Improving our knowledge of species interaction networks

Cédric Gaucherel based on reviews by Nicolas Deguines, Michael Lattorff and 3 anonymous reviewers

A recommendation of:

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Cite this recommendation as:

Ecosystems shelter a huge number of species, continuously interacting. Each species interact in various ways, with trophic interactions, but also non-trophic interactions, not mentioning the abiotic and anthropogenic interactions. In particular, pollination, competition, facilitation, parasitism and many other interaction types are simultaneously present at the same place in terrestrial ecosystems [1-2]. For this reason, we need today to improve our understanding of such complex interaction networks to later anticipate their responses. This program is a huge challenge facing ecologists and they today join their forces among experimentalists,

theoreticians and modelers. While some of us struggle in theoretical and modeling dimensions [3-4], some others perform brilliant works to observe and/or experiment on the same ecological objects [5-6]. In this nice study [6], Magrach et al. succeed in studying relatively large plant-pollinator interaction networks in the field, in Mediterranean ecosystems. For the first time to my knowledge, they study community-wide interactions instead of traditional and easier accessible pairwise interactions. On the basis of a statistically relevant survey, they focus on plant reproductive success and on the role of pollinator interactions in such a success. A more reductionist approach based on simpler pairwise interactions between plants and pollinators would not be able to highlight the interaction network structure (the topology) possibly impacting its responses [1,5], among which the reproductive success of some (plant) species. Yet, such a network analysis requires a fine control of probable biases, as those linked to size or autocorrelation between data of various sites. Here, Magrach et al. did a nice work in capturing rigorously the structures and trends behind this community-wide functioning. To grasp possible relationships between plant and pollinator species is a first mandatory step, but the next critical step requires understanding processes hidden behind such relationships. Here, the authors succeed to reach this step too, by starting interpreting the processes at stake in their studied plant-pollinator networks [7]. In particular, the niche complementarity has been demonstrated to play a determinant role in the plant reproductive success, and has a positive impact on it [6]. When will we be able to detect a community-wise process? This is one of my team's objectives, and we developed new kind of models with this aim. Also, authors focus here on plant-pollinator network, but the next step might be to gather every kind of interactions into a huge ecosystem network which we call the socio-ecosystemic graph [4]. Indeed, why to limit our view to certain interactions only? It will take time to grasp the whole interaction network an ecosystem is sheltering, but this should be our next challenge. And this paper of Magrach et al. [6] is a first fascinating step in this direction.

References

[1] Campbell, C., Yang, S., Albert, R., and Shea, K. (2011). A network model for plant–pollinator community assembly. Proceedings of the National Academy of Sciences, 108(1), 197-202. doi: 10.1073/pnas.1008204108   [2] Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A., and Berlow, E. L. (2016). How structured is the entangled bank? The surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. PLoS biology, 14(8), e1002527. doi: 10.1371/journal.pbio.1002527   [3] Gaucherel, C. (2019). The Languages of Nature. When nature writes to itself. Lulu editions, Paris, France. [4] Gaucherel, C., and Pommereau, F. Using discrete systems to exhaustively characterize the dynamics of an integrated ecosystem. Methods in Ecology and Evolution, 10(9), 1615-1627. doi: 10.1111/2041-210X.13242   [5] Bennett, J. M. et al. (2018). A review of European studies on pollination networks and pollen limitation, and a case study designed to fill in a gap. AoB Plants, 10(6), ply068. doi: 10.1093/aobpla/ply068   [6] Magrach, A., Molina, F. P., and Bartomeus, I. (2020). Niche complementarity among pollinators increases community-level plant reproductive success. bioRxiv, 629931, ver. 7 peer-reviewed and recommended by PCI Ecology. doi: 10.1101/629931   [7] Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., and Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature, 458(7241), 1018-1020. doi: 10.1038/nature07950

Reviewed by Nicolas Deguines, 2019-11-26 12:09

All my comments and interrogations have been addressed, and I have no further comments to make on this final version of the manuscript authored by Magrach & colleagues. This study will be a very interesting one added to the field of ecology and pollination ecology.

