

PLANT–POLLINATOR COMMUNITIES environmental gradients, trade-offs, and controllability

-Evaluation by Ignasi Bartomeus-

The thesis of Fernando Cagua provides a fresh look onto how plant-pollinator networks work. All three chapters are of high intellectual depth and are beautifully executed. Fernando uses cutting edge techniques, sometimes never applied to ecological problems before, to understand how the structure of plant-pollinator networks and how this knowledge can be used to better manage ecosystems. I specially value that he combines hard won observational data (Chapter 2), with synthetic analysis of a large compilation of datasets (Chapters 1 and 3) demonstrating his versatility. The quality of his work is already recognized, as chapter 3 is already published in *Journal of Ecology*, one of the leading journals in the area. The other two chapters are already available as preprints and I am sure they will be published soon. In addition, there is a further extra chapter already published where he actively collaborated. This collaboration shows he can be a good team player in collaborative projects. Given the complexity of the ecological problems posed, being able to collaborate with researchers with complementary expertise is a clear asset. Fernando has read a lot as he uses a variety of references, from theoretical studies, to field work studies and ranging from classic citations to modern articles. This is important to bridge theoretical ecology with empirical validations. As a minor nuance, there are a few editorial typos, specially in the introductory and discussion texts, for example a few latin species names are not italicized, something that is straightforward to fix and do not have more relevance than that.

Overall, the questions addressed are original and highly topical, the methodology uses state of the art statistics and often open new paths on how to approach network ecology. The results are clear and the thesis is very well written and easy to read. Hence, my comments mainly aim to fulfill my curiosity and to push the research further. Most chapters are quite novel regarding techniques used, so a lot of my questions try to think on how to interpret the results or how can those be further developed.

Chapter one deals on how species diet specialization changes with abiotic conditions. This is an original question that is answered at larger spatial scales. The introduction introduces two competing hypotheses showing that stress may increase or decrease specialization. As a general (and personal) reflexion, ecologists are a bit obsessed in finding general rules, but as you show later on, both hypotheses hold depending on the species analyses, and probably also depends on the type of stress considered. Hence, we shouldn't be disappointed if no general universal trend emerges from our analysis.

This chapter, specially the discussion, covers very well the network ecology perspective, but it may be interesting to also give a bit more of information on species biology. For example, specialists may broaden its diet ONLY if they can do that physiologically. Most bee specialists can't digest pollen other than the one they are specialized. In fact, despite that in the paper the metric used is clearly defined, for researchers working at species level, specialization may mean a very different thing, specially for bees. Traditionally, specialist bees are described regarding on how many plants they collect pollen to feed their progeny. Even pollen specialist bees collect nectar from very different plant species. As your measure is focused on visitation and not pollen use, you can't disentangle both processes. This is ok, as I expect pollen specialists to be detected visiting less plant species, but may be interesting to show you are aware of this discussion somewhere in the paper before its publication in a scientific journal. Furthermore, the fact that specialist bees increase its diet in high stress areas, may imply they are visiting more flowers, but those are useless for their progeny.

One question I have is about the interpretation that generalist species in low stress areas. Why should a generalist species not behave optimally when conditions are good? You mention that "Species with a large number of partners, on the other hand, should have a larger pool of available

partners and might, therefore, be more likely to specialise under environmental stress and focus on the most beneficial partners.” Alternatively, maybe in high stress areas they need to focus on the only available resources (not the most beneficial). I assume in high stress areas, they will be more likely to be outcompeted by competitors, and one of the theoretical expectations when competition is high is to reduce niche breadth to avoid using the resources copied by the best competitor. This is hard to test, but may be an alternative explanation that can be discussed.

The stress metric used is very clever, however I can help thinking it ignores local adaptations and populations differences. This is not a strong critique, as there is no way to control for that, but may be a nice caveat to add to the discussion. This stress metric is also dominated by climatic variables, and adding other stress sources such as land use transformation may be a promising avenue for the future.

Finally I have a few minor methodology questions, which are normal, giving your methods rely in several steps, each one with its own assumptions.

