

Reviewers comments

General comment from the PCI recommender Sylvain Billiard

Two reviewers and myself have thoroughly read your paper. We all find that your paper has the potential to be recommended by PCI Ecology. However, we all find that it lacks much clarity in the concepts used and the definitions, and in the model assumptions and calculations. You will find in the attached reviews, technical and conceptual comments and corrections, as well as other aspects such as suggestion of improvement of the paper organization. It is important to address these questions and comments in order to satisfy a large audience from empiricists to theoreticians.

You will also find detailed comments from my own reading of your paper. You will see that I insist on the following aspect: I think that your model is very general and, as a consequence, lacks specificity regarding the core of your message: the evolution of plant pollinator interactions. I would suggest to be less specific and more general in the introduction (it is not necessary to invoke global changes, pollinator declines, etc. to justify your work) and talk about what you really do: 1) develop an adaptive dynamics model for the evolution of the interaction rate between two mutualistic species, and especially study their conditions for coexistence, and 2) apply it to a specific question inspired from plant-pollinator interactions in a context of environmental degradation. I find particularly important to compare your model to previous ones which can be very close, for instance Ferrière et al. 2002 (Proceedings of the Royal Society B).

→ Dear PCI Recommender, we are glad you find our work interesting. We completely agree with you that the model is actually more general than a plant-pollinator system. We have therefore modified the introduction and discussion of our study following the structure you propose. We now present a mutualistic model where a focal species evolves and faces a decline of its interacting partner population. These results can be interpreted in the frame of the pollinator population decline and plant evolution. We have also added text linked to other types of mutualisms, notably plant-mycorrhizae interactions.

As recommended we link our model to previous theoretical studies, including that of Ferriere et al. 2002, as mentioned for example at line 54-60 in our introduction and line 232-254 in our discussion.

Detailed comments and corrections for the paper 'Plant eco-evolution weakens mutualistic interaction with declining pollinator populations' By A. Weinbach, N. Loeuille and R.P. Rohr

Sylvain Billiard

Abstract

- Do the author consider that “population decline” = “decrease of the intrinsic growth rate” as suggested in the abstract? I would rather think of population decline as the population size decrease rather than the intrinsic growth rate. I imagine that decreasing the growth rate gives a lower population size but a population decline can come from many other possible mechanisms, for instance fragmentation.

→ *As requested, we clarified the link between population decline and our model. The sentence is now: “We next assume an external disturbance that decreases the partner population by lowering its intrinsic growth rate.”.* Note that, differentiating the equilibrium population at equilibrium (A^* in system of equation (3)) shows that the population decline when the growth rate declines in the case of our model.

Introduction

- Line 32: ‘shown’ → ‘showed’, or ‘have shown’

→ *Corrected to showed in the manuscript.*

- Line 33: ‘already’ can be removed

→ *Corrected in the manuscript.*

- Line 36: ‘high’ → ‘height’

→ *Corrected in the manuscript.*

- Line 38: I am not sure these experiments consider ‘deterioration’ of pollinator communities. I would avoid the term.

→ *What we meant was that plant population can evolve in response to changes in the pollinator community. We modified our introduction and it does not include that sentence any more.*

- Line 46: Isn’t a little exaggerated to talk about a plant-pollinator community when considering a pair of species only?

→ *Corrected to “mutualistic system” in the manuscript. We follow the main recommendation to generalise our study.*

- Line 50: ‘Clarify’, why does one need clarification? Are there results not clear? Which ones? Be more explicit.

→ *We modified our introduction and it does not include that sentence any more.*

Model

- I am not sure that Fig. 1 is helpful. The model is simple enough and Eq. 1 are self-sufficient

→ *This figure is intended to the less theoretician of our readers, who might only be interested in our conclusions, but could also grasp in one glance the general structure of our model without having to read equations. Having presented similar model in conferences, we noticed that this type of figure help non-theoreticians, and we would like to keep it if you agree.*

- Lines 64-70: precise whether the parameters are supposed positive or not, especially the parameters γ . I suspect they’re supposed both positive?

