

Reviewer comments to authors

General comments

The manuscript authored by Magrach A. and colleagues investigates the drivers of plant reproductive success in natural ecosystems of SW Spain using a plant-pollinator network approach. Specifically, this manuscript looks at whether ‘simple’ metrics (pollinator richness, number of visits) can be used to predict reproductive success or if more complex metrics informing of the network structure can be more informative and provide clues to the mechanisms involved in the patterns observed. For this, they use their own dataset collected from 16 sites in SW Spain, each surveyed for 7 visits in 2015. The dataset is impressive and seems adequate for the aims of this study. The research presented here is quite novel as looking into how exactly the structure of plant-pollinator networks affect plant reproductive success in natural plant communities, which would allow to empirically validate previous theoretical and experimental works on this issue.

Overall, this manuscript is very interesting; I am largely positive about both the questions asked and the data used, and I am convinced it will be a nice addition to the literature. However, on a less positive note, there are issues that need to be addressed. There is some substantial work to be done to clarify a number of different points (e.g. reducing the possible confusions to readers between overlap and complementarity, statistical analyses: e.g. data transformation and choice of distribution family for inclusion in glmm’s) and to provide more details (e.g. choice of focal plant species for measuring reproductive success). I also thought the discussion did not address all the points raised by the results. The abstract states that simple metrics can be used for prediction purposes but I felt this was not enough backed up by both the results presented and the discussion, and would need more arguments in the discussion. I below provide detailed comments that I hope will help authors improve this manuscript.

Detailed comments

Title

I wonder if the title could be improved because when reading ‘Interaction network structure maximizes’, I thought: ‘what exactly in the structure?’.

Perhaps: “Niche complementarity in interaction networks maximizes community-level plant reproduction success”?

Abstract

L29-30: After reviewing the paper, I feel that this result (simple measures can be used for predictive purpose) is not enough backed-up and lacks specifics. Is it more suitable than complex ones or the latter do better? What’s the direction of the prediction? What are the implications (e.g. can we infer plant reproductive success from pollinator richness estimates based on captures from pan traps?) ? I provide complementary comments about this below.

Introduction

L58: change ‘but also they found that community structure had’ to ‘but community structure also had’

L75-78: I suggest being more specific here about exactly what is known from the literature on network structures and pollination. For example, authors wrote that ‘a prevalence of nested structures’ and ‘presence of asymmetric specialization as a pervasive feature’ shape mutualistic interactions: how exactly? What are the effects of nestedness and asymmetric specialization on mutualistic interactions? More stable or robust to extinctions? More efficient plant pollination? Also, there would be a need to define nestedness (and perhaps asymmetric specialization? It may be self-explanatory, I’m not sure).

L66-83: In this paragraph overall, I would suggest using less wordings such as ‘considerable understanding’ and instead try to be more specific on what is known. That would help readers understand what is not known and thus what’s interesting in the current MS. For example, L81 mentions it’s time to ‘use this knowledge’ but the paragraph does not provide clear facts. Also, it should be here emphasized that a strength of the paper is to answer questions with empirical data from natural communities (compared to theoretical or experimental, as said L336-338). Also, how is the approach different from papers cited at L337-338 – Valdovinos et al. 2016 or Poisot et al. 2013)

L87: change ‘at Mediterranean’ to ‘in Mediterranean’.

L88: what is the meaning of ‘area of influence’ of the Donana National Park? Is it a legal concept (e.g. outside the core area of the park but still has to be managed according to some rules from the parks) or do you mean ecological influence (e.g. not far from the park)?

From start to L97: I think I got confused because I understood that authors use ‘community’ and ‘network’ for the same meaning, as on L97 mentioning ‘community structure’. But from paragraph L66-83, nestedness and asymmetric specialization are characteristics or ‘attributes’ of interaction networks. I would suggest homogenizing, using rather network than community (the latter often used as a synonym of assemblage, e.g. bird assemblage or bird community).

L96-97: I think that about here somewhere, it should be clear to readers what measure of network structure authors will use.

Methods

L109: ‘area of influence’ again

L113: by ‘recorded’, do you mean ‘captured’?

