Examiner’s report

PhD candidate: Fernando Cagua

Examiner: Christopher Kaiser-Bunbury

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**Key questions**

The terms ‘specialists’ and ‘generalists’ assume a central role in this thesis. I’m wondering whether they are, as I understand, primarily defined by the number of links these species establish (Chapter 1: “…number of partner species […] as a metric of their level of specialisation.”), and if this is the case, how this differs from specialisation as a function of feeding niche breadth (realised and fundamental) or simply abundance/visitation frequency in pollination networks. The core question is, whether degree (or normalised degree) is the ‘best’ metric to express specialisation?

*Specialists and generalists are indeed primarily defined as the number of links a species has.*

*Agree that # of partners it is not the best metric to express specialisation in many contexts as it is a rather simplistic view. First it only accounts for the realised niche at the community level, and even then, it does so in a rough manner.*

*Nevertheless, this is primarily the perspective adopted in network ecology and therefore allowed us to better link the concept across chapters.*

*At a network level (community) it offers a decent approximation of the realised niche, at the meta-network level (larger spatial extents) it starts to move towards the fundamental part of the niche. The number of partners is related but is not the same as abundance or visitation frequency. It has the additional advantage that is easy to measure from a network perspective and easily understandable.*

Chapter 1, page 12, first paragraph: The adjustment of ‘coastal’ bioclimatic values, were these primarily from islands? Although the proportion of these occurrences is low compared to the overall number, I'm wondering whether there is the potential of generating a bias against island species and their stress responses.

*It is true that there is a potential bias and that it’s likely that these problems were more prevalent in small islands. We did not quantify it but there are reasons to suggest that the impact might have been minor. First even if using bioclimatic variables from an adjacent cell, they are still, from a global perspective, very close to those in the actual site. Second, it represented only a very small percentage. Third, it is possible, but unlikely that islands have a fundamentally different response to stress than non-island species. Fourth, our analysis required species to be present in multiple sites, so those that*

Chapter 1, page 13/14, last and first paragraph, resp.: “We included the number of known possible partners as a predictor in our models…” It is not entirely clear to me why this is necessary, and whether this includes some circularity in your argument, as both the degree (response) as well as predictor side of the model appears to constrain the potential response in change of degree due to environmental stress. I may be missing something here, but I would like to ask the candidate to elaborate more clearly on this point. In fact, the point made in the thesis “Controlling for the number of potential partners makes our model a particularly stringent test of our environmental-stress hypotheses because this variable could explain a large proportion of variance.” reflects exactly the dilemma that I currently have with this step in the analysis.

*We thought this was a good approach from two perspective:*

* *Environment determines which species are present in a community – species distribution, so we wanted to make sure the effects effect from stress in # of partners is because of changes in preferences rather than just species composition*
* *From a niche perspective which we touched on before, the number of potential partners serve as a proxy for the fundamental niche, while the number of partners serve as a proxy on the realised niche. Again, we wanted to make sure that changes due to the environment and not changes due to the fundamental niche being larger or smaller.*

Chapter 1, general comment: I question the suitability of the term ‘environmental stress’. Given that you define environmental stress as one minus the suitability to particular climatic conditions (most of the variables are climatic), would it not be more appropriate to talk about climatic stress? What are the reasons for using the term environmental stress, which lacks specificity and seems less meaningful?

*Primarily because we also include topographical information alongside the climatic variables to determine the stress. As we expect several other environmental variables (habitat, soil, hydrography, geology) to be related to climate. Admittedly it has nothing to do with other environmental variables like pollution, degradation, fragmentation. We might consider changing terms in future revisions.*

Chapter 1, page 23, second to last paragraph: Is a reduced nestedness plausible? Quantitatively, is it a ‘regression towards the mean’? Would you expect this if pp networks tend to have long-tailed degree distributions with many specialised species that will become more generalised, which may result in higher interaction redundancy, which in turn may increase robustness? What are your thoughts on this?

*This is a very provoking question and there was a lot of speculation on this paragraph, so we actually removed it from the discussion in a later revision. This is a reflection on how little we still know about the mechanisms of stability and robustness in ecological networks. Much literature about how nestedness and robustness seem to be correlated but it’s not necessarily the cause. From a theoretical perspective on mutualism, nested is better than random, but not better than a fully connected network.*

*In my mind because of the tails a “regression to the mean” might indeed imply a reduction of nestedness as nestedness requires an asymmetry in interactions to be reflected. Many specialists might become more generalised but also some generalists will become more specialised. Wether it is more robust or not depends on the arrangement, and how much the increase is.*

Chapter 1, general comment: Qualitative data – often niche broadening or narrowing is expressed through quantitative shifts in visitation frequency, but this is not taken into account here. Several previous studies have shown that models based on qualitative data are relatively unrealistic/overly conservative. Why did you decide to use qualitative data and would it be possible to use quantitative data with your approach, i.e. shifts in interaction strength rather than adding or removing links?

