Examiner’s report

PhD candidate: Fernando Cagua

Examiner: Christopher Kaiser-Bunbury

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**Overall assessment:**

Overall, the thesis is a well-communicated collection of linked, high-quality research studies which focus on understanding the processes that shape plant-pollination interactions at the community level using a network ecology approach. Specifically, the candidate focusses on the defining features of species that interact with many mutualist partners that emerge across plant-pollinator communities. Investigating the patterns and processes that are generated by ‘generalised’ species is the overarching connection between the three core data chapters of this thesis (Chapters 1-3). I particularly like the breadth of approaches and deep mechanistic and functional explorations that the candidate has applied in his work and, combined with input from collaborators, created strong, potentially highly influential contributions to the field of community ecology.

The thesis is largely well-written (but see below) and the quality of the science is very high. The thesis does come across as predominantly the candidate’s own work. Overall, the thesis is easily of sufficient quality to meet the criteria to be awarded the degree of Doctor of Philosophy. Below, I have listed the main strengths and some areas for improvement, a few sections that would benefit from amendments, and a list of questions that I’d like to discuss further with the candidate during the viva. I have also enclosed an annotated copy of the thesis with many in-text edits, comments, suggestions and questions, which the candidate may want to take into consideration for the final submission of his thesis.

Overall, I’d like to emphasise that this thesis is a great achievement with thought-provoking contributions.

**Strengths**

* Very confident and proficient use of complex analytical approaches to answer challenging ecological questions.
* Visualisation of complex results is novel and often very clear and convincing.
* Chapter 3 and Annex A are significant, well-formulated and -executed contributions to the network ecology literature which reflect the candidate’s ability to produce high-quality research.

**Areas to improve**

* Although the text is generally well written, there are relatively frequent dips in clarity, either from awkward word choice, by using jargon without explaining specific terms previously, or by being vague. I have highlighted many examples in the annotated thesis.
* Especially in the introduction my impression was that the candidate used too few references to support his statements. For example, paragraph 1 of the Chapter 2 introduction contains a couple of general statements which should cite the original work.

**Amendments**

* Abstracts/summaries are noticeably weaker in writing style and coherence than the main text of the chapters. These sections are important, and the abstracts of Chapter 1 and 2 should be improved to convey a stronger, clearer and more informative (quantitative) message.
* The introduction would benefit from a clearer definition of the specialisation concept, and justification of why this concept was selected over other concepts (see also the first question below).
* While the thesis is generally well written, I find it easier to follow and fully assimilate the more ‘technical parts’ of the chapters (methods and results) compared to those sections that convey the ecological rationale and interpretation of the results (Ch1 and Ch2 mainly). This does not necessarily reflect a break in logic or lack of hypothetical support, but is due to a lack of clarity of the writing. I’m convinced that the candidate’s understanding of the underlying rationale of the different chapters is advanced, but this understanding is not communicated in the clearest and most structured way. I’d like to emphasise that this critique is comparatively minor, but it is noticeable throughout and reflected in the many comments in the annotated document. Focussing efforts on revising these sections is likely to have the greatest benefit to the candidate’s skillset as well as to the scientific community who will engage with and potentially apply his research.
* I don’t know if this is the particular style at the Department/University, but I would strongly suggest that the supplementary material is, at least partially, included in the final thesis. The frequent references to an online archive is cumbersome and gives the impression of incompleteness.

**Minor amendments**

* I regularly stumble across the term ‘pollination service’, possibly because of its closeness to ‘ecosystem service’. It implies (and is often used in the literature) a service to humans. My impression from the text is that this is not what the candidate intends. I would recommend that the term where used is simply shortened to ‘pollination’, which appears more accurate in most cases.
* Chapter 2, section describing results depicted in Figure 2.2: I fail to fully understand the connection between the two model coefficients and how the difference in coefficients can be used to describe the association of a variable with the conspecific to heterospecific ratio. It would be worthwhile explaining this in more detail here, what exactly was done and how this can be used to draw the stated conclusions.

**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?
* 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.
* 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.
* 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?
* 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?
* 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?
* 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?
* 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?
* 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.
* 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.
* 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'?
* 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?
* 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?
* 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?
* 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?