

Answers to PCI Ecology second-round review of manuscript “Attracting pollinators vs escaping herbivores: eco-evolutionary dynamics of plants confronted with an ecological trade-off” by Y. Yacine and N. Loeuille

Dear recommender and referees,

First, we would like to thank you for acknowledging the effort made to improve our first manuscript version, following your initial comments and suggestions. In this second round of review, the main criticism relates to the fact that particular parameters may lead to biologically unrealistic population dynamics (i.e. unbounded growth). We acknowledge that this possibility and its implications were probably not made explicit enough. To correct this:

- We describe and comment on such outcomes when introducing the dynamics of our model (**L184-196**), notably mentioning that in such conditions “our model fails at producing biologically realistic dynamics” and highlighting possible missing components (**L187-190**).
- In terms of Methods, we made explicit in the main text **L271-274** that selection towards and within unbounded growth regions is described as stabilizing selection, in the sense that evolution selects for phenotypes closer to this region (i.e. convergence from an evolutionary point of view). It was previously mentioned briefly at the end of **Appendix B.II.1**. We now provide a clearer argumentation for such a choice (**L 274-281**, and detailed in **appendix B.II.1**). We also modified **Appendix B.II.1** and **Fig. B2** to give an explicit example of the characterization of the type of selection when unbounded growth occurs. We fully agree that when reaching such unstable situations (i.e. within unbounded growth regions), classical tools of adaptive dynamics cannot be used (now mentioned **L 276-277** and **appendix B.II.1 L 322-323**).
- Most importantly, because we have characterized the conditions for stable coexistence in a previous article (Yacine & Loeuille 2022), we can control the occurrence of such unbounded growth outcomes. In the new version, we test the robustness of our results to the occurrence of unbounded growth by considering a third ecological parameter set in which unbounded growth cannot happen (introduced **L 314-319**, detailed in **Appendix B.I, new Fig. B1 in particular**). Our results are robust to the occurrence of unbounded growth (**L319**).

In what follows, we address each comment on a point-by-point basis, notably detailing the points listed above. Please note also that as we reconducted our Monte-Carlo experiments with our new ecological parameter set, we found two additional (technical) points that needed to be fixed (but that do not modify our results), and these are presented at the very end of this document.

Hereinafter, the referees' or recommender's comments are in black; our responses are in green. We also took the liberty of switching the order between the comments of reviewer 1 and reviewer 2 as we felt it made our answers easier to follow.

Please note that the references to line numbers (thereafter) apply to the PDF file (on BioRxiv), or the word file (tracked changes) when changes are shown in minimal mode (when changes are shown in detail, the line numbering is a bit modified, sorry for that).

Comments by PCI recommender:

Dear colleagues,

two reviewers and myself have read the new version of your manuscript. We all agree that you did a very good work in responding our comments and modifying your manuscript after our suggestions.

I think we are close to a definitive version, pending you can answer the last comments of the reviewers, especially the one of reviewer 2 regarding the weakness of the way your model is built.

I recommend to follow reviewer 2's suggestion: either to modify your model fixing this flaw and assess whether it qualitatively changes your results (maybe in a small but significant parameter ranges), or to at least pinpoint the weakness, discuss it and make the reader aware of it.

We chose the second option. While we agree that unbounded growths are not biologically realistic, they are useful for our analysis. Indeed, in the (rather rare) cases where evolution leads to these unstable regions, they highlight a destabilizing role of evolution, which would be overlooked if such dynamics were prevented. We however went beyond simply clarifying the issue. We also tested the robustness of our results to the occurrence of unbounded growth, and found that our results are qualitatively robust to such a change.

To do so, we considered an ecological parameter set in which both plant and pollinator intraspecific competition rates are sufficiently strong to ensure stable systems (detailed in **Appendix B.I**, see **Fig. B1.A.c** notably). To put it precisely, irrespective of the sampled interspecific parameter set (Monte Carlo experiments, potential ranges provided in table 1), no region of phenotypic space gives unbounded population growth with this third ecological parameter set (introduced **L 318**). We found our results to be qualitatively robust (see **Appendix C**) as mentioned **L319, L415-416 and 443-445 and 472-473**.

I think in addition to reviewer 2, that you have to explicitly write in the main text that such "unbounded growth regions" exist, and how you managed them for the study of the evolutionary trajectories. In particular, as the adaptive dynamics framework assumes the community to be ecologically stable when the mutant is introduced, it is unclear how you did your analysis in

unbounded growth regions (i.e. if I am not wrong where P^* , M^* , H^* do not exist). You can certainly avoid them as initial conditions, of course, but the difficulty especially rises when evolutionary trajectories would lead the community to such unbounded growth regions.

