**Author's Reply:**

*Montpellier, November the 25th, 2023*

*To PCI Ecology Recommender: Pr. Francis Raoul*

*Re: Manuscript re-submission*

*Dear Recommender - Editor,*

*Attached is our revised research paper for your publication, a manuscript still entitled " Diagnosis of planktonic trophic network dynamics with sharp qualitative changes ".*

*We modified the initial version of our paper. This paper now better emphasizes the major comments of the reviews. In particular, we modified several illustrations and corrected the paragraphs describing in details our innovative method. By the way, the paper has been entirely edited to correct the English formulations.*

*We are therefore confident that the ecological and methodological facets of the paper convey general messages for PCI ecology and would resonate strongly in your publication.*

*We welcome any questions and comments that you may have.*

*Sincerely.*

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*by Francis Raoul, 02 Oct 2023 13:48*
Manuscript: **https://doi.org/10.1101/2023.06.29.547055** version 1

**Major revision needed**

Dear authors,

Your manuscript has now been reviewed by two colleagues. They both point out that the method you propose could potentially be useful to the scientific community for modelling trophic networks. However, they both agree about strong flaws of the manuscript in its present form, to a point where it is quite hard to appreciate the added value of your work: (i) the modelling method and its validation process remain **poorly explained and justified** (vs. other options) and are not detailed enough for the work to be repeated by others, (ii) many **terms are vague and/or left undefined** so that it is hard to guess their meaning, (iii) the **structure and flow of the article need to be revised**, (iv) the English seems to need a strong **editing**.

I have decided to follow the reviewers' opinion. I therefore encourage you to submit a new version of the manuscript that incorporates all suggestions made by them.

Best regards.

*Answer: Thank you for this opportunity to improve our manuscript. We did our best to answer point by point to the reviewer's comments.*

**Reviews**

*Reviewed by anonymous reviewer, 23 Aug 2023 15:04*

Overall: The manuscript presents a fascinating topic, but the difficulty lies in introducing a new method to the field of ecology. This is an incredibly high challenge to meet, as it's more than "just" giving the Methods. The manuscript lacks structure, with a clear explanation of (1) the **differences and advantages** of the method pursued here, (2) a perfectly **clear explanation** of the method and walked-through application comparing to a well-known ecological example, (3) an explanation of what tests will be done **to validate the method** (how do we know it worked), and (4) guidelines given clearly in advance of **what to expect** for the Results section.

*Answer: Thank you for your positive appreciation. We gave more details on each point, although one point was unreachable in this manuscript: to compare our method to another one. Not only the paper would become lengthy and unreadable, but it is also difficult to compare our qualitative, discrete-event and possibilistic method to other methods in ecology, being most of the time quantitative, continuous and deterministic or probabilistic! Nevertheless, we did our best to improve all methodological parts of the paper.*

I cite 2 other papers below that manage to meet this challenge (De Cáceres et al. 2019; Silk et al. 2022), but there is a long line of new methods being introduced to ecologists then applied. I strongly suggest finding one such of these papers to use as a template, and to follow the structure used to guide what elements to include. I'm afraid as written, I can't truly evaluate the method and application. The manuscript read a bit more as a linear description - it was difficult to evaluate the model and its validation on data without knowing how the model worked and how the validation would be performed in advance of the Results section. Moreover, I simply don't find the Methods meets the standard of "Include sufficient details for the work to be repeated", which is critical for any study.

*Answer: this is true. Nevertheless, let us briefly recall that this paper is NOT the first one using this method based on the EDEN framework: our pioneer methodological paper is the MEE 2019 paper, the first EDEN application is the Mao et al. 2021 paper and the recent improvements of the methods (with applications) are the Thomas et al. 2022 and Cosme et al. 2022 papers (see refs of the paper). Hence, in this PCI ecology submission, we intended to show the first ever published **validation** of the method on observed ecological dynamics (and not to entirely reexplain the method). In this way, we did not strongly modify the structure of the paper, but added information about the model and its validation.*

Abstract

Overall some typos (e.g. Line 29, "is assumed")

Line 19: Please be more precise about "to diagnose"

*Answer: Yes, good point. We suggested to use this term for describing the process to identify the contrasted possible network functioning regimes. From winter to summer regimes, many trophic networks and community functioning may appear, and our model is able to accurately identify them in the course of the dynamics. We added some sentences in the abstract and main text.*

Line 20-21: Please be a bit more specific with "welcome numerous feedbacks" and "are not frozen". I appreciate the language choice, as I can infer what you may mean, but its much easier to be precise. For example. "Such ecological networks have many direct and indirect connections between species and these connections are not fixed, but often vary with time"

*Answer: Thank you for this suggestion; now changed.*

Line 23: dynamic (singular)

*Answer: Thank you for this suggestion; now changed.*

Line 24, 26: I can say again that the ambiguity of what "diagnosing" a network exactly means makes these two lines difficult - I am not sure yet what exactly will be done in the paper. (is it estimating species interaction strengths / connection strengths?)

