ROMA TRE
UNIVERSITÀ DEGLI STUDI

Dipartimento di Scienze
Dr.ssa Marta Carboni

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

The PhD thesis by Eva Švamberková addresses assembly rules in grassland plant communities, mainly focusing on how plant species from a potential species pool are filtered into communities through (semi-)stochastic events or biotic and abiotic filters. This work is based on an impressive number of long-term experiments in the field, addressing priority and founder effects on community assembly, species pool estimation, the effect of competition vs. environmental filtering, below- vs. aboveground competition and the best method to correctly identify the pool of species which can survive locally with or without competition. While only chapter 2 is focused on stochastic priority effects, the following 3 chapters tackle deterministic assembly rules from the species pool. Chapters 3,4 and 5 all address more or less the same issue, though focusing on slightly different aspects of correctly identifying the species pool and community assembly processes. There is a progression in complexity and I was pleased that several of my concerns or ideas of improvement from chapter 3 were actually addressed in the following chapters. Overall I found this is a very interesting work, with a huge experimental effort, which also shows the progress of the student throughout the chapters and which has delivered a novel and very useful contribution to the study of community assembly in plant ecology. I outline a series of concerns and unclear points below, but note that these are mainly to provoke thought and stimulate the discussion.

A few general concerns/remarks

1) Community assembly is very complicated and requires making many assumptions. I found that though you designed and carried out elegant and clever experiments and nicely analyzed the results, the general conclusions remain in part a bit vague and/or difficult to interpret. I think the interpretation of results and conclusions would have greatly benefitted from either a conceptual figure or a clear outline of the different possible outcomes of your experiment and how you would interpret each. For example, what do you expect if competition is the most important filter in terms of the correlation with the beals index in gaps and in controls? What if it is important, but not the most important? You often state that you found that competition is the most important driver, but I'm left unconvinced. To me you find convincing evidence that it is important, but based on what can you say it is the most important? If you assign each possible outcome to a conclusion before-hand, then it is easier to understand results. Also, you often have contrasting trends for different species, so I'm missing a way to synthesize the results overall (for what percentage of species you find competition, etc.).

2) Throughout the chapters I found it was often not very clear how the initial species pool to sow in experiments was determined. Though this seems like a rather crucial step, since you aim to identify the best way of choosing the reference species pool… I'm aware you then use methods that do not necessarily need a crisp division of present/absent from the species pool. But still, you do need to select an appropriate pool of species to start from in your sowing experiments. If, like in chapter 2,

Dr.ssa Marta Carboni - tel. (+39) 06.5733-6434 - mobile az. (+39) 333.760.2091 – marta.carboni@uniroma3.it
DIPARTIMENTO DI SCIENZE, Viale Guglielmo Marconi, 446 - 00146 Roma - www.uniroma3.it - fax (+39) 06.5733.6321

you only choose species that are not resident, you might not have the correct comparison to see effects even in relative terms or you might be missing the correct species spool from the beginning.

3) You often seem to argue that with your experiments you demonstrate it is not possible to recover the correct signals of competition or environmental filtering from observational data. However, while in chapter 5 you do focus on species pool methods, you never actually compare your conclusions with those that would be obtained from full community assembly analyses involving different combinations of null models (or constrained null models), metrics (co-occurrence based or also trait-based) and species pools. These classical analyses are indeed not perfect and have many pitfalls, but I feel you have an opportunity here to truly see if/when they can correctly recover signals of assembly mechanisms. I would have been curious to see if the results would coincide with the experimental approach at least partially. I'm maybe optimistic, but I would bet that in many cases you would actually reach qualitatively similar conclusions (if you carefully choose the appropriate null model, species pool and metric combination for your scale of analysis, and tolerate at least some stochasticity). Maybe you could consider it for some follow up work?

Chapter 2

In this chapter you focus on priority and founder effects, and interestingly demonstrate they can have long-lasting consequences. I thought it is a bit a pity that this chapter is so detached from the others: it would have been interesting to see how you incorporate some of these findings in the following steps, since you conclude they are very important for community assembly. But I realize the set-up is very different in the other experiments and you cannot test everything, so perhaps this is something to consider for future work.