Revision round #2

2019-11-15

Dear Ainhoa Magrach,

Your preprint, entitled Interaction network structure maximizes community-level plant reproduction success via niche complementarity, has now been reviewed again. The referees' comments and the recommender's decision are shown on PCI site. As you can see, the recommender found your article interesting, but suggests a few (minor) revisions.

We shall, in principle, be happy to recommend your article as soon as it has been revised in response to the points raised by the referees, and in particular the second one. Once the recommender has read the revised version, he/she may decide to recommend it directly, in which case the editorial correspondence (reviews, recommender's decisions, authors' replies) and a recommendation text will be published by PCI Ecology under the license CC-BY-ND.

Alternatively, other rounds of reviews may be needed before the recommender reaches a favorable conclusion. He/she also might decide not to recommend your article. In this latter case, the reviews and decision will be sent to you, but they will not be published or publicly released by PCI Ecology. They will be safely stored in our database, to which only the Managing Board has access. You will be notified by e-mail at each stage in the procedure.

Thanks in advance for submitting your revised version. Yours sincerely, The Managing Board of PCI Ecology.

Preprint DOI: doi: https://doi.org/10.1101/629931
Reviewed by Nicolas Deguines, 2019-10-02 16:01

General comments

I would to thank the authors for their work on the revisions and for the clear Responses to reviewers file provided. Following previous reviews, the revised version is very much improved indeed.   My comments were mostly all considered, so I'll only focus on a few remaining points that I think need to be addressed. Specifically, I have three main remaining concerns: - are results qualitatively similar when using the same max(NODF) 'uncorrected' measure for all sites (instead of a new version for 13 sites but an uncorrected version for 3 sites)?   - I don't understand how GLMM Poisson models with response variables 'average

values of fruit and seed weight' that are (most likely) continuous (and not count-like data) can be used? - is the effect of pollinator richness on Fruit weight and Seed weight (Figure 4) still positive and is it statistically significant (or what's the confidence intervals for the estimates) when removing the site of maximum pollinator richness? More details are for these main points are provided below, along with minor comments. Also, I again had no access to the supplementary materials.

Detailed comments

Abstract I feel like the abstract is lacking a sentence of conclusion or perspective.

Introduction L89: change "these potential pathways" (i.e. nestedness and complementary specialisation) to "these potential attributes"? L109: delete 'of' in 'requires of the delivery'

Methods L199: perhaps change 'Here' to 'With this method,'? L220-223: Are results qualitatively similar when using the uncorrected version of max(NODF) for all sites (not only the three not meeting the assumption of number of links > number of species)? I'm concerned about not using the same calculation for all sites. L239-240: given GLMs were used for site-level analyses and GLMMs were used for species-level analyses, I suggest the following change at L239: "we used generalized linear mixed models (GLMMs) and generalized linear models (GLMs) respectively." L247-248: authors mentioned in their response that there had been an error in the first version of the MS and have corrected it. However, I still don't see how 'the average values of fruit and seed weight [which would almost inevitably produce decimal values, or am I missing something?] fitted to Poisson distributions' could work. Looking at R scripts provided by the authors (e.g. L324-330 in 'removing out obs.R'), I see the use of package glmmTMB when modeling the response variable 'mean.seedw' but Poisson distribution should only work with so-called count data (i.e. positive integer), as stated for example in a glmmTMB related paper: https://journal.r-project.org/archive/2017/RJ-2017-066/RJ-2017-066.pdf. This is an important concern here as I don't understand how this could work and this requires a clarification. L258-259: conversely to 'species-level models', here, average fruit and seed weight were modeled using a

Normal distribution and I agree with this. If it was an error above, did the R code also include an error then (i.e. are the results presented from a Poisson model as in the R code or a Gaussian model?)