*Answer: No, as our approach is fully qualitative, we are not intending to estimate interaction intensity or strength, rather than the presence/absence of interactions (and associated ecosystemic components). We added some sentences in this sense.*

Line 27: borrowing "from", not "to"

*Answer: Thank you for this suggestion; now changed.*

Line 32-34: I find this a bit speculative, and would prefer more quantitative conclusions. It should be a summary of the scientific findings

*Answer: Unfortunately, our innovative approach is not providing any quantitative information. Rather, it provides new and unexpected trajectories of the studied system as well as the whole possible dynamics. Hence, it justifies why we focused in this abstract on the additional information provided to experts. No change.*

Introduction:

Lines 66: You write that equation-based models aren't well adapted to handle dynamical systems, but some theoretical CS tools "are able to handle" sharp changing networks - can you better summarise or articulate why one can't and another can? If you need to reduce space, I think the first 2 sentences in paragraph 2 could be deleted.

*Answer: No, we insist on the main ability of our approach: to be able to handle dynamical systems ON dynamical structures. The word "on" is the most important as, obviously, equation-based are able to handle dynamical systems, yet on static/frozen structures. Our approach is indeed directly coming from CS tools (as mentioned at lines 65-66) and they are not differing to this stream. Some tools are able to handle changing network because they are formalizing the way components and interactions may appear and disappear in the modelled network. Hence, we added italic "on" in the sentences and highlighted even more this point with a new sentence.*

Line 67-69: Because you only introduced the field (theoretical CS) and the name of the approach (Petri net), the reader isn't brought in to understand exactly what you will do. Please better articulate the distinctions between the 2 approaches, a brief summary of what the theoretical CS (or Petri specifically) does. That will better set up the topic sentence you give here.

*Answer: OK, while we did not proceed so because we found the introduction already lengthy (and because many details are given in the Methods section). Nevertheless, we added one sentence rapidly setting up the Petri nets.*

Line 107: Not clear what "well instrumented" means

*Answer: well measured. Now added.*

Line 111: Same as above, the reader doesn't truly know what you will do given no explanation of the method and its distinction from existing approaches

*Answer: Now corrected at the first mention (above).*

Methods:

Overall - I'm afraid the delivery of these methods falls far short of what is needed to clearly understand how this type of model works. Many terms are left undefined, and even when they are defined, they are not always clear. A reader who sees "the rule is **fired**" might only make use of such a simplification if they already understand the entire process. I don't know exactly what edits to advise, but the section reads like someone explaining a very, very complicated figure and writing down what they say when explaining. Terms are only introduced right when they are critically needed to understand a given sentence, but no clear **overall summary** of how the methods works is given. The Petri net explanation could use much more structure, divided overall into the sections needed to understand this entire process.

*Answer: Sorry for this, we thought the explanations were clear enough, especially with the toy-model shown, but we have now divided the explanations into sub-sections and have changed many sentences for clarity.*

It's not because this is complicated that it can't be clearly explained. See for example another paper for an Ecology audience that walks the reader through their method:

De Cáceres, M., Coll, L., Legendre, P., Allen, R. B., Wiser, S. K., Fortin, M.-J., Condit, R., and Hubbell, S.. 2019. Trajectory analysis in community ecology. Ecological Monographs 89(2):e01350. 10.1002/ecm.1350

I can only say again that I can't advise how to structure this, but it's quite difficult to follow how the method works. I would advise to share the Methods section with a group of PhD students, and ask for their feedback. Complicated methods can still be shared with ecology readers in a way that they can follow, but this explanation is too linear.

*Answer: Actually, our approach is not complicated at all! And it is easy to explain orally. So, it only means that we were not clear enough, and we tried our best to improve these explanations (thank you for your advices and careful reading).*

Line 115: For Figure 1 - (i) The figure is too difficult to read, please change for clarity. (ii) Please raise the position of the inset / left part of the figure - so that the total dimensions of the image become smaller. (iii) Pardon me if I am mistaken, but the figure appears to be associated with Google Maps - is it thus under some kind of copyright? Check that you have permissions needed to use such an image.