The analysis in this chapter is complex to fit the constraints of the original experimental design and I'm not sure I get everything. But I do have some concerns or points where I would need some clarification or discussion:

- I feel that to the least there is a potential confounding effect between the density of sowing (which you account for in your analysis) and the diversity of the community (which you do not even discuss for this analysis, though it was at the basis of the original experiment). A part from the density of the sown species, however, the diversity of the overall community may also influence whether species can or cannot establish. This is also a classical discussion in ecology, that species rich communities are likely to be less invasible because more resources are used (largely independently of which species are there). Do you think you could have disentangled this effect, perhaps including a treatment factor in your analysis, or would this have been impossible because of the design? If indistinguishable, could you comment how this could have affected your results (or maybe it does not affect them)? Could you have missed some effects? Did you try to repeat the analysis only including the HD and NC plots? Or perhaps using sown species as binary variables instead of giving a different weight for sowing density?

- To assess significance of your RDAs you used constrained (hierarchical) permutations. I'm not sure I understand correctly, but when you say "We permuted only the whole-plots" it sounds like you are

Dr.ssa Marta Carboni - tel. (+39) 06.5733-6434 - mobile az. (+39) 333.760.2091 – marta.carboni@uniroma3.it
DIPARTIMENTO DI SCIENZE, Viale Guglielmo Marconi, 446 - 00146 Roma - www.uniroma3.it - fax (+39) 06.5733.6321

permuting the 5 plots, but (since all plots received the same treatments) you mean you are permuting across the treatment, right? or maybe I am misunderstanding something… Also if you only permute 5 plots, won't this strongly limit the power of the test, since you only have only few possible permutations?

- I'm not familiar with the PRC method, so I couldn't follow this analysis as you gave no explanation (I would have appreciated at least a brief intuitive explanation sentence. This is not a very commonly used method). What is the response variable here?

- The lack of an effect of sowing on itself for a species in different years is a bit difficult to interpret: it can mean either that the species spreads broadly to all plots (so sowing is very successful) OR (quite to the opposite) that it doesn't survive at all (so sowing is not successful at all), right?

- In the analyses of each single species dynamics the effect on itself is mixed with the effects of other species. The two types of effects seem conceptually very different (propagule pressure in one case and competition on the other). I wonder if you tried to (or could have) obtain some form of variance partitioning of the two (effect on itself vs competition/facilitation from other species).

TRAITS

- How do you reconcile your conclusion that traits are not important with the large literature that finds evidence of traits influencing species distributions and dominance in plant communities (for example for invasive species)?

- Since traits can't explain success because priority effects are so important, did you check if they can at least explain for which species priority effects are important? You have variation among your species: for some of them priority effects seem very important for others not at all. Is this variation predictable through traits? For example. maybe species that have very large seeds are not so influenced by priority effects because they have enough resources stored to overcome the limiting germination and seedling stage no matter what competitive species are present.

Chapter 3

- You note that, contrary to what is sometimes argued, Beals index does not only reflect species environmental preferences but also competitive processes, since it is calculated from observed species distributions and thus based on their realized niche. Taking this reasoning further, does it not also reflect species dispersal limitations? So species might not coexist because of different environmental preferences, but also because they compete and one excludes the other…but maybe they also just have geographically distinct distributions because they are dispersal limited. Could this affect your results or interpretations? So maybe species might have a low Beals index in your experimental locality neither because they are environmentally unsuitable, nor because competition excludes them, but just because they generally don't coexist with the local species because they are from far away.

Dr.ssa Marta Carboni - tel. (+39) 06.5733-6434 - mobile az. (+39) 333.760.2091 – marta.carboni@uniroma3.it
DIPARTIMENTO DI SCIENZE, Viale Guglielmo Marconi, 446 - 00146 Roma - www.uniroma3.it - fax (+39) 06.5733.6321

In this case, even species with low Beals index could potentially survive in both the controls and gaps… Do you think this plays a role in your results? Indeed, it is true that you show higher survival in the gaps, but you also have individuals/species survive in the controls. So competition is not telling the full story?

