Peer Community In Ecology

High-order interactions in food webs may strongly impact persistence of species

Cédric Gaucherel *based on peer reviews by* ***Jean-Christophe POGGIALE*** *and 1 anonymous reviewer*

Michael Raatz (2023) Provision of essential resources as a persistence strategy in food webs. bioRxiv, ver. 3, peer-reviewed and recommended by Peer Community in Ecology.
https://doi.org/10.1101/2023.01.27.525839

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Gaucherel, C. (2023) High-order interactions in food webs may strongly impact persistence of species. *Peer Community in Ecology*, 100527. 10.24072/pci.ecology.100527

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Michael Raatz (2023) provides here a relevant exploration of higher-order interactions, i.e. interactions involving more than two related species (Terry et al. 2019), in the case of food web and competition interactions. More precisely, he shows by modeling that essential resources may significantly mediate focal species' persistence. Simultaneously, the provision of essential resources may strongly affect the resulting community structure, by driving to extinction first the predator and then, depending on the higher-order interaction, potentially also the associated competitor.

Today, all ecologists should be aware of the potential effects of high-order interactions on species' (and likely on ecosystem's) fate (Golubski et al. 2016, Grilli et al. 2017). Yet, we should soon be prepared to include any high-order interaction into any interaction network (i.e. not only between species, but also between species and abiotic components, and between biotic, anthropogenic and abiotic components too). For this purpose, we will need innovative approaches such as hypergraphs (Golubski et al. 2016) and discrete-event models (Gaucherel and Pommereau 2019, Thomas et al. 2022) able to manage highly complex interactions, with numerous interacting components and variables. Such a rigorous study is a necessary and preliminary step in taking into account such a higher complexity.

References:

Gaucherel, C. and F. Pommereau. 2019. Using discrete systems to exhaustively characterize the dynamics of an integrated ecosystem. Methods in Ecology and Evolution 00:1–13. https://doi.org/10.1111/2041-210X.13242

Golubski, A. J., E. E. Westlund, J. Vandermeer, and M. Pascual. 2016. Ecological Networks over the Edge: Hypergraph Trait-Mediated Indirect Interaction (TMII) Structure trends in Ecology & Evolution 31:344-354. https://doi.org/10.1016/j.tree.2016.02.006

Grilli, J., G. Barabas, M. J. Michalska-Smith, and S. Allesina. 2017. Higher-order interactions stabilize dynamics in competitive network models. Nature 548:210-213. https://doi.org/10.1038/nature23273

Raatz, M. 2023. Provision of essential resources as a persistence strategy in food webs. bioRxiv, ver. 3 peer-reviewed and recommended by Peer Community in Ecology. https://doi.org/10.1101/2023.01.27.525839

Terry, J. C. D., R. J. Morris, and M. B. Bonsall. 2019. Interaction modifications lead to greater robustness than pairwise non-trophic effects in food webs. Journal of Animal Ecology 88:1732-1742. https://doi.org/10.1111/1365-2656.13057

Thomas, C., M. Cosme, C. Gaucherel, and F. Pommereau. 2022. Model-checking ecological state-transition graphs. PLoS Computational Biology 18:e1009657. https://doi.org/10.1371/journal.pcbi.1009657

Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.1101/2023.01.27.525839
Version of the preprint: 2

Authors' reply, 22 August 2023

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Decision by Cédric Gaucherel, posted 21 July 2023, validated 24 July 2023

minor revision

Dear author,

I would like you to answer to the points raised by the first reviewer, after which I will be in position to decide about your manuscript.

I thank you in advance. Best wishes.

Cédric Gaucherel.

Reviewed by anonymous reviewer 1, 11 July 2023

I thank the author for this revised version of the manuscript. Most of the points raised in the reviews have been satisfyingly addressed and the manuscript reads well and makes an interesting and important scientific contribution to trophic ecology.

In my opinion, two points could still be improved:

1) I feel it is not very satisfying to assess only visually the convergence of dynamics in a theoretical study. Can't the author give a quantitative criterium as it is usually done for simulations (e.g. on slope of a linear regression on time series + on variation of abundance ranges along time for oscillations)?

2) I am only partly convinced by the response of the author to my point 3 of previous review (about the mathematical implementation of the HOI of interest). I agree that the provision of essential resource could change the conversion efficiency of the predator only when feeding upon the competitor since the focal species already contains the essential resource. It thus assumes that the essential resource participates to a better assimilation of food that doesn't contain this essential resource (e.g. recalcitrant parts). But I don't see by which mechanism bringing an essential resource compare to not bringing an essential resource can improve the feeding rate of the predator solely when feeding upon the competitor and not when feeding upon the focal species. To me, if I am not wrong, the underlying assumption the author is making with the formulation of the model is that the provision of the essential resource is changing the preference of the predator to the detriment of the competitor. As it is not so intuitive, I would explicitly state it in the manuscript.