L114: ‘legitimately’ would need a definition here (the one used by fieldworkers when capturing pollinators). Indeed, there can be bumblebees robbing for example. However, how were considered flies from the Bombyliidae family or diurnal moths from the Sphingidae family for example? The two can take nectar from flowers without even landing and thus often without getting pollen grains on their bodies.

L115-117: How did authors know before the fieldwork what were the 19 most common species across the study area? Also, how could authors make sure they were following three individuals from the same species or that those three actually differed from other individuals without capturing them and identifying them? Finally, what information was recorded during those 3 minutes of focal observation / what was the purpose?

=> update: I understand know that *plant* individuals were followed, not pollinators. Authors should precise this. Also, the final comment remains: precise the information collected during the 3 minutes and how it was used. Were the ‘pollinator diversity’ and ‘total number of visits’ taken from those three minutes of observation?

L117-121: If not said later, readers would be interested in knowing how many such opportunistic interactions were recorded and included in the network (perhaps as an average % per site).

L109-125: This paragraphs lacks the ‘time of day’ information regarding sampling. Was each site sampled both in mornings and afternoons?

L127-132: I suppose there were more than 19 plant species in each transects. What are the species sampled? How were they chosen? I am not a plant expert but for practical reason (e.g. plants with long and differential flowering – not all flowers at the same time, i.e. fruits present over several weeks), could the choice of plant being sampled somehow bias the results if only some types of plants are sampled and appear to be those more visited by particular visitors? What about self-(in)compatibility of these plants?

L153: I had trouble understanding ‘which covers’. Change to ‘which is an estimation of / which measures’ maybe?

L179-184: This sentence needs to be divided.? Perhaps stop the first sentence after first mentioning of ‘NODFc’. Then starts with ‘NODFc is calculated as:’

L198-199: it is unclear to me to what refer ‘both at the species and the community-level’. The way it is, I thought it applied to reproductive success but in section ‘plant reproductive success’, there is no mention of a ‘community-level’. Then I suppose it may be the network metrics at species and community-level? But then, that would mean that L197 uses ‘community structure’ to encompass both species-level metrics and community-level metrics (see also my previous comments on using ‘community’ or ‘network’). This should be clarified.

L202-204: ‘All response variables’: so these are ‘reproductive success’, correct? I suggest having two sentences: the first specifying what are the response variable, and the second explaining that prior to be analyzed, each species reproductive success values were scaled (across sites then?).

L205-206: some paper present results in terms of both richness and diversity (e.g. Shannon index of diversity) so here I strongly suggest sticking to richness (i.e. the number of species, and thus using ‘Pollinator richness’) if this is what is used by authors, and not use ‘Pollinator diversity’.

L198 & L205: after reading the next paragraphs, data are first analyzed at the individual level: all individual values from all species are included in two models: model 1 and model 2. Then, shouldn’t it be ‘Models analyzing data at the individual level’ instead of ‘At the species level’ which I first understood as one model per species.

L208-209: what do the authors mean by ‘In this case’ ? Model 1? Model 2? Species level models 1 and 2?

L211-214: This should arrive prior to the explanatory variables: indeed, readers need to first understand that response variables include values at the plant individual level, taken from different species in different sites. Without this, the need for the random effect (L208-209) is unclear.

Also, I'm not sure I get what means the 'average values of', why not simply 'average fruit and seed weight'? Actually, a previous section mentioned 'the average seed weight per fruit'. Some clarifications are needed here.

Finally, Poisson distribution works with strictly positive integer values; averages of weights that had first been scaled should produce some negative values and decimal values. Unless I misunderstood the verb 'scaled' that I took as 'standardized' (i.e. subtracting the mean to each value and dividing by the standard deviation ; <https://www.rdocumentation.org/packages/base/versions/3.6.0/topics/scale>).

See also comments about L229 for the 'binomial' model with data that had been scaled (i.e. about ranging from -1 to 1 in my definition of scale, resulting from the above mentioned R function).

L220: 'average reproductive success' => authors mean 'per site', correct? I think here it needs to be clarified.

L229: is 'normalized' used as 'scaled'? or did the authors normalized to a given range (as done by <https://www.rdocumentation.org/packages/BBmisc/versions/1.10/topics/normalize>)? Perhaps this should be clarified to become obvious to readers what was done by scaling or normalizing, especially to understand which (g)lmm's were used. For example, I questioned above the use of the Poisson distribution and I realize now I should also have questioned the use of the binomial family given that values had been 'scaled', which I took as resulting to values approximately being between -1 and 1.

