Peer Community In Ecology

The role of phenology for determining plant-pollinator interactions along a latitudinal gradient

Anna Eklöf based on reviews by Ignasi Bartomeus, Phillip P.A. Staniczenko and 1 anonymous reviewer

A recommendation of:

Natasha de Manincor, Nina Hautekeete, Yves Piquot, Bertrand Schatz, Cédric Vanappelghem, François Massol. **Does phenology explain plant-pollinator interactions at different latitudes? An assessment of its explanatory power in plant-hoverfly networks in French calcareous grasslands** *(2019), Zenodo, 2543768, ver. 4 peer-reviewed by Peer Community in Ecology.*
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Increased knowledge of what factors are determining species interactions are of major importance for our understanding of dynamics and functionality of ecological communities [1]. Currently, when ongoing temperature modifications lead to changes in species temporal and spatial limits the subject gets increasingly topical. A species phenology determines whether it

thrive or survive in its environment. However, as the phenologies of different species are not necessarily equally affected by environmental changes, temporal or spatial mismatches can occur and affect the species-species interactions in the network [2] and as such the full network structure. In this preprint by Manincor et al. [3] the authors explore the effect of phenology overlap on a large network of species interactions in calcareous grasslands in France. They analyze if and how this effect varies along a latitudinal gradient using empirical data on six plant-hoverfly networks. When comparing ecological network along gradients a well-known problem is that the network metrics is dependent on network size [4]. Therefore, instead of focusing on complete network structure the authors here focus on the factors that determine the probability of interactions and interaction frequency (number of visits). The authors use Bayesian Structural Equation Models (SEM) to link the interaction probability and number of visits to phenology overlap and species abundance. SEM is a multivariate technique that can be used to test several hypotheses and evaluate multiple causal relationships using both observed and latent variables to explain some other observed variables. The authors provide a nice description of the approach for this type of study system. In addition, the study also tests whether phenology affects network compartmentalization, by analyzing species subgroups using a latent block model (LBM) which is a clustering method particularly well-suited for weighted networks. The authors identify phenology overlap as an important determinant of plant-pollinator interactions, but also conclude this factor alone is not sufficient to explain the species interactions. Species abundances was important for number of visits. Plant phenology drives the duration of the phenology overlap between plant and hoverflies in the studied system. This in turn influences either the probability of interaction or the expected number of visits, as well as network compartmentalization. Longer phenologies correspond to lower modularity inferring less constrained interactions, and shorter phenologies correspond to higher modularity inferring more constrained interactions. What make this study particularly interesting is the presentation of SEMs as an innovative approach to compare networks of different sizes along environmental gradients. The authors show that these methods can be a useful tool when the aim is to understand the structure of plant-pollinator networks and data is varying in complexities. During

the review process the authors carefully addressed to the comments from the two reviewers and the manuscript improved during the process. Both reviewers have expertise highly relevant for the research performed and the development of the manuscript. In my opinion this is a highly interesting and valuable piece of work both when it comes to the scientific question and the methodology. I look forward to further follow this research.

References

[1] Pascual, M., and Dunne, J. A. (Eds.). (2006). Ecological networks: linking structure to dynamics in food webs. Oxford University Press.   [2] Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology, 13(9), 1860-1872. doi: 10.1111/j.1365-2486.2007.01404.x   [3] de Manincor, N., Hautekeete, N., Piquot, Y., Schatz, B., Vanappelghem, C. and Massol, F. (2019). Does phenology explain plant-pollinator interactions at different latitudes? An assessment of its explanatory power in plant-hoverfly networks in French calcareous grasslands. Zenodo, 2543768, ver. 4 peer-reviewed and recommended by PCI Ecology. doi: 10.5281/zenodo.2543768   [4] Staniczenko, P. P., Kopp, J. C., and Allesina, S. (2013). The ghost of nestedness in ecological networks. Nature communications, 4, 1391. doi: 10.1038/ncomms2422

Revision round #2

2019-10-26

All comments have been addressed and the manuscript reads well. There are only a few minor comments to address from one of the reviewers.

