Review of the thesis by Miroslav Dvorský: Ecology of alpine plants in NW Himalaya

The thesis examines vegetation ecology high mountain ecology in Ladakh. The thesis revolves around three main subjects (i) vegetation description, including identification of main driving gradients that shape it, (ii) sheltering effects of a common cushion plant, *Thylacospermum caespitosum*, and (iii) soil crusts and their ecological significance, including nitrogen fixation.

Strong points of the thesis

Choice of the subject. The high mountain ecology has been built around a few frequently visited mountain regions, and misses data from ecologically different ranges. In this respect the work is really innovative and interesting.

Solid analysis of vegetation and vegetation environment relationship when it was needed. I appreciate that the author has not been lured into developing quasi-general theories or testing fancy hypotheses. Any ecological understanding rests on a good knowledge of the system, and in this respect the thesis (together with the work of the candidate's coworkers) makes a very solid foundation. The fact that vegetation description is obsolete in some parts of the world must not preclude its use in parts that are not well known. It is laudable this approach has not been forgotten and is used here in a qualified fashion.

Good data analysis. With the proviso of my questions below, I think that the author used correct and suitable statistical techniques and seems to be aware of the limits they have.

I appreciate the *amount of the work done*. The thesis is composed of six papers, out of which five have already been published. Although all of them are multiauthored (an inevitability given the harshness of conditions for field research), the candidate is the first author of three of them. I really appreciate the effort put not only in data collection and analysis , but also into paper writing and getting them published. It is clear that the contribution of the candidate in all papers was substantial. A thesis of six papers would be rather on the top in the theses that are submitted at our department. Still the papers are well-conceived and by far do not make the feeling that one topic was split into two papers to increase the paper number.

Weak points of the thesis

A thing I miss in the thesis is a treatment of (or at least a reference to) biogeographic/evolutionary issues. One would be interested to know where the species found at highest altitudes come from, where are their close relatives etc. Obviously, this cannot be addressed in full without molecular studies, but some information can be gleaned even from more classical sources (occurrence of congeneric species, distribution areas of the species in question etc.).

Questions to be discussed

(*) I am not very happy with the demonstration of the absence of the shelter effect by *Thylacospermum*. The core argument used is a shallower increase of the S-A relationship in

the cushions compared to the open space. However, the S-A relationship does not make very good sense if a large part of the "area" is actually occupied by another organism. In such a case, one should be comparing species-available area relationship. Of course I understand "available area" cannot be estimated (as it depends on plants themselves), but this does not undermine this argument. Other approaches should be used to demonstrate such effect. The same argument concerns a number of other analyses (e.g. at p. 109) which compare number of species per unit area inside and outside the cushions –comparisons should be done by comparing things that are comparable. Given these approaches are not fully correct, I wonder whether the candidate would propose a better approach to identification of a sheltering effect. (I do not argue that the sheltering effect exists – I am just asking for better ways how to demonstrate its absence or weak effect.)

(*) If the authors claim that conditions are so unfavourable that sheltering does not help the plants, why the species itself is forming cushions?

(*) is there any good analysis whether high altitude areas are really less prone to invasions (p. 154)? I presume that propagule pressure is very low there, which precludes any analysis of resistance. BTW, later the author speaks about non-native weeds (possibly up to 24 species out of 330 species), which – given the low propagule number – is well comparable to many central European habitat types.

(*) I really appreciate recording microclimatic conditions in the *Thylacospermum* study, because it is giving an idea of thermal regime in the habitat over the whole year. On the other hand, I am not convinced that these can demonstrate much – mainly because we do not know which climatic factors may be limiting individual species, and we have no clue how to interpret differences between the inner and outer parts. How would you say that a difference is "large" or "small"? What if there is no measured difference? - The devil's advocate's reply would be you did not measure the right thing.

Methodological comments

p. 21: assessment of the stand properties: I wonder to what degree these values involve circular argument. In particular, definitions of soil nutrients and substrate stability use vegetation parameters which is making circular argument likely. These parameters could be used for a passive projection over an indirect ordination, but not as an explanatory variable.

p. 36: the plotted relationship suffers from very unequal sampling of the x axis. There are many more points in the central part of the gradient which can possibly lead to curvilinear relationship due to a simple sampling effect (if there are more points in a part of the gradient, they are more likely to include extreme values, which will unduly influence the shape of the regression curve). I understand that better sampling may be difficult to obtain, but given the sampling other techniques should be used.

