1995), climate, productivity (Swift & Anderson, 1994), landscape heterogeneity (Turner, 1987), successional status and disturbance (Osbornová *et al.*, 1990; Huston, 1994; Bazzaz, 1996). These factors do not act separately but are, to a

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greater or lesser extent, mutually correlated (Whittaker, 1972; Ozenda, 1988), which makes it difficult to assess the role each plays in determining species richness (Kohn & Walsh, 1994).

The Czech Republic represents a suitable model for studies of diversity at a landscape scale. This territory has an extremely variable orography, climate and geology and a number of different habitats can be found even in small areas. Environmental conditions favour the development of a rich flora, typical of central Europe. The prevailing climate supports forest expansion (Hejný & Slavík, 1988). There is a long-term tradition of nature protection dating back as far as the nineteenth century, which has resulted in a dense network of nature reserves. At present, all major vegetation types are included in the Czech Republic's system of nature reserves, within a relatively large-scale and diverse region (Maršáková-Němejcová & Mihálik, 1977).

The present dataset is a highly representative sample of relatively undisturbed vegetation, covering a wide range of habitats with a high beta diversity (Whittaker, 1972; Kučera, 1997). Hence it represents a convenient model for studying the role of factors influencing species richness. Diversity is expressed in terms of the number of species, which is a commonly used measure in biogeographically orientated studies (Ricklefs & Schluter, 1993). These data have been analysed to determine the effects of individual factors, unbiased by correlations with other variables. The paper attempts to answer the following questions: (1) What is the overall pattern in species richness at different taxonomic levels? (2) Do particular vegetation types differ in the number of species they contain? (3) What are the main factors determining the number of species in central European landscapes? (4) What is the relative importance of particular groups of factors, especially those related to climate compared with those determined by habitat characteristics? (5) What is the relation between species richness, habitat diversity and reserve area? (6) Is the pattern of richness of native species different from that found for the complete species set, i.e. including aliens?

METHODS

Study subject: character of nature reserves

The study covers an area of 78 854 km^2 within the latitudinal range of 48°30′–51°05′ and the longitudinal range of 12°05′–18°50′. In 1996, there were 1757 small-sized nature reserves protected in the Czech Republic, covering an area of 823 km^2, i.e. 1.05% of the territory of the country (Kos & Maršáková, 1997). Of these, 302 had suitable data for the purpose of the present study and they represent 17.2% of the total number. However, the focus was on important reserves, which are usually larger in land area; therefore those that were sampled covered an area of 365 km^2 (accounting for 0.46% of the country's territory, and 44.2% of the total area of nature reserves). The set of reserves studied may be considered as a highly representative sample of the natural vegetation of the study area.

Data sources

Species lists were obtained for each of the 302 nature reserves in the study, using published records from particular reserves as well as unpublished floristic inventories deposited at the Agency for Landscape Protection of the Czech Republic, Praha. These inventories are carried out regularly by professional botanists who are asked to collect data with a special focus on obtaining complete species lists. The following data were recorded for each reserve: (i) total number of vascular plant species (ii) number of genera (iii) number of families, and (iv) number of native species (i.e. excluding alien species). The system of higher taxononomical units follows Mabberley (1999). For each nature reserve, the following characteristics were recorded (the range of values is in parentheses):

- reserve area (range 0.17–4280 ha);
- mean altitude, expressed as the middle value between minimum and maximum altitude recorded at the reserve territory (150–1362 m above sea level);
- altitudinal range, expressed as the difference between the minimum and maximum altitude (0–710 m);
- habitat diversity expressed as the number of major habitat types recorded in the reserve, based on the Czech national system of nature conservation and management habitat classification, with the higher levels of habitat type units being the so-called 'physiotypes' (Petříček, 1999). In this classification, 20 habitat types (physiotypes) are defined on the basis of physical characters of the site, using terms such as e.g. wetlands, arable land, rocky sites, sandy habitats, alpine habitats, ruderal habitats, alluvial, oak, beech and spruce forests, etc. (ranked 1–7 physiotypes);
- density of human population (number of inhabitants per km^2) in the region, included as a measure of severity of human impact (60–500 inhabitants per km^2);
- major vegetation type covering most of the reserve area (the following categories were recognized: pine forest; beech forest; oak forest; hornbeam forest; spruce forest; scree and ravine forests; humid grasslands, including pastures and saline habitats; wetlands, including pond shores and alder forests; peat bogs and fens; dry grassland, i.e. steppe vegetation including scrub in dry habitats, rock outcrops, heathland and serpentine habitats);
- phytogeopraphical region in which a reserve is located (three basic regions are recognized: thermophyticum, i.e. a region of thermophilous flora and vegetation; mesophyticum, with flora and vegetation of the temperate zone; oreophyticum, with mountain flora and vegetation — Hejný & Slavík, 1988);
- climatic district: warm, moderately warm and cold (Quitt, 1975);

- January isotherm (average temperature in January) (–7.5 to –1.0 °C);
- June isotherm (average temperature in June) (8.0–18.0 °C);
- mean annual temperature (1.0–9.5 °C);
- annual sum of precipitation (475–1700 mm);
- sum of precipitation during the growing season (April–September) (325–850 mm).

