

Answers to PCI Ecology 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,

We would first like to thank you for the comments and feedback on our manuscript, which we found very helpful and constructive. Thank you also for pointing out the quality of the Supplementary Material. We have tried as much as possible to modify our manuscript following your comments, and we really feel our manuscript has significantly improved. Before explicitly detailing how we tackled each comment, we would like to briefly summarize the most important changes we have made:

- One of the most crucial points highlighted in the reviews was the lack of clarity about our definition of the “ecological trade-off”. It is now defined early in the introduction. The last paragraph of the introduction was largely modified to clarify earlier the link between trade-off and animal phenotype dissimilarity. An utterly new paragraph entitled “Definition and emergence of ecological trade-offs” now opens the Method section. Following your suggestions, this paragraph includes the old Fig. B.1 (initially in appendix B, Supp. Info.) as a new Fig. 1.
- We clarified the biological interpretations/implications of the different simplifying assumptions of our modeling framework, and we are now explicitly discussing some of their limitations in a new paragraph of the Discussion.
- We reformulated the text in many places to be more precise in the wording so that the global clarity of our manuscript is improved.

In what follows, we address each comment on a point-by-point basis. The referees’ or recommender’s comments are in black; our responses are in **green**.

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:

Suggested major revisions

(1) Trade-off, dissimilarity: Trade-offs and dissimilarity are at the core of your paper and model but it is difficult to clearly understand how you define and modelize them. I agree with one reviewer who suggested to move App. B to the main text. I agree with the other reviewer that the presentation and justification of the link between dissimilarity and the trade-off should be improved.

A new paragraph entitled “Definition and emergence of an ecological trade-off” now starts the Method section (L197-216). This paragraph provides a clear definition of the meaning of ecological trade-off in our work (i.e. “a positive covariation between the strengths of pollination and herbivory”, L199-200), and how it plays out in our framework. In our framework, the ecological trade-off is not a direct input of our model, but rather something that intrinsically emerges from our modeling assumptions (which are presented in the Model section, i.e. population dynamics + interaction strengths that increase with plant-animal trait-matching). After showing the latter (L200-205), we explain why the dissimilarity between animal phenotypes can be considered a proxy for this emerging ecological trade-off (L206-216). This is essentially the explanation provided in Appendix B.I in the first submitted version, whose components are now included in the main text, as proposed. Following the suggestions, we also rely on an improved version of the old Fig. B1 (from Appendix B) which is now **Fig. 1**.

In addition to this new Method paragraph, we clarify the meaning of “ecological trade-off” in terms of costs and benefits when it first appears in the introduction (L89-92). The last paragraph of the introduction (L126-152) was also largely modified to be in line with the new Method paragraph: it provides a clear definition of the term (L135-137), clarify early in the manuscript that it is not a direct input but rather something that emerges within our framework, and how it is linked to animal phenotype dissimilarity, notably with the reference to Fig. 1 (L138-140). Finally, the first sentence of the discussion was reformulated in line with the clarifications mentioned above (L518-521).

(2) Modelling choices: Several strong assumptions are made and not explicitly highlighted: as the existence of an extrinsic intraspecific competition, none-evolution of the animals, and the absence of limit to the evolution of the plant trait. These assumptions should be made explicit, biologically justified or interpreted (e.g. the assumption that the animals do not evolve can be interpreted as much shorter time evolutionary scales for the plant than the animals because of differences in reproduction rate or lifespan), or at least discussed. In addition to the reviewer’s suggestions I would add other implicit assumptions to be highlighted: the animal species are supposed to be either ultra-specialist of the plant, or obligate mutualist.

The biological interpretations of our ecological assumptions (i.e. on growth rates and competition rates) are now clarified when introducing population dynamics (L160-169). Following the suggestions, we dropped the distinction autotroph vs. heterotrophs for the more

relevant one in our case: obligate vs. facultative. We also made explicit the biological reality encompassed by intraspecific competition rates (i.e. resources for the plant, interference for animals).

