Oponentský posudek disertační práce Mgr. Davida Zeleného
Patterns of vegetation diversity in deep valleys of the Bohemian Massif

Předložená disertační práce čítá 126 stran textu a jejím jádrem jsou čtyři články, z nichž imprimatur k publikaci dostaly dva, ze zbylých byl jeden podán k recenzi a ten zbývající to teprve čeká. U tří článků je spoluautorem Milan Chytrý, a už to zaručuje kvalitu. Práce se zabývá něčím hodně složitým, totiž studuje zejména vzájemné vztahy mezi heterogenitou prostředí, jeho fragmentací, mass efektem, species pool a jednotlivými úrovněmi diverzity, Tématizovat podobné věci je dneska jednak velmi módní a moderní, a to zejména z toho dobrého důvodu, že se na nic podobného zatím nikdo nedokázal zeptat.

Zásadní problém práce vidím ten, že právě proto není úplně triviální, na co se tedy autora ptát, a to je taky asi jediný důvod, proč jsem byl k oponentuře volán, totiž abych se ptal jinou metodou a z jiného hlediska, než jakým je tradiční kanonický přístup, kdy oponent je moudřejší než autor práce, takže dokáže jít hbitě po jeho stopách a v případě nalezení chyby či nedostatku to dokáže ukázat. Takový přístup je samozřejmě nutný a zásadní, jenže na to jsou tu naštěstí jiní. Mě tedy zřejmě patří role analogická tomu, co se nazývá soudce z lidu, který je u soudu právě proto, že nemá právnickou metodu a z ní plynoucí manýry.

Mě ta práce velmi potěšila, a na druhé straně drze přiznávám, že práci v zásadě nerozumím, a tak se budu spíš zvědavě a naivně ptát s důvěrou, že odpovědi na ty dotazy vysvětlí něco, co by jinak zůstalo stranou jako nezajímavé nebo nedotknutelné. S tím už souvisí první dotaz.:

Určitě existuje nebo se časem vynoří argument, že to je ideální věda, protože je sice o biologii, ale už se nemusíme zabývat mrzkými jednotlivostmi, jako jsou druhy, jména řek apod., a proto je to ideálně komunikativní. Kolik lidí tomu vlastně v Česku rozumí? Když je to tak komunikativní, jsou i mimo botaniku nebo dokonce mimo biologii? Ptám se jednak kvůli sociologii takové vědy, ale zejména proto, že by mě zajímalo, nakolik je takový způsob myšlení a bádání sdělný a možná inspirativní pro výzkum jiných analogických struktur třeba i mimo vegetaci.

Tématem práce je v podstatě geobotanika, ovšem matematicky vyvařená tak, že rostlinstvo úplně mizí a zbývá jen čirá geometrická esence. Na to, jaká je to čirá matematika, jak velmi je to abstraktní, jak málo se tam mluví o kytkách, tak mi tato práce a její přístup ukazuje být velmi příjemně nereduktivní. Chápu to správně, když se mi zdá že to realitu nezjednodušuje, ale skoro naopak, že to ukazuje to jemné vlastnosti vegetační mozaiky, které by se jinak přehlédly, anebo se naopak vysvětlily nějak triviálně? Anebo je to tím, že se zatím z této avantgardy nestal kánon, který se ale stejně jednou chopí moci a začne jako obvykle zásadně bránit jiným způsobům popisu?

Pak by mě ovšem zajímalo, o čem tato práce a tato věda vlastně jsou. Jsou dvě možnosti. Buď spějeme k poznání obecných vlastností vegetace. Věří autor, že nějaké obecné vlastnosti vegetace existují? Trochu by tomu nasvědčovalo, že v práci se nakonec o údolní vegetaci zas tolik nemluví, zdá se mi, že je to jen prostředek k obecné výpovědi. Je to tak? Jedna z příčin jsou samosebou ty články, kde se důsledky pro konkrétní krajinu nedají příliš diskutovat. Pokud by to tak bylo, neukáže se nakonec, že to obecné, po čem nyní paseme, nejsou vlastnosti vegetace, ale rovnou vlastnosti světa (resp. vlastnosti samotné matematiky, což je totéž)?

