

19<sup>th</sup> November 2019

Dear Editor,

You notified us on October 15, 2019 that we were encouraged to review and resubmit a revised version of our manuscript entitled “Stoichiometric constraints modulate the effects of temperature and nutrients on biomass distribution and community stability”.

We thank the editor and the two reviewers for their constructive comments that significantly improved the manuscript. We believe that the revised version satisfactorily addresses most of those comments (see our detailed point-by-point explanations below) and more concisely explains our main findings, which should be of a broad interest for the *PCI Ecology* readership. In addition to addressing the points made by reviewers, we have also made changes to improve the flow and clarity of the text without any impact on our main findings. If you have any questions, please do not hesitate to contact us. We really appreciate your assistance in this matter.

We would be grateful to you for reconsidering this manuscript and we hope that you would approve this new version. We look forward to hearing from you at your earliest convenience.

With kind regards,  
Arnaud Sentis on the behalf of all co-authors.

***Decision by the handling editor (Dr. Elisa Thebault).***

Dear authors, I have now received two reviews of your manuscript. Both reviewers and I are in agreement that this is an interesting study considering how flexible stoichiometry of primary producers affect the dynamics of primary producers and consumers in response to both nutrient enrichment and climate warming. However, several issues have been identified which, in my views, require revision before recommendation. Such revised contribution would need to address all of the reviewer comments. In particular, as outlined by reviewer #2, several points would deserve to be further clarified and discussed (e.g. better justification of the use of different extinction thresholds, robustness of the results to different sets of parameters, consequences of abiotic pools such as detritus).

**Our response:** We thank the handling Editor for the positive comments on our manuscript. As recommended, we have modified the manuscript to clarify the use of the extinction threshold, the robustness of the results to different parameter sets and the consequences of abiotic pools (see below and the blue font text in the main text).

***Handling editor***

In addition to the detailed suggestions of the reviewers, I have a few additional comments: - Lines 352-358: The definition of the static and dynamic effects are at first not fully clear. Is the part on consumer energetic efficiency (lines 358-378) related to the static effect while the following part (lines 382-393) relates to the dynamic effect? I better understood the difference between the static and dynamic effects later on (line 395), when these two effects are directly compared. I would suggest modifying this section (from lines 347 to 414) to make the distinction and the comparison between the static and dynamic effects clearer to the reader.

**Our response:** we modified this section to clarify the distinction between the static and dynamic effects (lines 352-357, 386-390, 411-415) and better explain why we are doing so (lines 402-405). We have limited the use of the terminology "static vs dynamic effects" to the feedbacks induced by the stoichiometric constraints, and that we do no longer use this terminology in the part on consumer energetic efficiency.

***Handling editor***

Lines 387-389 “When consumer population increases, this decreases resource population growth leading to a negative feedback on consumer population growth rate”: isn’t it also the case in the RM model? Please explain more precisely why this feedback is different in the SRM model.

**Our response:** We agree that, in the RM model, when the consumer population increases, this decreases the resource population growth rate, but this occurs only through direct predation. In contrast, for the SRM, the negative feedbacks occurs through direct predation (i.e. reduction in resource density) and through the competition for nutrients (i.e. reduction in resource quality). In other words, for the SRM model, when consumer population increases, this decreases resource population growth by reducing both resource density (through predation) and quality (through the total nutrient load) leading to a negative feedback on consumer population growth rate. In contrast, for the RM model, the negative consumer feedback is only driven by the reduction in resource density as resource quality is not considered. We clarified this point (lines 386-390).

***Handling editor***

Discussion on the effects of temperature on assimilation efficiency (lines 481-493): It could be interesting to discuss a little further which mechanisms lead to reduced assimilation efficiency of the consumer (in relation to reduced resource nutrient quota) at high temperature in the model. This result could potentially also be related to existing experimental and empirical literature on the effects of temperature on the stoichiometry of primary producers (although the mechanisms involved might be indeed different in the model).

**Our response:** as suggested we detailed the mechanisms leading to reduced assimilation efficiency and also related this finding to the empirical literature (lines 506-512, 515-519).

***Handling editor***

I am looking forward to seeing your revised manuscript addressing the reviewers’ comments, along with a point-by-point response.