As for our strong assumptions regarding the evolutionary process (i.e. no evolution for animals, no cost other than pollination and herbivory for plant evolution), we decided to discuss them in more detail in the discussion (L 555-560 + new paragraph L562-582). We provide biological interpretations and discuss their relevance (L563-569 & L576-580). We also highlight their implications notably for runaway dynamics as pointed out by the second reviewer: animal evolution and/or constraining plant phenotype to a viable space by accounting for other costs to changing plant phenotypes should dampen extinctions (L557-560 & L 580-582). More generally, we explicitly position our work as a first step towards the study of more realistic coevolutionary scenarios, pointing out the limits of our approach (L569-573).

(3)Cited literature: I agree with one of the reviewers who strongly suggested to better choose and more thoroughly present the empirical and experimental literature you cited in the discussion, and to better position in the introduction the present article in relation to the one you previously published (Yacine and Loeuille 2022). I suggest to improve the former point in the introduction (e.g. L97-98 and L103: a list of references rather than a single example is expected; also provide a more accurate and synthetic presentation of what has been shown in these papers that justify you own work). I also concur with the reviewer that you should position your model with the literature which consider mutualism as a product of a continuum of between-species interactions rather than as an input.

We agree and we now position our work within the literature on the mutualistic-antagonistic continuum as suggested by the first reviewer (L68-72) when introducing the context. We however did not do so later when introducing our model, because we believe this would be confusing as our model is not directly suitable to model cases when interaction outcomes are context-dependent. For example, in the example of nursing pollinators cited by the referee, the pollinator and the herbivore would be the same species, so their population dynamics should explicitly depend on each other (stage structure).

We went through the different pieces of empirical literature cited to support the notion of ecological trade-off, and while we acknowledge that not all papers explicitly mention the term “ecological trade-off”, all of them suggest a pattern of “positive covariation between the strength of pollination and herbivory”, which means that benefits from one interaction lead to costs in another, therefore corresponding to our definition of ecological trade-offs (L89-92, L135-137, and L198-200). We feel that a large part of the criticism about the cited empirical literature is due to the lack of clarity of our definition of ecological trade-off (and how it intrinsically emerges from our trait-matching framework), which we did our best to improve (see answer to major point 1 above). A large number of the empirical citations we provide indeed report shared pollinator and herbivore preferences for plant phenotypes, which implies a strong trade-off (see L 206-216 & Fig.1). In addition, when necessary, we provided a list of references (L108-109, L114-115), or reformulated the text to be more precise (L614-617).

Finally, we improved the positioning of our current manuscript in relationship with our previous one already at the end of the introduction (L145-148, in addition to what was already present L173-177). Our previous work did not consider phenotypes and solely focused on the ecological dynamics of antagonistic-mutualistic systems (i.e. no evolution was accounted for). In that work, we described the relationships between the strength of plant-animal interactions that would enable the stable coexistence of the 3 species (i.e. study of the dynamical system provided as equation 1). This analysis of ecological dynamics is needed so that evolution is studied over a region of phenotypic space where it makes sense (e.g. adaptive dynamics results and formulas require stability). It also helped us when making our predictions (as indicated L145-148), and in general when interpreting and discussing our results.

(4)Paper organization: I strongly suggest to modify one aspect of the paper with which I am uncomfortable. Your presentation of verbal 'predictions' (Fig. 1) that are later 'confirmed' by your results gives me the impression of something similar to 'Harking', something I would call 'Parking': 'Predicting after the results are known'. Of course I might be wrong and you might have effectively provided predictions before doing the model, and of course such a bias would be less important than in the case of an experiment. One drawback of your choice of presenting verbal 'predictions' is, when starting the "Results" section with "as predicted", to trivialize your results. In addition, one can argue that your verbal "predictions" are confirmed only because you introduced the necessary elements in your model to do so. I really do not think the organization of your paper needs to present Fig 1 as something you 'predicted'. I think Fig 1A and 1B. are good graphical summary of your work and results but should not be presented as a prediction. I think that it would be more important to replace Fig 1 and the associated text by Fig B1 and a text better explaining your definition and use of the trade-off.

