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Review of PhD thesis by Michał Bogdziewicz,
Entitled "Plant-animal interactions in dynamic environments: how tree masting and nitrogen deposition affect consumer populations, seed dispersal and see predation"

Overall assessment

I enjoyed reading this PhD thesis very much. While having myself experience in herbivore-plant interactions in a variety of systems and working in recent years especially on trophic cascading effects of large carnivores in temperate forest (Białowieża forest, Poland), this was a refreshing view on trophic cascades. While much work has focussed on top-down factors that create these trophic cascading effects, the work of Michał Bogdziewicz mainly used a bottom-up approach by showing how pulses in resource availability lead to cascading effects on other trophic levels; i.e. granivores and parasites. I am impressed by the overall quality of the performed studies, and the very decent international scientific journals they are published in. Especially, because all chapters of this thesis have already been published within the duration of the PhD project. According to the CV of Michał Bogdziewicz that I found on the internet, his PhD project started in 2012, meaning that all chapters were published within 4 years. That is an outstanding achievement. Furthermore, I am impressed by the smooth text and high standard of scientific English writing throughout this thesis. Big compliments and congratulations with this achievement!

The compilation of four already published chapters, in combination with a very clear and to-the-point summary, illustrates that the candidate has a thorough knowledge of the current state of the art within this discipline. Moreover, the candidate showed in the thesis chapters that he is able to use different sources of data for his analyses; from reviews of existing knowledge, to data acquired by ecological field studies and finally to the combination of field data with modern ways of acquiring indices via Google search volumes. I appreciated this original approach and the combination of different methods to answer ecological questions. It demonstrates that the candidate is able to create an original solution to solve a scientific problem. Furthermore, it shows evidence of the candidate's ability to place his work in a more general framework which makes these studies interesting for a general scientific audience and hence publishable in high standard scientific journals. Since the candidate is the leading author of all four publications in his thesis, he demonstrates that he is able to carry out these analyses and work with its results. So it illustrates the candidate's ability to carry out independent scientific research, and coordinate the work of different co-authors to come to a nice end result. Especially this last ability, is one of the most important skills that modern scientist should have to be able to compete in the increasingly competitive scientific community.

A bit more critical remark concerns the summary. First of all, I found this a very well-written and nice concise version of the work that is presented in the four thesis chapters. So for this my compliments. But what I missed was a synthesis of your results. What do all your four chapters teach us about masting effects and the consequences for trophic interactions or ecosystem functioning? You showed this bigger picture nicely for each chapter separately in the summary, but the strength of all four chapters forming a coherent body of scientific work, is not fully exploited in my opinion. Especially, considering the title of the thesis 'how tree masting and nitrogen deposition affect….', I would expect a final paragraph in which you

tried to combine all results. Maybe this was not a requirement for a thesis at the Adam Mickiewicz University of Poznan, but this is what I am used to from PhD theses from other West-European countries.

Assessment and discussion points per chapter

As mentioned above, I especially appreciated the variety of methods that were used to tackle the scientific problems. In Chapter 1 the candidate aims to answer three clearly-defined hypotheses on the basis of a review of existing knowledge. He used a more traditional approach based on a literature search in Web of Science, additionally he used an alternative approach by using a full-text search. In Chapter 2, field methods were used (live trapping and marking of yellow-necked mouse) in combination with a modern modelling approach (spatially explicit capture-recapture models) to study the effects of masting on space use of rodent. A very interesting and not so often used approach was used in Chapter 3. Here the candidate used temporal fluctuations in Google search volume as an index of rodent and tick abundance and the occurrence of lyme disease. I liked this demonstration of using this approach to show large scale ecological processes and their potential relationships, for the generation of hypotheses that need more detailed testing. Finally, in Chapter 4 a well-designed experimental approach was used to test the relationships between nitrogen deposition on the regeneration potential of oak trees. The candidate could nicely profit from a long-term experimental site in the USA. The results are very interesting and illustrate the complex nature of interactions that result from increasing nitrogen deposition, affecting seed number and size which on their turn affect both insect and rodent seed predators often in opposite directions. I appreciated these varied and original approaches to use available and self-gathered information to answer specific ecological questions.

All thesis chapters have already been published in high-standard scientific journals: Oikos (IF: 3.586), Ecology and Evolution (IF: 2.537), Basic and Applied Ecology (IF: 1.836), Journal of Ecology, IF: 6.180). Hence, they all went through a decent peer-review process and referees have already critically examined and commented on each chapter. Since they already passed the ultimate test that each scientific study has to go through, it feels for me unnecessary to comment in detail on each publication. Their acceptance in these high standard scientific journals sufficiently illustrates the quality of the work performed in my opinion.

