

## Diversity of beech forest vegetation in the Eastern Alps, Bohemian Massif and the Western Carpathians

Diverzita vegetace bučin ve Východních Alpách, Českém masivu a Západních Karpatech

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This study compares species composition, local species richness, beta diversity and species pool of beech-dominated forests in three main mountain systems in central Europe. We used a recently compiled representative data set of 5946 vegetation plots recorded in the Eastern Alps, Bohemian Massif and Western Carpathians. Effects of bedrock type, region, altitude and spatial variables represented by PCNM (principal coordinates of neighbour matrices) axes were analyzed. All the predictor variables studied had highly significant effects on species composition. Effect of altitude was largely independent of effects of bedrock and regions, which shared the majority of explained variation in species composition. Spatial (PCNM) variables together accounted for the largest part of the variation in species composition. Communities on carbonate bedrock were differentiated by numerous calcicolous species. Within the group of silicate bedrock types, beech forests on volcanic rocks were differentiated by occurrence of a set of eutrophic and nitrophilous species. The Alps and the Carpathians were similar in species pool size, beta diversity and increasing species richness with altitude, which is related to extensive areas of carbonate bedrock at high altitudes in these mountain systems. The highest local species richness occurred at high altitudes in the Alps. Beech forests in the Alps were floristically well differentiated from the other regions by a group of species restricted to this region, which is probably a consequence of the postglacial migration history. Limited species richness and species pool were found to be typical of the Bohemian Massif; they seem to be partly linked to predominance of siliceous bedrock in this region and partly to the greater distance to beech-forest glacial refugia.

**Key words:** altitude, bedrock, beta diversity, central Europe, *Fagus sylvatica*, spatial pattern, species pool, species richness

## Introduction

Deciduous beech-dominated forests are typical of the natural vegetation in the temperate zone of the northern hemisphere (Box & Fujiwara 2005). In Europe they are one of the most widespread natural habitats and are of considerable interest to nature conservation (Bohn et al. 2003, European Commission 2003, Brunet et al. 2010). European beech (*Fagus sylvatica*) dominates forests across a broad latitudinal, altitudinal and environmental range in the temperate zone of western and central Europe, which is enabled by its broad ecological amplitude and high competitiveness (Leuschner et al. 2006, Ellenberg & Leuschner 2010). Nevertheless, there are remarkable regional differences in diversity of beech-forest plant communities, partly related to the postglacial migration history of beech and its associated species from the glacial refugia on the southern fringes of the Alps, Carpathians and in the Dinaric Mountains (Pawłowski 1970, Hendrych & Hendrychová 1979, Šercelj 1996, Magri et al. 2006, Willner et al. 2009). Vascular plant species composition and richness of beech forests are highly variable among European regions and habitats. Both species-poor and extraordinarily species-rich beech forests can be found (Ewald 2003, 2008, Willner et al. 2004, Ujházyová & Ujházy 2012, Chytrý et al. 2015).

Apart from the very different vegetation histories of individual regions, there are several environmental drivers of species composition and diversity in European beech forests. One of the key factors is the bedrock type, which affects soil properties such as pH and water-holding capacity. Vascular plant species richness in central-European forests is particularly high on calcareous bedrocks, which give rise to soils with a high calcium content and high topsoil pH (Ewald 2003, 2008, Schuster & Diekmann 2003, Wohlgemuth & Gigon 2003, Kooijman 2010). Montane beech forests on carbonate bedrock, such as those in the Northern Alps and the Western Carpathians, can be very species-rich, particularly if enriched by acidophilous species, which grow in the surface organic layer that develops especially under the canopy of admixed coniferous trees (Wohlgemuth & Gigon 2003, Ewald 2008, Ujházyová & Ujházy 2012, Chytrý et al. 2015). Although the positive effect of calcareous bedrock on species diversity is well known, effects of other bedrock types with different chemical and physical properties on species diversity have been rarely studied, even though they may be very important (compare Rédei et al. 2003).

Another important driver of beech-forest vegetation diversity is altitudinal zonality, which correlates with climatic gradients in temperate mountains. Species richness is generally thought to decrease with increasing altitude (Brown & Lomolino 1998, Adams 2009) or to be unimodal with a mid-altitude peak (Rahbek 1995, 2005, Colwell & Lees 2000), but these general trends are often modified by various factors, such as transitions between vegetation types (Lomolino 2001, Grytnes 2003). For example, an inversely unimodal species richness-altitude relationship in the central Slovakian beech forests on volcanic bedrock has been reported by Hrivnák et al. (2014). However, no reliable analyses of general trends in species richness-altitude relationships across central-European beech forests are currently available.

The large-scale variability of central-European beech forests has been described mostly using formal syntaxonomy. However, national or regional vegetation surveys differ in the syntaxonomical concepts used (Oberdorfer 1992, Willner & Grabherr 2007, Ujházyová & Ujházy 2012, Chytrý 2013, Slezák et al. 2016), which makes them difficult to apply internationally. The first attempt to synthesize beech forest vegetation diversity across a broad

area in Europe was made by Willner (2002) and Willner et al. (2004), but these studies did not include the core area of the Western Carpathians, which is influenced by specific postglacial migration pathways (Hendrych & Hendrychová 1979, Willner et al. 2009). Recently established European vegetation-plot databases (Schaminée et al. 2009, Chytrý et al. 2016) make it possible to extend previous analyses of vegetation diversity. In particular, they enable rigorous tests of the relationships that were inferred from informal observations or analyses of local data sets, but never quantified for large areas.

Here we aim at quantifying the relative effects of the above-mentioned factors on diversity of beech-forest vegetation using a representative dataset of 5946 vegetation plots covering the major central-European mountain systems. It includes the whole altitudinal range of beech forests and a representative range of beech-forest site conditions and community types.

Specifically, we address the following questions: (i) How much variation in species composition of central-European beech-forest communities is explained by regional differences, bedrock, altitude and spatial patterns, and how do these factors affect the occurrence of individual species? (ii) Do local species richness, species pool size and beta diversity of beech forests differ among regions, bedrock types and altitudinal zones?

## Materials and methods

### *Study area*

We studied beech forests in three neighbouring regions in central Europe: the Eastern Alps (Austria), the Bohemian Massif (the Czech Republic and northern Austria) and the Western Carpathians (Slovakia and the eastern Czech Republic). These regions are geographically distinct mountain ranges and differ phytogeographically (Willner et al. 2009). The area studied covers a large part of the central-European geographical and ecological range of beech and beech-dominated forests (Fig. 1).

### *Data collection*

Vegetation plots from the Austrian, Czech and Slovak national vegetation databases (Chytrý & Rafajová 2003, Šibík 2012, Willner et al. 2012) in the Turboveg format (Hennekens & Schaminée 2001) and recently sampled unpublished plot data from Slovakia were used. Vegetation plots meeting the criterion of *Fagus sylvatica* cover greater than 50% in the tree layer were selected and analyzed using the Juice program (Tichý 2002). To reduce the possible confounding effects of variable plot size in the databases, we restricted our selection to plots of 200–625 m<sup>2</sup>, which were the most common plot sizes in the database. Also plots for which the size was not specified were included, assuming that most of them were from the accepted size range.

Altitude values were obtained from the plot-related information in the vegetation databases. Phytogeographical regions were identified according to Futák (1966), Skalický (1988) and Meusel & Jäger (1992). GIS layers for bedrock classification were created using digital maps for Austria (Geological Survey of Austria, 1:500 000), the Czech Republic (Czech Geological Survey 1:500 000) and Slovakia (State Geological Institute of Dionýz Štúr 1:50 000). Plots lacking geographic coordinates or altitude were excluded, resulting in a matrix of 5946 plots and 980 taxa of vascular plants.

