Structural controllability of ecological networks

JEcol-2017-0720 - Detailed response to comments

Fernando Cagua, Kate L. Wootton, Daniel B. Stouffer

We are thankful to the editors, David Gibson and Nicole Rafferty, and two anonymous reviewers for the insightful comments to improve the manuscript. In the following sections, you can find a detailed response to each comment raised during the previous round of review.

Editor comments

> "I agree with the AE and reviewers that this is an interesting and potentially important manuscript. I support the AE's decision to reject but invite resubmission for all the reasons mentioned. I encourage resubmission if you feel that you can better bring out the conceptual importance of their work for plant ecologists. If you wish to strengthen the applied focus with specific conservation recommendations then you may wish to submit to Journal of Applied Ecology. Reviewer 1 offers suggestions for both approaches. I hope that you choose the former."

Thanks to the Senior Editor, David Gibson, for his comments and his willingness to allow resubmission. After lengthy consideration of the two recommended alternatives, we have chosen to focus on the conceptual importance of our work in line with the editor's stated preference. To do this effectively, we ultimately ended up rewriting both the manuscript and the supplementary materials almost completely. We think the extra effort was worth it as we feel the current version does a much better job at explaining the utility and insights generated by the proposed approach.

Associate Editor comments

> "Both reviewers see potential value in the application of control theory to species interaction networks and found the work to be of interest. I agree that the method and its application to plant-pollinator networks are interesting, particularly the findings that contrast invaded vs uninvaded networks and use novel metrics to describe the influence of invasive species in networks. Both reviewers also note, however, that the current ms falls short of clearly and convincingly demonstrating the utility of control theory in making management decisions. They

> call for more in-depth exploration and illustration of what novel and important contributions this method would make to conservation. For these reasons, this work may be better-suited to a more applied journal (e.g., Journal of Applied Ecology), assuming the ms is revised in the recommended direction."

We thank the Associate Editor, Nicole Rafferty, for the constructive feedback and highlighting the strengths of the paper. As we noted above in our response to the Senior Editor, we opted to use our revisions to strengthen the conceptual component rather than emphasising its application in specific management and conservation scenarios. We opted to take this decision for two main reasons. First, the empirical data we use does not explicitly include any management or conservation scenarios. As a consequence and despite the potential of the approach, we currently lack *direct* evidence of the utility of the approach for management decisions. Second, we think that highlighting the conceptual approach offered a greater opportunity to draw attention to the strongest/most interesting aspects of the paper. Namely, the contrasts between invaded and uninvaded communities and the role of invasive species, as one of the reviewers points out.

Reviewer comments #1

> "The management of complex ecological networks is of vast importance for the conservation of the natural world. While the field of ecological networks is vast few have tackled this question in a practical way. This paper would make a significant contribution to a field that needs to change direction if it is to help inform conservation as often purported in studies from this field."

We are grateful to the reviewer for the positive feedback and encouraging words.

> "The control theory approach is very interesting. I think however there needs to be more clarity in the paper. It is hard to read. A reworking of it including using descriptions of the variable throughout instead of variable names would improve this."

Previously we used two sections to explain our approach: a section called "Theoretical framework" where we described the control methods, and another called "Methods" where we described their application on empirical data. At that moment, we thought this was the best approach; in hindsight, we realise that separating these two aspects made it hard to understand the core control concepts and their relationship with ecology. As mentioned by the reviewer, this problem was compounded by abundant jargon and mathematical notation. To improve clarity, we have now combined the two sections into a single "Methods" section in which we explain the theory alongside with the empirical application. We also spend more time

providing intuitive explanations of the concepts of control theory and have moved the most technical details to the supplementary information. This latter move (shifting the technical details to the supplementary information) allowed us to use far less jargon and simplify the notation. We hope that the reviewer agrees that the new version is easier to follow.

> "Better context needs to be given for previous work to look at the management of networks in ecology. There are a few papers and knowing how this one differs from these (not just the ones that look at node importance for example) is important. Some of these papers are mentioned in the discussion but in the intro, it is important to know what they do and why this paper is novel."

Thanks for this observation. In line with feedback from both editors, we have chosen to emphasise on the conceptual aspects of the work and reduced the core question of management applications to appear only in the discussion. Nevertheless, we have also rewritten the introduction and took care to be clear at explaining how this study relates to and differs from previous work. In particular, we set up the stage for our work by briefly explaining how keystoneness metrics are mainly based on centrality metrics and how the proposed work differs from it.

> "Finally I think it is important to provide context about what kind of decisions are being made and could be informed by this approach. Who is managing plant-pollinator networks and what choices would they actually be making. Some examples should be expanded on. And also how would the outputs of this work actual inform choices and guide prioritization"

As it was explained in the previous response, in this paper we chose not to emphasize the empirical application of structural controllability. We acknowledge however that the approach has potential to be applied in management and have hence added a couple of examples in the Discussion (line XXX).