We followed the suggestion and replaced the old **Fig.1** with the old Fig. B1 to clarify the link between animal phenotype dissimilarity and ecological trade-off (L219). The old Fig. 1 is now provided as a graphical summary of our work, and is presented as results rather than predictions. As for our predictions, they were reformulated in a simpler way so that we were able to present them in the last paragraph of the introduction without relying on any additional figure (L142-152).

5. Global clarity: I found that the text lacks clarity in many places:

- - L94: "stronger mutualism" is not clear. You mean obligate vs. facultative? Specialism vs. generalism? Is "stronger mutualism" synonymous to "better match"? If so this sentence is somewhat tautological.

"stronger mutualism" means that the mutualistic interaction increases in strength, as clarified L104-105. It indeed means "better match" if interaction strengths increase with trait-matching, as is the case in our model (see next comment and answer).

- - L95-106: your justification why mutualistic interactions should give stabilizing selection whereas predation should give runaway or disruptive selection should be

improved. Some situations can justify the reverse: for instance, how would it be possible to explain the dozens centimeters tongue length in some pollinators with stabilizing selection rather than runaway selection? Or one can imagine that some chemical component produced by a plant to repel its predator should exactly match its vision, olfaction or taste and thus should evolve because of stabilizing selection. Overall, I think you might want to explicitly present this as an assumption of your paper, supported by some empirical literature, rather than as an “obvious” and exclusive element.

We agree with the comment. The reasoning initially provided **L95-106** (now detailed **L97-118**) is only true if interaction strengths increase with plant-animal trait matching. We clarified this assumption and its relevance **L99-104**.

- - L38, L108, L180, L206: “constrain”: be more explicit, do you mean “shrinks the parameters space”?

The term “constrain” was replaced by a more precise term each time (**L 37, L120, L177**). The one **L 206** does no longer exist: this part of the text is now utterly reformulated as part of the new Method paragraph on the ecological trade-off.

- - L110, L137, L141, L143, L177, L179 and in the whole text: “balance between”, “correlated interactions”: this should be better defined, what do you mean by balance, similar predation and mutualistic interaction strengths? But at the individual or population level? (regarding the individual interaction rate or the global interaction rate?)

In the vast majority of cases (including the ones explicitly mentioned **L122, L148, L150**), the expression refers to similar interaction strengths (i.e. a_{pm} & a_{ph}) and this was made explicit each time by adding the term “strength” when missing. a_{pm} & a_{ph} are defined as individual interaction rates (they depend on the phenotypes), and as all individuals have the same phenotype in adaptive dynamics in between mutation events (i.e. no polymorphism, except in cases of branching), this would also correspond to the individual interaction rate at the population level (i.e. the individual interaction rate that would be measured at the population scale in the field for instance). We are pointing this out in case the latter rate is what you are referring to as “global interaction rate”. “Global interaction rate” could also refer to the terms $a_{pm}M$ & $a_{ph}H$ (M and H being animal densities). In this latter case, we are indeed referring to similar strengths of the “global interaction rate” when presenting the results derived from equations (3) and (4), as well as Fig. 3. We, however, feel that introducing a distinction between individual and global rates would be confusing, and prefer to point out to the terms we are referring to explicitly as already done (see equations 3 and 4, or Figure 3). Note finally that the distinction is not very relevant regarding the results presented in Fig. 3 as pointed out **L375-378**: other ratios of “pollination vs. herbivory” (including “individual rates” in the strict term) give similar results.

- - L112-L113: The question you are addressing seems to be only about species coexistence when the reader arrives at the end of the introduction. However, your model

addresses more general and numerous other questions, as suggested by the beginning of your introduction when you presented some phylogenetic works. You might want to better present the whole set of questions addressed in your paper especially in regards with the literature you already cited.