→ We added the sentence “ Because we consider mutualism as the net benefice obtain by both species, both γ parameters values are assumed positive in our model” at line 86-88.

- A main comment about the model derivation: you consider that mutualistic interactions have no cost, while it is well-known that it is never the case: mutualistic interactions can be defined as when the net benefit for both species is positive, which is not necessarily always true, in particular because the cost and benefits of the interspecific interactions can depend on species density. See for instance Holland and DeAngelis (2010). Considering the interaction between species as a resource exchange can help in avoiding the artificial positive feedback loop mentioned by the authors (Eq. 4). Even though I am aware the authors want the model to be as simple as possible, I think this is an important limitation of the current model which should either justified or discussed.

→ We agree that our model is very simple and that other functional responses would have definitely be possible. Many different functional responses have been proposed, just for pollination. In the model build by Holland and DeAngelis 2010, the intensity of the interaction is controlled by a saturating function. This prevent an explosion of the positive feedback loop that is observed in linear model such as ours. We have chosen a linear model to facilitate the mathematical analysis. To control for unlimited growth, we add the competition term, which is biologically relevant. In the new version of the manuscript, we have tried to explain why we kept the model simple and try to clarify its limits. We have also added a sentence to justify our choice of function at lines 113-115. Note also that while we do not allow the mutualistic interaction to become antagonistic, as some models do, we still have a benefit and a cost to mutualism and mutualism can be counterselected. Considering the fitness gradient (see equation 9) shows that the gains resulting from the mutualistic interaction (the $\gamma_A A^*(\hat{\alpha})$ parameter) are indeed dependent on the density of the species A. Below this density, costs resulting from the trade-off ($\frac{dr_p(\hat{\alpha})}{d\hat{\alpha}}$) offset the benefits, and mutualism is counterselected.

- Line 67: I tend to partially disagree that α represents attractiveness. It can be interpreted that way but I think it is much more general: it is the interaction rate, which might be affected by plant attractiveness, or many other mechanisms, for instance pollinator flight speed, or visitation speed, etc. For me it is not straightforward that introducing attractiveness in a model would result in Eq. 1. If one would start from the mechanistic point of view, it is not clear what assumptions should be made to obtain such equation (see for instance Fishman and Hadany 2010 TPB). I would expect more precise justification on the chosen form of equation 1.

→ We agree that α is an interaction rate and therefore contains other aspects than plant attractiveness. However, the assumption we make is that we model only the changes in α that are due to changes in plant attractiveness. We assume that other aspects of the interaction are contained in the gamma parameters. We have added these sentences to make our conception clearer starting at line 88. “We modulate the intensity of the interaction between the two species with the parameter α . While the interaction depend on biological traits from both interactors (pollinator morphology or flight capacities, plant attractiveness), we have chosen to model it as a plant dependant trait and have therefore linked it to other plant traits via a trade-off function. We interpret it here as the attractiveness of the plant for the pollinator, and it corresponds to the trait that will be under selection in the rest of the study.”

- Line 69: ‘encompasses’

→ Not in the manuscript anymore due to the rewriting of the introduction

- Line 75: ‘coexistence of the two species in time can be maintained’ could be replaced by ‘coexistence is stable’.

→ Corrected in the manuscript.

- Globally, I am not sure to understand why the authors focus their study on plant-pollinator. Indeed, their model is not specific to a plant-pollinator interaction but rather to any mutualistic interaction in a classic mutualistic Lotka-Volterra system with Holling Type I functional response where the interaction rate evolves. I would find more appropriate to present the paper and its model like this more general, and the authors could present their results regarding the decline of pollinator as an application of the general model, discussing the fact that their model lack plant-pollinator specificities.

