



## New insights into the role of nutrient cycling in food web dynamics

[Samraat Pawar](#) based on reviews by Jean-François Arnoldi, Wojciech Uszko and 1 anonymous reviewer

A recommendation of:

### Open Access

Pierre Quévreur, Sébastien Barot and Élisabeth Thébault. **Interplay between the paradox of enrichment and nutrient cycling in food webs (2020)**, *bioRxiv*, 276592, ver. 7 peer-reviewed and recommended by Peer Community in Ecology. [10.1101/276592](https://doi.org/10.1101/276592)

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Understanding the factors that govern the relationship between structure, stability and functioning of food webs has been a central problem in ecology for many decades. Historically, apart from microbial and soil food webs, the role of nutrient cycling has largely been ignored in theoretical and empirical food web studies. A prime example of this is the widespread use of Lotka-Volterra type models in theoretical studies; these models per se are not designed to capture the effect of nutrients being released back into the system by interacting populations. Thus overall, we still lack a general understanding of how nutrient cycling affects food web dynamics. A new study by Quévreur, Barot and Thébault [1]

tackles this problem by building a new food web model. This model features some important biological details: trophic interactions and vital rates constrained by species' body masses (using Ecological Metabolic Theory), adaptive foraging, and stoichiometric rules to ensure meaningful conversion between carbon and nutrient flows. The authors analyze the model through detailed simulations combined with thorough sensitivity analyses of model assumptions and parametrizations (including of allometric scaling relationships). I am happy to recommend this preprint because of the novelty of the work and its technical quality. The study yields interesting and novel findings. Overall, nutrient cycling does have a strong effect on community dynamics. Nutrient recycling is driven mostly by consumers at low mineral nutrient inputs, and by primary producers at high inputs. The extra nutrients made available through recycling increases species' persistence at low nutrient input levels, but decreases persistence at higher input levels by increasing population oscillations (a new, nuanced perspective on the classical "paradox of enrichment"). Also, for the same level of nutrient input, food webs with nutrient recycling show more fluctuations in primary producer biomass (and less at higher trophic levels) than those without recycling, with this effect weakening in more complex food webs. Overall, these results provide new insights, suggesting that nutrient cycling may enhance the positive effects of species richness on ecosystem stability, and point at interesting new directions for future theoretical and empirical studies.

## References

[1] Quévreur, P., Barot, S. and E. Thébault (2020) Interplay between the paradox of enrichment and nutrient cycling in food webs. bioRxiv, 276592, ver. 7 peer-reviewed and recommended by PCI Ecology. doi: [10.1101/276592](https://doi.org/10.1101/276592)

## Revision round #4

2020-02-10

Dear Authors,

Your response and edits clarifies somewhat, but I am concerned that you did not find values from the literature leading to a "satisfying species persistence". Can you please clarify what you mean by that?

Also, do your scaling relationships for search/attack rates and handling times match up with recent work by Carbone et al and Pawar et al (myself!)? The papers are:

- Carbone, C., Codron, D., Scofield, C., Clauss, M. & Bielby, J. Geometric factors influencing the diet of vertebrate predators in marine and terrestrial environments. *Ecol. Lett.* 17, 1553–9 (2014).
- Pawar, S., Dell, A. I., Lin, T., Wiczyński, D. J. & Savage, V. M. Interaction dimensionality scales up to generate bimodal consumer-resource size-ratio distributions in ecological communities. *Front. Ecol. Evol.* 7, 1–11 (2019).

These studies do find energetically and dynamically feasible regions of coexistence between consumers and resources using updated (relative to Yodzis and Innes and Brose et al) scaling equations for search rate and handling time.

I sincerely apologize for delaying this preprint's recommendation so much. However, the above is an important issue because future studies might want to use the scaling relationships you are using, and your results do rely strongly on them.

Best wishes,

Samraat

*Preprint DOI:* <https://doi.org/10.1101/276592>

**Author's reply:**

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## Revision round #3

2020-01-25

Dear Quévieux et al,

Thank you for your responses. I understand that the Supp Info issue is hard to resolve. Let's leave it at that.