Thanks for pointing this out. By reformulating the last paragraph (L126-152) of the introduction, we hope that we managed to make the different questions appear more clearly. We dropped the initial formulation with 3 bullet points for an encompassing formulation referring to the eco-evolutionary feedback between interactions, traits and coexistence (L126-129). We highlighted the special focus on the role of the ecological trade-off (L134-142, especially the last sentence). We also conclude the introduction by emphasizing the investigation regarding the potential for disruptive selection to occur, and to lead to a polymorphic plant population (L150-152).

- - L117-118: claim 3) seems contradictory to what was explained L95-106. Does stabilizing or disruptive selection depend on the type of interactions? Or on the trade-offs? Is it an output or an input of your model?

Claim 3, whose formulation was indeed rather confusing, was suppressed, and replaced by a more wordy but clearer question on the role of the ecological trade-off (L140-142).

As for the initial rationale, stabilizing or disruptive selection depends on the type of interaction as explained L97-118 in the case of one-interaction systems (i.e. comparing plant-herbivore to plant-pollinator system as done in Yoder & Nuismer (2010) for instance), which suggests that in a plant-pollinator-herbivore system, it would depend on the relative strength of pollination vs. herbivory, and hence on the strength of the ecological trade-off. Disruptive selection is an output of our model, as emphasized in the last sentence of the introduction (L150-152).

- - L138: “favored”, relatively to what? What does “coexistence favored” mean?

“rarely favored” means that coexistence becomes less likely. The formulation was rather confusing, and we changed that L145: “coexistence should be frequently disrupted”.

Minor comments

- L171: “heterotroph”: seems too restrictive. Might your model also be interpreted for specialist mutualistic or predator species? For obligate mutualistic species?

We dropped the distinction “autotroph vs. heterotroph” for the more relevant one given our modeling framework: “obligate vs. facultative” (L161-163).

- A direct and explicit link to the Appendix should be given within the text, and also for the files on the Dryad deposit server.

Done, at the end of the main text: data availability statement (L662), and supporting information statement (L 656).

- Table 1: The variable length L only appears in this table if I am not wrong. It should be defined and related to the model. Some notations would need to be changed to avoid confusion: M is used for mass and pollinator density, t for time and trait. t_h t_m described as “strength of ecological trade-off” in the table but as dissimilarity everywhere else (e.g. L205), which is confusing and inconsistent.

L, M and t were only abbreviations, not model variables or parameters. We abandoned the abbreviations and directly put the dimensions in the 5th column of table 1 (i.e. length, mass, and time). We clarified the meaning of $t_h - t_m$ in table 1 (i.e. dissimilarity & proxy for ecological trade-off), with a reference to the new method section where we detail how the ecological trade-off emerges in our framework, and how/why it is linked animal phenotype dissimilarity $t_h - t_m$.

- I am not sure to understand why you only talk about CSS and not ESS when the singular strategy are non-invasible but convergent.

An ESS is non-invasible but not necessarily convergent. As the notion of convergence does not exist in the framework from which the concept of ESS comes (i.e. evolutionary game theory (EGT), Maynard Smith & Price 1973), the distinction is not meaningful in EGT (but see Nowak 1990 for instance). In adaptive dynamics, a non-invasible singular strategy can be convergent (it is then called a CSS, Eshel 1983); or non-convergent (it is then called a “garden of Eden”: when it is lost, it is lost forever, e.g. Hofbauer & Sigmund 1990). We did not introduce the latter in our framework because the dynamics resulting from such a singularity (runaway dynamics) are qualitatively similar to those resulting from repellors given our investigation.

- Fig 1.: What you mean by “temporality” is unclear.

The formulation was rather confusing, we meant “over time”, which is now corrected in the graphical abstract (old Fig. 1).

- Fig. 5: “orgy” is not defined and not a classical term in Adaptive dynamics as far as I know.