→ *Your comment is very relevant, and we have rewritten our manuscript to make it about mutualism in general. See our first answer as a complement.*

- I am rather surprised that noone ever produced an adaptive dynamics model for the evolution of mutualism under the mutualistic Lotka-Volterra system. I am not a specialist of this literature, but it would be worth looking for such potential previous paper. If such a paper does not exist, then it is worth stressing about this in the paper. If the authors are the first to analyze such a simple and general model, the authors should state it. However, consider replacing the present work in older ones such as Ferrière et al. 2002 for instance.

→ *Thank you for giving us this bibliographical reference. We tried to take previous work into account all along our manuscript. We specify that we rely on discussion of previous articles, as stated for example at lines 54-60 in our introduction and line 232-254 in our discussion.*

Results: evolution of plant attractiveness

- Line 95: since the trade-off is the core of the model, I would not put the definition of the trade-off functions in Supp. Mat., but rather in the main text. Fig. 1 would be advantageously replaced by Fig. 1 in the SM.

→ *We agree that this is a very important aspect of the model. We have added the figure representing the shape of the trade-off depending on the value of the s parameter on figure 2, and the formula corresponding to the chosen trade of at lines 117-123.*

- Lines 98-137: The very classical and canonical adaptive dynamics methods are extensively described. I think this is not necessary: the description made here are not sufficient for the reader to be able to do the calculation by themselves, and this is the goal of the SM. I would remove this part, summarize it and place a summary in the model description section. Instead of giving a vague description of the method here, I would find more important to give the most important analytical results here, which could help the readers to better understand what's happening.

→ *We agree with you. We have tried to rework the text to make it more easy to read for non specialist and left the details for the supplementary informations. However, we preferred to keep the definition of fitness and the canonical equation in the main text, because we believe they may be useful for the reader to understand the analysis..*

Results: Consequences of pollinator population decline

-L 160: I suspect that α_{max} corresponds to α_{cl} from Eq. 4, I am exact?

→ *We apologize for the confusion. The terms α_{max} and α_{cl} encompass different biological realities, hence the different names. As explained at line 108-111 α_{max} value is strictly below that of α_{cl} , to prevent infinite growth that in reality is moderated by other phenomena (e.g. density dependent diseases).*

- L167: Reconsider rephrasing the sentence beginning by 'In this case'. The sentence is long and complex, and it is difficult to understand it. For instance, I suspect that a comma is missing as well as a 's' giving '...above the Garden of Eden value, the evolution converges ...', otherwise the sentence is hard to understand.

→ *As suggested by the editor, we have modified this sentence and split it into different ones.*

- L173: 'Now consider the environmental degradation': It was not clear that all the description of Fig. 3 before now was about a case without degradation. I would suggest to explicitly introduce the previous description of Fig. 3 as a 'reference' case.

→ *Figure 4 (old Figure 3) pictures all possible environments on the x-axis. Positive values of intrinsic growth rate correspond to a "good environment" because it means the pollinator sustains high populations, and negative values means that environmental conditions are unfavourable. We have tried to clarify this at lines 168-173 .*

To better emphasize this "good" vs "bad" dichotomy, we have added a part in the sentence before the one you mentioned "For positive pollinator intrinsic growth rates ($r_A > 0$), corresponding to a "good environment, the system converge toward..." at line 190.

- L178: Restoration has not been defined: what did the authors do exactly? What is it changed in the model?

→ *Restoration attempt is here modelled by an increase in the previously negative value of the intrinsic growth rate r_A . We added a sentence at lines 196-199 to specify what parameter is affected in the model, and to what it could correspond in a biological system.*

- There are important implicit assumptions regarding the timescales: do the authors really think that 'restorations' play on the same timescale than the eco-evolutionary feedbacks in their model? I do not think so. The implication of their results regarding the restoration should be taken with caution and justified and discussed further.

