

Dear Editor and Reviewers,

Please find the revised version of our article. We apologise for the delay of our second submission. The reasons for this significant delay are twofold:

First, while we were going back to the code of the food chain model, we noticed a mistake that changed our results on this matter. Our former results showing that feedback loops generated by nutrient cycling reduce the temporal variability of species biomass in a food chain are no longer true. Our new results show that feedback loops either decrease or increase species biomass CV depending on trophic levels and food chain length (see the Supporting information). Therefore, we redid all the analysis of the food chain model and these results are now presented in Supporting information rather than in the main text. We also had to rethink the interpretations of the effects of feedback loops in complex food webs that were related to the results of the food chain model. The parts lines 494 and 574 in the discussion have been modified according to these new interpretations. Please note that we re-checked carefully the code of the complex food web model and did not find any mistake. The core result of our manuscript, that is the general response of a complex food web model to nutrient cycling and nutrient enrichment, thus remains unchanged compared to the previous version of the manuscript.

Second, I was also just starting my first post-doc while we submitted our article (that was a part of my PhD project) to PCI. I was thus unable to achieve all the needed new analyses in a short time, thus explaining further the delay of this resubmission.

In spite of these changes regarding the food chain model, the remarks made by the three reviewers still hold and we took them into account to improve the manuscript. In particular, we added new analyses regarding the sensitivity of our results to the assumption of intraspecific density dependence (see detailed response to the three reviewers), adaptive foraging, number of food web replicates and extinction threshold (see detailed response to reviewers Uszko). We also included additional analyses to precise the effects of our two main recycling parameters (d and δ) in the main text. We also increased the focus of our paper on the effect of nutrient cycling on the paradox of enrichment (see response to reviewer Arnoldi).

Thank you for considering our manuscript for recommendation. We appreciate your time and look forward to your response.

Best regards,

Pierre Quévieux, on behalf of the authors

Response to reviewers - Round #1

Decision

by Samraat Pawar, 2018-12-15 08:38

Manuscript: <https://doi.org/10.1101/276592>

First decision on manuscript

Dear Authors,

I have now received three reviews of your manuscript. I am glad to say that all three reviewers have been very thorough and constructive. All three acknowledge the potential value of your manuscript, but also raise a number of technical issues that merit a significant revision. All three concur on two main issues that need to be addressed in particular: apparent parameter sensitivity (and in particular, the use of body-mass scaling) of the mathematical model's dynamical behaviors, and related to that, insufficient insights into mechanisms underlying these behaviors. These include your results about stability, and the role of intraspecific density dependence.

Some of these comments raise some fundamental technical questions that definitely need to be addressed. In particular, * Both Reviewer Uszko and the one Anonymous Reviewer raise concerns about the adaptive foraging model. * All three question the assumption of intraspecific density dependence across trophic levels. * The Anonymous Reviewer questions the use of model parametrization using body-mass scaling alone as it may not capture empirical reality to a sufficient extent. * Reviewer Arnoldi raises questions about your conclusions about stability, and suggests that you re-focus the paper (from stability) on the novel perspective that nutrient cycling provides on the classical paradox of enrichment in complex food webs. I leave it to you to make a decision about it though.

Overall, I think the reviewers have made a number of very clear, objective suggestions and comments, and I look forward to seeing a revised manuscript that addresses them, along with a set of point-by-point responses.

Best wishes,

Samraat

Thank you for these positive and constructive comments. We performed additional sensitivity analyses regarding different parameters (including adaptive foraging and intraspecific density dependence) to better understand the mechanisms underlying our results. Regarding the use of body-mass scaling, we agree that body mass does not control all the aspects of trophic interactions (as pointed out by Reviewer 2). However, many studies revealed the major role of predator-prey body mass ratios in structuring trophic interactions in real ecosystems (Brose et al., 2006, Brose 2010, Petchey et al., 2008, Vucic-Pestic et al., 2010, Barnes et al., 2010, Dell et al., 2011, Arim et al., 2009, 2010, Gravel et al., 2013). Body mass scaling provides simple rules with few parameters and have been largely used in previous models (see Heckmann et al., 2012 for instance). We thus think it is relevant to use a size-structured food web in our model. As outlined in our above cover letter, we also modified significantly the part corresponding to the results and discussion of the food chain model as we found a mistake in our previous analysis of this model. The results corresponding to the food web model remain unchanged, and our sensitivity analysis further strengthens our conclusion that the effects of nutrient cycling on food web stability are mainly related to enrichment effects.

You will find below our detailed point-by-point response to all the reviewers' comments.

Reviews

Reviewed by Jean-François Arnoldi, 2018-12-03 13:59

The manuscript by P. Quévreur et al focuses on the dynamical impacts of nutrient cycling in a complex food web model.

As I will argue below, In my opinion, the paper has potential. However, a restructuring of the narration as well as a more synthetic understanding of the dynamical behavior of the model, i.e. an identification of driving parameters and dynamical regimes leading to the observed patterns, might

be required for the paper to be recommended.

Summary of the paper

Methods: The authors base their findings on a metabolic model that defines trophic interactions from species body mass, allows for foraging strategies to adapt and, importantly, tracks the amount of nutrient contained in species biomass via their stoichiometry. This latter feature allows to add -or not- recycling pathways from species biomass to a global nutrient pool, on which primary producers grow.

