Eidg. Forschungsanstalt WSL
Institut fédéral de recherches WSL
Istituto federale di ricerca WSL
Swiss Federal Research Institute WSL
Ein Institut des ETH-Bereichs

Expertise on PhD thesis submitted by *Martin Macek*

Patterns and processes in spatial distribution of plant species across scales

Goals of the PhD research

The primary goal of this thesis is to analyze and identify factors shaping plant distributions at different (spatial) scales. This is done by using statistical models to explain such patterns from hypothesized predictors that provide causal explanations and by testing hypotheses useful to explain found patterns. The title is kept quite broadly, in order to summarize what has been achieved in 5 different research chapters. While the first two studies aim to explain small- to intermediate-scale spatial variation in factors responsible for patterns of plant distribution in Central Europe, the latter three are centered around explaining patterns and processes shaping larger-scale plant distributions along a huge elevation transect in Ladakh, Himalaya.

Structure, Content and Presentation

The thesis is structured into six major parts, namely: (1) a general introduction to the thesis based on a thorough literature review on the topics of the thesis, and (2) a series of five research papers on the core topic of the thesis among which three papers are published, one is submitted, and the last is available as a draft manuscript. The open research questions of the five following research chapter are partly but not always introduced in the first chapter, though not explicitly presented and not explicitly summarized at the end of the introduction. Among the five research papers, three were written by M. Macek as first author, and two as second author. In both papers for which M. Macek acted as co-author, he was responsible for data analyses, and helped design the study, thus provided a strong scientific contribution to these two papers.

The introduction to the thesis (first chapter) discusses a variety of topics directly relevant to the five different research papers (chapters 2-6) following the introduction. The topics vary broadly from patterns and processes responsible for the distribution at meter-scale (in chapter 2) to those responsible across large landscapes of hundreds of kilometers. In several chapters, environmental heterogeneity is a central driver identified to play a major role in structuring plant distribution. The relevant literature is well covered regarding the key aspects addressed when discussing the issues relevant for one or the other research chapters discussed and introduced. What I was missing maybe, is a more synthetic view of scale (what is scale, how does it vary, what have others found out about scale and the dependencies of patterns and processes in relation to scale). In addition, some aspects of the discussions are nice introductions of some papers, while other parts are nice introductions around general topics of interest covered by the thesis. But overall, I found that the introduction did not provide a well-structured introduction to the main research gaps and research questions for the thesis (I missed an overview of which research gaps the five chapters addressed), although the major research gaps relevant for the five chapters were generally touched and discussed throughout the introduction. However, each of the

Dr. Niklaus E. Zimmermann
Zürcherstrasse 111, CH-8903 Birmensdorf
Telefon +41-1-739-2337, Fax +41-1-739-2215, www.wsl.ch

following research chapters had a thorough introduction to the research topic followed by clear questions or hypotheses each that were regularly discussed again in the end of the chapter in the light of the found results. Well done!

In the first research paper (2nd chapter) of the thesis, a 12-year, massive dataset on post-disturbance (by bark beetles) regeneration was analyzed to assess whether pre-disturbance regeneration is primarily responsible for explaining the post-disturbance stand structure (H1) or whether microsite patterns dominate the establishment of stand structure (H2). To this second end, growth and survival patterns of seedlings across a range of microsites was analyzed. The study identified that both post- and pre-disturbance regeneration were rather unimportant (so H1 was rejected) and that the regeneration from during the disturbance was most important. Also, it was found that seedling mortality was affected by microsites while seedling growth rate was not. Post-disturbance regeneration was largely influenced by competition by graminoids that benefitted from the additional light in disturbed plots. H2 was thus supported, yet it was shown that the effect was driven by mortality rates, not growth rates. The study worked out very well in addition, how bark beetle disturbance is different from other, more abrupt types of disturbances, such as those caused by windthrow or fire. A huge advantage of this study over other similar ones is lies in the fact that the fate of seedlings was available over a long temporal period (12 years), which allowed more detailed analyses of interacting factors than if only data from a short temporal snapshot was available for analysis. This advantage allowed to disentangle in novel detail the reasons behind clumped regeneration patterns. The chapter finishes off with sound recommendations management of bark beetle disturbed mountainous spruce forests.

In the second paper (3rd chapter), the hypothesis was tested that canopy and microsite variation caused by topography has modifying effect on temperature and that such detailed temperature data better predicts understory community composition than coarse-scale interpolated climate data (as that from Worldclim). Microsite climate was measured in-situ at 46 sites during a whole year with vegetation composition having been sampled at the same time. 160 additional vegetation plots were available, and the annual minimum (5th percentile), mean climate (average) and maximum (95th percentile) was extrapolated to using regression techniques and elevation, topographic variables and canopy cover as predictors. The study found that the maximum temperature best explained vegetation composition, both in the 46 plots where temperature was measured and in the 160 test plots to which temperatures were extrapolated to, although the predictive performance of the temperature variables decreased on the 160 plots to which T variables were predicted to. When using coarse grained (1km) Worldclim data, the predictive power further declined, yet for all three tests the rank order of Tmax>Tave>Tmin was the same. The study didn't find an effect of canopy cover on measured understory temperature across the 46 sites. It is discussed that this might be due to a) huge topographic variability across the site, and b) more importantly due to the fact that all forests had a canopy closure of >75%, a threshold above which Zellweger et al. (2019) identified no more effect in canopy cover variation on understory temperatures.

