

PCIEvolBiol #654 : response to reviewers round 2

We would like to thank the reviewers for this second in-depth examination of our manuscript. We have made every effort to respond to the reviewers' comments, and we believe that the document has once again been corrected and improved.

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 the tracked changes.

1 PCIEvolBiol #654 (round 2) : Editorial decision

The review of the revised version are positive. I agree with their general assessment of the ms as well as with their suggestions for relatively minor changes. However, I spotted an oddity in the ms which suggests that a more thorough revision may still be needed. Specifically, in eq. 16 of the ms, a fomula is given for a correlation coefficient, and I would expect this formula to be of the standard form $\text{cov}(X,Y)/\sqrt{\text{var}(X)*\text{var}(Y)}$. The formula seems almost of this form (for zero-mean X and Y) except that it appears to have $\sqrt{\text{var}(X) \text{ 'plus' } \text{var}(Y)}$ in the denominator. So, unless I miss something trivial, the formula is wrong. I also looked at the matlab code (niche-overlap-AF.m) and it looks as if the problem is also in the code (but I am not a matlab programmer so I may misunderstand the code).

If there is an error in the code, the simulations on the effect of niche overlap need to be re-run and re-analyzed. If I missed something trivial, let me know.

Response : We apologize for this mistake, we actually replace a * by +. We have modified the definition of the niche overlap in the manuscript as well as in the matlab code. Our result changes for small value of PF trait as shown by Figs. 3.d, SI 3.d. In the present Figures, the PF evolution always decreases niche overlap and the decrease is enhanced when mean foraging trait increases.

Typos :

"consumers disappears" (l.329-330). Done

"systems... tolerates..." (l. 338-339). Done

Also the y axis labels of the top panels of fig. SI.3 conflicts with the presence of curves for resources in these panels.

Response : On the left-hand side of the top panels the y-axis corresponds to consumer biomass, but there is also a second y-axis on the right-hand side corresponding to resource biomass. The same applies to functional diversity. There is therefore a corresponding axis for each curve.

The font size of the main text appears to be 9, which is too small. Done, up to 11pt

2 Reviewed by anonymous reviewer, 16 Aug 2023 06 :32

I thank the authors for their changes, which I believe have improved their manuscript. I think the text flows much better. This makes reading the manuscript more enjoyable and understanding the study more straightforward. I do not have major comments left, only questions or remarks that came to mind as I read. Here there are in order of appearance :

Equations 1 and 2. There is an extra outer bracket on the right of F_R and F_C . Done

1. 159 and 161. There is a problem with extra dots and space. Done

Eq. 11. I still think this equation can be better explained. First, I was perplexed why the whole term should be proportional to the density of consumers C . Second, the two terms within brackets need to be intuitively and more slowly introduced. What does it mean exactly when this is positive or negative? What does each term within bracket correspond to exactly?

Response : We clarify this point by explaining more in details the different terms of the PF effort equation. We add the following explanations l.183 :

"The PF dynamics allow consumers to compare the benefits u received from different resources. More precisely, for a given resource y and a given consumer with traits x and z , if the benefits $u(t, x, y, z)$ from the resource y is larger than the benefit $u(t, x, y', z)$ from the resource y' , that is $[u(t, x, y, z) - u(t, x, y', z)]_+ > 0$, then the consumer will gain benefits by increasing its effort on resource y . Conversely, it will gain benefits by decreasing its effort on resource y' . Eq. (11) reflects the balance between the positive effects $[u(t, x, y, z) - u(t, x, y', z)]_+ > 0$ to increase the effort on resource y and the negative effects $-[u(t, x, y', z) - u(t, x, y, z)]_+ < 0$, to do it. As a result, consumers increase their efforts on the most beneficial resources and reduce them on sub-optimal resources. The comparison of resources is assumed time consuming. The efforts are therefore not adjusted instantaneously but exponentially fast at a rate that is proportional to the density of consumer C , with similar trait x and z , accounting for the use of social cues during foraging [Jones et al., 2018], and an intrinsic adjustment rate l_ϕ . When the intrinsic adjustment rate l_ϕ becomes large, the plastic foraging strategy becomes closer to the optimal foraging strategy maximizing the potential resource uptake u [MacArthur and Pianka, 1966, Loeuille, 2010]."

l. 220. "a positive correlation between total niche width and inter-individual niche variation" I found this remark interesting as doesn't it go against standard theory where only niche trait evolves? I mean isn't it the case that the greater sigma, the more generalist consumers can be, which disfavors the emergence of specialists and thus inter-individual niche variation?

Response : The theory underlying our remark is called "Niche Variation Hypothesis" and is now mentioned in the text l.243 :

"The evolution of plastic foraging may lead to contrasting foraging strategies among individuals, which increases inter-individual niche variation. This would then fit with the "Niche Variation Hypothesis" (NVH) according to which "populations with wider niches are more variable than populations with narrower niches" [Soule and Stewart, 1970]. The NVH was initially formulated by Leigh van Valen 1965 for morphological traits, although it appears better suited to behavioral traits like resource use [Bolnick et al., 2007]. Empirical support for the NVH was found for herbivores [Bison et al., 2015] and predators [Bolnick et al., 2007], with a positive correlation between total niche width and inter-individual niche variation."

l. 260 "variabililty" variability. Done

Eq. 17. There is an integral symbol missing in the numerator and denominator (i.e. its integrated over x and y). Done

The results below eq. 17 need to better explained. In particular why niche overlap initially increases and then decrease with z .