Best wishes, Elisa Thébault

**Our response:** thank you for the constructive comments. We look forward to hearing from you.

***Reviewer 1***

The manuscript investigates the influence of resource quality and temperature on consumer persistence in aquatic systems. For their theoretical investigations the authors extend the Rosenzweig-MacArthur model to include flexible stoichiometry at the resource level and temperature dependent resource and consumer rates. The authors follow published approaches and parameterizations. The study is well designed, the methods sound. The results are nicely explained and illustrated. As stated by the authors the presented study is a first step towards realistic theoretical approaches that are able to provide realistic predictions on the influence of climate warming and changes in nutrient regime on community dynamics and abundance patterns. The insight from this adapted resource consumer model with flexible stoichiometry and temperature dependent rates is very interesting. Due to its simplicity the changes in dynamics when moving from fixed to flexible stoichiometry for different temperature regimes

provides a mechanistic understanding of the underlying feedback mechanisms that lead to the observed shifts in coexistence, defined by nutrient availability and temperature, and consumer to resource ratios. The results highlight the necessity of including flexible stoichiometry and temperature dependence in ecological models that aim for predictions on community dynamics and species persistence along with climate change. What these results really imply with respect to management decisions will have to be investigated with more complex food web models. Apart from little typos I have no major remarks. Please find highlighted typos/small comments in the attached file.

[Download the review \(PDF file\)](#)

**Our response:** We thank reviewer 1 for the positive comments on our manuscript. We have corrected all the typos (see text in blue colour font in the main text) and better explained why in the SRM model more nutrients are needed to shift the system from a stable equilibrium to population cycles (lines 461-464, lines 386-390).

### ***Reviewer 2***

Sentis et al. have examined the interactive effect of temperature and nutrient stoichiometry on stability in the Rosenzweig-MacArthur Model. I enjoyed the manuscript, but was left with 9 concerns outlined below. I hope that these comments will help the authors as they revise their manuscript.

**Our response:** we thank reviewer 2 for the positive and constructive comments on our manuscript. We have modified the manuscript accordingly (see below for more details).

### ***Reviewer 2***

1) Most importantly, the authors need to clearly explain how their work differs from the work on Uszko et al. 2017. Uszko et al. also analyze the impact of stoichiometry (they account for both C and P) and temperature on a similar Rosenzweig-MacArthur model. They make many of the same assumptions (functional responses, temperature responses) or even consider multiple cases. They also assess questions of stability, limit cycles, and variation across the two constraints. Since the authors use many of the same parameters and as Uszko et al., it is especially important that they indicate how their work is different. I envision a few sentences telling the reader how this work builds upon this and other earlier work.

**Our response:** we agree that it is important to clarify how our work differs from Uszko et al. 2017. Uszko et al. addressed the effect of temperature on the Rosenzweig-MacArthur model (equation T1 and T2 in Uszko et al.) as well as a modified version of this model accounting for nutrient limitation in a closed or an open system (equations T4a, T5a and T5b in Uszko et al.). In this modified model, nutrients are stored in living biomass depending on fixed stoichiometric ratio, which is the usual approach in population dynamic models that consider nutrient dynamics. Put simply, in Uszko et al. the stoichiometric ratio is only a conversion parameter from nutrient to biomass. In other words, Uszko et al. model does not take into account neither flexible stoichiometric ratio nor the influence of flexible stoichiometric ratio on both the resource and consumer dynamics. It thus clearly differs from our work focusing on flexible resource stoichiometric ratio and its influence on both resource and consumer dynamics. We have now clarified this difference (lines 126-134).

### ***Reviewer 2***

2) I found the introduction to be repetitive. The authors have excellent content, but have at least 3 paragraphs making the point about the lack of studies with temperature x stoichiometry--this need only be said once. It could be collapsed into ~4 paragraphs instead of the current 7.

**Our response:** as suggested, we modified the introduction to avoid repetition and merged the two first paragraphs.

**Reviewer 2**

3) In most systems, the majority of nutrients are held in abiotic pools and biotic pools that have long turnover times (e.g. wood). Since you assume that there is a fixed amount of nutrients ( $N_{tot}$ ) that is shared between the resource and consumer, the only source of new nutrients for the resource (i.e. plants) is from dead consumers. I think this is a questionable assumption for most ecosystems, wherein consumer mediated recycling might be important but is certainly not the dominant source of nutrients accessed by autotrophs. In an aquatic system, the other nutrient pool would be dissolved organic (i.e. detritus) and inorganic nutrients. For example, Uszko et al.(2017) consider dissolved nutrients.