1- Regarding the use of Gbif data. I like that you remove duplicates, but do you think it's possible to correct for false absences, which are likely to occur in more isolated areas?

2- Did you considered using also d' as an specialization metric? I am not a big fan of this metric, but as is widely used, I am curious whether if you considered it or not.

3- The variable "number of known possible partners" tells you how generalized is a species at the species level. I wonder if the deviation of number of partners observed in a network/total known possible partners tell us something about variability in specialization. Just thinking aloud here.

Finally, it would be nice to cite taxize and rgbif in main text, as a way to give proper credit to the maintainers of this packages.

Chapter two is the more empirical one and tackles the effects of the network structure on pollination function. This is very topical as despite there is much theoretical expectations, very few empirical data is available on this topic. I have to say that the four factors analyzed make a very beautiful story, but I missed in the introduction a clear explanation on why are those metrics selected and not others. This is better thiged up in the discussion, but readers not familiar with this kind of metrics may appreciate a bit more of background here. I am thinking here on maximizing the readership of the paper, nothing that needs to be fixed for the dissertation.

Methodologically, I also missed some details on the protocols used for pollen identification in stigmas and pollen loads in pollinators. There is a reference to other papers, but a quick summary will be appreciated, as is important for the interpretation. For example, did you get pollen from the body of the bees, or from the scopa? Pollen from the scopa is usually useless for the plant. In fact, I am not familiar with this metric of visitation potential, and I am not sure if there are papers correlating pollen loads with visitation efficiency from the plant perspective, but I know pollen deposition and pollen load may differ highly because deposition depends on the matching of morphological parts of both partners. This is a caveat that can be added to the discussion.

The PCA results are very interesting to me in order to depict the context dependency of the strategies and maybe they can be presented first, to give them more importance. On the contrary, the pollen deposition data may be more limited because pollen deposition is not always a good proxy of plant fitness. You may have large amounts of heterospecific pollen and this be neutral for plant fitness. A measure closer to fitness such as pollen tubes developed would strengthen this part, but I understand this a large extra amount of work.

One think you can easely add is how much variance explain the fixed factors, as it would be good to understand the model performance.

Chapter three is probably the more ambitious, as it uses cutting edge methods developed in other disciplines applied to ecological problems. I think this is a promising avenue and a great advance for the literature. Time will tell us if this methodology ends up being relevant for ecology, but trying is brave and needs to be applauded.

A good discussion to have is how to further follow up with this approach. First, do you think it is worth to following it up? What would need to be the next steps? For me there are two main areas of interest. First validating the way you infer the directionality of the network, which now relies in a big assumption. Second, to experimentally or observationally test the controllability of a network, maybe using restoration or removal experiments. What do you think?

One easy check to make regarding directionality is performing some kind of sensitivity analysis. For example, by relaxing the conditions to decide directionality, for example when the observed asymmetry is low, you can also assume bidirectionally and see how much the results change. Maybe you already did that. The fact that controllability depends on asymmetry, and asymmetry is used to decide directionality makes me wonder how to brake this circularity in an elegant way.

The final chapter is very complete and robust. I particularly enjoyed that it matches my own findings with trait matching, which emerges at larger scales, but its blurred when only a subset of species is considered. This is not surprising as most traits are phylogenetically constrained.

One question that came to my mind is about the phylogenies used, which only capture the deep history, but not recent speciation events, right? Do you think using better phylogenies may change the picture? Specially regarding the results within modules, which contain taxa that are closer phylogenetically. However, on the tips, is precisely where your phylogenies are not well resolved, at least for pollinators. In other words, It could be that recent evolution is more important for modules cophylogeny?

Another very interesting finding is that exotic species do not break the cophylogenetic signal. I wonder if you think this is just because removing only one species makes little influence on the community pattern, or is it because invaders are not phylogenetically distinct? This can be probably tested, or you may already know the answer.

Overall, I don't think there is any major amendment that needs to be made and I congratulate Fernando and his supervisor for this splendid Thesis disertation.

Best,
Ignasi Bartomeus.