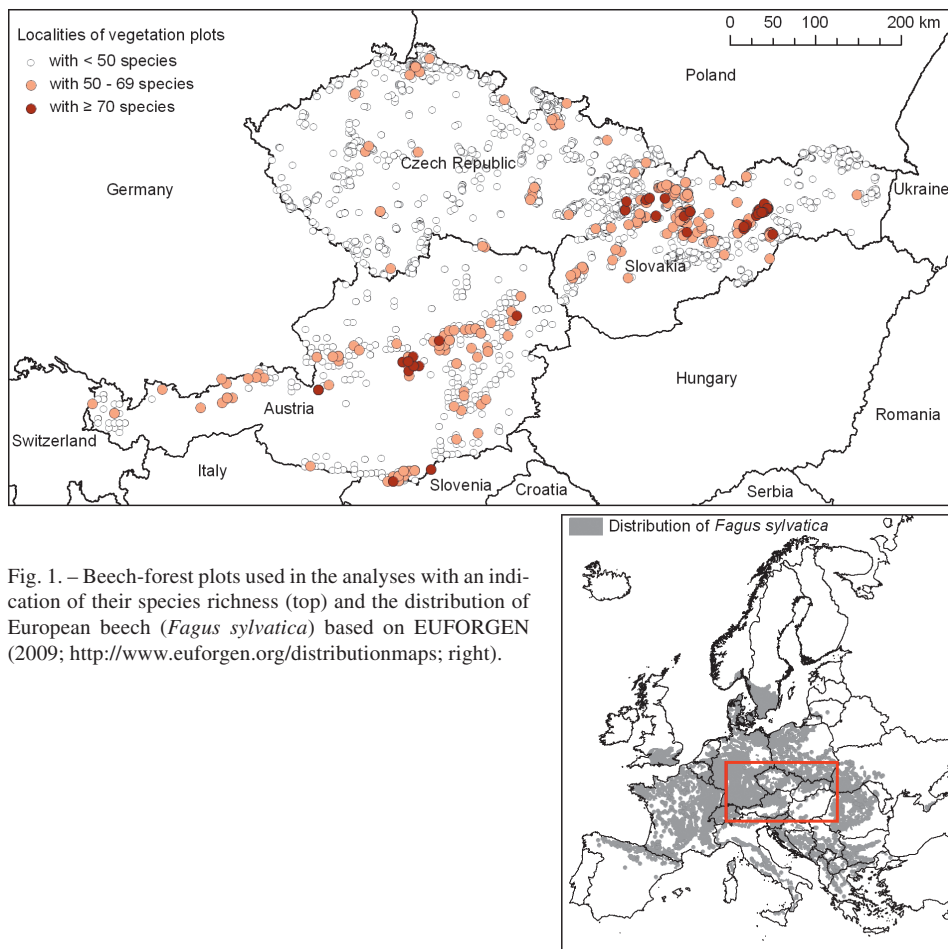


Fig. 1. – Beech-forest plots used in the analyses with an indication of their species richness (top) and the distribution of European beech (*Fagus sylvatica*) based on EUFORGEN (2009; <http://www.euforgen.org/distributionmaps>; right).

### Data processing and analyses

Taxonomic concepts used in different countries and by different authors were unified according to the Euro+Med PlantBase ([ww2.bgbm.org/EuroPlusMed](http://ww2.bgbm.org/EuroPlusMed)) and complemented using ThePlantList for the missing families ([www.theplantlist.org](http://www.theplantlist.org)). A list of the taxa merged into a higher taxonomic level is provided in Electronic Appendix 1. Species of vascular plants recorded in different vegetation layers were merged into one layer. Bryophytes and lichens were not recorded in the majority of plots, and therefore they were not included in the dataset. Species cover-abundance values originally recorded at various semi-quantitative scales were transformed into a nine-degree ordinal scale according to percentage covers underlying individual categories (van der Maarel 1979).

Plots were assigned to orographic/phytogeographical regions: Eastern Alps (Alps; 1204 plots), Bohemian Massif (BohMass; 2142 plots) and Western Carpathians (Carpat;

2600 plots). Plots from the Pannonian region of the Czech Republic, north-eastern Austria and Slovakia were combined with those from the Western Carpathian region. The south-eastern foreland of Styria (SE Austria) was combined with the Alps.

Bedrock information was simplified into six types: carbonate rocks, including all calcareous rocks (Carbo; 1759 plots); Quaternary colluvial and fluvial sediments (Quate; 265); extrusive igneous (volcanic) rocks (Volca; 315); sandstones, clay stones and flysch (Sands; 1517); metamorphic rocks, excluding marble (Metam; 1331); intrusive igneous (magmatic) rocks (Magma; 759).

Mean annual temperature and precipitation were obtained from the WorldClim database ([www.worldclim.org](http://www.worldclim.org)). Since regression analyses indicated a strong relationship between altitude and mean annual temperature ( $r = -0.77$ ,  $r^2 = 0.59$ ,  $P < 0.001$ ), and altitude and annual precipitation ( $r = 0.7$ ,  $r^2 = 0.49$ ,  $P < 0.001$ ), altitude was used to represent climatic factors. Three altitudinal zones were delimited, which correspond to the three beech-dominated altitudinal zones in central Europe recognized by Ellenberg & Leuschner (2010). The altitudinal boundaries of these zones were defined based on Willner & Grabherr (2007), Hlásny et al. (2011) and Hrivnák et al. (2014) as follows:  $< 500$  m (colline; 1387 plots),  $500\text{--}800$  m (submontane; 2541 plots),  $> 800$  m (montane; 2018 plots).

Relationships between species richness and altitude were modelled using a regression analysis. Besides simple linear models, polynomial models of the second and third order were tested using partial F tests. The most parsimonious models explaining variability in species richness were chosen based on Akaike Information Criterion.

We used PCNM (principal coordinates of neighbour matrices; Borcard & Legendre 2002) to identify spatial patterns across the whole range of scales discernible in our data set. This analysis generates eigenvectors that can be used as spatial explanatory variables in multiple regression (Borcard et al. 2004). The analysis involved several steps described by Borcard et al. (2004) and Dray et al. (2006). First, we computed a pairwise geographic (Euclidean) distance matrix from the geographic coordinates of the plot locations. Then we truncated the distance matrix just above the minimum distance (0.616 in our case), which keeps all the sites connected into a single network as defined by the minimum spanning tree algorithm. Any value higher than the truncation distance was replaced by the value of 2.46 ( $4 \times 0.616$ ) in the matrix. Subsequently, we performed principal coordinate analysis (PCoA) to compute the principal coordinates of this modified distance matrix. Only principal coordinates corresponding to positive eigenvalues were selected and used as spatial predictors (hereafter referred to as PCNM variables) in redundancy analysis (RDA). The total number of PCNM variables created by PCoA was 848.

Only significant PCNM variables ( $P < 0.05$ ) that accounted separately for more than 0.1% of the total variation in species data ( $R^2 > 0.001$ ) were selected by forward selection in order to obtain a manageable number of variables. The selection process retained 42 significant positive PCNM variables. The remaining explanatory variables (regions, bedrock types, altitudinal zones) were included in the final model if their marginal effect was significant ( $P < 0.05$ , Monte Carlo permutation test with 999 permutations). Finally, effects of regions, bedrock types, altitudinal zones and spatial (PCNM) variables on the overall pattern in species composition were analyzed using RDA. Ordinal cover values in the species matrix were transformed using the Hellinger transformation prior to the analysis. The variation partitioning algorithm proposed by Peres-Neto et al. (2006) was applied using RDA to quantify shared and unique effects of regions, bedrock types,

altitudinal zones and PCNM variables. This algorithm provides unbiased estimates of explained variation (adjusted  $R^2$ ) that control for unequal number of categories within the categorical variables and unequal numbers of variables in different groups. Significance of the marginal and pure effects of explanatory variables was tested using Monte Carlo test with 999 permutations.

Principal component analysis (PCA) with supplementary categorical variables was used to visualize the main trends of compositional variation in the species data set. Hellinger transformation of ordinal cover values was used for consistency with the RDA analysis.

To express floristic differentiation among the categories of explanatory variables, phi coefficient of association between species and groups of plots classified in these categories was computed using the JUICE 7.0 program (Tichý 2002). Additionally, Fisher's exact test was calculated to establish significances of these associations. Species significantly associated with particular categories with  $\phi > 0.15$  were considered as a specific (diagnostic) species of the categories.

Local species richness (alpha diversity) was calculated as the average number of species per plot within each region, bedrock type and altitudinal zone. Beta diversity was computed following Anderson et al. (2006) as the average distance (compositional dissimilarity) of all plots within each category to the category centroid. Bray-Curtis index was used as a measure of dissimilarity and centroids of the particular categories were obtained from the scores of principal coordinate analysis (PCoA). Differences in species richness and beta diversity among regions, bedrock types and altitudinal zones were tested using ANOVA and Tukey's HSD post hoc tests.

Species pool size was calculated using the JUICE 7.0 program (Tichý 2002) as the cumulative number of vascular plant species recorded in the plots belonging to individual categories. Rarefaction was performed to obtain species pool size estimates based on the same number of plots within categories (Colwell et al. 2004).

Analyses were performed and graphs drawn in the R language (R Core Team 2015), using the library vegan (Oksanen et al. 2014), and CANOCO 5 package (Šmilauer & Lepš 2014).