L256-258: different parameters can be extracted from a model and authors should precise to which parameter their expectation applies. I would suppose it's the beta estimates (i.e. the slope of the effect of the network predictor on equity).

Statistical analyses: In all models, authors should mention how assumptions were checked and if they were met; additionally, Variance Inflation Factors [see (Zuur et al. 2009)] should be computed to check collinearity between explanatory variables, especially perhaps between "niche overlap" and "niche complementarity" which I expect to be negatively correlated, somewhat strongly?

Results

L262-263: '1472 pollinator individuals belonging to 57 species of plants' appeared weird to me. I suggest instead '1472 plant-pollinator interactions involving 57 plant species and 277 pollinator species'.

L264: are % corresponding to species or abundance? Perhaps provide both?

L291-292: this is of debate I suppose, but I tend to conclude the contrary: the added complexity is useless because it does not improve the AIC, and therefore the simpler the better. Instead of choosing between the two models, did authors consider starting with a full model (i.e. model 2) and prune out explanatory variables with no significant effects? Or simply keeping it whole so that each estimate is adjusted for other variables. That would also simplify the method to not have to present two types of models. What I suggest is only valid if there is no collinearity among predictor variables; if there was then, the approach of the authors must be revised as well.

L291-296: typically, here and given Figure 3, could it be that niche complementarity and pollinator diversity are negatively correlated, so much that having them in the same model is not possible? This needs to be checked by computing VIF values.

L297: Is the effect of total number of visits in table 2B significant? It's not in bold there.

L300-303: I was not able to find Supplementary materials and could not check see those results. After reading the discussion, I strongly recommend moving those results in the main text. They are crucial to discuss the unexpected results of pollinator diversity and total number of visitation being negatively associated to fruit set.

L308: 'However' is misleading and confusing here and seems not appropriate with 'also' just after. If there was an expectation, either it should have been clearer before or perhaps authors can shortly re-state it here. Or if authors want to insist on the fact that it's similar to the effect from pollinator diversity on fruit set, then I suggest stating it here simply.

Additionally, information is missing: model 1 is best, but are there any significant effects besides pollinator species diversity using the 0.75 threshold?

L313: I had no access to Supplementary Materials so I am unable to see Figure S4, which is a shame.

Discussion

L318: 'a relationship' => 'relationships' given the generality of the sentence and current MS's results.

L320: I need to admit here that I am not enough aware of the literature to confirm or not that mechanisms have been elusive 'until now'. However, has there been no papers since Thompson et al. 2012? Especially given that the sentence does not precise which function and which attributes of network structure. If need be, authors should precise a little bit (e.g. mutualistic interactions; or plant-pollinator networks and plant reproduction in natural communities, ...). What of Valdovinos et al. 2016 for example?

L325: is niche complementarity between pollinators a measure of overlap or rather the contrary? The greater the 'Niche complementarity' indicator, the less overlap among pollinators, correct? If so, this sentence should be adjusted. Overall, I would suggest using more 'complementarity' throughout the MS than overlap so that most sentences can be read and understood in the same 'direction' (e.g. 'complementarity increased community-level fruit set' instead of 'overlap decreased community-level fruit set').

I'd like to insist on this point because both are used in the analyses but at different level: species-level, i.e. Table 1, test for an effect of 'Niche overlap' but community-level analysis, i.e. Table 2, test for an effect of 'Niche complementarity' (L208 & 219). Both consider plant niche (i.e. the first overlap in pollinator visitation, and the second complementarity in pollinator visits).

I realize I have been confused all along the MS and I here suggest choose to use overlap or complementarity in both (e.g. using "Morisita index x (-1)" to get a complementarity here as well?). I would further suggest to add 'plant' (leading to either 'plant niche overlap' or 'plant niche complementarity').

Additionally, L325: ‘niche complementarity between pollinators’ but L187-190: “[...] between plants”: so which is it? Niche complementarity among plants (for pollinator visit) or among pollinators (for plant resources)?