→ *We agree that timescales will likely be key in the outcome. We have tried to answer this comment in two ways. First by clarifying that in our analysis we implicitly assume that restoration is fast compared to the eco-evolutionary dynamics. Second, we have tried to better discuss the impact of rapid shifts and the various timescales of eco-evolutionary dynamics and restoration attempts, at lines 202-204, and in the discussion part at lines 290-296.*

- The paper lacks any technical information regarding how the authors obtained their results about environmental degradation and restoration. Which equations are used? How? How exactly are Fig. 3 and 4 obtained? Instead of describing very well-known adaptive dynamics in the previous section, I would find more appropriate that the authors give much more details about what makes the technical specificity of their paper: how to take into account environmental degradation and restoration. This remark is to be related with the previous one: more technical details would make more explicit the underlying assumptions concerning timescales.

→ *We apologize for the lack of clarity. We have used E3 diagrams to show effects of environmental changes (including deterioration and restoration) on the eco-evolutionary dynamics. These graphical tools have been used by several people in the past (for instance in references 1 and 37). We have tried to clarify this and make explicit references to these articles when describing the figures. Environmental degradation and restoration is here simply modelled by increasing and decreasing r_A value. We realize that this wasn't explicit enough in our previous manuscript, and we have added this precision to the results section at line 175-178 and 196-199.*

Discussion

- To my mind the first sentence of the Discussion summarizes very well the true objective of the paper: ' The present work highlights how evolution may play a critical role for mutualistic interaction maintenance in time'. Plant-pollinator responses to decline and restoration is an application of this model.

→ *As suggested, we revised our introduction and discussion. Our model is indeed more general and we now introduce it as a two species mutualistic system, that could for example be interpreted as a plant-pollinator one. In the method and result sections we keep the plant and pollinator denomination to*

make our paper more readable, but insist in the introduction and discussion part on the generality of our model.

Report on the paper Plant eco-evolution weakens mutualistic interaction with declining pollinator populations

by Avril Weinbach, Nicolas Loeuille and Rudolf P. Rohr

submitted for publication in PCI Ecology

This paper considers a system of two interacting species, a plant population and a pollinator population, represented by a system of two ordinary differential equations. Dynamics of both populations include intrinsic growth, intraspecific competition as well as mutualistic interactions between both species depending on plant attractiveness. Authors study evolution of plant attractiveness in an adaptive dynamics way. For that they consider a trade-off between the plant attractiveness and the plant intrinsic growth rate (justified because energy used for attractiveness is not used for intrinsic growth). They illustrate that changing the slope of the trade-off changes the nature of singular strategies of the system: for convex and linear studied tradeoffs, the singular strategy is a repellor; for concave studied trade-offs, there is a convergence-stable strategy (CSS) and eventually a Garden of Eden. Some analytical calculations are done in Appendix for a particular family of tradeoffs. For convex tradeoffs, they study the impact of pollinator population decline by studying CSS and Gardens of Eden w.r.t to the intrinsic growth rate r_A of pollinator population. They discuss the evolution of plant attractiveness in case of environmental degradation for pollinator population (i.e. r_A switches from positive to negative values): attractiveness converges towards 0, leading to pollinator extinction, except if a restoration plan is undertaken sufficiently fast (before a strong decreasing of attractiveness).

In my opinion this paper is interesting. However, I think that the analytical study (in Appendix) for one particular family of tradeoffs is not sufficient to make general conclusions about ESS w.r.t. the shape of the tradeoff as it is done at the end of Section 3. Moreover several misprints are to be corrected in the paper. I give several comments and modifications below that would, in my opinion, help to improve the content of the paper, which can deserve publication after these modifications.

→ Dear reviewer, thank you for the interest you express about our manuscript and for all the helpful comments you gave. We hope we addressed them accordingly, and that our paper will then deserve publication as you mentioned.

Comments

1. In System (1), N should be A in the first equation;

→ Corrected in the manuscript.

2. In System (3), α A should be c A in the second equation;

→ Corrected in the manuscript.

3. p.8, l.140: you say that “only concave allocative trade-offs leads to non-invasive strategies.”. However, you study only particular trade-offs on the form

$$r_p(\alpha) = \left(1 - \left(\frac{\alpha}{\alpha_{max}}\right)^s\right)^{\frac{1}{s}}$$

I think that it is not sufficient to generalize your results to all trade-off forms. I suggest to modify the sentence into something like “among the particular trade-

offs that we study (see Eq. (A2) in Appendix A), only concave allocative trade-offs leads to non-invasible strategies”.

