



## Phylogenetic approaches for reconstructing macroevolutionary scenarios of phytophagous insect diversification

**Open Access**

**Hervé Sauquet** based on reviews by Brian O'Meara and 1 anonymous reviewer

A recommendation of:

Emmanuelle Jouselin, Marianne Elias . **Testing host-plant driven speciation in phytophagous insects : a phylogenetic perspective (2019), arXiv, 1910.09510, ver. 1 peer-reviewed and recommended by Peer Community in Evolutionary Biology.**

<https://arxiv.org/abs/1910.09510v1>

*Submitted: 25 February 2019, Recommended: 08 October 2019*

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Plant-animal interactions have long been identified as a major driving force in evolution. However, only in the last two decades have rigorous macroevolutionary studies of the topic been made possible, thanks to the increasing availability of densely sampled molecular phylogenies and the substantial development of

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comparative methods. In this extensive and thoughtful perspective [1], Joussetin and Elias thoroughly review current hypotheses, data, and available macroevolutionary methods to understand how plant-insect interactions may have shaped the diversification of phytophagous insects. First, the authors review three main hypotheses that have been proposed to lead to host-plant driven speciation in phytophagous insects: the ‘escape and radiate’, ‘oscillation’, and ‘musical chairs’ scenarios, each with their own set of predictions. Joussetin and Elias then synthesize a vast core of recent studies on different clades of insects, where explicit phylogenetic approaches have been used. In doing so, they highlight heterogeneity in both the methods being used and predictions being tested across these studies and warn against the risk of subjective interpretation of the results. Lastly, they advocate for standardization of phylogenetic approaches and propose a series of simple tests for the predictions of host-driven speciation scenarios, including the characterization of host-plant range history and host breadth history, and diversification rate analyses. This helpful review will likely become a new point of reference in the field and undoubtedly help many researchers formalize and frame questions of plant-insect diversification in future studies of phytophagous insects.

## References

[1] Joussetin, E., Elias, M. (2019). Testing Host-Plant Driven Speciation in Phytophagous Insects: A Phylogenetic Perspective. arXiv, 1910.09510, ver. 1 peer-reviewed and recommended by PCI Evol Biol. <https://arxiv.org/abs/1910.09510v1>

## Revision round #2

2019-09-09

Dear authors,

Thank you very much for revising so thoroughly your preprint and taking into account the suggestions made by the two reviewers on the original version. One of them kindly agreed to check your revised version and was very positive, but

also suggested two final minor edits. While the first is not critical, the second point is important. Please see if there is a way to answer this comment and submit your final revision (or a strong rebuttal) before we proceed with recommendation.

Apologies for the delay in processing this manuscript.

Kind regards,

Herve

**Additional requirements of the managing board:** Please ignore this message if you already took these requirements into consideration. As indicated in the 'How does it work?' section and in the code of conduct, please make sure that: -Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad (to pay) or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data. -Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused. -Details on experimental procedures are available to readers in the text or as appendices. -Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is one of the PCI XXX recommenders."

*Preprint DOI:* <https://www.preprints.org/manuscript/201902.0215/v2>

Reviewed by anonymous reviewer, 2019-08-22 09:45

The authors did a very good job in the revision, I really like the new Table 2.

Just some minor things:

- You may want to add Nyman et al. 2019 (Early wasp plucks the flower: disparate extant diversity of sawfly superfamilies (Hymenoptera: ‘Symphyta’) may reflect asynchronous switching to angiosperm hosts.) to #6 in Table 2 – to add to the butterflies also a sawfly/hymenoptera study.
- Figure 2 is cool - a possible problem with c) scenario H1 and H2 is that H1 may still show adaptive radiations in morphology even if shifts in diversification are not detected – following your definition of adaptive radiation in the glossary (although it looks like all recent clades will show a diversification rate shift as compared to the background rate). And similarly, H2 would possibly show the fastest rate of diversification in the range 3 clade (opposite of what is suggested), because of the long branch suggesting extinction but also fast speciation (high turnover), whereas range 1 and 2 show gradual accumulation of diversity – and thus not necessarily adaptive radiation. Last, for the radiation to be adaptive, one would have to show that within the range there is partitioning of resources (e.g. through the reconstruction of traits related to this partitioning – comparable to the beak-size in Darwin finches), something that is currently missing.

### Author's reply:

Please find a revised version of our MS.  
<https://www.preprints.org/manuscript/201902.0215/v3>

We have followed the reviewer's comments and have redrawn Figure 2c, as this the only major change that we made we only uploaded figure 2 in the "track change" tab, as other changes were minor edits (i.e. references).

Many thanks for handling the manuscript. Sincerely Emmanuelle Jouselin

[Download author's reply \(PDF file\)](#)

## Revision round #1

2019-05-13

Dear authors,

Your preprint has now been reviewed by two experts, and I have also reviewed it myself. You will see that both reviewers are positive about the preprint and I agree with them that it will represent a thorough and very useful contribution to the field.