The climatic parameters were obtained from GIS layers built by digitizing the relevant maps. Climatic characteristics (50-year averages) were taken from Vesecký *et al.* (1958).

Statistical analysis

Data on species numbers were transformed by their square root to obtain an appropriate distribution for count data (e.g. Sokal & Rohlf, 1981: 421–423) and the adequacy of fitted statistics was confirmed by plotting standardized residuals against fitted values, and by the normal probability plots of the fitted values (Crawley, 1993). Calculations were made using general linear modelling in the commercial statistical package GLIM® v. 4 (Francis *et al.*, 1994). The intent of each analysis was to determine the minimal adequate model. In this model, all parameters were significantly ($P < 0.05$) different from zero and from one another. This was achieved by a stepwise process of model simplification, beginning with the maximal model (containing all factors, interactions and covariates that might be of interest), then proceeding by the elimination of non-significant terms (using deletion tests from the maximal model) and retention of significant terms. The transformed numbers of species or residuals were the response variables, and vegetation type, climatic district, phytogeographical region and climax community were factors. Reserve area, habitat diversity, density of human population, mean altitude, altitudinal range, annual precipitation, precipitation in the growing season, mean temperature, January isotherm and June isotherm were covariates. Because the explanatory variables were often highly correlated, and to prevent biases to the model structures caused by correlation, model simplifications were made by backward elimination from the maximal models by using stepwise analyses of deviance tables (e.g. Crawley, 1993: 192–197). In the maximal model, each covariate was regressed on each factor with a different intercept and a different slope. In the first step of model simplification, the different slopes of each covariate on each factor were in turn replaced by a common slope of each factor on each covariate. The common slopes were regressed on the factors one after another, and the changes in residual deviance caused by removal of the different slopes for each covariate were assessed. All covariates with a common slope were assessed, then all non-significantly different slopes were deleted, and a reduced model was assessed. The analysis then continued on the reduced model. In this model, all the remaining terms were deleted in turn from the reduced deviance table, and only those leading to a significant increase in residual deviance were retained. The deletion tests were repeated on the reduced models until, after removing from the last deviance table, the minimal adequate model that contained nothing but significant terms was determined. The results obtained were thus not affected by the order in which the explanatory variables were removed in the step-wise process of model simplification.

As nature reserves represent natural vegetation within the given region, and the presence of alien species can be driven by rather different factors than that of native species (Pyšek, 1998; Pyšek *et al.*, 2002), it was considered that the presence of aliens might change the relationships between species richness and environmental parameters. For that reason the same analysis applied to the total number of species was performed separately for the total number of native species.

Path analysis (e.g. Sokal & Rohlf, 1981; Kohn & Walsh, 1994) was used to explore the form of the interrelationship between species richness, reserve area and habitat diversity. The path analysis enabled assessment of the relative direct and indirect effects by which a reserve area contributes to species richness both directly and indirectly, through habitat diversity. The appropriate path model was suggested by regression analysis of square root-transformed species numbers, natural logarithms of reserve areas and ranked numbers of habitat types recorded in each reserve. To achieve a com-parable influence in absolute values, each parameter was standardized to have a zero mean and variance of one.

RESULTS

Number of taxa at different taxonomic levels

In total, 2152 taxa at the specific and subspecific levels were found, of which 92 are hybrids. The taxa belong to 663 genera and 135 families. Obviously, the vast majority of the Czech flora, containing about 2550 taxa (Holub & Procházka, 2000), is represented in the nature reserves in this study.