The authors focus on the fraction of surviving species (persistence) in assembled communities, and the relative amplitudes of biomass fluctuations of surviving species (variability). The authors then study the impact of nutrient cycling on persistence and variability, as a function of nutrient enrichment (which could represent an anthropogenic disturbance, such as fertilizer runoff). The analysis is performed by comparing the simulated outcome of assembly with and without nutrient cycling. Interestingly, a comparison is made between the outcome of assembly without recycling but with an additional nutrient input equivalent to the amount recycled in the full model. To assess the effect of complexity, the authors also consider a much simpler tri-trophic food chain, and study its dynamical state as a function of enrichment.

Results: The main finding is that cycling does have a strong effect on community assembly. It makes the paradox of enrichment more acute, as increasing enrichment, after allowing for more species to persist, rapidly leads to the extinction of most. Without nutrient cycling the effects on persistence are much less dramatic. In terms of variability, the effects are qualitatively similar (increase of variability with enrichment) although less impressive. Importantly, in the complex food web, this aggravation of the paradox of enrichment is entirely explained by the added influx of nutrients caused by recycling, the latter growing nonlinearly with enrichment. The simplified food chain model shows similar variability pattern but, contrary to the complex web, shows some (stabilizing) effects of cycling which are not equivalent to an added influx of nutrients. There is thus some simplicity emerging from the apparent complexity of the food web model.

Major comments:

I found the manuscript to be well written and the analysis rigorous. However, to propose a recommendation some major issues must first be addressed. Below I explain my criticisms and make some suggestions to answer them.

I) I find that the focus on stability substantially weakens this contribution. Stability is taken in a rather narrow sense (no perturbations are considered for instance) and the "stabilizing" effects of cycling are in fact very minimal and only present in the food chain model. In terms of persistence, over the range of parameters considered, it is clear that recycling is mostly destabilizing whereas the authors seem to desperately look for signs of stabilization (the "weak stabilizing effects" mentioned in the abstract). Instead of getting lost into what stability means and what is stabilizing and what is not, I believe that a much stronger contribution can be made: a novel perspective on the paradox of enrichment in complex food webs, and the fundamental role played by nutrient cycling.

We modified the title and the narration in the paper to stress on the interactions between nutrient cycling and paradox of enrichment. The questions at the end of the introduction now directly refer to these interactions:

“How nutrient cycling affect the overall nutrient availability in ecosystems and thus interact with the paradox of enrichment? Can the addition of feedback loops by nutrient cycling change the effects of the paradox of enrichment on species dynamics? Do the relative importance of direct and indirect nutrient cycling and the decomposition rate modulate these effects? “ (l.131-135 at the end of the introduction) and in the discussion (l.366-367)

The first section of the discussion is now devoted to the paradox of enrichment (l.377-409)

Regarding stability, we removed all our conclusions referring to the general stability of our system

and systematically refer to temporal variability when we speak about stabilising or destabilising effects (l.497-498, 566-568). We also explain more clearly that recycling is mostly destabilising through its enrichment effect, while additional effects of feedback loops on temporal variability are weak (see changes in abstract l.20-23, and in the main text l.368-372,495-497).

We also suggest in the discussion the interest of other stability measures including perturbations to go beyond the context of the paradox of enrichment: “Moreover, studies based on stochastic perturbations as in Shanafelt and Loreau (2018) would bring new knowledge on the effects of nutrient cycling on other stability components of food chains and webs.” (l.566-568).

II) A better understanding of the dynamical regimes that can lead to such paradoxical effects is required. For instance, in the analysis, variability is caused by the occurrence of limit-cycles. I'm guessing that such attractors do not occur for any choice of parameters but require strong top-down feedbacks. Such top-down feedbacks are strongly dependent on the strength of self-regulation (see a recent preprint by Barbier and Loreau, bioRxiv). In the manuscript those self-regulating effect were admittedly arbitrarily chosen and independent on species metabolism. It is this not impossible that an other parametrization of self-regulation would lead to different top-down effects and thus different conclusions regarding the effect of nutrient cycling. This is not necessarily true, but the fact that there is no way to know based on the manuscript is a problem.

As discussed in our manuscript, we fully agree that part of our results (e.g. decrease in persistence in response to nutrient cycling at high nutrient inputs) are related to the occurrence of limit-cycles associated to the paradox of enrichment in our food web model. Parameters determining the occurrence of such limit-cycles thus affect the food web response to nutrient cycling, as already shown by the different response of food web persistence to nutrient cycling when we use a type III functional response instead of a type II functional response (see Appendix l.1150-1162). When limit-cycles associated to the paradox of enrichment do not occur, the presence of nutrient cycling always increases persistence. However, as for other cases, the effects of nutrient cycling are mostly related to enrichment effects rather than by the presence of recycling loops.

To test the impact of self-regulation on our conclusions, we also ran simulation with $\beta=0$ (no self-regulation) and $\beta=0.1$ (strong self-regulation) and we found that “whatever the value of β , the enrichment effect of nutrient cycling is always dominant in explaining the difference between the C and the NC models as both curves representing the C and SC models overlap strongly” (l.1115-1118) (see Fig. S3-3).