Following the advice of referee 2, we are now using the expression “unbounded population growth” which is more appropriate (Fig.5, and in supp. info. L303 & L305) The term “orgy” appears in a book chapter (i.e. May 1981), to refer to the unbounded growth of populations in models of two interacting mutualistic species.

- L458-463, Eq. 5: this part is very unclear. α is not clearly defined, is it an input parameter, an output of a statistical analysis? Regarding Eq. 5, some elements are not

defined as c_{sim} . I was also unable to understand where does this equation come from, how it is used.

α is an input parameter. We are here actually reformulating our model by changing the expression of plant intraspecific competition c_p into a function that depends on the phenotype of competing plant morphs (the variables) and two new parameters α and σ_c . We clarified this by a new clear sentence **L492-493**, as well as **L494** (“now”), and by adding the arrow in equation (5). Moreover, to avoid confusion with the type II error threshold α in statistical analyses, we replace α by α_c (i.e. indexing by c for competition as done for σ_c).

- App. III, L320-325: rep1, rep2, css, etc. are not defined.

Thanks for pointing this out. Those are now clearly defined in the caption of Fig. B2, and a reference to this caption is given in the main text of the appendix (i.e. **L 274 of supp. info**).

- It is not easy to make the link between Fig.B3 and Figs. 1A, 2A, 5. I would suggest to combine both Fig 1A and Fig3B to better explain how you measured the proportion of the different regions, or even maybe replace Fig3B in 1D by a similar toy figure but in 2D.

Old Fig. **B3** (supp. info, appendix B, **now labeled Fig. B2**), was modified by adding a panel “a” showing a 2D eco-evolutionary landscape as suggested (i.e. as old Fig 1A). An eye icon indicates how the one-dimensional view (panel “b”) is obtained from the 2D panel.

Comments to the MS by Yacine & Loeuille

This MS presents a model about the stability of plant animal-interactions when there is an ecological trade-off between attracting pollinators and deterring herbivores. Authors use adaptive dynamic modelling and invasibility analysis to find a relationship between the intensity of this trade-off and the resulting natural selection (stabilizing, directional, or disruptive) on a plant trait that influences both pollinator attraction and herbivore deterrence. The main results are that a high pollination strength compared to herbivory leads to stabilizing selection and coexistence of pollinator and herbivore, while a high herbivory strength compared to pollination leads to directional selection and extinction of one of the interactors. In cases of strong ecological trade-off, disruptive selection can occur, with the evolution of polymorphism in plant traits.

I found this MS inspiring. It may be relevant, for example, in the analysis not only of ecological trade-offs in which pollinators and herbivores are different species, but also in those cases in which pollinators and herbivores are the same species, such as in nursing pollination systems (Table 1 in Hahn & Brühl, 2016), or in the case in which the outcome of the interaction is not always of the same sign (Gómez et al., 2023).

Thank you for finding our work inspiring, as well as for your helpful comments and feedback.

We positioned our work within the literature on the mutualistic-antagonistic continuum as suggested (L68-72). We did so early in the introduction (i.e. context), but not when introducing our modeling framework as the latter is not precisely appropriate (for instance, if herbivores and pollinators are the same species, their population dynamics should explicitly depend one on the other, e.g. Picot *et al.* 2019).

As an empirical ecologist, I will not deal with the modelling itself, but on the ecological framework of this study. This ecological framework requires some clarifications. First, when reading this MS I wondered if the model applies to all potential tripartite interactions of plants with pollinators and herbivores or specifically to those in which there is a trade-off in attraction of pollinators vs. deterrence of herbivores. In principle, this model applies to the latter scenario. However, authors refer to a gradient between a strong trade-off and a weak trade-off, which makes me think that in the limit, the trade-off disappears and the interaction of the plant with its pollinator(s) or its herbivore(s) are independent of each other. Whether this limit situation can be interpreted from this model or not is relevant because the empirical evidence for trade-offs between pollination attraction and herbivore deterrence is limited and biased to strong trade-offs.