My main comment is that the text as it stands is very long, especially part II, where a very long list of examples is cited and reviewed. Both reviewers have alluded to the same issue, but both have offered a very similar solution in the form of a summary table. I really like this idea and encourage you to explore it as an excellent way to make the text much more concise and easy to go through. The level of clarity and concision achieved in the Perspectives is ideal.

I also like the idea of reviewer #2 to present more clearly how to test the three macroevolutionary scenarios for a given dataset using the comparative toolbox currently available.

When you revise your preprint, please make sure to consider all other comments and suggestions made by the two reviewers, provide a point-by-point answer, and a version of the manuscript with your changes tracked or highlighted. Please note that I also attach an annotated copy of your manuscript with a few comments and typos highlighted, but no need to answer these specifically in your response (just make sure you correct the typos). I take this chance to apologize for the long delay it took us to process your submission, which is partly due to the difficulty of finding available reviewers.

I hope you find these comments helpful and look forward to handling your revised preprint.

Kind regards,

Herve.

**Additional requirements of the managing board:** As indicated in the 'How does it work?' section and in the code of conduct, please make sure that: -Data are

available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad (to pay) or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data.

-Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused. -Details on experimental procedures are available to readers in the text or as appendices.

-Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is one of the PCI XXX recommenders."

*Preprint DOI:* <https://www.preprints.org/manuscript/201902.0215/v1>

Reviewed by anonymous reviewer, 2019-03-26 14:23

Jousselin et al. give an interesting (and probably quite comprehensive) overview of hypotheses and studies testing phytophagous insect diversification in relation to their host plants. This is an interesting topic, and the review is generally clear and well written (could be a bit more concise in places, and needs in parts clarification, check for a couple of minor spelling mistakes, some I indicated below). I especially like the Perspectives part.

I have a couple of suggestions to improve the ms, indicated below. More generally, it may be useful to make a table indicating support for the different hypotheses (e.g. for different study groups/taxonomic groups [would be useful to use taxonomic symbols/silhouettes], and indicate the reference, and the method used, for example) (this would support the text with the sum-up of examples, which is quite long at the moment). The same (a table, or maybe better a figure) could perhaps be done for the Perspectives ideas.

Other comments:

L48 Not clear whether hybrids will thus be selected against, or that this intermediate phenotype has the potential to become a new species through reproductive isolation. Or both. In case of both, perhaps some more information about the commonness of ‘selection against hybrids’ vs. ‘hybrids become new species’ can be presented.

L76 This overview is interesting, but not particularly novel. To really move forward in this field, I guess it would be great to incorporate the available fossil evidence, to calibrate the radiations / estimate diversification rates, but perhaps also to obtain a better idea of insect-hostplant associations in the past, if such things fossilize (or co-occurrence of species through insect/plant fossil assemblages perhaps).

L78 an extra ‘and’

L88 Why only speciation rates? I would say diversification rates, which would include both speciation and extinction. I imagine certain host-plant relationships are less vulnerable to extinction (e.g. more generalized as opposed to specialized relationships?)

L174 less fewer

L182 The musical chairs hypothesis needs a bit more detail. For example, the description does not really match the figure (1c), and it’s only indicated how it differs from the second hypothesis, not how it differs from the first, and more importantly, what makes it ‘unique’.

L203 What about the methods that test for host switching and co-diversification – are those not required to test some of these hypotheses as well?

L212 insect insects

L220 But a lack of support for coevolution has also been often found, or?

L230 and more generally – some predictions remain quite vague and could do with a bit more detail. For example, concepts/terms such as ‘high lability’ (in speciose lineages breadth) high compared to what? ‘Few transitions in host breadth’ – few compared to what? What is, and how does one measure ‘lability in

host association'? 'following the capture of a new host-plant lineage' does that not directly indicate that there is host tracking? Or how can there be shifts to new host-lineages without tracking? 'Conservatism of host-plants' – compared to what? Conservatism in what? How does conservatism shift on a phylogeny – is it (or linked to) 'intrinsic' traits? 'recurrent transitions in host breadth' – what is recurrent, how often, how commonly?

In short – always make the comparison, i.e. larger (e.g. geographical range) than what. Make clear what 'lability' and 'conservatism' are – these are vague and difficult concepts.

L234 host-plant adapted traits – such as?

L237 But I guess these studies have not found support for all predictions from the hypothesis, or? Maybe write something about the methods they used and how reliable their conclusions are.

L265 How can host history be mapped on a tree when there are multiple associations per species? Or how are host associations classified?

L282 What if the host shift is to the nearest living relative of the current host plant? Or would that be called host tracking instead of host switching? Perhaps make clear.

L294-295 rephrase sentence

L300 few species of what? Plants? Angiosperms?

L326 I wonder whether the availability of (suitable, e.g. chemically matching) hosts also plays a role in the host-breadth evolution of insects. This therefore depends on the diversification of particular host plant lineages. Perhaps this could be mentioned here, or elsewhere.

L333 Here, and more generally: what is specialized and what is generalized? Should that always be in comparison to something else (e.g. other species or previous/ancestral state?)

