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Patterns of vegetation diversity in deep river valleys of the Bohemian Massif

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Ph.D. Thesis

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Annotation:
Vegetation in deep river valleys of the Bohemian Massif was studied from two viewpoints: from local perspective, trying to untangle effects of environmental factors on patterns of vegetation and species richness within the valleys, and from landscape perspective, putting species richness of topographically heterogeneous valleys into the context of surrounding homogeneous landscape.

Key-words:
landscape topographical heterogeneity, local species richness, spatial mass effect, species habitat specialization, vegetation-environment relationships.

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Preface

Czech scientists have a compulsive need for describing special landscape features as “the landscape phenomenon”. As a result, Czech scientific literature is rich for terms such as hill phenomenon, karst phenomenon, serpentine, loess, vulcanite or scree phenomenon and also phenomenon of frost hollows. Whenever there is some part of landscape somehow special, it gets its own name. For people abroad this may sound as a strange hobby, but in the context of the Czech landscape it seems to have perfect sense. Unless you are lucky or you know exactly where to go, travelling across Czech may give you the feeling that general landscape here is flat or at most softly undulating agriculture plain, alternating with areas of forest plantations. In such conditions, whatever is “different” is also “special”, so why not to produce a special term for that?

One of these “specialties” are deeply incised river valleys, commonly referred to as “the river phenomenon”. If you come from a country with mountainous and rugged landscape, you won’t feel that these valleys deserve such an attention - they are actually not so deep, not so large and not so wild compared to some of their colleagues in other parts of the world. However, in the context of the Czech landscape they are unique, and you don’t need to be an experienced scientist to recognize that. Deep river valleys are perfect place for trip, holidays or just a short escape from the rush of everyday live. My own experience with them started many years ago, when I frequently went for one or more day trip to valleys in the western Moravia, and not knowing why, these places attracted me to come back again and again. That’s why later I didn’t hesitate to choose vegetation of river valleys as the topic of my study and spent several years climbing up and down the valley slopes in several places of Czech. In this thesis, I will try to convince you at several places that it is important to study deep river valleys, because they are “the main source of the topographical heterogeneity in the middle elevations of the Czech Republic”, or that “there are no quantitative studies that test the predictions of the ’river phenomenon’ concept”. All this is true, but - in reality, the main reason, why I studied deep river valleys, is because I like them and I enjoyed. That’s it!

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General introduction

Vegetation-environment relationships

The main aim of studies dealing with vegetation-environment relationships is to reveal underlying ecological processes, resulting in appearance of given vegetation pattern in nature. Descriptive studies can untangle only correlative, i.e. not necessarily causal links in these relationships, as the latter are domain of experimental studies designed to separate the effect of the given environmental factor from the others. Still, inference based on descriptive studies is valuable, as it brings important insights into the potential processes. One of the most influential revolutions in vegetation ecology during the last century was development of direct and indirect ordination analysis (Whittaker 1956, Bray & Curtis 1957). Vegetation ecologists got a tool, allowing them to quantify the gradient-related patterns in vegetation, which are observed in the field but difficult to formulate in a non-verbal way. Fast development of computation power has resulted into today's situation when ordination analysis has become a standard for studies dealing with description of vegetation-environment relationships. However, there are still methodological challenges waiting to be solved, and recent state resembles situation of a wanderer at the crossroad: where to go, further or back? If going back, there are traditional ordination methods such as DCA or CCA, heavily used, but suffering from (for some people) not acceptable drawbacks, such as "lolly paper effect" in case of DCA, producing triangle or diamond shape of DCA ordination diagram as a result of detrending (Oksanen et al. 2006), or the fact that all ordination analyses assume bell-shaped response of species along gradients, even if this is in contrast to prevalence of asymmetric species response curves in real vegetation (Oksanen & Minchin 2002), or finally that most of ordination analyses perform poorly in case of very long ecological gradients (De'ath 1999). If going further, there are methods partly covered by fog, not commonly used and not accessible in readily available software packages, such as non-metric multidimensional scaling (NMDS, Minchin 1987), promising nonparametric alternative to DCA (but see Hirst & Jackson 2007 for disagreement), or hot news such as fuzzy set ordinations (FSO, Roberts 2008). However, I believe that recent development and growing use of open source projects, mainly the R program (R Development Core Team 2008), may bring these methods to everyday use.

Environmental variables may be classified into direct, indirect and resource gradients (Austin & Smith 1989). Direct variables are those having direct effect on plant growth, such as temperature, soil pH and other soil characteristics. Some of them are relatively easy to measure (pH) and their effect may be directly attributed to some kind of ecological processes (for effect of pH on plants, see Tyler 2003). Indirect variables, such as altitude and other topographical variables, have no direct effect on plant growth, and their importance results from their correlation with some kind of direct or resource variable (e.g. in case of altitude is correlated to moisture, temperature or soil pH; slope and aspect are good surrogates for habitat irradiation). Resource variables are those consumed by plants, such as light or nutrients (e.g. nitrogen and phosphorus). Light conditions can be measured rather easily by several more or less precise methods: single estimate of canopy cover in forest can give rather good information about availability of light for the undergrowth, and this can be further improved for example by analysis of canopy photography using fish-eye lenses or by direct measurement using LyCor sensors. In contrast, measuring availability of nutrients in soil is not an easy task, as it has been shown that results of soil analysis for basic chemical compounds do not have to mirror real uptake and desire of plants for these compounds (e.g. Van Duren & Pegtel 2000); promising solution of this problem seems to be bioassay experiments, when selected phytometer is grown in the greenhouse conditions in collected soil samples and consequent chemical analysis of its tissue gives estimate of real nutrient potential of given stand (for grassland vegetation types see Köhler et al. 2001 or Wesche et al. 2007). Alternative solution in case that measured variables are missing is using some kind of species indicator values, e.g. Ellenberg values for basic ecological gradients such as moisture, nutrients, soil reaction, light, continentality and temperature (EIVs; Ellenberg et al. 1992) frequently used mainly by European vegetation scientists. Some of them proved to be useful surrogates of measured environmental factors (Schaffers & Sýkora 2000; Diekmann 2003), even if their application requires particular attention due to potential circularity in reasoning.

Local diversity patterns

Why there are more species here than there? This question is a traditional part of introductions to textbooks dealing with biodiversity, and its answer consists of a broad range of different theories and explanations (for such review, see e.g. Palmer 1994). But what is actually the reason we should care about diversity? In the middle of the last century, the argument was relatively simple, as one of the main paradigms ruling vegetation ecology of that time stated that "diversity begets stability" (see Ives 2005 for a thorough review). It implied that if something is more diverse, it is also more stable and hence less vulnerable to the damage by human activities. However, while earlier theoretical studies seemed to match this intuitive view (MacArthur 1955, Elton 1958), later studies, including experimental ones, failed to support it by reliable evidence. Nowadays, it seems that this paradigm is death. The focus of diversity studies shifted from pointing up the diversity hotspots to searching for underlying mechanisms, which are responsible for creating existing diversity patterns. It has been recognized that processes maintaining diversity are scale dependent (Levin 1992), and the scale issue is also reflected in the focus of individual studies, ranging from microscale, often subjected to manipulative experiments, up to large scale studies examining macroecological processes. Diversity pattern at the mesoscale level are subject of numerous local descriptive studies, which can reveal only correlative, not causal relationships between diversity and environment and inference based on these studies is often of local validity only. However, because experiments at the mesoscale are extremely difficult to perform, such studies are still useful, as they offer an opportunity to test, if the pattern observed in real natural situation is explicable by set of available hypothesis; if it is not, then such studies draw attention to discrepancies between theory and reality.

Similarly to ordinations techniques mentioned above, important step in the development of analytical tools for diversity modeling was introduction of methods such as Generalized Linear Models (GLM; McCullagh & Nelder 1989), Generalized Additive Models (GAM; Hastie & Tibshirani 1990) or Classification and Regression Trees (CART; Breiman et al. 1984). Another important development is the change in paradigms of modeling itself, from the original search for the only "true model", best explaining collected data, to modeling based on the multimodal inference and information theory, mainly the measure called Akaike's information criterion (AIC; Akaike 1973). This approach views modeling as "exercise in the approximation of the explainable information in the empirical data, in the context of the data being a sample from some well-defined population or process" (Burnham & Anderson 2002). From this view, it is not so important to accept a single model with the best combination of predictors yielding the best explanatory power, because modeling itself is the way how to get deeper insight into the data structure. Again, availability of suitable software is essential for such developments.

Diversity and landscape topographical heterogeneity

Heterogeneity is considered to be one of the main drivers of biological diversity (Wiens 1976; Ricklefs 1977; Grime 1979; Tilman 1982; Huston 1994). Its importance is scale dependent, supposed to be highest at the mesoscale level (Sarr et al. 2005). Biodiversity at a particular site is expected to be affected by two aspects of environmental heterogeneity (Dufour et al. 2006): (1) the range of environmental variability influencing the number of available habitat types within the target site ("within-patch heterogeneity") and (2) spatial configuration of habitats in the landscape surrounding the site ("patch-surrounding heterogeneity"). The first (within-patch) aspect of environmental heterogeneity is well established in ecological theory, both in equilibrium and non-equilibrium models (Sarr et al. 2005). Equilibrium models predict that heterogeneity increases the capacity for richness due to higher niche separation in more heterogeneous environment, enabling coexistence of more species (Tilman 1982, 1994). Non-equilibrium models connect the importance of heterogeneity to other processes, e.g. the increase of spatial variability due to disturbances (Naiman et al. 1993; Pollock et al. 1998). While numerous studies focused "within-patch" aspect of environmental heterogeneity considering various scales and taxonomic groups (e.g. Vivian-Smith 1997; Burnett et al. 1998; Lundholm & Larson 2003), the second aspect, considering spatial context of the patch, still lacks robust theoretical background and remains relatively untouched by both field and theoretical studies (Gabriel et al. 2005; Mayer et al. 2005; Dufour 2006; Kumar et al. 2006).

Species richness of plots surrounded by a heterogeneous landscape seems to be mediated by the combination of processes linked to regional species pool and dispersal limitation. First, in localities that encompass a greater range in local conditions, either because they are larger or because they are more heterogeneous for a given size, more opportunities exist for the establishment of species from the regional pool (Freestone & Harrison 2006), resulting into increase of local species pool (for definition of regional and local species pool, see Zobel et al. 1998). Second, larger local species pool can affect the within-patch alpha diversity via spatial mass effect or vicinism (Shmida &

Ellner 1984; Cantero et al. 1999) – species can grow in a less favorable habitat due to the input of propagules from a nearby, more favorable habitat. Metapopulation ecology puts this process into the framework of more general sink-source dynamic, with source population in favourable and sink population in not favourable habitats (Shmida & Ellner 1984; Pulliam 1988; review by Dias 1996). Close vicinity of various habitats close to each other may increase the role of spatial mass effect in determining local species richness in heterogeneous landscapes. The spatial mass effect is known to be an important determinant of species composition of successional communities (e.g. Novák & Konvička 2006), however, it seems that it may play important role also in the established communities (Cantero et al. 1999). Openness of community to enrichment by species via spatial mass effect may be dependent also on local environmental factors, e.g. productivity (Freestone & Harrison 2006).

Weak point of landscape scale diversity studies is availability of good-quality data, covering sufficient spatial range and available for various vegetation types. In this case, data compiled in large vegetation databases (such as the Czech National Phytosociological Database, Chytrý & Rafajová 2003) plays important role as a source of large amount of vegetation data. However, as recognized already by Mueller-Dombois & Ellenberg (1974), information about actual species richness in these data may be significantly biased due to mostly subjective design of sampling. Together with the fact that phytosociological relevés are not random samples and hence they cannot be treated by any statistical test of significance, this was the main argument put forward by Lájer (2007) against the use of these data for diversity-related studies. Still, I believe that if we use wise analytical approaches and shift our focus from testing null hypotheses to searching for diversity patterns, phytosociological data are valuable material for inference about diversity at the landscape scale. And realistically, there are, at least recently, no better data sets.

Deep river valleys as a model for study of vegetation diversity patterns

In the middle elevations of the Czech Republic, deeply incised river valleys form distinct geomorphological feature, with steep slopes and sharp upper edges contrasting to the otherwise flat or softly undulating surrounding landscape. Most of these valleys are of late Tertiary and early Quaternary origin, when the uplift of the Bohemian Massif resulted into increased erosion power of rivers (Kopecký 1996). Geomorphology of these valleys was further shaped during Pleistocene periods of glaciation, when intensive frost weathering occurred as a result of periglacial climate (Kopecký 1996). Main abiotic features of these valleys are related to rugged topography and specific microclimatic conditions: steep slopes with exposed rocky outcrops, diversity of landform shapes, variability in slope aspect with sharp contrast between warm south and cold north facing slopes, and also frequent temperature inversions, resulting from the valley shape and pronouncing the contrast between cold and wet valley bottom and dry continental upper valley edges. Important biotic consequences of these features are (1) high diversity concentrated in these valleys due to concentration of various, often ecologically contrasting habitats, (2) occurrence of relict species, reflecting the role of valleys as a refuge during glacial and postglacial period, (3) function of river valley as migration corridors between mountains and lowlands, with migration of both downstream and upstream direction (the latter facilitated due to the frequent occurrence of suitable dry and warm habitats within the valleys in higher altitude), and finally also (4) conservation of vegetation less affected by human activities in hardly accessible sections of the valleys. Specific features of the vegetation pattern in these valleys were summarized under the heading "river phenomenon" in the descriptions provided by Czech vegetation scientists in the 1960's (Blažková 1964; Jeník & Slavíková 1964).

Concentration of strong ecological gradients within limited space of the valley together with the fact, that these valleys are the main source of the topographical heterogeneity in the middle elevations of the Czech Republic, makes them an interesting model for studies searching for environmental correlates of vegetation and plant diversity patterns at the landscape scale.

Outline of the thesis

This thesis tries to describe the vegetation of deep river valleys from two different viewpoints: from local perspective, trying to untangle effects of environmental factors on pattern of vegetation and species richness within the valleys, and from landscape perspective, putting species richness of topographically heterogeneous valleys into the context of surrounding homogeneous landscape. Thesis consists of four papers – three case studies and one methodological study; one of them is already published, one is in press, one is submitted and one is a manuscript. These are the main questions covered by individual papers:

1. What is the relationship between species composition of vegetation and the main ecological gradients in deep river valleys?
2. Which environmental factors are the best predictors of the local species richness in these valleys and how can be diversity-environment relationship influenced by differences in regional species pool?
3. What is the effect of landscape topographical heterogeneity on the local species richness and which ecological processes may cause this effect?

Paper 1 (published in *Preslia*) brings quantitative description of the vegetation-environment relationships in deep river valleys, using data from two areas differing markedly in both climatic and floristic characteristics. Performance of two main groups of environmental variables, topographical and soil, as explanatory variables in models describing the vegetation patterns in these valleys is assessed by set of canonical correspondence analyses. Link between particular environmental variables and main ecological gradients is analyzed by correlation analysis with Ellenberg indicator values. New method was invented for analysis of joint effect of two environmental variables on vegetation, in this case of aspect and the height above river valley.

Paper 2 (manuscript) analyze the pattern of local species richness within two deep river valleys and its environmental correlates. Using General Linear Models, we built two sets of models, one using only spatial variables and aiming to arrive to spatially explicit model of species richness within the valley, and the second using ecological (topographical and soil) variables. Similarities and dissimilarities between the two valleys are interpreted in terms of local ecological processes and differences in composition of regional species pools. Local species richness is compared to the size of regional species pool for individual forest habitat types, using published estimates of species pool for particular habitat types, based on data from large vegetation database and modified by expert knowledge.

Paper 3 (submitted manuscript) tries to answer a more ambitious, general question: does the species richness change along the gradient of landscape topographical heterogeneity between heterogeneous river valleys and homogeneous surroundings? Observed pattern is interpreted as a result of fragmentation, spatial mass effect and alternatively also shift in habitat ecological conditions and processes related to the patterns of species richness along environmental gradients. Ratio of habitat generalists and specialists is used as an indication of spatial mass effect.

Paper 4 (*Journal of Ecology*, in press) describes correction of the method used for the assessment of species habitat specialization. The method was invented by Fridley et al. (2007) and is based on co-occurrence data from large vegetation databases. However, I found that the original algorithm does not give reliable estimates of habitat specialization, as the used additive measure of beta diversity is affected by the size of the species pool. I proposed correction of this method, supported by results of both simulated and real data analyses. Corrected version of the algorithm was used in Paper 3 for estimation of species habitat specialization.

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Paper 1

Environmental control of the vegetation pattern in deep river valleys of the Bohemian Massif

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Environmental control of the vegetation pattern in deep river valleys of the Bohemian Massif

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Abstract

The pattern of natural vegetation on non-calcareous soils in two deep river valleys of the Bohemian Massif (Vltava and Dyje rivers, Czech Republic) was analyzed in order to determine the main topographic and soil variables affecting the composition of the vegetation. Vegetation data together with topographic and soil variables were collected along transects down the slope from the upper edge to the bottom of the valley. The distribution of vegetation types within the valleys was described using cluster analysis and non-metric multidimensional scaling (NMDS). Effects of topographic and soil variables were compared using a set of canonical correspondence analyses (CCAs) with explanatory variable selection based on the Akaike Information Criterion (AIC). In order to describe the non-linear interaction between the two topographic variables, elevation and aspect, a new method (moving window CCA) was introduced. This method assessed the explanatory power of aspect at various elevations above the valley bottom. Results show that main vegetation coenoclines are correlated with two complex environmental gradients: the moisture–nutrient–soil reaction and light–temperature–continentality gradients. Soil variables are slightly better predictors of vegetation composition than topographic variables. Altogether, these variables explain 18.8–21.6% of the total inertia. Although soil development depends on topography, the variation jointly explained by both groups of variables is only 3.9–5.2%, indicating that each of these two groups of variables influences vegetation pattern in a different way. Variables selected by the most parsimonious model for the Vltava valley are aspect, soil pH, soil type fluvisol and soil depth. For the Dyje valley the same variables as in Vltava valley were selected except for soil depth, which was replaced by soil type cambisol. Aspect has a strong effect on vegetation on the middle slopes but not on the lower slopes of the valleys. The results of all analyses are similar between the two valleys, suggesting that similar patterns may also occur in other deep river valleys of mid-altitudes of the Bohemian Massif.

Key-words: canonical correspondence analysis, cluster analysis, deep river valleys, non-metric multidimensional scaling, moving window CCA, vegetation-environment relationships.

Introduction

In the gently undulating landscape of the Bohemian Massif, which occupies a large part of the Czech Republic and adjacent areas of Germany and Austria, deep river valleys are a distinct topographic feature. Compared to other valley types, these are narrow, V-shaped valleys with steep slopes, large meanders and a narrow, discontinuously developed floodplain. They are sharply incised in the flat or hilly landscapes, predominantly formed of granite or gneiss bedrocks. These valleys are mainly found at middle altitudes between 200 and 700 m. All river valleys of this type are of Quaternary age, when the uplift of the Bohemian Massif increased the erosion power of rivers and caused the deepening of previously shallow and broad valleys into deep and narrow ones (Kopecký 1996).

Botanical diversity of deeply incised river valleys in the Bohemian Massif has the same general characteristics as other river corridors, such as high species richness (Gould & Walker 1999), linear plant migration (Naiman et al. 1993; Burkart 2001; Mouw et al. 2003) and sensitivity to alien plant invasions (Pyšek & Prach 1993; Planty-Tabacchi et al. 1996). Additionally, these valleys possess some additional characteristics, in particular a high beta diversity of the plant communities on hillsides, caused by high topographic, geological and mesoclimatic diversity (Chytrý & Tichý 1998). There are sharp environmental gradients within relatively small areas, some of which are large enough to include both extreme as well as intermediate values of environmental factors (e.g. different moisture in the floodplain and on the south-facing upper parts of the valley slopes, or soil pH on outcrops of siliceous and calcareous bedrocks). Consequently, deep river valleys represent local biodiversity hotspots in an otherwise rather uniform landscape in the middle altitudes of the Bohemian Massif.

The high biotic diversity in the Bohemian Massif deep river valleys is coupled with limited human impact in some places. This feature also sharply contrasts with the adjacent landscape, which is dominated by an intensively managed mosaic of arable fields and secondary forest plantations. Because of the limited accessibility due to the steep valley slopes, there are complete zonations of near-natural vegetation types, predominantly forests, in several sections of the valleys.

Strong topographic gradients in the river valleys affect the variation in several environmental variables, which directly affect plant growth, e.g. moisture, nutrient availability and pH. Thus, topography strongly co-varies with vegetation pattern, and at some scales, topographic variables can be robust predictors of vegetation patterns. Such relationships are clear in river valleys with broad floodplains (e.g. Sagers & Lyon 1997; Gould & Walker 1999; van Coller et al. 2000; Goebel et al. 2006), but may be accentuated in deep river valleys due to the complex topography of the slopes adjacent to the floodplain.

Specific features of the vegetation pattern of these deep river valleys were summarized under the heading "river phenomenon" in the descriptions provided by Czech vegetation scientists in the 1960s (Blažková 1964; Jeník & Slavíková 1964). The "river phenomenon" concept describes how topographic and mesoclimatic features of the deeply incised river valleys of the Bohemian Massif affect their vegetation diversity. Of the abiotic factors, this concept stresses the sharp contrast between the deep river valleys and adjacent gently undulating landscape, the pronounced effect of exposed rocks occurring on steep slopes on the vegetation, the contrast between the sunny and warm south-facing slopes and shaded and cold north-facing slopes, high diversity of various extreme habitats situated next to each other and specific mesoclimatic conditions causing temperature inversions. Of the vegetation features, the "river phenomenon" concept emphasizes (1) the high biodiversity in deep river valleys, (2) non-random distribution of vegetation types and species richness within the valleys, (3) concentration of relict species, resulting from the fact, that deep river valleys probably served as a Pleistocene refuges for plant and animal species, and (4) migration of plants and animals along the rivers, connecting mountains with lowlands. Although there are several published local descriptions of plant communities in the Bohemian Massif deep river valleys (Blažková 1964; Türk 1994; Chytrý & Vicherek 1995, 1996, 2003; Kolbek et al. 1997, 1999-2003), there are no quantitative studies that test the predictions of the "river phenomenon" concept (Blažková 1964; Jeník & Slavíková 1964) and summarize the general features of vegetation patterns and their driving environmental factors.

The aim of this study is to produce a quantitative description of the vegetation-environment relationships in deep river valleys of the Bohemian Massif, focusing on the patterns occurring in a cross-section of the valleys. To avoid the effect of local idiosyncrasies on the results, we studied two valleys, Vltava and Dyje, differing markedly in both climatic and floristic characteristics. Specifically, we analyzed correlations between vegetation pattern and topographic variables, measured soil factors and species indicator values, in order to reveal the most important factors determining the pattern of vegetation in deep river valleys.

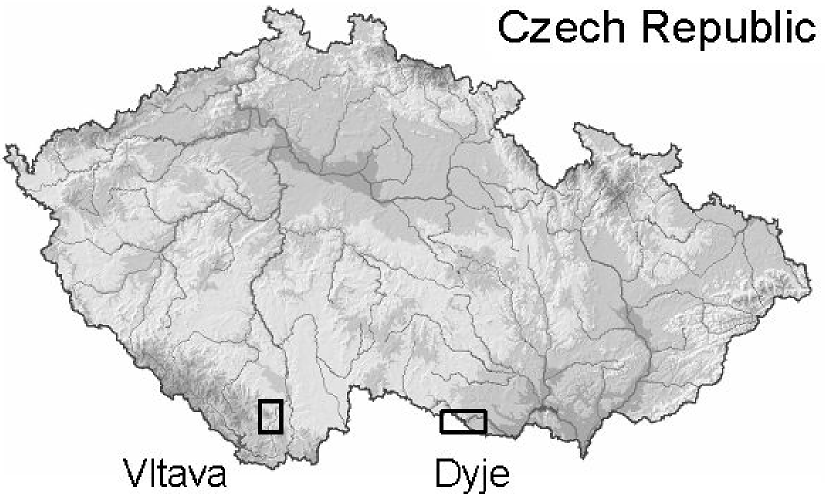

Figure 1: Location of the studied sections of the Vltava and Dyje valleys in the Czech Republic.

Methods

Study sites

One study site is a part of the Vltava river valley in South Bohemia, north of Český Krumlov (Fig. 1). The section of valley studied is situated between Zlatá Koruna (48°51' N, 14°22' E) and Boršov nad Vltavou (48°55' N, 14°26' E), with an altitudinal range of 400–540 m a.s.l. and maximum valley depth of around 100 m. Climate in this area is moderately warm, with mean January temperatures −3 to −1 °C and mean July temperatures 16–17 °C. Average annual precipitation is 550–600 mm (Tolasz 2007). Phytogeographically this area belongs to the Hercynian floristic region with some components of the forest flora of the Alps and continental thermophilous flora of Central Bohemia. Bedrock types include mainly acidic gneiss and granulite, with patchy occurrence of crystalline limestone (marble), serpentine and amphibolite (Chábera 1985).

The other site is located in the Dyje (in German Thaya) river valley in the Podyjí/Thayatal National Park on the border between the Czech Republic and Austria (Fig. 1). The studied section of this river valley is between the towns of Vranov nad Dyjí (48°54' N, 15°49' E) and Znojmo (48°52' N, 16°03' E) on the Czech and Austrian sides of the national border, respectively. Altitudinal range is 220–536 m a.s.l. and maximum valley depth almost 200 m. Climate in this area is generally warmer and more continental than at the previous site, with mean January temperatures ranging between -3 and -2 °C, mean July temperatures 18–19 °C and mean annual precipitation 550–600 mm (Tolasz 2007). This site is located close to the boundary of the Hercynian and Pannonian floristic regions (Chytrý et al. 1999) and therefore has a significant proportion of thermophilous and continental species. Geological characteristics are similar to those of the previous site. Predominant bedrocks include acidic gneiss and granite, with some restricted occurrences of crystalline limestone (Batík 1992).

Data sampling

Fieldwork was conducted in 1992–1993 by M. C. (Dyje valley) and 2001–2003 by D. Z. (Vltava valley). The standardized sampling protocol (Chytrý 1995) was applied in both valleys. Vegetation was sampled along transects from the upper edge to the bottom of the valley in places where there was no artificial or human-disturbed vegetation. Transect sites were selected to include the maximum diversity of habitat types occurring in the valleys. Along these transects, vegetation and environmental data were collected in plots of 10×15 m (with longer axis situated along the isohypse) placed equidistantly every 30 m in the Vltava valley and 40 m in the Dyje valley, which reflects the greater depth of the Dyje valley. In each plot, all the vascular plants were recorded, plus an estimate of the cover based on the nine-degree Braun-Blanquet scale (Westhoff & van der Maarel 1978). Nomenclature of plant taxa follows Kubát et al. (2002).