## Results

### *Response of species composition to explanatory variables*

The RDA model, consisting of regions, bedrock types, altitudinal zones and PCNM variables, accounted for 17.1% of the total variation in plant community composition. All variables had significant effects on species composition, although their explanatory power was different (Table 1). In RDA, the three categorical variables (regions, bedrock types, altitudinal zones) together accounted for 9.9% of overall variation in species composition. Bedrock had the largest and altitude the smallest marginal effect. However, spatial variables accounted for more of the variability than all the above mentioned categorical variables combined. The effect of spatial variables was partly shared with the effects of region, bedrock and altitude (Fig. 2). Region and bedrock also shared large parts of their explanatory power, but effect of altitude was almost independent of these two predictors.

Table 1. – Marginal and pure effects of regions, bedrocks, altitudinal zones, PCNM (principal coordinates of neighbour matrices), and of all variables combined, on the composition of vascular plant communities in central-European beech forests. Degrees of freedom, test statistics, probabilities of type I error and adjusted coefficient of determination ( $R^2$ ) values are given for each variable. The significances were tested using a Monte Carlo permutation test with 999 permutations.

Variables	Marginal effect				Pure effect			
	df	pseudo-F	P-value	adjusted $R^2$ (%)	df	pseudo-F	P-value	adjusted $R^2$ (%)
All variables	51	25.03	0.001	17.09	–	–	–	–
Regions	2	119.28	0.001	3.83	2	7.55	0.001	0.18
Bedrocks	5	60.80	0.001	4.78	5	17.95	0.001	1.19
Altitudinal zones	2	96.39	0.001	3.10	2	46.97	0.001	1.29
PCNM variables	42	24.56	0.001	14.27	42	13.35	0.001	7.24

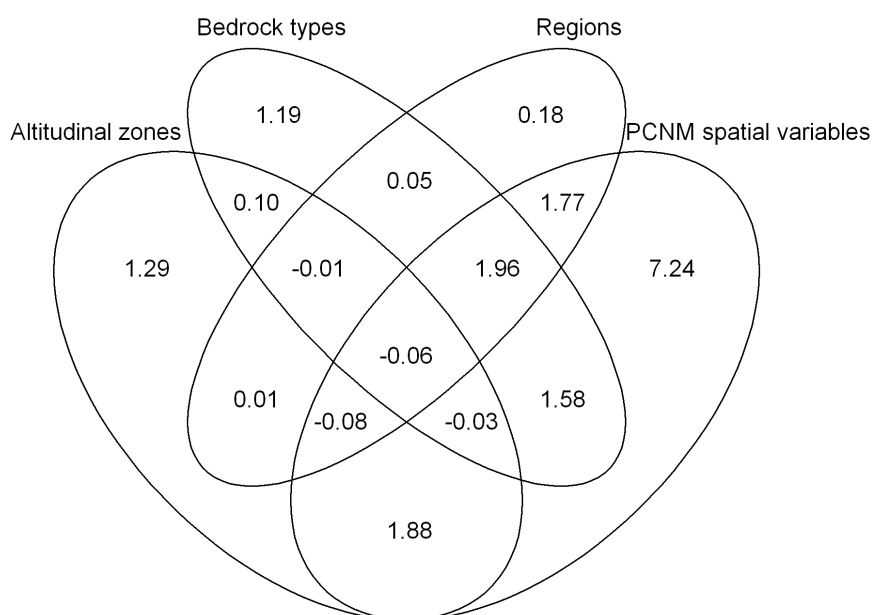


Fig. 2. – Variation partitioning showing the effects of regions, bedrock, altitudinal zones and space (PCNM variables) on the species composition in central-European beech forests. Adjusted  $R^2$  values (%) are given for each pure and shared fraction of explained variation. Low negative values of shared explained variation result from the subtraction of larger fractions (Legendre & Legendre 2012). The residual (unexplained) fraction was 82.9%.

Differences in species composition among the categories of explanatory variables are summarized in Tables 2–4. Twelve species had a frequency higher than 30% in all regions, and 69 species showed significantly higher concentration in a single region (most of them in the Alps) than in the rest of the data set ( $p < 0.05$ , Fisher's exact test). The Alps were characterized by a larger number of high-altitude calcicolous species, the Bohemian Massif by acidophilous/oligotrophic species with optima on magmatic and metamorphic bedrocks, and the Carpathians by a higher frequency of nitrophilous species with an ecological optimum in forests of the *Tilio-Acerion* alliance (Table 2). Among

the different bedrock types, the largest number of specific species was recorded on carbonate (45) and volcanic (13) bedrocks, and only 7 species reached a frequency > 30% on all bedrocks (Table 3). In addition to calcicolous species, thermophilous and eutrophic species were also specific to carbonates. Communities on volcanic rocks were differentiated by a high frequency of nitrophilous species. Species composition also well reflected the altitudinal zonation (Table 4). Most of the specific species were found in the highest zone (35), fewer in the lowest (13), while the intermediate zone had a transitional character and specific species were lacking there. Ten species were frequent (> 30%) in all zones.

In the ordination diagram of PCA (Fig. 3A), the most frequent species in central-European beech forests were arranged according to the nutrient and soil reaction requirements (1st axis) and altitude (2nd axis). Effects of bedrock types and regions were related especially to the 3rd axis, which contrasted the Alps and carbonates at one end to the other regions and other bedrock types at the opposite end (Fig. 3B). Eutrophic species (e.g. *Fraxinus excelsior*, *Geranium robertianum* and *Mercurialis perennis*) were specific to base-rich bedrocks, while acidophilous and oligotrophic species (e.g. *Avenella flexuosa* and *Vaccinium myrtillus*) were typical of poor siliceous bedrocks. Montane species most frequently occurred on carbonates in the Alps (*Adenostyles alpina*, *Calamagrostis varia* and *Valeriana tripteris*) and the eutrophic/nitrophilous species on volcanic rocks in the Western Carpathians (*Cardamine bulbifera* and *Impatiens noli-tangere*), and species on poor siliceous rocks in the Bohemian Massif (*Calamagrostis villosa* and *Luzula luzuloides*).

#### *Pattern of local species richness, beta diversity and species pool*

Local species richness in beech forests varied from 1 (only *Fagus sylvatica*) to 100 vascular species of plants per plot. It significantly differed among regions (Fig. 4A). Average number of species was highest in the Alps (32) and lowest in the Bohemian Massif (21), where the lowest variance in values was also recorded (Table 5). The species-richest communities (43 plots exceeding 70 species) were recorded in the Alps and Carpathians exclusively on carbonate bedrock (Fig. 1). Average species richness was also highest on carbonates (37) and lowest on intrusive igneous (magmatic) rocks (18; Fig. 4B).

Species richness increased with altitude in the whole area. Average values were highest (31) at altitudes over 800 m (Fig. 4C), where the maximum richness was also recorded. Minimum average richness (23) occurred below 500 m a.s.l. However, extremely species-poor plots were recorded in all zones. There were significant relationships between species richness and altitude in all regions (Fig. 5), with a monotonously increasing trend in the Alps and Carpathians, and weak inversely unimodal relationship in the Bohemian Massif.

Beta diversity was higher in the Alps and the Carpathians than in the Bohemian Massif (Fig. 6A). Splitting the plots into three altitudinal zones revealed that beta diversity decreased from the lowest (up to 500 m a.s.l.) to the highest zone (above 800 m a.s.l.; Fig. 6C). Considering the bedrock, the highest beta diversity was recorded on Quaternary alluvial and colluvial sediments, and it was also high on carbonate bedrocks. The lowest beta diversity was recorded on volcanic and crystalline siliceous bedrocks (Table 5, Fig. 6B).



Table 2. – Floristic differentiation among the three regions studied (Eastern Alps, Bohemian Massif, Western Carpathians). Numbers are percentage occurrence frequencies and asterisks indicate species concentration in plots of particular categories measured by the phi coefficient of association (\* 0.15–0.30, \*\* > 0.30). Only significant concentrations (Fisher's exact test,  $P < 0.05$ ) are shown. Species with a frequency > 30% that are not associated with any region are shown in the top part and the rest of the species are ordered by decreasing fidelity within the regions. Only species with a frequency  $\geq 10\%$  in at least one column are shown.