Results   L347-349: Was the positive effect statistically significant? I could not access Tables S7-8 (no access to spuuplementary materials). However, when looking at Figure 4, I am concerned about the influence of a single site on the overall relationships (panel A and B). Indeed, the site with scaled pollinator richness at ~2 appears well above and apart from all others and I am worried that any significant effect would disappear without this site (or even become negative in case of effect of pollinator richness on Fruit Weight).   I strongly suggest running again both models (1 and 2) for both response variables without that extreme site and check if results are robust.

Tables   Table 1: I read answers of authors to my previous comment on including or not p-values (especially from mixed-effects models) and confidence intervals. Taking the example of Centrality, the 'large effect' (0.46) seems also associated with large variation (SE = 0.25), and a confidence interval would help to interpret how likely the effect is (especially because SE are not so easily interpretable for non-Gaussian model).   Also, I suspect grey bands in Figure 2-4 represent confidence intervals (they often do as it's easily interpretable). If so, if used in these figures, I think CIs could be added to tables showing model results. This was recently suggested in Conservation Letters (Fidler et al. 2018) to improve statistical transparency. So I still suggest to add 95% confidence intervals.

Figures   Figure 2:   Relative to my previous comment on panel A: points don't go over 1 but the prediction line does. I see two issues with this panel: 1) what is the grey band surrounding the black line? I understand it describes uncertainty around the predicted effect, but is it a confidence interval and at which level (95% or 99%)?   2) given these are results from a glmm based on a binomial distribution (L245-247), neither the estimated effect (the black line) nor its uncertainty (grey band) should be predicted at values >1. For example, when using function predict() or add_ci() (package ciTools) in R on a binomial gl(m)m model, predicted values stay within the boundaries of the its associated distribution.

Reference used above

Fidler, F. et al. 2018. Improving the transparency of statistical reporting in Conservation Letters. - Conserv. Lett. 11: e12453.

Reviewed by anonymous reviewer, 2019-09-04 21:23

The revised version has successfully addressed all of my concerns. I especially enjoyed reading the added discussion of the challenges in linking network and function empirically. I believe this paper presented important advancements on an important topic.

One last suggestion is to expand the figure captions. The current captions are too brief to be understood by someone skipping the papers.

Author's reply:

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Revision round #1

2019-06-17

Recommendation: Major revision   This paper is well written and addresses interesting ecological questions. Yet, as stated by all reviewers, it deserves additional analyses and requires the writing to be more rigorous.

The R3 has made an impressive work by listing all locations at which the authors should add justifications and explanations for readers. Many other precisions are required to follow the study and make it fully reproducible. The R4 added the point of view of an experimenter and suggests to include more details on the measurements (be it in the supplementary materials). R2 has mentioned the possible biases coming from the non-exhaustive sampling of the species network. This point may be generalized by the question of the possible biases of the study. How to reduce the uncertainty coming from all the possible co-variables? Elevation has been mentioned by reviewers, as well as other species (outside the

most common plant sp.) or possible evolutionary effects. In addition, R4 reminds that wind-pollination and self-pollination may bias the study, and should be addressed or at least argued. While R2 mentioned the danger to use the term "prediction", which was not discussed in the paper, R1 mentioned the danger to use the term "mechanistic" when based on correlative studies. Authors have no choice but to remove these terms or to complete their analyses and provide all the details required to convince the readers. As an ecologist, I am also surprised that authors did not comment the possible autocorrelation between sites. Even with a 7km averaged inter-distance in a forested landscape, I guess we can easily hypothesize a partial redundancy between sites due to spatial links. Unfortunately, autocorrelation is one of the most difficult issues in statistics and in particular in GLM models (see Dorman et al. papers). Authors should mention this point, as some other limitations: in particular, GLM are assuming linear relationships whereas ecological relationships are often non-linear. Authors should probably control this issue too. Finally, one point I am particularly aware is that ecological networks are not static at all, although they are often hypothesized so. Even on a short term as in this study, networks may change their structure (not only their fluxes, but also species and species interactions involved) due to frequent local extinctions and invasions. Furthermore, what if a specific relationships is not stable (shifting from positive to negative for a while)? This observation is neglected by most ecologists today and should be at least commented in the discussion.