We clarified our ecological framework notably by having a new paragraph in Methods whose aim is to precisely define “ecological trade-off” in our framework (L197-216). As highlighted in this new paragraph, the ecological trade-off emerges in our framework from the trait-matching assumption (interaction strength increases with plant-animal phenotype matching).

Our model thus applies to any tripartite interaction community with the latter assumption. Note that any dissimilarity in animal traits will lead to situations in which a trade-off occurs (outside the two traits) or no trade-off occurs (in between the two traits), so that our model actually covers both situations. Clarifications about “ecological trade-off” were also incorporated earlier in the text (in the introduction, **L89-92**, and in the largely rewritten last paragraph of the introduction **L135-137**).

Thus, authors should be careful in choosing the empirical references cited in the discussion; not any study including pollinators and herbivores is necessarily relevant, as many interactions may not entail a trade-off.

We chose all our empirical references carefully so that the reported patterns suggest an ecological trade-off. We believe that this was not clearly visible owing to the fact our initially submitted manuscript version did not precisely define “ecological trade-off” and how it emerged in our framework. It is now clearly defined **L89-92**, **L135-137**, and **L198-200**: “a positive covariation between the strengths of pollination and herbivory”. When such positive covariations occur, benefits from one interaction are traded against costs in the other interactions, providing a rationale for ecological trade-offs (see Strauss *et al.* 2002). While it is true that many empirical references do not use the term “ecological trade-off”, the reported patterns suggest a positive covariation between pollination and herbivory strengths, most often as a result of both pollinators and herbivores having the same preference for plant phenotypes (table 7.1 in Strauss & Whittall 2006; Fig. 2 in Theis *et al.* 2014). Other references (**L615-616**: Melián *et al.* 2009; Sauve *et al.* 2016) reporting the topology of empirical plant-pollinator-herbivore networks indicate a positive correlation between the number or strength of plant-pollinator and plant-herbivore interactions for various plant species, again suggesting a positive covariation between pollination and herbivory strengths. We reformulated the sentence **L614-617** to be precisely in line with the results of those papers. All in all, while we acknowledge that not all cited references explicitly refer to an ecological trade-off, we feel they are nevertheless relevant once our definition of ecological trade-off is clearly provided.

Second, a clarification about the meaning of the trait match between plant and animals is needed, early in the methods section. On page 21, line 406, trait match is mathematically described as $t_p - t_m$ or $t_p - t_h$ but (a) this description is given too late for readers to follow the argument and (b) the ecological meaning of t is uncertain; I found myself thinking sometimes in actual values of a trait (e.g., phenology) and sometimes in terms of (behavioural, chemical) preferences of both kinds of animals towards the plant (actually, it is easier to define t in the same "units" for the animals - t_p vs. t_h - than for any comparison between the animals and the plant).

Thanks for pointing out that our formulation of trait-matching is not explicit enough early in the manuscript. We clarified this formulation earlier (in Model, **L181-183**). Moreover, the ecological meaning of the plant and animal phenotypes is left general on purpose, which we

believe to be one advantage of modeling approaches. Any plant trait (1) subject to evolution, (2) that is involved in both pollination and herbivory and (3) which relates to plant-animal interaction according to a trait-matching set up (L181-183) is a priori relevant. That is why we provide several examples of such traits L183-186.

Third, a clarification about the connection between animal dissimilarity and the strength of the trade-off should be provided. In particular, what do the authors mean by dissimilarity? Taxonomic, morphological, behavioural, in their preference for the plant, in the chemical receptors used to locate the plant, all of it, any of it?

Dissimilarity refers to the difference between animal species in their phenotype (i.e. preference for the plant phenotype t_p , so what it is exactly depends on what is considered for t_p in any specific case (see previous comment)). Precisely, it is the model term $t_h - t_m$, as has notably been corrected in line 7 of Table 1. It is here a proxy for the strength of ecological trade-off as clarified L137-140, and L206-216 and with Fig. 1.