Various topographic and soil factors were either measured directly, estimated or calculated (Table 1). Of them, heat index (Parker 1988) measures relative differences in the solar energy arriving at the different sites. It is calculated from the slope and aspect, using the formula $heat\ index = cos(aspect - 202.5°) \times tg(slope)$, where 202.5° represents the warmest SSW aspect. Although in theory solar irradiance in the northern hemisphere peaks at solar noon and a 180° aspect, delayed ground heating is responsible for the fact that the highest diurnal heat load is experienced on SW–SSW facing slopes (Geiger 1966). Aspect, due to its circular nature, was not used per se, but calculated as the deviance of the measured plot aspect from 22.5° (NNE), thus reaching the highest value of 180° on SSW slopes.

Within each plot, five measurements of soil depth were made using a metal gouge auger with an operational length of 70 cm and a diameter of 1.5 cm; the five values were averaged and used as an estimate of soil depth (note that the actual soil depth may

Table 1: Explanatory variables used in the study.

Topographic variables (quantitative and ordinal variables):	
Elevation	relative elevation above the valley bottom (range 0–1, 0 for the valley bottom, 1 for the upper edge)
Aspect	aspect, expressed as deviation of plot aspect from 22.5° (NNE); it reaches the highest value for the supposedly warmest SSW aspect
Slope	slope inclination (°); observed range: Vltava 0–88°, Dyje 5–77°.
Heat index	heat index = cos (aspect $-$ 202.5°) $\times$ tg (slope)
Surface SL	landform shape in the downslope direction (three-degree ordinal scale: -1 concave, 0 flat, 1 convex)
Surface ISO	landform shape along an isohypse (three-degree ordinal scale: -1 concave, 0 flat, 1 convex)
Soil variables and soil types (quantitative and categorical variables):	
pH	active soil pH measured in water solution
Soil depth	soil depth, expressed as log [soil depth (cm)]
Fluvisol	Fluvisols (water-influenced soils formed from alluvial deposits)
Skeletic	skeletic and hyperskeletic Leptosols (stony soils on scree accumulations)
Cambisol	Cambisols (well-developed zonal soils)
Lithic	lithic Leptosols (shallow soils near rock outcrops)

be underestimated when the auger is used in stony soils). Due to a strongly skewed distribution, this variable was log-transformed before further analyses. At each plot, five soil samples from the A-horizon (depth 0–10 cm after litter removal) were collected from different places, mixed together and used to measure soil pH in water solution (dried samples were placed in distilled water for 24 hours; weight ratio of soil/water = 0.4). For each plot, soil types according to ISSS-ISRIC-FAO (1998) were recorded, using a simplified categorization of the following four broadly conceived classes: fluvisol – fluvisols, i.e. soils directly affected by a river water regime, with fluvic soil material (inspected using the auger); skeletic – skeletic and hyperskeletic leptosols on steep scree slopes, containing various proportions of gravel or coarse stones; cambisol – deeper and matured cambisols on slight slopes; lithic – shallow and undeveloped lithic leptosols on and near to rocky outcrops. As most plots were on acidic bedrock, data from transects containing plots on calcareous soils were removed from the data set (3 plots in the Vltava and 22 in the Dyje valley). These plots, representing vegetation types sharply different from those on acidic soils, might produce an undesirable outlier effect. The data set used for the analyses included 94 plots situated along 26 transects in the Vltava valley and 82 plots from 14 transects in the Dyje valley.

Classification and indirect ordination

To identify the main vegetation types, plots were classified by cluster analysis, performed separately on the data sets from each valley. Several pilot analyses with various combination of clustering methods and distance measures were calculated. For presentation, the relative Euclidean (chord) distance and Ward's clustering algorithm based on square-root transformed percentage cover data were used, because they best reflected the pattern of vegetation differentiation as judged by expert knowledge. The resulting classifications were projected onto an ordination diagram using non-metric multidimensional scaling (NMDS; Minchin 1987) performed on a matrix of Bray-Curtis dissimilarities between relevés, together with passively projected Ellenberg indicator values (EIV; Ellenberg et al. 1992) calculated as non-weighted averages of the values for all species in merged vegetation layers. NMDS was calculated using the advanced algorithm proposed by Minchin (1987). It includes several random calculations in order to search for a robust global solution and post-analysis rotation of NMDS axes based on principal components analysis so that the variance of points is maximized on the first dimension (for more details see Oksanen et al. 2006). Polarity of axes in resulting diagrams was adjusted in order to unify the directions of EIV and signs of correlations with axes in both valleys. Clusters obtained for each valley were ordered along the moisture gradient (according to cluster median EIV for moisture) from the driest (Cluster 1) to the wettest (Cluster 5) to ensure that in both valleys the clusters with the same numbers represent analogous vegetation types. Interpretation of particular clusters in terms of vegetation types was based on expert judgement, supported by the list of diagnostic, constant and dominant species identified for each cluster (not shown; diagnostic species were determined using the phi coefficient of association, corrected for even group sizes according to Tichý & Chytrý 2006).

Correlation among explanatory variables and Ellenberg indicator values

Correlation matrix of all explanatory variables and EIV was calculated, using Spearman rank coefficients for all variables except the relationships between binary variables (soil types); these were calculated using contingency tables, with significance derived from Pearson's Chi-square test with Yates's continuity correction (Sokal & Rohlf 1995). Correlations between explanatory variables were based on data merged from both valleys, while correlations of explanatory variables and EIV were made separately for each valley in order to detect local differences in observed patterns.

Variation partitioning between topographic and soil variables

Relationships between vegetation composition and environmental variables were analyzed using canonical correspondence analysis (CCA; ter Braak 1986), a method modified to handle unimodal species responses. In the first step, models based only on topographic (model V.topo for Vltava and *D.topo* for Dyje valley, respectively) and only on soil variables (models *V.soil* and *D.soil*) were developed for each valley in order to assess the amount of variation explained by each of these two types of explanatory variables. Models were built using a stepwise algorithm, combining forward and backward selection of explanatory variables. Evaluation of models' parsimony was based on the Akaike Information Criterion (AIC; Akaike 1973) as implemented in the R package Vegan (Oksanen et al. 2006). Conditional and shared effects of selected topographic and soil variables were calculated by partial CCA, using topographic variables as explanatory variables and soil variables as covariables (models *V.topo.cond* and *D.topo.cond*) and vice versa (*V.soil.cond* and *D.soil.cond*). In order to quantify the amount of variation explained by the model, the ratio of the sum of the constrained eigenvalues to total inertia was used. Like Økland (1999), this ratio was not interpreted as the proportion of the explained variation, but as the fraction of the total inertia explained by the model. A stepwise algorithm was used also to build a parsimonious model that combined both topographic and soil variables.

Moving window CCA: quantifying interaction between aspect and elevation

Preliminary analyses indicated that species composition mainly varies along two gradients, directly influenced by the topographic position in the valley – relative elevation above the valley bottom and aspect. However, aspect may have a different effect on vegetation in deeper, shaded parts of the valley, where it plays a less important role than in the upper parts, where the contrast in irradiation between north-facing and south-facing slopes is much more pronounced. To test this hypothesis, we proposed a method inspired by the moving window regression analysis (e.g. Walker et al. 2003; Palmer 2006), which was originally designed to detect changes in vegetation composition along transects. However, our analysis did not employ linear regression, but CCA with one explanatory variable, which analyzed the changes in explanatory power of this variable along a gradient of another variable. We call this method "moving window CCA". In our case, the method was used to quantify changes in the explanatory power of aspect when moving from the bottom to the upper edge of the valley. Plots were sorted by their relative elevation above the valley bottom (from 0 to 1) and a virtual moving window was set at the beginning of this series. The window then moved by steps of constant length toward the opposite end of the relative elevation interval (elevation). In each step, CCA analysis of the plots included in the window, with aspect as an explanatory variable, was calculated to quantify the amount of variation explained by aspect at particular elevations above the valley bottom, measured by the fraction of total inertia explained by the first axis of CCA. The size of the window and hence the gradient length was kept constant in all steps, which resulted in different numbers of plots being included in the window in particular steps. However, to make the analyses of all steps comparable (in the sense of variation explained by aspect), it was essential to keep constant the number of plots in each analysis. This was done by random selection (without replacement) of a constant number of plots in each particular step within the virtual window. This random selection was repeated 20 times and averaged fractions of total inertia together with confidence intervals were plotted against the relative elevation. Generally, the shape of the analyzed relationship depends on the gradient length (or size of the window) analyzed in each step, which corresponds to the scale of the studied relationship. To make the results comparable, this parameter was kept the same in both valleys. After several pre-analysis runs, the size of the window was set to 0.35 units of relative elevation, the number of steps of the window towards the end of the elevation gradient to 20 and number of plots randomly selected per window and used in CCA in a particular step to 17 in both valleys. To visualize the trend, the averages of the explained variation were smoothed by a curve fitted using a general additive model with three degrees of freedom (Hastie & Tibshirani 1990).

Software

TURBOVEG 2 database program (Hennekens & Schaminée 2001) was used for storing vegetation data, JUICE 6.3 (Tichý 2002) for data editing and calculation of Ellenberg indicator values and PC-ORD 4 (McCune & Mefford 1999) for processing cluster analysis. The calculation routine for moving window CCA analysis was written in R language and run in R software (R Development Core Team 2005) with vegan package (Oksanen et al. 2006). R software was used also for calculating and drawing NMDS and CCA ordinations.

Results

Vegetation types and their ecological relationships

Differentiation of the vegetation types in the river valleys is illustrated in Fig. 2, which combines the results of cluster analysis and NMDS ordination with passively projected Ellenberg indicator values (see Table 2 for explanation of vegetation types).

Number of clusters was arbitrarily set to five in both valleys. There are corresponding patterns in both valleys, with major vegetation types similarly scattered in the ordination diagrams. The first axes show strong correlations with EIV for moisture, nutrients and soil reaction, whereas the second axes correlate with light, temperature and continentality (although not so clearly in the Dyje valley). Central position in both ordination diagrams is occupied by ravine and oak-hornbeam forests (Cluster 3). The most dry, nutrient-poor, light and warm habitats are occupied by thermophilous oak forests (Cluster 1). More acidic and cooler habitats support acidophilous pine and oak forests (Clus-

Table 2: Brief description of the clusters revealed by the cluster analysis of the Vltava and Dyje vegetation plot data, including number of plots in each cluster, average values ± S.D. of selected environmental variables (slope, soil pH, soil depth) and the two most frequently occurring soil types (see Table 1 for abbreviations).

Cluster	Vegetation characteristics	No. of plots	Slope (°)	pH	Soil depth (cm)	Two most frequent soil types
Vltava						
1	thermophilous oak forests (*Quercus petraea, Q. robur*)	6	35±8	4.4±0.5	22±8	cambisol/lithic
2	acidophilous pine and oak forests (*Pinus sylvestris*, *Quercus petraea*)	24	41±18	3.8±0.2	16±9	cambisol/lithic
3	ravine and oak-hornbeam forests (*Acer, Tilia, Quercus petraea*)	29	39±10	4.2±0.4	23±8	cambisol/skeletic
4	fir forests (*Abies alba*)	18	35±8	4.1±0.3	31±10	cambisol/skeletic
5	alluvial alder forests (*Alnus glutinosa*)	17	26±25	4.6±0.4	33±17	fluvisol/skeletic
Dyje						
1	thermophilous oak forests (*Quercus petraea*)	14	36±8	4.5±0.4	21±9	cambisol/lithic
2	acidophilous pine and oak forests (*Pinus sylvestris, Quercus petraea*)	17	39±13	4.1±0.2	22±14	cambisol/lithic
3	ravine and oak-hornbeam forests (*Acer, Tilia, Carpinus betulus, Quercus petraea*)	25	35±12	5.0±0.7	28±16	cambisol/skeletic
4	beech forests (*Fagus sylvatica*)	19	33±6	5.0±0.5	40±9	cambisol/skeletic
5	alluvial alder forests (*Alnus glutinosa*)	7	10±6	5.2±0.6	65±27	fluvisol/skeletic

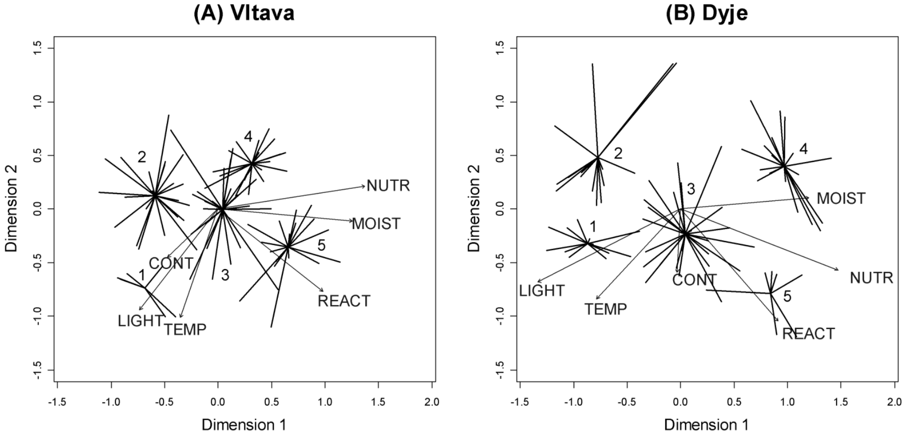

Figure 2: Non-metric multi-dimensional scaling (NMDS) ordination diagrams of vegetation plots from the Vltava and Dyje valleys with projected cluster membership (1-5; see Table 2 for cluster descriptions). Each spider connects individual plots with the average score for plots belonging to the same cluster. Ellenberg indicator values for LIGHT, TEMPerature, CONTinentality, MOISTure, soil REACTion and NUTRients are passively projected onto these ordination diagrams.

ter 2). The opposite part of the ordination diagrams, with wet and nutrient-rich habitats, is occupied by alluvial forests (Cluster 5). The vegetation in the coolest and most shady habitats, on the north-facing slopes, is in Cluster 4 and occupies similar habitats in both valleys, but with different species composition: in the Vltava valley, this cluster includes ravine forest dominated by fir with the tall forb *Lunaria rediviva* dominating the herb layer, whereas in the Dyje valley it is represented by beech forests. The spatial pattern of the distribution of particular vegetation types in idealized space of river valley is presented in “iris diagrams” (Fig. 3). The difference between the vegetation in the two valleys is shown in Fig. 4, with the Dyje valley being generally warmer.

Correlations among explanatory variables and Ellenberg indicator values

Distribution of soil types strongly depends on topographic features: fluvisols and (hyper)skeletic leptosols are found in the lower and bottom parts of the valleys, while lithic leptosols and cambisols are confined to the middle and upper slopes. Lithic leptosols are shallow soils with low pH and are restricted to steep, upward convex and sun-exposed slopes. Fluvisols in the floodplain are deeper and less acid and together with hyper-

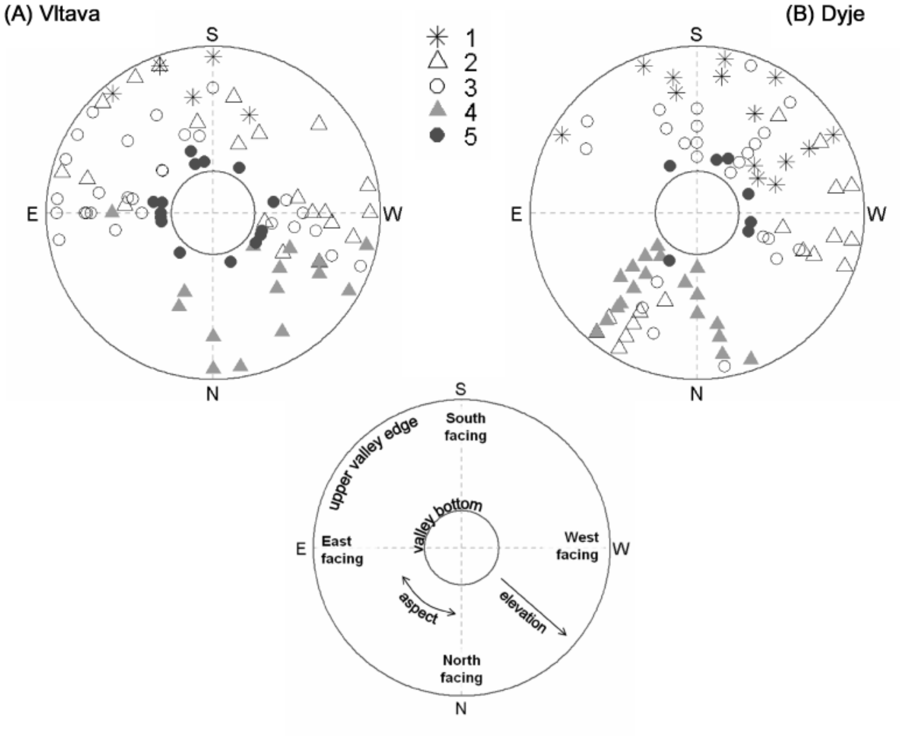

Figure 3: "Iris diagrams" showing distribution of particular vegetation types (clusters) in idealized space of the deep river valleys. Diagrams combine aspect and relative elevation above the valley bottom in the following way: centre of the circle represents valley bottom, outer margin represents upper edge of the valley and the direction from the centre represents the direction, in which the slopes face (see the scheme in the middle). Point types refer to the vegetation types described in Table 2.

skeletic leptosols of stony screes occupy concave landforms. Elevation is strongly connected with soil reaction, with base-rich soils in the lower parts of the valleys. Slope is also negatively correlated with pH, with more acidic soils found on steeper slopes.

Table 3: Correlations between all explanatory variables and correlations between explanatory variables and Ellenberg indicator values (the latter calculated separately for the Vltava and Dyje valley). Spearman rank coefficients are used for all correlations except soil type categories (Fluvisol, Skeletic, Cambisol and Lithic), for which the chi-square test is used. Positive correlation: +++ $P < 0.001$, ++ $P < 0.01$, + $P < 0.05$; negative correlation: − − − $P < 0.001$, −− $P < 0.01$, − $P < 0.05$. Meaning of P: for correlation of categorical soil variables - significance of Pearson's chi-squared test with Yates' continuity correction derived from a contingency table; for the others - significance of Spearman rank coefficient. Ellenberg indicator values for LIGHT, TEMPerature, CONTinentality, MOISTure, REACTion and NUTRients are used. For abbreviations of environmental variables, see Table 1.

Elevation	x											
Slope	n.s.	x										
Aspect	n.s.	n.s.	x									
Heat index	n.s.	n.s.	+++	x								
Surface SL	+++	+++	n.s.	n.s.	x							
Surface ISO	++	n.s.	n.s.	n.s.	+++	x						
Soil depth	−−	− − −	− − −	− − −	−	n.s.	x					
pH	− − −	−−	n.s.	n.s.	−	n.s.	+++	x				
Fluvisol	− − −	− − −	n.s.	n.s.	− − −	n.s.	+++	+++	x			
Skeletic	− − −	n.s.	n.s.	n.s.	− − −	− − −	n.s.	+	+	x		
Cambisol	+++	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−	−−	− − −	x	
Lithic	+++	+++	+++	+++	+++	n.s.	− − −	− − −	−−	− − −	n.s.	x
	Elev.	Slope	Aspect	Heat index	Surface SL	Surface ISO	Soil depth	pH	Fluvisol	Skeletic	Cambis.	Lithic
Vltava												
Light	n.s.	n.s.	+++	+++	n.s.	+	− − −	n.s.	n.s.	−−	n.s.	+
Temperat.	n.s.	n.s.	+++	+++	n.s.	n.s.	−	n.s.	n.s.	n.s.	n.s.	+
Continent.	n.s.	n.s.	+++	+++	n.s.	n.s.	−−	n.s.	n.s.	n.s.	n.s.	n.s.
Moisture	− − −	− − −	− − −	− − −	− − −	n.s.	+++	+++	+++	+++	−	− − −
Reaction	−−	−−	n.s.	n.s.	− − −	n.s.	+++	+++	+++	+	n.s.	− − −
Nutrients	−	− − −	− − −	− − −	− − −	n.s.	+++	+++	+++	+++	n.s.	− − −
Dyje												
Light	+++	n.s.	+++	+++	n.s.	n.s.	− − −	− − −	n.s.	n.s.	n.s.	+++
Temperat.	+	n.s.	+++	+++	n.s.	n.s.	− − −	−−	n.s.	−	n.s.	++
Continent.	− − −	n.s.	+++	+++	n.s.	n.s.	n.s.	++	+	n.s.	n.s.	n.s.
Moisture	− − −	− − −	−−	− − −	−−	−	+++	+++	+++	++	− − −	− − −
Reaction	− − −	− − −	+	n.s.	−	n.s.	+++	+++	+++	n.s.	n.s.	−−
Nutrients	− − −	− − −	n.s.	−−	−−	n.s.	+++	+++	+++	++	−−	− − −

Correlations between Ellenberg indicator values and explanatory variables were (in contrast to the correlation of explanatory variables with one another) calculated for separate data sets from each river valley (Table 3). Even though the results are generally consistent between valleys, they show some regional differences. EIVs are closely associated with topography: sites with warmer aspects and higher heat index values are positively correlated with EIVs for light, temperature and continentality, and negatively correlated with EIVs for moisture and nutrients. The bottom of the Vltava valley is cold and shaded (in terms of EIVs) and in both valleys the bottom is more wet, basic and nutrient-rich. Convex topography and slope are negatively correlated with moisture, soil reaction and nutrient availability. Soil variables also correlate with several EIVs: fluvisols are wet, basic and nutrient-rich; lithic leptosols are dry, acidic and nutrient-poor; hyperskeletic leptosols are wetter and richer in nutrients. Soil depth in both valleys is negatively correlated with EIVs for light and temperature, and positively with moisture, soil reaction and nutrients. In both valleys measured soil pH is strongly positively correlated with EIVs for soil reaction, moisture and nutrients; only in the Dyje valley is pH negatively correlated with EIVs for light and temperature.

Effect of topographic and soil variables on vegetation

Table 4 shows the results of direct ordination analyses, processed separately for data from each river valley and each set of topographic and soil explanatory variables. The most parsimonious model (based on AIC), including only topographic variables, explains 10.3% of total inertia in the Vltava valley (V.topo) and 12.0% in the Dyje valley (D.topo), while models including only soil variables explain slightly more – 12.5% in the Vltava valley (V.soil) and 14.8% in the Dyje valley (D.soil). Partial CCA revealed conditional and shared effects of these models (Fig. 5). Full models, including all topographic and soil variables selected by previous topographic and soil models, explain 18.8% in the Vltava (V.full) and 21.6% in the Dyje valley (D.full). However, these models are not parsimonious, as measured by the AIC criterion. Parsimonious models including both topographic and soil variables (V.parsim and D.parsim, respectively) include only four out of the seven explanatory variables included in the full models and explain 13.8% in the Vltava valley (V.parsim) and 16.8% in the Dyje valley (D.parsim).

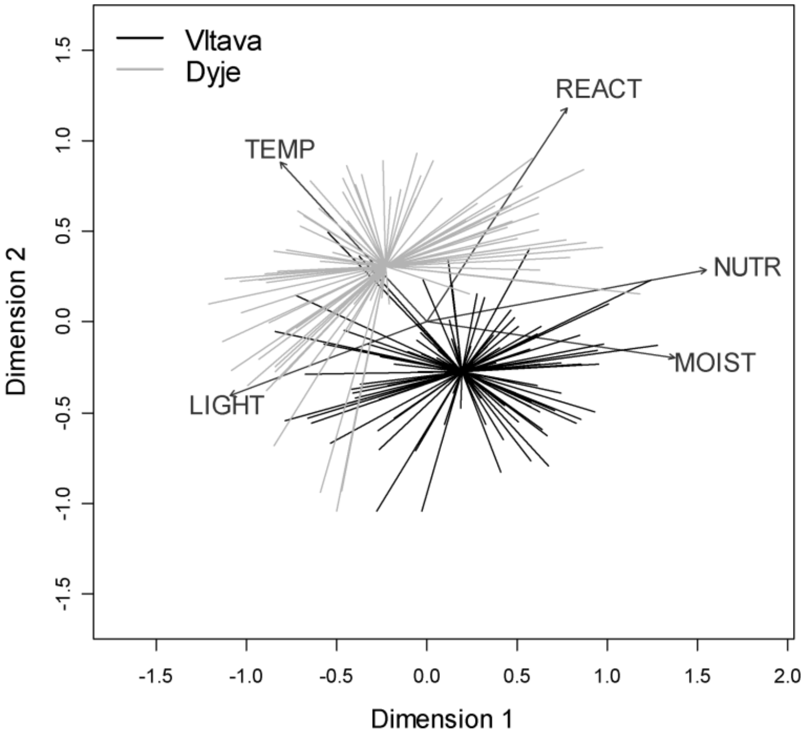

Figure 4: Joint NMDS ordination of all plots from the Vltava and Dyje valleys. Each spider connects individual plots with the average score for plots from each valley. Ellenberg indicator values are passively projected onto this ordination diagram (for abbreviations see Fig. 2).

Relationship between vegetation, elevation and aspect: moving window CCA

Although elevation and aspect are not correlated, moving window CCA revealed that the explanatory power of aspect changes at different elevations above the valley bottom (Fig. 6). Explanatory power of aspect is lowest near the valley bottom, reaches the maximum half way up the side of the valley and decreases again near the top. Fractions of total inertia explained by ASPECT in particular steps range between 7–13% in the Vltava and 9.5–13% in the Dyje valley.

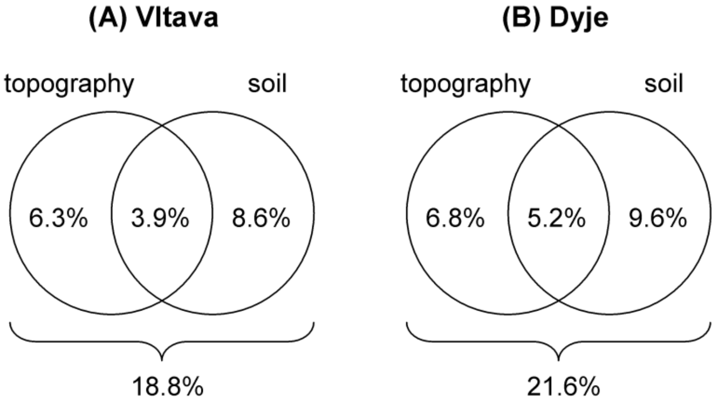

Figure 5: Venn diagrams showing conditional and shared effects of the groups of topographic and soil variables as fractions of the total inertia.