→ *As suggested, we have added this clarification to the manuscript, at line 158.*

4. p.8, l.141 It is not clear why long-term coexistence occurs only for non-invasible strategies. Moreover, from Figure 2, it seems that if α is initially larger than the repeller, it will converge toward α_{max} leading to the coexistence of both species.

→ *You are right, coexistence is not only guaranteed with a CSS, it is coexistence at intermediate parameters values that is guaranteed. We have therefore corrected our sentences. Among the four types of singularities, invasible strategies (repeller) ultimately lead to extreme situations, with either $\alpha=0$ or $\alpha=\alpha_{max}$. When $\alpha=0$ interaction is no longer maintained between the species, and they will coexist only if mutualism is non-obligate (i.e. $r_A > 0$), but the mutualistic interaction will not exist. When $\alpha=\alpha_{max}$ there is still coexistence if the pollinator is sufficiently numerous to maintain the plant population, whose growth then only depends on the mutualistic interaction. However, note that evolution in these instances pushes us toward the stability limit α_{cl} where the ecological equilibrium (3) becomes unstable (ie, the mutualistic interaction is so powerful that fast growth is expected for the two populations and other components should be added to the model). We have tried to clarify these aspects at lines 160-173.*

5. Figure 2. For panels a and b, it seems that $\alpha = 0$ and $\alpha = \alpha_{max}$ are both CSS.

→ *These two points cannot be considered CSS because they do not correspond to the singular strategies (the fitness function isn't null at those points). However they are still endpoints of evolution for convex trade-off, and we have added this information at lines 168-173.*

6. Figures 3 and 4: I think that $\hat{\alpha} = 0$ is a CSS for $r_A < 0$ (as illustrated for example by arrows (4) and (7)).

→ *As explained above in that case the fitness function is not null, therefore by definition it cannot be a singular strategy.*

7. p.13, l.184. Is $s = 2$ a threshold for the existence of Garden of Edens? What is the landscape for $s = 2$?

→ *The reviewer is right when suggesting that $s = 2$ is a threshold for the existence of Garden of Edens and, therefore, can be a bifurcation point. However, the full mathematical study of this bifurcation seems quite difficult, and may clearly be the topic of another manuscript. We made some computation indicating that this is certainly the case, but not full mathematical proof yet:*

We computed the invasion gradient for $r_A = 0$:

$$\left. \frac{\partial \omega^2(\alpha_m, \alpha)}{(\partial \alpha_m)^2} \right|_{\alpha_m, \alpha \rightarrow \hat{\alpha}} = \frac{(1-s) \left(\frac{\hat{\alpha}}{\alpha_{max}} \right)^s \left(1 - \left(\frac{\hat{\alpha}}{\alpha_{max}} \right)^s \right)^{\frac{1}{s}-2}}{\hat{\alpha}^2} < 0$$

If $1 < s \leq 2$, then it has only one root ($\alpha = 0$), while if $s > 2$, a second root appears

$$\alpha = \frac{c_A * c_P}{\gamma_A * \gamma_P * \alpha_m^s}^{\frac{1}{(2-s)}}$$

Then, we would need to evaluate the second and cross derivative at this singular strategy value, and finally extend our results for value of r_A around 0.

We decided to not incorporate this computation, as this is also not the focus of our manuscript. However, we present the leads of these computations in the electronic supplementary material.

8. p.15, l.217 to l.225. I don't think that this result is surprising. In fact evolution of attractiveness is in favor of plant population, whereas degradation of environment affects pollinator population. If pollinator population is not abundant, the benefit of mutualism for plant population is very low. The best strategy for plant population is then to decrease attractiveness in order to increase its intrinsic growth rate.

