

PCIEvolBiol #654 : response to reviewers

We would like to thank the reviewers for a thorough and thoughtful review to our manuscript. We have worked on addressing the reviewers' comments and believe that the paper has significantly improved as a result. Since some comments are redundant, we refer to other comment's responses in our answers. Below, you will find the reviewers' comments in black, and our responses in blue. The line numbers in our responses refer to the revised manuscript with tracked changes.

1 Recommender

1.1 Gaussian function

See notably the comment "As far as I could see, the results were obtained using Gaussian functions for the resource growth and resource utilisation functions..." It would be nice to provide additional results checking the robustness of key findings of the ms with respect to this assumption.

Response: please refer to our response to comment 3.5.

1.2 Trade-off with mortality

See also the comment l. 283 "We are nevertheless confident that similar results would have been obtained if the trade-off had concerned mortality"... Readers should not be interested in the authors' confidence in their results but rather in the information provided about the strength of these results.

Response: We agree that this sentence needs justifications. From the modelling point of view, adding a linear trade-off between PF and mortality brings similar terms as the trade-off used in our manuscript. We add the section B in the appendix to explain this point. We propose formal computation to see the similarity and we also numerically compare the emergence of resource consumer system with the same parameters as in Fig.1 but with a trade-off on mortality. In addition, we look at the effect of plastic foraging when it is fixed on the different characteristics of the model. Finally, we reformulate the sentence in the section 2.2 (l. 227)

"If the PF strategy had increased mortality d instead of handling time, this would have also reduced resource absorption (see Appendix B for a formal derivation of the model). A trade-off between PF and mortality therefore provided similar results (Fig. SI.4 and SI.5)."

1.3 Adaptive foraging

I agree with one reviewer's comment that the term adaptive foraging is used in a confusing way. I would just not reserve the term "adaptive" for traits shaped by natural selection, otherwise one can no longer say that natural selection is an explanation for adaptation (old semantic argument); but beyond that I see only reasons to tie adaptation to fitness increase, despite what the current introduction says.

Response: please refer to our response comment 2.1.

2 Reviewer 1

2.1 Plastic rather than adaptive foraging

First, I found the use of the term "adaptive foraging" to refer to plasticity misleading and confusing. What it gives for a provocative title, it takes away from the main text as one must systematically remember that "adaptive foraging" is not necessarily adaptive. The adjective "adaptive" should in my opinion be reserved for traits shaped by natural selection, especially within an evolutionary model. Why not refer to "foraging plasticity" throughout?

Response: The term "adaptive foraging" was used in the previous version because this is the established term in the literature. We agree that this can be misleading, this is indeed one of our main points in the manuscript. We followed the suggestion and now use the term "plastic foraging", the drawback being that the connection with the "adaptive foraging" literature is blurred. In the manuscript, this has been added in the introduction :

"The ability to adjust relative foraging efforts is a type of behavioural plasticity which has been called *adaptive foraging* in the literature [Valdovinos et al., 2013, Loeuille, 2010]. However, this term can be misleading because "*adaptive*" generally refers to traits shaped by natural selection. Here, the term *plastic foraging* (PF) will be used for clarity, moreover because its evolutionary dynamics will be explored." (l. 40)

Elsewhere in the text, "AF" has been replaced by "PF", "adaptive" by "plastic" and "adaptatively" by "plastically".

2.2 Introduction

Second, the introduction was difficult to parse, rapidly technical, and lacked linearity. For instance, the very first line (l. 29) introduces plasticity as a way to mitigate environmental changes. But the rest of the first paragraph is concerned with rather technical definitions concerning foraging theory. The notion of environmental changes is in fact not re-explored until the end of the third paragraph, and not in the sense that plasticity can mitigate its effects, but rather that foraging plasticity may evolve in response to environmental changes (l. 69). Such lack of linearity made the introduction difficult to follow. I would therefore encourage the authors to revisit and streamline their introduction.

Response: We agree that the reference to the mitigation of environmental changes was misplaced, and moved this point later in the introduction. However, we believe that it is important to clarify terminological issues as soon as possible (as evidenced by comment 2.1) in order to connect the present work to the rest of the literature. We therefore kept the definitions in the first paragraph.

2.3 Plasticity equation

The model section 2.1 is fairly dense and sometimes hard to understand. This particularly true of the key equation (eq. 7) describing plasticity. I would recommend explaining this equation clearly for the reader to grasp how plasticity works in the model. It may also be worth expanding on the definition of u as "potential gain". What does u measure exactly? More generally, it would also be useful where possible to give the units of these different quantities.

