Peer Community In Evolutionary Biology

Evolution and consequences of plastic foraging behavior in consumer-resource ecosystems

François Rousset based on peer reviews by 2 anonymous reviewers

Léo Ledru, Jimmy Garnier, Océane Guillot, Erwan Faou, Camille Noûs, Sébastien Ibanez (2023) The evolutionary dynamics of plastic foraging and its ecological consequences: a resource-consumer model. EcoEvoRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://doi.org/10.32942/X2QG7M

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Plastic responses of organisms to their environment may be maladaptive in particular when organisms are exposed to new environments. Phenotypic plasticity may also have opposite effects on the adaptive response of organisms to environmental changes: whether phenotypic plasticity favors or hinders such adaptation depends on a balance between the ability of the population to respond to the change non-genetically in the short term, and the weakened genetic response to environmental change. These topics have received continued attention, particularly in the context of climate change (e.g., Chevin et al. 2013, Duputié et al., 2015, Vinton et al . 2022).

In their work, Ledru et al. focus on the adaptive nature of plastic behavior and on its consequences in a consumer-resource ecosystem. As they emphasize, previous works have found that plastic foraging promotes community stability, but these did not consider plasticity as an evolving trait, so Ledru et al. set out to test whether this conclusion holds when both plastic foraging and niche traits of consumers and resources evolve (though ultimately, their new conclusions may not all depend on plasticity evolving). Along the way, they first seek to clarify when such plasticity will evolve, and how it affects the evolution of the niche diversity of consumers and resources, before turning to the question of consumer persistence.

The model is rather complex, as three traits are allowed to evolve, and the resource uptake expressed through plastic behavior has its own dynamics affected by some form of social learning. Classically, in models of niche evolution, a consumer's efficiency in exploiting a resource characterized by a trait y (here, the resource's individual niche trait), has been described in terms of location-scale (typically Gaussian) kernels, with mean *x* (the consumer's individual niche trait) specifying the most efficiently exploited resource, and with variance characterizing individual niche breadth. The evolution of the variance has been considered in some previous models but is assumed to be fixed here. Rather, the new model considers the evolution of the distribution of resource traits, of the consumer's individual niche trait (which is not plastic), and of a "plastic foraging trait" that controls the relative time spent foraging plastically versus foraging randomly. When foraging plastically, the consumers modify their foraging effort towards the type of resource that maximizes their energy intake. in some previous models, the effect of variation in the extent of plastic foraging was already considered, but the evolution of allocation to a plastic foraging strategy versus random foraging was not considered. The model is formulated through reaction-diffusion equations, and its dynamics is investigated by numerical integration.

Foraging plasticity readily evolves, when resources vary widely enough, competition for resources is strong, and the cost of plasticity is weak. This means in particular that a large individual niche width of consumers selects for increased plastic foraging, as the evolution of plastic foraging leads to reduced niche overlap between consumers. The evolution of plastic foraging itself generally, though not always, favors the diversification of the niche traits of consumers and of resources. There is thus a positive feedback loop between plastic foraging and resource diversity. Ledru et al. conclude that the total niche width of the consumer population should also correlate with the evolution of plastic foraging, an implication which they relate to the so-called niche variation hypothesis and to empirical tests of it.

The joint evolution of the consumer's individual niche trait and plastic foraging trait generates a striking pattern within populations: consumers whose individual niche trait is at an edge of the resource distribution forage more plastically. The authors observe that this relatively simple prediction has not been subjected to any empirical test.

Returning to the question of consumer persistence, Ledru et al. evaluate this persistence when consumer mortality increases, and in response to either gradual or sudden environmental changes. These different perturbations all reduce the benefits of plastic foraging. The effect of plastic foraging on stability are complex, being negative or positive effect depending on the type of disturbance, and in particular the ecosystem has a lower sustainable rate of environmental change in the presence of plastic foraging. However, allowing the evolutionary regression of plastic foraging then has a comparatively positive effect on persistence.

Despite the substantial effort devoted to analyzing this complex model, relaxing some of its assumptions would likely reveal further complexities. Notably, the overall effect of plasticity on consumer persistence depends on effects already encountered in models of the adaptive response of single species to environmental change: a fast non-genetic response in the short term versus a weakened genetic response in the longer term. The overall balance between these opposite effects on adaptation may be difficult to predict robustly. In the case of a constant rate of environmental change, the results of the present model depend on a lag load between the trait changes of consumer and resource populations, and the extent of the lag may also depend on many factors, such as the extent of genetic variation (e.g., Bürger & Lynch, 1995) for niche traits in consumers and resources. Here, the same variance of mutational effects was assumed for all three evolving traits. Further, spatial environmental variation, a central issue in studies of adaptive responses to environmental changes (e.g., Parmesan, 2006, Zhu et al., 2012), was not considered. Finally, the rate of adjustment of effort by consumers with given niche trait and plastic foraging trait values was assumed proportional to the density of consumers with such trait values. This was justified as a way of accounting for the use of social cues during foraging, but to the extent that they occur, social effects could manifest themselves through other learning dynamics.

In conclusion, Ledru et al. have addressed a broad range of questions, suggesting new empirical tests of behavioural patterns on one side, and recovering in the context of community response to environmental changes a complexity that could be expected from earlier works on adaptive responses of organisms but that has been overlooked by previous works on community effects of phenotypic plasticity.

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Reviews

Evaluation round #2

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Version of the preprint: 3

Authors' reply, 19 September 2023

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Decision by François Rousset, posted 25 August 2023, validated 28 August 2023

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 cov(X,Y)/sqrt[var(X)*var(Y)]. The formula seems almost of this form (for zero-mean X and Y) except that it appears to have sqrt[var(X) 'plus' 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.