There was a close correlation between the number of species and the number of genera and families, respectively (Fig. 1). We focused on phylogenetic distinctiveness (using taxonomy as a correlate of phylogeny) of present species so that species without close relatives were given special attention. Such an approach can contribute to understanding how the overall evolutionary variation is maintained. As the relationship between the number of species in the reserves and that of genera was very close (Pearson's correlation coefficient, square-rooted numbers = 0.99, $n = 302$), an additional separate analysis was performed only for the number of families, which had a lower correlation value with species richness (Pearson's correlation coefficient, square-rooted numbers = 0.91, $n = 302$). The statistical analysis of richness at the level of families, using the same models as for the

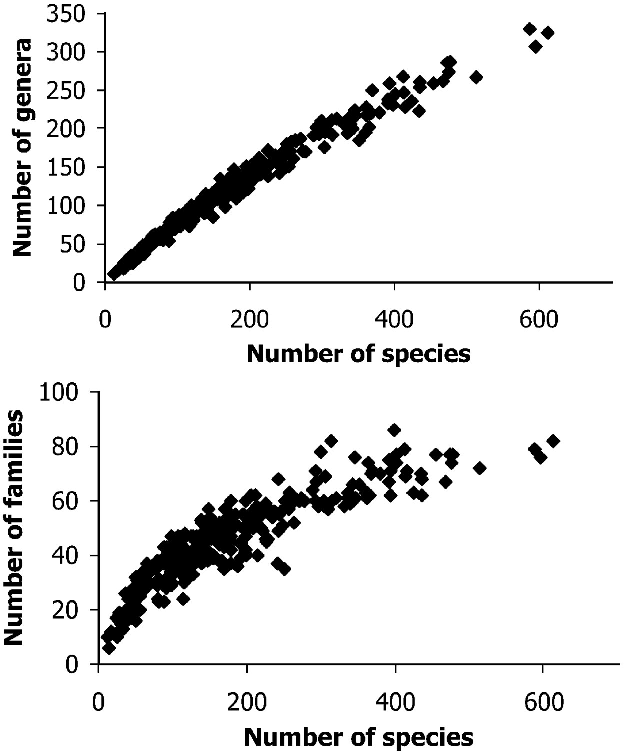

Fig. 1 Relationship between the number of species recorded in the reserve and that of higher taxa. Pearson's correlation coefficient (on square root transformed numbers, $n = 302$) was 0.99 for species vs. genera (top), 0.91 for species vs. families (bottom), and 0.94 for genera vs. families (not shown here).

number of species, none the less always yielded similar, but less significant results, explaining a lower proportion of the variance. These results indicate that the number of families in regional floras is determined by the same factors as of species. Thus further analyses are not reported herein.

Table 1 Species richness in nature reserves located in particular phytogeographical regions, climatic districts and with prevailing vegetation types. Mean species numbers per reserve of a given type are shown. Number of reserves is indicated (n). See text for comments

Factor	Level	n	Mean ± SD
Vegetation type	Spruce forest	4	258.5 ± 218.0
	Dry grassland	72	244.0 ± 138.4
	Hornbeam forest	16	212.6 ± 98.8
	Wetland	45	205.2 ± 111.9
	Oak forest	10	200.9 ± 68.5
	Humid grassland	19	159.9 ± 51.6
	Pine forest	12	154.3 ± 91.1
	Scree forest	15	154.3 ± 59.9
	Peat bogs	52	137.0 ± 113.4
	Beech forest	57	109.8 ± 57.8
Phytogeographical region	Thermophyticum	78	237.0 ± 128.4
	Mesophyticum	159	171.5 ± 99.7
	Oreophyticum	65	124.3 ± 107.4
Climatic district	Warm	67	235.4 ± 129.3
	Moderate	156	181.6 ± 104.5
	Cold	79	123.1 ± 100.5

Species richness in various vegetation types and different climate districts

Mean species number in the reserves was 178.2 ± 115.9 (mean ± SD), maximum species number was 612. The most species rich nature reserves were those with prevailing dry grasslands, wetlands and oak and hornbeam forests (Table 1). The high mean species richness of spruce forest reserves is explained by the fact that two large, complex reserves in the mountain regions have a high diversity of available habitats such as alpine grasslands, open rocks and scree, with a large number of relict species of natural open habitats (e.g. an extremely rich glacial cirque), but were classified into this group.

Nature reserves in the warm regions, defined both climatically and phytogeographically, harbour more species than reserves located in either moderate or cold conditions (Table 1).