Discussion

Indirect ordination revealed that in both river valleys, the main gradients in vegetation composition are similar – the first NMDS axis represents a complex nutrient–moisture–soil reaction gradient and the second a light–temperature–continentality gradient. Distribution of vegetation types determined by cluster analysis along these gradients also displays similar patterns in both valleys, both in ordination space (Fig. 2) and the idealized spatial model of a deep valley (Fig. 3). This degree of similarity between the two river valleys accords with the results of previous phytosociological studies from deep river valleys (e.g. Blažková 1964; Türk 1994; Chytrý 1995; Chytrý & Vicherek 1995, 1996; Kolbek et al. 1997; Kolbek 1999–2003) and suggests that the patterns described in this study are general for river valleys of the Bohemian Massif, and not a result of local coincidences of vegetation and environment. Vegetation patterns in the Vltava and Dyje valleys are similar in spite of the fact that the former is situated in a cooler and wetter macroclimatic region than the latter (Fig. 4).

This analysis shows that soil and topographic variables are both good predictors of vegetation pattern in river valleys, but the former explains slightly more variation. While topographic variables can be derived from high resolution digital elevation maps, soil variables need detailed field inspection, which is more time and budget demanding. If money or time are limiting factors, topographic variables itself, such as elevation above the valley bottom, aspect and slope (or landform shape), can be still considered

Table 4: CCA models with various combinations of explanatory variables and covariables. Total inertia: Vltava = 7.144, Dyje = 7.898. See Table 1 for variable abbreviations. AIC = value of (generalized) Akaike Information Criterion; $\sum$ eig. = sum of all canonical eigenvalues; % expl. = fraction of total inertia explained by the model. All models (excluding conditional effect models, which have not been tested) are significant when subjected to the Monte Carlo permutation test ($p < 0.001$, 1000 permutations). Model abbreviations: *V.topo*, *D.topo* – explanatory variables including topographic factors only for Vltava and Dyje valleys, respectively; *V.soil*, *D.soil* – explanatory variables including soil factors only; *V.topo.cond*, *D.topo.cond* – conditional effects of topographic variables with soil variables as covariables; *V.soil.cond*, *D.soil.cond* – conditional effects of soil variables with topographic variables as covariables; *V.full*, *D.full* – combines topographic and soil variables from *V.topo*, *D.topo* and *V.soil*, *D.soil*; *V.parsim*, *D.parsim* – the most parsimonious models including both topographic and soil variables.

	Explanatory variables	Covariables	AIC	$\sum$ eig	% expl.
Vltava					
V.topo	elevation + aspect + surface SL	–	447.00	0.733	10.3
V.soil	skeletic + fluvisol + soil depth + pH	–	446.59	0.896	12.5
V.topo.cond	elevation + aspect + surface SL	skeletic + fluvisol + soil depth + pH		0.452	6.3
V.soil.cond	skeletic + fluvisol + soil depth + pH	elevation + aspect + surface SL		0.615	8.6
V.full	elevation + aspect + surface SL + skeletic + fluvisol + soil depth + pH	–		1.347	18.8
V.parsim	aspect + fluvisol + soil depth + pH	–	445.21	0.987	13.8
Dyje					
D.topo	elevation + aspect + slope	–	384.42	0.945	12.0
D.soil	cambisol + fluvisol + soil depth + pH	–	383.78	1.166	14.8
D.topo.cond	elevation + aspect + slope	cambisol + fluvisol + soil depth + pH		0.537	6.8
D.soil.cond	cambisol + fluvisol + soil depth + pH	elevation + aspect + slope		0.758	9.6
D.full	elevation + aspect + slope + cambisol + fluvisol + soil depth + pH	–		1.703	21.6
D.parsim	aspect + cambisol + fluvisol + pH	–	381.83	1.324	16.8

as good predictors of vegetation pattern (Tichý 1999a). These variables have no direct effect on plants, but exert a strong control on the distribution of resources and conditions necessary for plant growth, such as moisture availability, nutrients or temperature (Pabst & Spies 1998). Aspect and elevation determine mesoclimatic conditions such as incoming solar radiation (Austin et al. 1984) or formation of temperature inversions in river valleys (Quitt 1996; Chytrý & Tichý 1998; Tichý 1999b). Slope is closely related to disturbance, caused by falling rocks, soil creep, surface erosion etc. (Rejmánek et

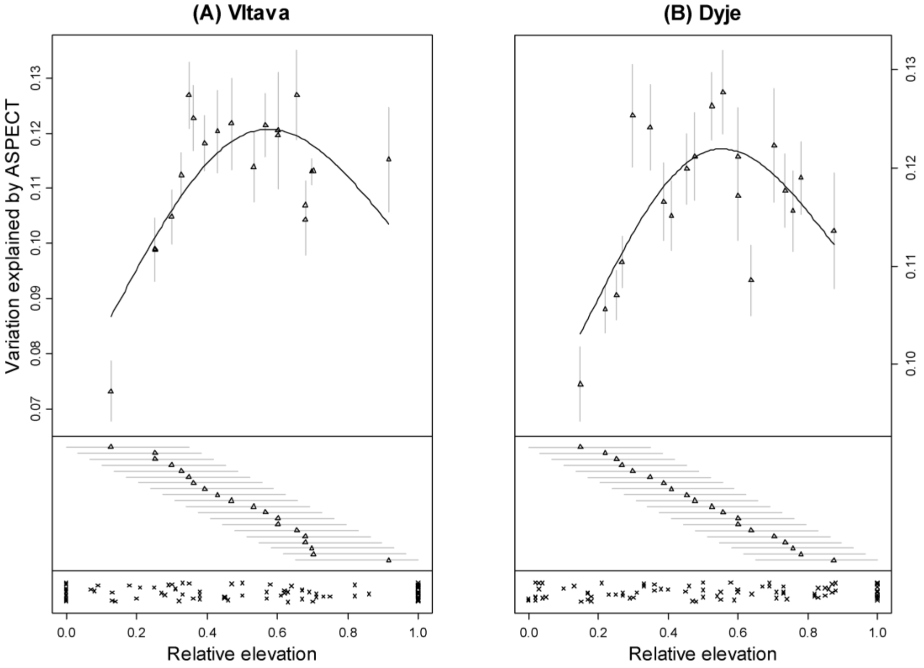

Figure 6: Joint effect of aspect and relative elevation above the valley bottom on species composition, analyzed using moving window CCA for the Vltava and Dyje river valleys. Horizontal axis is relative elevation above the valley bottom. The bottom parts of the diagrams show distribution of elevation (the points are slightly jittered along the vertical line to visualize overlapping values). The middle parts demonstrate the position of each moving window along the gradient of elevation (triangle shows the mean of all the values in a particular window). The upper part shows the explained variation (the fraction of total inertia explained by aspect), calculated by CCA for a given step; for each step of the moving window, mean (triangle) and confidence interval (vertical bar) of the explained variation, calculated using the random sub-samples, are shown; the positions of triangles along the horizontal axis correspond in the middle and upper part of the diagram.

al. 2004). The down slope increase in soil pH revealed in this study is probably also connected with down slope mass and nutrient migration, induced both by groundwater flow (Campbell 1973; Zinko et al. 2006) and superficial erosion (Cox et al. 2002), causing increased leaching of the upper slopes, followed by transport and accumulation of soluble base cations in the lower parts of the valley (Silver et al. 1994; Chen et al. 1997). Surface erosion is perhaps also responsible for the negative correlation between soil pH and slope, as steep slopes on acidic bedrock support the development of shallow soils with an acidic reaction. Apart from this, nutrient accumulation in the lower parts of the valleys is connected with flooding (in the case of fluvisols) or more intensive microbial activity in the highly skeletic soils of ravine forests on the lower slopes (Ellenberg 1996).

Due to the complex topography of the valleys, the effects of some topographic variables on vegetation pattern are not easy to identify. In particular, the non-linear interaction between the elevation above the valley bottom and aspect can mask the effect of the latter when standard procedures of constrained ordination are used. The new method of moving window CCA, proposed here, proved successful in disentangling the complex effect of these two variables on vegetation (Fig. 6). It clearly showed that near the valley bottom, where the valley is rather narrow and shaded by the adjacent slopes in many places, aspect does not explain much of the variation in vegetation. Moving up the valley sides, the importance of aspect as a determinant of species composition increases, because of the more pronounced contrast between the dry and warm south-facing and more shaded, wetter and cooler north-facing slopes. At the upper edges of the valley, the importance of aspect decreases again, as the difference in insolation of south-facing and north-facing slopes diminishes due to the less steep topography.

Despite the strong correlations between several topographic and soil variables (Table 3), the shared fraction of variation in species composition explained by both topographic and soil variables is relatively low (Fig. 5). It means that soil variables explain a different part of the variability in vegetation than topography. Therefore, recording several simple soil variables, such as pH, soil depth and soil type, can significantly improve the explanatory power of vegetation-environment models, even in a landscape with strong topographic contrasts.

Conclusions

The similarity of the vegetation patterns between the two river valleys studied and their correspondence with the earlier phytosociological studies indicate that the patterns revealed in the present study are reasonably robust and can be generalized for most deep river valleys on non-calcareous soils at middle altitudes of the Bohemian Massif. Main topographic factors driving vegetation pattern are elevation above the valley bottom, aspect (being more important half way up the valley sides) and slope. Soil variables such as measured pH and soil type (mainly fluvisols vs. the others) may significantly improve vegetation-environment models for these valleys. The vegetation pattern of the valleys can be briefly summarized as follows:

(1) Floodplain forests, mostly dominated by *Alnus glutinosa*, occur on the valley

bottom on deep and moist fluvisols, which are rich in nutrients and have a relatively high pH.

(2) On lower valley slopes, there is usually a small difference in the vegetation on south-facing and north-facing slopes. Here the main factor is slope, which determines whether cambisols (on less steep slopes) or skeletic leptosols (on steeper slopes) develop, with the former supporting oak-hornbeam forests and the latter ravine forests of *Acer*, *Tilia* and *Carpinus betulus* (*Carpinus* being locally absent in the Vltava valley).

(3) Half way up the valley sides and to a lesser extent further up, there is a striking contrast between the vegetation on southern and northern slopes. The warmest south-facing slopes support thermophilous oak forests with *Quercus petraea*, which are better developed in the warmer and more continental Dyje valley. In contrast, north-facing slopes support forests dominated by fir (Vltava) or beech (Dyje) on relatively deep and nutrient-rich cambisols.

(4) Other habitats in deep river valleys are covered with acidophilous oak and/or pine forests on more or less shallow lithic leptosols of various aspects and pure pine stands restricted to extreme habitats on rocky outcrops.

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Paper 2

Pattern of species richness in the topographically complex landscape of deep river valleys in the Bohemian Massif

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manuscript

Pattern of species richness in the topographically complex landscape of deep river valleys in the Bohemian Massif

David Zelený & Milan Chytrý

Abstract

Deep river valleys in the Bohemian Massif combine features of river corridors and landscapes with rugged topography, making the pattern of diversity within these valleys and processes possibly linked to this pattern more complex. We compared the pattern of local species richness within two climatically different deep river valleys in the Czech Republic and using General Linear Models we searched for the spatial and ecological (topographical and soil) variables best predicting this pattern. Additional correlation analyses used Ellenberg indicator values as surrogates for main ecological gradients and also compared local species richness with estimated size of species pool for particular forest habitat types. Spatial pattern of species richness show similarities between the valleys, with the highest richness located in the valley bottom and south or west facing upper valley edges. Models based on topographical and soil variables and correlation analysis using Ellenberg indicator values show important differences between valleys, with species richness best explained by soil pH in case of the Vltava valley and continentality in case of the Dyje valley. These differences are attributed to generally higher values of soil pH in Dyje valley as a result of warmer and dryer climate and also to differences in regional species pools between valleys.

Key-words: Akaike Information Criterion, Ellenberg indicator values, Generalized Linear Models, habitat types, species pool.

Introduction

River corridors are worldwide recognized as diversity hotspots, concentrating remarkable proportions of species from regional species pools (Nilsson et al. 1989; Tabacchi et al. 1990; Goebel et al. 2003; Mouw & Alaback 2003). From the landscape perspective, the reason for such high diversity is their spatio-temporal heterogeneity and habitat connectivity (Gregory et al. 1991; Nilsson et al. 1998; Pollock et al. 1998; Ward

1998; Brinson & Verhoeven 1999). The main processes driving diversity of floodplains at local scale are related to intensity and frequency of floods, small scale variation in topography resulting from lateral movement of river channels, variation of climate due to river flowing from higher to lower elevation and specific disturbance regime (Naiman et al. 1993). Diversity is further increased by linear plant migration (Naiman et al. 1993; Burkart 2001; Mouw & Alaback 2003) and higher sensitivity of riparian zones to invasions (Pyšek & Prach 1993; Planty-Tabacchi et al. 1996; Brown & Peet 2003).

In Central Europe, Cenozoic geological uplift of the Variscan platform gave origin to deeply incised V-shaped river valleys with narrow floodplains and steep slopes (Kopecký 1996). They represent a unique geomorphological feature, differing from other valley types mainly by the abrupt upper edge that clearly separates the valley from the surrounding uniform plains or gently undulating landscapes. Unlike in the valleys with extensive floodplains, in the deep river valleys of the Bohemian Massif the effect of periodic and stochastic floods is restricted to narrow strips of floodplains at the valley bottoms, with other parts of the valleys shaped mainly by various slope processes. They combine features of river corridors and landscapes with complex topography, making the pattern of diversity within these valleys and processes possibly linked to this pattern more complex. Most of the studies dealing with species richness within the river corridors focused on the floodplains, e.g. areas directly influenced by the activity of river (e.g. Tabacchi et al. 1990; Schnitzler 1996; Pollock et al. 1998), with only few exceptions including also adjacent valley slopes, terraces and upland (Lyon & Sagers 1998; Decocq 2002; Goebel et al. 2003).

Uniqueness of the deep river valleys in the Bohemian Massif in the context of the softly undulating and mostly agricultural landscape of Central Europe was recognized by Jeník & Slavíková (1964) as a result of the studies of negative impacts of building of large water dams. These authors proposed the concept of ’river phenomenon’ summarizing specific features of vegetation pattern in these valleys. Along with several descriptive studies of flora and vegetation, general features of vegetation pattern in these valleys were summarized in models of phenological pattern (Chytrý & Tichý 1998), potential natural vegetation (Tichý 1999a) and actual vegetation (Zelený & Chytrý 2007).

In this study, we extend the existing knowledge of vegetation patterns in these river valleys by exploring the pattern of plant species richness on the gradient from the floodplains at the valley bottom through the slopes to the upper edges, and by searching for its spatial and environmental correlates. We employed modelling approach, building several alternative sets of models using either spatial or ecological (non-spatial) explanatory variables. Given complex topography of deep river valleys, we expected that the pattern of species richness is well predicted using only spatial information about the position within the valley (elevation above the valley bottom and slope aspect). However, other environmental variables, such as those characterizing topography and soil, may add significant explanatory power to spatial models. Additionally, some of these variables may be used as surrogates for general ecological gradients such as moisture, productivity and temperature, hence offering an opportunity to interpret observed pattern of species richness using general theories of biodiversity. However, species richness of local plant communities is also known to be strongly influenced by regional species pool (Eriksson 1993; Pärtel et al. 1996; Zobel 1997), and local species richness is therefore not only result of processes operating at the local scale (i.e. competition or small scale variation in ecological gradients), but also large scale and evolutionary processes, shaping the size of regional species pool. In order to get better insight into the observed pattern, we also examined the relationship between estimated size of regional species pools for particular habitat types (Sádlo et al. 2007) and their local species richness.

The main aim of this study is to (1) build models of local species richness pattern in deep river valleys using spatial and ecological (topographical and soil) parameters as explanatory variables; (2) interpret the species richness pattern in the context of current diversity theories, including the species pool hypothesis.

Methods

Study sites

The study was conducted in two deep river valleys located in climatically distinct regions in the Czech Republic and Austria. The first study site is in the Vltava river valley in the south-western part of the Czech Republic, north of Český Krumlov (Fig. 1). The studied section of the valley is situated between Zlatá Koruna (48°51' N, 14°22' E) and Boršov nad Vltavou (48°55' N, 14°26' E), with an altitudinal range of 400–540 m a.s.l. and maximum valley depth of around 100 m. Climate in this area is moderately warm, with mean January temperatures −3 to −1 °C, mean July temperatures 16–17 °C and average annual precipitation is 550–600 mm (Tolasz et al. 2007). Phytogeographically this area belongs to the Hercynian floristic region, dominated by Central European mesophilous flora with some components of the forest flora of the Alps and thermophilous flora of

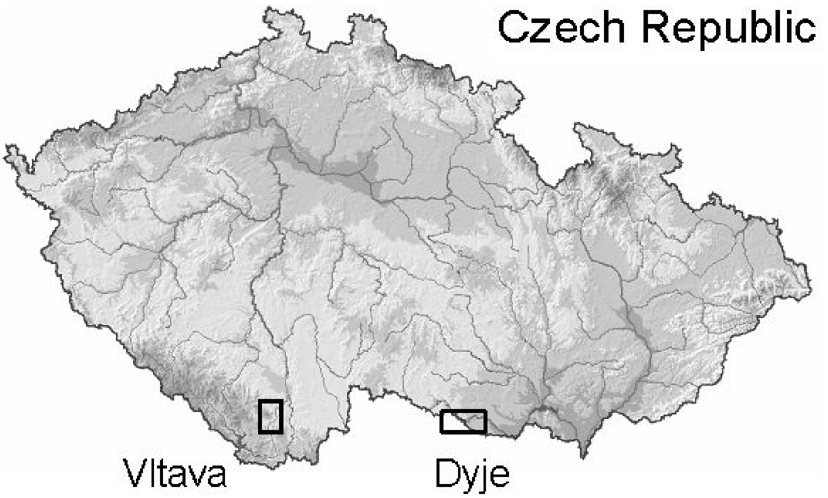

Figure 1: Location of the studied sections of the Vltava and Dyje river valleys.

Central Bohemia. Bedrock types include mainly acidic gneiss and granulite, with patchy occurrences of crystalline limestone (marble), serpentine and amphibolite.

The second study site is located in the Dyje (Thaya) river valley in the Podyjí/Thayatal National Park on the border between the Czech Republic and Austria (Fig. 1). The studied section of this river valley is between the towns of Vranov nad Dyjí (48°54’ N, 15°49’ E) and Znojmo (48°52’ N, 16°03’ E) on the Czech and Austrian sides of the national border, respectively. Altitudinal range is 220–536 m a.s.l. and maximum valley depth almost 200 m. Climate in this area is generally warmer and more continental than at the previous site, with mean January temperatures ranging between −3 and −2 °C, mean July temperatures 18–19 °C and mean annual precipitation 550–600 mm (Tolasz et al. 2007). This site is located close to the boundary of the Hercynian and Pannonian floristic regions (Chytrý et al. 1999) and therefore it contains a significant proportion of thermophilous and continental species, in addition to predominant Central European mesophilous species. Geological characteristics are similar to those of the previous site, with predominant bedrocks including acidic gneiss and granite and with restricted occurrences of crystalline limestone.

Data sampling

Fieldwork was conducted in 1992–1993 by M. C. (Dyje valley) and 2001–2003 by D. Z. (Vltava valley), with standardized sampling protocol (Chytrý 1995) applied in both valleys. Vegetation sampling was carried out along transects from the upper edge to the bottom of the valley. Positions of transects were selected in order to avoid localities with heavily disturbed or planted forests and to maximize the diversity of habitats and the range of environmental factors, occurring in the valleys. Along these transects, vegetation and environmental data were collected in plots of size 10×15 m (with longer axis situated along the isohypse) placed equidistantly every 30 m in the Vltava valley and 40 m in the Dyje valley, reflecting the greater depth of the Dyje valley.

In each plot, all the vascular plants were recorded and their cover estimated using the nine-degree Braun-Blanquet scale (Westhoff & van der Maarel 1978). Additionally, various topographic and soil variables were measured, estimated or calculated (Table 1). Of them, elevation is expressed by relative value ranging from 0 to 1 (0 for valley bottom, 1 for upper edge of the valley), as the relative measure better reflects topographical situation in the valleys. Aspect, due to its circular nature, was not used per se, but calculated as the deviance of the measured plot aspect from 22.5° (NNE), thus reaching the highest value of 180° on SSW slopes (“folded aspect”, McCune & Keon 2002). Although in theory solar irradiance in the northern hemisphere peaks at solar noon and a 180° aspect, delayed ground heating is responsible for the fact that the highest diurnal heat load is experienced on SW-SSW facing slopes (Geiger 1966). Heat load (McCune & Keon 2002) is a measure combining the potential direct incident radiation with the effect of ground heating delay, taking into account latitude, aspect (here the aspect “folded” along the SSW–NNE axis) and slope and using exponential values derived from the equation given by McCune & Keon (2002).

Within each plot, five measurements of soil depth were made using a metal gouge auger with an operational length of 70 cm and a diameter of 1.5 cm. These five values were averaged and their logarithmic values were used as an estimate of soil depth, even if this value may underestimate the real soil depth when the auger is used in stony soils. For soil chemical analysis, five soil samples from the A-horizon (depth of 0–10 cm after litter removal) were collected from different places within each plot, mixed together and used for measuring the soil pH in water solution (dried samples were placed in distilled water for 24 hours; weight ratio of soil/water = 0.4). For each plot, soil types were recorded using categorization based on ISSS-ISRIC-FAO (1998), simplified into the following four broadly conceived classes: Fluvisol – fluvisols, i.e. soils directly affected by a river water regime, with fluvic soil material (inspected using the auger); Skeletic – skeletic and hyperskeletic leptosols on steep scree slopes, containing various proportions of gravel or coarse stones; Cambisol – deeper and matured cambisols on gentle slopes; Lithic – shallow and undeveloped lithic leptosols on and near to rocky outcrops. As most plots were on acidic bedrock, all data from transects containing plots on calcareous soils (3 plots in the Vltava and 22 in the Dyje valley) were not included in further analysis, as they may produce an undesirable outlier effect. The data set used for the analyses included 94 plots situated along 26 transects in the Vltava valley and 82 plots from 14 transects in the Dyje valley.

Data analysis

As a measure of local species richness, we used the number of herb-layer species recorded in each vegetation plot. Species of different vegetation layers may respond to different environmental variables and on different scales (McCune & Antos 1981; Sagers & Lyon 1997), and therefore it is better to treat the data from different vegetation layers separately. However, in the cool-temperate forests such as those in the study area, herb-layer species account for dominant proportion of the overall local species richness due to low number of shrub and tree species. Spring therophytes and geophytes were removed from the data set to avoid possible confounding effect caused by differences in sampling time of particular plots during the growing season.

General Linear Models (GLM; McCullagh & Nelder 1989), with combination of Poisson distribution and logarithmic link function, were used as the main analytical tool for modelling local species richness as dependent variable. Our modelling approach reflects the fact that our data consist of two separate data sets originating from two different areas, and while similarities in pattern detected in both data sets can be used as the basis for generalisation, differences between and uniqueness within each valley may have itself an interesting ecological interpretation. For this reason, rather than searching for the most parsimonious predictive model describing the pattern of species richness in each valley, we built several alternative models corresponding to alternative hypotheses. Construction of the models was based on the combination of *ad hoc* decisions and forward selection, while the search for the best predictive variables was done on the pre-selected subsets of variables and selection of particular variable was evaluated by Akaike Information Criterion (AIC; Akaike 1973). According to our empirical experi-

Table 1: Measured, estimated and calculated spatial and ecological (topographic and soil) variables.

Spatial variables	
Elevation	relative elevation above the valley bottom (range 0–1, 0 for the valley bottom, 1 for the upper edge of valley)
Aspect	folded aspect, expressed as deviation of plot aspect from one of the following aspects: 180°(southerness), 202.5°(SSW-erness), 225°(SW-erness), 257.5°(WSE-erness), 270°(westerness), 292.5°(WNW-erness) and 315°(NW-erness)
Non-spatial (microtopographical and soil) variables	
Slope	slope inclination (°)
Heat load	heat load $= exp(-1.467 + 1.582 \times cos(latitude) \times cos(slope) - 1.5 \times cos(aspect) \times sin(slope) \times sin(latitude) - 0.262 \times sin(latitude) \times sin(slope) + 0.607 \times sin(aspect) \times sin(slope))$ (following McCune & Keon, 2002)
Surface SL	landform shape in the downslope direction (three-degree ordinal scale: -1 concave, 0 flat, 1 convex)
Surface ISO	landform shape along an isohypse (three-degree ordinal scale: -1 concave, 0 flat, 1 convex)
pH	active soil pH measured in water solution
Soil depth	soil depth, expressed as log [soil depth (cm)]
Fluvisol	Fluvisols (water-influenced soils formed from alluvial deposits)
Skeletic	skeletic and hyperskeletic Leptosols (stony soils on scree accumulations)
Cambisol	Cambisols (well-developed zonal soils)
Lithic	lithic Leptosols (shallow soils near rock outcrops)

ence, using AIC as the only criterion for model construction may result in models with too many explanatory variables, as the behaviour of this criterion is quite liberal. To avoid this, inclusion of the candidate variable into the model during the process of forward selection was also approved using analysis of deviance and finally only significant variables were included. An additional criterion was employed to avoid inclusion of two highly intercorrelated variables in the same model: if the candidate variable had significant Spearman's correlation coefficient with any of the variables already included in the model and this coefficient was larger than 0.5, this variable was excluded.

Two types of explanatory variables were used for forward selection: (1) spatial variables, including elevation (either linear or as a polynom of the 2^nd order) and eight alternative folded aspects: along S–N, SSW–NNE, SW–NE, WSW–ENE, W–E, WNW–ESE, NW–SE and NNW–SSE axis, respectively, and (2) ecological variables, including measured soil and topographic variables and calculated heat load (see Table 1). Resulting spatial models were used for projection of the spatial pattern of species richness into an idealized model of the river valley, which was designed to summarize the effect of two main spatial variables – relative elevation within the valley and aspect. For resemblance with donut, we call the resulting diagram "donut diagram".

An additional ecological explanation of the observed pattern in local species richness has been assessed using the Ellenberg indicator values (EIVs; Ellenberg et al. 1992) as proxy measures of moisture, nutrients, soil reaction, temperature, continentality and light. Mean EIVs for each plot were calculated as non-weighted means of tabulated EIVs for species presented in the plot and compared with species richness using Pearson's correlation coefficients.