→ You are right. That is in fact the way we interpret our results, as we specify it at line 192-196.

9. p.16, l.235. Decreasing plant attractiveness decreases pollinator abundance, however does it increase plant abundance? I think that it is the reason why the strategy of the plant evolves toward lower values of attractiveness.

→ Figure 4 panel b represent the plant biomass density at ecological equilibrium. The colour gradient is quite light but as you can see decreasing plant attractiveness for negative pollinator intrinsic growth doesn't seem to increase plant abundance. Furthermore, in adaptive dynamics, traits may be favoured that actually decrease population size or even lead to extinction (evolutionary suicide, see e.g. Parvinen 2005)

10. the term $\alpha_N \alpha_P - \hat{\epsilon}^2 \gamma_N \gamma_P$ should be $c_A c_P - \alpha^2 \gamma_A \gamma_P$ in Eq. (B7);

→ Corrected in the appendix.

11. Equation (B11) is derived from (B4) rather than (B6);

You are right, we first derive (B4) in the general case and then make α_m and α tend toward $\hat{\alpha}$.

12. the term $2c_P \gamma_A r_A$ should be $2c_P \gamma_A r_A \alpha$ (α is missing) in the numerator of (B12);

→ Corrected in the appendix.

13. unless I'm mistaken, the derivative of r_P is

$$r'_P(\hat{\alpha}) = r_P(\hat{\alpha}) \frac{1}{\alpha \left(1 - \left(\frac{\hat{\alpha}}{\alpha_{max}}\right)^{-s}\right)}$$

→ We indeed forgot an α , it has been corrected.

14. I don't understand how Equation (B14) is derived. However, in order to conclude on the sign of the derivative term, I think that it is better to let $(c_A c_P - \hat{\alpha} \gamma_A \gamma_P)^2$

at the denominator: As $\gamma_A r_A - \frac{c_A}{\alpha_{max}} = \frac{-\hat{\alpha} \gamma_A \gamma_P}{c_P}$, the derivative term is equal

to

$$\frac{\gamma_A \gamma_P}{(c_A c_P - \hat{\alpha} \gamma_A \gamma_P)^2} [c_A c_P + \hat{\alpha}^2 \gamma_A \gamma_P - 2 c_P \hat{\alpha} \frac{\hat{\alpha} \gamma_A \gamma_P}{c_P}] = \frac{\gamma_A^2 \gamma_P^2}{(c_A c_P - \hat{\alpha} \gamma_A \gamma_P)^2} - [\frac{c_A c_P}{\gamma_A \gamma_P} - \hat{\alpha}^2]$$

which is positive (when $\hat{\alpha}$ exists) because $\hat{\alpha} \leq \alpha_{max} < \alpha_{cl}$.

→ *This has been added in the appendix.*

15. Please, go back over all the appendix and correct the layout, for example:

I equation B12 → Equation (B12) (idem for all equation citations);

→ *References to the equations in the appendix have been updated.*

I one bracket is missing in the paragraph between Eq. (B3) and Eq. (B4);

→ *Corrected in the appendix*

I you refer to annex A, then name your sections by letters;

→ *We added letters to our appendix sections.*

Review of the manuscript entitled “Plant eco-evolution weakens mutualistic interaction with declining pollinator populations” by Weinbach, Loeuille & Rohr

Using an eco-evolutionary dynamics model, this work investigates how the evolution of attractiveness can impact plant and pollinator populations persistence. Different evolutionary scenarios are possible according to (i) the shape of the trade-off between attractiveness and plant intrinsic growth rate and (ii) the degree of pollinator decline. In general, I think this paper is clearly written and that it is easy to understand the frame and purpose of the study. While there is a wealth of literature about the demographic effects of pollinators decline on plant populations persistence, the potential effect of plants trait evolution remains understudied to date. This is especially true for floral traits that are linked to pollinator attraction. I however think there is a lack of clarity regarding the definitions of the plant intrinsic growth rate and the allocation trade-off. Because these terms are key concepts of the paper, I think the authors should explain more precisely the biological hypothesis behind those. This would allow empiricists, such as myself, to better understand the significance of the results presented in the manuscript.