L330-332: Given the materials provided, I’m not convinced by the predictive power of the simple visitation metrics. Readers would be very interesting in knowing such metrics can be used but I feel that more information is needed. For example, to predict Fruit set at the community level, is using Pollinator species diversity as efficient as Niche complementarity? If using those in bivariate regressions, what would be the R^2 ? This is thus true for what’s shown in Figure 3 and Figure 4.

This paragraph, with more specific information on which of the simple metrics can be used for informing on what, would be better placed toward the end of the discussion as this is more of an ‘application output’ while the main message of the MS is about the role of Niche complementarity in plant reproductive success?

Additionally, more than the predictive power, there is a need to describe and explain the relationships between the ‘simple’ metrics and the ‘network’ metrics. In particular, they do not measure the same things, but I felt the paper presented the comparison as a test for using simple ones as substitute for more complex time-consuming ones.

L334-335: To avoid redundancy, I would erase the end of this sentence (i.e. stop right before “and, in particular”]) because this is explained from L336.

L342-346: In my opinion, the general idea in the literature is that diversity increases functions and services (many articles from D. Tilman, or (Cardinale et al. 2002) for example). Here however, pollinator species diversity is associated to lower fruit set and equity in fruit set. A convincing explanation is provided but I think it’s worth to note and discuss the discrepancy (from my knowledge of the literature) with previous research. Similarly, greater abundance of pollinators on flowers (nb of visitation) usually leads to greater fruit set (Garibaldi et al. 2013) but that is not what is found here (Fig. 3), so why is this? In particular, if ‘total number of visits’ can be used for predictive purposes, it is not in the direction that is usually thought (i.e. more visitation leading to better fruit set, not the contrary as found in Fig. 3B).

L341: remove “values” from “greater fruit set values” ? “fruit set” alone is understood.

L342: in “species requires of the”, remove “of”

L342 + L345-346: The first states that reproductive success needs conspecific pollen, and the second state a somehow opposite idea that there can be interference with conspecific pollen. This requires more explanation. This relates to a previous comment above about the choice of plants that requires more details. For example, did authors choose self-incompatible plant species, i.e. “the ability of plants to reject their own pollen” (Tovar-Mendez and McClure 2016)? In that same Dispatch paper from Tovar-Mendez & McClure, they argue that domesticated plants (i.e. crops) were selected for self-compatibility. Would that explain why the present MS found that pollinator diversity and total number of visits have negative effects on fruit set whereas Garibaldi & colleagues (2013) (among others) found the opposite for crops? I strongly recommend adding more information from a plant perspective in the introduction, the methods, and the discussion. It is critical for understanding the function (plant pollination) authors seek to explain with measures of reproductive success.

L354-369: I feel this whole paragraph could be reduced as the point for looking at equity in fruit set was well-made before in the MS. I suggest to then lump it with the next one discussing what is found here.

L373: unfortunately, I could not see this ‘dramatic’ effect. It is the first time I read about fruit set equity and I think it’s a very important facet of the pollination function and the community-level plant reproductive success. There are already five figures; however, if possible, moving Figure S4 (which I did not see) to the main text could be useful given it is discussed and given the importance of fruit set equity. Unless authors think that with “only” six species maximum per community, it is not enough for making a strong point presently (in which case then perhaps using ‘dramatically’ is too much and more caution should be used).

L378-380: given my previous comments, I suggest discussing the unexpected results before. Then, only once this is ‘cleared’, discuss other things. Also, currently, it’s not clear if there were significant effects when using a different threshold than 0.75.

L381: from the sentences at L205-207 and L284, I understood that pollinator species diversity was the one found visiting each focal plant species; as for total number of visits. But with L381, I become uncertain: did authors test for an effect of overall pollinator diversity in a community with fruit set of each focal plant species (in its community)? I would understand testing the latter* but in which case, it would be very important to clarify this throughout the MS and show clearly results of both and explaining why it would be interesting to look at this.

*For example, it could be interesting when sampling pollinators with pan traps and therefore without the information of plant visitation, as a way to consider resulting diversity as an index of plant pollination.

L385-386: Could authors detail the mechanism(s) here by which there could be a reduction in the reproductive success of the dominant species? Is it related to plant self-(in)compatibility or type of reproduction?