Region	Eastern Alps	Bohemian Massif	Western Carpathians
No. of plots	1204	2142	2600
Frequent species			
<i>Fagus sylvatica</i>	100	100	100
<i>Acer pseudoplatanus</i>	73	55	68
<i>Oxalis acetosella</i>	58	69	53
<i>Mercurialis perennis</i>	56	39	50
<i>Lactuca muralis</i>	51	38	57
<i>Athyrium filix-femina</i>	38	45	48
<i>Senecio nemorensis</i> agg.	45	54	54
<i>Viola reichenbachiana</i>	50	35	47
<i>Lamium galeobdolon</i> agg.	46	41	44
Species associated with particular regions			
<i>Cyclamen purpurascens</i>	36**	2	.
<i>Adenostyles alpina</i>	27**	.	.
<i>Helleborus niger</i>	25**	.	.
<i>Veronica urticifolia</i>	24**	.	.
<i>Cardamine trifolia</i>	22**	1	1
<i>Hepatica nobilis</i>	28**	9	1
<i>Aposeris foetida</i>	16**	.	1
<i>Calamagrostis varia</i>	31**	.	10
<i>Carex alba</i>	28**	.	9
<i>Anemone trifolia</i>	12*	.	.
<i>Lonicera alpigena</i>	11*	.	1
<i>Phyteuma spicatum</i>	26*	5	7
<i>Larix decidua</i>	20*	4	3
<i>Galium sylvaticum</i>	18*	5	1
<i>Polygala chamaebuxus</i>	10*	1	.
<i>Picea abies</i>	69*	50	34
<i>Valeriana tripteris</i>	22*	.	9
<i>Asplenium viride</i>	13*	.	2
<i>Abies alba</i>	52*	19	30
<i>Solidago virgaurea</i>	35*	13	14
<i>Polystichum aculeatum</i> agg.	23*	2	10
<i>Gymnocarpium robertianum</i>	10*	1	2
<i>Daphne mezereum</i>	39*	12	23
<i>Prenanthes purpurea</i>	63*	44	37
<i>Salvia glutinosa</i>	31*	1	22
<i>Gentiana asclepiadea</i>	17*	1	7
<i>Carex digitata</i>	32*	8	18
<i>Cardamine enneaphyllos</i>	31*	12	14
<i>Clematis vitalba</i>	13*	1	4
<i>Sanicula europaea</i>	36*	13	20
<i>Veratrum album</i>	10*	1	2
<i>Aconitum lycoctonum</i>	10*	1	3
<i>Ranunculus polyanthemus</i> subsp. <i>nemorosus</i>	10*	.	3
<i>Fraxinus excelsior</i>	50*	25	35
<i>Sesleria caerulea</i>	12*	1	5
<i>Neottia nidus-avis</i>	24*	4	14
<i>Luzula sylvatica</i>	13*	2	5

Region	Eastern Alps	Bohemian Massiff	Western Carpathians
<i>Sorbus aria</i> agg.	19*	1	16
<i>Primula elatior</i>	16*	2	10
<i>Calamagrostis villosa</i>	1	21**	1
<i>Avenella flexuosa</i>	6	31**	5
<i>Drymochloa sylvatica</i>	7	27**	4
<i>Calamagrostis arundinacea</i>	8	27*	11
<i>Dryopteris carthusiana</i> agg.	15	45*	31
<i>Poa nemoralis</i>	13	35*	24
<i>Gymnocarpium dryopteris</i>	14	25*	11
<i>Milium effusum</i>	5	18*	9
<i>Moehringia trinervia</i>	4	16*	8
<i>Sorbus aucuparia</i>	27	44*	30
<i>Maianthemum bifolium</i>	15	31*	19
<i>Cardamine bulbifera</i>	14	22	57**
<i>Asarum europaeum</i>	12	9	38**
<i>Galium intermedium</i>	1	1	19**
<i>Geranium robertianum</i>	14	19	37*
<i>Cardamine glandulifera</i>	.	1	10*
<i>Pulmonaria officinalis</i>	12	10	29*
<i>Glechoma hederacea</i> agg.	1	1	11*
<i>Campanula rapunculoides</i>	8	4	19*
<i>Dryopteris filix-mas</i>	43	42	63*
<i>Rubus</i> sect. <i>Rubus</i>	11	17	30*
<i>Carex pilosa</i>	10	4	19*
<i>Heracleum sphondylium</i>	5	2	13*
<i>Galium odoratum</i>	49	51	68*
<i>Acer campestre</i>	8	3	15*
<i>Melittis melissophyllum</i>	9	1	14*
<i>Melica uniflora</i>	4	8	15*
<i>Lathyrus vernus</i>	14	13	26*
<i>Myosotis sylvatica</i> agg.	2	4	10*
<i>Euphorbia amygdaloides</i>	35*	2	34*

Table 3. – Floristic differentiation of beech forests on different bedrocks. See Table 2 for details.

Bedrock	Carbonate	Quaternary	Volcanic	Sandstone	Metamorphic	Magmatic
No. of plots	1759	265	315	1517	1331	759
Frequent species						
<i>Fagus sylvatica</i>	100	100	100	100	100	100
<i>Senecio nemorensis</i> agg.	55	37	54	45	62	44
<i>Lactuca muralis</i>	65	50	61	40	42	39
<i>Viola reichenbachiana</i>	47	51	57	46	37	31
<i>Oxalis acetosella</i>	46	46	52	65	74	65
Species associated with particular bedrocks						
<i>Calamagrostis varia</i>	32**	14	.	1	1	1
<i>Cirsium erisithales</i>	19**	1	1	1	1	1
<i>Sorbus aria</i> agg.	31**	13	3	3	1	1
<i>Valeriana tripteris</i>	25**	10	1	1	1	1
<i>Daphne mezereum</i>	48**	23	14	12	12	4
<i>Lilium martagon</i>	29**	9	3	4	6	1
<i>Cyclamen purpurascens</i>	22**	3	.	3	3	1
<i>Epipactis helleborine</i> agg.	26*	9	4	4	4	1
<i>Campanula rapunculoides</i>	28*	12	8	4	2	3

Bedrock	Carbonate	Quaternary	Volcanic	Sandstone	Metamorphic	Magmatic
<i>Euphorbia amygdaloides</i>	46*	26	17	22	2	6
<i>Heracleum sphondylium</i>	20*	8	3	2	2	1
<i>Carex digitata</i>	37*	26	11	11	5	5
<i>Rosa pendulina</i>	15*	2	7	1	1	1
<i>Campanula trachelium</i>	28*	15	8	6	5	4
<i>Cephalanthera damasonium</i>	13*	4	.	1	2	1
<i>Vincetoxicum hirsundinaria</i>	17*	11	2	2	1	.
<i>Cornus mas</i>	11*	3	.	2	.	.
<i>Pimpinella major</i>	10*	3	.	1	1	.
<i>Melica nutans</i>	32*	16	8	11	11	4
<i>Neottia nidus-avis</i>	28*	14	16	5	3	4
<i>Primula elatior</i>	19*	7	5	5	2	1
<i>Cephalanthera rubra</i>	14*	8	1	1	1	.
<i>Melittis melissophyllum</i>	21*	12	8	4	1	1
<i>Mercurialis perennis</i>	69*	44	48	39	41	23
<i>Digitalis grandiflora</i>	13*	5	1	1	3	1
<i>Sesleria caerulea</i>	13*	8	.	2	1	.
<i>Asplenium viride</i>	10*	5	.	1	1	1
<i>Laserpitium latifolium</i>	10*	4	1	1	1	.
<i>Galium intermedium</i>	21*	10	11	4	1	1
<i>Fragaria vesca</i>	35*	23	22	9	11	6
<i>Solidago virgaurea</i>	32*	22	4	8	20	9
<i>Gentiana asclepiadea</i>	15*	7	2	3	3	2
<i>Lonicera xylosteum</i>	24*	16	16	5	2	1
<i>Platanthera bifolia</i>	10*	2	2	2	1	1
<i>Cardamine trifolia</i>	12*	6	.	1	2	3
<i>Asarum europaeum</i>	38*	25	23	19	11	12
<i>Tanacetum corymbosum</i> agg.	11*	7	2	2	1	1
<i>Convallaria majalis</i>	16*	12	4	4	2	2
<i>Cardamine enneaphyllos</i>	27*	15	4	15	14	7
<i>Larix decidua</i>	13*	4	2	4	5	3
<i>Lathyrus vernus</i>	32*	21	23	16	11	6
<i>Polystichum aculeatum</i> agg.	19*	11	4	10	3	2
<i>Acer pseudoplatanus</i>	79*	57	64	61	60	49
<i>Ranunculus lanuginosus</i>	12*	4	3	2	4	2
<i>Phyteuma spicatum</i>	19*	17	2	7	9	1
<i>Veronica urticifolia</i>	11*	11	.	2	2	.
<i>Campanula persicifolia</i>	15*	9	5	3	4	3
<i>Aposeris foetida</i>	7	21**	1	1	1	.
<i>Hepatica nobilis</i>	18	22*	3	5	6	1
<i>Hedera helix</i>	20	23*	8	7	3	2
<i>Glechoma hederacea</i> agg.	4	5	25*	6	1	3
<i>Ribes uva-crispa</i>	7	5	22*	2	2	1
<i>Geranium robertianum</i>	25	23	55*	29	21	21
<i>Dryopteris filix-mas</i>	47	49	82*	53	50	47
<i>Urtica dioica</i>	11	10	42*	18	22	20
<i>Cardamine bulbifera</i>	35	25	61*	46	25	26
<i>Stachys sylvatica</i>	6	10	28*	15	12	9
<i>Acer platanoides</i>	27	23	41*	17	22	16
<i>Sambucus racemosa</i>	2	2	15*	4	8	6
<i>Galium odoratum</i>	57	45	78*	68	54	42
<i>Alliaria petiolata</i>	7	6	17*	5	4	5
<i>Circea lutetiana</i>	5	17	25*	18	6	5
<i>Sambucus nigra</i>	7	16	26*	19	5	8
<i>Rubus</i> sect. <i>Rubus</i>	8	23	43*	36	19	23
<i>Rubus idaeus</i>	19	11	40*	24	32	27