Local species richness of particular forest types in the Vltava and Dyje valleys was compared with published estimates of the number of species that constitute regional species pools, based on the relevé data from the Czech National Phytosociological Database and modified by expert knowledge (Sádlo et al. 2007). For the purpose of this comparison, vegetation plots from both valleys were manually classified into the same habitat types as used by Sádlo et al. (2007). Because tabulated values of species pool size include also species of shrub and tree layer, we used the number of all species in merged vegetation layers (with juveniles removed) as a measure of local species richness in this analysis. Sizes of species pools including both native and alien species were projected against local species richness of plots classified into particular habitat types.

Plot data were edited and mean Ellenberg indicator values were calculated in the JUICE program (Tichý 2002); all statistical analyses and figure drawings were carried out in the R program (R Development Core Team 2008).

Results

GLM equations including either spatial or ecological environmental variables are summarized in Table 2. The best spatial predictor of local species richness in both valleys is the polynomial form of elevation, performing better than the linear form and explaining 32% and 22% of variance in the Vltava and Dyje valley, respectively. In case of the Dyje valley, the second best spatial predictor is aspect folded along S–N axis (southerness), which adds more than 10% to the total variance explained by the model. In the Vltava valley the forward selection resulted in inclusion of WNW-erness, which however does not bring too much additional explained variance ($< 2\%$). Donut diagrams (Fig. 2) illustrate similarities and differences in spatial patterns of local species richness between the valleys. The distance from the centre is related to relative elevation above the river valley and the angle to plot aspect. Values of local species richness predicted by particular

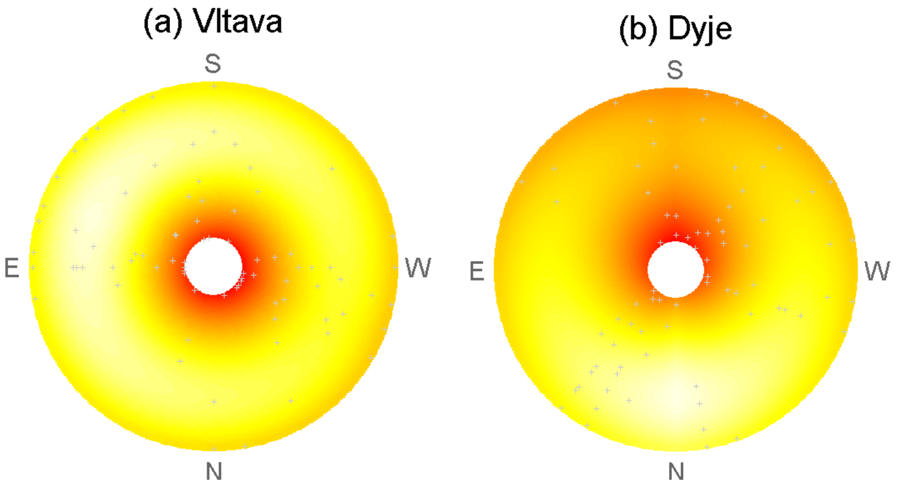

Figure 2: Donut diagrams - projection of spatial distribution of local species richness pattern, modeled using GLMs with relative elevation above the river and aspect as explanatory variables, into idealized model of deep river valley. The diagram should be imagined as a bowl with the empty circle inside being bottom, rising up to the bowl edges. Diagram summarizes two main spatial gradients in the valley – elevation above the valley bottom (distance from the centre of the diagram) and the aspect of the valley slopes (main aspects are indicated by letters at the donut periphery). Colour scale from white to red indicates the gradient from low to high species richness. Grey crosses represent positions of sample plots within the valley.

GLM models are drawn into the space defined by elevation and aspect as a surface with reversed heat colours (red – high values, white – low values). Both diagrams show the polynomial effect of elevation: the highest richness is at the bottom of the valley (centre of the diagram) and in the upper edge of the valley slope (periphery of the “donut”). Due to additional effect of aspect in the model, the second peak of species richness at the upper slopes is not distributed evenly, being most pronounced at the west-facing upper slopes in the Vltava valley and south-facing upper slopes in the Dyje valley. Lowest species richness is found in the middle parts of east-facing slopes in the Vltava valley and the middle parts of north-facing slopes in the Dyje valley.

Of the ecological (topographical and soil) variables, soil pH has the highest explanatory power for local species richness in the Vltava valley, with quadratic polynomial form performing significantly better than the linear one (47.4% of explained variance by quadratic term vs. 30.8% by linear term). In contrast, soil pH behaves as a very weak predictor in the Dyje valley, and forward selection included it as one of the latest vari-

Table 2: Spatial and non-spatial models (GLM) of the herb-layer species richness. The order of explanatory variables follows the steps of forward selection. *AIC* – value of the model's Akaike Information Criterion after adding the given variable (AIC values of null models are given in brackets); *explained* – cumulative percentage variance explained by the model after adding the given variable, *chi-square* – analysis of deviance tests whether the addition of the given variable brings significant increase in the model's explanatory power; *** – $p < 0.001$, ** – $p < 0.01$, * – $p < 0.05$.

Spatial models					
Vltava					
	Elevation + Elevation^2		WNW		
coefficient	−1.6, 1.5		0.001		
AIC (815.4)	703.5		699.6		
explained	31.95		33.6		
chi-square	***		*		
Dyje					
	Elevation + Elevation^2		South		
coefficient	−1.34, 1.2		0.003		
AIC (666.8)	602.4		571.6		
explained	22.1		32.7		
chi-square	***		***		
Non-spatial models					
Vltava – model with pH					
	pH + pH^2	Fluvisol	Heat load		
coefficient	2.02, −1.44	0.38	0.24		
AIC (815.4)	625.6	603.6	600.7		
explained	47.4	54.6	56.1		
chi-square	***	***	*		
Vltava – model without pH					
	Fluvisol	Lithic	Heat load	Surface ISO	
coefficient	0.53	−0.18	0.23	−0.07	
AIC (815.4)	693.6	683.7	681.6	679.8	
explained	26.29	29.87	31.1	32.25	
chi-square	***	***	*	*	
Dyje – model with pH					
	Fluvisol	Cambisol	Heat load	pH + pH^2	Lithic
coefficient	0.51	0.44	0.42	0.67, −0.78	0.22
AIC (666.8)	633.7	599.2	581.7	571.6	566.56
explained	11.33	23.14	29.42	34.01	36.27
chi-square	***	***	***	***	**
Dyje – model without pH					
	Fluvisol	Cambisol	Heat load		
coefficient	0.51	0.44	0.42		
AIC (666.8)	633.7	599.2	581.7		
explained	11.33	23.14	29.42		
chi-square	***	***	***		

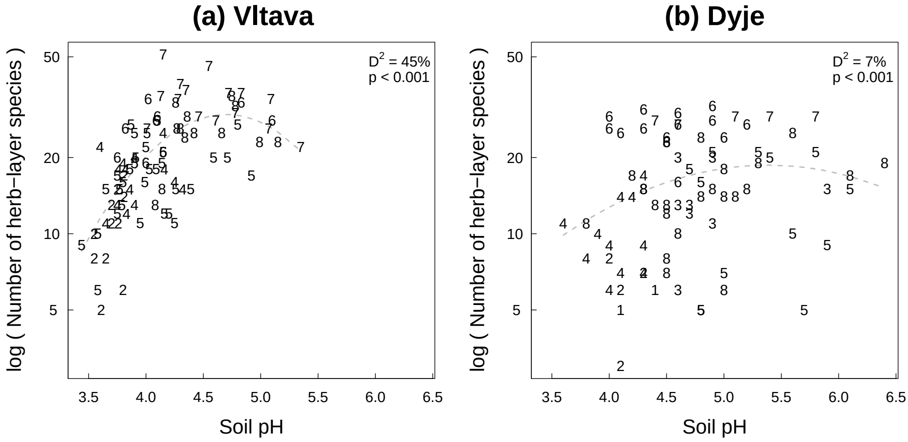

Figure 3: Relationship between the number of herb-layer species in plots and measured soil pH for (a) the Vltava and (b) the Dyje valley. In accordance with the GLM models built by forward selection, second-order polynomial is used to fit the values. Note that y axis is log-scaled. D^2 – deviance explained by the model, p – significance level of the analysis of deviance. Numbers refer to classification of plots into habitat types, following Sádlo et al. (2007): 1 – acidophilous beech forests, 2 – boreo-continental pine forests, 3 – herb-rich beech forests, 4 – acidophilous oak forests, 5 – ravine forests, 6 – thermophilous oak forests, 7 – alluvial forests and 8 – oak-hornbeam forests.

ables; if put independently, soil pH (also in the quadratic form) explains slightly over 7%. These differences in importance of pH for local species richness may be observed also from Fig. 3, showing the relationship between local species richness and soil pH (in GLMs, which were used for fitting the polynomial relationship, explained variance equals the proportion of explained deviance). From the symbols of forest types plotted on Fig. 3 it may be observed that in the Dyje valley the relationship between species richness and soil pH deviates from positive due to two habitat types: thermophilous oak forests (type 6) with low pH and high species richness, and ravine forests (type 5) with high pH and low species richness.

In the Dyje valley, the strongest ecological explanatory variables are soil types Fluvisol and Cambisol, together explaining over 23% of variance. Also in the Vltava valley, when the model is built without soil pH, the best explanatory variable is Fluvisol, explaining over 26% of variance. Another important variable in both valleys is heat load, being more important in the Dyje valley (here it explains 8.5%, while in the Vltava valley it explains only 1.1%). If soil pH is excluded, both models for the Vltava and Dyje

Table 3: Correlations between local species richness (number of herb-layer species) and Ellenberg indicator values (EIVs). Pearson's correlation coefficients and their significances are provided. Bold values are the best correlates of EIVs with herb-layer richness for the particular valley. *** – $P < 0.001$, ** – $P < 0.01$, * – $P < 0.05$, n.s. – not significant result.

	Number of herb-layer species			
EIVs	Vltava		Dyje	
Light	0.27	**	0.28	*
Continentality	n.s.		**0.52**	***
Temperature	0.22	*	0.28	*
Moisture	0.45	***	n.s.	
Nutrients	0.28	**	n.s.	
Reaction	**0.58**	***	0.38	***

valley are quite similar, sharing Fluvisol and heat load and differing by the presence of Lithic and topographical shape along the isohypse (surface ISO) in the Vltava valley and presence of Cambisol in the Dyje valley.

Correlations with the EIVs reveal the most important differences between the valleys: while the species richness pattern of the Vltava valley is shaped mainly by soil pH (as already shown by GLMs including ecological variables), species richness in the Dyje valley is best correlated with continentality, which has no significant effect in the Vltava valley (Table 3). It seems that the best alternative to continentality from spatial variables is slope aspect ('southerness' in case of the Dyje valley), having relatively high explanatory power in spatial model of the Dyje valley, while performing as a very poor predictor in case of the Vltava valley. From ecological ecological variables, possible alternative to continentality may be heat load (in the Dyje valley, 'southerness' and heat load explain 12.5% and 8.5% of variance, respectively). In the Vltava valley, the model based on ecological variables can explain almost all variance explained by the model based purely on spatial variables (shared variability is 31.9%) with additional 25% of net variance explained by only ecological variables (Fig. 4). In the Dyje valley, the model based on ecological variables has significantly lower explanatory power, indicating that some important factor was not measured: models based on only spatial and only ecological variables explain 32.7% and 36.3% of variance, respectively, while sharing only 19.6% of explained variance.

The relationship between local species richness and the size of species pool estimated for particular habitat types is generally positive, although the variability of local species richness within habitat types is quite large (Fig. 5). The most significant exception from this pattern are oak-hornbeam forests – although having the largest estimated species

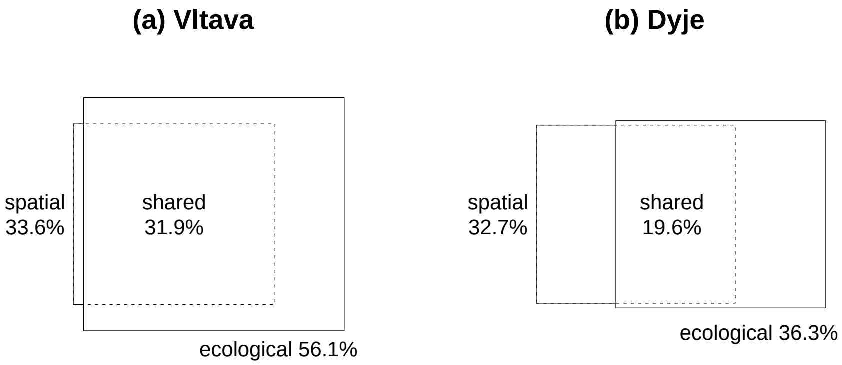

Figure 4: Venn diagrams, showing the proportion of variance in GLM models explained by spatial and ecological variables and variance shared by both model types. Size of squares proportionally reflects the amount of explained variance.

pool, realized local species richness is significantly lower than that of alluvial forests. Another remarkable pattern is higher local species richness in the Vltava valley, observed in all habitat types except thermophilous oak forests.

Discussion

Several studies dealing with the pattern of species richness in river valleys report a strong relationship between species richness and elevation, mainly as a result of decreasing frequency and severity of floods towards the edges of the floodplain (Pollock et al. 1998; van Looy et al. 2003). Situation in deep river valleys of the Bohemian Massif is different because the effect of floods is limited to the valley bottoms. However, our study also showed strong effect of elevation on species richness, having in both valleys a non-linear relationship, with one peak in species richness at low elevation (valley bottom) and the other at high elevation (upper edge of the valley slopes). Species richness at the upper edge of the valley is further modified by aspect, with higher richness located on south- and west-facing upper slopes and slope edges. One possible explanation is that the peaks in species richness at the valley bottom and at south and west-facing upper edges of the valley may result from their ecotonal position. The valley bottom

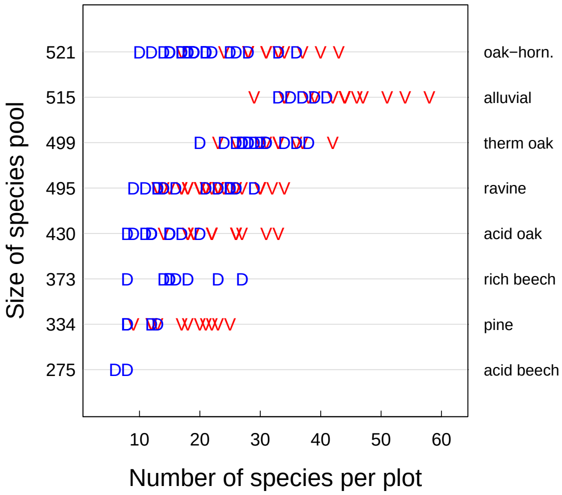

Figure 5: Comparison of local species richness (number of all species per plot) with the regional species pool size estimated for selected habitats by Sádlo et al. (2007). Plots are indicated by V for the Vltava valley and D for the Dyje valley. For explanation of abbreviated names of forest types, see Fig. 3.

is located on the boundary between river-influenced habitats (floodplain) and slopes, while the upper edges of the valley are located between habitats of the valley slopes and the surrounding flat uplands. However, at the same time the upper edges of the valley host rather unique habitats, which are dry, exposed and often rocky, with distinct vegetation types such as thermophilous and acidophilous oak forests and pine forests. While spatial models show significant similarities between both valleys, employment of ecological (topographical and soil) variables reveals the major difference between valleys: effect of soil pH. In case of the Vltava valley, pH is a strong explanatory variable, explaining itself more than 47% of variance in species richness. This is consistent with the empirical positive relationship between species richness and soil pH, observed in several studies from temperate forests (reviewed e.g. by Pärtel 2002) and often attributed to larger species pools of calcicole than calcifuge species in modern floras, probably resulting from predominance of base-rich soils during past glacial periods (Ewald 2003). In the Dyje valley, this relationship was also positive and relatively strong when plots from crystalline limestones were retained in the data set (Chytrý 1995), but it became weak when plots from limestones were removed in this study. Although the removal of the limestone plots made the data sets from both valleys very similar in terms of geology, average soil pH in the Vltava valley is significantly lower than in the Dyje valley (Fig. 3). We suggest that the main reason for this difference is climate: the Dyje valley with lower average altitude is generally warmer and drier than the Vltava valley. Higher soil evapotranspiration due to higher average temperatures may result into higher content of cations in soil and hence higher pH (e.g. Chytrý et al. 2007). At the same time, effect of soil pH on species richness is known to be more pronounced on low-pH soils (active pH < 4.5–5) as a consequence of strong increase in concentration of toxic Al^{3+} cations under this threshold (Tyler 2003), and this fact may explain the differences between valleys in the effect of soil pH on local species richness.

When omitting soil pH from the model, the best explanatory variable in both valleys is occurrence of Fluvisols. These soils develop under direct effect of periodic and stochastic floods and fluctuating ground water table. Floods bring nutrients, help water-dispersed plant species to spread and also cause disturbances of floodplain vegetation. High productivity and certain level of disturbance combined with high dispersal potential of water-dispersed plants may be the main reasons of high species richness of floodplains (Ward 1998). However, separating the effect of productivity on species richness from the effect of soil pH and possibly also moisture is not possible, as all these factors are correlated, forming complex environmental gradient linked to elevation above the valley bottom (Zelený & Chytrý 2007).

Generally lower performance of models with ecological variables in case of the Dyje valley indicates that some factor important for prediction of species richness pattern within the valley was not measured. Correlation analysis of species richness with EIVs shows that in case of the Dyje valley, species richness is strongly correlated with continentality, which does not play any role in the Vltava valley. This contrast may be attributed to the effect of between-valleys differences in species pool, resulting from their geographical (and phytogeographical, respectively) localization within the Czech Republic. The Vltava valley has rather isolated location in South Bohemia, with species pool predominantly derived from elements of Hercynian floristic district and due to close vicinity to mountainous area also enriched by several species from higher altitude, but generally lacking markedly thermophilous species. In contrast, the Dyje valley is located on the boundary of the Hercynian and Pannonian floristic districts, the second being rich source of continental thermophilous species (Chytrý et al. 1999). In the Vltava valley, lack of continental thermophilous species may result in the pattern with the most species-rich habitats in lower parts of the valley, which experience less continental mesoclimate (Chytrý & Tichý 1998; Tichý 1999b). At the same time, the habitats at the valley bottom have higher soil pH, which complies with the generally positive richness–pH relationship. Contrary to this, surplus of continental thermophilous species in the Dyje valley may result in the higher species richness in the upper (mainly south-facing) and relatively acid parts of the valley slopes, which may possibly result into obscured richness–pH relationship. These regional differences in species pools may also explain why the effect of aspect on species richness in spatial models is significantly higher in the Dyje than in the Vltava valley, as aspect is an important variable influencing occurrence of dry and warm habitats with continental mesoclimate, being more important in the Dyje valley.

An analysis comparing estimated regional species pool size with local species richness after separating into habitat types reveals that even if within-type variability in species richness is high, the general relationship is positive, with oak-hornbeam forests being the most distinctive exception. One possible explanation for lower local species richness of oak-hornbeam forests than those expected from the size of their species pool would be that the size of regional species pool for oak-hornbeam forests is overestimated. However, the whole problem is probably more complicated. Estimation of the regional species pool for certain habitat type may be influenced by commonness of this habitat in landscape: the larger the total area where given habitat type occurs, the higher the number of species as a simple consequence of species-area curve (e.g. Rosenzweig 1995), resulting either from the effect of increasing internal heterogeneity and hence occurrence of species with different niches (as already discussed in Sádlo et al. 2007), or simply as an effect of area *per se*. Another explanation may be internal compositional heterogeneity within particular habitat types: from the definition, the size of gamma diversity (which is an analogy to regional species pool) results from the effect of alpha diversity (here local species richness) and beta diversity (heterogeneity), and high gamma diversity may be result of high beta diversity and low alpha diversity. At regional scale, high beta diversity may be caused by strong geographical differentiation of vegetation types within given habitat type, which is also the case of oak-hornbeam forests (Knollová & Chytrý 2004).

Local species richness in the Dyje valley is significantly lower than in the Vltava valley, and this holds true within all compared habitat types except thermophilous oak forests (Fig. 5). There may be slight differences in species richness between valleys, caused by the fact that each valley was sampled by different author, but we do not think that these differences would be as pronounced and as systematic as observed in our data. Possible interpretation is probably again in the differences of local species pools between the valleys. The fact that Dyje valley has generally warmer and drier climate may be reflected in the species structure of its species pool, with increased proportion of continental species of dry and warm habitats and partial lack of species of mesophytic and eutrophic habitats.

Conclusions

Using modelling approach, we found similarities in patterns of local specie richness between both valleys, which may be attributed to similar distribution of local environmental factors within the valleys, such as nutrients, moisture and soil pH. At the same time, we observed also significant differences between valleys, which may be at least partly explained by the effect of species pool.

Acknowledgements

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Paper 3

Pattern of plant species richness along the gradient of landscape topographical heterogeneity: result of spatial mass effect or environmental shift?

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submitted manuscript

Pattern of plant species richness along the gradient of landscape topographical heterogeneity: result of spatial mass effect or environmental shift?

David Zelený, Ching-Feng Li & Milan Chytrý

Abstract

Several processes, such as spatial mass effect and habitat fragmentation, are hypothesised to mediate the relationship between local (microsite) plant species richness and topographical heterogeneity of surrounding landscape. In topographically heterogeneous landscape with various habitats concentrated in close vicinity of each other, local species richness may be enriched for species from surrounding habitats due to the spatial mass effect (sink-source dynamic). Contrary to this, habitat fragmentation increasing with spatial heterogeneity may have negative effect on species richness. Spatial mass effect is assumed to be pronounced in communities with higher ratio of generalists, as generalists will more probably establish viable population at sink habitats. To reveal the pattern of local species richness along the gradient of landscape heterogeneity in middle elevations of the Bohemian Massif, we used 2551 vegetation plots stored in the Czech National Phytosociological Database. We developed analytical approach relating the pattern of local species richness within homogeneous vegetation groups to the gradient of landscape heterogeneity. Increase or decrease of species richness along increasing landscape heterogeneity was related to the changes in ratio of habitat generalists and specialists, and also to the changes in soil pH and nutrient availability estimated by Ellenberg indicator values. Generally, local species richness along the gradient of increasing landscape heterogeneity increases in the case of nutrient-poor vegetation types and decreases in the case of nutrient-rich vegetation types, with several exceptions. Nutrient-poor vegetation types, such as thermophilous and acidophilous oak forests, have also high proportion of habitat generalists, supporting the hypothesis that increased richness in heterogeneous landscape may be result of spatial mass effect. However, the same pattern may be alternatively explained by the shift in environmental conditions of habitat along increasing heterogeneity gradient, such as consistently increasing soil reaction and also increasing productivity of nutrient-rich vegetation types. In discussion, we weight available evidence and conclude that both set of explanation doesn't need to be mutually exclusive.

Key-words: alpha diversity, Central Europe, Ellenberg indicator values, landscape heterogeneity, soil reaction.

Introduction

Environmental heterogeneity is considered as one of the most important drivers of biological diversity (Huston 1994; Rosenzweig 1995; Sarr et al. 2005). Topographic heterogeneity is a special case, as it strongly affects other types of landscape heterogeneity, e.g. variation in mesoclimate, natural disturbances, soil conditions or intensity of human impact. The main effect of landscape-scale topographic heterogeneity on local (microsite) species richness can be seen in the control over the spatial configuration of habitats surrounding the target site. In a topographically homogeneous landscape, site neighbourhood will contain the same or similar habitats, while in a heterogeneous landscape very different habitats may be found in the close vicinity of the site. The effect of spatial configuration of neighbourhood habitats on local species richness has been demonstrated in a number of empirical studies (e.g. Gabriel et al. 2005; Kumar et al. 2006) as well as simulation models (Palmer 1992; Steiner & Köhler 2003). Fewer studies evaluated directly the effect of topographic heterogeneity (Jobbágy et al. 1996; Dufour et al. 2006; Hofer et al. 2008).

Large-scale patterns of species richness are practically impossible to approach experimentally, which increases the importance of empirical descriptive studies. Even though correlative results of these studies cannot untangle causal relationships, they can still bring valuable insights. It is important to consider the effect of landscape context on local species richness separately for different vegetation types. There are two reasons for this: first, the effect could vary between vegetation types in its direction, and the analysis on joint data could be obscured by contradictory results within different vegetation types; and second, different vegetation types differ in the size of their species pools, thus comparison of species richness across vegetation types (and therefore across species pools of different sizes) may reflect the effects of species pool rather than of landscape context. Therefore, we developed a method capable of identifying species richness patterns along the gradient of landscape heterogeneity, based on the separate analyses of data subsets with similar vegetation composition. If we consider species composition as the best descriptor of habitat conditions, similarity of species composition within compared sites also ensures environmental similarity of these sites.

There are several processes, which may drive species richness patterns along the gradient of landscape heterogeneity. Increasing topographic heterogeneity will result not only into higher diversity of habitats occurring close to each other, but also into the reduction of size of particular habitat patches and therefore into their fragmentation. The Theory of Island Biogeography (MacArthur & Wilson 1967) predicts that increasing habitat fragmentation in heterogeneous landscapes would itself result into the decreasing local species richness, as smaller and isolated habitat fragments are more prone to species extinction than large ones and therefore are species poorer (for review of effect of habitat fragmentation on biodiversity see Fahrig 2003). However, habitat fragments in a heterogeneous landscape differ from the islands in the sea in that they are rarely surrounded by completely different habitats. Thus, another important process with contradictory effect on species richness which may play a role is the spatial mass effect (or vicinism; Shmida & Ellner 1984; Zonneveld 1995; van der Maarel 1995). It assumes that species can occur in an unfavourable habitat where it cannot regenerate due to influx of propagules from a vital source population in a nearby favourable habitat (Shmida & Ellner 1984). In a heterogeneous landscape, where more habitats occur close to each other, the probability of the spatial mass effect to happen increases, and the enrichment of the target habitat for vicinists (species from surrounding habitats) increases too. As a result, local species richness can be higher in a heterogeneous landscape.

In their simulation study, Steiner & Köhler (2003) showed that the importance of spatial mass effect on species richness increases with increasing proportion of habitat generalists in community, as generalists can survive in a variety of habitats (Holt 1997). Therefore, we hypothesized that the changes in the ratio of generalists and specialists along the gradient of landscape heterogeneity, measured within vegetation types, give a reasonable indication that the spatial mass effect plays a role. For this purpose, we used the measure of species habitat specialization based on the co-occurrence method introduced by Fridley et al. (2007), which is based on the assumption that habitat specialists consistently occur in habitats with similar set of ecological conditions, while habitat generalists occur in a variety of different habitats. If we assume that similarity of habitats in terms of their ecological conditions is reflected in similarity of their species composition, then, in large a dataset, habitat specialists will systematically co-occur with a similar set of species, while habitat generalists will co-occur with a wider range of other species (Fridley et al. 2007). When corrected for the effect of species pool (Zelený 2008), this method provides a reasonable estimate of realized species niche breaths if large datasets of species co-occurrences are available.