Response : As pointed out by the editor, there was an error in our formula for calculating niche overlap (see section 1). Having corrected this error, the relationship between the niche overlap and the mean foraging trait of the system with PF evolution is monotonically decreasing (Figure 3, panel d), so that the niche overlap is lower with PF evolution than without :

l.334 *"The evolution of PF also decreases the niche overlap between consumers by about 90% as soon as the mean foraging trait exceeds 0.2."*

l. 315-326 I thought that the approach could be better explained :

— What does " niche center is displaced at constant speed c " mean exactly? Is that changing the mode of $K(y)$?

Response : Yes, that is what we meant. We first have specify that y_0 is the mode of the carrying capacity function and it represents the resource niche center. In the equation, we have written $K(y - y_0)$, where K is a normal distribution with mean 0 and variance σ_K^2 . We now specified l.350 that perturbation affects the mode y_0 of the carrying capacity function. The sudden shift corresponds to y_0 that becomes $y_0 + \Delta y$. The displacement at a constant speed corresponds to a mode that moves as follows : $y_0 + ct$.

- What parameters were used exactly? All those of Table 1 including varying all of those in the first row?
Response : The parameters are those in Table 1 column "Values for the response to disturbances", we are now specifying it in the text.
- Did you wait for the population to go to equilibrium before perturbing it? In that case, why initializing with $z = 0.9$?
Response : Indeed, the disturbances are initialized from a simulation up to equilibrium (one with PF evolution and one without), but the text was not clear. We replace it 1.359 with :
"Before the perturbation, we start with a resource-consumer system at equilibrium for each system : with PF evolution and with fixed RF, that is the foraging trait of consumers is monomorphic ($z = 0$) and does not evolve ($\partial_z^2 C = 0$). In the system with PF evolution, the mean PF trait is stabilized around a high value, $\bar{z} \approx 0.9$, with the parameters set in Table 1. For each disturbance strength and type, we wait until a new equilibrium is reached. The stability metrics of the system with PF evolution is compared to those of the system with fixed RF at this new equilibrium. For all disturbance types, the disturbance strength is increased until the consumer population goes to extinction, in order to compute the maximal disturbance level that the system can tolerate. Monomorphic systems for different foraging trait values are also initialized to test their response to disturbances.
- The treatment with PF fixed (right column of Figure 4) isn't entirely clear from the text. Actually, it's hardly mentioned in the text. Was the population set to be monomorphic for a given value of z , left to go to equilibrium, and then perturbed? Response : Yes that is right. As the method was added in response to the previous comment, we add 1.369 :
"Monomorphic systems for different foraging trait values are also initialized to test their response to disturbances." after it in the text.

1. 336 " at each mortality increase, consumers in the system with PF evolution gradually reduce their foraging trait " Is this because with high mortality, density of consumers decrease and thus competition for resources decrease? Response : This is certainly one of the processes involved in reducing mean PF trait. Added to this is the fact that, with increased mortality, it becomes impossible for consumers to survive at the edge of the niche, where a high PF is needed to exploit the resources present, leading to a reduction of the mean PF trait. We add 1.376 :
"Indeed, increased mortality leads to reduced competition between consumers via their reduced density, and to the non-viability of the niche edge for consumers, both leading to a reduction in PF trait."

1. 353 " in addition PF imposes a second lag load, corresponding to the time needed for the evolutionary regression of PF. In the case of ecosystem disturbance, however, since optimal foragers quickly turn into random foragers, both types of foraging strategies respond in a similar way " I am not sure I understand why in one case the population can quickly evolve from PF to RF but not in the other. Can you please explain?

Response : This was indeed very unclear. We modified this paragraph 1.397, which now reads :
"In figures 4b and d PF is fixed, but when PF can evolve, it gradually decreases in function of the intensity of the disturbances (see color scales in Figures 4 a and c), although for different reasons. In the case of ecosystem disturbance, plastic foragers located at the edge of the niche trait distribution (Figure 2b) disappear progressively due to increases in mortality. The average PF trait therefore decreases (Figure 4a) due to demographic changes of a pre-existing trait diversity. In the case of a constant environmental change, however, the typical trait distribution depicted in Figure 2b no longer exists because niche traits constantly run after those of resources, which corresponds to an evolutionary lag load. In that case, consumers do not have enough time to reduce their PF searching behaviour and become extinct slightly earlier (Figure 4c); PF therefore imposes a second lag load, corresponding to the time needed for the evolutionary regression of PF.

3 Reviewed by anonymous reviewer, 01 Aug 2023 15 :56

This is a much improved version of a very interesting theoretical manuscript investigating the evolutionary dynamics of plastic foraging. The authors have taken into account all my previous comments, and I am happy about the current version of the manuscript. I have a few minor quibbles that I think could be addressed in a revision.