Anebo se vrátíme ke konkrétnějším jevům, třeba obloukem přes tu vegetační metafyziku. Vegetačních pattern je spousta, jak by asi dopadla podobná práce věnovaná např. rašeliništím? Pokud je možná, správná, ideologicky snesitelná atp. tato druhá možnost, co se dá říci dodatečně o vegetaci našich údolí? Mě je sympatické, že si autor sám sebral data a ostatně mimo tuto disertaci se věnuje mimo jiné i celkem tradiční geobotanice. Jistě tedy měl nějakou zpětnou referenci o tom, co je triviální a co ne, co skutečně v daném vegetačním typu nebo na dané řece funguje a co jen tak vyšlo.

Naproti tomu některé výsledky jsou trochu triviální – že světová strana vysvětluje vegetaci nejlíp ve střední části svahu, na to stačí selský rozum bez matematiky a spousty dat, i když chápu, že takto to vypadá lépe a víc vědecky. Jaký je tedy vztah mezi tím, co se o údolním fenoménu vědělo (a spíš říkalo než psalo, viz ty citace) a mezi tím, co autor zjistil? Je tam nějaký posun, a zejména podařilo se přijít na nějaký tradovaný omyl?

Práce prokazuje tvůrčí schopnosti a splňuje požadavky kladené na disertační práci. Na tomto základě doporučuji práci Davida Zeleného k obhajobě.

RNDr. Jiří Sádlo, CSc., Botanický ústav AVČR Průhonice

Sádlo

Review of doctoral thesis: D. Zelený (2008), Patterns of vegetation diversity of deep river valleys in the Bohemian Massif

As a reviewer, I must reveal at the start that I am not a vegetation scientist. I spend most of my time with work related to statistical analysis of data coming from various fields of ecology. Accordingly, I cannot examine author's deep understanding of the vegetation science or current theories of diversity. My review is focused on the methods that author adopted in the presented studies and their suitabilitz within the framework of questions being asked. I hope this is appropriate in the context of the obvious joy that sophisticated statistical torture of his data bring to the defendant.

Whole thesis is build around four reseach papers either already published or likely to be in the near future, but it starts with a "General Introduction" chapter. It provides (perhaps too) brief introduction to research paradigms from which the presented studies started. Unlike the following, peer-reviewed papers, this part asks for thorough language revision, to eliminate funny statements, such as the morbid claim on page 3, where reader learns that the current research paradigm for diversity studies is (the) death. More importantly, this part is a rather unsorted mixture of very general ecological statements (such as the scale dependency of diversity patterns) with rather practical hints (such as those about appropriate selection of varibles into statistical models). This is a very frequent fault of Czech (and Moravian) doctoral theses, where their introductory and concluding parts are created in the frenzy of several missed deadlines for thesis submission and do not play the synthesizing and knowledge-forwarding role.

Paper 1 about environmental control of vegetation in river valleys, coauthored by Milan Chytrý, represents a traditional study, in which measured environmental factors are used to explain variation in vegetation composition.

The first issue I have with this paper is that two river valley are compared, but sampled ten years apart (1992-3 vs. 2001-3) and by different persons, with possibly different field experience and plant determination ability. In this way, location effects in the studies can be confounded with the collector and time effect. There were many changes in the landscape management in the time between these two studies. *As the paper keeps silent about the confounding effects, could the defendant comment on these?*

Chosen plant community space metrics vary wildly and one would say "ad hoc" in this study: cluster analysis used Chord distance, unconstrained ordination (by NMDS) used Bray-Curtis distance, and constrained CCA used – inevitably so – chi-square distance metric. *Could the author justify those choices, pressumably stressing different aspects of vegetation variation. I fail to see any such justification in the paper itself.*

Concerning the variation partitioning and explanatory variable selection in CCA, *why did the authors use the directional stepwise selection, instead of evaluating AIC for all possible models?* I wonder because the author clearly suggests such approach in his General Introduction chapter and it would be quite feasible here, given the limited number of variables.