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Reviewed by anonymous reviewer, 2019-10-13 20:29

Review of revised "Does phenology explain plant-pollinator interactions at different latitudes? An assessment of its explanatory power in plant-hoverfly networks in French calcareous grasslands" by Manicor et al.

I have read the revised manuscript and authors' response letter. I appreciate the authors' thoughtful response to my comments and their edits to the manuscript. I have no further comments.

Reviewed by Ignasi Bartomeus, 2019-10-23 19:38

Thanks for the detailed response. The authors clarified all my comments and I especially appreciate the cross-validation analysis added. In this new version, I only spotted a few editorial errors.

Line 39. maybe is better "phenological" Line 455. Something is misisng before "evinces a clear effect of PO" Fig 2 and 3 species names can be spelled out for publication. It will look nicer. Fig S1, I only spot 5 red dots.

Best,

Author's reply:

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Revision round #1

2019-03-14

Dear authors, Thank you very much for submitting your preprint to PCI Ecology. Two reviewers have now commented on your preprint and they were both positive to the research questions and your scientific approach. I indeed do agree with this. But both reviewers also have some comments and suggestions of ways to improve your contribution. When reading the preprint there were two issues I find crucial to address. First, I experienced that there was a lack of details regarding the description of SEM, and it seems like the authors assume the reader is already quite familiar with the methodology. I think this will usually not be the

case. Therefore, I think it is necessary to add some text and go a bit deeper into explanations of this (this is also a comment from Reviewer #1). Second, to me (as for Reviewer #2) the connection to phenology seems a bit secondary As I see it there are to ways to address this; either make the connection to phenology much more clear and stronger in the text or to actually turn around the focus more towards the method on estimating probabilities of occurrence of interactions for informing models. In addition to these comments the reviewers have additional suggestions that the authors should address in order to further improve their contribution. As such, I would like to invite the authors to submit a revised manuscript before a decision is made about a recommendation.

Best regards, Anna Eklöf .

Reviewed by Ignasi Bartomeus, 2019-02-25 11:18

The paper shows an interesting approach to model species interactions and applies such approach to 6 plant-pollinator networks using species abundances and phenology as starting points. Overall the paper is well written and the approach sound (but I am no expert in Bayesian statistics) and I have a general comment and a few minor questions I would like to understand better. My general comment is that despite the paper is easy to read, it may benefit from a more clear structure. For example, the title highlights "latitude", but with only 6 data points (clustered in 3 regions), the authors do not make a direct analysis of how latitude affect interactions. This is fine, and I agree on not asking to much to the data, but then, the effect of latitude can be de-emphasised. On the other hand, for me, the strength of the paper is on focusing on predicting plant-pollinator interactions. As noted by Olito and Fox (cited by the authors), null models often predict the right network structures, but not pairwise interactions. My own work (Bartomeus et al. 2016, also already cited) moves into that direction by assessing species probability of interaction based on trait-matching. Here, the authors model not only probability of interaction, but also visitation frequency. I would focus the discussion around this core issue, and not around phenology (which is just one more predictor, and with lower power than species

abundances). This is just a suggestion, and nothing that should be changed if the authors prefer to focus on phenology.

Minor questions: - Why focusing only on hoverflies? This is ok, but having also the Bee data, sounds as you are missing the opportunity to test a more complete dataset. Maybe a justification in methods would help the reader understanding the choice.

- Why using Sirph the Net for flies phenology? This is something that I am worried about. Hoverfly phenology changes with latitude, yearly (depending on weather) and with microclimatic conditions (site specific). Using a general species phenology may introduce large biases, specially as plant phenology is estimated locally. For your realized networks, I would suggest using directly observed phenology. You can approximate species observed phenology to a normal distribution and estimate start and end dates if you want to be more precise.