We made the occurrence of such behaviors more explicit when introducing population dynamics (Model section) **L185-187**. We mention it as a model weakness, provide some elements of interpretation and point towards our previous ecological study in which this issue has been extensively discussed (**L187-190**).

The adaptive dynamics framework indeed assumes stable ecological equilibria, and (P^* , M^* , H^*) defined as stable equilibrium does not exist in unbounded growth regions (an equilibrium exists but is either not feasible (i.e. negative) or unstable). As such, our analytical study (e.g. equation (3)) is only conducted over regions of three-species stable coexistence. For our numerical analysis, we choose to describe directional selection towards and within unbounded growth regions as stabilizing in the evolutionary sense (**L 271-274**), which seems to us mathematically (i.e. attractiveness) and biologically (i.e. coexistence maintenance) coherent as detailed in the manuscript (**L 274-281**) and supporting information (**appendix B.II.1 L322-338**). An explicit calculation of the proportion of phenotypic space under each type of selection in the case where an unbounded growth region exists is now given in **appendix B.II.1 (Fig. B2.c)**.

Hence, in order for your paper to be of high quality and to be appreciated in the long run by both theoreticians and empiricists, I would recommend that you modify your model in such a way to remove this flaw, check whether it has strong implication for your results in a limited parameter range, or at least make this limitation explicit and describe better how you dealt with it. Otherwise, I am afraid it would limit the impact of your paper and results.

Best regards,
Pr. Sylvain Billiard

Review by [Yaroslav Ispolatov](#), 23 Jan 2024 06:52

I think the Authors did a good job addressing most of the comments from the previous round of reviews. Nevertheless, it appears that one issue persisted.

I wrote in my previous review, perhaps not in entirely clear terms, that the model defined by Eqs. 1 has a serious design flaw: When the conversion coefficient e_m and the rate $a_{\{pm\}}$ are sufficiently large compared to the corresponding quadratic "death" rates c_m and c_p , both P and M catalyze each other and grow indefinitely. In terms of "natural" variables, it definitely makes no sense: No matter how well-pollinated a plant is, neither the plant nor the pollinator can increase their densities indefinitely.

We agree that our model has the weakness of producing biologically unrealistic population dynamics in the form of unbounded growth. The mentioned relationship (i.e. $c_p c_m -$

$e_m a_{pm}(t_p)^2 < 0$) is indeed necessary for such unrealistic behavior, but it is not sufficient. As now clarified **190-193**, this is actually one of the main results of our previous study (Yacine & Loeuille 2022): the plant-herbivore interaction can stabilize the plant-pollinator unbounded growth dynamics, making, in our opinion, the investigation of the evolutionary dynamics in this “extended” stable coexistence region relevant.

I also suggested one of infinitely many possible ways to fix this flaw, preserving the phenomenon similar to what is observed in the regime when the divergence is absent and ensures convergence for all values of the rates. Naturally, I have not expected the simulations and adaptive dynamics analysis to be redone to correct this flaw, but I insist that it has to be acknowledged. Writing in resubmission letter that "Other published theoretical works (e.g. Thébault & Fontaine 2010) have made similar assumptions." seems like a lame excuse for a pure theoretical work. So I strongly suggest to replace the vague terms "unstable community dynamics" and "unbound growth" in lines 445, 452 and Fig. 5 by something more self-critical, as, for example, "failure of the model", explain it and propose ways to fix it in the Discussion.

We have followed the referee’s suggestion and now more clearly highlight such dynamics and their implications. Their occurrence can actually be controlled. Taking advantage of the fact that $c_p c_m - e_m a_{pm}(t_p)^2 < 0$ is necessary for unbounded growth to be produced, we reconducted our Monte Carlo experiments with a third ecological parameter set in which the above relationship can never be satisfied, and found our results to be qualitatively in line with our main conclusions (see **Fig. 3 & 4, Appendix C**). Please also refer to our answers to the recommender’s comments.

We would also like to point out that there has been a misunderstanding about the sentence "Other published theoretical works (e.g. Thébault & Fontaine 2010) have made similar assumptions." in our previous reply: this sentence was exclusively about interpreting negative quadratic terms as intraspecific competition.

