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PCI Ecology
Dr. Simon Blanchet

Manuscript number: MS#93

**Submission of a revised version of "Size-dependent eco-evolutionary feedback loops in exploited ecosystems"**, authored by Eric Edeline and Nicolas Loeuille.

Dear Simon Blanchet,

We very much appreciated the insightful and constructive comments provided by you, Jean-François Arnoldi and the anonymous reviewer. These comments made us realize that the paper was far too long and complex. In the process of solving this issue, we have profoundly rearranged the whole text. Specifically, in carefully addressing the comments we have:

- shortened the whole text from 7721 to less than 6800 words,
- reduced the number of figures from six to four,
- reworked the whole text so as to provide more explanations or remove unnecessary complexities where needed,
- provided the general objectives and overview of the paper in the last paragraph of the introduction,
- moved the section describing size-dependent natural selection in the first section,
- removed the whole sections dealing with intraguild predation and alternative stable states,
- clarified our framework for describing antagonistic and synergistic EEFLs in Fig. 2,
- refined the description of EEFLs involved in predator-prey co-evolution (Section 3), including providing a new version of the associated figure (now Fig. 4),
- added in Section 4 a Box 2 providing guidance on how to advance our empirical knowledge of EEFLs.

We feel that these changes strongly improved the quality of our manuscript. As requested, we provide a point-by-point response to tour and the reviewers' comments (enclosed).

All persons entitled to authorship have been included and both Nicolas Loeuille and I have read and approved the revised version of this manuscript.

On behalf of Nicolas Loeuille,

Sincerely yours,

Eric Edeline

Point-by-point responses to the reviewers' comments for manuscript MS#93, "Size-dependent eco-evolutionary feedback loops in exploited ecosystems" authored by Eric Edeline and Nicolas Loeuille.

COMMENTS FROM REVIEWERS IN PLAIN TEXT, OUR RESPONSES LISTED DIRECTLY BELOW IN BOLD TEXT:

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Round #1
Author's Reply:
by Simon Blanchet, 2020-05-23 08:54
Manuscript: https://doi.org/10.1101/2020.04.03.022905
Revision required

Dear Authors,

Two reviewers have now read the MS, and as you will see both of them found it interesting and timely. I also read it and I also found it very interesting. However, they both raised some concerns that were mostly related to the clarity of the text; one of the referee found it "long" and the other one read it "three times" to fully grasp the story. As a result, they both suggest finding a way to simplify the message and/or re-organize the MS, without providing clear guidance. I must admit that the MS is long and that it needs full concentration to be read at once. I would suggest authors re-working on the introduction (last paragraph at the least) to provide a more thorough plan of the paper with extremely clear objectives. This is important for this type of paper that objectives are clear from the introduction and that a plan is provided (there is currently a plan but it is not elaborated enough).

**We have now profoundly reorganized and extensively rewritten our manuscript so as to better structure, to shorten and to clarify the whole text. In this process, and despite adding a new Box 2 (see below) containing 733 words, we still managed to reduce the total number of words from 7721 to less than 6800. Additionally, we reduced the number of figures from six to four. Following your advice, we now more clearly provide the global objective and a detailed outline of the paper in the last paragraph of the introduction (lines 79-90). Natural selection on body size is now treated in the first section, so that the reader is more smoothly introduced**

**with the basic framework for size-dependent EEFLs. In opening this Section 1 (lines 92-199), we provide a summary table (Table 1), such that the readers uninterested in the details can simply look at the table and directly move to the next section. Sections 2 (lines 201-357) and 3 (lines 358-480) now gently take the reader through an increasing complexity gradient. In Section 2 we examine EEFLs in the relatively simple case where only one species evolves in response to one single density-dependent environmental variable. In Section 3 we now briefly touch on the additional complexities that may arise when more evolving species interact. Finally, in the last section (lines 481-582) we shortly discuss some management implications of size-dependent EEFLs, and we provide a new Box 2 presenting an extensive overview of the empirical approaches needed to advance our knowledge in the field. Throughout the whole text, we paid particular attention to clarifying our arguments, adding extra explanations or removing unnecessary complexities where appropriate. It is our feeling that these extensive changes have greatly improved the quality and readability of our manuscript, and make it now much more accessible to a wide readership in ecology and evolution.**

Also, I would suggest synthesizing further section 2 (size-dependent selection) that is important but a bit away from the main objective (perhaps including this information in a box ?).
**As advised, we have now made this section on size-dependent natural selection more compact, mainly through further refining and clarifying the text. Additionally, this section now more naturally comes first (now Section 1), i.e., comes *before* presenting the theory. Finally, we now open this Section 1 with summary Table 1, which readers may read rapidly and directly jump to Section 2 if they are not interested in the details of natural selection.**