However (iv) the image doesn't capture these are wetlands. Is there some kind of GIS layer that better shows the aquatic habitats? That information is more relevant than the road, town, and marine labels included. The text in lines 115-119 paint a rich aquatic picture of habitat and connectivity that the figure simply doesn't show.

*Answer: Yes, we changed the Figure 1 to resize it and better highlight the wetlands. In terms of data properties, it's all public, and the sources are cited in the figure 1. The base map belongs to open street map (OSM), the hydrographic network is an adaptation of an IGN layer and the perimeters of AS are traced by UNIMA.*

Line 119-122: Trajectories of what? Also the description here doesn't inform the reader the date of the samples

*Answer: Good point, we changed the sentence into: "Samples of the planktonic trophic network were recorded at two stations (stations A and B) at successive dates (28 February to 17 April 2012, during*

*winter and spring 2012) to reconstruct the network trajectories along time (more details, see Masclaux et al. 2014)".*

Line 127: I didn't realise before this point that the trophic model would include environmental drivers - how can you better present this so we know to anticipate this? I argue above to give a better verbal preview of what the model is / does. Then here, you can simply list the information needed to reproduce the environmental measures. More detail needs to be given on how the model was constructed - where did this come from? What biological support is there for this model?

*Answer: All the details for the methodology on plankton analysis are given in Masclaux et al. (2014). The model was constructed with different parameters clearly mentioned in our Figure 2: Phytoplankton, Zooplankton, Resources, Microbes, Abiotic components. Yet, we also added some words in the introduction and largely modified the first paragraph in the Materials & Methods."*

Line 127-141: I am not sure what to advise, but I really could not follow this verbal description of the model. It didn't help me understand Figure 2, and was difficult to read. I also advise that the information needed to follow the model (abbreviations etc) appear in the Figure 2 caption. In the Figure 2 caption, what does "upward" and "downward" mean? Also, you refer to abiotic components as "trophic"? This is very difficult for me to understand.

*Answer: This seems to us surprising, as this figure displays a simple interaction network. So, nodes are species (or abiotic variables) and edges are (mostly) predation interactions, that is "who eats who". Yet, it is true that colours and component categories were not in perfect agreement. We rephrased this paragraph, and aligned it with the Fig. 2 caption and clarified its presentation.*

Line 150: What is "the leading question"?

*Answer: Here, the leading question refers to any question addressed by the EDEN models (In our case, the leading question is: "what are all the possible trajectories of such an aquatic trophic network?"). now clarified. And we also added two sub-questions in the introduction.*

Line 150-151: I find it awkward to be this far along and still not have any information on what a Petri net is.

*Answer: precisely. The following paragraph is detailing how Petri nets are functioning and how they will be used. In this former paragraph, we just describe the overall strategy.*

Line 151: What does it mean to normalize a rule? I think there is a lack of description of what is done that is reproducible for a reader. This continues for Python automatically building a Petri net - how? Where are the full methods we need to evaluate this method, how does it build this?

*Answer: You are right, this point was far more technical for an ecological paper; hence, we removed it. We also focused more rapidly on the functioning of the method and thus largely modified the structure of the Methods section.*

I can see you give more detail in the subsequent sections, but it would be easier for you to state explicitly that this is a summary and more detail for each step is given subsequently.

*Answer: Yes, now done. Kindly notice that the model is freely available on GitHub (provided at the end of the main text) and that it would not be easy for a user to rebuild the model from scratch. Hence, the ecologist reader is not intended to redevelop the whole EDEN framework (requiring the technical papers listed in references: Pommereau et al.), rather than being able to reproduce the application of the proposed model (i.e., tables 1-2).*

Line 164: What is "2#nodes"?

*Answer: Now corrected.*

Line 167: Its much too confusing to describe e.g. socioeconomic processes. We need the exact information needed to evaluate this study. I am struggling to really understand what methods this study uses, and having such general information at this point in the Methods is more confusing than clarifying.

*Answer: Sorry for that, but we did not want to enter into details regarding to non-ecological processes (social-economical processes may be human interactions, economic decisions, managements, etc.), and so, we removed such mentions. They have been treated into complementary studies now briefly cited at the end of the paper (e.g., Cosme et al. and Mao et al.).*

Line 168-169: What does "neglectable" mean?