L349 Why would these be the result of range expansion? What is that based on?



L378 disruptive selection to what - host plants? Make explicit, because disruptive selection could have still played a role during speciation.

L438 I wonder whether it may not be just phytophagy vs. non-phytophagy driving the high diversification rates, but phytophagy in interaction with other (extrinsic, or intrinsic) traits (such as host plant diversification / availability). This would require more sophisticated trait and interaction-dependent diversification models. Or, alternatively, a similar trait-based approach to Onstein et al. 2017 (Nature Ecology & Evolution) could be taken, in which the authors infer speciation rates based on important interaction-relevant traits (in that case of frugivory). Those traits would tell you something about the interaction (e.g. chemical traits, phytophagy and or host-breadth) as well as the consequence for speciation based on host-plant characteristics (e.g. host-plant diversity or diversification, or their variation in chemical traits).

L498 changed changes

L509 geography, or other factors. Explain why geography is likely in this case.

L591 Is such a phylogeny available?

L735 Indicate which definition of adaptive radiation you follow – in some cases the radiation does not have to be rapid, just morphologically. Rapid refers to the necessity to also test for a shift in diversification rate at that point in time, which was not mentioned in the main text.

L747 What is a 'wide niche'? And what a 'narrow niche'?

Reviewed by [Brian O'Meara](#), 2019-05-07 22:47

This paper is an important contribution: it goes beyond the hand waving arguments for diversification to get at which mechanisms may credibly lead to observed patterns.

Major suggestions

A persistent problem throughout the paper is that diversification and speciation are treated as synonymous, but they are not. For example, one idea for escape

and radiate is not that the plant speciation rate would go up (for what it's worth, I agree with the authors that this probably wouldn't happen) but extinction rate of plants could go down (less herbivore pressure). Both would increase diversification; only one relates to speciation. I would go through and any time there is diversification, change it to speciation if that is meant; if that is not meant, think about how varying extinction could lead to a diversification pattern.

I would love another table: scenario on the rows, papers on the columns, and a symbol indicating which hypotheses were examined and which ones were supported. Much of the text is a verbal description of this, but doing a table like this would really help clarify the results: in situations where both hypothesis A and C were evaluated, C won 75% of the time, but comparing B and C, C won 17% of the time. One could lump the columns by focal taxon (butterflies, beetles, etc.). It would also help highlight which hypotheses have not been examined much, and which ones have been only looked at on their own without rigorous comparison to others.

Lines 289-313: an important caveat is that methods looking at host shifts and speciation shifts will miss some: a shift, then a shift back, for example. I suspect that missed speciation events are far more common than missed host shifts -- if anything, multiple missed speciation events and still few host shifts is even more support for the idea that most speciation doesn't involve a host shift, supporting the conclusion. I'd still mention this caveat. It also comes into the discussion on 321-325 -- one problem with these approaches is they assume all speciation events and host switches are on the tree, which is not true (it makes me wary of such methods).

One caveat about diversification models that could be more strongly emphasized is that under any of these models where phytophagy affects diversification rate, we don't expect that is the ONLY factor (this could be relevant to bring up around line 451). Gaining or losing flight likely has a substantial effect on diversification rate, for example, and that this happens sometimes does not mean phytophagy does or does not also matter.

The interaction network approach is compelling -- I am glad it is in this paper.

Table 1 is a good contribution.

The paper would be stronger if there were a section explaining more clearly how to compare the models in Table 1 in one study (this related to line 707: the paper argues for a standardization of these predictions, but show better how this can be used in practice). Say I have a fairly well sampled insect phylogeny where I have host families for all of them. What parameters, model selection, would help me select which macroevolutionary scenario best explains my data? Some of the predictions in table 1 are vague ("high lability", "few transitions", "conservatism") -- how do these work operationally?

Minor suggestions

Line 162: Figure misspelled

Line 553: "hwas" typo.

Line 557: Shouldn't be parentheses around author names

I would say BiSSE and related methods are referred to more as SSE or \*SSE rather than -SSE methods.

Line 613: This is a good point, but it's even worse than that: there could be many changes and it's still not robust to say a state led to a diversification rate increase. See Beaulieu & Donoghue (2013) <https://doi.org/10.1111/evo.12180> -- a single change in one clade that correlates with diversification increase could make it seem like that change always increases rate, but it's not true.

615: I'm not sure sister group comparisons are "very" sensitive to sampling biases in the way SSE models are. Sensitive, yes -- but when one is comparing a clade of 1000 vs one with 50, you'd have to do some pretty extreme sampling to get the wrong sign.

Closing on transcriptomes was odd -- it's not bad, but I could see counter reasoning (selection in the present doesn't necessarily correlate with selection when switching hosts; this does not get at the speciation genes). It does not mean cut this, only that I might move this somewhere less prominent -- it's an approach, not the ultimate approach.



Line 717: should be sister lineages.

Left align the contents of Table 1: justified looks terrible

### **Author's reply:**

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