**Our response:** we agree that, in natural system, nutrients are often held in abiotic and biotic pools. As in Uszko et al. (2017), we considered dissolved inorganic nutrients and their dynamics (see text S1 where we detailed the full model considering the nutrient dynamics). As our objective was to compare predictions from the Rosenweig-McArthur model (that is not considering nutrient dynamics) to the simplest stoichiometric model, we simplified the full model (equations S1-S4) by assuming that inorganic nutrients are quickly uptaken by the primary producers. In other words, we assumed nutrient recycling to be faster than the population dynamics of the primary producer and the consumer. This assumption is realistic for the algae-grazer system considered here, and resembles the fast-flow energy channels modelled in aquatic systems, where system dynamics are fast and consequently nutrients are quickly recycled and uptaken (Rooney *et al.* 2006; Rip & McCann 2011).

Considering the nutrient held in the abiotic pool would not change the equilibrium densities of primary producers and grazer if nutrients are released in the environment proportionally to their density stored in the abiotic pool. It would only change the population fluctuations by probably reducing them. All our results related to equilibrium densities would thus not change if the abiotic nutrient pool was considered. We discussed this limitation in the revised version (Lines 484-490).

**Reviewer 2**

4) I do not understand the extinction threshold. The authors set an extinction threshold in the methods section. They say that considering data below this threshold lead to unrealistic results (Line 280). However, in the results section they use that threshold to contrast the SRM versus RM. I think these two approaches are in conflict. Can the authors resolve this?

**Our response:** We apologize for the lack of clarity. We did not mean that it leads to unrealistic results. It leads to unrealistically low biomass densities below which the population should be considered as extinct. We clarified this point in the revised version (line 279).

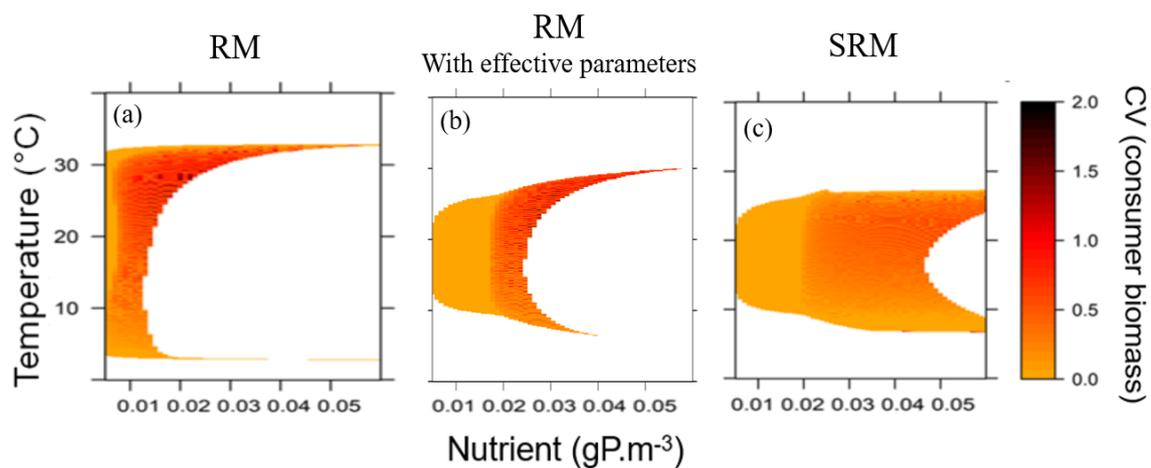
**Reviewer 2**

5) The excitation threshold is also very low ( $10^{-9}$ ). Therefore, I believe that the statement in the methods (that low populations should be considered extinct) is correct. The authors say that they simulated the SRM model (Line 271), but do not tell us how. Depending on the solver they used, these simulations could have different levels of precision. However, often the precision