Overall, this paper seems to be a relevant attempt to include community analysis into more traditional species-centered studies. For this reason, it should be considered. But reviewers mentioned a large number of points that authors should address before recommendation. For this reason, on behalf of PCI ecology, I suggest a Major revision to be sent.

Best wishes. CG.

Preprint DOI: https://www.biorxiv.org/content/10.1101/629931v1

Reviewed by Nicolas Deguines, 2019-05-28 14:18

Download the review (PDF file)

Reviewed by [Michael Lattorff](#), 2019-06-13 19:47

Reviewed by anonymous reviewer, 2019-05-10 22:31

The manuscript by Magrach et al. addresses how community-level plant reproduction is linked with pollinator visitation. The authors found evidence that visitation alone can well explain some pattern, while niche complementarity offers a mechanistic understanding of what ecological process is responsible for determining the differences in reproductive outputs. The paper is clearly written and I find the research questions to be well-defined and of broad interests. As I am a theoretical ecologist, my review would only focus on the theoretical part of the paper.

One major concern I have is the robustness of the results. As stated in the abstract, this paper has focused on community dynamics, which is a broad and complex issue. The authors have only considered niche complementarity and nestedness, and it is unclear to me why the authors picked only these two possibilities. Furthermore, nestedness, as the authors have admitted, may not be a meaningful metric for this study because of the small network size. Therefore, it is not entirely convincing that the authors have proved their main claim. I suggest the authors test other metrics as well, such as the ones proposed in 10.1101/604868. Of course, the authors are free to choose any other metrics, but the bottom line is that more metrics must be tested to convince the readers. Again, I am not doubting that correctness of the findings in the manuscript, but rather encourage the authors to run more tests.

Other major concern I have is the repetitive use of "prediction". One of the central claims of the paper is that `information on simple visitation metrics is sufficient for prediction purposes'. Yet, it falls short in two important aspects. First, regression analysis of in-sample inference does show its predictive power (which has to be based on the out-of-sample forecast). I cannot find any forecast analysis in both the main text and the supplementary material. Second, no R^2 or any other similar statistic is reported. Table 1 and 2 only show if a variable is

statistically significant, but it does not show if the model explains the data well. Please correct me if I miss something,

Minor points:

- Despite the clarity in the flow of the paper, many points need more explanations. For example, What is the definition of the asymptotic number of species (line 135)? What is the Morisita index (line 159)? Please excuse me if these questions are well-known concepts in the empirical field, but I believe adding more explanations would never hurt the paper.
- Title. Maximization may not be entirely appropriate here. I think the authors found evidence that niche complementarity increases plant reproduction success, but not maximizes.
- Line 50. 10.1111/ele.13091 and 10.1002/ecy.2708 are relevant recent works on the importance of indirect interactions via shared resources.
- Line 98. I suggest to remove 'us'.
- Line 127 and many other similar places. Please specify what is the error around the mean. I assume it is standard deviation, but it does not hurt to be precise.
- Line 176-184. Recently 10.1111/1365-2656.12963 have come up with a new algorithm to compute the normalized NODF. Although the difference between the two algorithms appears to be small (10.1111/1365-2656.12964), I suggest the authors to re-compute the normalized NODF for the sake of accuracy (the code can be found in github.com/CHoeppke/maxnodf).
- Line 199. Is it "generalized" or "general"?
- Line 249. Perhaps 'small' is better than 'low'?
- Line 349. I am not sure if James et al. 2012 have claimed that nestedness destabilizes the dynamics. Instead, I think they have claimed nestedness has an almost null effect on the dynamics.

Reviewed by anonymous reviewer, 2019-06-10 21:21

I reviewed the manuscript of Magrach et al. submitted to PCI Ecol. The authors analyze a number of network metrics and their relationship with plant

reproductive success in an attempt to decipher the putative link between network theory and community-level processes. In my opinion, the authors, after extensive fieldwork provide strong evidence that some network metrics, such as centralization and niche overlap, have a significant effect on variation in fruit set and seed number per fruit. However, other metrics often calculated in network-based studies (e.g., nestedness) do not provide significant association with plant reproduction, hence lacking easy interpretation in ecosystem function. This is an interesting result.