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2023.01.27.525839
Version of the preprint: 1

Authors' reply, 29 June 2023

Dear Dr. Gaucherel,

Thanks a lot for handling this manuscript and your supportive assessment, as well as providing me with this positive and constructive feedback! Indeed, I have probably kept the discussion of general HOIs (both NTIs and TMIIs) too short in the original submission. I now added multiple references to this field, as well as a discussion paragraph that embeds my findings better into the complexity of HOI effects on stability (l. 282-293). Regarding the interactions of multiple HOIs, this definitely presents an interesting aspect but I feel like this should be investigated separately (I added this perspective in line 295). Also, to clarify the focus, I changed the title of the paper to "Provision of essential resources as a persistence strategy in food webs".
Please see also my point-by-point response to the reviewers' comments below.

Kind regards,
Michael Raatz

Reviews

Reviewed by Jean-Christophe POGGIALE, 21 Apr 2023 12:27

This work aims to analyze the effect of provision of an essential resource by a so called "focal species" (another consumer) on the structure and dynamics of a resource - consumer - predator system.

The paper is clear and well written. It deals with how and when a species providing an essential resource can invade and how it may change the structure of the resident community. As said by the author, pairwise interactions in food webs can be modulated by a third species and this phenomenon is strongly related to what is called the Trait Mediated Indirect Interactions (TMII's). References as Werner and Scott (2003), which provides a review of TMII's in ecological communities and Bolker et al., (2003), making a connection between theoretical and empirical studies of TMII's could profit to the discussion of the present manuscript. Here however, the author focuses the study on the provision of an essential resource which may modify some traits of a resident competitor and/or of a predator. An original concept introduced in the present work is the essentiality, which

is clearly defined in the method section and discussed in relation with possible experiments in the discussion section. This concept is an important contribution of the manuscript because it allows to summarize the effects of the focal prey in an elegant and understandable way. It also provides a quantitative tool to measure these effects.

Thank you for this positive assessment and the appreciation of the essentiality concept. I added the given references and related my findings to TMIIs, thanks for the suggestion!

Considering the title of the paper, I find that it does not really serve the content of the paper. Indeed, it is rather intuitive that providing essential resource to a system where it was lacking can benefit the system and enhance its stability and persistence. For instance, from a conceptual point of view, we can see the focal species as a species exhibiting a unidirectional direct interaction as commensalist : it can help the competitor when it is included in the system by directly modifiying its uptake rate or its conversion efficiency. And this type of interaction is known to stabilize network stability (see Mougi, 2016 for instance). However, the paper shows that the effect of the provision of essential resource is more subtle and may be detrimental, may induce multi-stability, etc.

I changed the title to make the focus on persistence of the focal prey more apparent.

The abstract is clear and focused on the main ideas of the paper.

The introduction is well written with a well description of the state of art and the hypothesis that are tested in the manuscript are well stated.

The method is based on the one hand on the use of a rather simple model with 4 state variables (a resource, a consumer and a predator to which a focal prey providing the essential resource is added), and on the other hand on the concept of essentiality which is a measure of the relative reduction of upake rates or conversion efficiencies in the absence of the focal species. On this basis, the author studies the invasibility of the resident system by the focal species, which provides a simple tool to understand the richness of the outputs of the model. This is done via four scenario that are complementary and allow to understand situations where the focal species (a consumer) is more or less competitive than the resident consumer and situation where the focal species is prefered or not by the predator. In the present work, only one indirect interaction may take place at once (changing either the competitor uptake rate, or the conversion efficiency of the competitor, or the predator uptake rate or the predation conversion efficiency). Thus the work does not consider the combination of several indirect effects, it is why only one essentiality suffices.

The simulations done in the paper are well described and can be easily reproduced. They provide figures that adequately illustrate the results.

The results are clear and presented for each of the 4 previous scenarios. Some of the results are mainly intuitive, others are more subtle like for instance in scenario II, the dynamics of the community when the higher - order interaction increases the uptake rate of the predator presented in Figure 7b. Here multi-stability can be observed and then it is important to know when reintroducing the predator to get a persistent community.

The discussion reminds some works that show the existence of the MTII's concerning provision of an essential resource and experimental works that may be extended by using the results of the present paper. It highliths the interest of the concept of essentiality. However, I am not sure to really catch the sentence from line 278 to 280 ("One of the benefits from this definition is that the density-dependent functional form of the higher-order interactions does not need to be specified..."). This is indeed true when focusing on the invasibility (may be it is what the author meant) but of course, it is wrong for results where the focal species is in the system (like figures 5b and others for instance).