Bedrock	Carbonate	Quaternary	Volcanic	Sandstone	Metamorphic	Magmatic
<i>Lamium maculatum</i>	4	1	10*	2	1	3
<i>Cardamine glanduligera</i>	3	2	3	11*	1	1
<i>Carex sylvatica</i>	14	24	10	32*	16	9
<i>Carex pilosa</i>	8	15	23	24*	3	3
<i>Drymochloa sylvatica</i>	5	1	3	8	30*	19
<i>Calamagrostis arundinacea</i>	7	5	13	13	34*	19
<i>Carex pilulifera</i>	1	1	1	2	4	15*
<i>Carex alba</i>	28*	24*	.	2	1	1
<i>Helleborus niger</i>	15*	14*	.	1	1	.
<i>Adenostyles alpina</i>	15*	14*	.	2	1	.
<i>Calamagrostis villosa</i>	1	.	2	1	19*	26*
<i>Avenella flexuosa</i>	3	8	4	8	31*	34*

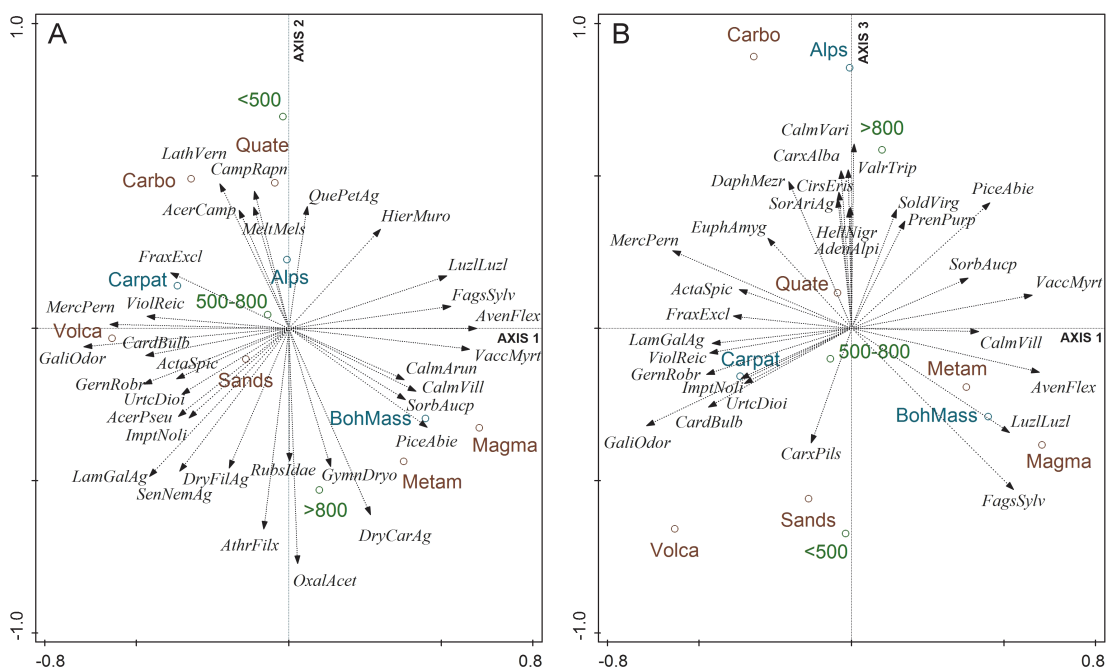


Fig. 3. – Principal components analysis (PCA) of central-European beech forest vegetation with passively projected variables. Plotted ordination axes accounted for 8.6% (axis 1), 7.5% (axis 2) and 4.9% (axis 3) of total variance. The biplot A (axis 1 and 2) shows the 32 most important species (fit  $\geq 16\%$ ), and the biplot B (axis 1 and 3) shows the 28 most important species (fit  $\geq 15\%$ ). For abbreviations of explanatory variables see Methods. Abbreviations of species names: *AcerPlat* – *Acer platanoides*, *AcerPseu* – *Acer pseudoplatanus*, *ActaSpic* – *Actaea spicata*, *AdenAlpi* – *Adenostyles alpina*, *AthrFilx* – *Athyrium filix-femina*, *AvenFlex* – *Avenella flexuosa*, *CalmArun* – *Calamagrostis arundinacea*, *CalmVill* – *Calamagrostis villosa*, *CampRapn* – *Campanula rapunculoides*, *CardBulb* – *Cardamine bulbifera*, *CarxAlba* – *Carex alba*, *CarxPils* – *Carex pilosa*, *CirsEris* – *Cirsium erisithales*, *DaphMezr* – *Daphne mezereum*, *DryCarAg* – *Dryopteris carthusiana* agg., *DryFilAg* – *Dryopteris filix-mas* agg., *EuphAmyg* – *Euphorbia amygdaloides*, *FagsSylv* – *Fagus sylvatica*, *FraxExcl* – *Fraxinus excelsior*, *GaliOdor* – *Galium odoratum*, *GernRobr* – *Geranium robertianum*, *GymnDryo* – *Gymnocarpium dryopteris*, *HierMuro* – *Hieracium murorum*, *HellNigr* – *Helleborus niger*, *ImptNoli* – *Impatiens noli-tangere*, *LamGalAg* – *Lamium galeobdolon* agg., *LathVern* – *Lathyrus vernus*, *LuzLuzl* – *Luzula luzuloides*, *MeltMels* – *Melittis melissophyllum*, *MercPern* – *Mercurialis perennis*, *OxalAcet* – *Oxalis acetosella*, *PiceAbie* – *Picea abies*, *PrenPurp* – *Prenanthes purpurea*, *QuePetAg* – *Quercus petraea* agg., *RubsIdae* – *Rubus idaeus*, *SenNemAg* – *Senecio nemorensis* agg., *SoldVirg* – *Solidago virgaurea*, *SorbAucp* – *Sorbus aucuparia*, *SorAriAg* – *Sorbus aria* agg., *UrtcDioi* – *Urtica dioica*, *VaccMyrt* – *Vaccinium myrtillus*, *ValrTrip* – *Valeriana tripteris*, *ViolReic* – *Viola reichenbachiana*.

Table 4. – Floristic differentiation in beech forests in different altitudinal zones. See Table 2 for details.

Altitudinal zone	< 500	500–800	> 800
No. of plots	1387	2541	2018
Frequent species			
<i>Fagus sylvatica</i>	100	100	100
<i>Galium odoratum</i>	63	60	52
<i>Viola reichenbachiana</i>	47	45	38
<i>Lactuca muralis</i>	48	52	47
<i>Hieracium murorum</i>	36	36	32
<i>Cardamine bulbifera</i>	30	39	34
<i>Mercurialis perennis</i>	34	52	49
Species associated with particular altitudinal zones			
<i>Carpinus betulus</i>	34**	10	1
<i>Quercus petraea</i> agg.	36**	12	1
<i>Carex pilosa</i>	32**	9	1
<i>Tilia cordata</i>	20*	5	1
<i>Impatiens parviflora</i>	14*	2	1
<i>Acer campestre</i>	21*	10	1
<i>Melica uniflora</i>	22*	11	2
<i>Lathyrus vernus</i>	31*	21	8
<i>Hedera helix</i>	19*	12	2
<i>Dactylis glomerata</i> agg.	11*	3	2
<i>Luzula luzuloides</i>	38*	28	18
<i>Galium sylvaticum</i>	12*	4	4
<i>Acer platanoides</i>	33*	27	10
<i>Polygonatum verticillatum</i>	2	17	50**
<i>Picea abies</i>	23	43	69**
<i>Stellaria nemorum</i>	1	4	21**
<i>Oxalis acetosella</i>	39	55	80**
<i>Valeriana tripteris</i>	1	3	20**
<i>Luzula sylvatica</i>	1	1	15**
<i>Prenanthes purpurea</i>	20	44	63*
<i>Abies alba</i>	13	27	48*
<i>Rubus idaeus</i>	10	21	40*
<i>Senecio nemorensis</i> agg.	23	55	68*
<i>Petasites albus</i>	3	9	23*
<i>Lactuca alpina</i>	.	1	10*
<i>Polystichum aculeatum</i> agg.	2	7	20*
<i>Adenostyles alpina</i>	1	2	13*
<i>Gentiana asclepiadea</i>	1	4	15*
<i>Cardamine trifolia</i>	1	2	12*
<i>Calamagrostis varia</i>	2	8	20*
<i>Rosa pendulina</i>	1	3	12*
<i>Phyteuma spicatum</i>	2	8	19*
<i>Athyrium filix-femina</i>	28	44	59*
<i>Dryopteris carthusiana</i> agg.	17	32	46*
<i>Veronica urticifolia</i>	1	2	11*
<i>Lamium galeobdolon</i> agg.	30	40	57*
<i>Gymnocarpium dryopteris</i>	7	14	27*
<i>Helleborus niger</i>	1	3	11*
<i>Ranunculus lanuginosus</i>	2	2	12*
<i>Paris quadrifolia</i>	8	16	29*
<i>Cirsium erisithales</i>	1	4	12*
<i>Sorbus aucuparia</i>	19	34	46*
<i>Cardamine enneaphyllos</i>	7	15	26*