- How good are the Best models? The LOO approach is a nice way of testing the models, but I would like to see the predictive power yielded in a clear way. It is fine to select the best models, but I would like to know how good are those models. For example, both Olito and Fox and Bartomeus et al. show that the predictive power for predicting plant-pollinator interactions is quite poor. Are your models being better descriptors of those interactions? Or do you still observe a large unexplained variability? If the models are good, I would challenge the authors to make a hard test on the models and use parameters calculated in one network to predict the second one based on abundances and phenology overlap. This is a really hard test on the models, and I don't expect to achieve high predictability, but would be super cool if they did.

- What about false absences? If I am right, your model assumes that the absence of interaction are true absences, but we know there is sampling error (See my own work cited above, but also Weinstein, B. G. and C. H Graham. Traits, abundance, and the detectability of species interaction networks. Foodwebs. 2017). A caveat in the discussion would be good to add.

- Specialization and modularity analysis. This is a neat analysis using state of the art methods, but it's difficult to integrate with the main question about predicting species interactions. I have mix feelings weather suggesting to remove it or not, so I left it to the authors to think if it strengthen the ms, or can be a distraction to the main point.

In line comments:

line 38-39: I am not sure the commas are needed. line 56: add space before (Hutchings) line 79: I would replace "the output" by something more specific. e.g. the probability of interaction? or the predicted visitation rates? lines 81-82: There are already a few examples and this do not add much to your intro, so I would remove it. lines 88-89: "as well as pollen or nectar specialists". This is unclear, I would remove this part or explain better. As far as I know there are almost no nectar true specialists in any taxa. line 90: "serial specialized diets". I would suggest looking for another word to describe this. At least I was not familiar with this term. line 107: By using the work "pollinator" you create the expectation all pollinators would be considered. line 138 (and elsewhere): Unify hoverfly - syrphids. line 141-146: This can be much clearly stated. You DO have proof of interactions with fabaceae, right? Then, just state that. line 158-160: This is interesting, but It took me a while to grasp. Can you clarify that you used d-value and dmax-value from the function, but calculated d' manually (this is what you did, right?) line 181: "their" of the plants or of the hoverflies? Clarify. line 182: Why average and not sum? line 195: I was not familiar with the term dyad. Consider "pairwise interaction" or explain it on the first time mentioned. line 206: Did you considered Ah and Ap to could affect also probability of interaction? line 226: Thanks for making the code available! line 229: "that included all combinations between 0 and 4..." line 265; Can this be an artefact of using Syrph the Net for estimating hoverfly phenology? line 293: "suggesting". You know the effect size, right? Then would be better to state it, rather than referring to a "suggestion". line 303-305: But your study do not fix this, but circumvent the problem by focusing on probability of interaction, rather than on overall structure. I would suggest to be clear on this. Other studies have focused also on pairwise interactions and both approaches are complementary. Figure 2: Phenology and

blocks are not that congruent as first sight (e.g. first two columns have contrasting overlap, but belong to the same block). Can you formally test for this?

Best, Ignasi Bartomeus

Reviewed by Phillip P.A. Staniczenko, 2019-02-06 16:05

Review of "Does phenology explain plant-pollinator interactions at different latitudes? An assessment of its explanatory power in plant-hoverfly networks in French calcareous grasslands" by Manicor et al.

The authors use Bayesian Structural Equation Models (SEMs) to study the explanatory power of phenology and species' abundances for understanding the structure of six plant-pollinator networks that span a latitudinal gradient. In their SEMs, they propose phenology and species-specific random effects for explaining the presence of an interspecific interaction and phenology and insect and plant abundances for explaining the intensity (number of visits) of an interspecific interaction. They find that species' abundances were able to explain interaction intensity in most networks but results were more variable for phenology, with greater explanatory power at higher latitudes.

The manuscript describes a nice application of SEMs that could---and should---be extended to include more realistic ecological processes and be applied to a wider range of ecological communities. I have three major comments: (i) provide more description of SEMs in the introduction and methods, (ii) consider other model structures, such as zero-inflated Poisson models, and (iii) add additional discussion of the result that insect abundance provides the strongest explanatory power, in order to avoid critiques of circular reasoning. I expand on these major comments, below, and offer some minor comments.