The reviewer understood precisely what I meant. I now also modified the description of this fact in the Methods (l. 152).

Bolker, B., Holyoak, B., Krivan, V., Rowe, L., Schmitz, O., 2003, Connecting theoretical and empirical studies of trait-mediated interactions, Ecology, 1101-1114.

Mougi, A., 2016, The roles of amensalistic and commensalistic interactions in large ecological network stability, Scientific Reports, 6, 29929.

Werner E.E. and Peacor S.D., 2003, A review of trait-mediated indirect interactions in ecological communities, Ecology, 24 (5), 1083-1100.

Reviewed by anonymous reviewer, 21 May 2023 07:56

Species interact through a diversity of trophic and non-trophic interactions. While initially studied in isolation, ecological theory has now recognized the multiplexity of interaction types in communities. Here, the author presents an analysis of a diamond shape module with non-trophic interactions mediated by a prey enhancing the uptake rate or conversion efficiency of either its predator or its competitor. Exploring a wide range of scenarios, the author provides evidence that such non-trophic interactions can allow a prey to invade and persist in this small module despite a defavorable apparent competition with the other competitor. In addition, the author shows that this facilitating effect allow prey to create the conditions for the persistence of its predator in some specific conditions. Finally, the results demonstrate that the higher order interactions can also be detrimental to the persistence of its initiator in case it decreases predator efficiency to regulate a dominant competitor.

General Comments:

The author contributes to an important problem of food-web theory: unveiling the role of non-trophic interactions on coexistence, functioning and stability of communities. The model is simple, the manuscript is in good shape and the methods are clear and allow to separate the effects of trophic structure from non-trophic interactions (essentiality) on the persistence of this small module. Aside from minor comments, I have four more general comments that I think could help clarify the manuscript and its messages.

I'd like to thank the reviewer for the supportive assessment and the valuable comments. Please see my point-by-point response below.

1) The author motivates the model structure and the inclusion of the non-trophic interactions for aquatic ecosystems. Yet, we lose this motivation in the introduction. Maybe it could be more explained in the introduction why such model is particularly well suited to aquatic rather than terrestrial communities. For instance, if I think about plant facilitation in arid ecosystems, a nurse species could definitively fit into the focal prey of this model by enhancing water uptake of a beneficiary species. So, I think this point needs to be clarified in the introduction at some point.

I removed the reference to aquatic systems in the abstract to avoid this confusion. The model might be applicable to terrestrial systems as well, and in fact I'm referencing terrestrial systems as examples (e.g. the moth larvae in Eberl et al. (2020)). The problem might be that the model assumes well-mixed states and a high mortality on each species, as it's essentially a chemostat model.

2) There is a number of studies that have studied the effects of non-trophic interactions on community persistence. Among others, I could think about Sauve et al., Theoretical Ecology 2016, Gross 2008 Ecology letters, Aubier 2020 Elife, Kéfi et al., 2012 Ecology letters. How the study complements these studies? I think the results needs to be discussed in the light of other theoretical studies asking related questions. Currently, its barely the case.

Indeed, some embedding into the HOI literature has been missing and was now added (l. 300-312). Thank you for the suggestions, particularly the Gross paper is a good addition which I wasn't aware of before. I didn't include the Sauve paper, as here the authors are focusing on indirect interactions, and the Aubier paper as it discusses intraspecific facilitation.

3) I like the simplicity and elegance of the model, but I have a concern about one point of its formulation: I think the correct transcription of the empirical examples motivating the study of these higher order interactions

would need the performance of the predator to be equally affected by essentiality when attacking or converting the biomass of either prey, including the focal one. If the predator's uptake rate or conversion efficiency is improved in the presence of the focal prey, why only when attacking the competitor. I think the author should show the robustness or variation of the results with the "more realistic" alternative formulation of multiplying the predation term upon X1 by μ_Y(X1), and eps_Y(X1) in the equation of the predator.

The modelled mechanism here is the provision of the limiting resource, and not the case when the focal prey would also lack the essential resource (in which case the reviewer would be absolutely correct and an additional limitation term should indeed appear also for the conversion of the focal prey). I am however considering a scenario where the composition of the focal prey is given, and the question is whether the competitor can also provide the complete set of essential resources.

To avoid future confusion, I have extended the motivation (l. 78-80) and included a remark on this (l. 118-121).

4) Lastly, I acknowledge that it is further analysis so the author may decide whether going one step further, but we naturally wonder about the interacting effects of these high order interactions? It would be interesting to investigate it since all studies I could think of studied the effect of different non-trophic interactions in isolation.

