

Decision

by Dominique Gravel, 2018-09-26 18:07

Manuscript: [10.1101/373332](https://doi.org/10.1101/373332)

Recommendation for St-Gelais et al.

The manuscript reports an investigation of the co-distribution of phytoplankton and zooplankton communities in boreal lakes of Northern Québec, Canada. It aims at testing the hypothesis that trophic regulation by zooplankton should impact the distribution of phytoplankton, the main prediction being a correlation between community compositions. This is a big problem in biogeography right now, explored in many systems with a wide variety of approaches, ranging from species pairs analysis with sophisticated distribution models to the exploration of food web beta-diversity. The originality of the study is the simultaneous analysis of taxonomic and functional co-distribution between groups. The observation that both aspects of community structure are correlated among trophic levels, but that this correlation disappears once the effect of the abiotic environment is taken out, is interpreted as evidence that trophic interactions do not matter at this spatial scale for community distribution.

Both reviewers and myself agree that there is a lot of potential with the manuscript and would be happy to provide a positive recommendation after appropriate corrections. The reviewers are constructive and provide several specific ways to improve the manuscript. I invite the authors to consider each of them in their reply, but more specifically, I would like the authors to consider explicitly the limitation of the analysis of correlation between trophic levels (a point that is common to both reviews). I personally think that this point would be best addressed with a better explicit review of theory in the introduction, in order to formulate specific and discriminant predictions to test (and relate them to the statistical analysis). In particular, I would like the authors to compare the expected co-distributions in situation of a bottom-up assembly of food webs (which I think should lead to a positive correlation between traits) and a top-down assembly (leading to a negative correlation). Statements such as "It is also important to acknowledge that the coupling between plankton groups that we attribute to environmental factors could mask the effect of trophic interactions." are vague and likely the result of inadequate predictions.

In addition to the different comments of the reviewers, I would encourage the authors to explore the possibility of using Joint Species Distribution Models such as the one described in Ovaskainen et al. 2017 in Ecology Letters. It is mentioned in the introduction that "We expected that using functional traits characterizing the trophic interaction would improve our ability to detect joint distributions". This is very precisely the objective JSDMs, and a much more powerful approach to describe multivariate (community) data than RDAs. Such models aim at representing the covariance among species and groups once controlling for the environment. Such analysis use latent variables to deal with missing predictors (a point raised by one of the reviewers) and allows a much more detailed representation of the data structure.

The "spatial" model also needs revision because it is way too simple to either use euclidean distance among sites or lat/long coordinates as predictors. There are much more flexible

algorithms that could be used to represent spatial autocorrelation. Further, the underlying hypothesis must be better explained and the interpretation of "space = dispersal limitations" taken with caution. That was a standard approach 15 years ago, but we now have a much better understanding of the potential drivers of spatial autocorrelation.

I would also like to personally thank the authors for encouraging the new publishing model proposed by PCI and wish them success with the communication of their study.

Reply:

We agree that we need to better state the limitations of the approach, which we did mainly by better explaining our framework and how we tested our hypotheses. We also did a more general review in the Introduction instead of mainly focussing on plankton.

Thank you for suggesting of using Joint Species Distribution Models, it is a very interesting approach. It took us quite some time first to use the script because there is a known bug in the code so that it isn't possible to run the analysis for abundance data with traits. However, in the end, we realized that the way we approach functional traits is different; we use taxonomic and trait classifications similarly to compare what we observe at the two levels, which is not what is tested using the Joint Species Distribution Models. In order to compare both approaches, we did the joint Species Distribution Modelling on taxonomic data (without traits), code which is working, and we also did the modelling for each trait (by summing the biomass in each trait class). We obtained similar results to what we have now, which is interesting, but we do not see an added value to changing the methods in the manuscript because the analyses on taxa and traits must still be done separately.

We also agree that the way we deal with space is far from ideal. However, we are restricted to this because of the sampling design (3 distinct regions, see figure 1) that makes it challenging to fit other spatial models.

R1- AM

Reviewed by Anthony Maire, 2018-08-13 16:54

Summary

This paper aims at investigating the influence of trophic interactions between zooplankton and phytoplankton taxa on their spatial distribution in lakes at the landscape level. The authors hypothesized that regarding biogeographical distribution of plankton taxa and plankton functional traits, the major and determining trophic interaction would be between primary producers (phytoplankton) and consumers (zooplankton), which seems reasonable and coherent. However, in overall, the results point out that the initially supposed most important trophic interaction between zooplankton and phytoplankton does not significantly explain the observed distribution of taxa and traits, or at least not after accounting for the effects of environmental drivers. Instead, they conclude that it seems more likely that the directly upper (predators on zooplankton) and directly lower (resources on phytoplankton) interactions are the essential drivers of the biogeographical distribution of the studied taxa. Nevertheless, this result represents an interesting input to better understand trophic

interactions within lake food webs, and is likely to contribute to better apprehend the cascading influence of global changes (e.g. species invasions or water warming) on these ecosystems.