- l. 54 : "Although the PF strategy tends to increase fitness, in some situations PF may reduce it". Given the examples that follow, I wonder what the authors mean by fitness. Do they mean typical fitness proxies such as fecundity or survival? That is, the ability to do PF can e.g. be assumed to be costly and modelled as trading-off with survival? Or maybe I misunderstood. Please clarify.

Response : This is indeed what we had in mind. The corresponding section 1.57 now reads :

"Although the PF strategy increases energy intake, it may also be costly, e.g. by increasing predation risk, preventing efficient thermoregulation [du Plessis et al., 2012, Van de Ven et al., 2019] or increasing searching time for resources [Randolph and Cameron, 2001, Bergman et al., 2001, Fortin et al., 2004]. Since PF faces several trade-offs with life-history components, its evolution should depend on ecological parameters such as mortality rate, resource searching time or consumer niche width."

- eqn (7) : bold mathematical symbols are often used to denote vectors or matrices, so the notation is perhaps not the best. Same for $R(t)$ in Table SI.1. In addition, it is weird to use $\bar{C}(t, x)$ for the integral over z of $C(t, x, z)$ and $\mathbf{C}(t)$ for the integral of $\bar{C}(t, x)$ over x . And we probably want to keep the bar notation to denote trait averages. Alternatively, perhaps we don't need these notations at all. At least in the main text, the notation $\mathbf{C}(t)$ only appears in eqn (7), and the notation $\bar{C}(t, x)$ in eqn (14), as far as I could see. In both cases, you could use the double integrals, as you do in eqn (13). So perhaps less notation is better here. In the table SI.1, $\bar{x}(t)$ and $\bar{z}(t)$ could be defined in the same way (with double integrals), so you don't need the notation $\bar{C}(t, x)$, and then you can either write the denominator as a double integral as in the main text or use the notation C_T and R_T for the total biomasses if you really want to. Anyway, this is very subjective, but perhaps worth thinking about.

Response : We agree that these notations are not classical and may confuse the reader. So we decide to remove them and replace them by the integral notations that are more intuitive.

Other minor points :

- l. 38 : correspondS. [Done](#)

4 Additional changes

Change "AF" to "PF" in x-axis labels of Figure 3 panels, Figure SI.8 panels, and Figure SI.9.

Références

- C.M. Bergman, J.M. Fryxell, C.C. Gates, and D. Fortin. Ungulate foraging strategies : Energy maximizing or time minimizing? *Journal of Animal Ecology*, 70(2) :289–300, 2001. doi : 10.1111/j.1365-2656.2001.00496.x.
- M. Bison, S. Ibanez, C. Redjadj, F. Boyer, E. Coissac, C. Miquel, D. Rioux, S. Said, D. Maillard, P. Taberlet, N.G. Yoccoz, and A. Loison. Upscaling the niche variation hypothesis from the intra- to the inter-specific level. *Oecologia*, 179(3) :835–842, 2015. doi : 10.1007/s00442-015-3390-7.
- D.I. Bolnick, R. Svanbäck, M.S. Araújo, and L. Persson. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences*, 104(24) :10075–10079, 2007. doi : 10.1073/pnas.0703743104.
- K.L. du Plessis, R.O. Martin, P.A.R. Hockey, S.J. Cunningham, and A.R. Ridley. The costs of keeping cool in a warming world : Implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, 18(10) :3063–3070, 2012. doi : 10.1111/j.1365-2486.2012.02778.x.
- D. Fortin, M.S. Boyce, E.H. Merrill, and J.M. Fryxell. Foraging costs of vigilance in large mammalian herbivores. *Oikos*, 107(1) :172–180, 2004. doi : 10.1111/j.0030-1299.2004.12976.x.
- T.B. Jones, S.C. Patrick, J.P.Y. Arnould, M.A. Rodríguez-Malagón, M.R. Wells, and J.A. Green. Evidence of sociality in the timing and location of foraging in a colonial seabird. *Biology Letters*, 14(7) : 20180214, 2018. doi : 10.1098/rsbl.2018.0214.
- 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.
- R.H. MacArthur and E.R. Pianka. On optimal use of a patchy environment. *The American Naturalist*, 100(916) :603–609, 1966.
- J.C. Randolph and G.N. Cameron. Consequences of diet choice by a small generalist herbivore. *Ecological Monographs*, 71(1) :117–136, 2001. doi : 10.1890/0012-9615(2001)071[0117 :CODCBA]2.0.CO ;2.
- M. Soule and B.R. Stewart. The "Niche-Variation" Hypothesis : A Test and Alternatives. *The American Naturalist*, 104(935) :85–97, January 1970. doi : 10.1086/282642.
- T.M. Van de Ven, A.E. McKechnie, and S. Cunningham. The costs of keeping cool : Behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*, 191(1) :205–215, 2019. doi : 10.1007/s00442-019-04486-x.
- L. Van Valen. Morphological variation and width of ecological niche. *American Naturalist*, pages 377–390, 1965.