Sujet :

PCI Ecology: Decision concerning your submission

De :

PCI Ecology Contact <contact@ecology.peercommunityin.org>

Date :

15/03/2019 à 08:16

Pour :

<natasha.de-manincor@univ-lille.fr>

Dear Natasha de Manincor,

Your preprint, entitled Does phenology explain plant-pollinator interactions at different latitudes? An assessment of its explanatory power in plant-hoverfly networks in French calcareous grasslands, has now been reviewed. The referees' comments and the recommender's decision are shown below. As you can see, the recommender found your article very interesting, but suggests certain 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.

When your revised article is ready, please:

1) Upload the new version of your manuscript onto your favorite preprint server;

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4) Write, copy/paste or upload (as a PDF file) your reply to the recommender's and reviewers' comments by clicking on the 'Write, edit or upload your reply to recommender' button. You can also upload (as a PDF file) a revised version of your preprint, with the modifications indicated in TrackChanges mode;

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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 In this latter case, the reviews and decision will be sent to you, but they will not be published or publicly released by PCI Ecology.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

article picture

Does phenology explain plant-pollinator interactions at different latitudes? An assessment of its explanatory power in plant-hoverfly networks in French calcareous grasslands

Natasha de Manincor, Nina Hautekeete, Yves Piquot, Bertrand Schatz, Cédric Vanappelghem, François Massol

Submitted by Natasha de Manincor 2019-01-18 19:02

Abstract

For plant-pollinator interactions to occur, the flowering of plants and the flying period of pollinators (i.e. their phenologies) have to overlap. Yet, few models make use of this principle to predict interactions and fewer still are able to compare interaction networks of different sizes. Here, we tackled both challenges using Bayesian Structural Equation Models (SEM), incorporating the effect of phenology overlap, in six plant-hoverfly networks. Insect and plant abundances were strong determinants of the number of visits, while phenology overlap alone was not sufficient, but significantly improved model fit. Phenology overlap was a stronger determinant of plant-pollinator interactions in sites where the average overlap was longer and network compartmentalization was weaker, i.e. at higher latitudes. Our approach highlights the advantages of using Bayesian SEMs to compare interaction networks of different sizes along environmental gradients and articulates the various steps needed to do so.

Round #1

Author's Reply:

Decision by Anna Eklöf, 2019-03-14 13:56

Manuscript: 10.5281/zenodo.2543769

Revision round #1

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).

We thank the Editor and Reviewer 1 for the suggestion. We added more details about the SEM methodology in the introduction and in the material and methods paragraphs.

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.

We thank the Editor and Reviewer 2 for this comment. Our view is that the effect of phenology is not secondary to estimate the number of the probability of interaction, and our objective was not to make a comparison between the effect of phenology overlap vs. the effect of abundance, but rather to test whether PO could improve a simple model only based on abundances. In other words, we used insect and plant abundances to make a more "solid" null model than the model with no explanatory factors. The fact that all the best models included PO means that its effect is not due to chance. We now make this connection clearer in the main text.

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.

We thank the Editor and the reviewers for all the suggestions. We replied to them in this document and we will submit the revised version.

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.

We thank the reviewer for the suggestion. In this study we cannot test directly how latitude affects interactions, due to the low number of sites. We did not use the latitude as an explicative variable, but to clarify that the data used in this study were not collected in the same site/region. We considered that latitude can influence the network diversity and thus it might influence indirectly the probability and the intensity of interaction that we tested in this study.

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.

We thank the reviewer for this suggestion. In this study we used the species phenology and phenology overlap to test if it could influence pairwise interactions. Even if phenology alone is not sufficient to explain the probability and the intensity of the visits, its explanatory power change along the gradient, which is a new result that we want to highlight. We agree with the reviewer that the visitation frequency is also a unique asset, but it was not the core of the study.

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.

We focused on hoverflies because at the moment of the study we did not have the identification at the species level for bee data. One of our perspective is to apply this model to bee data.

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.

We did not use only the Syrph the Net phenology, but we completed the phenology that we observed in the field (based on the sampling) with information on phenology found in the Syrph the Net database. We preferred to complete the phenology to avoid the problem of data circularity, *i.e.* phenology explains all the visits. For this reason, our estimates of the effect size of PO are quite conservative – in reality, insect phenology could be locally shorter than the duration we used, and PO could thus have had more leverage on interaction probability and visitation intensity in the best models.

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.