General appraisal

First, I must acknowledge that I have only limited knowledge about zoo/phytoplankton ecology, so I won't be of much help/expertise on this specific aspect of the paper. I have however tried to focus on aspects I am more comfortable with such as community ecology and functional biogeography.

Overall, I enjoyed reading this paper. Despite a perhaps too quick focus on the present subject of the study (see comment #4), the introduction is very well constructed, the issue raised pedagogically and the hypotheses clearly set. The reader should thus well understand the interests and challenges of the study in the broader context of species trophic interactions in lake ecosystems. The authors analyzed a large dataset of lake plankton communities (>100 lakes) at a pretty large spatial scale (Québec, CA). A set of analysis methods have been used to test the formulated hypotheses, which to me represents one possibility of analytical approach among others, but the authors have made choices, and I found that these choices make sense. The results presented here are rather descriptive but remain both concise and comprehensive. The discussion is interesting and, to me, well covered the main aspects of the study. Overall, the manuscript is very well written and of good quality. This study indeed provides interesting new inputs to our knowledge of trophic interactions between plankton taxa in boreal lakes, and more broadly of interactions in lake food webs.

Given those elements, I would recommend this manuscript for further consideration by PCI Ecology recommenders. I have provided more detailed comments below. The main comments that specifically requires clarifications or attention are comments #2, #4 and #11.

Detailed comments

Overall

C1: Please add line numbering to make the reviewing easier.

Reply: We are sorry for this oversight! In the replies, we specify lines in the updated version.

Abstract

C2: p.2 second sentence ("*However, the influence of such interactions on the biogeographical distribution of taxa or functional traits has never been explicitly tested*") - I doubt that this is globally true (e.g. some of the references listed in comment #3), but it is perhaps true for plankton in lakes. I may be wrong, but in this case it would mean that the sentence is not accurate enough since I am almost sure that a pretty large number of studies have investigated the influence of trophic interactions on the spatial distribution or co-existence of species, and probably also on their ecological traits. Please modify this

sentence to either specify in which context (environment, taxa, ...) the influence of such interactions have never been tested or detail more what aspect of such interactions you focused on has never been tested. For instance as it is stated in the last sentence of the 1st paragraph of the introduction.

Reply: We modified the second sentence to be more specific (lines 23-24).

C3: p.2 sentence "The lack of support for the role of trophic interactions as a driver coupling the distribution of plankton communities across boreal lakes indicates that taxon-specific and functional trait driven ecological interactions do not modulate large-scale spatial patterns of phytoplankton and zooplankton in a coordinated way." - Careful here, it is not because you did not find any significant coupling residuals that could be attributed to trophic interactions that it does not exist. You can only say, and have to stick to it, that the data considered and the analyses performed, which both seem quite robust, did not bring evidence of such phenomenon. Consequently, I would suggest to at least qualify/nuance this statement, for instance as follows: "[...] across boreal lakes suggests that taxon-specific and functional trait driven ecological interactions may not modulate large-scale spatial patterns [...]"

Reply (lines 34-37): We agree that this sentence lacked nuance, but we think that adding "suggests" and "may not" weaken the sentence too much, we kept "indicates" and then modify the last part of the sentence with may not as the reviewer suggests: "[...] across boreal lakes indicates that taxon-specific and functional trait driven ecological interactions may not modulate large-scale [...]"

Introduction

C4: The introduction seems to me too precise too quickly (i.e. lakes are the topic of the first sentence of the introduction). It may be fine for a journal specialized in limnology, but it might not be appropriate for a generalist journal in ecology. Thus, a slight widening (through a new first paragraph) of the context of trophic interaction between different levels of food webs in other ecosystems than lakes would make the article more suitable for a wider panel of scientists, which does not seem very challenging given the large number of studies dealing with this topic in terrestrial, marine and freshwater environments (here some possible references I found after a quick bibliographic research, which are probably not all relevant and would deserve a more serious inventory: Holt 1996; Srivastava 2006; Gotelli et al. 2010; Gravel et al. 2011).