p. 105: I doubt that the competition/performance indices can be used meaningfully for the field data. First, it is not fully clear from the paper how the indices were calculated, namely, what was the performance measure used. Were these species covers? Second, the use of these indices is restricted to situations where the performance measure (whatever it is - cover, biomass, growth rate etc.) can be meaningfully compared, such as designed experiments with a well-defined start. In the field, different performance values could be due to, e.g., different

ages of the plants. if one assumes full equilibrium, indices can possibly be used (as age distribution of plants in and out would be the same), but are these assumptions likely?

p. 159, Fig. 5: which technique is used to fit the line? Although different smoothing techniques could give similar results, their fits are often strongly parameter-dependent. Let alone the issue that fitting a line to a badly sampled x axis is doubtful anyway, the more so given very unequal variance along the x axis.

p. 168. It is not clear from the paper how the nivality index was defined and calculated – which is odd given its analysis is one of the main components of the paper. From Fig. 12 I presume it ranges from zero to one, which makes its variance to depend on its mean in a highly non-linear fashion. Use of linear models for its analysis is then very inappropriate.

Conclusion

In summary, the thesis convincingly demonstrates ability of the candidate to perform good research in plant ecology. It is based on a solid amount of field, laboratory and analytical work, it shows a good understanding of the subject and the ability to present results in the form of scientific papers. I am fully convinced that the candidate deserves a PhD. title and wish him success with further work.

I am happy to recommend the thesis for defence.

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7 March, 2012

Review by Markus Bernhardt-Römermann

With his PhD-thesis „Ecology of alpine plants in NW Himalaya" Miroslav Dvorský closes a gap in the ecological understanding of the drivers of vegetation differentiation in relation to elevation. The study area is characterized by extreme environmental conditions like very short vegetation periods with partly daily frost-defrost cycles at extremely low precipitation (<100 mm). Previous research in this region of the Himalaya mainly focused on lower altitudes. In his PhD-thesis Miroslav Dvorský extended the elevation gradient to the upper boundary of vascular plant life to derive a complete understanding of the ecology of alpine plant life at its limits.

In his thesis he focused on various aspects of alpine plant live. This includes a description - together with the identification of the most important environmental drivers - of vegetation types along an elevation gradient (Chapter II) and at extreme elevations of the subnival zone (Chapter VII). These chapters include basic ecological interpretations based on proportions of plant growth forms. More in depth functional interpretations are presented in Chapter III for clonal growth organs and summed up by an ecological characterization of biological soil crusts (Chapter VI). In general the environmental drivers are carved out very well; however, only a very brief comprehensive summary of the ecologically relevant processes driving the assembly of the plant communities is presented. Such information can be found at several places in the different chapters of the thesis, but an additional overview on the whole elevation gradient would be great. However, this issue should not be stressed too much, as all necessary information can be found in the thesis.
Furthermore the thesis (Chapters IV and V) focuses on the stress-gradient hypothesis and facilitation of cushion plants. From an ecological point of view these two chapters add most to the understanding of the alpine ecosystem as they present hypothesis driven research on an important aspect shaping the occurrence of vegetation assemblages at extreme altitudes: competition and facilitation.

In general the thesis is very well written and makes a valid contribution to the literature in this field of ecology. It was stimulating to read and I started thinking about various aspects of alpine plant life I did not consider before. I do not have any serious concerns; I strongly recommend this work to be defended. Comparing with typical German PhD-theses, the research (number and quality of already published papers) included in thesis of Miroslav Dvorský is huge. Below some minor points that may be discussed during the defense (1-3 directly related; 4-5 as discussions of the generality of the approved results):

1. Looking at the time when the different chapters were published, an evolution in the complexity of applied statistical methods can be found. I would like to learn more about different clustering methods for vegetation samples with a special focus on the use of a TWINSPAN. This method has been criticized by several authors, the same for DCA.
2. Provocative question: At some points the thesis reads like a report of hunting for records in high elevation observations of vascular plant life. What is the ecological justification for such research? Is there a difference between physiological and ecological constraints comparing lower and highest altitudes?
3. The thesis focused mainly on growth forms and clonal traits. What about applying other functional traits related to the plants ability to grow or to resource use efficiency? What is the role of competition (intra- and interspecific), and how do you expect this will change with elevation?

4. What do you think: What are the most important differences between the Himalaya alpine ecosystem and other alpine regions of the world? At which level could your results be transferred to other alpine ecosystems?
5. The ecosystems studied in your theses are also called alpine deserts. Can the results of this thesis be transferred to other desert ecosystems of the world? E.g. deserts with very limited water access, but extremely high temperatures instead of extensive frost periods? What are the main differences to Arctic and Antarctic ecosystems?