However, the spatial mass effect may not be the only process responsible for changes in species richness along the gradient of landscape heterogeneity. Our analytical approach assumes that the similarity in species composition among plots in one analysed group reflects also similarity in habitat conditions of these plots; however, even within narrow range of ecological variability within the group, systematic shift in ecological parameters along the gradient of landscape heterogeneity may occur and this shift itself can result in changes of local species richness. Here, we particularly focus on the gradual shift of local soil pH and productivity, as both of these variables are known to exert strong control on species richness. The pattern of species richness along pH gradient in the temperate and boreal zones is most frequently documented to have positively linear relationship (Gilbert & Lechowicz 2005; Pärtel 2002), although across the entire range of pH it is ultimately unimodal (Chytrý et al. 2007; Hájek et al. 2007). The pattern of species richness along the productivity gradient is usually reported as unimodal (Waide et al. 1999; Gough et al. 2000; Mittelbach et al. 2001; but see Gillman & Wright 2006). While for productivity-diversity pattern there are at least two sets of possible interpretations, one based on local biotic interactions (see review by Grace 1999) and the second based on the species pool hypothesis (Schamp et al. 2002, 2003), explanation of pH-diversity pattern is based solely on species pool hypothesis (Pärtel 2002; Ewald 2003 or Peet et al. 2003).

In this study, we address the following questions: 1) What is the pattern of local species richness along the gradient of increasing topographic heterogeneity of landscape for different vegetation types? 2) Can this pattern result from the spatial mass effect? 3) Can this pattern be also attributed to the systematic shift in local habitat conditions?

Methods

Vegetation data

All analyses in this paper are based on the data from the Czech National Phytosociological Database, containing more than 85 000 vegetation survey plots (relevés) of various vegetation types recorded following the Braun-Blanquet approach (Westhoff & van der Maarel 1978) at the territory of the Czech Republic since the 1920s (Chytrý & Rafajová 2003). We used only forest plots with geographic localization, which have been assigned by their authors to some of the phytosociological vegetation units at least at the class level. To ensure that no forest vegetation type is represented by disproportionately high number of plots from a small area and to limit the effect of spatial autocorrelation, for which it is not controlled further in the analysis, the dataset was geographically stratified (Knollová et al. 2005). This stratification was performed in the geographical grid of 1.25 minutes of longitude $\times$ 0.75 minutes of latitude (approximately 1.5 $\times$ 1.4 km) in the following way: if more plots assigned by their authors to the same phytosociological association fell within the same grid cell, only one of them was selected for the resulting dataset, preferring more recent plots. Records of mosses, lichens, juveniles and seedlings were deleted and occurrences of the same species in different vegetation layers were merged together. To limit the effect of altitude, only plots from the altitudinal range of 250–480 m a.s.l. were included into further analysis. Plots smaller than 100 m^2 or larger than 400 m^2 were removed. Further removed were plots from rare or ecologically extreme forest types (e.g. thermophilous oak forests on base-rich bedrock and peatland pine forests) and artificial forestry plantations. The resulting dataset used for the analysis included 2551 plots (Fig. 1).

Local species richness and estimation of soil reaction and productivity

The number of all vascular species occurring in each plot was used as the measure of local species richness. To remove for the effect of different plot sizes (within the range of 100–400 m^2) on species richness, we used linear regression of species richness on the log-transformed plot size. Plot species richness, as referred in the further text, is standardized residual of species richness after accounting for plot size, based on this regression model. Soil reaction and productivity for each plot were calculated as non-weighted mean Ellenberg indicator values (EIV; Ellenberg et al. 1992) for soil reaction and nutrients, respectively. Here, EIVs for nutrients are referred to as a measure of productivity, following suggestions of Hill & Carey (1997) and Schaffers & Sýkora (2000).

Landscape heterogeneity

The heterogeneity of the landscape surrounding each plot was calculated using Terrain Ruggedness Index developed by Riley et al. (1999) and calculated from the digital terrain model of the Czech Republic (with pixel resolution of 50 $\times$ 50 m) using the ArcGIS 8.3 software (ESRI, Redlands, California, USA). The position of each plot was projected onto digital terrain model. For a circle of fixed radius around it, square rooted mean of squared differences between the elevation of the central grid cell and other cells falling within the circle was calculated. We arbitrarily set the circle radius corresponding

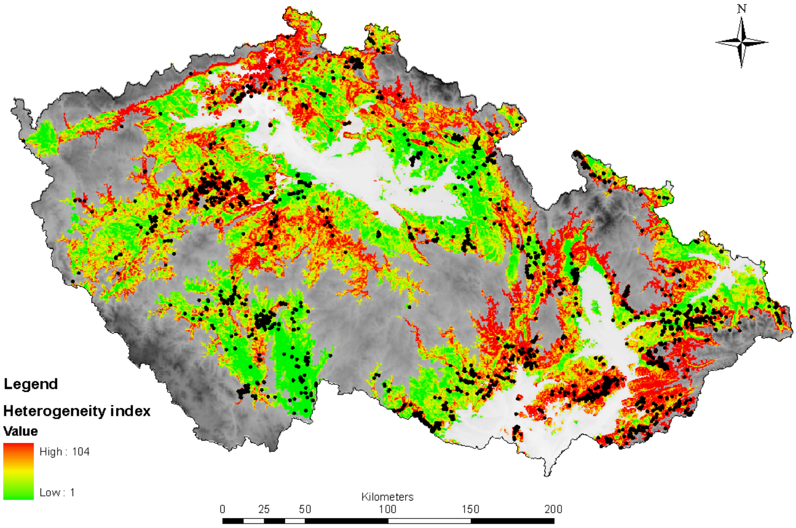


Figure 1: Map of the Czech Republic, with locations of vegetation plots used in the analysis and projection of topographic landscape heterogeneity from low (green) to high (red) in the area falling within the altitudinal range of 250–480 m.

to the length of 6 grid cells (300 m), following results of Kumar et al. (2006) showing the best predictive power of landscape heterogeneity on species richness when calculated from the circle radius of 240 m.

Species habitat specialization

We used the measure of species habitat specialization proposed by Fridley et al. (2007), based on the species co-occurrence data from large dataset. This measure assumes that habitat specialists, growing in specific habitats, will systematically co-occur with a limited number of other species, specialized on the same habitat, whereas habitat generalists, which are able to grow in a wide range of various habitats, will co-occur with many species in a large dataset. The metric, called theta (θ) value, is in fact beta diversity of the set of plots that contain the target species, accounting for the differences in species frequencies in the dataset: low θ value (low beta diversity) indicates a habitat specialist;

high θ value (high beta diversity) indicates a habitat generalist. The original algorithm, as published by Fridley et al. (2007), used beta diversity based on additive partitioning of diversity, which is, however, affected by the size of species pool. In this paper, we used a modified version of original algorithm according to Zelený (2008), which replaces the additive partitioning measure with Whittaker's beta diversity measure, thus removing the confounding effect of variation in species pool size. This algorithm was applied on a geographically stratified dataset of 43 814 plots of all vegetation types from the Czech National Phytosociological Database. θ value was calculated for all species with more than 10 occurrences. One third of species (occurring in the dataset of 2551 plots) with the highest θ values were considered to be generalists, and the proportion of generalists to the total number of species was calculated for each plot.

Statistical analyses

As local species richness of different vegetation types is derived from species pools of various sizes, we developed a method which enables to analyze the pattern of local species richness (and other variables) along the gradient of landscape heterogeneity for each vegetation type separately. For each of the 2551 plots we generated a group including this plot and 99 most similar plots according to the Bray-Curtis dissimilarities, calculated between all plot pairs on the square rooted percentage cover data (Fig. 2, Step 1). For further analyses, we compared all groups with each other and if two groups shared more than two thirds (66) of plots, we randomly deleted one of them, resulting into 1684 groups. To allow the interpretation of the pattern also on the level of vegetation types, we classified all plots into six groups, using cluster analysis based on the flexible beta linkage method (beta = –0.25) and Bray-Curtis distance applied to the square rooted species cover data. The method used, the number of resulting groups and their delimitation were selected subjectively based on the preliminary analyses and expert judgment, in order to distinguish the major vegetation types of broadleaf and mixed coniferous forest of the middle elevations in the Czech Republic, among others also reflecting empirical differences in their regional species pools (Sádlo et al. 2007). Each group of 100 plots was assigned in the vegetation type that was most common within the group, and the result was projected onto the ordination diagram of the 2551 plots, based on non-metric multidimensional scaling (NMDS; Minchin 1987; Oksanen et al. 2008), calculated using the Bray-Curtis dissimilarities and square rooted species cover data. Fitted vectors of Ellenberg indicator values for moisture, nutrients, soil reaction,

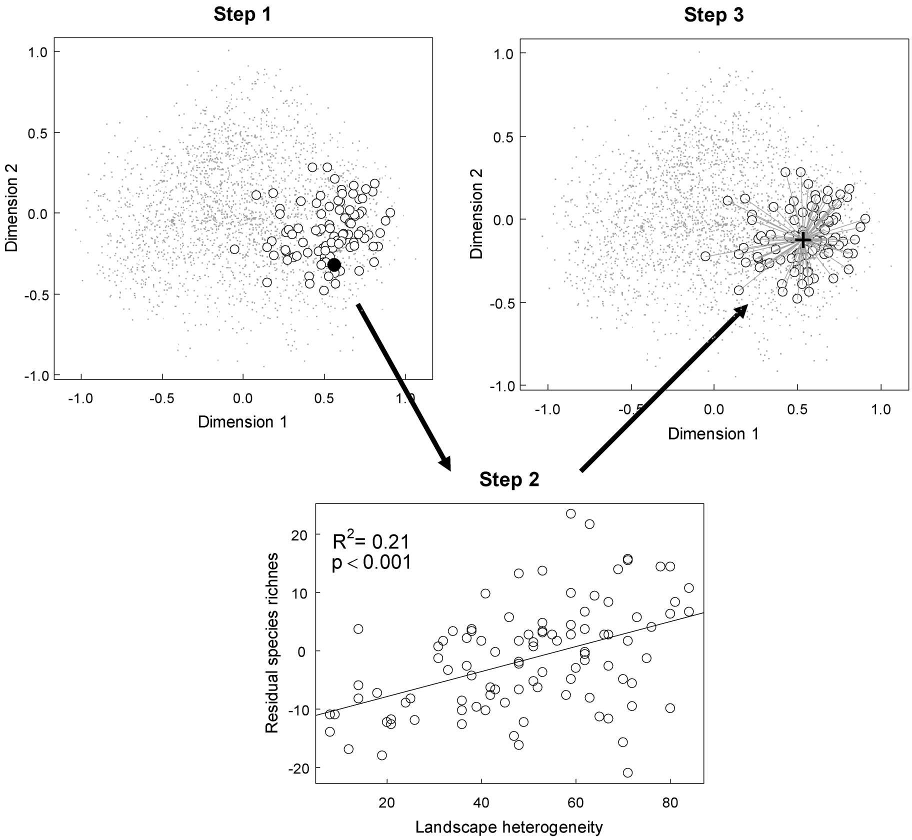


Figure 2: Step-by-step scheme of the repeated-correlation analysis. Dark full circle in the upper left figure indicates the position of randomly selected plot in the space of NMDS ordination diagram. For this plot, 99 plots with most similar species composition are selected, with position indicated by empty circles (Step 1). Selected relevés are used for correlation analysis between (in this case) residual species richness and landscape heterogeneity (Step 2). The result of this analysis is significant and positive, and this information is projected back into the original ordination diagram as a plus symbol in the weighted centroid of the analyzed plots (Step 3); minus sign would be projected in case of significant negative correlation and empty circle in case of non-significant relationship.

light and temperature were also projected on this diagram to ease its interpretation.

For plots of each group, we calculated correlations between landscape heterogeneity and (1) local species richness (Fig. 2, Step 2), (2) soil reaction, (3) nutrients (productivity) and (4) proportion of generalists. Both significant ($P < 0.05$) and non-significant results of correlations were projected onto the NMDS ordination diagram (Fig. 2, Step 3). In this diagram, the result of the correlation within each group of plots was indicated as a symbol in the centroid position of the group. Significant results were plotted as plus signs in the case of positive and minus signs in the case of negative correlation, non-significant results were indicated by empty grey circle. Further, this analysis is referred to as repeated-correlation analysis.

It is important to note that the whole analysis is designed to reveal pattern in the data, not to test and reject null hypotheses. We are aware of the fact that phytosociological data, obtained by non-random sampling, may violate basic assumption of traditional statistical tests, and the significance values calculated by these tests may not be reliable (Lájer 2007). Here, a threshold is set up in order to quantify the result of repeated-correlations analysis and simplify its interpretation, which is based on the counts of correlations with t-value exceeding the threshold. This threshold is arbitrarily set up at the significance level of $P < 0.05$. In fact, this repeated-correlation analysis is a multidimensional variant of moving window regression (e.g. Walker et al. 2003; Palmer 2006). The original method of moving window regression is designed for one gradient and moving window sliding along this gradient, with the samples falling within this window in each step subjected to regression analysis. Here, the sliding is done in a hypothetical multidimensional ecospace, with each window containing plots with similar species composition and two windows close to each other sharing up to 66% of plots.

As each analysis consists of 1684 independent correlations, some kind of correction for multiple comparisons is necessary. Therefore we performed Monte Carlo permutation test for each analysis: values of both dependent and independent variable were randomized and the same set of 1684 correlations were calculated. This procedure was repeated 199 times in order to get the distribution of the number of significant correlations from each run. Based on this distribution, we were able to determine the probability that the given number of significant correlations in the analysis results from random effects. For interpretation of the resulting pattern within particular vegetation types we took only the results based on so high numbers of significant correlations that their probability of being derived from random distribution as calculated by Monte Carlo permutation test was less than 5%. The fact that the partial correlations within the repeated-correlation analysis are not independent, as they may share up to 66% of samples, may unpredictably violate the results of the Monte Carlo permutation test, which requires independent samples. However, the whole analysis is descriptive, and the threshold set up for interpretation has only informative character, without ambitions being the significance threshold for rejecting null hypothesis.

The aim of the last-mentioned analysis was to visualize the pattern of local species richness along the gradient of landscape heterogeneity and to interpret it in terms of changes in soil reaction, nutrient status and species pool. We established a two-dimensional ecospace, defined by Ellenberg indicator values for nutrients on horizontal and soil reaction on vertical axis. For each group of 100 plots, we plotted the position of each plot in this ecospace and calculated the direction of a vector correlated with the changes in landscape heterogeneity within the group. The significance of the fitted vectors was assessed using the Monte Carlo test based on the permutation of heterogeneity values among plots within each group and the criterion of goodness of fit based on the squared correlation coefficients (Oksanen et al. 2008). This procedure was repeated for all plot groups. Only significant vectors, each representing one group of plots, were considered. Of these, we selected only the vectors for groups that had significant correlation between species richness and landscape heterogeneity, and projected them onto the ecospace, pointing in the direction of increasing landscape heterogeneity within the group. Additionally we drew the isolines of estimated species pool size within the ecospace. The estimate of species pool was based on the information from the geographically stratified dataset from the Czech National Phytosociological Database including 4644 forest plots from the elevation range of 250–480 m a.s.l. All plots were drawn onto the ecospace, position of each being defined by its mean Ellenberg indicator value for soil reaction and nutrients. Then we generated 1000 random locations within the ecospace, took one of them, surrounded it by a circle of constant diameter, randomly selected 10 plots falling within this circle and counted the number of species occurring in these plots as an estimate of species pool size in the given location of ecospace. This procedure was repeated for all 1000 locations and results were fitted by smooth surface using thinplate spline fitting (Oksanen et al. 2008).

All statistical analyses were carried out in the R program (R Development Core Team 2008). Plot data were edited and mean Ellenberg indicator values were calculated in the JUICE program (Tichý 2002), and vegetation classification was done in PC-ORD 5 (McCune and Mefford 1999).

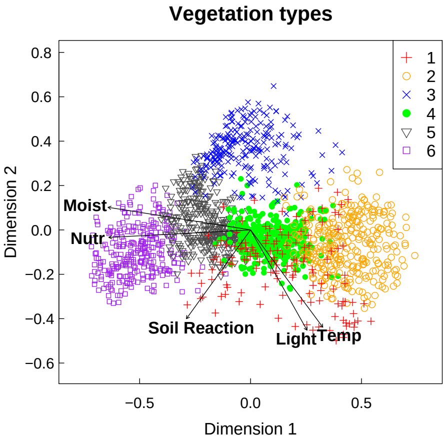


Figure 3: Vegetation types in the space of NMDS ordination diagram, with passively projected Ellenberg indicator values for moisture (Moist), nutrients (Nutr), soil reaction, light and temperature (Temp). Particular vegetation types are: 1 – thermophilous oak forests, 2 – acidophilous oak forests, 3 – beech forests, 4 – oak-hornbeam forests, 5 – ravine forests and 6 – alluvial forests.

Results

The NMDS ordination diagram (Fig. 3) reveals the relationships between the distinguished forest vegetation types in terms of main ecological gradients, described by Ellenberg indicator values. The first ordination axis is correlated with nutrients and moisture, separating (from the left to the right) alluvial forests, ravine forests, oak-hornbeam forests and oak forests. Second axis is correlated with soil reaction, light and temperature, with thermophilous oak forests placed in the warmer and base-rich part of this gradient (bottom) and beech forests in colder and more acid conditions (top).

Generally, nutrient-poor and nutrient-rich forest types differ in their pattern of species richness along the gradient of increasing landscape heterogeneity (Fig. 4). With a few exceptions, which will be mentioned further, nutrient-rich vegetation types at the left part of the ordination diagram have generally lower species richness in heterogeneous than in homogeneous landscapes, while nutrient poor vegetation types in the right part of the diagram show the opposite pattern – they are more species-rich in heterogeneous landscapes (Fig. 4a). In terms of vegetation types, negative relationship between species richness and landscape heterogeneity is more common in beech, oak-hornbeam and ravine forests, while positive relationship is more common in acidophilous and thermophilous

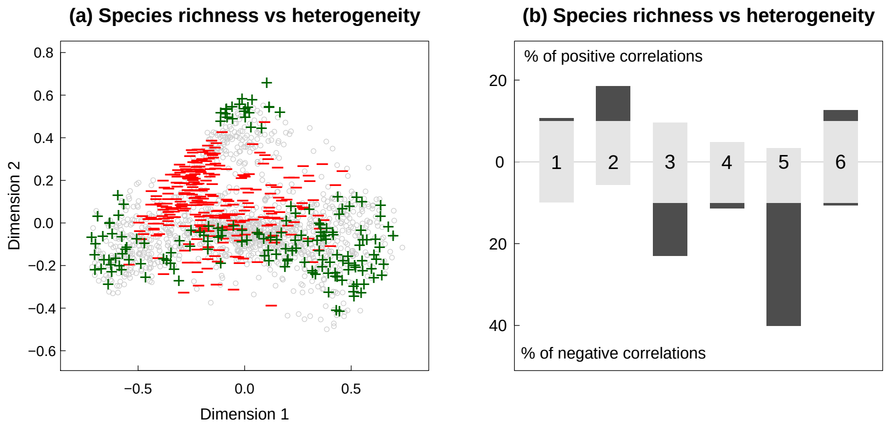


Figure 4: Results of the repeated-correlation analysis between species richness and landscape topographic heterogeneity projected onto the NMDS ordination diagram (a) and expressed as the percentage number of positive or negative correlations within particular vegetation type (b). Plus symbols in the left diagram indicate significant positive correlations within each group of 100 plots, minus symbols are for significant negative correlations and open grey circles for non-significant correlations. The height of boxes in the right diagram reflects the percentage proportion of significant positive (upwards) or negative (downwards) correlations; the black part of the boxes indicates the proportion above 10% (interpretation threshold set up by Monte Carlo test). Particular vegetation types are: 1 – thermophilous oak forests, 2 – acidophilous oak forests, 3 – beech forests, 4 – oak-hornbeam forests, 5 – ravine forests and 6 – alluvial forests.

oak forests (Fig. 4b). Response of alluvial forests is ambiguous, with both positive and negative correlations. The threshold for interpretation determined by the Monte Carlo permutation test was set up to 10% of significant correlations per analysis and vegetation type – it means that only the patterns of vegetation types with more than 10% of negative or positive correlations are interpreted, because the probability that such number or correlations would occur randomly is reasonably low.

There are two main exceptions in the general pattern described above: several positive correlations within the group of alluvial forests (left part of the scatter in Fig. 4a) and within the group of beech forests (upper part of the scatter). Detailed inspection of particular plots revealed probable explanation for these exceptions. In the case of the alluvial forests, increasing species richness is due to increasing frequency of species from other, mainly ravine forest types, reflecting the topographical vicinity of these vegetation types in heterogeneous landscapes of river valleys. In the case of beech forests, positive correlations probably mirror the management status of beech forests across landscape –

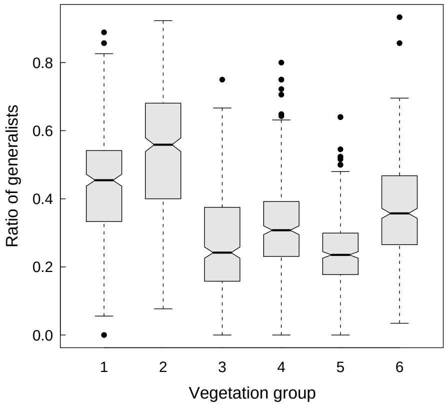
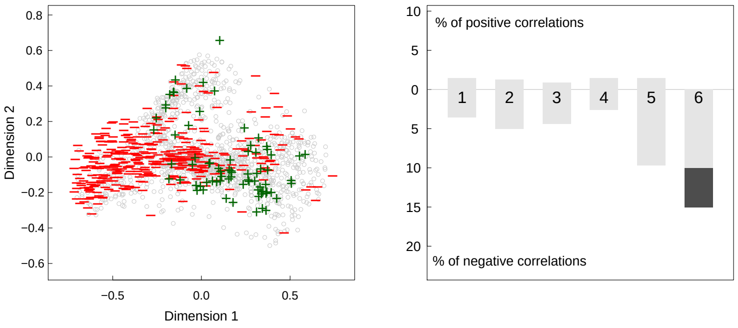


Figure 5: Ratio of generalists in relevés of different vegetation types. Notches in the boxes indicate significance of between-group differences: if notches of two groups do not overlap it is a strong evidence that medians of these groups significantly differs. Particular vegetation types are: 1 – thermophilous oak forests, 2 – acidophilous oak forests, 3 – beech forests, 4 – oak-hornbeam forests, 5 – ravine forests and 6 – alluvial forests.

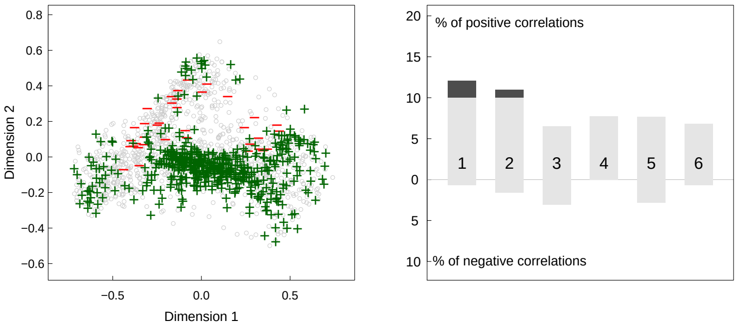
monotonous and species-poor managed beech forests typical of homogeneous landscape shift into less intensively managed and more diverse beech stands in the heterogeneous landscapes.

The differences between vegetation types in the proportion of generalists have a similar pattern as the changes in local species richness along the gradient of landscape heterogeneity (Fig. 5). Generally, both thermophilous and acidophilous oak forests have high proportion of generalists, while beech forests, oak-hornbeam forests and ravine forests have high proportion of habitat specialists. Proportion of generalists is mainly negatively correlated with landscape heterogeneity in the nutrient-rich (left) part of the vegetation continuum, with some positive correlations in the nutrient-poor (right) part (Fig. 6). Generally, in nutrient rich vegetation types, moving toward more heterogeneous landscape, the proportion of generalists in vegetation tends to decrease (prevalence of minus signs in Fig. 6a), with exception of beech forests, where there is no obvious trend. However, when only the results with significant both correlations of productivity and landscape heterogeneity (Fig. 6a) and of species richness and landscape heterogeneity (Fig. 4a) are selected (Fig. 6b), it appears that no vegetation type has markedly increasing proportion of generalists in heterogeneous landscape related to changes in local species



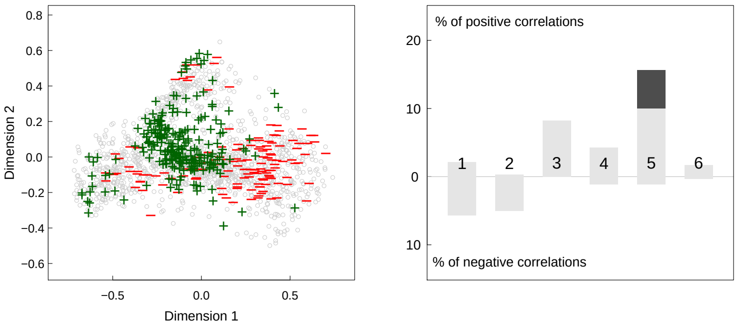
(a) Proportion of generalists vs heterogeneity

(b) Proportion of generalists vs heterogeneity



(c) Soil reaction vs heterogeneity

(d) Soil reaction vs heterogeneity



(e) Productivity vs heterogeneity

(f) Productivity vs heterogeneity

Figure 6: Results of the repeated-correlation analysis projected onto the NMDS ordination diagram (left column) and as the percentage of positive or negative correlations within particular vegetation type (right column). Correlation were calculated between the landscape heterogeneity and (a, b) proportion of generalists, (c, d) soil reaction and (e, f) productivity. See caption of Fig. 4 for further explanation and numbering of vegetation types.

richness, and only alluvial forests and partly also ravine forests have remarkable decrease in proportion of generalists.