Section 4 (multispecific EEFLS could be reduced in length; it is the most speculative, the less documented and I think there a re few redundancy in the text.
**As advised, we have now shortened and simplified this section (now section 3). This process reduced the number of words from 2205 to less than 1400. Additionally, we took care to remove any redundancy between this and other sections.**

As another note, I what a bit disappointed not to see a section or box about what we must/should do next from an empirical, experimental or theoretical point of view. I think this type of "speculative" paper should provide guidance for future researches as it paves the way toward new research avenues.
**As advised, we have now written a new Box 2 (lines 494-552), where we provide a detailed account of the approaches needed to improve our empirical knowledge of size-dependent EEFLs.**

Finally, the paper is about harvest (which includes fishery but not only) but almost all examples and all biological foundation (section 2) are fish-based. The paper is actually about fishery and this should make it clear from the beginning. After the introduction I was expecting examples about mammal harvesting or any other types of harvests, but no, it is mainly about fish (which is fine for me!). So if it is about fish, tell it explicitly. Note that I also attached a pdf file with some minor comments.
**We have now changed the title to “Size-dependent eco-evolutionary feedbacks in fisheries”. Additionally, we have paid attention to implement all the changes suggested from the pdf file when they were still applicable to the new, deeply reorganized version of the manuscript.**

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Reviewed by anonymous reviewer, 2020-05-06 12:29

I think the topic of this review was rather interesting and touches upon a timely question. I really enjoyed the idea of integrating natural selection with fisheries selection, and particularly how natural selection could further change due to eco-evolutionary feedback loops.

However, I must say that I read the manuscript three times and was still rather confused how the different mechanisms driving the feedback loops led to changes in natural selection.
**We have now deeply reworked our manuscript in order to shorten, simplify and clarify the whole text. It is our feeling that these reorganizations have strongly improved the readability of our paper (please, see also our answers to Simon Blanchet and Jean-François Arnoldi).**

Exploitative competition and fisheries selection favor small body size. Because of size-selective fisheries, there will be lots of small fish in the population. How does this decrease exploitative competition? If anything, shouldn't it increase that? Therefore, it was not clear to me how these two selection forces together increase the probability of extinction. Interference and cannibalism select for large body size. Removing large, dominant, cannibalistic individuals creates better conditions for small fish and increase their fitness. This idea I get.
**Our hypothesis is that harvesting always decreases densities. In order to lift any ambiguity on this point, we now make it crystal clear throughout the manuscript that we assume harvesting to decrease population density and, hence, to relax competition (lines 48-51, 303-306, 309, 329-332, 430-432). We think that, maybe, the ambiguity stemmed from the previous version of the manuscript presenting harvest selection and the theory of EEFLs before natural selection. It is probably more intuitive to reverse the order and present natural selection first, then EEFLs, and last to add harvest selection into the play. This is the sequence we now adopt in the revised manuscript: we present size-dependent natural selection first (Section 1), then the theory of EEFLs (Box 1, opening of Section 2) and, last, we add harvesting into the EEFL with Figs. 1 and 2.**

As the authors also acknowledge, all of the processes they introduce will likely occur simultaneously and therefore it is difficult to make any clear, realistic predictions. However, it is good to identify these processes although those occurring in the food web likely requires a network model. As I mentioned, I read the manuscript several times, yet I was left rather confused and not super convinced. I think the authors need to clarify the text a lot and perhaps add concrete examples of the processes. It is not easy to explain in a simple way eco-evolutionary processes but there must be a way. If possible, the review could be more focused.
**We agree with the referee. We have deeply reorganized and extensively rewritten the manuscript to improve clarity, including the network part (please, see also our answers to Simon Blanchet and Jean-François Arnoldi).**

##==========
Reviewed by Jean-François Arnoldi, 2020-05-18 12:36

This manuscript by Edeline and Loeuille focuses on the role of evolution in shaping the responses of fish populations to harvesting. In particular, they review many plausible scenarios of adaptive responses driven by eco-evolutionary feedbacks (EEFL) where harvesting can alter not only the target population but also the natural selective forces acting upon it.

The paper proceeds as a review, both of empirical evidence (not only in fish) for various mechanisms entering in EEFL and eco-evolutionary models used to describe them. Overall it is

quite interesting, well written and extremely well documented. It should be noted, however, that I am not an expert of neither fisheries nor evolutionary dynamics, so I cannot vouch for the relevance of the literature cited. I do have two main points that I believe should be addressed, one conceptual, one presentational.