Therefore, I discuss below some points that came to me while reading the thesis, and do not discuss each chapter in detail. I do not ask to revise these points in the current thesis, but I would like to hear how the candidate thinks about these discussion points.

1) Full text search approach versus traditional literature search (Chapter 1)

In Chapter 1, the candidate used for his review of existing knowledge a more traditional approach bases on a literature search in Web of Science. As an alternative he used a full-text search. In the results it turns out that for the three hypotheses tested, for two the outcome did not differ across search methods. Only for one hypothesis (nr. 1) the relationships differed marginally with search method. In the discussion is only pointed at one advantage of the full search text method, i.e. that these results did not show that there was a strong bias towards granivorous rodents and their food webs when it comes to their response to mast seeding events (2nd sentence of discussion). This indeed suggests that the effects of mast seeding are much more diverse and affect many more species than is often assumed.

Although I see the advantages of this full text search, I also see some problems that might lead to erroneous conclusion regarding this potential bias. The down-side of the full text search is that you include a large-body of studies making, often not tested, claims on the effects of masting on species (groups). These studies were not designed to test for these

effects and they are some kind of side-result or maybe only based on observations or impressions. Hence, I feel that with this approach you move more in the direction of a science that is not based on carefully designed experiments to test for relationships between factors. You run the risk of providing a scientific bases for ideas that have never been properly tested. In other words, what many people say or think as being true, becomes the truth.

I missed a careful discussion in the conclusions of this chapter/article regarding this point, and would like to hear what the candidate thinks about these potential biases that may be introduced by the full-text search. Also I would like to know what is really the added value that this full-text search method provides next to the more traditional search for peer-reviewed articles?

2) Changed trophic structure or interactions as a result of experimental N-deposition, and their consequences for the results (Chapter 4)

In chapter 4 (entitled 'Effects of nitrogen deposition on reproduction in a masting tree:...'), an experimental site at Harvard Forest (USA) was used to study the effects of long-term nitrogen fertilization on the reproductive ecology of red oaks (*Quercus rubra*). At this experimental site they applied for more than 25 years different levels (0, 50 and 150 kg ha^{-1} $year^{-1}$) of monthly nitrogen. The authors estimated the acorn production, acorn traits and determined weevil predation. With an acorn tracking experiment they evaluated the effects of nitrogen fertilization on the rodent dispersal behaviour. Finally, to evaluate the effects on acorn germination they used a seed sowing experiments in which they planted uninfected seeds on experimental plots. Established seedlings were determined a year later. This chapter very nicely illustrated the importance of indirect effects and consumer interactions when considering the effects of environmental change on plant populations.

The long-term, different levels of N that were applied to the experimental plots, likely have resulted in many changes in the local communities on the experimental plots. The study gives insight in some of them; weevil predation, acorn production, acorn dimensions, rodent caching behaviour. But likely there are many more changes that can have large effects on the survival of seeds and their recruitment potential. I wonder how these trophic cascading (bottom-up) effects of N have affected some of the results of this study. I think for example about the following likely effects.

Firstly, differences in N application often directly affect herbaceous plant production and hence plant cover. Since tree seedlings compete with herbaceous plants in their early stages of establishment, plant cover is a main factor determining recruitment potential to larger size classes (Kuijper et al. 2010). Based on the description of the experimental design and discussion, it is unclear to me whether this factor of increased competition with herbaceous vegetation as result of the higher N-deposition was taken into account.

Secondly, since ungulate herbivores can be an important factor determining recruitment success of tree seedlings and saplings in natural forest systems, their effects cannot be ignored. Since ungulates base their foraging decisions largely on plant chemical quality (especially N content), the N-treatments likely strongly interact with ungulate herbivory and likely intensify herbivore browsing intensity. As the acorns in this experiment were sown inside cages, ungulate browsing effects have been excluded. How would they have affected the outcomes of the experiment when their effects would have been included (they are a natural component of these kind of forest systems I assume)?

Thirdly, the N treatments likely have affected rodent numbers or changed the granivorous community structure. Since plant cover is an important determinant for rodent densities and their caching behaviour (as mentioned in the discussion), differences in plant cover and vegetation species composition between N-treatments likely affect the food abundance for different species of rodents and hence their community structure. That such

changes in rodent abundance or community structure could be important is hinted at by Fig. 4. Rodents seem a main factor determining seedling establishment probability at control plots, but what determines the large drop in establishment at Low and High-N treatments? A simple answer would be a higher weevil predation, but that does not seem to fit with the more gradual increase of weevil prevalence from control to low to high N (Fig. 2). Moreover, weevil prevalence is higher at the High-N compared with the Low-N treatment (Fig. 2), whereas establishment probability tends to increase from Low-N to High-N (Fig. 4). Also rodents seem to have again a larger effect on establishment probability at High-N versus Low-N (compare closed and open plots in Fig. 4). Does this suggest that there are more changes in the community structure, for example in rodent population (or mesopredators), that are responsible for explaining part of the observed patterns?