→ Dear reviewer, thank you for the time you spent on our manuscript and for the interesting comments and corrections. We appreciate your interest in our work. We have tried to take your comments into account. Particularly, we have reworked the presentation of the model and tried to clarify the aspects you are mentioning. However, following the editor’s major comment, we enlarged the scope of our manuscript, presenting now our study has a model of two mutualistic species. We keep plants and pollinators as an example to interpret our model, but aim at more generality regarding the model goal, structure and results. Therefore, we choose to stay general on the evolving trait, that is not necessarily a plant trait, but definitely affect the strength of the interaction with the mutualistic partner.

MAJOR COMMENTS

Comment 1 – My first concern is about the plant intrinsic growth rate. As said in L60 “we assume r_p to be strictly positive because of other reproduction means, e.g. vegetative reproduction or autogamy”. I think this is a reasonable assumption except if individuals suffer from inbreeding depression. In this case, one can imagine that plant intrinsic growth rates could decrease to negative values because of mortality before reproduction or infertility.

→ We completely agree. While we do not explicitly model the genetic background of our two interacting species (as we rely on adaptive dynamics), we have tried to better discuss this. This work has been done by Lepers and collaborators (Lepers et al. 2014) . We refer to their work in the introduction (lines 54-57), but more notably we now discuss and compare their findings to ours in the discussion part at lines 234-240.

The exact definition of “plant intrinsic growth rate” should be clarified throughout the manuscript. For instance, the abstract suggests that it impacts plant biomass (L6), but this term is never used again in the rest of the paper and it seems that the authors modeled the plant intrinsic growth rate as the capacity of plants to reproduce only. I also found it confusing that in the section entitled “Plant-pollinator model and ecological dynamics”, r_p seems to be a population-level parameter, while in the section about “Evolution of plant attractiveness”, the same parameter is used in the allocation trade off as an individual-level parameter (the authors explain that “The plant has a given quantity of energy, divided

into different functions; some energy is allocated to intrinsic growth and to self-reproduction, and some to attractiveness”).

→ *The confusion you express arose from a lack of precision on our side that has now been corrected. All our ecological equations are following biomass variation, hence r_p corresponds to the plant biomass variation resulting from asexual reproduction and vegetative growth. As for the link with evolution, one main assumption of adaptive dynamics (that we present in the annex part on adaptive dynamics, and that we discuss in the discussion part), is a decoupling of ecological and evolutionary times. In between each evolving steps the system is assumed to reach the ecological equilibrium. Therefore, the equilibrium corresponds to a monomorphic population (the resident population with resident trait), which means that the individual trait α , being adopted by the whole population, affects its growth r_p .*

Comment 2 – My second concern is about the resource allocation trade-off between attractiveness and plant intrinsic growth rate. L72, the authors list various traits that are classically involved in attractiveness when defining parameter α . That list includes flower number, which has indeed been shown to play a crucial role in pollinator attraction in many systems. However, this trait should increase both functions: on one hand plants with a lot of flowers should attract more pollinators, but on the other hand plants with large displays will also produce more gametes and so should present a higher intrinsic growth rate. The exact definition of the two terms of the trade-off needs to be clarified. It would also be good to cite empirical work studying such tradeoffs and to acknowledge that, while tradeoffs are expected to be frequent, they might not be ubiquitous. Trade-offs can indeed be masked by a high inter-individual variance in the ability to acquire resources, or by inbreeding depression which could establish positive correlations among traits, independently of any resources allocation strategy.