Altitudinal zone	< 500	500–800	> 800
<i>Vaccinium myrtillus</i>	11	13	27*
<i>Primula elatior</i>	3	6	15*
<i>Acer pseudoplatanus</i>	48	65	75*
<i>Phlegopteris connectilis</i>	1	4	10*
<i>Dryopteris filix-mas</i>	35	53	60*

Table 5. – Species pool sizes (estimated by rarefaction corresponding to the number of plots in the smallest group), average species richness (average number of species per plot) and beta diversity (average distance to the group centroid) in the different regions, on different bedrocks and in individual altitudinal zones. Total number of species recorded in all plots of a given category is also provided.

	No. of plots	Total no. of species	Estimated species pool	Average species richness	Beta diversity
<b>Regions</b>					
Eastern Alps	1204	632	632	31.9	0.496
Bohemian Massif	2142	530	463	20.7	0.481
Western Carpathians	2600	748	629	28.9	0.498
<b>Bedrocks</b>					
Carbonate	1759	792	519	36.9	0.505
Quaternary	265	437	437	26.7	0.518
Volcanic	315	325	310	26.6	0.466
Sandstone	1517	507	375	22.5	0.484
Metamorphic	1331	511	336	22.3	0.473
Magmatic	759	362	281	18.3	0.474
<b>Altitudinal zones</b>					
< 500 m	1387	633	633	23.2	0.507
500–800 m	2541	752	651	25.6	0.499
> 800 m	2018	708	651	30.2	0.481

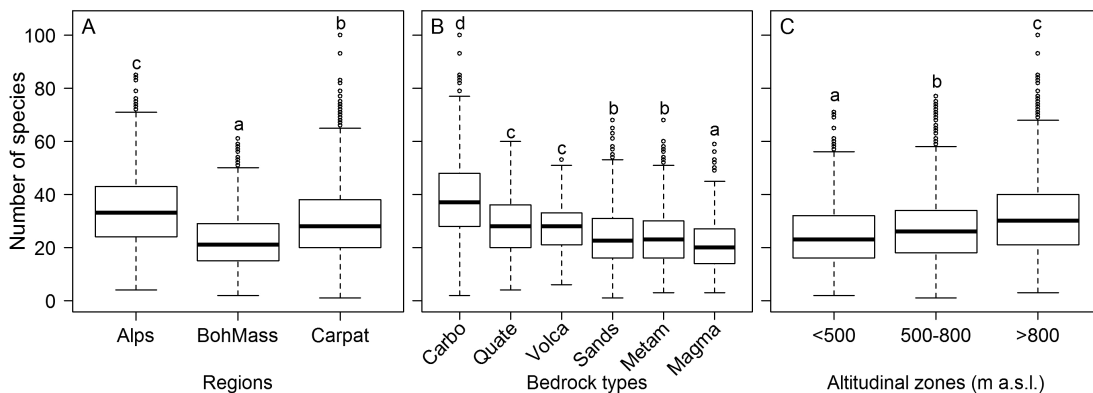


Fig. 4. – Species richness of vascular plants in beech forests divided by regions, bedrock and altitudinal zones. The same letters indicate homogeneous groups (Tukey's HSD post hoc test,  $P < 0.05$ ). Boxes in boxplots include 25–75% of values, horizontal lines are medians, whiskers show the range of non-outlying values (1.5 times the interquartile range from the 25th and 75th percentiles) and points represent outliers. Carbo – carbonate rocks; Magma – intrusive igneous rocks; Metam – metamorphic rocks; Quate – Quaternary sediments; Sands – sandstones, claystones and flysch; Volca – extrusive igneous rocks.

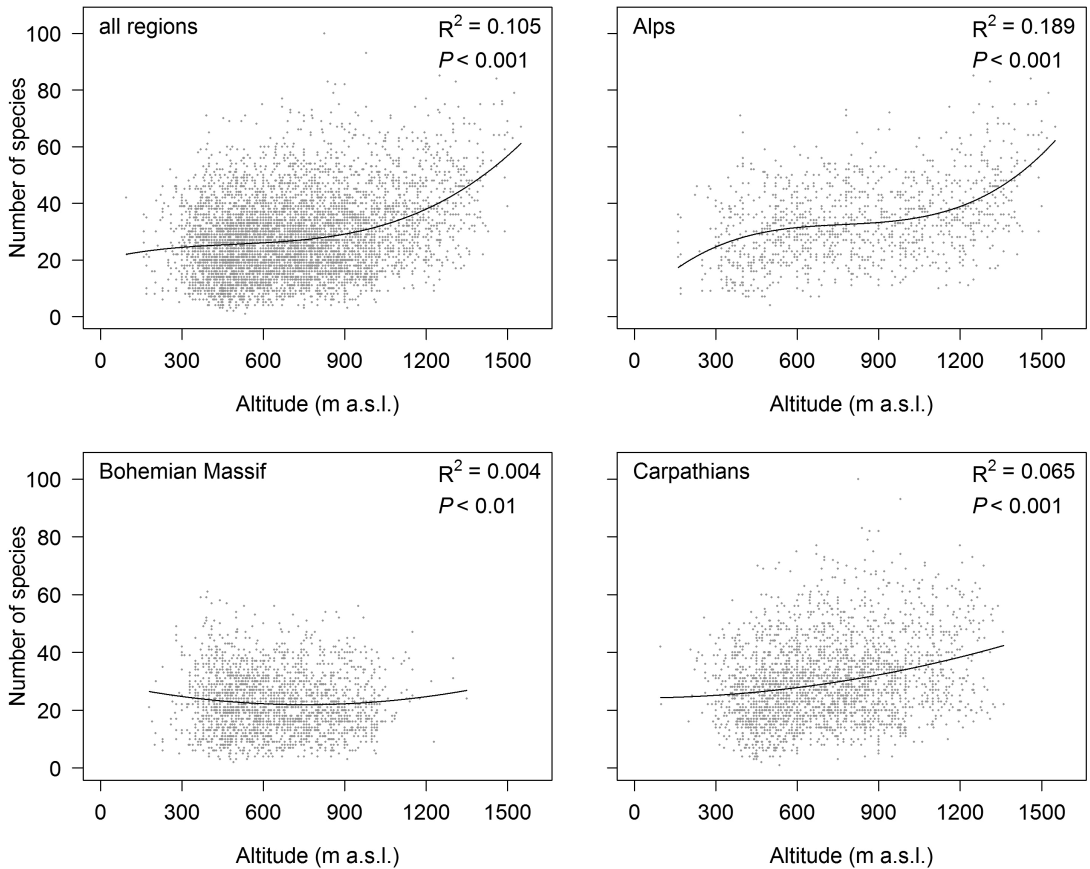


Fig. 5. – Species richness of vascular plants in beech forests in relation to altitude. Trends were fitted using either second (Bohemian Massif and Carpathians) or third-order polynomial regressions (all regions and the Alps) selected based on the Akaike Information Criterion.