The allometric parameters commonly used in this kind of model lead to limit-cycles (see Brose et al., 2006, Otto et al. 2007 or Boit et al., 2012), density-dependent mortality ensuring a reasonable species persistence. As we did not find in the literature any value for β , we set it arbitrary such that to maximize the persistence domain without removing the limit cycles (see Fig. S3-5). Please note also that density dependent mortality is in fact allometric in our model, we had made a mistake when we retranscribed the parameters from our code. This mistake is now corrected in the revised version of the manuscript (l.186 and equation (4c)).

III) Make the theory empirical testable: Once the the key parameters (or combination of parameters) driving the paradox of enrichment in the complex model have been identified, this might enable the authors to propose empirically accessible conditions predicting the importance of nutrient cycling and the ensuing vulnerability of complex food webs to enrichment. For instance, a condition could be that a given community exhibits trophic cascades, supposing that top-down feed backs are key features. Such work would greatly increase the scope and importance of this contribution.

We agree it would be very interesting to understand which key parameters (and their combination)

determine the paradox of enrichment in our model. We now discuss more clearly the importance of model parameters on this issue (l.398-400).

However, although going fully in this direction would be very interesting, it would have required to vary many other parameters than the ones we already vary. Testing combinations between all the food web parameters and the nutrient cycling parameters and looking at all the output variables we presented would be a very large and long task, especially regarding the long running time of our simulations. In addition, we feel that such results, in addition to our already existing results, would not fit in a single manuscript. Our aim for the present manuscript was to include nutrient cycling in this kind of model that is known to be affected by the paradox of enrichment and to explore how it interacts with it. However, what you propose would be an interesting future direction to have a broader understanding of our results. Using a simpler representation of nutrient cycling and a food chain model similar to Barbier et al. 2019 would maybe be more suitable.

IV) Clarify the emerging simplicity (This last point might be slightly off-topic). The authors may want to take a step further in the understanding of emerging simplicity in complex food webs, at least when focusing at collective observables (such as the fraction of surviving species following assembly). This is indeed already suggested by the fact that the impact of optimal foraging is inexistent in terms of the output of interests, and cycling loops are equivalent to an additional nutrient influx, whereas it is not the case in the food chain. There are possibly many other details that do not matter for the outcome of assembly, the latter possibly driven by some aggregate features of the ecosystem (due to self-averaging effects allowed by complexity -see the work by Guy Bunin for instance).

We agree that it would be very interesting to clarify which parameters (or aggregated parameters) determine the outcome of assembly and effects of nutrient cycling in our model. However, we think that such approach is beyond the scope of our study. To outline the perspectives of our study in relation to the notion of emerging simplicity, we now discuss the work of Barbier et al. 2018 “Overall, our results suggest that simplicity emerges from food web dynamics, making the prediction of the impact of nutrient cycling on ecosystem functioning easier in complex food webs than in food chains. Barbier et al., 2018 found that food web properties such as biomass distribution can be assessed thanks to the statistical distribution of species physiological and ecological parameters. From their results, adding the statistical distribution of recycling parameters (δ is fixed in our study but it must vary between species) would enable us to evaluate the quantity of recycled nutrients I_{recy} and thus to assess ecosystem functioning just by knowing the overall characteristics of the community living in the ecosystem.” (l.550-557).

The emergence of aggregated process could also be tackled in future studies by “new models based on simple food chains and manipulating both food chain length and horizontal diversity are needed to fully understand the effects of nutrient cycling on dynamics.” (l.560-562)

Minor points:

1) I was left wondering why the species were going extinct, is it entirely due to the amplitude of the cycles? In this case the two stability notions, variability and persistence, are not complementary (as stated in the introduction) but are the two sides of the same coin.

Species extinctions are indeed due to the amplitude of the cycles. We have added an analysis in supplementary material showing that increasing the extinction threshold further increases the number of species extinct (Fig S3-2). Indeed, variability and persistence are thus related in our study, and we accordingly removed the term “complementary” (l.235).

2) Does it really matter whether there are one or two abiotic compartments (Mineral nutrients and

detritus)? I would expect that the decomposition rate (d) from detritus into mineral nutrients can be integrated as a part of the fraction of recycled nutrients (δ). Indeed, Fig. 4 shows that d and δ are interchangeable since persistence is a function of their difference.

We extended our analysis to other combinations of d and δ values to further test this issue. We showed that d and δ impact differently the outcome of nutrient cycling and thus are not interchangeable. For instance, the detritus compartment size does not depend on the decomposition rate d (Fig. S2-4D) and “keeps nutrient unavailable for primary producers and tends to smooth nutrient cycling dynamics (see Fig. S2-1B and S2-1D in the supporting information)” (l.503-505). In addition, the stabilising or destabilising effects (even if they are weak) depend on the fraction of direct recycling δ (see Fig. 5, S2-5 and S2-6). As it “shortens feedback loops and then increases the coupling between each trophic levels and mineral nutrients. Such a coupling can be seen in the increased biomass CV difference between the C and SC models (see Fig. S2-6 in the supporting information) and in the increase of the total quantity of recycled nutrient CV due to the larger contribution of species direct recycling that have high CV.” (l.505-510). Concretely, the mere existence of the detritus compartment changes the interactions between nutrient cycling and the food web.

Reviewed by anonymous reviewer, 2018-11-27 18:44

This preprint presents results of simulations of a variants of food-web model that do or do not include explicit representations of nutrient cycling. The authors ask to what extent this affects persistence of species and variability of population abundance in the dynamic steady state of assemblages of random species.