My conceptual point is about the notion of fitness landscape, as represented in Fig.2 which is at the base of most of the paper.

The way I understand what a fitness landscape is, in relation to adaptive dynamics (Box 1), is that its gradient represents how invadable the resident population is, by closely related phenotypes (here body size). Thus, along evolutionary dynamics, the phenotype climbs the fitness landscape until it reaches an uninvadable point (or branches out). Fitness is relative to the surrounding phenotypes. But in figure 2, it seems that fitness is an absolute feature of the resident population, related to its persistence, such as its growth rate, or population size (see the line representing an extinction threshold in Fig. 2). I probably misunderstood completely the authors point, but just to be clear, If fitness is resident growth rate, we run into trouble if the resident population is stationary and thus its growth rate is zero, no matter what the fitness landscape may be (in the sense of adaptive dynamics). If we think of fitness as related to population size, it is easy to imagine scenarios in which evolution (which increases fitness by definition) would nonetheless lead to smaller population sizes. Thus, I urge the authors to make crystal clear the assumptions that go into drawing their figure, and lay the basis for their subsequent reasoning.

**We thank Jean-François Arnoldi for pointing to us this important conceptual gap in our manuscript. We now define the framework of Fig. 2 much more carefully. In particular, we now make it fully explicit that Fig. 2 represents fitness landscapes in terms of absolute fitness for given phenotypes, therefore ignoring frequency dependence as is often done in quantitative genetics (lines 258-260, y axes in Fig. 2), and justify this choice on practical grounds (lines 263-266). Specifically, if ones assumes that any point on the fitness landscape in Fig. 2 provides the phenotype of a monomorphic population, the connection from absolute to relative fitness is easily visualized from the relative position of trait value on the fitness landscape (explained lines 260-263). We agree that Fig. 2 sketches evolutionary optimization (i.e., maximisation of fitness and population size), while frequency-dependent selection often does not optimize (Metz et al. 2008) and may even lead to evolutionary suicide (Ferrière and Legendre 2013). Specifically, evolution optimizes only when the environmental feedback is one-dimensional (Metz et al. 2008). Therefore, we now make it clear in the text that the evolutionary dynamics sketched in Fig. 2 hold true only when the environmental feedback is one-dimensional (lines 20, 275-277, 384-386, Fig. 2 caption). We made this choice because this type of fitness landscape allows us to directly visualize the implications of evolution for the maintenance of the harvested population, which would be harder with the adaptive dynamics (invasion) fitness definition. Finally, we have further justified the functional forms of the selection functions represented in Fig. 2 (lines 269-275). It is our feeling that these changes now clarify the assumptions that go into drawing Fig. 2.**

**References:**

**Metz, J. A. J. et al. 2008. When does evolution optimize? - Evolutionary Ecology Research 10: 629–654.**

**Ferrière, R. and Legendre, S. 2013. Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. - Philosophical Transactions of the Royal Society of London B: Biological Sciences 368: 20120081.**

My presentational point is about the length and structure of the paper.

I find the paper very long, and hard to follow since was not clear to me, at first reading, what the authors contribution was. After a while I understood that they were reviewing many plausible scenarios, without going too much in the details of any, about EEFL. This is fine, but should be announced very clearly. And since one doesn't not need to known one scenario to understand another, the structure of the paper should be designed so that it becomes easily consulted, depending on what teh reader is interested in. I'm not sure how to do that, since I never wrote a paper of the kind, but I am convinced that giving some serious thoughts into crafting an appropriate reader-friendly structure would greatly benefit the paper.

**This comment by Jean-François Arnoldi echoes comments from the anonymous reviewer and from Simon Blanchet, making it very clear that the first version of our manuscript was far too long and complex. We therefore put strong efforts into shortening, simplifying and clarifying the whole text (see also our answers above). The text is now considerably shorter and, we feel, clearer. Additionally, as advised here we now more clearly present the objectives (lines 79-80), approach (lines 80-83) and map (lines 83-90) of the paper in the last paragraph of the introduction. Furthermore, as advised, we have tried to further "disconnect" Section 1 (size-dependent natural selection) from other sections using a summary table (Table 1), which allows the reader to rapidly skim through the results from this section and jump to the next ones. Finally, Section 3 (multispecies EEFLs) includes a short introduction that makes it relatively self-sustaining and, we feel, understandable without having to read the whole manuscript.**