*One of the main constrain was data availability. Many of the networks we included do not have information about visitation frequency. We considered using only quantitative networks but that would have severely limited the number of species and the number of sites where they are present. I think it would be valid to use quantitative data using a similar approach and would be very valuable. One is that visitation frequency has its own problems to account for niche, for example is presumably more closely related to abundance, so it’s possible valid interpretation would need this piece of information too.*

Chapter 1, Page 23, last paragraph: You acknowledge that your methodological filter includes species that are overall relatively generalised on a gradient of specialisation, although you distinguish between specialists and generalists, in relative terms. The 'fourth group’ is ecologically highly relevant, but here its sensitivity to climatic stress appears to be neglected. How could you modify your study to include these species? Would you expect a different result if you include the full spectrum of specialists vs generalists in a similar study?

*This is something that I considered in multiple occasions. As it is an obvious bias in the data. It is however a problem we found very hard to address. One would need to have information about places where a species is present but has no interactions as well as some information about places where the species would is absent, but would otherwise be present if it had partners.*

*The first requires independent surveys complementary to the interaction data in each of our sites. Not only interatction presence, but also interaction absence. The second would require detailed information about the distribution of every species included in the model. There are ways around it. Generating species distributions for single species or species groups is usually done with much caution and expert knowledge input and is rarely attempted in automated fashion as it would be attempted in our case. This is further complicated by the fact that most geographic data is presences not absences in GBIF.*

*I have to confess that I don’t know what the result would be if we were to include that. The high amount of zeroes will most likely warrant appropriate statistical modelling but presumably if we manage to separate the effect of environment zeroes and non-zeroes we should see a similar pattern.*

Chapter 2, Introduction: I find the thoughts and processes of intra- and interspecific indirect interactions very interesting. In a pollination context, I feel, however, that you may be overlooking interactions on the individual level. That means, species and individuals may show quite different patterns of floral and/or plant species fidelity. This is an aspect that doesn’t seem to be considered here – at least at this stage of the chapter. How do you think this may affect the proposed trade-off between pollination benefits of pollinator sharing?

*This is actually a very exciting question. I am currently working in a manuscript that shows that the specialisation might look very different when including individuals and it goes one step further and shows that the partitioning of pollen of different species across a pollinator’s body is not random. So, this is another strategy plants have to minimise this trade-off.*

*So in hindsight I think this might be exactly the reason why the # of species shared is a relatively poor predictor of pollen quantity and purity compared to the others. I believe that if we were to include a more detailed metric of specialisation based on individuals the effect would be much stronger. Sadly, this is something we cannot incorporate straightforward fashion as the visitation networks are not constructed at the individual pollinator level. We do have individuals level data for the pollen transfer, but identifying pollen at the individual level is a tremendous amount of effort and was only achieved for a subset of species and there is no complete overlap between the species in the visitation and the transfer network.*

Chapter 2, section 2.3.1: It would probably be useful to spell out here the rationale behind the flower manipulation described in the last sentence of the first paragraph. Why were the other flowers removed? Did you consider their presence irrelevant for your questions or did you aim to actively control for an effect? With the information provided so far I can’t fully appreciate the reasons for the manipulation.

*My understanding is that this was done purely for practical reasons, some plants have multiple flowers per inflorescence and many inflorescences per individual. Removing old flowers allowed an easier identification of the buds that became flower in the following days. Leaving all flowers there would have made it very challenging to distinguish recent flowers with older ones. As the time allowed was standardised.*

Chapter 2, section 2.3.2, calculating floral abundance 3rd paragraph: It's mentioned below (functional originality paragraph) that phenology is taken into account, but if floral counts are aggregated and then weighted, it has the potential to ecologically distort the data. Would you be able to expand on this rationale? Further, is the phenology trait included as a fixed effect in the models? How does a weight of 1/5 account for non-independence? Some rewording is required to communicate the reasons for the procedure more clearly.

*Thanks for the feedback. The weighting was done such that phenology has the same weight of the other traits we included in the study when calculating originality. Otherwise functional originality would have taken over by phenology and not reflect the other traits. We agree we need to improve how we state this.*

Chapter 2, Discussion, page 41, first sentence: It’s not clear whether this pattern could also be generated by changes in the pollinator community, which mediates these apparent different plant species responses. Could you elaborate on this and explain why the observed patterns are driven by plant species 'flexibility'?