*Answer: Each variable is associated to a given threshold, allowing to qualify it into Boolean states (+ and -). So, "neglectable" means below the chosen threshold (even if not precisely known). We now reformulated each sentence related to these variable thresholds.*

Lines 179: "were unlabelled arcs" - this sentence is not complete. Are the s0, s1, s2 all system states encountered? If so, indicate this abbreviation here in the legend. It's not clear to me why these are inactive rules. What is missing in Figure 3c between S0 and S1? It appears to be a "2" but the grey is partially blocked.

*Answer: Good point, sorry. All of this has now been corrected.*

Line 182: What is a token circulation?

*Answer: Yes, we reexplained this point too: the token is a marking associated to places (round shape nodes in the Petri net, Fig. 3), which will move according to the transitions (square shape nodes) they are connected to. Now changed.*

Line 186: What does "a realisation parts" mean?

*Answer: As explained in the sentence, the realization is the right-hand part of the rule (after >> symbol), and stands for what should be changed in the modelled system if the rule is fired (is applied). We tried to reformulate many terms in this paragraph which, we understand, is not straightforward for ecologists.*

Line 220: The reasoning for these 2 tests is not given.

*Answer: Actually, it is given at the end of the sentence: i.e. we wanted to be able to stop the dynamics "before" returning to the winter conditions and see whether the model was able to recover the expected summer regime. Now corrected.*

Results:

Overall: I struggled (as I have indicated) that no general summary of the Petri net approach was given, before the detailed and difficult to follow explanation of the method. Many, many new terms are introduced and in some instances not defined. For this reason, it is almost impossible to know **what to expect in the Results section**. Sentences such as "when rule zero is deactivated, the model gets stuck into a high number of structural stabilities." I ask the authors to paint a better picture of what the

model does, what the tests to the model consist of, and what the reader can expect to evaluate the results. It reads a bit too much like a descriptive report, and less like a systematic test of some hypothesis.

*Answer: OK, we understand and apologize (although we already did some efforts in describing the use of the model. For ex. We wrote a clear sentence in the methodology part stating "As a validation stage, we intend not only to detect these successive states in the modelled state space, but also to detect them in the correct succession orders". Fig. 5 clearly shows the corresponding states listed in the tables of Supp. Mat.). We now detailed more how the model is computing the successive states of the system and better explain what was expected. Basically, the idea was to compute all the states following the chosen initial state.*

Line 261: How was this figure generated? Did the authors describe how they decide to merge state spaces? How does this figure help readers better understand trophic networks in plankton? I would suggest some kind of alternative, perhaps a Figure 1 that sketches a clear, well-known aquatic scenario, with some figure showing a traditional NPZ approach, and a 2nd figure showing a Petri approach, with some description of what can be learned using this alternate approach.

*Answer: True, we did not want to go into details about the production of such figures (quite technical and already present in our technical papers), although their principles were explained a few lines before (ln 237-245). (to compare a NPZ model to our approach would be too difficult and even useless, as we are modelling qualitative dynamics. But we keep this suggestion in mind.) Each merged node is a set of nodes mutually reachable and by definition belonging to the same (structural) stability. We now explain in details how to identify these stabilities at the end of the "Methods" section.*

Line 271: This to me captures the difficulty I have with the manuscript - an "immature regime" is never defined. The amount of terms needed to follow grows too large, and I question what is gained by this approach. Even if you inform the reader an "immature regime" is a "biological winter", it means I search backwards until I can find what "biological winter" means. It is quite difficult to follow.

*Answer: Yes, we understand and removed this "immature" term. Details of the planktonic trophic network are to be found in Masclaux et al. (2014). Yet, we added sentences in the "materials and methods" section to redefine these regimes.*

Line 293: I would again advise that the reader simply doesn't know what to expect when this very complex figure emerges. The method wasn't easy to follow, and only a very long list of Rules was given - what are the small black lines coming from the red nodes? How exactly can a plankton ecologist look at this figure and understand how it clarifies seasonal dynamics?

*Answer: Concerning the ecological study for validation, all the details were in the paper of Masclaux et al. (2014) in figure 7. But, to be clearer, we added a paragraph in Material and methods part "Aquatic trophic networks". In addition, the idea here was to "show" that all states of the theoretical/observed trajectories were computed and recovered by the model. It was not for the reader to "check" the computed states. The Fig. 4 (and Tables Suppl. Mat.) should be sufficient to convince the reader, while Fig. 5 is only showing that the model computed correctly. We corrected this point and comments in the main text (and better explained what was expected in the state space).*

Line 301-302: It was confusing for me that this term was used in the Abstract, but only defined here.