(i) Provide more description of SEMs

The introduction should include some background and references on SEMs and Latent Block Models. Then, in the methods section the authors should describe the general principles of SEMs and provide definitions of "latent variables" and "latent tables" and how they implement them in their SEMs. Please also provide

clear definitions of the parameters E_i *and* E_j: are they categorical variables (L202, L208) or numerical species' degrees (L393)?

The authors should also consider mentioning two other approaches to modelling network structure: Staniczenko et al. (2017) and Cirtwill et al. (2018). This second reference in particular would also be useful for informing other possible SEMs, as detailed below.

Staniczenko, P.P.A., Lewis, O.T., Tylianakis, J.M., Albrecht, M., Coudrain, V., Klein, A.-M. & Reed-Tsochas, F. (2017). Predicting the effect of habitat modification on networks of interacting species. Nature Communications, 8, 792.

Cirtwill, A., Eklöf, A., Roslin, T., Wootton, K. & Gravel, D. (2018). A quantitative framework for investigating the reliability of network construction. bioRxiv 332536, doi: https://doi.org/10.1101/332536

(ii) Consider other model structures

In addition to phenology, the authors consider species-specific random effects for explaining the presence/absence of an interaction and insect and plant abundances for explaining the number of visits. This model structure does not really make any strong statement about what ecological processes distinguish the presence of an interaction from its intensity. For example, one could consider presence/absence as being related to the concept of "forbidden interactions" (i.e., some interactions are not possible whatsoever) or, alternatively, are simply absent due to too low abundance of interacting species to be observed. Thus, the presence/absence modelling component could be based on species' traits (as the authors themselves mention, L373) or also include species' abundances as parameters. Additionally, the authors could consider different model structures, such as zero-inflated Poisson models (and replacing the Poisson distribution with a negative binomial distribution).

It is worth investigating if the reason phenology is not found to consistently and strongly explain network structure (P13) is because the authors' SEMs don't reflect the possibility for "forbidden interactions" or allow for observational limitations associated with low species abundance.

(iii) Discuss results for insect abundance

The authors suggest that "the most important [factor] affecting pollinator visits was insect abundance" (L311). But their measure of insect abundance was calculated from visitation data (L180). The authors need to mention this and argue how this does not fall into the logical fallacy of circular reasoning. It is also worth stressing that relative abundance estimates calculated from visitation data (L180) are likely to differ from those from non-visitation-based sampling methods.

Looking at Figures 2 and 3, the maximum number of visits is quite low and most interactions are only represented by 1 or 2 visits. How might this limited range of visitation intensity affect results? Also, is this limited range a fair reflection of the expected distribution of visits in these communities?

Finally, the authors should add in the results section how their results correlate with latitude, to foreshadow the more speculative discussion they provide in the discussion section.

Minor comments

L56. Space missing after "pollination"

L90. Clarify what "generalisation" is referring to---at the species level?

L114. Briefly describe the NATURA 2000 network

L126. Briefly describe Braun-Blanquet coefficients and provide a reference

L158. The authors write that they "did not use the d' values provided by [the bipartite] package" but they present values (L259)---did they get values from somewhere else?

L163. I suggest rewriting this sentence to: "Modularity optimization can help identify strong, simple divisions of a network into relatively independent sub-networks by looking for highly interconnected sub-networks."

L203. Define "degree"

L231. Briefly describe the "leave-one-out cross-validation criterion"

L241. The authors need to mention that they also refer to W_H values as "evidence ratios" (e.g., Table 2)

L248. The authors should present connectance values (binary interactions / #species) as well as the maximum number of visits recorded in each network

L295. I suggest rewriting this sentence to: "Latitude affects seasonality, with advancing species phenologies at higher latitudes, and thus, latitude can be a limiting factor..."

L311. I suggest replacing "effect" by "factor"

Author's reply:

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