*This is a very good point and something we actually have some data to explore this. We would be keen to see whether this is something we could incorporate when the paper comes back from review. As of now we cannot really tell how much it is due to pollinator composition and how much to plant flexibility. Some of our metrics, visitation, and shared pollinators are sensitive to this, but others like functional originality and relative abundance should be more insensitive to pollinators. So certainly there is some flexibility, but we don't know exactly how much.*

*It certainly won’t be a straightforward task as I cannot think on a simple statistical test to perform this, but perhaps is something that could be investigated using a fourth corner analysis of the pollinator-community composition matrix.*

Chapter 3, general: This chapter sheds light on the ability of invasive species changing the controllability of a network. In the discussion it is also said that invasive species and their native counterparts are equally likely to have high control capacity. But, does the candidate have insights into how exotic but not invasive species behave in terms controllability? Do exotic species that may become invasive show early signs of control capacity in the networks?

*This is a very tantalising question and I think it would be the case. Invasive species all are critical for control and a large asymmetry in their interactions. Some native ones do have this as well and anecdotally they tend to be well established. So there is indeed a good reason to believe that if an exotic shows these signs could very well become invasive in the community or at least well established.*

Chapter 3, general: Most empirical pp networks do not show pollinator abundance but use the number of visits as a proxy. As the role of a species in the controllability concept is partly defined through the species’ ability to control abundances of other species, do you think that the lack of ‘abundance’ information actually compromises the ecological interpretability of the concept?

*I think abundance information could bring new perspectives to the work. However part of the strengths but also drawbacks is that it uses only topological information to assess the controllability of a network and the control capacity. So it gives that piece of information but tell us nothing about what exactly an intervention would look like. Or what interventions would be better than others, for that you need a better understanding of the population dynamics in the community and also lots of information about the species that inhabit it. So yes it limits the usefulness but also makes it stronger by being useful with limited information.*

*Abundance is used heavily when determining the asymmetries (indirectly via visitation). In this case we are interested in the part of the abundance that interacts with other species, and in that regard that might be an OK assumption.*

Chapter 3, Results, last sentence: Would you have not expected that critical species in full networks are also critical in a rarefied network? If so, why?

*This is what we expected but not what some of the reviewers expected. I think the reviewer was afraid that the control capacity was a fragile metric, more so than the controllability of the network. Particularly for important species with only a few interactions. We showed that this might not be the case.*

Chapter 3, Discussion: Is the species' ability to control abundance linked to the fact that a species itself has to be abundant? If so, is abundance a relatively good predictor of the species' role in network controllability?

*I believe it would be a good predictor in the same fashion as centrality metrics. Very central species (generalists) tend to have high control capacity. So abundant species are more likely to have high asymmetry and also be central, but one of the surprises of the research and takeaways is that these are not the* ***only*** *ones. There was a good number of species that were very important from the controllability perspective and interacted only with a few species. Other things like contribution to nestedness tended to be better predictors than centrality and I suspect it would be the same with abundance.*

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***Nacho***

Chapter 1: 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 coped by the best competitor. This is hard to test, but may be an alternative explanation that can be disussed.

*This is a good point. We account for the number of resources by including the number of potential partners in our model, so it appears that generalists are indeed concentrating into a subset of partners under high environmental conditions. We do not test however whether there is an association between the environmental stress and the number of available partners. On the other hand, it is indeed possible that generalists focus on low stress areas but will only do so if competition is high, which presumably is more likely to happen in high stress areas.*

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.

*This is true and is related to Chris observation about environmental and climatic suitability. Initially we identified habitat composition as an important metric but failed to secure a dataset that provided the coverage we needed for such an endeavour. I think that looking at habitat, soil, and other environmental variables not examined by us would be a good idea in a continental or regional basis.*

*As anecdote, in the initial stages of the project we toyed with the possibility of exploring this idea in fruit dispersal networks in New Zealand, for which there is good habitat information and networks.*

Finally I have a few minor methodology questions, which are normal, giving your methods rely in several septs, 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?

*While this is a more important aspect to correct in species distributions models, the our understanding of the “niche factor analysis” we employed is that it is less sensitive to this. While a species distribution model needs to account for absences/ and generating pseudo-absences is a quite challenging thing on its own. It’s not that bad for our method because we are essentially just calculating a bi-dimensional density distribution of the presences.*

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 weather if you considered it or not.

*This question is related to a previous question by Chris. D’ would have been a good candidate had we used quantitative visitation data.*

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.

This is a good point

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 thighed 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

*Thanks for the suggestion! We will address this caveat in future versions of the paper. For you punctual question: care was taken to not include parts of the body not available for pollination like scopas in female bees*

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 discusion.

*They do differ but it’s worth to keep in mind that pollen transfer might be more closely related to the outcome of pollination than visitation.*

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?

I agree the next steps must be experimental. Even if from a synthetic point of view. It should be possible to simulate the population dynamics

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.

This was something we explored but it would be a great way to follow up. Not only that but also exploring other metrics of asymmetry that have been proposed in the literature and might be more adequate.

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?

I think is possible that using better phylogenies would improve the resolution, I think the improvements would be marginal as even if the signature were recent, one would need to find

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.