Environmental models of species richness

The minimal adequate model of species richness explained 53.9% of the total variance (Table 2). Only four of the 14 explanatory variables appeared significant and they included:

Table 2 Significant explanatory variables of minimal adequate models of species richness. Covariates are indicated by slope ± one standard error (SE). Total explained variance by the minimal adequate models including intercepts (not shown) is $R^2 = 53.9\%$

Explanatory variables	Slope ± SE	F	d.f.	P	R^2 (%)
Reserve area (natural log)	1.20 ± 0.12	98.56	1, 290	< 0.0001	15.7
Mean altitude	−0.0065 ± 0.00088	55.39	1, 290	< 0.0001	8.8
Vegetation type	—	4.14	9, 298	< 0.0001	5.9
Habitat diversity	0.75 ± 0.20	14.06	1, 290	< 0.001	2.2

Table 3 Proportion of explained variance (%) of particular models used to explain the number of species recorded in a reserve. All models were significant at $P < 0.0001$

Model	Explanatory variables	Factors removed	Explained variance (%)
1	Vegetation type	Area	29.6
2	Habitat diversity	Area	15.6
3	Habitat diversity + climatic district	Area + vegetation type	10.3
4	Phytogeographical region + altitude + climatic parameters	Area + habitat diversity + climatic district	9.4
5	Area	Vegetation type + mean altitude	30.8
6	Habitat diversity	Vegetation type + mean altitude	14.3
7	Area + habitat diversity	Vegetation type + mean altitude	34.0

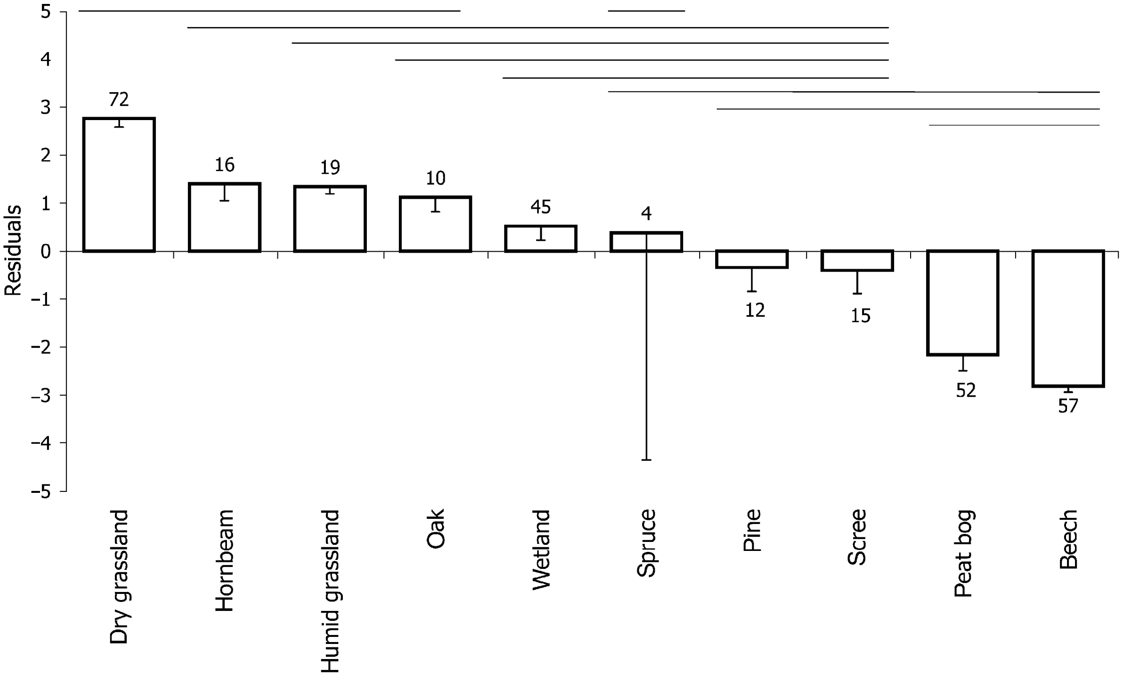

Fig. 2 Species richness in vegetation types independent of reserve area. Standardized residuals from the square root of species numbers in particular vegetation types after removing the effect of reserve area (Model 1, Table 3). The horizontal lines show groups not significantly different by least significant differences (LSD). Sample sizes are displayed on top of the bars, standard errors are indicated. $F = 11.35$; d.f. = 6, 292; $P < 0.0001$; $R^2 = 29.6\%$.

natural log of reserve area, mean altitude, prevailing vegetation type and habitat diversity. The effect of reserve area, mean altitude and habitat diversity covaried similarly in all vegetation types, and reserve area explained more of the variance than did the other factors. For further analyses, these factors were filtered out to reveal the unbiased effects of other factors on species richness.