The third paper (4th chapter) evaluates to what degree asymmetric niche shapes along elevation gradients are an exception or rather the rule, and whether left-skewed (skewed towards low temperatures) shapes are more or less frequent than right skewed (skewed towards high temperatures, i.e. drought-prone environments in the study region of Ladakh). The study finds that symmetric response shapes were the most dominant ones (61%), primarily though at low elevations. Asymmetric response shapes – representing the asymmetric abiotic stress limitation hypothesis – are important overall (36%) among all studied 395 plant species, and that the AASL hypothesis primarily holds for the cold limit, while it was rare towards the dry limit. The left skew was more important at high than at low elevation. Right skew was unimportant and also increased with elevation. The manuscript well discusses possible reasons for the lack of right-skewed responses towards dry conditions along the elevation gradient.

The fourth paper (5th chapter) used the same dataset as paper 3 and tested Rapoport's rule of increasing range size of species with increasing mean elevation. For 781 species (at least 10 occurrences per spp.) the local elevation range was analyzed and the relationship of elevation range with elevation was assessed for the Ladakh data. In addition, elevation ranges were constructed both for a regional dataset of the same Ladakh species by assessing elevation ranges from various databases neighboring Ladakh (regional floras, GBIF, etc). In order to avoid biased results from sampling effects and geometric constraints, a null model was constructed and randomizations based on this null model were applied. Upper local elevation limits agreed for most species with their regional upper limits, while the lower limit was truncated locally, compared to the regional lower limit. As found in other studies before, but by applying null models carefully and by using two different approaches (Steven's and "bin" method), no evidence for Rapoport's rule along elevation gradients was found. Contrary to expectation, the elevation range decreased from low to high elevation in the regional dataset, and in- and then decreased for the local dataset (from low to high elevation). This trend was generally stronger for the "bin" than for Steven's method. Both patterns were predicted by the null model and observed data only marginally deviated from this expectation. While Rapoport's rule posits that increasing "temperature variability" is responsible for the hypothesized pattern, in-situ measurements in the Ladakh region indicate no change in seasonal or diurnal temperature variability with elevation, which could explain, why Rapoport's rule did not apply. In addition, the study demonstrates the distorting effect on both the null model and the observed patterns, when truncated elevation data is used.

Paper five (6th chapter) assessed to what degree the novel "mid-point attractor model" (MPA) can explain unimodal species richness patterns in the Ladakh region better than the "mid-domain effect model" (MDE). Both models use geometric constraints for null models expected species distributions for testing realized distributions, yet the MPA method is more flexible and has additionally been adjusted lately for truncated domains. The model was tested using 1054 species of the same dataset as the previous two chapters. Both versions of MPA (with 2 variants each) clearly better explained observed species richness than did the MDE method. The study discusses the fact the monotonic decline in species richness with elevation is likely driven by physiological constraints, while the decrease in richness towards the lowest altitudes likely originates from geometric constraints imposed by the niche truncation due to the geographic setting (extent) of the region.

Evaluation

I judge the PhD thesis to be of **high quality**, of **substantiated originality**, providing **critical insights** into a complex set of topics. I suggest **acceptance independent of the minor changes** I suggest below. The listed issues do not diminish the value of the current thesis. The thesis **fulfills all formal requirements** and is **very well written**. The material is presented in a clear manner and the relevant literature is covered well.

Overall, the PhD thesis is presented in a clear and structured manner, and it discusses and presents a variety of topics with concise text. I enjoyed reading it. I may have had some different views in parts regarding the aspects discussed in the paper's discussion sections. This is normal: discussions are here to present different views. In my eyes, the weakest part is the introduction. It suffers from the difficulty to cover a huge breath of topics in the introduction that are presented in the 5 different research chapters. But it suffers also a bit from a lack of clear structure. On the other hand, I am impressed (reading the CV) by how M. Macek has worked for a variety of projects during his PhD period. He has been involved in many different projects, has contributed to numerous additional papers not listed in the PhD, and therefore had to choose from these many contributions those that make his PhD. Such broad involvement and the necessity to work for these diverse projects make it more difficult to unambiguously focus on one single and well-structured PhD topic. Given this background, the thesis is well done.

I found the first and the last research paper (both first-authored by M. Macek) the most innovative, while I found the second research paper least novel. Yet, from experience, I know how hard it is to present novelty in each research chapter. All papers were primarily analyzed by M. Macek and the analyses are always very carefully done and are scientifically sound, both from a theoretical and from a statistical viewpoint. This indicates clear scientific maturity of M. Macek. I like to further mention positively that 3 papers are already published (2 as first author) and all in good journals of the field of research. The two unpublished manuscripts have certainly the potential to be published in good scientific journals. In addition, M. Macek has a CV that reflects well the many contributions to different projects, with around 30 ISI papers published (many as co-author) and an h-index (WoS) of 10. This is beyond what you usually expect after a PhD.

Suggested Changes

I am overall very happy with the quality of the thesis manuscript. I primarily request that the text is checked carefully for small typo's and missing words.

Request

In summary, I request acceptance of the PhD irrespective of further changes and without reservation.

Prof. Dr. Niklaus E. Zimmermann
Birmensdorf, August 31st 2020