While I have no concerns regarding the technical correctness of the results, I am worried that the empirical motivation and/or validation of the model are too weak to justify the strong conclusion that the authors draw.

The recommendation is therefore that the authors might want to substantially moderate the strength of the wording of their conclusions they draw or more seriously engage in model validation (and probably reconstruction).

We understand this general comment and have checked that the discussion is not too positive about the applications of our findings to real ecosystems. Nevertheless, we think that the way we have written our manuscript is in line with the way theoretical papers about food webs are written. Of course, our results strongly depend on the modelling hypotheses we have made (which is always the case). What is important is to criticise in the discussion the aspects of the model that are the most disputable and that would deserve new research and modelling efforts. We believe to have done so.

To demonstrate this point, let me first collect a few conclusions:

116: "We found that nutrient cycling can provide more than 50% of the total nutrient supply of the food web, ..."

This sentence has been replaced by “We found that nutrient cycling can provide a significant part of the total nutrient supply of the food web” (l.17)

1405: "Our results highlight that effects of nutrient cycling on nutrient availability are key to understand consequences of nutrient cycling on food web dynamics in ecosystems."

This sentence has been deleted.

1518: "In an ecosystem model linking population dynamics in a food web to ecosystem functioning, we found strong effects of nutrient cycling on food web stability. Thus, ecologists need to incorporate nutrient cycling in theoretical and empirical work to better predict food web stability."

This sentence has been replaced by "Thus, ecologists should consider nutrient cycling in theoretical and empirical work to better predict food web response to nutrient inputs as nutrient cycling deeply changes the overall nutrient availability" (l.583-585)

These are statements about what processes are important in REAL systems. To support such conclusions, the model used should be sufficiently realistic. So let's have a look at the model.

The authors parametrise trophic link absence/presence and strength based on predator and prey body mass alone. They motivate this by writing

124: "Models parametrised with such allometric relations have been increasingly used to study food web dynamics and stability, especially because they allow recreating observed patterns and dynamics of complex food webs (Boit et al., 2012; Hudson & Reuman, 2013)."

However, Boit et al. (2012) do NOT reproduce "patterns and dynamics of complex food webs". They simplify complex food webs into a small number of compartments. Hudson & Reuman (2013) use OBSERVED presence/absence data for trophic links to link species in their model (and then body for to adjust link strengths), and predicted abundances typically differ from observations by a factor 10. So, neither reference supports the statement. To the contrary, there is strong evidence that link presence/absence is not primarily affected by body mass: <http://doi.org/10.1098/rspb.2012.0327> <http://doi.org/10.1016/j.jtbi.2005.12.021> .

We nuanced our sentence referring to the studies of Boit et al. and Hudson & Reuman : "Models parametrised with such allometric relations have been increasingly used to study food web dynamics and stability, especially because they give better approximations, even though still simplified, of observed patterns and dynamics of complex food webs (Boit et al., 2012; Hudson and Reuman, 2013)." (l.123-126). We agree that these models did not reproduce exact ecosystem dynamics and were simplified versions of observed food webs but this is the case for any food web model aiming to be simple and general enough. We are also aware that the ratio of predator/prey mass is not the only determinant of trophic interactions but a large number of studies have highlighted its key role as predictor of food web structure (Brose et al., 2006, Brose 2010, Petchey et al., 2008, Vucic-Pestic et al., 2010, Barnes et al., 2010, Dell et al., 2011, Arim et al., 2009, 2010, Gravel et al., 2013).

The model for adaptive foraging used (Eq. (6)) does not appear have a good empirical justification. I am concerned that it might yields diets that are much less diverse (in terms of the distribution of the size of diet proportions) than those observed (e.g. Secs. 12.3, 12.4 in <http://doi.org/10.1002/9781118502181>), which unclear consequences.

Our results (see Fig. S3-5 in the appendix) show that the presence of adaptive foraging in our model does not affect our conclusions. Indeed, even if the presence of adaptive foraging increases overall species persistence when compared with a model without adaptive foraging, the effects of nutrient cycling on persistence and species temporal variability are the same in both cases.

Most importantly, I am concerned about the Intraspecific competition term (with constant coefficient β) that is included the dynamics for all species. It is worth pointing out that the model by Hudson & Reuman (2013) cited above and other realistic food-web models do NOT contain such terms. Indeed, it is hard to image what kind of ecological phenomenon this term could represent, given that it describes effects of individuals on conspecifics that do NOT affect any other species. To the contrary, the observed power-law structure of size spectra (which follows from feeding being

the only form of density-dependence) and the observed strong coupling of species richness across trophic levels (Sec 18.6 <http://doi.org/10.1002/9781118502181>) both provide good empirical evidence for the absence of such exclusively intraspecific, non-trophic competition. As the authors show in Fig S3-1, the strength of Intraspecific competition can strongly affect system properties. The choice of β could easily affect the qualitative nature of conclusions, such as in the following passage:

l286: "At low nutrient enrichment levels, consumers are responsible for most of the recycling. However, at high nutrient enrichment levels, the quantity of nutrient recycled by consumers stops increasing while the total quantity of nutrient recycled still increases linearly with the external nutrient input I due to a large increase in the quantity of nutrient cycled by primary producers. A similar relation is observed for the primary and the secondary productions (see Fig. S2-4C in supporting information)."