I like the moving window CCA method – it is an interesting invention. But I have some doubts about the decision to select same-sized subsets of samples by a selection procedure <u>without replacement</u>. What can be learned from the theory of statistical bootstrap, suggests that resampling with replacement provides subsets with lower bias of estimated explained variation and higher precision for calculated confidence intervals.

Authors correctly recognize in this paper that it is difficult to compare explained variation among ordinations differing in the number of analysed plots, but similar problem occurs also when the data tables differ in species richness (for the same number of samples, datasets with lower richness tend to give a higher explained variation). *How large were the differences in species richness across the elevational gradient and could this create an artefact in the presented results?*

I liked the use of "iris diagrams" and also the many-legged spiders in ordination plots. They give the nice warm feeling of Christmas time (to me, not particularly liking the spiders).

Paper 2 about relation of species richnes to deep valleys topology (Milan Chytrý again as coauthor) is the second major paper in this thesis, devoted to river valleys. I must admit I did not like much the way the regression models, which form the core of the research evidence presented in this paper, were sought. Authors decided to guide model selection by the parsimony of candidate models (which is fine with me), but it looks they were not happy with the obtained results, so they attached further filters. They required that a variable included into a model must be also significant from the point of view of "inferential statistics" (deviance based test) and the authors also explicitly checked, whether the candidate variable is not too much correlated with those already present in the model. I consider both choices to be horrible mistakes. The first one, mixing parsimony and hypotheses test in a single model selection, is a sort of heresy, so we might easily ignore it here, in our infidel environment. But the latter step, judging a candidate variable "too much correlated" by looking at the correlation extent (must be over 0.5) and its significance, at the same time, looks very unprofessional to me. *I do not ask any question about the gross model selection strategy, but the defendant is welcome to comment on it, if he wants to.*

What I would be interested to hear, nevertheless, is the explanation why - when comparing sample averages of Ellenberg indicator values with species richness – the Pearson's correlation coefficient was used, but within the stepwise model selection the interdependence of candidate explanatory variables was judged by a rank correlation coefficient of Spearman? What the defendant thinks about the nature / linearity of these relations and why to take this into consideration one time and not the other?

An interesting result of this study is that of much lower contribution of measured environmental variables to the explanation of species richness in Thaya valley data, compared with Vltava valley. The authors suggest this might be due to "some important factor not being measured" for the former dataset. I was looking forward to see in the Discussion authors' suggestions about which factor (or factors) this might be. But the only thing I find there is the stressed higher correlation of richness with Ellenberg continentality in the Thaya dataset. *Well, you cannot go into the field and measure continentality at the plot level – or can you? Perhaps the defendant could suggest, which environmental factors would be best to measure in Thaya valley to improve explanation of richness patterns?*

I am also wondering what was the point of including the comparison of alpha diversity of the study plots with the whole-country estimates of species-pool size for various habitat types. My impression from how the authors discuss the contents of Figure 5 is that they wanted to test a hypothesis of positive correlation between pool size and the local richness. *But why was not such a test done?* While the discussion contains many valid statements about relations between alpha-, beta-, and gamma diversity, these hardly profit from the information provided by the data in Figure 5. And the discussion of this figure' contents seems to shrink merely to the question of why the horn-beam forests do not follow the general pattern …

Paper 3 (about the patterns of species richness along the gradient of landscape topographical heterogeneity, and with two coauthors) has nothing to do with the deep river valleys, as far as

I can see (of course, some plots from the national database might come from them). Instead, it deals with species richness and plant communities at the levels quite different from the preceding two papers.

I would like to know what should the index of landscape heterogeneity express? It is calculated as a measure of variation in altitude (using central pixel as a reference value). I wonder whether it is, for the defendant, an acceptable view that a level, flat area is less heterogenenous than a monotonously raising slope? In other words, would not be better to detrend the elevation data for each GIS sample (circle with 300 m radius) using a linear surface, and calculate the index from the residuals?