> "And finally I think mentioning the extreme uncertainty mostly seen in networks in the real world is key, how can approaches deal with this needs to be discussed. What do we need to think about in terms of key information to use this approach?"

In the previous manuscript, we discussed this uncertainty but it was buried in the Supporting Information. We have now added a subsection in the Methods describing how we evaluate the impact of the uncertainty induced by using visitation as a proxy of species interdependence and that induced by incomplete sampling of rare interactions (page 11, line 268). We found that the structural controllability approach is robust to these two sources of uncertainty (page **??**, line **??**). Further details can be found in the Supporting Information Section S5 and S6. In addition, we also included a reference to the key information needed to apply the method in the Discussion (XXX).

Reviewer comments #2

> "I read with great interest the manuscript by Cagua et al. on 'Quantifying the manageability of pollination networks in an invasion context'. The authors use control theory to develop an approach to assess how ecological networks – here pollination networks – can be managed, and test the approach on ten pairs of invaded and uninvaded plant-pollinator communities. Overall, the methodological approach appears to be sound (I'm not familiar with control theory, so I'll have to leave in-depth assessment to an expert), the descriptions and rationale behind the assumptions used to develop the methods are logical and reasonable, and the illustration of the concept using published networks seems appropriate. Also, although the manuscript may require a few minor edits it is well and clearly written. I do, however, have some concerns about the applicability of the approach and the findings, which I'll describe in more detail below."

We are thankful to the reviewer for indicating the aspects which they believe were strengths of our work. We maintain the methodological approach in the latest version and have used these details to determine which elements were essential to maintain in the current revision.

> "When I first read the title and the abstract of the manuscript I was excited about the prospect of reading about a way forward using ecological networks to improve ecosystem conservation. Now, having read the manuscript twice, I'm not persuaded that the proposed approach really advances our ability to conserve or restore ecological communities as the authors claim, or whether the approach provides primarily another, rather complex, way of analysing networks and describing the role of species in networks. As it is, the authors fail to convince me that the developed approach really advances our ability to prioritise species for ecosystem conservation, nor does the manuscript offer novel insights into the role and importance of certain species in a network and for ecosystem functioning. I've little doubt that there are ecological and theoretical justifications for combining control and network theory, but the authors don't yet show that their proposed methods are overly useful in applied conservation."

> "I can see two ways forward: the authors re-arrange and re-word the manuscript to focus on the ecological advances that such an approach would bring to explaining and predicting network structure; or the authors describe in more detail a few scenarios in which conservation practitioners and managers could apply the proposed method to 'improve' management strategies or measure the efficacy of interventions. The latter would require a stronger justification of the advantages of control-theory approach compared to the classic species-level

network metrics."

We are very thankful for the insightful identification of the manuscript weaknesses and especially for clearly identifying possible pathways to fix them. Following this suggestion and that of the editors, we chose to focus on how structural controllability offers a new perspective to understand the role of species in their community in the context of species "keystoneness". Despite this decision, we still discuss previous metrics as we found that being explicit about how the approach differs from classic centrality metrics to estimate species importance made the paper much clearer. These differences are discussed more in the light of network structure than in the design of efficient management interventions.

> "In short, I feel that the manuscript is currently a hybrid between ecological theory and applied conservation without being fully beneficial for either of the two disciplines. With a few changes to the manuscript, the interpretation and presentation of the results, and a re-write of the discussion with more tangible points and concrete examples from practical experience, the manuscript has the potential to be a solid contribution to the field of applied ecology."

As mentioned earlier in a response to the editor, we found that in order to address effectively all concerns, a rewrite of the whole paper was needed. Although we have not gone in the applied ecology direction, we hope the current version addresses the fundamental reviewers concerns satisfactorily.

> "One last minor remark, the authors have overlooked some key references in the field of restoration/conservation and ecological interactions/networks, which would strengthen the manuscript further, e.g.

- Harvey, E., Gounand, I., Ward, C.L. & Altermatt, F. (2017) Bridging ecology and conservation: from ecological networks to ecosystem function. Journal of Applied Ecology, 54, 371-379;
- Devoto, M., Bailey, S., Craze, P. & Memmott, J. (2012) Understanding and planning ecological restoration of plant-pollinator networks. Ecology Letters, 15, 319-32;
- Kaiser-Bunbury, C.N., Mougal, J., Whittington, A.E., Valentin, T., Gabriel, R., Olesen, J.M. & Blüthgen, N. (2017) Ecosystem restoration strengthens pollination network resilience and function. Nature, 542, 223-227;
- Pires, M.M., Marquitti, F.M.D. & Guimarães Jr, P.R. (2017) The friendship paradox in species-rich ecological networks: Implications for conservation and monitoring. Biological Conservation, 209, 245-252.

Thanks for these references. We have used them to strengthen the Discussion (lines XXX).