The effect of vegetation type on species richness can be assessed after removing the effect of area (Table 3: Model 1). Species numbers independent of area (Fig. 2) indicate a higher species richness in dry and humid grasslands and hornbeam and oak forests. By contrast, peat bogs and beech forests were least diverse. Spruce forests were excluded from further analysis because of the low sample number and extremely high variation in species numbers.

The effect of habitat diversity was assessed independently of reserve area (Table 3: Model 2). Species richness increased with habitat diversity ($F = 54.6$; d.f. = 1, 295; $P < 0.0001$) (Fig. 3) and Model 2 accounted for 15.6% of the variation in the dataset.

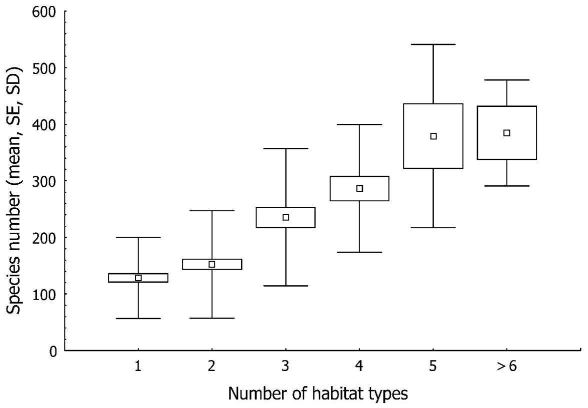

Fig. 3 Number of species in nature reserves classified according to the number of habitats present in a reserve.

As a next step, both the effect of reserve area and prevailing vegetation type were removed to assess the effect of habitat diversity and its interaction with climate (Table 3: Model 3). The increase in species richness with habitat diversity remained highly significant ($F = 10.6$; d.f. = 1, 299; $P = 0.001$) and directed towards warm climatic districts ($F = 9.09$; d.f. = 2, 300; $P = 0.0001$). This model explained 10.3% of the variation.

Finally, we studied how species richness in the three phytogeographically distinct regions of the central European flora may be influenced by altitude, and the role played by specific climatic parameters. In this model (Table 3: Model 4), a significant effect of altitude and climate on species richness in phytogeographical regions was found after filtering out the effect of reserve area, habitat diversity and climatic district ($F = 6.11$; d.f. = 5, 296; $P < 0.0001$). With these effects removed, the regions of thermophilous, temperate and mountain floras did not differ from each other in the number of species ($F_{\text{residuals}} = 1.41$; d.f. = 2, 289; $P = 0.25$). However, within-region differences in species richness were found. Species richness in mountain floras significantly decreased with mean altitude of the reserve (regression slope = −0.0062 ± 0.0024) ($F = 6.90$; d.f. = 1, 297; $P = 0.009$) but increased ($F = 3.43$; d.f. = 2, 298; $P = 0.03$) with the altitudinal range of the reserve in regions of both temperate (regression slope = 0.0069 ± 0.0035) and thermophilous floras (regression slope = 0.01 ± 0.0054). When evaluating particular climatic parameters, the effect of annual precipitation ($F = 10.53$; d.f. = 1, 295; $P = 0.001$) and especially that of January temperature ($F = 21.76$; d.f. = 1, 297; $P < 0.0001$) was significant for the region of the mountain flora: species richness decreased with increasing precipitation (regression slope = −0.0069 ± 0.0021) and with decreasing January temperature (regression slope = –2.78 ± 0.60).

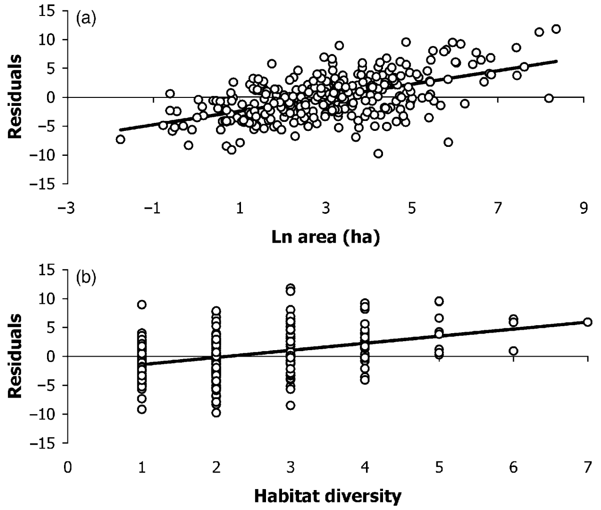

Fig. 4 Relationship between species richness and area (a) and species richness and habitat diversity (b). Species richness is represented by residuals from the square root of species numbers after removing the effect of vegetation type and mean altitude. (a) Residuals = −3.59 ± 0.36 + 1.17 ± 0.10 ln (area) ($F = 133.30$; d.f. = 1, 300; $P < 0.0001$; $R^2 = 30.8\%$). (b) Residuals = –2.60 ± 0.42 + 1.22 ± 0.17 ln (area) ($F = 50.23$; d.f. = 1, 300; $P < 0.0001$; $R^2 = 14.3\%$).