- I was surprised, given your aim, that you chose to sow almost exclusively species that are not from the species pool (according to classical methods). Why not also use more control species that are expected to be there? I notice you changed this design in the experiments in the next chapters, which makes more sense to me.

- Why did you decide no to weed from the beginning? As you show elsewhere, there can be stochastic effects and the first life stages might undergo high mortality. Thus, the few seasons without competition might not truly reflect the true outcome of establishment. Maybe those seedlings would have died off even without overgrowing of the surrounding vegetation (i.e. irrespective of competition or not). In addition, the species might be able to establish, but then not reproduce and thus not found a lasting population. In the natural environment the inability to survive and reproduce in the long-run (even if it can germinate and establish as seedling) would also determine the absence of the species, and thus determine a low beals index. In other words, it seems that it is difficult this way to truly say that the gaps represent the effect of environmental filtering at the beginning and of competition later…

- I was also wondering if the effects of the disturbance itself in the gaps (this applies here and in the other experiments) could have other effects than just removing competitors…for example, less compact soil, activated micro-organisms, etc. Did you consider this?

- In the results you find correlation of the beals index with success of species, but this is true both with and without competition, so how can we say this is evidence of competition being reflected in the beals index? In the competition plots you have both competition and environmental filtering together, so I would expect this correlation anyways (even if the beals index only reflected environmental preferences). When reading I thought it would make better sense to check if the competitive effect itself, calculated as a log ration of your competion/control treatments would allow to better see if you have the signature of competition in your beals index. Then I was happy to see you actually did this in the following chapters. In retrospect, did you try it for this data too? I think it could provide better support for your conclusions.

Chapter 4

- You mention in your introduction that low favourability can be overcome by high propagule pressure. Since in your experiments you do provide very high propagule pressure, can we then really conclude that seedlings can tolerate the environment if they establish? Perhaps the estimates of survival are overly optimistic here (which might explain why you often observe survival of species with low BI)?

- In this chapter you included both residents and non-residents. This way in comparison you can see that actually the competition effect is even stronger for the residents than for the non-residents. How do you explain/reconcile this? So competition is not so important for the species pool definition after all?

- In the analysis, why did you choose to average across your replicates instead of using both? Also, why did you not include species as a random effect in the analysis? Is there a specific reason for these choices, or was it just not to complicate analyses too much?

I was intrigued by the fact that the correlation of survival with the BI was not significant when gaps were not weeded anymore, while in other instances the correlation is significant even in the control (also in chapter 3)... so why is this the case?

- here you say that the fact that the correlation between BI and survival is stronger with competition than in gaps is evidence that competition is the most important factor for determining the BI. But I'm not very convinced by this, because in the control you have both competition and environmental filtering, so this just says that both together are more important than just environmental filtering, not necessarily that competition is more important... I find it difficult to see whether you can find a way of deciding which filtering mechanisms is best reflected by you beals index... I guess just the log-ratios give an estimate of the pure competitive effect, but I couldn't districate well enough the results of these analyses, and it's thus difficult to say if these correlations were stronger than the ones for the environmental filtering (gaps).

Chapter 5

This is the most complete analysis, and I really enjoyed reading it and finding some practical guidance for the best method to use for species pool estimations. As I mentioned in my general comments it would have been nice to see these methods combined e.g. with null models to see what filtering mechanism would emerge as important using the classical community assembly approach from purely observational data. But I realize this was already a huge work.

Just a minor point: In your general ANOVA of the correlation coefficient between seedling/transplant survival and different methods of species pool determination you did not include a "time" effect. Did you use an average across time or just maybe the last time-point or did you just mix together different times? I realize time was not significant in the other analysis, but won't using separate data points of different times introduce some pseudo-replication (it is basically the same point repeated many times, which apparently doesn't change)?

Overall I enjoyed reading this Thesis and I think it is great work. I hope my comments help in preparing for the defense.

Sincerely,

Dr.ssa Marta Carboni - tel. (+39) 06.5733-6434 - mobile az. (+39) 333.760.2091 – marta.carboni@uniroma3.it
DIPARTIMENTO DI SCIENZE, Viale Guglielmo Marconi, 446 - 00146 Roma - www.uniroma3.it - fax (+39) 06.5733.6321