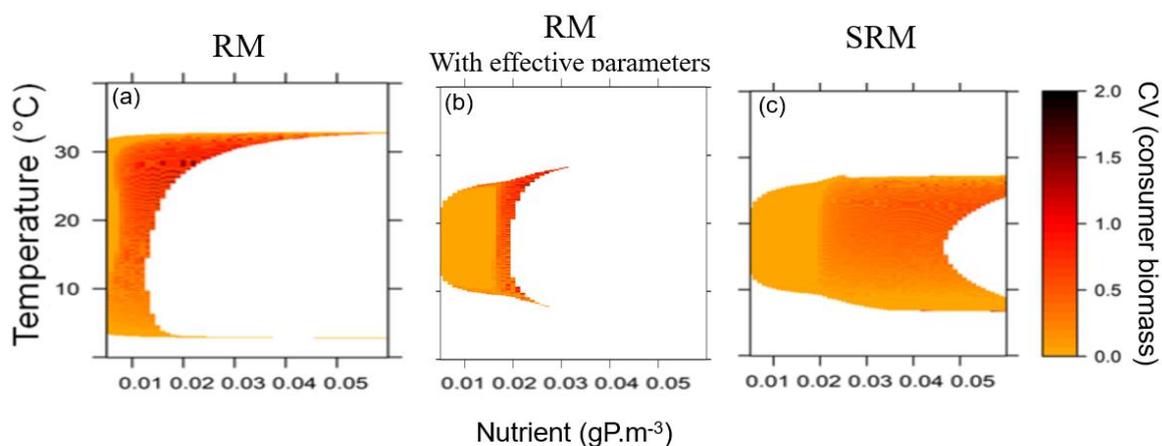
is only good to  $10^{-5}$  (R package "deSolve"), so the analysis of results below  $10^{-9}$  might not be acceptable. The authors can clear this up by providing information on the solver they used and its precision.

**Our response:** as suggested, we added information on the solver used (Desolve package) and the precision parameter used (lines 281-283). In the original version we used the default precision for both the absolute and relative error tolerance ( $10^{-6}$ ), we thus simulated again the dynamics using an absolute error tolerance of  $10^{-10}$  and a relative error tolerance of  $10^{-6}$ . The results remain unchanged, except for the RM with effective parameter for which we found that the system can persist at higher nutrient levels than in the original simulations. Nevertheless, this difference was independent of the error tolerance used as we found exactly the same results with an absolute error tolerance of  $10^{-6}$  or  $10^{-10}$ . The difference can thus be explain by either a coding mistake or a new R version (as R was reinstalled in-between the original submission and the revised submission) or new versions of the R packages used. Overall, these simulation differences were only quantitative and our conclusions remain unchanged.

**Figure 4 NEW simulations.** Population fluctuations (consumer biomass coefficient of variation) across the temperature (y axis) and nutrient (x axis) gradients as predicted by the Rosenzweig-MacArthur (RM; panel a), the RM with effective parameters (panel b), and the Stoichiometric Rosenzweig-MacArthur (SRM; panel c) models.



**Figure 4. Original version (first submission)**



**Reviewer 2**

6) The biomass ratios of the RM model are a function of parameters, so the RM could predict a biomass ratio of below 1 with different parameters. This leads me to ask: how general are the parameters used and how different would they need to be for the RM model to predict a biomass ratio below 1? If the assimilation efficiency, attack rate were low or the mortality or handling time were higher, the biomass pyramid would probably be inverted. SRM likely predicts a biomass ratios below 1, because the nutrient and temperature ratios chosen adjust these parameters to values that make consumers less abundant than their resources. I am left wondering, do the models always produces these differences, or is it based on parameter choices? (I also suggest calling these biomass ratios, because pyramid suggests more than two species.)

[Our response:](#) as suggested, we changed the pyramid for biomass ratios. We also added a mathematical demonstration that the SRM model always predicts lower biomass ratio than the RM model, independently of the parameter set (see text S2 and lines 344-347).

**Reviewer 2**

7) Figure 1: Since the number of species is discrete, I suggest using a discrete color scheme.

[Our response:](#) we modified Figure 1 as suggested.

**Reviewer 2**

8) I do not understand how the effective RM and SRM are different. Can you clarify this explanation?

[Our response:](#) we clarified the difference between these two models (lines 411-415).

**Reviewer 2**

9) You say that your model demonstrates that assimilation efficiency is temperature dependent in contrast to other evidence (Line 484-486). However, assimilation efficiency is temperature dependent in your model because of the structural assumptions you make. Consequently, your model hypothesizes what dynamics would look like if assimilation efficiency were temperature dependent. I think it is circular to suggest, in the absence of empirical data related assimilation efficiency and temperature, that your model demonstrates temperature dependence.

[Our response:](#) we agree and have modified the manuscript to clarify our contribution (lines 504-510).

**References**

- Rip, J.M.K. & McCann, K.S. (2011). Cross-ecosystem differences in stability and the principle of energy flux. *Ecology Letters*, 14, 733-740.
- Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, 442, 265-269.