We also made more explicit the occurrence of unbounded growth directly after introducing the population dynamics of our model **L184-198**, mentioning that “our model fails at producing biologically realistic dynamics” **L187-188** (this is also mentioned **L 279** and in the caption of **Fig. 5**). The vague term “unstable” **L487 & L494-495** is now completed by the explicit mention of unbounded growth, which should now be clear given it is emphasized early in the manuscript.

Finally, we feel that the changes made to increase the reader’s awareness about this weakness of our model (i.e. occurrence of unbounded growth), and importantly the fact that our results are robust in the absence of unbounded growth, makes extending our discussion not strictly necessary, the occurrence of such dynamics being not tightly linked to our main results. We briefly provide some elements before referring to the extensive discussion on the topic provided in Yacine & Loeuille (2022) (**L187-190**).

I see this issue as important and easily fixable, and making the discussion about it public appears to me as one of the merits of transparency of the new reviewing protocol.

We agree and we hope that the new version is more satisfactory in this regard.

Review by [Marcos Mendez](#), 24 Jan 2024 10:11

Comments to the MS by Yacine & Loeuille

I thank the authors for taking into account my suggestions about their MS. I only have a few minor suggestions for improving clarity.

1. If this model is not suitable for extreme cases in which the pollinator and the herbivore are the same species, it is worth mentioning it early in the description of the model, e.g., when the Lotka-Volterra equations are provided. Empirical pollination biologists will appreciate this clarification, because the study of "nursing pollination" is a hot topic in pollination biology.

We followed the suggestion **L179-182**.

2. About match of phenotypes, I appreciate the clarifications of the authors. I understand that authors prefer to use a terminology which allows broader interpretations, to gain generality. However, I believe that it is clearer, and equally broad, to talk about a match between plant phenotypes and animal preferences (instead of animal phenotypes). Talking about dissimilarity in preferences of pollinators and herbivores would definitely improve clarity for empirical pollination biologists (e.g. in the first mention of animal phenotypes on L. 139). Please, consider changing animal phenotype to animal preference.

We have tried to make our terminology clearer. At the first mention of animal phenotypes (**L138**), the sentence was modified into "each interaction increases in strength with the matching between plant phenotype and animal preferences (or more generally and henceforth, animal phenotypes)." This seemed to us as a good compromise, but we prefer to keep the generality of our formulation for the rest of the manuscript.

3. Thanks for explicitly including reference to your previous modeling efforts. I wonder if this reference should be placed before the paragraph in which you state your goals. I believe readers will understand better the novelty of your model if the results of the previous model are introduced earlier.

Following the suggestion, we introduce our previous ecological study earlier and with more details (**130-141**), emphasizing the novelty and interest of the current eco-evolutionary extension.

4. A final comment, hopefully not too picky, is that your paragraphs in the Introduction are almost one page long, which can decrease readability. In particular, the last paragraph is over a page long. Please, try to split it or reducing its length.

Thanks for pointing this out. We divided the paragraph into two paragraphs (L142).

Sincerely,
Marcos Méndez
January 2024

Finally, two additional points:

(1) in the case of our first Monte Carlo experiment (MC1), the numerical precision used to find evolutionary singularities (i.e. solving *Selection gradient* = 0) was insufficient: in some cases (a few dozen cases over more than 10 000), the equivalent equation A.3 (appendix A) was not numerically verified. This was corrected by changing the value of the parameter *tol* of R function *uniroot.all* (package *rootSolve*) from its default value *Machine\$double.eps*^{0.2} to *Machine\$double.eps*^{0.7}. Consequently, MC1 was reconducted for our first two initial ecological parameter sets, and our results (*Fig. 3, table S1, Fig. C1.A and table C1*) were marginally and only quantitatively (i.e. not qualitatively) altered (e.g. in **Fig. 3**, Kruskal Wallis effect size changes from 68 to 67%).

(2) while reconducting our second Monte Carlo experiment (MC2) for our additional ecological parameter set, we realized that animal phenotype dissimilarity $t_h - t_m$ was actually constrained within [0, 1.5] (and not [0, 3]) when the focal interspecific parameter was one of the other four (i.e. a_{pm0} , a_{ph0} , σ_{Pol} , σ_{Her}). This was done to better capture the effects of the other interspecific parameters on disruptive selection, the latter being hardly observed for high animal phenotype dissimilarities (*Fig. 4A*), but this information was somehow lost during the process of reediting/improving/correcting our manuscript. We apologize for that. The information is now provided in the captions of **Fig. 4, C2 & C3**, as well as when detailing MC2 **L404-409 in Appendix B.II.3**.