My major concern is the complete lack of reference to classic niche and competition theory. Indeed, one can easily interpret the results by omitting network jargon and focusing on the theory developed in the 60s-70s. As I suppose network theory provides a new way to reveal and understand community patterns, I would expect that new patterns should emerge. For example, the observation that "niche complementarity is key in determining differences in reproductive outputs. Indeed, we find that communities where there is less overlap in the niches occupied by pollinator species had greater values of reproductive success, both greater fruit set values and larger numbers of seeds per fruit." (Lines338-341) is entirely accountable by niche and competition theory. Likewise, "At the community level, however, we find that niche complementarity between pollinators, a measure of the overlap in the niches of different species in terms of plant coverage, has an important effect for average fruit set." (Lines 324-327). Again, by definition the extent of resource partitioning among consumers is expected to have a substantial impact on resource dynamics and fitness.

In consequence, I would suggest that in order to improve the quality of their manuscript, the authors should try to reinforce the idea that some findings are in line with seminal advances in competition and niche theory by MacArthur, Pianka, Levin, (e.g., niche complementarity, niche overlap, resource partitioning, competition release, etc).

Reviewed by anonymous reviewer, 2019-05-22 14:53

The paper clearly has several merits. Approaching the functioning of plant-pollination network using species and community based indices in parallel is

clever. The specific objective addressed (exploring the explanatory power of community structure as opposed to more classical diversity indices) is also stimulating.

I however see several limits and needs for additional justifications.

A major limit is, according to me, the mismatch between the main objective, the results, and the conclusions. It is claimed that using community structure will help to shed light on overlooked mechanisms. Yet, those mechanisms are still very unclear after several readings. The study remains correlative and how species interact and what and how potential mechanisms contribute to increase the reproductive success is still very speculative and not really inferred from the results.

The general conclusion, therefore, is I think very expected (eg end of the abstract or L328-335). Indeed, the fact that other metrics (than simple visitation) are needed to understand community level processes is not surprising. But this does not provide in itself "a mechanistic understanding of the pathways through which pollinator diversity translate into changes in reproductive success". Dispersion, competition, trades off between specialization and pollination success, habitat filtering, co-evolution are few among the many processes that could be studied explicitly for such a mechanistic understanding. The metrics in itself are only tools to capture potential processes. In this respect, that additional metrics are needed to capture multiple processes is not making a very strong case.

A potentially key missing information for this framework are the environmental variables. Unless I have missed something 16 sites are described and equated to 16 networks. Therefore the pure effect of site is confounded with the network property. If an environmental co-variate both influence the plant and insect diversity, then part (and potentially most) of the results derive from the spatial distribution of this co-variate, not from any network functioning. It is likely, for instance, that altitude (Figure 1) is both affecting plant and pollinator diversity similarly, driving the correlation between the two components of the network. I was surprised that this is completely neglected.

The paper remains largely inconclusive for many relationships. More precisely, for important descriptors of reproductive success (fruit and seed weight, L282) and for community level, model 1 and 2 ie (ie including simple visitation metrics or information on community structure) are equally good (L291) or model 1 is even better for weight variables. This, together with other intriguing results (eg negative effect of pollinator diversity on fruit set) cast some doubts on the robustness of the conclusion that major gains of information and a better understanding of the mechanisms involved are provided by considering metrics of community structure. It probably does. But the results are not that clear on that perspective. My understanding is that even more confusion is produced.

Overall, it seems that this paper is a nice methodological contribution with an important message: approaching network functioning necessitates integrative descriptors. But the extent to which it helped to access to a better understanding of ecosystem functioning as claimed, is at this stage overstretched and deserve more justifications. My feeling is that the authors need to better delineate their strategy towards a more rigorous test of alternative candidate processes or develop the methodological side of the paper further. But the mixture is I think not really convincing or would deserve more nuanced conclusions and more justifications.

Author's reply:

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