Response: We decompose the model section into two subsections (2.1 Resource-consumer niche model and 2.2 Foraging strategies) to clarify the manuscript. Then the key equation (7) now (11) is embedded in a different section focusing on the foraging strategy only. In addition, we have added some comments on the dynamics of the dynamics of the plastic foraging effort ϕ_{PF} . In particular, we describe the term u which corresponds to the resource uptake if the consumer puts all this effort on this resource. And we stress that the increase or decrease of the effort on a resource depends on the average difference between the uptake from the resource and from the other resource. We add the following sentences (l. 160):

"Conversely, when using PF, consumers actively search for resources, that maximize their energy intake. More precisely, they modify their foraging effort according to the potential resource uptake u , that corresponds to the amount of resource taken by the consumer, if its foraging effort only focus on this resource. It depends on the resource availability and suitability [e.g. Sundell et al., 2003]. A consumer will reduce its effort on a resource if the uptake from that resource is lower than the uptake from an other resource, that is if the difference between potential resource uptakes is negative. The resulting relative foraging efforts ϕ_{PF} may change over time according to the average difference between resource uptake, weighted by the foraging effort per resource and the amount of resource as follows "

2.4 Manuscript structure

The results section, while clear, reads to me a bit too much like a list of disconnected observations. This is perhaps a matter of taste, but I would appreciate some biological interpretation of results as they appear instead of having to wait until the discussion section. This would allow readers to gain intuition about the results. For example, sentences like " Niche width fostered AF because consumers depleted

the whole range of resources when their niche width was large, therefore competition between consumers was more intense, which led to the evolution of AF" (l. 291) could belong to the results rather than the discussion. More broadly, I think the results section could be improved by providing explanations and intuition behind the observations.

Response: We have profoundly reorganised the manuscript in line with the above suggestions. Please refer to our answer to comment 3.4

2.5 Minor comments

l. 88 "directly or indirectly" What direct and indirect effects are we referring to here? I know that this is explained much later in the discussion but at this stage, in the introduction, it comes out of nowhere.

Response : this sentence now reads: "it is uncertain whether the evolution of PF stabilises communities directly, by altering food-web structure, or indirectly, through its effects on functional diversity."

l. 210 "A typical outcome" ok but how typical? And what happens in other cases and why?

Response : this sentence now reads "Given the parameter ranges given in Table 1, the eco-evolutionary dynamics of the model lead to the diversification of resources and consumers along the ecological gradient"

Legend of figure 4: "chanhe" → change

Response : done

l. 278 " $S_m ax$ " → $s_m ax$

Response : we have fixed the problem.

l. 283 " We are nevertheless confident that similar results would have been obtained if the trade-off had concerned mortality" It would be nicer if this statement were supported by some argument.

Response : please refer to our response to comment 1.2.

l. 307 "scarce resources located at the niche edge were consumed significantly by adaptive foragers only, whereas abundant resources located at the niche center could be consumed in large amounts by random foragers" there needs to be more explanation of why this pattern.

Response : we specified this occurs "because random foragers cannot choose infrequent resources".

l. 321 " At the intraspecific level, niche overlap between individuals of the same species decreases in function of their abundance (Svanback and Bolnick, 2007; Tur et al., 2014), suggesting the existence of a plastic behavior." Why necessarily plastic? Could it not be genetic polymorphism?

Response : Yes indeed, in principle, by not in the case of Svanback and Bolnick, 2007. We added : "Short-term experimental time scales suggest this pattern is caused by plastic behavior (Svanback and Bolnick, 2007), although in the long-term this pattern may also be due to genetic diversification."

l. 351 " the mechanisms responsible for this observation also rely on the dynamical nature of the interaction webs produced by AF, but not on the emergence of robust topologies" The notion of robust topologies needs to be explained.

Response : we were referring to the previous sentence, where this notion was explained. Both sentences have now been reorganised in order to make this point clear :

"Previous theoretical studies have shown that PF can stabilize food-webs by favoring topologies able to buffer environmental disturbances, but in the present model such inherently robust topologies have not been observed. Instead, the mechanisms responsible for the stabilising effect of PF rely on the dynamical nature of the interaction webs produced by PF."

3 Reviewer 2

3.1 Notations

First, I think the paper would greatly benefit from some simplified notations. For instance, using R and C (capital letters) for the densities would allow a graphic distinction between the ecological vari-

ables and the traits x , y , and z (lowercase letters). For the mutation terms, equations (1) and (2) could be simplified by using the notations $\mathcal{M}_R(t, y)$ instead of $\mathcal{M}_y(r)(t, y)$ and $\mathcal{M}_C(t, x, z)$ instead of $\mathcal{M}_x(c)(t, x, z) + \mathcal{M}_z(c)(t, x, y)$ (incidentally, I think there is a typo in the last term of eqn (2)). Using r_e instead of r_{eff} would also be simpler, and I think you could use $F_C(t, y)$ and $F_R(t, x, z)$ instead of $F_r[r, c, \phi](t, y)$ and $F_c[t, \phi](t, x, z)$.