*Answer: True, we removed this sentence, focusing on another relevant property of our models, but which would send the reader in another (and confusing) direction. We now focus on the qualitative and discrete properties of our EDEN models.*

Line 305-306: A difficulty is that the model is introduced to readers in a complex description, and proof isn't presented that the model can find states better than the experts identified here - how can we evaluate whether the trajectories identified by the model actually occurred?

*Answer: This is simple and is demonstrated in Table 2 Supplementary Materials! This table lists the observed states, and these states are displayed in the Fig. 5b and 5c. Moreover, they are in prefect agreement with the theoretical knowledge summarized into the Table 1 Supp Mat. And highlighted in Fig. 4 (and Fig. 5a). Fig. 2 Supp Mat is even listing the components absent in each structural stability encountered (so, it is complementary to Fig. 2 for interpreting the dynamics). We have now better explained such comparisons between tables and figures.*

Discussion:

Line 349-350: Because it is the 1st time to introduce this method, the burden is on this manuscript to make absolutely sure the methods is perfectly clear to ecology (and not computer science) readers. There are other instances where new methods are introduced to ecologists, but special care must be given in this case. Here is one example:

*Answer: No, we are afraid this is not the first time our method is described, as we now have almost ten papers introducing it in various case studies and technical papers. **It is the first time the method has been validated!** Yet, we understand here the paper should stand alone and be clear enough for explaining the method, thus explaining why we carefully followed your advices.*

https://onlinelibrary.wiley.com/doi/full/10.1111/ele.14079

Silk, M.J., Wilber, M.Q. & Fefferman, N.H. (2022) Capturing complex interactions in disease ecology with simplicial sets. Ecology Letters, 25, 2217–2231

*Answer: We would like to warmly thank the reviewer having taken the time to carefully read the paper and to patiently provided advices to improve it. We hope it is much clearer now, but feel free to come back to us if not.*

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*Reviewed by Tim Coulson, 20 Sep 2023 12:52*

The manuscript reports a new methodological approach based on directed graphs to parameterise temporally varying trophic networks. The approach is validated using a simulation, before it is then applied to real data. The approach does appear work well on the simple **simulation**, and does return results that appear sensible. Having said that, I did struggle to work out what was done.

*Thank you for the positive appreciation. We worked hard to improve the manuscript.*

The paper is hard going and rather poorly organised. I never like criticising language for researchers whose first language is not English, but this paper really needs review by a native English speaker. There are many places where I think translation from French has resulted in phrases that make little sense in English. As an example, the second line in the abstract states "Such ecological networks **welcome** numerous feedbacks between species and populations and are not frozen at all, as soon as we observe them over a long enough term." The verb welcome is not correct, the frozen at all sentence refers to (I think) that most networks are treated as being static in time, but are dynamic. I could do this for most sentence in the manuscript. The clunky English make it very difficult to assess the work because it is hard to work out what has been done. I consequently found it rather hard to work out what has gone on.

*Answer: we now corrected the English language by an English native speaker. As our method is radically new, it is indeed highly unusual and hard to understand without any oral presentation. Yet, we now have several papers explaining how it works and we would be delighted to have another illustration in PCI ecology.*

If my understanding is correct, a directed graph of the trophic network is **constructed**. I can't work out whether the initial graph contains all possible link, or is **put together** with expert knowledge. The initial model is then **sampled** using some sort of state-space **formulation** and a "**best'** model identified. The model can contain **temporal** variation for each path in the model, and the temporal variation can **be explained** with an environmental driver. Is that correct?

*Answer: Yes, this is globally correct (although some terms, in bold, are misused). We try to rephrase here your comment and rewrote the whole manuscript in this sense: 1) the directed graph you talk about is just the representation of the trophic interactions; 2) the expert knowledge is gathered into the rules of the model; 3) There is only one model (which is not the best but the sole one combining all the rules), which aims at computing all possible temporal changes of the previously mentioned directed graph; 4) as all the graph changes are kept (recorded), we are indeed able to explain all changes (and environmental drivers, actually processes, that are responsible for the graph changes).*

I would be pleased to review a revised version of the manuscript once the English has been made more accessible. I think this will be important for the authors, because if the method is to become widely used, which is clearly the hope of the authors, the manuscript needs to be accessible. My summary is I think there is the glimmer of a great idea here, but it is very hard to assess and work out what has been done.

*Comment: We would like to warmly thank both reviewers for their constructive and very helpful advices.*

*Best wishes. The co-authors.*