University of South Bohemia
Faculty of Science

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

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Summary of 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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Full text: http://sci.muni.cz/botany/zeleny/publ/Zeleny2008-PhD.pdf

1 Introduction

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.

2 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.

3 Abstracts

Paper 1: Environmental control of the vegetation pattern in deep river valleys of the Bohemian Massif

David Zelený & Milan Chytrý

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.

Paper 2: Pattern of species richness in the topographically complex landscape of deep river valleys in the Bohemian Massif

David Zelený & Milan Chytrý

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.

Paper 3: 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

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.

Paper 4: Co-occurrence based assessment of species habitat specialization is affected by the size of species pool: reply to Fridley et al. (2007)

David Zelený

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.

4 Conclusions

The answers to the main questions outlined in the 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 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.

5 References

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6 Curriculum vitae

David Zelený, Mgr.

Born July 26, 1978 in Třebíč, Czech Republic

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, consulted with Milan Chytrý (*Factors influencing the vegetation in the Vltava river valley north of Zlatá Koruna, Czech Republic*).
2002–?: 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.

7 List of publications

Publications in SCI papers:

Zelený D. (2008) Co-occurrence-based assessment of species habitat specialization is affected by the size of species pool: reply to Fridley et al. (2007). *Journal of Ecology*, in press.

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