Review of the thesis by Eva Švamberková: Assembly rules in plant communities

The thesis examines the role of species pool in structuring (grassland) communities. The species pool has been an extremely stimulative concept in ecology, but its operational treatment has been (and still is) difficult. Researchers on species pool have been struggling both with statistical issues of determination using observational data and with unfeasibility of experimental methods due to their short time span and laboriousness. The thesis brings a fresh light into the field, by focusing solely on experimental testing whether a species belongs to the species pool of the community. The key question in the thesis is the use of experimental method as a yardstick against which the other, more indirect methods could be compared. Part of the thesis consequently has a kind of a methodological focus, examining and comparing several methods for species pool determination.

It has a general introduction of 14 pages (excl. references), and four chapters in the journal contribution style, three of which have already been published in respectable journals. Three papers are dealing with experiments as tools to examine the species pool with similar questions and experimental design over a range of grassland communities. These papers are complemented by one paper (the first paper in the thesis), which addresses long-term changes in newly established vegetation from sowing seed mixtures of different species richness (and different species pools) examining their long term effects on the community composition. This paper makes use of the admirable long-term data collected by the team of her supervisor (and himself personally).

Strong points of the thesis

Strong focus on one subject. When reviewing PhD theses, quite often one sees theses composed of good papers (or to-be papers), but with weak conceptual links. The presented thesis is a clear example of the opposite type: all the papers address similar questions, using either different experimental systems, with slightly different approaches, but having very strong links (also clear from citations across individual papers). It pursues its subject with a kind of bulldog determination, showing that conclusions reached in one experimental setting hold also in another. This really makes the thesis substantial contribution to the species pool analysis.

Conceptual framework. I appreciate the courage of the candidate to delve into the quagmire of the species pool literature and not to get lost in it. Eva does not spend much time with the statistical issues of species pool (generally unsolvable and dependent all too much on the opinion of individual scholars) and devotes her primary attention on the experimental testing of it.

Separation of aboveground and belowground processes. I really appreciate (in the last paper) the attempt to identify whether the limitation on species establishment comes from aboveground or belowground interactions. The comparisons of three treatments (gap, aboveground and control)

with respect to their prediction by the species pool estimates are really enlightening and a pleasure to read.

Weak points of the thesis

There is nothing in the thesis I would label as a weak point in its true meaning. I am raising a few points in the section below, but they do not present weaknesses – I see them more as stimuli for discussion and further thinking.

Among points I perhaps did not like that much is that the introduction might have been written more in-depth. It might have presented the link between the species pool and assembly rules in a more focused way. It is not clear how – given that we have a technique how to determine whether a species belongs to the species – these species are filtered to make the actual community of coexisting species. I would also appreciate clearer discussion of individual filters in the species pool, namely making clear that the filters are not organized hierarchically (although they are often portrayed as such in literature). Finally, I must say that I find the title of the thesis ("Assembly rules in plant communities") a sort of confounding – most of the thesis deals with species pool and methods of its estimation, whereas assembly rules come in only indirectly (by comparison of experiments with and without biotic filter). Symptomatically, the term assembly (or assembly rules) is almost never used in the papers proper (I checked using the "Find" feature in Acrobat Reader :-))

Questions and comments for the discussion

In the thesis, the experimental approach has served as a kind of a yardstick against which the more indirect methods of species pool estimation are compared. I am not so confident that the experimental approach is really the ultimate method how to determine species pool. While I feel that the candidate may disagree with me, I'd like to hear some of weaknesses that the experimental approach has, and an outline how to deal with them.

I would like to know the candidate's opinion on the definition of the species pool: should it include also the filter of biotic interactions or not? Further, biotic interactions are presented mainly (or exclusively) as competition. How would e.g. interactions with the soil biota modify the species pool? Should they be considered or not?

Do species pool definitions based on including definitions based on functional plant traits (de Bello et al., 2012), Ellenberg indicator values (Zobel, 1997; Zobel et al., 1998) necessarily include also biotic filters? Could you please articulate arguments why it should or should not?