Jena, 06.04.2014

M. Bemmerlein-Rein

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Vienna, April 07 2014

Review report on the

PhD thesis Miroslav Dvorský: Ecology of alpine plants in NW-Himalaya

The thesis is based on five published papers, all in ISI-referenced peer-reviewed journals, and one submitted manuscript. The introductory chapter gives a detailed description of the study region, its botanical exploration and a thorough overview on the research topics and how they link to each other. Chapters two and three deal with the vegetation types of East Ladakh, their species composition and especially emphasize on growth forms with a focus on clonality. Chapters four and five deal with the potential role of cushion plants as facilitators of other vascular plant species, chapter six with soil crust communities and their function for soil fertility and plant colonisation and, finally, chapter seven with the extreme altitudinal limits of vascular plant life.

The presented thesis provides a comprehensive and detailed insight into the vascular plant life in one of the most extreme environments concerning both low-temperature and aridity. As such, the work deserves particular attention, as it contributes to research in a little studied and remote region, where data collection requires special preparations, precautions and endurance. Throughout the papers, the results were discussed with previous regional papers and studies of other mountain regions. Moreover, the thesis contributed to testing ecological theory, such as the stress-gradient hypothesis.

The thesis certainly much benefited from and is partly based on previous ecological research and the tremendous data sets collected by Leoš Klimeš and colleagues already since the 1990s. As such, the thesis also represents a fine example of continued research into long-term studies, which is an often neglected but essential component in ecology.

I do not see much reason to raising particular concern regarding the study designs, results and conclusions made. Rather, the papers of the thesis stimulate for further discussion and questions such as: on the role of past and increasing present pasturing for the composition of the current vegetation, on the most determining factors leading to a reduced importance of clonal growth, on the relevance of combined temperate/aridity effects for weak or no positive interactions among species, and for the exceptionally high upper limits of vascular plant growth. Below I append some more specific questions.

Altogether, this is an impressing research effort, which I can very much recommend to be defended.

With best regards,

Harald Pauli, Vienna, April 07 2014

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Some further statements and questions in more detail for the defence which may be communicated to the candidate.

(1) Traditional pasturing practices are century-old traditions in the region: (1a) Are alpine grasslands and the subnival vegetation originating from a co-evolution with human pasturing activities, as proposed by Miehe et al.? (1b) Apart from animal resting places, are there any indicator species in zonal vegetation types, which point to increased pastoralism? (1c) Which are the socio-economic factors for a recent increase in livestock grazing and which vegetation types are most affected?

(2) Given the absence of a forest belt, the distinction of and delimitation between the steppe vegetation of 'lower' elevations and the alpine screes and subnival vegetation may be difficult, owing to the generally low vegetation cover and the large vertical ranges of several subdominant species. What as the most important differential species, life forms and abiotic habitat factors distinguishing between lower elevation to lower alpine, upper alpine, and subalpine belts ?

(3) Your results indicate that the proportion clonal growth forms is unequally distributed over the vegetation types and that vegetative propagation is less common compared to other low-temperature regions, such as in alpine environments of central European mountains and the Arctic. (3a) Which ecological factors are the most effective determinants of clonal growth respectively which conditions could restrict it? (3b) What might be a functional advantage of non-clonal species with spreading below-ground branches, such as the pleiocorm plant Saussurea gnaphalodes, compared to clonal plants such as hypogeogenous rhizomes (Poa tibetica-type) at zonal high-elevation habitats of Ladakh?

(4) Your thesis includes results that challenge the general validity of the stress-gradient hypothesis. Two studies in your thesis with different experimental designs and from different regions of Ladakh, provide consistent evidence that facilitative effects were not increasing with increasing environmental stress. Briefly describe the ecological factors considered in these studies and explain the supposed reasons of the lack of positive interactions between the common cushion plant Thylacospermum caespitosum and other vascular plant species under extreme conditions?

(5) In the recent manuscript of the thesis, you report on one of Earth's highest limit of vascular plants, with five species found at 6150m a.s.l., exceeding any known uppermost site occurrence in the Andes, and is only surpassed by a few much earlier observations in central

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Himalaya, where altitude readings might be questionable: (5a) Why so high in Ladakh? - Can you explain the key-climatic and geomorphological features, which may support such high occurrences?

Only two out of the five upper-limit species are restricted to the subnival zone, whereas the others extend downwards for <1000m into the upper alpine belt. On the other hand, several subnival species with more narrow vertical ranges above the alpine zone hardly reach 6000m. (5b) Are there any traits which could restrict these subnival species in reaching the uppermost limit of vascular plant growth or other traits which support the high-elevation champions.