Response: We have simplified the notations, thanks to the reviewer's propositions, and we explain separately the different terms of the model to clarify the model section.

3.2 Foraging trait

Second, I think the reader needs to be told early on that the foraging trait ϕ is generically a function of t , x , y , and z . This is a key ingredient of the model and needs to be spelled out for the reader. Then, after equations (1)-(2), it would be helpful to have four paragraphs which explicitly mirror the different terms in the equations: (a) resource growth (where K and r_{eff} are discussed), (b) resource consumption and absorption (where F_C and F_R are discussed), (c) mortality and competition, and (d) mutation. Consider also using $\rho(t, y)$ and $\delta(t)$ for the resource growth and mortality/competition terms in eqns (1) and (2) respectively. Also, when defining F_C and F_R , it could be advantageous to define the quantity $b\phi\Delta/(1 + sb \int \phi\Delta R dy)$ (where I have dropped the function arguments for simplicity).

Response: We have reorganized the model section as proposed by the reviewer. We also provided some explanation about the foraging effort ϕ and the resource uptake per consumer U . We have added the following sentences (l. 127):

"In the presence of consumers, resources are exploited at rate F_R , whereas the consumer density increases through resource absorption at a rate F_C . On the one hand, these rates depend on the consumers foraging efforts $\phi(t, x, y, z)$, which characterize the time spent by a consumer of niche trait x and foraging trait z on a resource of trait y during a period t . On the other hand, they vary with the effective interaction strength $\Delta(x, y)$ between consumer and resource individuals. The function Δ is normally distributed around 0 with a variance σ , which measures the extend to which consumers can deal with a variety of resource types (Table A1). The variance parameter σ is chosen similarly to previous models [see e.g. Dieckmann and Doebeli, 1999, Egas et al., 2005], but it is not subject to evolution as in Egas et al. [2005]. The interactions are described by a Holling type II functional response, which provides the following consumption and absorption rates:

$$F_R(t, y) = \iint U(t, x, y, z)C(t, x, z)dx dz \quad \text{and} \quad F_C(t, x, z) = \alpha \int U(t, x, y, z)R(t, y)dy \quad (1)$$

$$\text{with } U(t, x, y, z) = \frac{b\phi(t, x, y, z)\Delta(x, y)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)R(t, y)dy} \quad (2)$$

with α the conversion coefficient, b the extraction coefficient and $s(z)$ the searching time, which depends on the foraging trait z as explained below. The quantity U corresponds to the uptake per resource of type y from a consumer of traits (x, z) ."

3.3 Definitions

Third, I would defer the definitions of RF and AF to a specific section about foraging strategies, because this is the key specificity of the model you propose, as far as I can see, so it makes sense to clearly devote a section to how foraging strategies are modelled.

Response: We defined the foraging strategies in a separate section (section 1.2).

3.4 Manuscript structure

The manuscript follows the classical "Methods/Results" structure, which I don't think works so well for theoretical papers in general, and clearly complicates matters for the reader in this specific case. The reason is that section 2.2 dumps on the reader a host of notations and definitions which are only used later in section 3 (the Results section), and I think it would make much more sense to introduce these

definitions only when they are needed to investigate a specific biological question. Hence, I would suggest to restructure the manuscript as follows:

1. A resource-consumer niche model
2. Foraging strategies
3. Evolution of adaptive foraging (current section 3.1, with some elements of the section "Sensitivity analysis on the mean foraging trait" thrown in, and others moved to an Appendix)
4. Effect of AF on trait diversity (section 3.2 + definitions of FDis, Prod and so on in eqns 12-15)
5. Effect of environmental disturbances (section 3.3 + last paragraph of section 2).

The advantage of this structure is that it roughly follows the organisation around three questions (Q1, Q2, Q3) that is announced in the introduction and also used to structure the discussion. Granted, some adjustments will be required, but I don't foresee many difficulties. The overall goal is to organise the argument around biological questions instead of the artificial Methods/Results dichotomy, and to introduce new definitions and concepts only when they are needed to answer a specific question

Response: We agree this is easier to follow, and have reorganised accordingly.

3.5 Model assumptions

As far as I could see, the results were obtained using Gaussian functions for the resource growth and resource utilisation functions. This is in line with classical theory on resource-consumer dynamics, but this is also a very special case which can lead to structural instability (Sasaki & Ellner 1995; Meszena et al 2006; Pigolotti et al 2009; Sasaki & Dieckmann 2011). I encourage the authors to discuss their results in the light of this earlier literature, to justify why they believe that their results provide a robust prediction, and possibly to speculate on how other functional shapes could alter their predictions.