We extended our sensitivity analysis with new simulations exploring the effects of $\beta=0$ (no self-regulation) and $\beta=0,1$ (strong self-regulation) (see Fig. S3-3 in the appendix). Even if increasing β promotes species persistence by decreasing the temporal variability of species biomasses, "the enrichment effect of nutrient cycling is always dominant to explain the difference between the C and the NC models as both curves representing the C and SC models overlap strongly as in Fig. 3B in the main text, making our results robust to β ." (l.1116-1118).

The intraspecific competition term can represent territoriality or pathogen accumulation for instance and it has been used in other food web models such as Heckmann et al. (2012) or in Barbier et al. (2019) for instance. Many other models do not use this term but they use a predator interference term in the functional response instead (Beddington-DeAngelis functional response) as in Hudson et al. (2013). However we agree that these two different options would impact differently nutrient cycling:

- Intraspecific competition β increases mortality and thus increases excreted nutrients*
- predator interference lowers the growth rate and may lead to less recycled nutrients by consequently reducing the flow of matter passing through the species compartment.*

Such a difference could for example change the size of the mineral nutrient and detritus compartments: by reducing species growth, predator-interference could lead to the accumulation of unconsumed mineral nutrient while the intraspecific competition could lead to the production of a lot of detritus. This interesting question deserves an entire study to be fully answered. We added a paragraph in the discussion to tackle this point:

"In addition, density dependent mortality seems to have a strong impact on nutrient cycling in our model as it drastically increases the quantity of nutrients flowing out of the species compartment. Although it does not affect the qualitative response of species persistence and biomass CV to nutrient enrichment (see Fig. S3-3 in the supporting information), it drastically increases the quantity of nutrients flowing out of the species compartment and then through the entire ecosystem. Other mechanisms limiting species biomass such as predator interference in the Beddington-DeAngelis functional response (Beddington, 1975; DeAngelis et al., 1975) decrease the net growth rate by reducing the resource uptake rate instead of increasing the death rate. As a consequence, such a mechanism would lead to reduced nutrient flows in the ecosystem, thus changing nutrient cycling. Such effects of population dynamics modelling on ecosystem functioning must be explored in future studies." (l.444-454)

Besides, the authors argue consistently based on the hypothesis that extinctions are caused by high-amplitude population oscillations, despite there being a strong body of evidence that most extinctions are caused by populations slowly and gradually approaching zero. The mechanisms

causing the latter is very different from that causing the oscillations. This, as well might have a strong bearing on the validity of the conclusions.

The populations in our model are actually experiencing large biomass oscillations (see Fig. S2-1A in the supporting information) whose amplitude increases with nutrient inputs, which is consistent with previous results.

To demonstrate that extinctions are due in our model to increased oscillation amplitude, we added a section testing the effect of the extinction threshold on species persistence:

“We raised the extinction threshold up to 10^{-15} kg.v⁻¹ (Fig. S3-2B) compared to the value used in the main study (10^{-30} kg.v⁻¹) (Fig. S3-2A). Species persistence is lower with this new threshold only at high nutrient inputs when species CVs increase with nutrient inputs. This demonstrates that extinctions are due to increased oscillation amplitudes that push species biomasses close to the extinction threshold.” (l.1099-1103)

We also discuss more clearly the importance of the occurrence of limit-cycles on our results:

“Thus, parameters determining the occurrence of limit-cycles in complex food webs should strongly determine food web response to increased external nutrient inputs as well as nutrient cycling. In accordance with our model results, the paradox of enrichment has been found in complex food web models with type II functional responses (Rall et al., 2008, Binzer et al., 2016).” (l.398-402).

Other notes:

144: "... but they never include a complete nutrient cycling." -> I am surprise the authors write don't consider <https://doi.org/10.1073/pnas.2434847100>

Our study takes place in the context of size structured food webs with allometric scaling of biological rates. Thébault and Loreau (2013) does not use such a model.

Para starting 71: it is really unclear where the authors are referring to empirical evidence and where to evidence from models. Can models alone support strong statements such as "Effects on nutrient availability thus clearly need to be accounted for when studying nutrient cycling effects on food web stability"?

We mainly have two statements on the effects of nutrient availability, both supported by models and empirical observations:

First: “it fuels primary production and increases the energy transfer to consumers, leading to a higher species persistence and sustaining higher trophic levels as supported by models (Abrams 1993, Binzer et al., 2011) and empirical observations (Yodzis 1984, Doi 2012)” (l.75-77).

Second: “On the other hand, nutrient overabundance tends to increase the amplitude of population oscillations, which increases the risk of extinction. This characterises the paradox of enrichment (Rosenzweig, 1971; Rip and McCann, 2011) predicted by several food chain and food web models (Roy and Chattopadhyay, 2007; Rall et al., 2008; Hauzy et al., 2013; Gounand et al., 2014; Binzer et al., 2016) and some experiments (Fussmann et al., 2000; Persson et al., 2001).” (l.77-82).

In addition, nutrient cycling affects nutrient availability through an enrichment effect:

“First, the recycled nutrients (i.e. excreted nutrients that return to the mineral pool available for primary producers) are added to the external inputs of mineral nutrients and could lead to an enrichment effect (Loreau 2010).” (l.72-74)

Therefore, as nutrient availability strongly affects food web structure and dynamics, we can expect the impact of nutrient cycling to be mediated by its impact on nutrient availability.