However, I am still unsure about how you got the scaling constants for search (what you call "attack") rate and handling time. Table 1 gives what seems to be a very low value for  $a_i$  (given that it is in units of  $\text{year}^{-1}$ ), and no value for  $h_j$ . *The SI does not clarify either. You cite "Arbitrary" for the source of these parameterizations, which suggests that the model results are insensitive to these parameterizations. However, the sensitivity analysis is directly on the values of  $a_i$  (and none for handling time), not the scaling constants or exponents.*

Can you please clarify the sources and derivations (being explicit about the unit conversions if relevant) of the parametrizations of  $a_i$ , and sensitivity of the results to  $h_j$ ?

Thanks,

Samraat

Preprint DOI: <https://doi.org/10.1101/276592>

### **Author's reply:**

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## Revision round #2

2020-01-16

Dear Authors,

I think you have done a thorough job of addressing reviewers' comments and revising the paper.

I have two further suggestions/comments before I feel comfortable with recommending this preprint:

- What is the scaling of search rate ( $a_i$ )? *Authors say "Following classical allometric food web models (Brose, 2008; Heckmann et al., 2012), that are*

*based on carbon flows, species biological parameters and trophic interactions scale with species body mass.", but I see no scaling relationship defined. None of the reviewers noticed this, but a model with scaling of birth and death rates but not of interaction rates would behave very differently than one with. As such, the scaling of handling time and search rates can have a significant impact on system dynamics, and the direct sensitivity analysis of  $a_i$  will likely not capture the variation introduced by variation in the scaling model structure and parameter values of  $a_i$  (or the scaling model/parameters of  $h_i$ ). Can the authors please clarify? For an example of a paper with scaling of all parameters, see Tang, et al. 2014. "Correlation between Interaction Strengths Drives Stability in Large Ecological Networks." Ecology Letters 17 (9): 1094–1100. <https://doi.org/10.1111/ele.12312>.*

- The SI has four different files, and not all of the sections/files are cited, as far as I can tell. And even if they are, it's hard to follow the structure of the SI, so I suggest that you combine them into one document with a TOC.

Thanks,

Samraat

Preprint DOI: <https://doi.org/10.1101/276592>

### **Author's reply:**

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## Revision round #1

2018-12-15

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

*Preprint DOI:* <https://doi.org/10.1101/276592>

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. Bellow 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). In stead 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.

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.

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.

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).

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.

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 ( $\delta$ ) Indeed, Fig. 4 shows that  $d$  and  $\delta$  are interchangeable since persistence is a function of their difference.

**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).

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

l16: "We found that nutrient cycling can provide more than 50% of the total nutrient supply of the food web, ..."

l405: "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."

l518: "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."

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 parameterise 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> .

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.

Most importantly, I am concerned about the Intraspecific competition term (with constant coefficient  $\beta$ ) 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  $\beta$  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)."

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.

Other notes:

l44: "... but they never include a complete nutrient cycling." -> I am surprise the authors write don't consider <https://doi.org/10.1073/pnas.2434847100>

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"?

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

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.

l539: "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>

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.

- 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.
- 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.
- 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.

- 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.
- 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.

- 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?
- (caption to Fig. 2) It should read “dashed lines“, not “dotted lines“.
- (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!
- (Figs. 3, 4, 5). I suggest, for better readability, to add parameter symbols next to their names on axis labels, i.e., letters “l”, “d” and “delta“.
- (line 24) It should read “opens“, not “open“.
- (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  $i$ “.
- (line 193) In fact, type III response arises for all  $q > 1$ , not only  $q = 2$ .
- (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?
- (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.

- (line 319) I do not agree that the average CV of species biomass “stays at its maximum value” with increasing “d” and “delta” in Fig. 4 B (“l”=40). Clearly there are lighter squares in the upper right corner!
- (Fig. 5 A; SC food chain) Why the green line has a little ‘disconnected’ part around “l”=18? It looks like all other species are already extinct.
- How many food webs were tested in every case in Appendix S3? Also 100?
- (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?
- (Fig. 3A) It would be helpful to state explicitly, even though it seems obvious, that this panel shows results from the C food web.

## Author's reply:

[Download author's reply \(PDF file\)](#)