I like the approach taken to visualize the change of relation between the landscape heterogeneity, diversity, frequency of generalists, and the environmental control factors. But I do wonder about two things:

(a) why to choose the groups of 100 samples in such overly complicated way (i.e. trying each sample as a "seed" and then excluding generated groups too much similar to others)? This exclusion based on pairwise comparisons will, in fact, be quite similar (in its faults) to the forward stepwise selection in regression analysis: depending on which of the "too-close" group-pairs I choose first to reduce, I will affect, to a certain extent, which other groups will be excluded. *So, why not to use an approach similar to what the local regression does, i.e. put a regular grid of reference points over the NMDS plane (within which are all the results interpreted anyway) and select N nearest neighbours for each grid location?* This would also allow for further improvements, such as varying the weight of individual observations, depending on their distance from the reference point, much like the local regression does.

(b) *given the main topic of this paper, would not be better to show, in Figure 6, the variation in relations between soil reaction and species diversity (rather than soil reaction and landscape heterogeneity), and similarly to show the relation between productivity and diversity, rather than the relation between productivity and heterogeneity?* I mean, when you try to predict something using multiple, partially correlated predictors, you might want to understand better to their cross-correlations, but the primary aim for the reader is to understand how their effects on the primary response variable (here the diversity) differ.

In the Discussion, I was intrigued by the claim on page 79 (about line 8), that negative correlations between richness and heterogeneity prevail in nutrient-rich conditions, while positive ones prevail in nutrient-poor conditions. Are we really talking here about the contents of Figure 4, compared with the leftward pointing "Nutr" arrow in Figure 3? (As a off-topic, this diagram of NMDS shows a nice triangular artifact, for which the defendant despises DCA method in his General introduction). Perhaps unlike the authors, I see substantial clouds of green plus signs at the far left and the middle-top corners of the scatter triangle, and a continuous band of them at the lower edge of that triangle. If anything, I would rather see the tendency of positive relations to occur at the margins of the variation in the studied forest vegetation. And this would say something about mass effect, with immigration sources being in non-forest vegetation. *What is the view of defendant?*

Finally, I must mention that I am worried that the paper uses so advanced methods to answer these complex questions, that a typical Joe Ecologist will not have enough time and/or courage to understand the methods to the extent (s)he would grasp the contents of presented results. But I guess this is a complaint rather about the ecologists than about the paper…

Paper 4 (for which the defendant is the only author) is a kind of letter to editor, pointing out the limitations of a published method and suggesting its possible improvement. Although this is strictly not a standard research paper, in which the defendant demonstrates ability to formulate hypothesis, collect data, and present the outcome to the scientific world in a rigorous way, writing this kind of papers is a welcome part of researcher's job. And I predict this paper will collect more citations than the earlier three papers together.

To summarize my review, the four research paper manuscripts produced by David Zelený during his doctoral studies are just partly related to the deep river valleys of the Bohemian massif and these two which do are based on a dataset collected only from half by the defendant. Therefore in this thesis, David Zelený profiles himself as a researcher focusing on synthesis and effective utilisation of someone else data. I cannot say that I am entirely impressed by the way he does it (see my specific comments about papers 1 to 3 above), but I certainly agree that he proves he will be able to find his own, independent niche in the current field of quantitative vegetation sciences and so I recommend this thesis for its defence.

P. Šmilauer

Petr Šmilauer, České Budějovice 29 August 2008

Institute of Ecology and Botany of the
Hungarian Academy of Sciences
Alkotmány u. 2-4., Vácrátót, H-2163, Hungary
Tel: (36) 28 – 360 122 Fax: (36) 28 – 360 110
http://www.botanika.hu

Review on David Zeleny's PhD Thesis

Describing and explaining diversity patterns belong to the main topics of community ecology. David Zeleny's PhD thesis contributes these efforts by three case studies and one methodological paper.

The thesis starts with a general introduction that consists of well-written short reviews of different topics, but the relations between sections remain unclear for me. These good reviews indicate that David Zeleny knows well the recent ecological literature. I disagree only with three points:

- Fuzzy set ordination is not really "hot news", since it was first proposed in 1986 by Roberts. (Roberts, D.W. 1986. Ordination on the basis of fuzzy set theory. *Vegetatio* **66**: 123-131.)
- I propose alternative classification of gradients. In first level direct and indirect gradients should be distinguished, then within direct gradients the gradients of resources (or more generally speaking regulating factors) and conditional (non-regulating) factors. Recent article by Meszéna and his co-authors gives detailed explanation on the distinction between regulating and non-regulating factors (Meszéna, G., Gyllenberg, M. Pásztor, L. & Metz, J.A.J. (2006) Competitive exclusion and limiting similarity: a unified theory. *Theoretical Population Biology* **69**: 68-87)
- He used terms equilibrium and non-equilibrium situation in agreement of field ecological literature. However, theoretical articles highlight that limiting similarity should be regarded more general than the recent literature do. The co-existing species may differ in their reaction to disturbances, and such differences also enhance the co-existence. By this interpretation of limiting similarity, the applicability of niche theory can be expanded to the so-called non-equilibrium situations too.

The main part of the thesis consists of four papers. All of them suitable for publication in peer-reviewed journals, some of them have already been published. Therefore, I do not have to emphasize their merits; rather I will highlight their weak points.

Paper 1:

- The skewed distribution of soil depth, or any independent variable would not cause any problem in statistical analyses, thus log transformation was not necessary. It should be noted that this transformation did not influence the Spearman rank correlation, since logarithmic function is monotonic.
- It would be logical using same dissimilarity function in ordination and classification. He admit that the applied classification method was chosen because it was "best reflected the pattern of vegetation differentiation as judged by expert knowledge". Regarding the high number of dissimilarity functions and classification methods, it is always possible to find numerical classification similar to expert's one. However, in my opinion, in this case, the numerical classification is only illustration of the expert knowledge, and it does not give new information on the structure of our data.
- Why are soil type treated as four independent binary variable and not one nominal (multi-state) variable with four categories? Can more than one soil type occur in one plot?

Paper 2:

- In page 42 it is stated that high invisibility of river valleys is one of the reasons of their high diversity. In my opinion, invasion is more often decrease than increase diversity.
- Why did you choose forward selection? Backward selection is often better method.
- Description of model selection is not sufficient: If AIC is regarded to too liberal, Bayes Information Criteria could be used. It is not clear how analysis of deviance applied in variable selection. Is it applied before entering a new variable, or was one final test done for excluding non-significant variables? Does analysis of deviance mean likelihood ratio test?
- Correlated variables does not cause problems in forward selection, thus selection criteria based on correlation would not be necessary.
- How was the percentage of explained variation measured? McFadden's pseudo-R2 would be an appropriate measure of explained variance.
- Not regional, rather habitat species pool size was used in the paper, since same pool size was used in both valleys for shared habitats.
- It would be interesting study effect of environmental variable after removing effect of species pool size. It would be possible if species pool size was used as co-variable.

Paper 3:

- Effect of plot size should be eliminated by using it as co-variable rather than using standardized residuals. The two approach results in the same parameter estimation only if plot size totally independent from other variables. If standardized plot size was used as co-variable, parameter estimates would relate to relationship at mean plot size, thus their interpretation would be easier.
- The statistical term "significance level" was used incorrectly in the paper. Statistical tests never calculate significance level. They calculate probability of Type I error. Significance level is the threshold for Type I error (for example 5%) established arbitrary by the researcher. Unfortunately, this mistake is very often in the literature, and it occurs even in output of statistical programs.
- The observed relationship between local richness and soil pH/soil nutrient richness was interpreted as indirect effect through species pool size. It is strange for me, since the effect of species pool size was eliminated by an interesting new method.

Paper 4:

There are two forms of species pool that should have been distinguished in this paper: species pool in certain point of an environmental gradient, and species pool of a section in the gradient. Local species richness depends on the first one, and not the second as Zeleny hypothesized, while beta-diversity is calculated from the second form. Fortunately, if gradient length is measured in half-change units, there is a simple relationship between two forms of species pool, and the main conclusion of the paper, that is in unsaturated communities Whittaker's beta diversity results in unbiased estimation of niche width, remains valid despite of this mistake.

In spite of the above mentioned weak points, the four papers indicate that David Zeleny deserves the PhD degree.

Zoltán Botta-Dukát

Zoltán Botta-Dukát, PhD
senior researcher
Head of Department of Plant Ecology
Institute of Ecology and Botany
Hungarian Academy of Sciences

Vácrátót, September 14, 2008