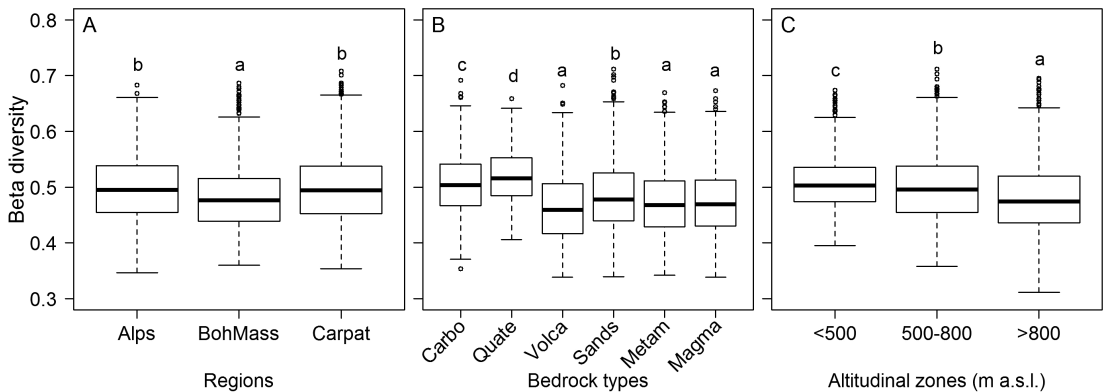


Fig. 6. – Beta diversity of vascular plant species in the three regions, on different bedrocks and in three altitudinal zones. Beta diversity was computed as the average distance (compositional dissimilarity) of individual plots to their group centroid. The same letters indicate homogeneous groups (Tukey's post hoc test,  $P < 0.05$ ).

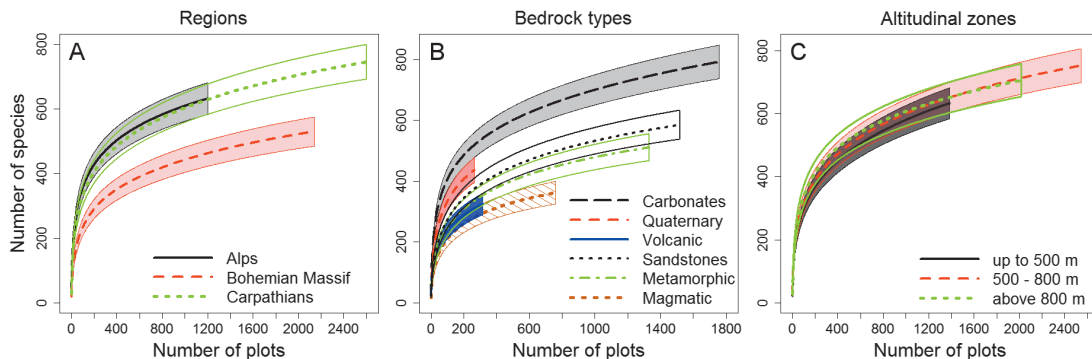


Fig. 7. – Sample-based rarefaction curves of the number of species in the three regions, on different bedrocks and in three altitudinal zones. Means and 95% confidence intervals are shown.

Species pool sizes in the Alps and the Carpathians did not differ significantly when the same numbers of plots were compared using rarefaction, but lower values were recorded in the Bohemian Massif (Fig. 7A, Table 5). Species pool sizes significantly differed among bedrock types with a maximum on carbonates and minimum on magmatic rocks (Fig. 7B, Table 5). However, there were no significant differences in the species pool sizes among altitudinal zones (Fig. 7C, Table 5).

## Discussion

### *Patterns in the species composition*

We confirmed that phytogeographical regions, bedrock and altitude are significant drivers of the species composition in central-European beech forests (Bohn et al. 2003, Ellenberg & Leuschner 2010). The proportion of variation explained by these three variables was relatively low, most probably due to the general decrease in proportion of explained variation with increasing data set size in direct ordination (Økland 1999, Fischer et al. 2014).

We corroborated the results of previous studies that bedrock is an important driver of species composition in beech forests (e.g. Wohlgemuth 1998, Lobo et al. 2001, Bruun et al. 2003, Moser et al. 2005) and for the first time quantified these relationships for a large central-European area. In particular, the contrast between base-rich (calcareous, volcanic) and poor siliceous (magmatic or metamorphic) rocks accounted for the highest proportion of the variation in the species composition. Effect of bedrock is linked to soil pH and nutrient availability. Since *Fagus sylvatica* dominates over a wide range of soil pH in central Europe (Härdtle et al. 2004, Leuschner et al. 2006, Ellenberg & Leuschner 2010, Packham et al. 2012), beech forests provide habitats for species with very different relationships with soil chemistry. Soil reaction is reported as a significant driver of species composition in beech-forest understorey in various regional studies (e.g. Ujházy et al. 2004, Mölder et al. 2008, Fischer et al. 2014, Slezák et al. 2016) and phytosociological classification uses the distinction between basic/nutrient-rich and acidic/nutrient-poor soils as the main criterion to identify beech forest vegetation at the alliance or suballiance level (Willner & Grabherr 2007, Boublík et al. 2013).



Communities on the other bedrock types are less specific than those on carbonates. Quaternary sediments are a heterogeneous group of bedrocks, most frequently occurring as colluvial and alluvial deposits in the valleys and foothills in the Alps and Carpathians. As these sediments often originate from calcareous sources, they share the majority of species with carbonate bedrocks in neighbouring areas. The flysch zone, with heavier soils on sandstones and claystones, harbours only very few beech-forest species confined to this bedrock type. Nevertheless, the continuous flysch belt probably served as a postglacial migration corridor for forest herbaceous plants from the Dacian refugia to the Western Carpathians (Hendrych & Hendrychová 1979). The optimum of *Cardamine glanduligera*, a Carpathian subendemic (Kliment et al. 2016), in the Western-Carpathian flysch zone, is an example.

Mineral richness of andesite (prevailing volcanic rock) is higher than that of granite (prevailing intrusive igneous rock) or metamorphic crystalline rocks (Húsenica 1964). Communities on volcanic bedrock are well differentiated by a large group of eutrophic species, which are linked especially to scree forests (Jarolímek & Šibík 2008). Higher mineral content, pH and organic matter content enable better nitrification of forest soils (Nugroho et al. 2007), which is the case for rocky soils on andesites.

Altitudinal zonation is another significant factor affecting the species composition in beech forests in central-European mountain systems (Willner 2002, Leuschner et al. 2006, Ewald 2008, Ellenberg & Leuschner 2010, Fischer et al. 2014, Hrivnák et al. 2014, Slezák et al. 2016). Species typical of oak and oak-hornbeam forests differentiate beech forests in the colline zone, while species of montane forests and subalpine tall-herb vegetation differentiate the forests in the montane zone. In the Alps, the latter zone can be further divided into the middle-montane (800–1200 m) and the supra-montane (1200–1600 m) zone as subalpine species are mostly absent in the middle-montane fir-beech forests (Willner 2002). Typical shade-tolerant beech-forest species have their optima at mid-altitudes with a relatively mild climate strongly dominated by beech, while species of neighbouring communities enrich beech-dominated communities at both ends of the altitudinal gradient (Hrivnák et al. 2014).

Variation partitioning indicates that species differentiation in beech-forest communities is determined mainly by the spatial variables. To some extent, spatial variables may include effects of other environmental variables that were not included in this study. Nevertheless, the most important PCNM variable accounted for less variation than the marginal effect of regions. This means that phytogeographical regions represent more than just large-scale spatial variation. Effect of biogeography on the variation in species composition clearly increases with the scale of a study. Species composition is related indirectly to geographical position, due to inter-regional differences in macroclimate and vegetation history (Stephenson 1998, Willner et al. 2009, Marinšek et al. 2013). In contrast to local and regional studies, in which edaphic and altitudinal gradients are stressed (Carr et al. 2009, Fischer et al. 2014), latitude and longitude play an important role in compositional change at larger scales (Marinšek et al. 2013).

Gradual change in species composition in European beech-forest communities from south to north can be partly explained by proximity of the most important glacial refugium for beech and possibly also of several beech-forest species in the north-western part of the Dinaric Mountains (Magri et al. 2006) and by the effect of postglacial migration that resulted in a lower number of beech-forest specialists dispersed at greater

distances from these refugia (Willner et al. 2009). Hypothetical glacial refugia for beech in the Western Carpathians (and perhaps even in the southern Bohemian Massif; Magri et al. 2006) probably enabled particular taxa to persist (such as *Cyclamen fatrense*; Slovák et al. 2012), but were too small to allow the survival of the majority of specialized beech forest species. Migration of beech-forest flora is probably limited by landscape barriers such as the Danube River and the Pannonian lowlands, which may have partly isolated the Alps from more northerly regions.