The logic of this model seems to build on a previous model by the same authors (Yacine & Loeuille, 2022). It would be advisable to clearly present in the Introduction how the present study advances the arguments provided in the previous work.

We clarified (L145-148) that our previous work (Yacine & Loeuille 2022) on plant-pollinator-herbivore communities was exclusively on the study of ecological dynamics (equation (1)). In that model, neither phenotypes nor (their) evolution were considered. The population dynamics arising from equation (1) can be rather complex, and we wanted to have an in-depth understanding of such dynamics (coexistence, stability) before addressing the question of phenotype evolution. The distinction between this previous study and the current one is again reminded L173-177.

Other minor aspects of the MS that need to be addressed:

1. Lines 91-113 should be a single paragraph. Corrected L97-124.
2. Fig. 1. Please, in the figure caption make clear that panel A pictures an eco-evolutionary landscape. It was difficult to read this panel at first. Old Fig.1 is now the graphical abstract, but we explicitly mentioned panel A is an eco-evolutionary landscape.
3. Results are rather long. I advise to add headings for the various kinds of results presented, at lines 265, 308, 353, and 407. Thanks for the suggestion. We added headings and L290, L335, L381 & L478.
4. Lines 340-346, please, add strength after pollination or herbivory, to avoid confusion. Same in line 378. Same on the title of panel A in Fig. 6. Actually, in these cases, the ratio of pollination

to herbivory is not that of strengths strictly speaking (i.e. a_{pm}/a_{ph} given our model formulation), but rather the one presented in **Fig. 3** ($a_{pm}^M/a_{ph} H$). We therefore kept the formulation in rather general terms, but added several references to **Fig. 3** to avoid confusion (**L367-369**). Note that the term “strength” was added each time we are referring to a_{pm}/a_{ph} (See also our answer to one comment by the recommender on global clarity).

5. Line 380, "toward the pollinator phenotype and away from the herbivore one". Corrected **L408**.

6. Line 564, *Nicotiana*, instead of *Nicotinia*. Corrected **L619**.

I hope these comments will be useful to the authors.

Marcos Méndez May 2023

References

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- Hahn, M.; Brühl, C. A. (2016). The secret pollinators: an overview of moth pollination with focus on Europe and North America. *Arthropod-Plant Interactions* 10: 21-28.
- Yacine, Y.; Loeuille, N. (2022). Stable coexistence in plant-pollinator-herbivore communities requires balanced mutualistic vs antagonistic interactions. *Ecological Modelling* 465: 109857.

Reviewed by Yaroslav Ispolatov, 22 May 2023 16:44

I am very sorry for the delay.

The manuscript 'Attracting pollinators vs escaping herbivores: eco-evolutionary dynamics of plants confronted with an ecological trade-off' presents a very thorough analysis of an eco-evolutionary model of 3 species: a prey, prey's cooperators, and a predator. Apparently for definiteness, these species are designated as flowering plants, their pollinators, and herbivores. The model is phenotype-based and only prey can evolve. A "tradeoff" is defined as what occurs in a scenario when the selection pressures on the plant phenotype from the pollinator and herbivore act in opposite directions. The Authors present the quite intuitive adaptive dynamics prediction of the various evolutionary regimes and then confirm and build on the intuitive predictions doing a complete numerical sampling of the multidimensional parameter space of the model. And a special praise should be given to the clarity and excellent organization of the Supplementary Materials.

Thank you for your helpful comments and feedback, as well as for the special praise on our Supporting Material.

That all said, there are several serious drawbacks of the manuscript that to some extent devalue its merits.

The first, and apparently the easy fixable one is to be more precise with the term "tradeoff". This word has become quite loaded and a reader, seeing it in the Title, first lines of the Abstract, and then numerous in the Introduction could quite feasibly be left puzzled by how the tradeoff is played out in the model. I suggest to move the explanation from the first paragraphs of Appendix B to the main text to make the definition of tradeoff more specific and precise. I would also look for perhaps more wordy yet more specific definition of the main quest of the manuscript very early in the text.