Relationships between species richness, reserve area and habitat diversity

There were strong positive, pairwise relationships between species richness, reserve area and habitat diversity. Habitat diversity increased significantly with reserve area (habitat diversity = 1.37 ± 0.12 + 0.25 ± 0.035 ln (area); $F = 50.98$; d.f. = 1, 300; $P < 0.0001$, $R^2 = 14.5\%$), and species richness increased significantly both with reserve area and habitat diversity (Table 2). However, as indicated in Table 2, species richness was also significantly influenced by mean altitude and vegetation type. To assess unambiguously the relationship between species number, habitat diversity and area, the effects of vegetation type and mean altitude were removed (Table 3: Models 5 and 6).

After removing the effects of vegetation type and mean altitude, species richness was still significantly related to both reserve area and habitat diversity (Fig. 4). When species richness was related together with both these variables (Table 2: Model 7), the multiple regression of residuals from the square root of species numbers yielded the following relationship:

Residuals of species richness = −4.45 ± 0.42 + 0.63 ± 0.16 habitat diversity + 1.01 ± 0.11 ln (area).

This multiple regression was highly significant ($F = 77.16$; d.f. = 2, 299; $P < 0.0001$; $R^2 = 34.0\%$), and the same can be said for both of its explanatory variables, i.e. reserve area ($F = 89.33$; d.f. = 1, 300; < 0.0001; $R^2 = 19.7\%$) and habitat diversity ($F = 14.85$; d.f. = 1, 300; < 0.001; $R^2 = 3.3\%$).

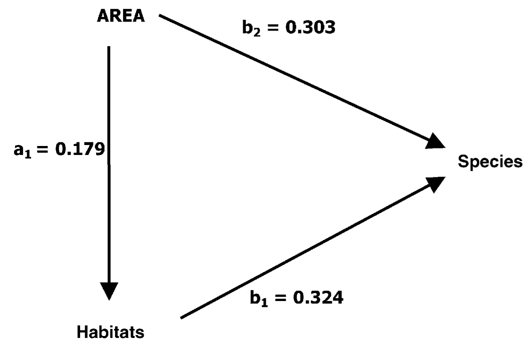

Fig. 5 Path model and path coefficients of species richness as a function of reserve area (natural log of ha) and habitat diversity (number of habitat/vegetation types recorded in the reserve). Reserve area directly affects habitat diversity and both area and habitat directly affect species richness.

Based on the significance of the two terms in the multiple regression, it is evident that both reserve area and habitat diversity contribute to species richness. Suggested relationships among the three variables are presented in a path model (Fig. 5). The direct area effect on species richness (0.303) is more than five times larger than the indirect area effect (0.058). The direct habitat effect on species richness (0.324) is approximately equal to the direct area effect (0.303), but the total effect of area, when direct and indirect effects are summed, slightly exceeds the effect of habitat (0.361) (Table 4).

The effect of area on species richness (independent of habitat diversity) was further explored by examining species–area curves for the reserves with a given number of habitat types, i.e. holding habitat diversity constant (Table 5). The slope of the species-area curves indicated increasing species richness with increasing reserve area.

Pattern of richness in native species

In total, 1831 native taxa were found, representing 74.7% of taxa recorded in all of the nature reserves. On average, native taxa contributed 93.0 ± 5.5% (mean ± SD) to the total number of species found in the reserve (Pyšek *et al.*, 2002).

Analysis of factors affecting species richness, taking only native species into account, yielded results similar to those obtained for the complete species set. The only striking difference appeared in the variance explained by mean altitude. The explanatory power of the regression slope of altitude on species richness was 8.8% when taking all species into account, but only 2.1% in the case of native species.