Typos: ”consumers disappears” (l.329-330) ”systems... tolerates...” (l. 338-339). Also the y axis labels of the top panels of fig. SI.3 conflicts with the presence of curves for resources in these panels.

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

Reviewed by anonymous reviewer 1, 16 August 2023

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

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

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?

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 ?

l. 260 ” variabililty” variability

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

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

l. 315-326 I thought that the approach could be better explained. 1. What does ” niche center is displaced at constant speed c” mean exactly? Is that changing the mode of K(y)? 2. What parameters were used exactly? All those of Table 1 including varying all of those in the first row? 3. Did you wait for the population to go to equilibrium before perturbing it? In that case, why initializing with z = 0.9? 4. 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?

l. 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?

l. 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?

Reviewed by anonymous reviewer 2, 01 August 2023

This is a much improved version of a very interesting theoretical manuscript investigating the eco-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 PG 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.

- 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.

Other minor points:

- l. 38: correspondS

Evaluation round #1

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Version of the preprint: 1

Authors' reply, 20 July 2023

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Decision by François Rousset, posted 19 June 2023, validated 26 June 2023

Decision for "Is adaptive foraging adaptive?..." by Ledru et al. (ms # 654, version 1)

The two reviews concur on the interest of the topic and the appropriateness of the results given. They also constructively comment on a number of issues relating to the presentation, and to a lesser extent to the substance, of the results. I largely agree with these comments and therefore encourage the authors to resubmit a revised version that takes them into account.

Specific points:

Please pay particular attention to comments to call for additional information. 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 ot provide additional results checking the robustness of key findings of the ms with respect ot this assumption. 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.

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.

Reviewed by anonymous reviewer 1, 05 May 2023

The manuscript, entitled "Is adaptive foraging adaptive? A resource-consumer eco-evolutionary model", investigates the emergence and consequences of plastic foraging strategy in a resource-consumer co-evolutionary model. It is found that foraging plasticity readily evolves, where resources vary a lot, competition for resources is strong, and the cost to plasticity is weak. The population at equilibrium varies phenotypically with individuals that forage randomly at the center of the niche (i.e. with traits that allow them to most efficiently forage the average resource), and others that forage plastically at the edge of the niche (i.e. with traits that allow them to most efficiently forage more extreme resource types). Such plasticity tends to increase and decrease the biomass of consumers and resources, respectively, and boost functional diversity. Finally, plasticity can facilitate or hinder persistence to external disturbances, depending on the nature of such disturbances.

I have enjoyed reading this manuscript. The evolution of plastic foraging is interesting and understudied and the model proposed here seems appropriate to this problem. My issues are mostly editorial.

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?

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.

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.

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.

Minor points:

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.

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

Legend of figure 4: "chanhe" -> change

l. 278 "S_max" -> s_max

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.

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.

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

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.

Reviewed by anonymous reviewer 2, 06 June 2023

In this interesting theoretical paper, the authors study the eco-evolutionary dynamics of adaptive foraging (AF), that is the ability of consumers to adjust relative foraging efforts towards more profitable resources. Three types of questions are investigated: (Q1) under which ecological conditions does AF evolve by natural selection?? (Q2) what is the effect of AF on trait diversity? (Q3) what is the effect of AF on the stability of the resource-consumer system? The authors model the interactions between resources and consumers using reaction-diffusion equations, which they analyse using numerical integration in order to study these three questions.

Overall, the paper appears to rely on a sound framework and to be well grounded in the vast literature on resource-consumer interactions, although the lack of analytical results makes it difficult to fully check the validity of the results. The key results of the paper are that (1) a high niche width of consumers selects for increased AF, (2) the evolution of AF leads to reduced niche overlap between consumers (i.e. niche partitioning), and therefore higher functional diversity of both consumers and resources, and (3) AF may have a negative or positive effect on community stability in response to a disturbance, depending on the type of disturbance. I think these results form an interesting contribution to the literature. Overall, the results are well presented, the figures are clear, and the results are put in the broader context of earlier theoretical and empirical studies. There are also nice summaries of the key messages throughout the paper.

However, I do have some concerns with the current version of the manuscript, and I think addressing them could help the authors improve the clarity of their paper. These concerns pertain to the presentation of the mathematical model, the structure of the manuscript, and some assumptions of the model.

(1) Model presentation

Understanding the model requires a lot of effort for the reader, and this is in part due to complex notational choices, the order in which variables and parameters are presented, and the structure of the manuscript.

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 variables 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 instaed of $r_\eff\$ would also be simpler, and I think you could use $F_C(t,y)$ and $F_R(tx,z)$ instead of $F_r[r,c,\phi](t,y)$ and $F_c[t,phi](t,x,z)$.

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/cometition terms in eqns (1) and (2) respectively. Also, when defining F_C and F_R, it could be advantageous to define the quantity $b \phi\Delta/(1+s b \int \phi \Delta R dy)$ (where I have dropped the function arguments for simplicity).

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.

Taken together, all these small adjustments could greatly improve the accessibility of the model for a random reader.

(2) 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 aroung biological questions instead of the artificial Methods/Results dichotomoy, and to introduce new definitions and concepts only when they are needed to answer a specific question.

(3) 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 unstability (Sasaki & Ellner 1995; Meszéna 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.

(4) Minor points:

- l. 30 : ”mitigate environmental change”. This is rather vague. Could you be more specific?
- l. 33: it is not immediate what you mean by ”defence” here.
- 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 plasiticity or something else?
- 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.
- eqn (7). Define the notation $[]_\+\$.
- 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.
- First line of caption of Fig 4: ”chanhe” -> ”change”

To conclude, I think this is an interesting theoretical study which is worthy of publication, but some further work on model presentation and structure is needed to improve the clarify of the paper.