3) Differences in preference for acorns between weevils and rodents (Chapter 4)

The results of the study in Chapter 4 also showed that, after controlling for differences in acorn volume, weevils infect more acorns with increasing N-deposition (Fig. 2). Interestingly, based on the tracking of acorns collected at the different experimental plots, rodent predation of control acorns was higher than that of both Low-N and High-N. This last, was mainly interpreted as rodents maximizing their energy intake by removing higher energy, larger and less spherical seeds, which are found on the control plots. However, N-deposition increased overall acorn production at each site (Fig. 1). The effects and possible interactions between the size (and energy content) per acorn and the number that is produced have not been taken into account in the acorn tracking experiment, since 15 acorns were presented of each N treatment at experimental plots. The optimal foraging theory predicts a maximization of energy intake based on the costs and benefits of foraging. As a result, rodents might in a natural setting be better off in collecting much more but lower quality acorns from higher N sites. At these High-N sites, the costs of finding another acorn are very low because of the high numbers available. Hence, the choice that they make in a natural setting, in which both energy content per acorn (benefits) and the number available (costs for collection) is considered in their foraging decisions, might differ from the choice they make in the tracking experiment. When rodents are offered equal numbers of acorns from each N-treatment, they may simply go for the highest quality acorn (from the control plots). How do you think, caching behaviour and seed predation might look like when these effects of differences in total acorn production in relation to N-deposition are taken into account?

4) Filling the gap of knowledge on the effects of N-deposition on tree recruitment (summary, Chapter 4)

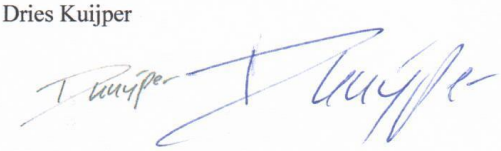
The candidate mentions in his summary and in Chapter 4, that numerous studies inform that anthropogenic global changes (f.e. nitrogen deposition) drive increases in plant seed production. However, it is not clear whether this increase translates in higher plant recruitment. Chapter four aimed to fill this gap of knowledge. However, the results of that study do not justify conclusions on tree recruitment, in my opinion. Whereas only the survival has been estimated and the potential for seedling emergence (after 1 year) in a seed sowing experiment, the results are presented as showing oak establishment and recruitment (f.e. Fig. 5). In the discussion the authors also conclude that 'long-term nitrogen fertilization has a strong potential to decrease the recruitment of masting trees'. I find this conclusion problematic since the study focussed entirely on the initial stages of recruitment, i.e. the seedling emergence phase, and therefore ignored the crucial steps that happen during later stages in the life cycle that really determine whether a seedling successfully established or not.

For example, our studies in the Białowieża forest illustrated that plant cover is a main factor determining recruitment from seedlings to larger tree saplings (Kuijper et al. 2010). When tree seedlings outgrow the herbaceous vegetation layer, ungulate herbivory is the main factor that determines recruitment to taller size classes (Kuijper et al. 2010ab).Ungulate herbivore seems to play a dominant role in determining recruitment rates of tree saplings towards taller size classes, with strong interactive effects with light levels (Churski et al. 2017). When trees grow above the browsing line of c. 150-200 cm (Kuijper et al. 2013) they again become exposed to completely different processes that determine their successful recruitment into the tree canopy (f.e. competition for light, self-thinning, etc.). Hence, when do you call it successful 'recruitment'? For sure establishment in the initial stages from seed does not guarantee much of the future recruitment process. Successful establishment or recruitment for a tree would rather mean successful recruitment into the tree canopy. Your results are very clear and nice in Chapter 4, and for sure allow conclusions on the effects on N-deposition on the emergence of tree seedlings, but what do you think these results teach us of the recruitment potential of these trees? Is there any correlation between the chance of 1st year establishment and future successful establishment?

Summarizing and conclusion

To conclude, I declare that the thesis submitted by Michał Bogdziewicz, entitled "Plant-animal interactions in dynamic environments: how tree masting and nitrogen deposition affect consumer populations, seed dispersal and see predation" illustrates his ability to carry out independent scientific research of high quality according to the requirements stipulated in **Article 13, section 1** of the Act of 14 March 2003 on academic titles and degrees. Therefore I recommend Michał Bogdziewicz to be awarded with the title of doctor in biological sciences ("doctor nauk biologicznych w zakresie ekologii"). Looking at the high quality of this thesis, especially based on the fact that all chapters have been published already in high standard scientific journals, I would also like to recommend Michał Bogdziewicz for an award of this work with an appropriate prize or with a 'judicium cum laude', when possible.

Dries Kuijper



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