We rephrased the sentence to make these implications more clear:

“Thus, the enrichment effect of nutrient cycling may be a major component of its effects on food

webs (McCann 2011).” (l.86-87)

Eq 7a and elsewhere: "i=diversity" ; "i=primary producer" -> poor notation.

We modified the notations in Equation 7a and other equations following the reviewer comment (equations (3), (5), (6) and (7)).

426: "At low nutrient inputs, consumers are the main contributors to nutrient cycling, in agreement with experimental and empirical studies (Vanni, 2002; Schmitz et al., 2010)." -> Good.

Thank you.

1539: "The predictions of our model should be tested experimentally." -> My feeling is there is some good empirical evidence already, one just needs to look at the problem from an empiricist's perspective. Here is an examples: [https://doi.org/10.1890/0012-9615\(2003\)073\[0301:ECSAEI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2003)073[0301:ECSAEI]2.0.CO;2) <https://lter.limnology.wisc.edu/data>
<https://doi.org/10.2307/1942450>

Thank you for proposing these references but in our text we thought about experiments manipulating nutrient cycling. The experiments you mentioned referred to bottom-up (nutrient enrichment) and/or top-down (top-predator removal) experiments only. We changed our sentence to better explain the aim of these potential experiments:

“Experiments designed to test the effects of the mechanisms involved in our model would be interesting” (l.598)

Reviewed by Wojciech Uszko, 2018-11-26 15:20

Persistence and stability of food webs have been one of the central research problems in ecology for many decades. Despite the importance of these subjects, we still lack the knowledge of how explicitly considered nutrient cycling affects food webs. We need more resource-based models studying how dynamic nutrient cycling potentially alters model predictions compared to classic approaches which do not take into account the nutrient currency.

Quévreur, Barot and Thébault approach this problem in a rigorous way by building and simulating food web models with different assumptions on nutrient recycling. They do so in four subsequent steps. First, they construct food webs consisting of 50 species linked by feeding relationships based on their body masses. The species dynamics is described by nutrient-explicit models, and species persistence and population stability is investigated at the end of the simulation time. Second, they consider three types of models which differ in if and how nutrients are recycled: (i) without nutrient cycling (NC), (ii) with full nutrient cycling loops (C), (iii) with nutrient cycling simulated through addition of mineral nutrients to food webs as calculated from the C model (SC). Especially the models C and SC give an opportunity to compare the effects of nutrient cycling which arise from the dynamic feedback loops vs. a simple enrichment effect, respectively. Third, the authors compare the modeling results from complex food webs (up to 50 species) to results from three-level food chains. And fourth, sensitivity analysis is run with different assumption on model parameters.

The authors report several important findings. The amount of recycled nutrients always exceeds the supplied mineral nutrients, and the recycling is driven mostly by consumers at low mineral nutrient inputs, and by primary producers at high inputs. This extra nutrient input through recycling increases the species persistence at low mineral nutrient input levels, but decreases it towards higher inputs. The mechanism behind the latter result is that additional nutrients destabilize food webs ('paradox of enrichment') by increasing population oscillations, leading to species extinctions.

However, when comparing the C and SC food webs (with dynamic nutrient cycling pathways vs. with simulated extra nutrient input, respectively), the SC food webs are more variable and less persistent than the C ones.

The manuscript is written clearly and in a comprehensive way. The figures are well designed, and convey the results to the reader very efficiently. I have however a number of comments, mostly considering the model formulation and the details of methods, which I believe can further improve the readability and broaden the scope of this already very valuable work.

1. The food web model is divided into two compartments: carbon-based and nutrient-based (Fig. 1, lines 139 onward). However, it is important to notice that this division is just an artifact of the units used for species biomasses. Given that both primary producers and consumers are assumed to have fixed C:N ratios, the translation of nitrogen to carbon mass for the living part of the food web is redundant, and does not change the model behavior itself. In other words, one could just as well represent the entire model in nitrogen units, and nothing would change. With that said, I think it is fine to make such a division of modeled food webs, but maybe add a statement that the existence of these two compartments is somehow artificial as carbon is a 'passive' player in the model, and its fluxes are not explicitly considered. What I believe is much more important to mention early in the methods section, is the fact that all species are assumed to have fixed C:N ratios. This information is at the moment somewhat hidden in Table 1.

You are absolutely right and we made it clearer in the M&M that all species are assumed to have fixed C:N ratio. We added "Constant" in table 1 and we added the following sentence :

"For simplicity, we assume here that species carbon to nutrient ratio (C:N) α_i are constant over time. Please note that we could have expressed directly the species biomasses in nutrient instead (as in Zou et al. (2016)), without changing the model behaviour. However, we chose to keep species biomasses based on carbon to relate more clearly our equations with classical allometric food web models." (l.211-215)

2. Changing the assumption of fixed to flexible nutrient stoichiometry of primary producers seems to me as potentially the most fundamental possible extension of the presented model. Flexible plant C:N ratio will influence the behavior of food webs not only through changes in detritus stoichiometry as the authors have already mentioned, but also it opens for a possibility of nutrient limitation of consumers. This in turn will dynamically affect the entire food web in a way that is hard to deduce from just considering different, but still fixed and not dynamic, producer C:N ratios as the authors have analyzed in Appendix S3. Of course, extending the model to flexible C:N ratios of producers is likely outside the scope of this paper. However, I suggest to extend the relevant points in the discussion section, with stronger emphasis of other effects of flexible producer nutrient quotas, different than just the detritus quality.