→ *Our trade-off description was mainly in the annexe part, we now moved this part to the section “3 – Evolution of plant attractiveness” to present more clearly to what it biologically corresponds to and the underlying formula. Here we oppose two potential types of population growth of our focal species, a reproduction that is dependent of the interaction with the mutualism (here pollination for example), and a growth that is independent of the interaction (for plants it is both vegetative growth and selfing). We modified our explanation of the trade-off at lines 117-123 to make it more explicit. Note that results of assuming no trade-off can be easily perceived using our analysis. Consider equation 9. If there is no trade-off, the first term is 0, and the gradient of fitness is always positive. More attractive individuals will then always be selected, leading to an orgy of mutualism (equation 9 is always positive when α increase, the increasing trait is then always selected).*

Comment 3 – My third concern is about the hypothesis advanced by the authors concerning the evolutionary response of plant to pollinator decline. They only cite two possible scenarios: evolution towards more attractiveness or evolution towards selfing (and so less attractiveness). What about species which cannot evolve towards selfing, like dioecious species or self-incompatible species where self-incompatibility has not been bypassed? Is evolution towards increased wind pollination also a possible outcome?

→ *Using adaptive dynamics, we cannot explicitly model these components. In the introduction, according to your advice, we mention the work of Thomann et al. 2013 who present the possible genetic outcome of a pollinator decline, including an increase in autogamy. We also discuss these genetic consequences at lines 234-240 of the discussion part. Also, because we have tried to enlarge*

our model to account for mutualisms in general and not just pollination, we cannot account easily for such aspects in the new form of the manuscript.

MINOR COMMENTS

L1-2 – I think that the wording “recent pollinator declines [...] greatly impact plant-pollinator coevolution” may be too strong. To the best of my knowledge, there are not that many empirical studies showing a micro-evolutionary plant response to pollinator decline itself.

→ We modified our introduction and it does not include that sentence any more.

L28 – Maybe the authors should not mention climate change in the introduction section, since their model focuses on absolute pollinator decline rather than on phenological shifts.

→ We modified our introduction and it does not include that sentence any more.

L32 – “showed” instead of “shown”

→ Corrected in the manuscript.

L36 – “Flora size” should be replaced by “flower size”

→ Corrected in the manuscript.

L45 – The authors should consider citing Thomann et al. (2013) to emphasize the two different evolutionary plant responses under pollinator decline (i.e., evolution towards autonomous selfing or reinforced interaction to pollinators).

→ This paper is definitely in line with our project, and we have added it to the introduction, starting at line 57-60.

Equation (1) – I think there is a mistake in equation (1): N should be replaced by A

→ Corrected in the manuscript.

L72 – The amount and quality (sugar concentration for example) of nectar should also be cited because it is an important reward for pollinators.

→ We added the suggested information to that sentence at line 96.

Figure 1 – It is the only time in the article that the intrinsic plant growth rate r_P is written as $r_P(\alpha)$.

→ We have separated presentation of ecological and evolutionary dynamics, to try and make it clear. In the ecological part of our manuscript (equation 1 to 4) r_P is written without this precision. When we present the evolutionary trait α we specify that r_P is in a trade-off with α and could be written as a function of that trait. We replaced $r_P(\alpha)$ by r_P in Figure 1 to make these two part homogeneous.

L158 – Parameters values are indeed the same except for s (s = 3 versus s = 2.5)

→ We added this clarification to the manuscript.

L158 – Figure descriptions should only appear in the legend.

→ We suppressed from the paragraph the part presenting explicitly the figure and kept the explanations of the results it presents.

Figure 4 – “More concave trade-offs allow a larger coexistence domain”; this should not appear in the legend but rather in the results or discussion section.

→ We suppressed that information from the figure and specify such results at line 206.

L253 – I think that this should read “an increase in autonomous selfing”.

→ *With the modification that sentence does not appear anymore in our manuscript.*

Citation 42 – The name of the first author is Bodbyl Roels.

→ *Corrected in the manuscript.*

Electronic Supplementary Material

The allocation trade-off – I am not sure I understand the meaning of [1] and [2] in the first sentence.

→ *These two references correspond to a book chapter presenting the trade-offs associated to the pollination mechanism and an article with trade-offs and the evolution of clonal growth. This part is now in the main manuscript and correspond to references 30 and 31.*

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