Other two analyses reveal the pattern of changes in soil reaction and productivity along the gradient of landscape heterogeneity. Soil reaction, as expressed by Ellenberg indicator values, generally increases with increasing landscape heterogeneity, the pattern being strongest for both thermophilous and acidophilous oak forests, ravine forests and oak-hornbeam forests, less significant for alluvial forests and almost non-significant for beech forests (Fig. 6d). In contrast, the pattern of correlations between Ellenberg indicator values for nutrients and landscape heterogeneity (Fig. 6e) differs among vegetation types, being negative for both thermophilous and acidophilous oak forests, positive for ravine forests, less pronounced but still positive for beech and oak-hornbeam forests, and with no trend in alluvial forests. These results include all significant correlations between Ellenberg indicator values and landscape heterogeneity. If we consider only groups with significant results of correlation between EIVs and landscape heterogeneity, showing at the same time significant correlation between species richness and landscape heterogeneity, the pattern gets simpler: soil reaction is correlated with heterogeneity only in thermophilous and acidophilous oak forests (Fig 6d), and nutrients only in ravine forests (Fig. 6f).

The results of vector analysis (Fig. 7) illustrate how changes in landscape heterogeneity within groups of 100 plots relate to changes of soil reaction and nutrients. Only vectors for the groups with significant positive (Fig. 7a) or significant negative (Fig 7b) correlations between species richness and landscape heterogeneity are drawn. Most of the vectors in Fig. 7a points toward higher soil reaction and less so toward lower productivity, which means that the increase in species richness in more heterogeneous landscapes goes mainly with the increase in soil reaction. In contrast, most of the vectors in Fig. 7b are pointing toward higher productivity and slightly toward lower soil reaction, which means that if local species richness is lower in heterogeneous than in homogeneous landscape, this pattern is related to higher productivity of local vegetation stands in the heterogeneous landscape. The vectors in Fig. 7a represent mainly thermophilous and acidophilous oak forests, and those in Fig. 7b are mainly ravine and less often beech and alluvial forests. Projection of the species pool size estimated on the basis of large vegetation database onto the two dimensional ecospace illustrates how does the size of species pool changes when moving within the ecospace from one combination of gradient values to another. Most of the vectors in Fig. 7a point toward larger species pools,

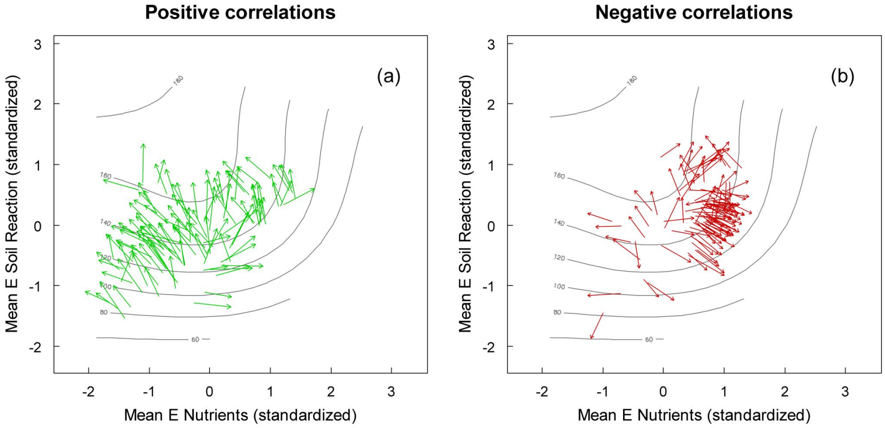


Figure 7: Results of the vector analysis, illustrating the within-group shift in soil reaction and productivity along the gradient of landscape heterogeneity and associated changes in species pool size. Each arrow represents the vector of increasing landscape heterogeneity within a group of 100 plots; figure (a) shows only the vectors of groups with significant positive correlation between species richness and landscape heterogeneity, figure (b) shows only groups with significant negative correlation. Background isolines represent smoothed estimate of the species pool size in given combinations of productivity and soil reaction values.

while most of the vectors in Fig. 7b point toward smaller species pools, suggesting a relationship between the species pool size and local species richness.

Discussion

There is no direct way how to prove, at least using the available non-experimental data, that local species richness changes along the gradient of landscape heterogeneity as a result of particular processes. However, we can compare the observed patterns with the predictions of relevant hypotheses derived from ecological theory and, while acknowledging the context of the present study, to explore which explanations appear to be more consistent with the data. The hypotheses we will consider are the island effect on species extinction in fragmented habitats (MacArthur & Wilson 1967), spatial mass effect (Shmida & Ellner 1984), species pool effect (Taylor et al. 1990; Eriksson 1993; Zobel 1997) and the hump-back relationship between species richness and productivity (Grime 1979).

Our original assumption was that changes in species richness along the gradient of landscape heterogeneity are driven by two processes with opposite effects: habitat fragmentation, which is higher in topographically heterogeneous landscape and results in lower local species richness, and spatial mass effect, which result in higher local species richness in a heterogeneous landscape with accumulation of different habitats close to each others. In the absence of the spatial mass effect we could expect generally negative correlations between species richness and landscape heterogeneity across vegetation types. The pattern resulting from this study indicates that both processes may play a role, but with different intensity in different vegetation types: negative correlations (suggesting the fragmentation effect) prevail in nutrient-rich vegetation and positive correlations (suggesting the spatial mass effect) dominate in nutrient-poor vegetation. The same pattern was observed in the proportion of generalists, which is low in nutrient-rich and high in nutrient-poor vegetation types. The simulation study of Steiner & Köhler (2003) showed that spatial mass effect will more probably result in higher species richness in communities with higher proportion of generalists, and this gives the ground for interpretation of the observed species richness pattern as a result of combination of spatial mass effect and fragmentation effect.

Additionally, we expected that vegetation types with higher local species richness in heterogeneous landscapes will also contain more generalists there; however, this pattern does not occur in every vegetation type (Fig. 6a, b). The reason may be that beside the spatial mass effect, which presumably increases the proportion of generalists, this proportion can be affected by the function of heterogeneous landscapes (here represented mainly by river valleys) as a historical species refuge. From the glacial and postglacial perspective, accumulation of diverse habitats in heterogeneous landscapes may have played an important role for survival of particular species during the periods of climatic changes. Due to changing climate some habitats may become unfavourable for species survival, while others can simultaneously become good alternatives, and spatial proximity of alternative habitats in a heterogeneous landscape allow species to migrate to alternative habitats and thus to reduce their extinction risk. We suggest that this process is probably more important for habitat specialists than generalists, due to specialist's higher sensitivity to environmental change; therefore it may result in higher proportion of specialists in heterogeneous landscapes. Our finding that nutrient-poor vegetation types have slightly increased proportion of generalists in heterogeneous landscapes can be interpreted as a combined result of the spatial mass effect and the 'refuge effect', while increased proportion of specialists in nutrient-rich vegetation types in heterogeneous landscape probably results from the 'refuge effect' alone.

Openness of local communities to species enrichment via spatial mass effect is expected to differ among vegetation types, as documented by both experimental (Foster & Dickson 2004) and observational studies (Cantero et al. 1999). This can be explained by the shift in relative importance of the main factors responsible for local species richness from the species pool effects (e.g. dispersal limitation) to local ecological processes (competition) when moving from low-productive to high-productive habitats (Foster & Dickson 2004). The pattern of local species richness observed in this study fits to this theoretical framework, as the increase in species richness which may be explained by the spatial mass effect occurs only in low-productive vegetation types such as oak forests.

The analysis of changes in local ecological conditions along the gradient of landscape heterogeneity, as judged by Ellenberg indicator values (Fig. 6), reveals an alternative explanation of the species richness pattern. The habitats of the same vegetation type are generally less acid in heterogeneous than in homogeneous landscapes. This holds true with various strength for all vegetation types, being less pronounced in alluvial and beech forests. An obvious explanation is that in a topographically heterogeneous landscape, more intensive denudation and erosion causes relief rejuvenation, resulting into intense weathering and cation release, which is absent in a homogeneous landscape. Due to higher erosion in heterogeneous landscapes, chemical properties of the bedrock have more direct effect on vegetation, while in homogeneous landscapes the bedrock is covered by thick, often leached soils. Because Central European forest flora contains larger species pools of calcicole than calcifuge species (Pärtel 2002; Chytrý et al. 2003; Ewald 2003; Schuster & Diekmann 2003), higher local species richness of oak forests in a more heterogeneous landscape (Fig. 6c, d) may simply result from the effect of larger species pool existing for more base-rich sites which are more widespread in more heterogeneous landscapes.

If we consider only soil reaction, increasing local species richness along the gradient of topographic heterogeneity should occur also in other vegetation types, as does the increasing soil reaction. However, this pattern doesn't show in our result. The clue for this discrepancy may offer the second controlled environmental factor: productivity. Moving into more heterogeneous landscapes, habitats of particular vegetation types are shifted toward more extreme ecological conditions: nutrient-poor vegetation types (thermophilous and acidophilous oak forests) are becoming even more oligotrophic, while mesotrophic and nutrient-rich vegetation types (oak-hornbeam, beech and ravine forests)

Table 1: Topographically heterogeneous landscape, compared to homogeneous landscape

Landscape properties	Species richness	Possible explanation of the species richness pattern	Evidence from the current study
Different habitats are closer to each other	+	Historical refuge effect	Not studied
		Spatial mass effect	Consistent (only valid for low-productive vegetation types)
Habitats are more fragmented	−	Island effect	No clear evidence
Soils are more basic	+	Species pool effect	Consistent (only valid for low-productive vegetation types)
Nutrient-rich soils get richer	−	Hump-back model of diversity-productivity. species pool effect	Consistent (only valid for high-productive vegetation types)
Nutrient-poor soils get poorer	±	Hump-back model of diversity-productivity, species pool effect	No clear evidence

are further enriched in nutrients. This pattern results from the topographical position of particular vegetation types in heterogeneous landscapes, represented here mainly by river valleys: while oak forests are restricted to the upper and exposed parts of slopes, the other vegetation types mainly occupy footslopes and lower parts of the valleys (Zelený & Chytrý 2007). Higher productivity is coupled with lower species richness only for nutrient-rich vegetation types (Fig. 6f), mainly ravine and beech forests. This is consistent with the unimodal relationship between local species richness and productivity, as described by Grime (1979) and also confirmed for Central European deciduous forests (Schuster & Diekmann 2005). Although the traditional explanation of this pattern is increased competition in more productive habitats (Grime 1979), effects of smaller species pools of plants adapted to nutrient-rich habitats (Aarssen 2001; Schamp et al. 2002) are also possible (Fig. 7b).

Conclusions (see also Table 1)

The pattern of species richness along the gradient of increasing landscape topographical heterogeneity surrounding the target site differs among vegetation types: low productive vegetation types have higher, while medium and high-productive types have lower local species richness in heterogeneous landscapes. We offer two alternative sets of explanations, which are not mutually exclusive: the first based on the combination of processes resulting from spatial mass effect and habitat fragmentation, and the second pointing to the fact that the changes in species richness are coupled with the shift in habitat soil reaction and productivity, which itself may be driving factors of processes influencing species richness. Hence, caution should be taken when interpreting landscape-scale patterns in non-experimental data in terms of processes linked to dispersal limitation, as such interpretation may be confounded by changes in those local environmental factors for which it is not controlled. It may be hard to test the hypotheses presented as a result of the current study experimentally, but at least more observational studies performed in other areas and different landscape contexts could explore whether the patterns reported here have a more general validity.

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Paper 4

Co-occurrence based assessment of species habitat specialization is affected by the size of species pool: reply to Fridley et al. (2007)

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Co-occurrence based assessment of species habitat specialization is affected by the size of species pool: reply to Fridley et al. (2007)

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Abstract

1. Fridley et al. (2007) introduced a technique of species habitat specialization assessment based on co-occurrence analysis of large species-plot matrixes, with a continuous metric (θ value) intended to reflect relative species niche width.
2. They used simulated data in order to demonstrate the functionality of the new method. I repeated their simulation and introduced three alternative scenarios with various patterns of species pool size along a simulated gradient. Results indicated that the co-occurrence based estimation of species niche width is dependent on the size of species pool at the position of species optima. This relationship was also revealed in an analysis of a real data set with Ellenberg indicator values as surrogates for environmental gradients.
3. I introduced a modification of the original algorithm, which corrects the effect of the species pool on the estimation of species niche width: the beta diversity measure based on additive partitioning was replaced with the multiplicative Whittaker's beta. Even after this, the method can satisfactorily recover the real pattern of species specialization only for unsaturated communities with a linear relationship between local and regional species richness.
Synthesis: This paper corrects the algorithm for co-occurrence based estimation of species specialization, introduced by Fridley et al. (2007), which was sensitive to the changes in species pool size along environmental gradients.

Key-words: additive partitioning, beta diversity, Ellenberg indicator values, generalists, habitat diversity, local-regional species richness relationship, simulation, specialists, theta value, Whittaker's beta.

Introduction

In their recent work, Fridley et al. (2007) introduced a novel technique to assess habitat generalists and specialists, based on analysis of co-occurrence data extracted from large vegetation data sets. The theory is simple and straightforward: for species occupying many different habitats – generalists – the rate of species turnover among plots in which they occur will be relatively high, while for species restricted to specific habitats – specialists – the species turnover rate will be relatively low, simply because they consistently occur with a limited number of other species. A continuous metric of habitat specialization proposed by Fridley et al. (2007) is called “theta” (θ) and its calculation is based on a measure of beta diversity among the plots with given species. The θ value should be an estimate of species niche width. However, given that real vegetation data are used to calculate θ, the results will reveal realized, not fundamental, species niche, and their validity will be limited to the data set used for analysis. The main advantage of this method is that there is no need for information about the ecological gradient and species position along this gradient. Instead, only a sufficiently large data set of vegetation plots and an algorithm written in R by Fridley et al. (2007) is required. Fridley et al. (2007) also tested the effectiveness of the proposed θ metric using a simulation of species abundance along a single gradient with known species niche widths. They concluded that the method recovers the simulated pattern of species niche widths and it is fairly robust considering sampling bias and various shapes of species response curves. Taking these results as proof of the ability of the θ metric to recover the real pattern, Fridley et al. (2007) analyzed vegetation data sets together with species trait databases and interpreted species habitat specialization by mean of species life histories.

The original simulation algorithm of Fridley et al. (2007) assumes that the optima of simulated species response curves are situated along the environmental gradient in a random fashion (see Table 1, p. 711 of their paper), which (with a low number of simulated species response curves and sampled plots) results in a relatively even pattern of species pool size along the gradient. However, numerous studies (for example Aarssen & Schamp 2002; Ewald 2003; Peet et al. 2003; Hájek et al. 2007) have reported uneven patterns of species pool size along gradients, indicating that changes in species pool size along gradients must be taken into account. Here, I define the size of the species pool in a particular position along (or section of, respectively) the gradient as the number of species having at this position (or section, respectively) non-zero probability of occurrence (and being thus a subset of the overall species pool, which includes all species in the study).

In this paper, I address the questions of how and why changes of species pool size along environmental gradients affect the results of the co-occurrence based estimation of habitat specialization. First, using a modification of the simulation algorithm of Fridley et al. (2007), I show that with uneven patterns of species pool size along the gradients the original algorithm does not satisfactorily recover the simulated pattern of species niche widths. An identical effect is also documented by analysis of an extensive vegetation data set. Subsequently, I propose a modification of the original algorithm, which is less affected by the variation in species pool size along the gradients. Finally, I discuss the conditions under which this method gives reliable estimates of species niche widths.

Relationship between estimated θ value, actual niche width and species pool size

In their simulation, Fridley et al. (2007) compared four scenarios focused on shape of species response curves (symmetrical or skewed) and sampling bias (samples distributed along the gradient randomly or strongly biased to one end). I used the same simulation algorithm, but modified the assumption about the distribution of species response curves along the gradient in order to produce an uneven pattern of species pool size along this gradient, and asked the following question: how will the uneven pattern of species pool size affect the results of the co-occurrence method of habitat specialization assessment?

From the simulation scenarios used by Fridley et al. (2007), I selected the one with symmetrical species response curves and samples randomly distributed along the gradient. To alter the pattern of species pool size changes along the gradient, I introduced three alternative scenarios with various distributions of species optima along the gradient: (1) species optima distributed randomly along the gradient, identical to the original algorithm (Fig. 1a), (2) species optima concentrated in the central part of the gradient (Fig. 1c), and (3) species optima distribution strongly skewed towards one end of the gradient (Fig. 1e). While Fridley et al. (2007) in their simulation used 50 species and 500 plots, I increased these numbers to 300 species and 3000 plots. Technical aspects of the algorithm modification are described in Appendix S1. All calculations in this paper have been carried out in the R program (R Development Core Team 2007).

Figure 1 illustrates the effect of three simulation scenarios with various species optima distribution on changes in species pool size along the gradient. Species pool in a particular position of the gradient is defined as the sum of species with nonzero probability of occurrence in this position. Even in the case of random distribution of species optima along the gradient (Fig. 1a), the species pool shows a hump-back shape with a maximum close to the gradient midpoint (Fig. 1b). The hump-back shape is even

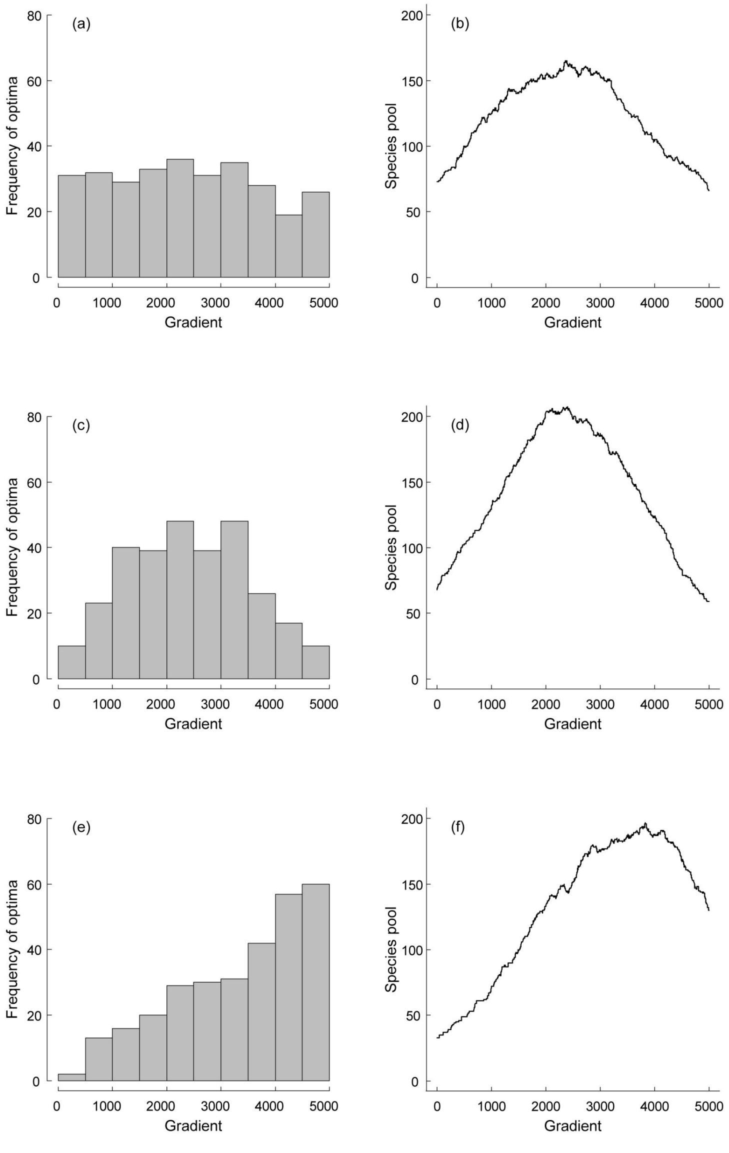

Figure 1: Changes in the size of species pool along the gradient for three simulation scenarios, differing by the distribution pattern of species optima along the gradient: species optima distributed randomly along the gradient (a, b), species optima concentrated along the gradient midpoint (c, d) and distribution of species optima skewed towards one end of the gradient (e, f). Figures in the left column show distribution of species optima along the gradient, figures in the right column represent the resulting pattern of changes in species pool size along the gradient. The size of the species pool at a particular gradient position corresponds to the number of species with non-zero probability of occurrence.

more pronounced if species optima are concentrated in the central part of the gradient (Figs. 1c, d). The skewed distribution of species optima along the gradient (Fig. 1e) results in a similarly skewed response in species pool size (Figs. 1e, f). The degree to which the estimated θ value reflects the actual niche width and species pool is shown in Fig. 2. The estimated θ value is best correlated with the actual niche width in the case of random distribution of species optima along the gradient (Fig. 2a, R^2 = 0.83), while in the case of skewed distribution of species optima the correlation is rather weak (Fig. 2e, R^2 = 0.35). The less the θ value reflects the actual niche width, the more it correlates with the size of species pool at the given position along the gradient: while in the first scenario (random distribution of species optima) the species pool explains 35% of variability (Fig. 2b), in the case of the second and third scenarios (non-random distribution of species optima) it is around 60% (Figs. 2d, f). The reason for the fact that there is a correlation between θ values and the size of species pool even in case of random distribution of species optima along the gradient is a hump-back shape of species pool size along the gradient, a pattern which could be interpreted as a mid-domain effect: species ranges overlap increasingly toward the centre of a bounded domain, in our case an environmental gradient (e.g. Colwell & Lees 2000). An identical mechanism is perhaps responsible for the decline of the species pool near the end of the gradient in the case of skewed distribution of species optima (Fig. 1f).

In Figs. 2a, c and e, the size of the species pool at the position of the given species optima is proportional to the size of circle for that species. Especially in scenarios with a non-random distribution of species optima along the gradient, the larger circles tend to be above the regression line, and smaller circles below. This means that for species with optima in the part of the gradient with a larger species pool, the θ value tends to overestimate the real species niche width, while for species with optima in the part of the gradient with a smaller species pool the real niche width will be underestimated.

Analysis of real vegetation data with Ellenberg indicator values as surrogates for environmental gradients

The following example will illustrate the effect of species pool size on the estimation of species niche width, using the method of Fridley et al. (2007). Let us suppose that the Ellenberg indicator values for vascular plants (EIVs; Ellenberg et al. 1992) can be taken as satisfactory surrogates for basic environmental factors. Most of the Central European species have been assigned in one of 9(12) ordinal classes of EIVs for moisture,

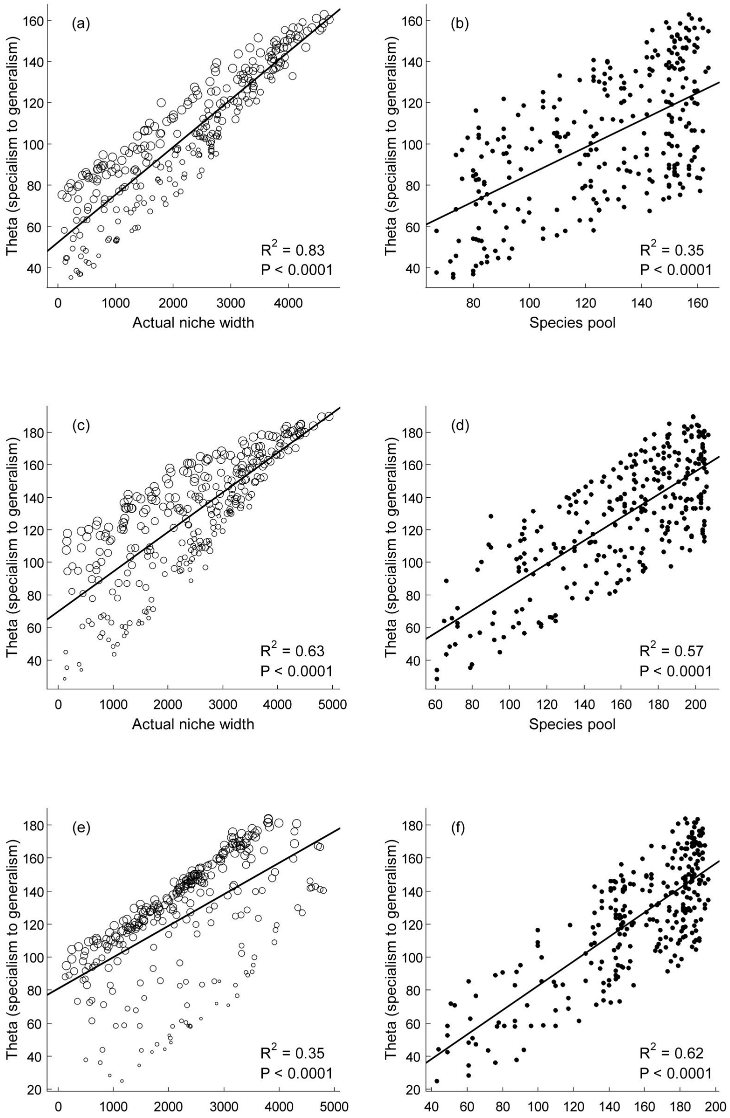

Figure 2: Results of three simulation scenarios, differing in the distribution of species optima along the gradient: species optima distributed randomly along the gradient (a, b), species optima concentrated along the gradient midpoint (c, d), and distribution of species optima skewed towards one end of the gradient (e, f). Figures in the left column display the correlations between the calculated θ value and simulated species niche width, with circle sizes corresponding to the size of species pool at the position of the given species optimum. Figures in the right column show the correlations between the calculated θ value and size of species pool at the particular gradient position. Simulation models are identical to those used in Fig. 1.

nutrients, soil reaction, temperature, continentality and light according to the position of their ecological optima along these gradients. Classes of particular EIVs are known to contain different numbers of species (e.g. Aarssen & Schamp 2002; Ewald 2003) which reflects changes in species pool size along particular gradients. EIVs indicate the position of species optima along gradients but contain no information on niche width. As such the number of species in particular EIV classes underestimates the real species pool size in a given position on the gradient. However, in this study, relative changes in species pool size along the gradient are of main importance, and these are reasonably reflected by the numbers of species assigned to particular EIV classes. Using extensive vegetation data sets, I calculated the θ value for more than 700 species in the list of EIVs and try to answer the question: how is the estimated θ value for species in given class of EIV dependent on the size of species pool (number of species) of this class?

I used a data set of 43807 phytosociological relevés, which carry information about co-occurrence patterns of more than 2200 species in small plots (4–400 m2, depending on vegetation type; Chytrý & Otýpková 2003). This data set results from geographically stratified resampling (Knollová et al. 2005) of more than 80000 relevés stored in the Czech National Vegetation Database (Chytrý & Rafajová 2003) and contains all vegetation types recorded in the Czech Republic over the past 90 years. For all species occurring in at least 20 relevés (all together 1428 species), I calculated θ values using the algorithm proposed by Fridley et al. (2007). For 705 of these species with assigned EIVs, I plotted their θ values against EIVs for soil reaction, nutrients and moisture (Figs. 3a, c, e). Afterwards, I plotted median θ values for species in particular EIV classes against the number of species in these classes (Figs. 3b, d, f).