We agree including flexible nutrient stoichiometry of primary producers is an important perspective and we now develop this point in the discussion:

"In addition, primary producer stoichiometry can be a flexible trait responding to nutrient limitation or herbivory, which can limit herbivore assimilation efficiency (Branco et al., 2018), thus affecting the energy transfer in the food chain." (l.490-492).

And at the very end of the perspective section

"To go further, the flexible stoichiometry of primary producers (and phytoplankton in particular) can also deeply affect food web dynamics and consumer persistence as it can limit herbivore assimilation efficiency (Loladze et al., 2000, Branco et al., 2018). In fact, Urabe et al. (1996) demonstrated experimentally that increasing light availability first increases phytoplankton and

zooplankton biomass productions but then led to zooplankton extinction because of the low nutritional quality of phytoplankton biomass if the light to nutrient ratio was too high.” (l.615-6121).

3. Apart from metabolic and feeding losses, all species in the modeled food webs experience an additional, density-dependent mortality with coefficient “beta” defined as the intraspecific competition coefficient. The authors should give an explanation why they decided to include such term in their generic model. Both intra- and interspecific competition is already taken into account through resource uptake/prey consumption of producers/consumers. Why then adding an extra density-dependent loss term? My intuition tells me that such term can have strong effects on system stability. This also emerges from patterns shown in Appendix Fig. S3-1, which however does not consider a scenario with “beta”=0. As the choice of “beta” values is arbitrary (i.e., not empirically based), is there any other reason the authors used this term, apart from aiming for reasonably persistent food webs? Whatever the reasons are, I think they should be stated in the methods section as to not leave the reader wondering why a particular model formulation has been chosen.

Indeed, self-regulation enables us to have food webs with a “reasonable species persistence, see Fig. S3-3 in the supporting information” (l.181). We also added more precision in the sensitivity analysis where we now consider a case with $\beta=0$ (Fig. S3-3). The results of this additional sensitivity analysis are discussed lines 1106-1118.

4. The authors do not give any explanation of why their models were tested on the set of only 100 different food webs. Intuitively, 100 is a very small number given the potential degree of variability of generated food webs. Is 100 a big enough number to exhaust qualitatively, and get enough replicates quantitatively, of all possible food web configurations? Were the authors in any way limited by computational time? Whatever the reason is for choosing the number 100, it should be explicitly stated. If there are no particular reasons, then why not test the model on many more (1000? 10,000? 100,000? 1,000,000?) food webs? Note that the number of analyzed food webs stands at the very core of this study, and potentially strongly influences the results.

Our simulations were quite long to run (up to three hours per replicate for a given parameter set) and we could not run thousands of replicates as the computation time is limited on the HPC of the university. We used old simulations (some output variables were added later in the history of this study) to have extra replicates and see the effect of the number of replicates on the confidence interval of six important output variables (species persistence, average quantity of recycled nutrients, average primary and secondary productions, average quantity of nutrient directly recycled by primary producers and consumers) (Fig. S3-1). Doubling the number of replicates from 100 replicates to 200 leads to a change close to 1% in the mean and less than 10% in the standard deviation (l.1092-1093). Thus, 100 simulated food webs are enough to capture the accurate response of the model for our variables of interest.

5. As far as I understand the procedure, the food webs were constructed in a few steps. First, 50 species were assigned random body masses spanning 6 orders of magnitude. Then, feeding links were assigned. However, if there is no matching prey for a consumer of a particular body size, this species is removed in the beginning, which is not counted as extinction. Am I right? How often did the assembled food webs go through this ‘thinning’ procedure before the actual dynamic simulations? This could mean that not all food webs have 50 as their starting number of species. What I also believe would be very helpful is a histogram showing how many food webs of how many species are left after the simulations, i.e., a histogram with number of persistent species after 10,000 years on the x-axis, and number of

food webs with a respective number of species in them on the y-axis.

Actually, we did not try to have our 50 initial species connected by trophic interactions. If a consumer has no prey, we let it die. Thus we never have 100% species persistence after 10,000 years. These extinctions are taken into account in the measured persistence and do not biased our results as there are present in all our simulations. We added more details to clarify the preliminary phase of our simulations:

“Simulations were run as follow: first, 50 species are attributed a body mass (the five smallest being primary producers) and trophic links were set depending on predator-prey body mass ratios (see equation 2). We did not seek for food webs with our 50 species linked by trophic interaction, thus consumer without prey got extinct during simulations. Then, simulations were run a for 9000 years to let the ecosystem reach a steady state. We kept in our results all resulting food webs even when some of the initial 50 species got extinct (see Fig. S3-1C in the supporting information). Species were considered as extinct if their biomass fell below 10^{-30} kg.v⁻¹ and consumers without prey got extinct. After this preliminary phase, outputs were recorded for 1000 years.”(261-269).