#### *Patterns in species richness, beta diversity and species pool*

It seems to be a general rule in the European temperate zone that species specific to calcareous habitats tend to be more numerous than those specific to acidic habitats (Pärtel 2002, Ewald 2003, Wohlgemuth & Gigon 2003, Ujházyová & Ujházy 2012). It has been shown that 50–64% of regional floras in central Europe (Borhidi 1995, Ewald 2003, Karrer unpubl.) consist of species preferring calcareous or base-rich soils (Ewald 2003). This pattern is reflected in a higher local species richness on base-rich than on base-poor soils (Wohlgemuth 1998, Pärtel 2002, Ewald 2008, Kooijman 2010). Our example of beech forests in central-European mountain systems unequivocally confirms this pattern, as we recorded both a higher species richness and larger species pool size on calcareous and base-rich bedrocks. Larger species pool on carbonates and in the Alps can also be explained by the glacial and post-glacial history of central-European forest vegetation. The calcicolous species survived glaciations in refugia characterized by high-pH soils (Willner et al. 2004, 2009), such as in the beech refugium in the calcareous Dinarides (Šercelj 1996). If any glacial refugia in the Bohemian Massif or Western Carpathians existed (Magri et al. 2006), they were small and probably did not contain many specialist herbaceous species. Postglacial migration lags due to barriers such as the Danube river valley partly explain the larger species pool in beech forests in the montane calcareous Eastern Alps as opposed to the Western Carpathians, because suitable habitats are clearly available in both regions. In contrast, the differentiation between the geographically well connected Bohemian Massif and Western Carpathians is more likely due to different bedrocks and altitudinal range.

Calicolous communities tend to be enriched by oligotrophic and acidophilous species (Wohlgemuth & Gigon 2003), particularly at high altitudes in fir-beech forests. The admixture of coniferous trees in such communities (especially in the Alps) is another important factor increasing local species richness by promoting specific niches by altering light and topsoil properties for understorey species (Ewald 2000, Máliš et al. 2012). Effect of admixture of other canopy tree species was also used by Hrivnák et al. (2014) to explain enrichment of beech-forest communities at the lower end of their altitudinal range in Slovakia.

The highest average species richness recorded in the Austrian Eastern Alps is consistent with results from the neighbouring calcareous Bavarian Alps (Ewald 2008). It is apparently linked to the high percentage of carbonate bedrock (ca 60% of plots in the Austrian Alps), and probably also to the richer high-mountain flora in the Alps (Taberlet et al. 2012), which can enrich the species pool of montane forests. For instance, the calcicolous “*Seslerio-Fagetum*” is the most species-rich plant association of forest vegetation in the Bavarian Alps, containing on average 55 species per 144 m<sup>2</sup> (Ewald 2008). Nevertheless, species richness in Western Carpathian beech forests is also high, in spite of the fact that the percentage of the area on carbonate bedrock is lower there (35% of

plots). Average richness in beech forests on carbonates was 39 species per plot both in the Alps and Western Carpathians. Forest communities with beech admixture in the Western Carpathians are among the most species-rich communities in the Czech and Slovak Republics (up to 109 vascular plant species per 400 m<sup>2</sup> and 118 per 500 m<sup>2</sup>; Chytrý et al. 2015). High species pool and beta diversity in the Western Carpathians seems to be related to a high heterogeneity of the bedrock as recorded in many case studies in other regions (Wohlgemuth 1998, Lobo et al. 2001, Bruun et al. 2003, Moser et al. 2005).

We also found that species richness increases with altitude in central-European beech forests (Fig. 5). Our findings probably do not contradict the hump-shaped trends presented by Rahbek (2005), as beech forests cover only a limited section of the altitudinal gradient (colline to montane zone). The linear correlation between species richness and altitude was not significant in a previous study of a larger and partly overlapping area of European beech forests (Willner et al. 2004). This can be explained by the sensitivity of analyses to data selection, as the relationship differs among regions (Fig. 5). In our case, there was weak relationship between species richness and altitude in the Bohemian Massif, where the altitudinal range of beech forests is the lowest, and magmatic and metamorphic rocks of pre-Permian age prevail. In contrast, increasing richness with altitude is typical of the geologically younger Alps and Carpathians with broader altitudinal gradients and large areas of carbonate bedrock in the montane zone. Nevertheless, there can be local deviations from the monotonically increasing trend valid for the whole Eastern Alps and Western Carpathians, for example the inversely unimodal species richness-altitude relationship reported by Hrivnák et al. (2014) for the volcanic region of central Slovakia.

## Conclusions

Species composition of central-European beech forests is significantly related to differences among regions, bedrock types and altitude. Effect of altitude on species composition is relatively independent, while effects of regions and bedrocks are coupled to a large extent. Purely spatial configuration unrelated to regions, bedrocks and altitude explains another significant part of compositional variation.

Beech forests in the Eastern Alps and Western Carpathians have similar species pool sizes and beta diversity. Those in the Alps have the highest local species richness and are floristically well differentiated from the beech forests in other regions by a group of specific species. The highest species richness and largest species pools are recorded on calcareous bedrocks in the Alps and the Carpathians. These regions are similar also in the significant increase in species richness with altitude, probably due to extensive areas of carbonate bedrocks at high altitudes, while almost no relationship with altitude was recorded in the Bohemian Massif. Limited species pool and species richness in the Bohemian Massif is linked to the predominance of poor siliceous bedrocks. Beech-forest communities on carbonates are strongly differentiated from those on other bedrocks. Communities on volcanic bedrock in the Western Carpathians are also well differentiated by a high frequency of eutrophic and nitrophilous species.

See [www.preslia.cz](http://www.preslia.cz) for Electronic Appendix 1

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## Souhrn

Studie srovnává floristické složení, lokální druhové bohatství, beta diverzitu a celkový počet druhů („species pool“) bukových lesů ve třech hlavních horských systémech střední Evropy a kvantifikuje jejich rozdíly na základě reprezentativního souboru 5946 fytoecologických snímků obsahujících 980 taxonů cévnatých rostlin. Porovnávali jsme společenstva s pokryvností buku lesního (*Fagus sylvatica*) ve stromovém patře nad 50 % v jednotlivých regionech, na šesti typech podloží a ve třech výškových stupních. Rozdíly jsme testovali analýzou rozptylu (ANOVA) a mnohonásobným porovnáváním (Tukey HSD). Vztah druhového bohatství a nadmořské výšky jsme navíc hodnotili pomocí regresní analýzy. Phi koeficient a Fisherův exaktní test jsme využili k vymezení diagnostických druhů bučin pro jednotlivé regiony, typy podloží a výškové stupně. Vliv regionu, podloží, nadmořské výšky a prostorových proměnných reprezentovaných osami PCNM analýzy na floristické složení bukových lesů jsme hodnotili pomocí ordinačních analýz (RDA a PCA). Výsledky ukázaly, že floristické složení bučin střední Evropy se významně liší podle fyto geografických regionů, typů podloží a nadmořské výšky. Vliv nadmořské výšky na floristické složení je do značné míry nezávislý na vlivu regionů a podloží, které naopak větší část svého vlivu na floristické složení navzájem sdílejí. Společenstva na karbonátových horninách se odlišují velkým počtem vápnomilných a částečně i teplomilných druhů. V rámci skupiny silikátových hornin se nejvíce liší společenstva na vulkanických horninách, častá zejména v Západních Karpatech, a to výskytem poměrně početné skupiny eutrofních a nitrofilních druhů. I když byl v analýzách vliv regionů, podloží a nadmořské výšky vysoce významný, největší část variability floristického složení vysvětlily prostorové proměnné (PCNM). Významné rozdíly byly zaznamenány i v hodnotách ukazatelů druhové diverzity. Největší druhové bohatství a největší celkový počet druhů se váže na vápnité horniny. Beta diverzita je však největší na kvartérních sedimentech, což zřejmě souvisí s přirozenou heterogenitou tohoto typu podloží. Alpská a karpatiská společenstva jsou si navzájem podobná celkovým počtem druhů, beta diverzitou i zvětšujícím se druhovým bohatstvím podél nadmořské výšky, což souvisí s velkým podílem karbonátových hornin, a to i v nejvyšším stupni výskytu bučin. Bukové lesy vystupují nejvýše právě v Alpách, kde bylo zaznamenáno největší druhové bohatství. Bučiny Alp jsou navíc floristicky dobře odlišeny od bučin ostatních horstev skupinou druhů omezených v rámci studované oblasti jen na toto pohoří, což je pravděpodobně důsledkem postglaciálního vývoje vegetace a blízkosti glaciálních refugií. V bučinách Českého masivu jsme nenalezli výrazný vztah mezi druhovým bohatstvím a nadmořskou výškou. Menší průměrné druhové bohatství a celkový počet druhů v tomto regionu částečně souvisí s převahou silikátového podloží, absencí karbonátů ve vyšších polohách a pravděpodobně i s delší vzdáleností od glaciálních refugií buku a jeho průvodních druhů.

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