Ok, I see one mechanism is introduced right after. Perhaps then modify this sentence, so that readers get there are mechanisms you will be discussing. Also, are there others or can there be more details on how density-dependence could play a role?

L387: ‘those evaluated in this study’ => as previously mentioned, details needed in the method.

L390-391: very interesting! I strongly suggest putting more results in the main MS rather than in the supplementary. At the very least in a table if there are too many figures.

L400: it may be because I’m not a plant expert but I would need slightly more details on what authors meant exactly by heritability. For example, which traits do they think researchers would need to focus on? Or is it about the effects of plant-pollinator network structure on the evolution of plant reproduction strategy?

Missing from the discussion: How come at the ‘species-level’ (measures at the individual level used) there is a positive association between plant niche *overlap* and seeds per fruit (Fig 2B), but there is also a positive association between plant niche *complementarity* and seeds per fruit (Fig 4B). Niche overlap and complementarity should be negatively correlated and so these two results are opposite, right?

So in the discussion, on top of clarifying throughout the MS the overlap or complementarity wordings, here there is a need to discuss these results which appear to me as contradictory.

Tables

Table 1:

I am vaguely aware of some debate about providing or not p-values associated to mixed-effects models (or to any models nowadays), but I would prefer to have a p-value here as z. or t.values are not as straightforward. Given table 2A, I take it authors have no strong feeling against p-values. 95% confidence intervals would also be better than SE because they can be interpreted directly.

This applies to Table 2 as well. If resulting tables become too wide to fit in the page, I suggest SE can be removed (provided there are 95% CI instead) and z or t values as well.

Finally, unless this is against PCI Ecology editing rules, I would lump Table 1A and 1B and adding a 'Response variable' column to more easily what predictor affect which response. Same for Table 2A and B.

Table 2:

Some tested predictors are in bold but not others and it does not seem to correspond to being a significance? (Conversely to what is said in legend of table 1).

Figures

Figure 1:

I think authors should add a north arrow somewhere, for readership not familiar with the European geography. Also, size font for the scalebar and the Elevation range should be increased; for the elevation range and color scale, consider placing it in an inset as well or to add a black line framing each colored rectangles: currently, colors are not easily seen because not differentiated from the map

Figure 2-5: I am not familiar with partial residual plots and this was not described in the methods. When looking at values on x- and y-axes, it seemed to me the data were plotted and that the predicted model effect was added.

Figure 2:

Font size for plant species is way too small for reading correctly. It would be better if imagining using a four panels-figure and spread the plant species across the full width and height that take panels A and B, but below (as if there were panels C and D)

More importantly, fruit set was said to be modelled with family=binomial but the effect of centrality goes beyond 1.0, which is not possible under this distribution. I suppose this is a plotting issue, as authors did use a glmm (as explained in the methods)?

To avoid any confusion, I suggest replacing, in B, 'seeds/fruit' by 'seeds per fruit'. Also in Figure 4

Figure 3:

Y-axis should be kept equal across panels A to C ; as is, it's hard to compare the strength of each predictor.

In 'Pollinator sps diversity', might change depending on answer to a previous comment: but sps likely can be removed to have only 'Pollinator richness' or 'Pollinator diversity'. Also in Figure 5.

Figure 4:

Is the effect of Total number of visits significant?

Y-axis should be kept equal across panels A to B; as is, it's hard to compare the strength of each predictor.

Supplementary information

I had no access to the supplementary either on PCI Ecology website or on biorxiv website. Did I miss them somehow or were they not available?

Data availability and details of quantitative analyses

According to guidelines of PCI Ecology to reviewers, I here state I did not see that data were made available on an open data repository yet. Similarly, I did not find a link to R (or similar) scripts for redoing the analyses.

References used above

- Cardinale, B. J. et al. 2002. Species diversity enhances ecosystem functioning through interspecies facilitation. - *Nature* 415: 426–429.
- Garibaldi, L. A. et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. - *Science* (80-.). 340: 1608–1611.
- Tovar-Mendez, A. and McClure, B. 2016. Plant Reproduction: Self-Incompatibility to Go. - *Curr. Biol.* 26: R115–R117.
- Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. - Springer-Verlag.