The histogram you propose actually corresponds to our persistence graphs (Fig. 3B). Instead, we added an histogram of the distribution of the number of extinctions during this phase to justify the duration of our simulations (Fig. S3-1C), most of the extinctions occurring during the first 2,500 years of simulation.

6. How is species extinction defined? What is the biomass threshold below which a species is considered extinct? I guess in the simulated ODE model, biomasses cannot reach zero. However, as can be seen in Fig. 5A, species do go extinct when the cycle amplitude is very high (i.e., densities get very close to 0). What is the limit here?

Sorry, we had forgotten to indicate this information in our previous version. The information about the extinction threshold has now been added in the M&M line 267 and we added a section in supplementary appendix testing the effect of the extinction threshold on species persistence to demonstrate extinctions were due to increased oscillation amplitude:

“We raised the extinction threshold up to 10^{-15} kg.v⁻¹ (Fig. S3-2B) compared to the value used in the main study (10^{-30} kg.v⁻¹) (Fig. S3-2A). Species persistence is lower with this new threshold only at high nutrient inputs when species CVs increase with nutrient inputs. This demonstrates that extinction are due to increased oscillation amplitude that push species biomasses close to the extinction threshold.” (l.1099-1103)

7. (caption to Fig. 2) It should read “dashed lines“, not “dotted lines”.

Captions have been corrected.

8. (Fig. 3 A-C) I do not see why the light and dark grey shading areas would be in any way useful here. Is there something the readers should look for when comparing the range of the shaded areas? Their exact placement seems rather subjective and defined based on visual judgement only. I think the reader does not need to be guided towards any particular way of looking at these graphs, especially because the graphs are so well done already!

These areas where remains of an older version we forgot to remove. Thank you for noticing it.

9. (Figs. 3, 4, 5). I suggest, for better readability, to add parameter symbols next to their names on axis labels, i.e., letters “T”, “d” and “delta”.

This has been done.

10.(line 24) It should read “opens”, not “open”.

Corrected.

11.(line 191) Why is the functional response F_{ij} defined as “the fraction of species j consumed by i ”? I think it should rather be “the rate of consumption of species j by i ”.

Our original definition was wrong, this is actually “the contribution of species j in the eaten biomass per unit species i biomass” (l.189).

12.(line 193) In fact, type III response arises for all $q > 1$, not only $q = 2$.

Corrected.

13.(lines 268-272) Why not take averages of species densities in the last 1000 years, and use them as initial conditions for the SC model, instead of taking densities at exactly 9000 years? Does it matter?

It enables to compare both C and SC models with the exact same initial conditions but what you propose would have been another option. Otherwise, we believe that the two options would lead to the same results.

14.(lines 304-313) Some of the words used here are either wrong or too subjective. The average CV of species biomass in the NC model (Fig. 3C, orange line) does not increase monotonically, it rather shows an increasing trend. The CV of the C model in the same figure (brown line) does not clearly saturate. It maybe shows such a trend, but it also shows wider confidence intervals at higher mineral nutrient inputs. Lastly, the black line there seems somewhat hump-shaped, but is this hump significant (however this significance would be defined)? I believe it is better to skip such description, and rather point at general trends.

This figure is now Fig. 4A as we changed our narration due to the new results from the food chain model. We also now weight the biomass CVs by the average relative biomass of the corresponding species to give more importance to primary producers that are fewer than consumer but have a higher average biomass. However, the results remain similar and we adapted their descriptions by following your advises (lines 310-320).

15.(line 319) I do not agree that the average CV of species biomass “stays at its maximum value” with increasing “ d ” and “ δ ” in Fig. 4 B (“ I ”=40). Clearly there are lighter squares in the upper right corner!

This figure does not exist any more (Fig. 4A now) in this new version. As we had access to the HPC of the university, we ran additional simulations over a nutrient input gradient for four combination of d (0.2 and 0.8) and δ (0.2 and 0.8). This gave us a better description of the interactions between d and δ and nutrient availability “At high d and δ , the increase and decrease of species persistence and biomass CV with increasing nutrient input I are sharper. However, the general response of the food web remains qualitatively unchanged. In addition, unlike d , high values of δ amplify the destabilising and stabilising effects of feedback loops on primary producer (Fig. 5A)

and consumer (Fig. 5B) dynamics respectively (this aspect is detailed in the following).” (l.332-340).

16.(Fig. 5 A; SC food chain) Why the green line has a little ‘disconnected’ part around “T”=18?
It looks like all other species are already extinct.

This figure does not exist any more in this new version as our results from the food chain model changed. Then, we removed these new results from the main text (they are in the appendix section now Fig. S2-8 to S2-11). However, the discontinuities were due to the extinctions in the C model, the I_{recy} value that fed the SC model was changed and thus led to a discontinuity.

17.How many food webs were tested in every case in Appendix S3? Also 100?

We indeed tested 100 food web replicates in the sensitivity analysis (except for primary producer C:N ratios that were tested with 36 replicates) and added the information in figure captions of Appendix S3.

18.(line 456) Why would the C:N ratios used in Appendix S3 be “average”? What are they averaged across if the producer C:N ratios are fixed?

We agree “average” was confusing and we remove it. Indeed the producer C:N ratios are fixed.

19.(Fig. 3A) It would be helpful to state explicitly, even though it seems obvious, that this panel shows results from the C food web.

We precised it in the captions of Fig. 3A and 4B.