We thank the reviewer for the suggestion and we accepted the challenge. We performed the predicted power analysis to compare sites which are in the same region and to compare the results for the species which are shared by the two sites. We used the best models (LOO < 4) found for each site to predict the interactions in the other site, using a simple threshold on probability of occurrence to find which interactions should be deemed as existing. We observed that the AUC values, both for the self-validation and the cross-validation, were higher than 0.5, thus our results are better than predicted by chance. We included the methodology in the materials and methods paragraph and we briefly presented the results in the main text. However, the accuracy tables (reporting sensitivities, specificities, etc.) are presented in the supplementary materials since it was not the main objective of the study.

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.

In our study we only considered as true absence the lack of phenological coupling between species (i.e. forbidden links). We added in the discussion an explanation about true/false absence considered in the model as request by the reviewer.

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.

We thank the reviewer for this comment. We used these indices to give information about the network structure as most network papers do. As reviewer #2 suggested, we also integrated the connectance values and the maximum number of visits recorded in each network in the main text.

In line comments:

line 38-39: I am not sure the commas are needed.

We removed the commas.

line 56: add space before (Hutchings)

Done.

line 79: I would replace "the output" by something more specific. e.g. the probability of interaction? or the predicted visitation rates?

We replaced "output" with "the probability of interaction" as suggested.

lines 81-82: There are already a few examples and this do not add much to your intro, so I would remove it.

We removed the sentence as suggested.

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.

We modified the sentence as suggested. We replaced with "i.e. from being pollen generalists to specialists".

line 90: "serial specialized diets". I would suggest looking for another word to describe this. At least I was not familiar with this term.

We replaced the sentence with "individually specialized diet".

line 107: By using the work "pollinator" you create the expectation all pollinators would be considered.

We thank the reviewer for the suggestion and we replaced the word "pollinator" with "hoverfly" in the main text.

line 138 (and elsewhere): Unify hoverfly - syrphids.

We replaced syrphids with hoverfly as suggested.

line 141-146: This can be much clearly stated. You DO have proof of interactions with fabaceae, right? Then, just state that.

We modified the sentence to state the interaction between hoverfly and Fabaceae.

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?)

Yes, it is what we did. We modified the sentence to clarify the methodological approach to calculate d' manually.

line 181: "their" of the plants or of the hoverflies? Clarify.

In this sentence "their" stands for plants.

line 182: Why average and not sum?

With the sum, the score gives an idea of mean abundance (when present) x phenology length, which is going to be much correlated with all phenology variables already used in this manuscript. With the average, we obtain an estimator of mean abundance when present which ought to be independent from phenology length (in principle and provided detectability is not pathologically linked with phenology and abundance).

line 195: I was not familiar with the term dyad. Consider "pairwise interaction" or explain it on the first time mentioned.

We replaced the term "dyad" with "species pair".

line 206: Did you considered Ah and Ap to could affect also probability of interaction?

No, we did not consider that, because we considered that the species abundances could have a stronger effect on the number of visits rather than on the interaction probability.

In theory, this could be considered but it would radically change the interpretation of the "probability of interaction" part of the model. Currently, this part is only concerned about true/ideal interactions explained by environmental/ecological factors. If we added abundances to its predictors, this model would then be construed as a model of "actual interactions", taking into account the contingencies of low/high local species abundances.

line 226: Thanks for making the code available!

You are welcome!

line 229: "that included all combinations between 0 and 4..."

We added "all combinations" to the sentence as suggested by the reviewer.

line 265: Can this be an artefact of using Syrph the Net for estimating hoverfly phenology?

It could be an artefact, but we used Syrph the Net to complete the phenology of hoverflies recorded in the field (based on the sampling) since for some species we had "presence gaps" among months. If, for example, a species was captured in April and then in June, with Syrph the net we completed its phenology by adding the month of May and the other months indicated (e.g. until August). However, we did the same thing with plant phenology, using the entire recorded phenology (based on the botanical inventory) and not only the moment which a plant species was visited by an insect during the sampling (i.e. we considered the plant presence independently from the fact that it was visited by an insect). We preferred to use the entire species phenology (i) to avoid methodological problem and data circularity in our model when we predicted species interactions and (ii) to rely on conservative estimates of the effect of PO on interactions and visits – given the rarity of interactions between two random species, if an effect is detected with a longer phenology, it should be even stronger in reality.

line 293: "suggesting". You know the effect size, right? Then would be better to state it, rather than referring to a "suggestion".

We remove the term "suggesting" and replace with "showing".

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.

We thank the reviewer for the suggestion and we added a sentence to explain that we focused on the probability of interaction.

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?