The resulting pattern is quite clear: except for a few marginal classes (class 9 for soil reaction and class 1 for moisture) there is a positive relationship between median θ value and the number of species in particular EIV classes. Interpretation of these results is identical to the interpretation of the simulation results: species occurring in EIV classes with more species (that is, at the position of the gradient with the larger species pool) have systematically higher θ values. With the method of Fridley et al. (2007) they would be misinterpreted as more generalist than species occurring in classes with lower species frequencies.

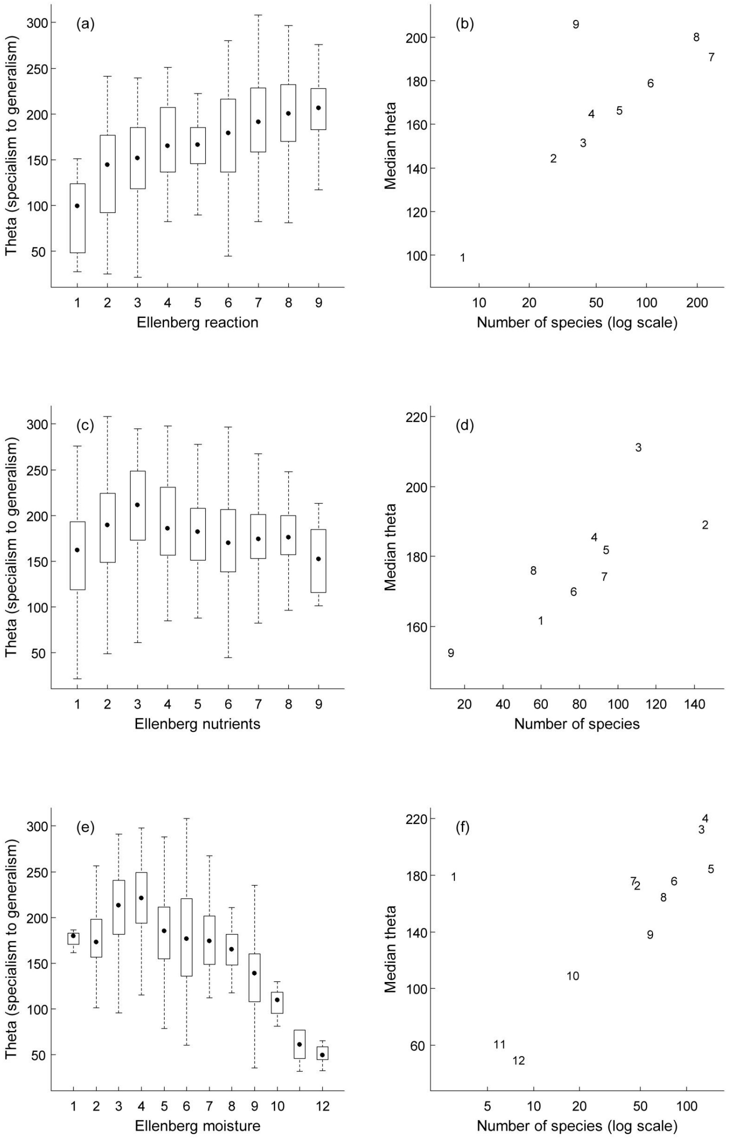

Figure 3: Relationship between co-occurrence based estimate of niche width (θ) of species, calculated from a large matrix of 43807 relevés, and Ellenberg indicator values for (a) reaction, (c) nutrients and (e) moisture. The corresponding figures in the right column (b, d, f) display the correlation between the median θ value, calculated for species from particular classes of the given Ellenberg values, and the number of species in these classes (numbers displayed in the plot correspond to the class numbers). The axes with species numbers in Figs. (b) and (f) are log scaled.

Main pitfalls of the method, possible corrections and conditions of use

The critical aspect of the algorithm proposed by Fridley et al. (2007) seems to be the selection of a beta diversity measure based on 'additive partitioning' of diversity components. The method of co-occurrence based estimation of species specialization compares beta diversities among groups of plots and each of these groups can be derived from species pools of different size. Therefore, the beta diversity measure used must be independent of the size of species pool. As discussed further, beta diversity measure based on additive partitioning does not fulfil this criterion.

The conceptual model in Fig. 4 shows an effect of the local-regional species richness relationship on the calculation of beta diversity using additive partitioning and multiplicative partitioning approaches. Suppose that we study the unsaturated community (Fig. 4a, solid line) with a linear relationship between local and regional species richness (e.g. Srivastava 1999), which can be expressed by the following equation:

$$\mu(\alpha) = k\gamma \qquad \text{(eqn 1)}$$

where $\mu(\alpha)$ is local species richness (mean alpha diversity), γ is regional species richness (or size of species pool), and k is the slope of the correlation between local and regional species richness. Beta diversity β_a based on additive partitioning of diversity (e.g. Veech et al. 2002) is expressed as:

$$\beta_a = \gamma - \mu(\alpha) \qquad \text{(eqn 2a)}$$

and Whittaker's beta diversity β_w (Whittaker 1960) as:

$$\beta_w = \gamma / \mu(\alpha) \qquad \text{(eqn 3a)}$$

By combining eqn 1 with eqns 2a and 3a we get:

$$\beta_a = \gamma - \mu(\alpha) = \gamma - k\gamma = \gamma(1 - k) \qquad \text{(eqn 2b)}$$

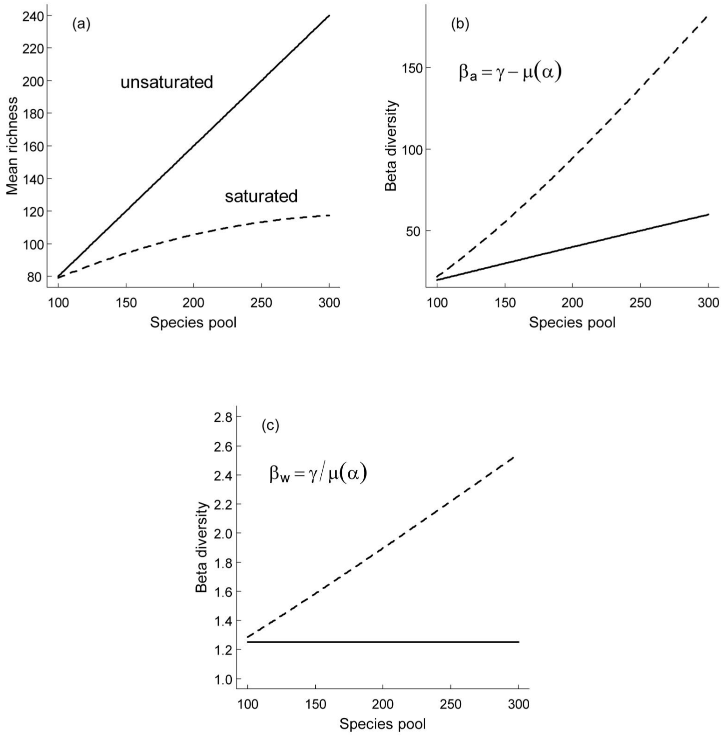

Figure 4: Effect of local-regional species richness relationship (Fig. a) on the calculation of beta diversity based on (b) additive partitioning of diversity components and (c) multiplicative partitioning using Whittaker's beta. In all figures, the solid line represents an unsaturated community with a linear relationship between regional and local species richness, while the dashed line represents a saturated community with a curvilinear local-regional richness relationship.

$$\beta_w = \gamma/\mu(\alpha) = \gamma/k\gamma = 1/k \qquad \text{(eqn 3b)}$$

For a community with a linear relationship between local and regional species richness, k will be constant. A beta diversity measure based on additive partitioning (Fig. 4b, solid line) will increase with the size of species pool (Gaston et al. 2007), while Whittaker's multiplicative measure of beta diversity (Fig. 4c, solid line) will not be affected by the changing size of species pool (Srivastava 1999).

Therefore, I modified the original algorithm of the θ calculation proposed by Fridley et al. (2007), replacing the additive measure of beta diversity with Whittaker's beta (Appendix S2). I re-ran the simulation described at the beginning of this paper, particularly the third scenario with species optima distribution strongly skewed towards one end of the gradient (Fig. 1e). The results are shown in Figs. 5a, b. Compared to the result of the original simulation (Figs. 2e, f), the correlation between simulated niche widths and beta diversity measure became significantly stronger (R^2 = 0.75 vs. original R^2 = 0.35) and the correlation between species pool and beta diversity became weaker (R^2 = 0.15 vs. 0.62). I used this modified algorithm for θ calculation and for recalculation of the analysis with real vegetation data and EIVs. The results showed there was no correlation between estimated θ value and number of species in particular EIV class (not shown).

However, as is obvious from the distribution of circle sizes in Fig. 5a, the effect of species pool size has not been removed completely, as the smaller circles are still found below the regression line and the larger circles above (circle size increases with the size of the species pool). The reason for this lies in the original simulation algorithm, responsible for the projection of simulated species pool sizes into the species richness of individual plots. This algorithm randomly assigned a given number of individuals (around 100) to species according to a simulated probability of species occurrence in the given gradient position, whereas more than one individual could be assigned to the same species. This will result in the non-linear shape of the local-regional species richness relationship (Fig. 4a, dashed line), which is typical for saturated communities (Srivastava 1999). In this relationship, the slope k of the local-regional species richness relationship is not constant, but it is a function of species pool size:

$$k = f(\gamma) \tag{eqn 4}$$

Modified equations for additive (eqn 2b) and Whittaker's (multiplicative; eqn 3b) beta diversity measures will be:

$$\beta_a = \gamma(1-k) = \gamma(1-f(\gamma)) \tag{eqn 2c}$$

$$\beta_w = 1/k = 1/f(\gamma) \tag{eqn 3c}$$

which means that for a curvilinear pattern of the local-regional richness relationship, both additive and multiplicative measures of beta diversity will be affected by the size of

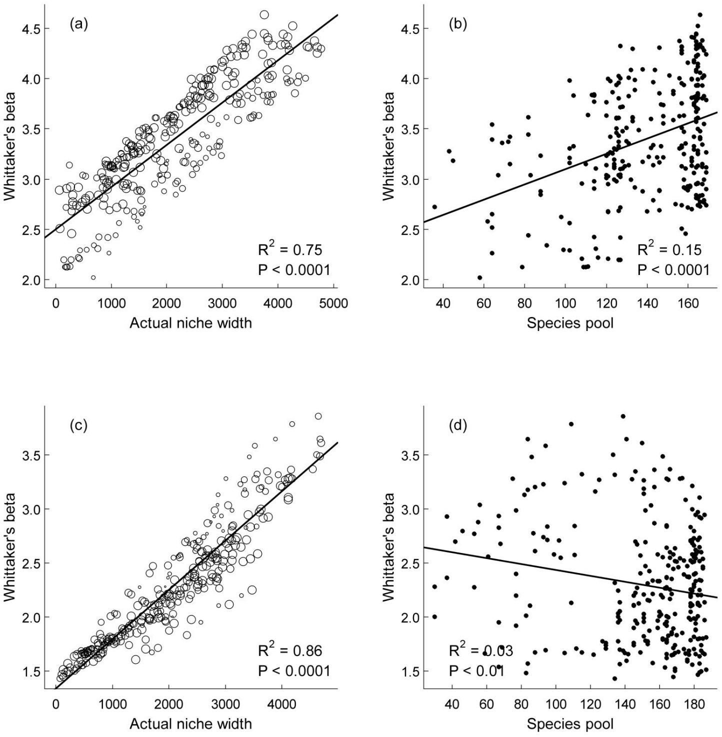

Figure 5: Results of the simulation with a left skewed distribution of species optima along the gradient, where additive beta diversity measure was replaced with multiplicative Whittaker's beta. Figures in left columns show the relationship between simulated species niche width and Whittaker's beta, with the size of the circles corresponding to the size of the species pool at the position of a given species optima. Figures in right column show the relationship between the species pool size and Whittaker's beta. Figures (a) and (b) are the result of a simulation using the original algorithm with a curvilinear local-regional species richness relationship (Fig. 4a, dashed line).Figures (c) and (d) are based on the modified simulation algorithm with a linear local-regional species richness pattern (Fig. 4a, solid line).

species pool (Figs. 4b, c, dashed line; see also Srivastava 1999). If we modify the original simulation algorithm by replacing the curvilinear local-regional richness relationship for the linear one (see Appendix S3), the effect of species pool size on the estimation of niche width will disappear (Figs. 5c, d).

Conclusions

The algorithm for estimating species niche width from co-occurrence data, as introduced by Fridley et al. (2007), is sensitive to the variation in species pool size along the gradient, resulting in strongly biased estimates of species niche width. I propose a modification of this algorithm, which reduces the effect of the species pool size. It replaces the original beta diversity measure based on additive partitioning of diversity components with Whittaker's beta diversity, which is a multiplicative measure. However, even after this modification, the method will satisfactorily recover the real pattern of species specialization only for unsaturated communities, that is, those with a linear relationship between local and regional species richness. As available empirical evidence indicates that unsaturated communities prevail in nature (e.g. Cornell & Lawton 1992; Caley & Schluter 1997; Lawton 1999), the method of Fridley et al. (2007) with the modification proposed here will give reliable results for most studies.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Modified R code for niche width simulations.

Appendix S2 Modified R code from Appendix S1 with multiplicative measure of beta diversity (Whittaker's beta).

Appendix S3 Modified R code from Appendix S1 for simulation of unsaturated community.

Appendix S1

```
1   #Appendix S1: Modified R code for niche width simulations
2
3   # This is a copy of the original R code, written by Jason Fridley (Fridley et al. 2007,
4    Appendix S2), with modification introduced by David Zelený (e-mail: zeleny@sci.muni.cz).
5   # From the original code, only the scenario with "normal" niche distribution type and random
6   sample intervals along gradient is retained, while three new scenarios are introduced - with
7   "even" distribution of species optima, with "unimodal" distribution and with "skewed"
8   distribution.
9   # Modified parts of the original script are marked by boxes .
10  # If not changed, the algorithm will calculate the scenario with "even" distribution of species
11  optima. For other two scenarios, activate the script on line 37 (for "unimodal") or 39 (for
12  "skewed") together with line 54 (in case of both scenarios).
13
14
15  ########################################################################
16  #Generalist-Specialist Metric "test" simulation, Jason Fridley, January 2007; email:
17  fridley@syr.edu
18  #Implemented in R 2.3.1
19
20  #Creates coenoclines
21  #Creates survey designs (random, uniform, or biased exponentially along gradient)
22  #Creates plot-spp matrix based on survey design
23  #Uses matrix in GS algorithm
24  #Outputs graphs
25  #Loops through "random" and "exponential (biased)" survey designs
26
27  #Choose niche distribution type: "normal", "skewed", or "random"
28  niche.type<-"normal"
29  totS<- 300         #total species in simulation
30  #This is beta function for generating niches
31  curve <- function(Ao,m,r,a,g)        {
32          (Ao*((((x-m)/r)+(a/(a+g)))^a)*((1-(((x-m)/r)+(a/(a+g))))^g))/(((a/(a+g))^a)*((1-
33  (a/(a+g)))^g))
34  }
35  x <- seq(1,5000,by=1) # gradient (abscissa)
36
37  #biased <- c(20,40,60,80,100,100,80,60,40,20)                # use this for "unimodal" distribution
38  scenario
39  #biased <- c(20, 40, 60, 80, 100, 120, 140, 160, 180, 200)   # use this for "skewed"
40  distribution scenario
41  pool.biased <- NULL
42  for (i in seq (5,4995, by = 500))
43    {
44    pool.biased <- append(pool.biased, sample (i:(i+500), biased[(i-1)/500+1], replace = T))
45    }
46    pool.biased <- pool.biased[!(pool.biased > 4995 | pool.biased < 5)]
47
48  # species values for normal niches
49  if(niche.type=="normal") {
50  S<-totS                                         #number of species
51  Ao<-rlnorm(S,2,1)                         #amplitude vector (lognormal distribution)
52  m<-sample(seq(5:max(x)-5),S)                #location of optima, use for ``even'' distribution of
53  species optima along gradient
54  #m <- sample (pool.biased, S)        # use this for ``unimodal'' or ``skewed'' scenario
55  r<-runif(S,min=10,max=max(x))                #range along gradient (niche breadth)
56  a<-rep(1.99,S)                                #shape parameter (alpha)
57  g<-rep(1.99,S)                                #shape parameter (gamma)
58  }
59
60  A <- matrix(0,nrow=length(x),ncol=S) #response abundances
61  for(L in 1:S){
62          A[,L] <- curve(Ao[L],m[L],r[L],a[L],g[L])
63  }
```

```

#Summary stats for each species
p.mat<-A
p.mat.NA<-is.na(p.mat)
p.mat[p.mat.NA]<-0
a.mat<-p.mat                        #abundance matrix with zeros
p.mat[p.mat>0]<-1                #presence-absence matrix

ranges<-colSums(p.mat)                #total ranges (niche breadth) for each species
richness<-rowSums(p.mat)        #richness gradient


#------Summary plotting:
#par(mfrow=c(2,2))

#Species distributions along gradient
plot(x,A[,1],xlim=c(0,max(x)),ylim=c(0,max(Ao)),type="l",xlab="Gradient",ylab="Abundan
ce",cex.lab=1.7,cex.axis=1.5,lwd=2)
        for(L in 2:S) {
                lines(x,A[,L])
        }
lines(x,A[,51],lwd=3,col=2)
lines(x,A[,52],lwd=3,col=3)

#Richness along gradient
plot(x,richness)

#Rank-abundance of niche breadths
plot(c(1:S),rev(sort(ranges)))


##SAMPLING FROM GENERATED CURVES
#---------------------------------
Np<- 3000                #number of sample plots
sppmat <- data.frame(c(1:S),paste("S",c(1:S),sep=""))

#Random sample intervals along gradient
rand.sample.x <- sort(trunc(sample(c(2:max(x))-1,Np)))

#Distribution of # inds per local community along gradient
        #from beta distribution (see above)
density.curve<-curve(100,max(x)/2,max(x),.25,.25)

#Number of inds in each plot for each above sampling schemes
draws.rand <- round(rnorm(Np,mean=density.curve[rand.sample.x],sd=1))

#output data frames
samp.out.rand <- matrix(0,nrow=Np,ncol=S)

#Sampling for random-sample-interval
for(i in 1:Np) {
        samp.prob<-a.mat[rand.sample.x[i],]                #probabilities of sampling each
species in given location (based on rel abundance)
        tab.samp <- table(sample(c(1:S),size=draws.rand[i],prob=samp.prob,replace=T))
        #tabulated vector of spp identities after choosing "draws" no. of individuals
        samp.out.rand[i,][as.numeric(names(tab.samp))] <- tab.samp
}
rand.pa <- samp.out.rand
rand.pa[rand.pa>0] <- 1                #presence-absence version

#converted to 2-column list:
spp.vec<-NULL
plot.vec<-NULL
for(i in 1:Np) {
        vec.true<-as.logical(rand.pa[i,])
        plot.vec<-c(plot.vec,rep(i,length=sum(rand.pa[i,])))
        spp.vec<-c(spp.vec,c(1:S)[vec.true])
}
```

```
out.rand <- data.frame(plot.vec,spp.vec)

######################################################################
#Put into G-S analysis (calculate thetas)

#INPUT parameters
reps<-100                                #number of random samples per species
psample<-20                                #min plot occurrences for a species to be analyzed

#par(mfrow=c(2,1))                        #for final graph

#Loop through two survey designs, random and exponential
#THETA<-list(NULL)
c.range<-list(NULL)
sp.loop <- 1
GOSmat<-out.rand

SppMat<-data.frame(sort(unique(GOSmat[,2])),paste("S",sort(unique(GOSmat[,2])),sep=""))
#column 1 is numeric SppID (links to above col 2), col 2 is species label (name, etc)
plotID<-factor(GOSmat[,1])                #factorized plot vector
SppID<-GOSmat[,2]                        #species per plot as numbers or codes
Nplots<-length(levels(plotID))                #number of plots
richness<-tapply(SppID,plotID,length)        #vector of number of species in each plot
max.rich<-max(richness)                        #maximum local richness value
metacom<-table(plotID,SppID)                #plot x species matrix

#Select subset of species for analysis that occur in "plot.cut" # of plots or more
plots.per.spp<-tapply(plotID,SppID,length)                         #vector of number plot occurrences for each species
Species<-sort(unique(GOSmat[,2]))[plots.per.spp>=psample]         #vector of selected species
Nspp<-length(Species)                                                 #number of selected
species

#SPECIES LOOP

sci.name<-rep(0,Nspp)
meanco<-rep(0,Nspp)
meanco.sd<-rep(0,Nspp)
local.avgS<-rep(0,Nspp)
tot.cooccur<-rep(0,Nspp)
occur.freq<-rep(0,Nspp)
GS<-rep(0,Nspp)
GS.sd<-rep(0,Nspp)

for(sp in 1:Nspp) {

print(sp)

#Plot selection
lab<-as.numeric(labels(metacom)[2][[1]])
xlab<-c(1:dim(metacom)[2])
metacol<-xlab[lab==Species[sp]]
sp.plots<-as.logical(metacom[,metacol])
sp.metacom<-metacom[sp.plots,]
Np<-dim(sp.metacom)[1]
wide<-length(xlab)

#Monte Carlo procedure

rpmat<-matrix(c(1:Np),reps,Np,byrow=T)                                         #"reps" rows of plot
sequences
rpmat<-t(apply(rpmat,1,function(x)sample(x,psample))        )                #randomize plot
sequence orders, taking "psample" plots
mc.mat<-array(0,dim=c(psample,wide,reps))                                 #monte carlo matrix:
psamples (eg 20) x #allspecies (178) x #reps (eg 100)
for(i in 1:reps) {
        mc.mat[,,i]<-sp.metacom[rpmat[i,],]
}
#-----------
```

```
colsum<-apply(mc.mat,c(2,3),sum)                #sum columns of each rep, reps become columns
colsum[colsum>0]<-1                                #convert >0 values to ones
rich.vec<-colSums(colsum)-1                        #vector of # cooccurrences for each rep
mc.mat[mc.mat>0]<-1                                #convert species numbers to ones
rowsum<-apply(mc.mat,c(1,3),sum)                #sum rows of each rep, reps become columns
Walpha.vec<-colMeans(rowsum)                        #vector of "avg local richness" (Whittaker's alpha) for each rep
Wbeta.vec<-rich.vec-Walpha.vec

GS[sp]<-mean(Wbeta.vec)                                #mean THETA value for all reps (G-S
metric)
GS.sd[sp]<-sd(Wbeta.vec)                        #s.d. of above
meanco[sp]<-mean(rich.vec)                        #mean # cooccurrences in "psample" plots
meanco.sd[sp]<-sd(rich.vec)                        #s.d. of above

sci.name[sp]<-as.character(SppMat[,2][SppMat[,1]==Species[sp]])                #scientific
name
local.avgS[sp]<-mean(rowSums(sp.metacom))                                #approximate mean
local richness
occur.vec<-colSums(sp.metacom)
tot.cooccur[sp]<-length(occur.vec[occur.vec>0])-1                        #total number of species
co-occurrences
occur.freq[sp]<-Np                                                        #total number of plots
}

#Actual range in simulation
Range<-ranges[Species]

#Output matrix
meanco.u<-qnorm(.975,mean=meanco,sd=meanco.sd)                        #97.5% confidence
limit
meanco.l<-qnorm(.025,mean=meanco,sd=meanco.sd)                        #2.5% confidence
limit
Theta.out<-data.frame(sci.name,local.avgS,tot.cooccur,occur.freq,meanco,meanco.sd,meanco.u,meanco.l,
GS,GS.sd,Range)
#THETA[[s.loop]]<-Theta.out

#Results
par (mar = c(5,6,4,2))
plot(Theta.out$GS,Theta.out$Range,xlab="Theta (specialism to
generalism)",ylab=NA,cex.lab=1.7,cex.axis=1.5,lwd=2,cex=1.3,pch=16, axes = F)
title (ylab = list('Actual niche width', cex = 1.7),line = 4)
abline(lsfit(Theta.out$GS,Theta.out$Range),lwd=3)
axis (1, tck = 0.015, at = seq (trunc (min (Theta.out$GS)/20)*20-20, max (Theta.out$GS)+20,
by = 20), cex.axis = 1.5)
axis (2, tck = 0.015, at = seq (trunc (min (Theta.out$Range)/1000)*1000, max
(Theta.out$Range)+1000, by = 1000), cex.axis = 1.5, las = 1, hadj = 0.8)
legend ('topleft', '(d)', box.lty = 0,cex = 1.7)

cmat<-cor(Theta.out[,-1])
c.range[[s.loop]]<-cmat[,dim(cmat)[2]]


#end
```

Appendix S2

```
#Appendix S2: Modified R code from Appendix S1 with multiplicative measure of beta
diversity (Whittaker's beta)

# This is a copy of part of the original R code, written by Jason Fridley (Fridley et al. 2007,
Appendix S2), with modification introduced by David Zelený (e-mail: zeleny@sci.muni.cz).
# Lines 200-208 from Appendix S1 is reproduced here, with modification marked by boxes.


############################################################################
```

```
colsum<-apply(mc.mat,c(2,3),sum)               #sum columns of each rep, reps become columns
colsum[colsum>0]<-1                               #convert >0 values to ones
rich.vec<-colSums(colsum)-1                       #vector of # cooccurrences for each rep
mc.mat[mc.mat>0]<-1                               #convert species numbers to ones
rowsum<-apply(mc.mat,c(1,3),sum)               #sum rows of each rep, reps become columns
Walpha.vec<-colMeans(rowsum)                       #vector of "avg local richness"
(Whittaker's alpha) for each rep
Wbeta.vec<-rich.vec / Walpha.vec
```

Appendix S3

```
#Appendix S3: Modified R code from Appendix S1 for unsaturated community

# This is a copy of part of the original R code, written by Jason Fridley (Fridley et al. 2007,
Appendix S2), with modification introduced by David Zelený (e-mail: zeleny@sci.muni.cz).
# Lines 95-132 from Appendix S1 are reproduced here, with introduced modifications
resulting into the simulation of unsaturated community marked boxes.


###########################################################################
##SAMPLING FROM GENERATED CURVES
#---------------------------------
Np<-3000                #number of sample plots
sppmat <- data.frame(c(1:S),paste("S",c(1:S),sep=""))

#Random sample intervals along gradient
rand.sample.x <- sort(trunc(sample(c(2:max(x))-1,Np)))

#Distribution of # inds per local community along gradient
        #from beta distribution (see above)
# density.curve<-curve(100,max(x)/2,max(x),.25,.25)

#Number of inds in each plot for each above sampling schemes
# draws.rand <- round(rnorm(Np,mean=density.curve[rand.sample.x],sd=1))

#output data frames
samp.out.rand <- matrix(0,nrow=Np,ncol=S)

#Sampling for random-sample-interval
for(i in 1:Np) {
        samp.prob<-a.mat[rand.sample.x[i],]                #probabilities of sampling each
species in given location (based on rel abundance)
        spec.pool.size.temp <- sum (as.numeric(samp.prob>1))
        spec.richness.temp <- round(rnorm(1,k*spec.pool.size.temp))
        present.species <- (1:S)[samp.prob>1]
        tab.samp <- table(sample(present.species, spec.richness.temp))
        samp.out.rand[i,][as.numeric(names(tab.samp))] <- tab.samp
}
rand.pa <- samp.out.rand
rand.pa[rand.pa>0] <- 1                #presence-absence version

#converted to 2-column list:
spp.vec<-NULL
plot.vec<-NULL
for(i in 1:Np) {
        vec.true<-as.logical(rand.pa[i,])
        plot.vec<-c(plot.vec,rep(i,length=sum(rand.pa[i,])))
        spp.vec<-c(spp.vec,c(1:S)[vec.true])
}
out.rand <- data.frame(plot.vec,spp.vec)
```

General conclusions

The answers to the main questions outlined in the General introduction can be summarized in the following points:

1. Relationship between species composition of vegetation and main environmental factors within the valleys:
    - (a) vegetation in deep river valleys is structured along two main complex ecological gradients: the moisture–nutrients–soil pH and the light–temperature–continentality; the first one is related to the elevation above valley bottom, the second one is related to aspect;
    - (b) the effect of aspect is pronounced the most in the middle parts of the valley slopes, while being lowest at the shaded valley bottoms;
    - (c) among the other important topographical variables are (in addition to the elevation above valley bottom and aspect) slope and landform shape of the plot in downslope direction; among important soil variables are occurrence of Fluvisols, Cambisols and skeletic soils, soil depth and measured soil pH;
2. Relationship between local species richness and environmental variables within the valleys:
    - (a) the highest local species richness within the valley is located at the valley bottom and at the south and west facing upper edges of the valley slopes;
    - (b) soil pH is a strong predictor of species richness, but only in case of Vltava river valley with predominating acid soils with values of $\mathrm{pH} < 4.5$; in case of Dyje valley, where the soils are generally more basic (perhaps as a result

    of drier and warmer climate due to lower elevation), the effect of soil pH on species richness is negligible;

    (c) important factor related to the high local species richness in case of the Dyje valley is continentality, resulting probably from the higher proportion of continental species in regional species pool of Dyje valley due to its geographical location at the boundaries between Hercynian and Pannonian floristic district;

    (d) local species richness is positively correlated with the size of regional species pool estimated for particular habitat types (with exception of oak-hornbeam forests); this indicates that estimates of species pool size itself may be a good predictor of real local species richness;

3. Relationship between landscape topographical heterogeneity and local species richness of particular vegetation types:

    (a) generally, nutrient-poor vegetation types are more species rich in topographically heterogeneous landscape, while the opposite is true for nutrient-rich vegetation types;

    (b) nutrient-poor vegetation types (e.g. oak forests) have high proportion of habitat generalists, indicating that their higher species richness in heterogeneous landscape may be result of pronounced spatial mass effect;

    (c) the pattern of local species richness along the gradient of landscape topographical heterogeneity may be also attributed to the shifts in stand ecological conditions: at heterogeneous landscape, the stands have higher soil reaction (valid for almost all vegetation types), and also higher productivity (valid only for nutrient-rich vegetation types).