Table 4 Path and effect coefficients of the path model of species richness as a function of reserve area and habitat diversity depicted in Fig. 5. The path coefficients a_1, b_1 and b_2 represent direct effects; a_1 is the regression slope from Fig. 5 for the standardized variables habitat diversity and reserve area; b_1 and b_2 are standardized regression slopes from the multiple regression of species richness as a function of reserve area and habitat diversity (Model 7, Table 2). Indirect effects are calculated as the product of the path coefficients along the links between causal variables and the response variable through other causal variables. Effect coefficients are the sum of direct and indirect effects

Path coefficients:	
a_1, area effect on habitat diversity (direct)	0.179
b_1, habitat diversity effect on species richness (direct)	0.324
b_2, area effect on species richness (direct)	0.303
a_1b_1, area effect on species richness (indirect)	0.058
Effect coefficients:	
$b_2 + a_1b_1$, area effect on species richness (total)	0.361
b_1, habitat diversity effect on species richness (total)	0.324

DISCUSSION

Nature of the data and validity of the results

Floristic surveys have provided important information about the species diversity of the studied region, as the number of species is related closely to vegetation diversity, and both are convenient characteristics reflecting habitat diversity and the nature of ecological gradients (Pyšek, 1993; Kučera, 1997).

Table 5 Species (square-rooted)–area (log hectares) regression relationships for reserves grouped to hold habitat diversity constant. The reserves are ranked by increasing habitat diversity expressed as the number of habitat types. Performed only for habitat diversity groups with sufficient number of samples

Habitat diversity	Intercept ± SE	Slope ± SE	*F*	d.f.	*P*
1	−3.03 ± 0.46	0.91 ± 0.17	27.79	1, 102	< 0.0001
2	−3.61 ± 0.64	0.90 ± 0.18	24.65	1, 110	< 0.0001
3	−3.44 ± 1.12	1.31 ± 0.26	25.54	1, 44	< 0.0001
4	−2.86 ± 1.47	1.22 ± 0.33	13.87	1, 26	< 0.001
5	−6.37 ± 4.32	2.63 ± 1.02	6.62	1, 6	< 0.05

Even if we take into account that some vegetation types preserved in the central-European system of nature conservation are of human origin (such as meadows or some wetlands), nature reserves can be considered as representing remnants of natural vegetation in the landscape and centres of species diversity. Therefore they reflect, unlike other habitat types affected more severely by humans, a more or less natural distribution pattern of plant species. It can be assumed that in nature reserves, factors affecting species distribution in particular vegetation types are less biased by human-related factors operating in the present central-European landscape. The data from nature reserves are thus better suited for analyses attempting to separate the effects of factors determining species richness than are complete floristic surveys across all habitats of a given region. The set of reserves studied is a highly representative sample of natural vegetation of the study area and the pattern found in the present study has therefore general validity in terms of central European vegetation. Moreover, in previously published analyses the effects of explanatory variables were often masked by their covariance structure. The statistical approach used in this paper allows us to evaluate the effects of particular factors, independent of other variables. The analysis thus gives a sound basis for unbiased discussion of regional patterns of plant species richness.

Concerning possible bias in the quality of species lists given by the identities of the data collectors, this is inevitably associated with any study based on secondary data. None the less, the results presented here are robust enough not to be affected by this.

Effect of climate and altitude on species richness

In regional studies attempting to explain floristic or vegetation diversity, various factors have been found as important, e.g. precipitation, radiation and altitude in a study comparing lowland and mountain landscapes in Patagonia (Jobbágy *et al.*, 1996); and climate, regional topography, geological substrate and human activity in the Scottish highlands (Thompson & Brown, 1992; Brown *et al.*, 1993a,b). Factors considered in the present study explained more than 50% of the variation in floristic diversity. By separating the role of particular variables, we have shown that not only the reserve area (see e.g. Rosenzweig & Ziv, 1999) but also other factors associated with habitat diversity (as a measure of spatial and resource heterogeneity), climatic variation and environmental harshness (reflected in the higher altitude) have *per se* a highly significant effect on the species number and explain a remarkable proportion of variation.

The effect of altitudinal gradients on species richness has often been studied (see Rahbek, 1995 for a review). However, the sampling method and size of the area sampled may influence strongly the results of particular studies (Rahbek, 1995). This shortcoming was overcome in our research by filtering out the effect of area. The results still indicated that altitude affected the pattern of species richness and that this effect was different in particular phytogeographical districts. In the region of the mountain flora, species number decreased with altitude, which suggests a relationship between species diversity and productivity (Brown & Gibson, 1983; Currie, 1991; Cox & Moore, 1993). The results of this paper show further that the effect of altitude on species richness in a temperate landscape is context-dependent because at lower altitudes, i.e. in regions of temperate and thermophilous flora, an increase in altitudinal range contributes to the enrichment of floristic diversity. In dealing with particular climatic parameters, low winter temperatures, characterized by the January isotherm, and high precipitation were found as significant predictors of species richness of the mountain flora in the Czech Republic. In western Norway, species richness was predicted well by mean July and January temperatures and mean annual precipitation, and a linear relationship between July temperature and the number of vascular plants was found between 700 and 1500 m of altitude (Odland & Birks, 1999). In a study on diversity of woody plants in southern Africa, climate accounted for 74–79% of variation in species richness (O'Brien *et al.*, 1998). Richness of vascular plants in Fennoscandia, sampled in squares of standard size, was correlated closely with geographical (latitude and longitude) and climatic variables, explaining over 80% of the variation (Grytnes *et al.*, 1999).