We tested the congruence between the classifications given by node membership (obtained using the latent block model (LBM) methodology explained in the main text) of the visit matrix and each of the 10,000 simulated phenology overlap matrices, using the normalized mutual information (NMI) method. The distribution of NMIs were used to compute the probability (p-value) that the NMI between the visits and PO clustering was significantly lower than expected from the null model. We observed that in the two southern sites the p-value was significantly inferior to the null model expectation, which means that the classification induced by latent blocks was significantly different between the visits and the phenology overlap matrices. These results confirm the fact that we did not find any effect of PO on the number of visits in the two southern sites (lines 335-337). In the Figure 2 we can then observe that the blocks of visits are not congruent with longer phenology overlap.

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.

We thank the reviewer for the suggestions and we replied to his comments below.

(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.

We thank the reviewer for the suggestion. We included some background and references of SEM and LBM in the introduction and we describe the general principle of SEM in the methods section.

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

We clarified the definitions of the parameters (and we removed the term "degree").

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

We thank the reviewer for the suggestion. We now mention the two papers in the introduction.

(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.

Thank you for the suggestion. Actually, the problem with using other model specifications, such as zero-inflated Poisson for instance, is twofold: (1) they would change the balance of the ecological processes captured by the two parts of the model; (2) they would lead to statistical problems (identifiability). For instance, with the ZIP model for visitation intensity and Bernoulli for interactions, there would be two ways of getting zeros in the number of visits (either set the probability of interaction very low in the Bernoulli or set the probability of zero very high in the ZIP). Because the ZIP has one more parameter than the Poisson, it is arguably possible then to tune all ZIP (for all dyads) in such a way that you could simultaneously assign 1 to all probabilities of the Bernoulli (i.e. remove the interaction part of the model), and yet recover the same predictions. In other words, the extra parameter of the ZIP would be very much redundant with the probability of the Bernoulli, and thus comparing the two parts of the model would lead to comparing artefacts borne out of different parameterizations.

(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.

Given that insect abundances are given by visitation data (and thus reflect a "cumulated number of interactions"), the most straightforward intuition about interactions is that they should positively depend on these abundances and we can interpret our findings using this as a "null model" of sorts. We do not over-interpret the fact that this factor is the most important because it is intuitively expected; however, the fact that another factor such as phenological overlap can add statistical fit on top of what is predicted by abundances is worth being discussed.

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?

Figures 2 and 3 are just examples of the LBM clustering and the other sites are presented in the supplementary materials (Fig. S2-S5). In general, in all our sites we recorded more than 10 visits at least for one pair of insect and plant species. The two southern sites showed the lowest numbers of visits (12 in the site of F and 10 in the site of BF, Fig. 2 and S2). The two sites in Normandie showed the highest number of visits, with a maximum of 22 visits recorded (for two pair of hoverfly-plant species) in the site of CG (Fig. 3) and in the site of Falaises the maximum number of visits was 47, which is quite high. Thus, we did not think that the presence of 1 or 2 visits could affect the results of the model and indeed is a fair reflection of the expected distribution of visits in the community. However, as in most studies, some links could have been missed during the sampling.

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.

In our study we only have 6 data points (clustered in 3 regions) so we could not make a direct analysis of how latitude affect interactions. As the first reviewer suggested we prefer to de-emphasise the effect of latitude.

Minor comments

L56. Space missing after "pollination"

Done.

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

We clarified the sentence and we modified "generalisation" with "generalist behaviour".

L114. Briefly describe the NATURA 2000 network

We integrated a brief description of the network NATURA 2000 in the main text.

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

We provided a brief description of the method and three references (Van Der Maarel 1975, 1979; Mucina et al. 2000). The description of the coefficients is provided in the main text and the converted values in the Table S1.

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?

We used d-value and dmax-value from the function dprime, but we calculated d' manually. We modified the sentence in the main text.

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."

We modified the sentence as suggested by the reviewer.

L203. Define "degree"

We provided a definition in the main text.

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

We provided a briefly description in the main text as request by the reviewer.

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

We replaced the term "evidence ratios" with "effects weight" and "wH". It was actually a small mistake since we initially envisaged using evidence ratios and then switched to effect weights because all tested effects are equally present in the set of all tested models (using evidence ratios is only relevant when this is not the case, e.g. when only a subset of interactions between explanatory variables are considered).

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

We presented the connectance values and the maximum number of visits as request by the reviewer at the beginning of the results section.

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..."

We modified the sentence as suggested by the reviewer.

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

We replaced the word "effect" with "factor" as suggested.