Additionally to the three case studies also one methodological study was included (Paper 4). It points up the problem of the method for estimation of species habitat specialization, as originally published by Fridley et al. (2007), showing that the result is affected by the size of species pool. Corrected version, using multiplicative beta diversity measure alternatively to the originally used additive measure, is proposed.

Český souhrn

Diverzita vegetace v hlubokých říčních údolích Českého masivu.

Pro hluboká ostře zaříznutá říční údolí, která jsou od okolních mělce zvlněných pahorkatin oddělená ostrou údolní hranou, se v české vegetační a krajinně ekologické literatuře ujal termín „říční fenomén” (Jeník & Slavíková 1964; Blažková 1964). Ten je souhrnem následujících abiotických a biotických charakteristik: (1) různě strmé údolní svahy s vypreparovanými geologickými odkryvy dávají vyniknout fyzikálním a chemickým vlastnostem matečné horniny, která je mimo údolí často překryta několikametrovým zvětralinovým pláštěm; (2) zaklesnuté meandry mají za následek střídání svahů různých orientací, s prudkými mikroklimatickými kontrasty mezi chladnými severními a výslunnými jižními svahy; (3) převažující „V” tvar říčních údolí má vliv na usměrnění vzdušného proudění a vytváření charakteristických teplotních inverzí; (4) údolí funguje jako migrační cesta, umožňující migraci nelesních společenstev a teplomilných druhů z nížin do vyšších nadmořských výšek a naopak sestup horských prvků do nížin; (5) údolí plnily funkci refugií pro druhy v klimaticky nepříznivých obdobích; a (6) některé úseky hlubokých údolí si díky špatné přístupnosti zachovaly vegetaci málo ovlivněnou lidskými zásahy. Shrnuto dohromady, hluboká říční údolí představují krajinný útvar s pestrou mozaikou vegetačních typů, která vznikla pod vlivem několika výrazných ekologických gradientů a díky tomu je zajímavým modelovým objektem pro studium vztahů mezi vegetací a faktory prostředí.

Cílem této práce je nahlédnout vegetaci hlubokých říčních údolí ze dvou hledisek: z lokálního hlediska, zabývajícího se popisem ekologických vazeb a prostorového uspořádání vegetace a druhové bohatosti v rámci údolí, a z krajinného hlediska, hledajícího souvislost mezi druhovou bohatostí a gradientem topografické heterogenity, a to srovnáním druhové bohatosti jednotlivých vegetačních typů v rámci údolí a mimo ně. Dílčí studie hledají odpovědi na následující otázky:

1. Jaký je vztah mezi druhovým složením vegetace a faktory prostředí v rámci hlubokých říčních údolí?
2. Které prostorové a ekologické proměnné nejlépe vysvětlují rozložení diverzity rostlin v rámci údolí a jak je tento vztah ovlivněn velikostí a vlastnostmi species pool?
3. Jaký je vliv topografické heterogenity krajiny na lokální druhovou bohatost jednotlivých vegetačních typů a které procesy mohou být za tento vztah zodpovědné?

Studie č. 1: Vliv faktorů prostředí na vegetaci hlubokých říčních údolí Českého masivu

Cílem této studie je kvantitativní popis faktorů prostředí, které zásadním způsobem ovlivňují druhové složení a prostorové rozmístění vegetace v hlubokých říčních údolích Českého masivu s vyvinutými projevy tzv. „říčního fenoménu”. Problematika byla studována ve dvou klimaticky odlišných územích: údolí Vltavy v jižních Čechách a údolí Dyje na jižní Moravě. Data o vegetaci a proměnných prostředí byla sbírána na transektech vedených po spádnici údolních svahů z horní hrany údolí k bázi svahu. Vegetační data byla analyzována kombinací shlukové analýzy a nepřímé ordinace (nemetrického mnohorozměrného škálování, NMDS). Vliv geomorfologických a půdních proměnných na vegetaci byl porovnáván sérií kanonických korespondenčních analýz (CCA) s metodou postupného výběru vysvětlujících proměnných založenou na Akaikeho informačním kritériu (AIC). Pro analýzu vlivu nelineárních interakcí mezi dvěmi proměnnými prostředí na vegetaci byla navržena nová metoda nazvaná „moving window CCA”. Tato metoda ukazuje, jak se mění vysvětlující síla jedné proměnné (orientace svahu) na složení vegetace se změnou druhé proměnné (výšky nad řekou). Hlavní směry variability ve vegetaci jsou v hlubokých říčních údolích korelovány s dvěma komplexními gradienty proměnných prostředí: vlhkost–živiny–půdní reakce a světlo–teplota–kontinentalita. Přímá ordinační analýza ukázala, že půdní faktory lépe korelují s druhovým složením vegetace než geomorfologie terénu, přičemž dohromady obě tyto skupiny proměnných vysvětlily 18.8-21.6% celkové variability v druhovém složení vegetace. Ačkoliv některé půdní a geomorfologické proměnné těsně korelují, množství variability vysvětlené sdíleným vlivem obou skupin není příliš vysoké (3.9-5.2%), což znamená, že každá skupina proměnných ovlivňuje vegetaci poněkud jiným způsobem. Nejlepší (nejvíce parsimonní) model CCA pro údolí Vltavy vysvětluje druhové složení vegetace pomocí následujících faktorů: orientace svahu, půdní pH, přítomnost fluvizemě a hloubka půdy; pro údolí Dyje vypadá model podobně, jen faktor hloubka půdy je nahrazen přítomností kambizemě. „Moving windows CCA" ukázala, že orientace svahu má na vegetaci vliv nejvíce ve střední části údolního svahu a nejméně při bázi svahu. Výsledky všech analýz ukazují výraznou shodu ve vztazích mezi vegetací a prostředím v obou říčních údolích, což naznačuje možnosti zobecnění popsaných vztahů i na další hluboká říční údolí Českého masivu.

Studie č. 2: Modelování druhové bohatosti rostlin v topograficky komplexní krajině hlubokých říčních údolí Českého masivu

Cílem této studie je popsat prostorové rozmístění druhové bohatosti rostlin v hlubokých říčních údolích a modelovat vztah druhové bohatosti k ekologickým (topografickým a půdním) proměnným prostředí. Zároveň byla provedena analýza srovnávající vztah mezi počtem druhů na jednotlivých plochách (lokální druhovou bohatostí) a odhadem velikosti species pool pro jednotlivé typy stanovišť. Pro účely této studie byly použity data z transektů vedených napříč údolími Vltavy a Dyje. Vztah mezi druhovou bohatostí vs. prostorovými nebo ekologickými vysvětlujícími proměnnými byl modelován zobecněnými lineárními modely (GLM); jednotlivé modely byly budovány postupným výběrem proměnných na základě Akaikeho informačního kritéria (AIC). Z prostorových proměnných je nejlepší relativní výška řekou, a to ve formě polynomu druhého řádu; druhou nejlepší proměnnou je orientace svahu. Druhově nejbohatší plochy se tedy v rámci údolí vyskytují při bázi údolních svahů a na jižně (Dyje) respektive západně (Vltava) orientovaných horních hranách svahů. V modelech zahrnujících ekologické proměnné vysvětlilo v případě Vltavy nejvíce variability půdní pH (47,4% celkové variability), zatímco na Dyji se pH chovalo jako velmi slabý prediktor (samo o sobě vysvětlilo 7,7% celkové variability). Pokud se půdní pH do modelů nezahrnulo, výběr proměnných byl u obou údolí do určité míry podobný (přítomnost fluvizemí a tepelný požitek plochy). Rozdílné chování druhové bohatosti ve vztahu k půdnímu pH může souviset s tím, že půdy na Vltavě jsou (zřejmě vzhledem k vyšší nadmořské výšce) obecně kyselejší, přičemž toxicita kyselých půd se obecně projevuje při pH $<$ 4,5 (na Vltavě má nižší pH více než polovina ploch, na Dyji méně než třetina). Možným vysvětlením by mohl být ale i rozdíl ve species pool jednotlivých oblastí: zatímco species pool Vltavy zahrnuje hlavně Hercynské druhy, species pool Dyje je díky geografické pozici na rozhranní Panonské a Hercynské oblasti nasycen Panonskými druhy s kontinentální tendencí. Porovnání druhové bohatosti a velikosti species pool ukázalo, že až na výjimky (dubohabřiny) platí pozitivní vztah mezi lokální druhovou bohatostí jednotlivých stanovištních typů a odhadovanou velikostí jejich species pool. Korelace druhové bohatosti a Ellenbergových indikačních hodnot potvrdila rozdíl mezi Vltavou a Dyjí – zatímco na Vltavě je druhová bohatost nejsilněji korelována s půdní reakcí, na Dyji je nejlépe korelovaná s kontinentalitou. Fytogenografické rozdíly mezi flórami obou údolí mohou tedy překrýt lokální efekty těch ekologických faktorů, které mají obvykle zásadní vliv na druhovou bohatost (např. půdní pH).

Studie č. 3: Jsou změny v druhové bohatosti podél gradientu topografické heterogenity výsledkem prostorového mass efektu nebo posunu ekologických podmínek stanoviště?

Topografická heterogenita krajiny může mít přímý vliv na lokální druhovou bohatost jednotlivých vegetačních typů. Jedním z důsledků vysoké topografické heterogenity krajiny je nahloučení rozdílných stanovišť v těsné blízkosti. Výsledkem může být vyšší migrace rostlinných druhů mezi těmito stanovišti v rámci tzv. dynamiky propadu a zdroje: stabilní populace druhu na optimálním (zdrojovém) stanovišti může díky mass-efektu podporovat existenci nestabilních, přechodných populací na (propadových) stanovištích, na kterých by druh díky nepříhodným ekologickým podmínkám nebyl bez neustálého přísunu diaspor z okolí růst. Definujme si mikrolokalitu analogicky fytocenologickému snímku jako výsek vegetace daného biotopu o konstantní ploše. Mikrolokality v heterogenní krajině, kde jsou obklopené mozaikou různých biotopů coby potenciálních zdrojů diaspor, by mohly být díky tomuto procesu druhově bohatší než mikrolokality analogického biotopu v krajině homogenní. Opačný vliv na druhovou bohatost může mít jiný důsledek krajinné heterogenity, a tím je vysoká fragmentace jednotlivých biotopů. Teorie ostrovní biogeografie předpokládá, že čím je daný fragment biotopu menší a izolovanější, tím menší počet druhů se na něm bude vyskytovat. Celková nízká druhová bohatost daného fragmentu může negativně ovlivňovat i lokální druhovou bohatost jednotlivých mikrolokalit. V naší studii jsme použili rozsáhlý datový soubor, obsahujících 2551 fytocenologických snímků z České národní fytocenologické databáze, který zahrnuje vegetaci různých lesních typů na gradientu topografické heterogenity krajiny, který je důsledkem výskytu hlubokých říčních údolí v jinak poměrně málo heterogenní krajině Českého masivu. Použily jsme statistickou analýzu, která umožnila popsat v rámci úzce vymezených relativně homogenních vegetačních typů vztah mezi druhovou bohatostí jednotlivých mikrolokalit (fytocenologických snímků) a topografickou heterogenitou okolní krajiny. Ukázalo se, že vztah mezi diverzitou a heterogenitou se liší podle produktivity daného vegetačního typu: oligotrofní vegetační typy (teplomilné a acidofilní doubravy) mají v heterogenní krajině systematicky vyšší druhovou bohatost než v krajinně homogenní, zatímco pro eutrofní vegetační typy platí (až na výjimky) pravý opak. Zároveň s analýzou druhové bohatosti jsme se zaměřili i na poměr mezi stanovištními generalisty a specialisty v jednotlivých vegetačních typech. Publikované teoretické studie předpokládají, že vliv mass efektu je vyšší u vegetace s vyšší proporcí generalistů, kteří mají větší schopnost migrovat mezi stanovišti coby důsledek dynamiky zdroje a propadu. Naše výsledky ukazují, že vegetační typy, které jsou v heterogenní krajině druhově bohatší, mají zároveň vyšší proporci stanovištních generalistů, což je v souladu s výše zmíněným předpokladem teoretických studií. Homogenní vegetační typy, v jejichž rámci byly jednotlivé analýzy prováděny, byly definovány jako skupiny snímků shloučených na základě jejich podobnosti v druhovém složení, což garantuje podobnost v ekologických parametrech stanovišť jednotlivých snímků. I přes to se ale může stát, že v rámci této skupiny se budou stanovištní parametry jednotlivých mikrolikalit lišit, a pokud budou tyto rozdíly podél gradientu topografické heterogenity systematické, mohou mít samy o sobě za následek rozdíly v jejich druhové bohatosti. Analýza dvou proměnných prostředí, půdní reakce a produktivity (odhadované pomocí Ellenbergových indikačních hodnot), ukázala, že podobné systematické trendy se v datech skutečně vyskytují: půdní reakce je u téměř všech vegetačních typů systematicky vyšší v heterogenní než v homogenní krajině. Naopak v případě produktivity se dané trendy liší podle úživnosti stanoviště, a to tak, že jednotlivé vegetační typy se směrem do heterogenní krajiny stávají extrémnějšími: oligotrofní typy jsou ještě chudší, mezotrofní a eutrofní typy se naopak směrem do heterogenní krajiny stávají ještě úživnějšími. Po propojení pozorovaných rozdílů v ekologických podmínkách stanoviště se znalostí obecných vztahů mezi druhovou bohatostí a pH (pozitivní) a druhovou bohatostí a produktivitou (unimodální) se ukazuje, že odhalené trendy v druhové bohatosti podél gradientu topografické heterogenity je možné vysvětlit těmito rozdíly v ekologických podmínách stanoviště docela dobře vysvětlit. Existují tedy dva alternativní soubory hypotéz, které by mohly podat vysvětlení rozdílů v druhové bohatosti mikrolokality zasazené do kontextu topograficky heterogenní a homogenní krajiny.

Studie č. 4: Míra stanovištní specializace druhu stanovená na základě společného výskytu druhů ve velkých datových souborech je ovlivněna velikostí species pool: reakce na článek Fridley et al. 2007

Tato metodická studie vznikla při práci na předchozí studii (č. 3) a zabývá se korekcí metody stanovení míry stanovištní specializace druhu na základě dat z rozsáhlých vegetačních databází. Fridley et al. (2008) vytvořily efektivní metodu, která umožňuje stanovit míru, do jaké se daný druh chová jako stanovištní generalista nebo specialista. Metoda je založená na myšlence, že pokud se vegetace různých lokalit, na kterých se druh vyskytuje, navzájem výrazně liší, druh je spíše stanovištní generalista, tolerující širší spektrum ekologických podmínek. Naopak pokud se druh na různých lokalitách vyskytuje ve vegetaci stále se opakujícího druhového složení, bude se jednat o stanovištního specialisty s úzkou ekologickou nikou. Tradiční nevýhodou různých způsobů měření šířky druhové niky je nutnost vybrat ekologický gradient, ke kterému se bude šířka niky vztahovat; není ale zároveň snadné objektivně rozhodnout, podél kterého gradientu a proč by se druhová nika měla měřit. Velkou výhodou navržené metody je fakt, že je bezrozměrná a nevztahuje se přímo k žádnému z ekologických gradientů. Informaci o společném výskytu druhů na různých lokalitách je možné získat z rozsáhlých vegetačních databází, které jsou dnes často k dispozici, a výsledná míra, označovaná jako theta (θ), přímo odráží beta diverzitu druhového složení snímků obsahujících daný druh. Autoři otestovali robustnost nové metody simulačním modelem a následně ji použily v případové studii, kde vztáhli míru stanovištní specializace druhů s jejich vybranými funkčními vlastnostmi.

Při práci s touto mírou stanovištní specializace jsem došel k závěru, že metoda tak, jak ji byla původně navržena, podává zkreslený odhad reálné míry stanovištní specializace druhu. Upravené simulační modely ukazují, že vypočtené hodnoty specializace jsou ovlivněné velikostí species poolu vegetačních typů, ve kterých se daný druh vyskytuje. Pokud má druh v modelu úzkou ekologickou niku, ale vyskytuje se ve vegetaci která má velký species pool, výsledkem bude nadhodnocení simulované šířky niky tohoto druhu. Naopak, u druhů z vegetačních typů majících malý species pool tomu bude naopak. Vedle simulačního modelu ukazuje tento artefakt i analýza založená na reálných datech: na základě datového souboru 43807 fytocenologických snímků z České národní fytocenologické databáze jsem spočítal míru specializace (θ) pro 705 druhů, a tyto hodnoty byly následně dány do souvislosti s Ellenbergovými indikačními hodnotami pro tyto druhy. Ukázalo se, že druhy v těch kategoriích jednotlivých Ellenbergových hodnot, které zahrnují větší množství druhů (větší species pool), mají na základě výpočtu míry stanovištní specializace širší niku než druhy z kategorií s malým počtem druhů. Teoretický rozbor ukázal, že podstatou problému je použití aditivní míry beta diverzity. Její nahrazení multiplikativní mírou, jako je Whittakerova beta diverzita, závislost na velikosti species pool odstraňuje. I po zabudování navržené korekce do výpočetního algoritmu je daná metoda schopná odhadovat míru druhové specializace jen v případě nesaturovaných společenstev, které mají lineární vztah mezi lokální a regionální druhovou bohatostí; empirické studie však ukazují, že nesaturovaná společenstva se v přírodě vyskytují nejčastěji.

Obecné závěry

Odpovědi na jednotlivé otázky formulované v úvodu je možné shrnout do několika bodů:

1. vztah mezi druhovým složením vegetace a faktory prostředí:
    (a) vegetace v hlubokých říčních údolích je strukturovaná podél dvou hlavních komplexních gradientů: gradientu vlhkosti-živin-pH a světla-teploty-kontinentality, přičemž první z těchto gradientů odpovídá výšce nad řekou a druhý orientaci svahu;
    (b) vliv orientace svahu na složení vegetace je nejvyšší ve střední části údolního svahu, naopak nejnižší na zastíněné bázi svahu;
    (c) mezi důležité topografické proměnné ovlivňující složení vegetace patří vedle výšky nad řekou a orientace i svažitost a tvar plochy po svážnici; naopak mezi důležité půdní faktory patří výskyt fluvizemě, kambizemě a suťových půd, hloubka půdy a půdní pH;
2. vztah mezi lokální druhovou bohatostí a faktory prostředí:
    (a) nejvyšší druhová bohatost v rámci říčních údolí je soustředěna při bázi údolních svahů a na jižně resp. západně orientovaných horních údolních hranách;

(b) půdní pH je silným prediktorem druhové bohatosti, ale pouze v případě údolí Vltavy, kde převažují kyselejší půdy s hodnotami pH ¡ 4.5; v údolí Dyje, které má (zřejmě díky nižší nadmořské výšce) bazičtější půdy, je vliv pH na druhovou bohatost malý;

(c) výrazným faktorem korelovaným s vysokou druhovou bohatostí je v případě Dyje kontinentalita, což je zřejmě důsledkem vyššího podílu kontinentálně laděných druhů ve species pool údolí Dyje díky jeho geografické poloze na rozhranní Hercynské a Pannonské fytogeografické oblasti;

(d) lokální druhová bohatost je pozitivně korelovaná s velikostí species pool pro jednotlivé stanovištní typy (s výjimkou dubohabřin), což ukazuje na to, že odhad velikosti species pool pro jednotlivá stanoviště může být sám o sobě dobrým prediktorem lokální druhové bohatosti;

3. vztah mezi topografickou heterogenitou krajiny a lokální druhovou bohatostí jednotlivých vegetačních typů:

   (a) obecně platí, že živinami chudé vegetační typy jsou v topograficky heterogenní krajině druhově bohatší než v topograficky homogenní krajině, zatímco u živinami bohatších vegetačních typů je tomu naopak;

   (b) živinami chudé vegetační typy (doubravy) mají zároveň vysoké zastoupení stanovištních generalistů, což naznačuje, že jejich vyšší druhová bohatost v heterogenní krajině může být důsledkem zvýšené role prostorového mass efektu v heterogenní krajině (ten způsobuje, že druhová bohatost na daném mikrostanovišti je zvyšována přítomností druhů z okolních, ekologicky odlišných stanovišť, přičemž přetrvání těchto druhů na daném mikrostanovišti je možné jen díky intenzivnímu přísunu diaspor tohoto druhu z okolí);

   (c) zároveň ale platí, že stanoviště daných vegetačních typů se od sebe v heterogenní a homogenní krajině liší některými ekologickými parametry, které samy o sobě mohou vysvětlit popsané rozdíly v druhové bohatosti: stanoviště v heterogenní krajině mají obecně vyšší půdní reakci (platí pro téměř všechny vegetační typy) a také vyšší produktivitu (platí pro živinami bohaté stanoviště).

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Curriculum vitae

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Education:

1996 – 1999: Faculty of Biological Sciences in České Budějovice, bachelor study under the supervision of prof. Jan Lepš (*Effect of biotically generated heterogeneity on the seedling recruitment in grasslands*).
1999 – 2002: Faculty of Biological Sciences in České Budějovice, master study under the supervision of Milan Štech and Milan Chytrý (*Factors influencing the vegetation in the Vltava river valley north of Zlatá Koruna, Czech Republic*).
2002 – (2008): Department of Botany, Faculty of Biological Sciences in České Budějovice, PhD study under the supervision of Milan Chytrý (Masaryk University Brno).

Work experience:

2001: participation on the project "*The influence of management changes and atmospheric deposition on the ecosystem quality in mountainous areas*" – collection and analysis of vegetation data (Dr. J. Květ, Institute of Botany, Czech Academy of Sciences);
2002: participation on the project "*Direct succession on previously arable land*", CLUE – field work, vegetation sampling (Martin Bezemeer – NIOO, Heteren, Holland);
2001–2004: field vegetation mapping in three different parts of the Czech Republic – project NATURA 2000 (J. Wimmer – AOPK Č. Budějovice, J. Juřička and D. Cigánek – AOPK Havlíčkův Brod);

October 2002 – February 2003: volunteer participation on the project of the New Zealand Department of Conservation, studying the browsing effect of introduced mammals on the regeneration processes of native beech forest – preparation and coordination of the local project in Rangataua forest in Tongariro National Park, establishment of experimental plots (Steve Deverell and Sean Husheer – Department of Conservation, Turangi, NZ);
2004–2005: participation on the project VISTA – *Vulnerability of Ecosystem Services to Land Use Change in Traditional Agricultural Landscapes* (prof. Jan Lepš, Faculty of Biological Sciences in České Budějovice);
September – November 2005: working stay in Taiwan, introduction of European vegetation survey methods in terms of *Taiwan national vegetation diversity inventory and mapping project* (invited by Forestry Bureau, COA);
September–December 2007 – working stay in Taiwan, field work as a part of the study for revealing the effect of cloud on diversity of mountain subtropical cloud forests, together with Ching-Feng Li (Masaryk University Brno).
from September 2005: research assistant at the Department of Botany, Masaryk University Brno (doc. Milan Chytrý, Masaryk University Brno).

Field experience:

except of Europe also northern Russia, Turkey, Morocco, New Zealand and Taiwan.

Research interests:

ecological processes maintaining diversity, analysis of data from large vegetation data bases, phytocoenology (mainly forest vegetation), ecology of subtropical forests, the effect of historical management on the vegetation during the postglacial period.

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