My apologies, but I must say I see the comparison of establishment and survival probabilities of species that strongly differ in their affinities to the test community a bit trivial. I would not expect that *Filipendula vulgaris* or *Aphanes arvensis* would establish in a wet sedge community, but I agree that it is worth testing in more borderline cases. However, I do not fully understand

why the candidate assumes there is an interaction between this affinity and the action of the biotic filter – why should distance from the community act more strongly for biotic filters? Why should this be the case? This is one of the core arguments in the thesis (see e.g. p. 107).

One of the key things addressed by the thesis is the priority effect, i.e. a founder controlled community structure. Could the candidate outline how such effects can be incorporated into the current coexistence theory, which is largely based on the "ability to increase when rare"? Are the priority effects more likely to be due to aboveground or belowground interactions?

In the papers two to four (The "species pool papers"), the authors examine fitness parameters of the tested species as predicted by treatment and residence (plus plot and time if appropriate), but does not include any predictor such as Beals index or Ellenberg- or trait-based distance from the community in the formal analysis of fitness. These measures are used only *ex post*. I suspect this is based on a deliberate decision, but I would like to hear the rationale for it.

I find puzzling that the correlation of fitness with the Beals index declines over time (p 120, 121). How shall I understand it? I would expect that at the beginning, a number of species will establish, but the long-term survival of those that do not occur in such vegetation type will be bad. If I understand it well, such process would increase the correlation. Decline of correlation seems to imply that species with high affinities to the community survived relatively worse over time. Or is this reasoning wrong?

I should say that I find the concept of limiting similarity difficult to apply for plant coexistence, namely when talking about plant traits. I would appreciate hearing some examples where limiting similarity could really structure plant communities.

In the thesis, there are repeated references to expert-estimated species pools (Sádlo et al.), but nowhere they are used to predict species pool for the experiments reported here. Is this due to the essentially qualitative nature of the Sádlo et al. paper, or does it have some other reason?

Review-type comments (not necessarily to be discussed at the defence)

p. 33: "Data from 2006 are unavailable". This is quite expected with a long-term data (I know from my own experience only too well), but the lines in Figures do not show a break for 2006 – how were the missing data handled? Data imputation? Line interpolation?

p. 35: I agree that randomization test can take account for the hierarchical design, but why the author has not used mixed model analysis, which is perhaps more standard approach and is able to do the same?

p. 75 Why was the log transformation of germination success used instead of the more straightforward generalized linear model with binomial distribution? The multiplicative constant used in the latter formula (x*200+1) was changed for species in which different sowing densities were used?

p. 81 "Interestingly, the species with the lowest Beals index value in the first experiment was the only species which reached the reproductive stage." I do not find it that surprising, as it was an annual, which is bound to reach maturity soon (*Aphanes arvensis* if I understand well)

Paper two: I really miss an ANOVA table – reading individual F-statistics in the text is annoying and difficult.

Why there is no germination test in the papers three and four? I really do not think this is any serious omission, I only would like to know why germination tests were done for some experiments, whereas not in some other experiments.

p 114: anova table - is this based both on transplants and seeds? (Or do I read the legend in a wrong manner?) I would definitely include transplant/seed as a predictor.

p 116: How shall I understand occasional increases in the survival curve: is it due to overlooked seedlings earlier or delayed germination? (I understand that this may be difficult to distinguish, but I'd like to know the author's opinion/comments)

p 167: I would appreciate if the essence of the UNO method is explained more clearly. (Even the original paper by Brown et al. is not very informative unless one checks the supplementary material I am sorry to say)

p. 168. It is clear that some correlations between a trait and a fitness measure may be negative. This may be due to a poor predictive power of the trait, but also due to the naturally inverse relationship between the trait and fitness (e.g. for seed size). Have you tried to identify these two different causes? Why the absolute value of the correlation coefficient was used instead of the standard R2?

p. 176. I am lost here where the degrees of freedom come from in the table. It is an analysis of correlations coefficients (between species likelihood to be in the species pool and their performance) if I am getting it right – are the correlations calculated independently for plots/localities? (The text at p. 169 did not help very much in this respect. I am sorry for my incompetence.)

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 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 her success with further work.

I am happy to recommend the thesis for defence.

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