Response: We agree that in the absence of animals, different carrying capacity functions may generate different distribution of resources along the niche. Indeed, the Gaussian function generates a bell shaped continuous distribution of resources while a quartic function of the form $K(y) = \exp(-y^4/\sigma_K^4)$ generates a discrete resource distribution picked at given values spaced by $1.4\sigma_K$ see (Hernandez-Garcia et al 2009, Sasaki and Diekmann 2011). Those distribution remain valid even if we add mutation between resources. In addition, the kurtosis tends to broaden the resource distribution, that will enhance the effect of plastic foraging strategy as we show in appendix A.5.

When we add the consumers, the dynamics with Gaussian functions is truly modified and it looks like the dynamics with a platokurtic function (see appendix C.1). When we look at the effect of a fixed foraging trait, which corresponds to a fixed plastic foraging strategy, the effect of plastic foraging does not change qualitatively with the kurtosis when looking at the biomass and the niche overlap. However, the effect changes when looking at the productivity and functional diversity. However, for any characteristic, the kurtosis enhances the effect of plastic foraging strategy (see appendix C.2). Similar results are obtained with full eco-evolutionary model.

We have incorporated this discussion in the section "Assumptions and limitations of the model". Our discussion is based on the literature given by the reviewer, that we would like to thank, and new numerical results. We numerically investigate the effect of the plastic foraging strategy with a quartic carrying capacity function of the form

$$K(y) = K_0 e^{-\frac{y^4}{12\sigma_K^4}} \quad (3)$$

Please refer to the last paragraph of the section "Assumptions and limitations of the model" for the details (l. 444).

3.6 Minor comments

- l. 30 : "mitigate environmental change". This is rather vague. Could you be more specific?

Response : the sentence now reads "phenotypic plasticity may help populations to cope with environmental changes".

- l. 33: it is not immediate what you mean by "defence" here.

Response : the sentence now reads "which depends on the (mis)match between the resources' defensive and consumers' counter-defensive traits"

- l. 42-43: "phenotypic plasticity often results from evolution by natural selection, but not always". Please clarify. Do you mean that other evolutionary forces (mutation, migration) can lead to phenotypic plasticity or something else?

Response : the related sentence now reads "In particular, phenotypic plasticity may help populations to cope with environmental changes, although empirical evidence is sometimes questionable"

- l. 90-95: I find this very clear, and as argued above I think it should be used to more clearly organise the results. However, it seems that later you treat the question "How do environmental disturbances alter the evolution of AF" in Q3 rather than Q1. Please clarify.

Response : this is right. Q1 now simply reads: "Under which ecological conditions is PF evolutionary adaptive?" and the reference to environmental changes has been moved to Q3.

- eqn (7). Define the notation $[\]_+$.

Response : We have added the definition of the positive part as follows:

"where $[u(y) - u(y')]_+ = \max \{ (u(y) - u(y')), 0 \}$ is the positive part of the difference between potential resource uptake."

- eqn (12). There is a strange notation "(t,x)" to denote the biomass of consumers with trait x. Is this a typo? If not, please consider a more straightforward notation.

Response : We have fixed this problem.

- First line of caption of Fig 4: "chanhe" → "change"

Response : done

4 Additional changes

Effect on productivity and niche overlap We realized that the codes for the computation of productivity and niche overlap were wrong. We have corrected them, which slightly modifies the results on the effects on the productivity.

"However, when \bar{z} is above 0.4, the productivity gain does not change on average, because consumers with high foraging trait impact resources too heavily."

References

- U. Dieckmann and M. Doebeli. On the origin of species by sympatric speciation. *Nature*, 400(6742):354, 1999. doi: 10.1038/22521.
- M. Egas, M.W. Sabelis, and U. Dieckmann. Evolution of specialization and ecological character displacement of herbivores along a gradient of plant quality. *Evolution*, 59(3):507–520, 2005. doi: 10.1111/j.0014-3820.2005.tb01011.x.
- N. Loeuille. Consequences of adaptive foraging in diverse communities. *Functional Ecology*, 24(1):18–27, February 2010. doi: 10.1111/j.1365-2435.2009.01617.x.
- J. Sundell, J.A. Eccard, R. Tiilikainen, and H. Ylönen. Predation rate, prey preference and predator switching: Experiments on voles and weasels. *Oikos*, 101(3):615–623, 2003. doi: 10.1034/j.1600-0706.2003.12264.x.
- F.S. Valdovinos, P. Moisset de Espanés, J.D. Flores, and R. Ramos-Jiliberto. Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos*, 122(6):907–917, 2013. doi: 10.1111/j.1600-0706.2012.20830.x.