We clarified the term "ecological trade-off" by providing a definition early in the introduction **L89-92**. The last paragraph of the introduction was largely modified notably to give a better grasp on how the ecological trade-off plays out in our modeling framework **L135-142**. Finally, a novel paragraph **L197-216** "Definition and emergence of ecological trade-off" now starts the Method section. Following your suggestion, this paragraph essentially corresponds to what was initially in **appendix B**, and relies on an improved version of the **old Fig. B1**, now presented as **Fig. 1**. This paragraph notably clarifies that the ecological trade-off emerges from our trait-matching assumption.

Second, way more attention should be given to the quantitative definition of the model. What are the meanings of the logistic (negative quadratic) terms for the pollinator and herbivore? Do those species compete for space? Such a term is essential for the stability of the model and could also be biologically justified for the plant, but why for the animals? The "orgy", coyly

mentioned in the main text, which apparently is way better described as "unlimited population growth" in the Supplementary materials, could be totally avoided by making the plant birth rate saturating in the limit of the infinite population of pollinator. I think this is totally justified empirically and could be implemented in a multitude of ways, for example, defining the per capita birth rate as $r_p(1-c*\exp(-a_{pm}*M))$. This or any other realistic definition of the limited plant birth rate will also make the c_m and c_h terms unnecessary for the stability. \(\ \)

We used a rather general formulation of negative density dependence that we proposed to interpret as competition, and we now provide biological interpretations as suggested L164-167 (namely space, water and nutrients for plants, and interference competition for animals). Other published theoretical works (e.g. Thébault & Fontaine 2010) have made similar assumptions. We however rewrote the sentences L 163-169 to put forth that these negative quadratic terms can be more generally interpreted, acknowledging that the different populations can be regulated by other aspects that are not explicitly modeled (other predators, other resources not accounted for, diseases...).

Third. Unfortunately, it is assumed that the plant evolution has no cost, that is, the plant's phenotype can change indefinitely without affecting the plant's birth and death rates. Besides being totally unrealistic biologically, this assumption also results in evolutionary regimes, such as a runaway evolution, that will not be possible if the plant phenotype were confined to an ecologically "liveable" interval. Again, there are many simple and "canonical" ways to take the ecological costs of changing phenotype into account, i.e. phenotype-dependent birth rate r_p or carrying capacity ($1/c_p$) that have a single (or even several) maxima and decay to zero away from those maxima.

Forth, are there any justifications for fixing the phenotypes of both animal species? Is it justified empirically? Are there any differences between animal/insect and plant genetics explaining that? A saying goes that a predator is evolutionary doomed if it evolved slower than its prey. In the presented work, in several scenarios the doom is circumnavigated by confining the prey phenotype to the favourable for the predator zone via its attraction to the pollination optimum. Allowing all three phenotypes to evolve will dramatically alter the evolutionary and ecological "phase diagrams", resulting in many non-stationary scenarios.

Given that I'm not reviewing the manuscript for any particular journal, I don't think I am in a position to make requests about the last 3 limitations. At the same time, I feel that independent of the target journal, those issues should be thoroughly discussed. Presumably, the authors have accumulated a lot of intuition about the model's dynamics that could allow them to qualitatively discuss what happens in more general cases that are free of those assumptions.

Regarding the evolutionary assumptions of our model (no animal evolution, no cost for plant evolution except pollination & herbivory), we followed the advice and discussed the meaning and implications of these two assumptions (L555-560 and new Discussion paragraph L562-582). We provide biological interpretations of these assumptions (L576-579 & L596-599, and

highlight, as advised, the limitation, notably regarding the occurrence (L580-682) or ecological consequences (L557-560) of runaway selection. We also explicitly present our work as a first step before more complex coevolutionary scenarios are explored and highlight the difficulty of deriving coevolutionary predictions from our work. (L567-573). Many theoretical works investigate the evolution of a given species, without necessarily tackling the coevolution of other species.

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