Effect of habitat and area on species richness

The effect of habitat diversity (as a measure of landscape heterogeneity) on species diversity has been studied thoroughly on islands (e.g. Connor & McCoy, 1979; van der Werf, 1983). For instance, close positive correlations have been observed between species number, island area and the number of habitat types on the Shetland islands (Kohn & Walsh, 1994). In a sense, nature reserves in the agricultural/industrial landscape of central Europe can be considered as habitat islands (Begon *et al.*, 1990), i.e. islands of remnants of natural vegetation surrounded by a landscape of remarkably distinct features. For many species, the surrounding landscape represents a dispersal barrier (Forman, 1995). There is agreement about the probable joint importance of area and habitat diversity, but their simultaneous effect on species numbers has rarely been considered. Kohn & Walsh (1994) reported that area affected species numbers on islands both directly and indirectly, through habitat diversity, and that while the direct effects of area and habitat on species were of about the same magnitude, the total effect of area was nearly twice that of habitats. Kohn & Walsh's conclusion corresponds to our results in that there was about the same direct effect of area and of habitat diversity on species number in both studies, but the indirect effect of area in our study was very low and consequently the total effect of area was only slightly higher than that of habitat diversity. Also, the direct effect of area on the number of habitats reported for the Shetland islands (Kohn & Walsh, 1994) was five times stronger than the value found in mainland central-European reserves (0.915 vs. 0.179). It must be borne in mind that both the sampling scale and the definition of habitats are probably crucial to the nature of resulting relationships. Nevertheless, the habitat classification adopted by Kohn & Walsh (1994) corresponds more or less to that used in the present study (both in terms of detail and classification criteria). Hence it can be concluded that on an island, area exerts a much more powerful effect on habitat diversity than in large mainland reserves, and this relationship has a profound effect on the pattern of species diversity. As suggested by Kohn & Walsh (1994), straightforward relationships in the island system may derive from their relative simplicity, while in other systems the relationships between species, area and habitats may be obscured.

Particular vegetation types differ in their species richness when reserve area is filtered out, with dry grassland being the richest, and humid grassland as well as hornbeam and oak forests also harbouring high numbers of species. Climax vegetation in the region covered by the present study is represented by forests (Neuhäuslová & Moravec, 1997). However, it should be borne in mind that when explaining number of species in forests, and consequently in reserves covered to a large extent by forest communities, the importance of the forest's continuity for species diversity should be taken into account (Lawesson *et al.*, 1998).

Pattern of species richness: effect of immigration status and taxonomic level

We assumed that the native species, which have a common evolutionary past, might respond to the factors affecting species richness in a more transparent way than do introduced species exhibiting a much closer relationship to human activities. Therefore, not only the total species number but also native species were analysed separately. Both approaches, however, yielded similar results. This may be explained by (a) a relatively low contribution of aliens to the total species number (Pyšek *et al.*, 2002) and (b) the fact that alien species contribute to the total species number by occupying vacant niches, which form an integral part of the habitats studied and would otherwise possibly be occupied by other (native) species. The only marked difference between both data sets was that when aliens were excluded, the explanatory power of altitude decreased, reflecting the confinement of introduced species to warmer situations in central Europe (Pyšek *et al.*, 1995).

We found closely corresponding results for species and family richness, indicating that in temperate floras there is a very close relationship between diversity measured at different taxonomic levels and that this diversity is driven by the same ecological factors. Similarly, O'Brien *et al.* (1998) reported on similar effects at the three taxonomic levels (species, generic and family). This is caused by a very close correlation between number of taxa at particular taxonomic levels. In other studies, family richness was a good predictor of species richness for a variety of groups and regions (Williams & Gaston, 1994) and the correlation between species richness and that of genera ($r = 0.97$) and families ($r = 0.89$), respectively, in the British Isles, yielded values very similar to those reported in this study. These results indicate that in central Europe, conservation measures adopted to maintain species diversity effectively contribute to maintenance of overall evolutionary variation of the regional flora.

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