This is indeed an interesting and natural extension, which would merit an exploration in a separate study. Particularly the food web scenarios where the HOI targeting the competitor favours persistence but the HOI targeting the predator is detrimental for focal prey persistence should provide some interesting dynamics.

Minor comments

L37: I found difficult in the intro to catch tight away what is the difference between an essential resource and a limiting resource. May be the author could add a sentence to highlighting the difference?

This has now been defined better in line 35.

L119 and L143: change "we" for "I" to be consistent.

Thanks!

L125: replace "should go" by "had gone"?

Thanks!

L 133: add a coma after "prey".

Done.

L134: How was the convergence to the attractor tested?

I added "Convergence was determined visually."

L153: add ", see black arrows" in the parenthesis, to guide the reader more accurately. Moreover, could the author use only 2 widths of black arrows in figure 2 for clarity?

Thanks for the suggestions, I implemented them both.

170: add a "s" to scenario?

I think it's correct without the "s".

L172: "independently" or "irrespective" instead of "independent"?

Thanks, I replaced by irrespective.

L182 and L127: Change "our" to my.

Thanks.

Figure 4: While it is clear in the legend, I think it would be nice to have more distinctiveness between the two types of dashed lines (analytic predictions and bifurcation point). In addition, analytical solutions should appear at some point in the appendix and be referred to in the main text if they are used in a Figure. Currently, because I don't have mathematica, I can't see them.

I revised Fig. 4 and made the lines more distinctive. The analytical expressions are very long and uninstructive. I now provide a pdf representation of the Mathematica scripts as appendices from which the formulae are accessible.

L219: Maybe precise what "not too high" means here.

Thanks, I rephrased to: “If the resource competitiveness of the competitor is only slightly exceeding the resource competitiveness of the focal prey the invasion growth rate of the focal prey is positive even for zero essentiality and only increases further for higher essentiality (Fig. 4).”

L231 a “s” to “affect”?

Thanks.

L237 “can increase” instead of “increases”

Changed.

L252-254 are these examples transferrable to the model?

Generally speaking yes. If for example secretion the essential resource acts as a chemoattractant or generally increases the foraging effort this would lead to a higher uptake rate of the competitor in the presence of the focal prey.

L278: delete the “s” of “definitions”

Thanks for noticing this!

L 283 add a “s” to “constrain”?

True, thanks.

L307-308: a coma missing: “herbivores, limitation”?

In fact, the coma was missing after biochemicals and has now been added.

L311: This sentence definitively needs a citation if that was already done in the literature.

To my knowledge, this hasn’t been done before but in Rosenbaum et al. (2019) we have shown that uptake rate and conversion efficiency can be disentangled with Bayesian inference, which should allow their inference across a supplementation gradient. I have extended the description of this approach in lines 332-335.

L330: it would be more comfortable for the reader to put first the last name of the first author in the references to better see the alphabetic order.

I changed the bibliography style accordingly.

Download tracked changes file

Decision by Cédric Gaucherel, posted 05 June 2023, validated 05 June 2023

This paper should be published into PCI ecology, after being revised by minor changes.

dear author,

I have now received the two reviews of your paper. Overall, I find that your paper is interesting and should be published into PCI ecology. Yet, the reviewers mentioned several points that may improve the present version of the paper.

In terms of bibliography, you could add some of the publications that reviewers have mentioned. The TMII concept is generating an important litterature (see for ex. the Golubski et al. article in TREE 2016). You should discuss more deeply your motivation, and improve your discussion about non-trophic interactions and their impact on community persistence. It seems that you could also improve the discussion about the combination of several indirect effects, and higher order of interaction.

Additionaly, you could also modify the title of your paper, as well as use the minor comments kindly suggested by both reviewers.

Best wishes. CG.

Reviewed by **Jean-Christophe POGGIALE**, 21 April 2023

This work aims to analyze the effect of provision of an essential resource by a so called "focal species" (another consumer) on the structure and dynamics of a resource - consumer - predator system.

The paper is clear and well written. It deals with how and when a species providing an essential resource can invade and how it may change the structure of the resident community. As said by the author, pairwise interactions in food webs can be modulated by a third species and this phenomenon is strongly related to what is called the Trait Mediated Indirect Interactions (TMII's). References as Werner and Scott (2003), which provides a review of TMII's in ecological communities and Bolker *et al.*, (2003), making a connection between theoretical and empirical studies of TMII's could profit to the discussion of the present manuscript. Here however, the author focuses the study on the provision of an essential resource which may modify some traits of a resident competitor and/or of a predator. An original concept introduced in the present work is the essentiality, which is clearly defined in the method section and discussed in relation with possible experiments in the discussion section. This concept is an important contribution of the manuscript because it allows to summarize the effects of the focal prey in an elegant and understandable way. It also provides a quantitative tool to measure these effects.

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