Reply (lines 42-47) : Good point, furthermore I think that our results can definitely be of interest to a broader public. We modified the first paragraph as suggested. Thank you for providing relevant references!

C5: p.6 last paragraph, first sentence - Perhaps "the relative importance of trophic interactions between planktonic organisms compared to the effects of environment and dispersal" is more correct?

Reply (lines 45-47) : Done

C6: p.6 last paragraph, last sentence - "Our study covers a large biogeographical scale (1 228 km)" Should not it be in km² for an area measurement? Please correct or specify what this figure corresponds to.

Reply (lines 127-130): Because we sampled three regions, it is hard to meaningfully define the total sampled area in this way. Consequently, what we report now is the longest distance between two lakes. We clarified the sentence.

Material and Methods

C7: You did not specify why only a subset of the 104 lakes was sampled for phytoplankton. Are the reasons for this only practical (cost, opportunity, data initially sampled to address another research question, ...), or are there other reasons? Behind my curiosity, I would like to make sure that there are no confounding reasons (e.g. absence or scarcity of phytoplankton, lake situation, unsuitable environmental features, ...) which have prevented the sampling of phytoplankton in these lakes. This would possibly have a strong effect on the results and on their interpretation.

Reply (lines 139-149): The lack of complete sampling in all lakes was purely a function of cost. Many of these lakes are remote and difficult to access. Some were accessed with floatplanes, wherein the time for sampling was limited by the high cost of pilot time. As part of a much larger project (CarBBAS: Chair in Carbon Biogeochemistry in Boreal Aquatic systems) there were many other parameters measured in each lake. As a consequence, some parameters were measured in every lake (i.e. zooplankton) while others (i.e. phytoplankton) were only measured in a representative subset of lakes.

Within this project a representative subset of lakes were selected for which multiple additional parameters were measured, and phytoplankton samples were identified for this subset of lakes.

C8: p.7 middle of the second paragraph - "We used a multiparameter sonde (YSI, Yellow Springs Instruments, OH, USA) to measure pH (at 0.5m) and temperature (at 0.5m, then averaged over the water column). Water samples were collected at 0.5m to measure [...]" Specify at 0.5m depth, because it can also be the distance to the shoreline.

Reply (lines 159-161): Done

C9: p.8 lines 4-5 - I find it odd to 'interpolate' (inputted using a random forest procedure) the missing values of some environmental variables, given the low number of lakes concerned (5 lakes max, 2 lakes min depending on co-missing values for the same lake). Usually, elements (here lakes) without available data are discarded for the part of the analysis in which these data are used. I fully concede that this probably has a negligible impact on the results, but yet it seems more likely to lead to additional biases rather than additional ecological sense. Please explain why you chose to proceed this way.

Reply (lines 170-172): We agree that here, because the proportion of missing data is small, the effect on the results is minor. However, imputing data is an approach that is preferable to removing sites with missing observation, even if that is a longer-used approach in ecology, because, “this approach reduces statistical power and increases estimation bias” (Nakagawa and Freckleton 2008). Using random forests has been shown more recently to be a flexible and powerful imputation method (Stekhoven and Bühlmann 2012). However, if the reviewer feels extremely strongly about removing these data, we could do so.

C10: p.8 and Figure 1 caption - Please move the sentence “Catchment slope was estimated using a Digital Elevation Model (Canadian Digital Elevation Data)” from the caption of Figure 1 to the Materials and Methods section. ‘was estimated’ was also written twice. Please also specify how you calculated the lake maximum depth (Zmax) or from where you retrieved this variable (+ reference).

Reply (lines 172-175): We moved the section on catchment slope to the Methods section and specified how lake depth was measured.

C11: An information is missing about the repartition and representativeness of the 48 lakes for which both zooplankton and phytoplankton samples were done. Especially regarding the 3 subsets of lakes (regions). I strongly encourage to make appear in the text or with an additional table the number of lakes sampled for zooplankton and/or for phytoplankton. A table like the one below would do the job (see attached file for the table example) and would let the reader assess whether the subsampling of phytoplankton was representative of the whole studied set of 104 lakes. This would also lead to fewer questions about the comparison between the patterns observed for zooplankton on the 104 lakes and for phytoplankton on the subset of 48 lakes.

Region/subset N_lakes_zooplankton N_lakes_phytoplankton

Abitibi

Chicoutimi

Schefferville

Total

104

48

Reply (lines): Great suggestion, we modified Table 1 first to enable the reader to understand the distribution of lakes between the three regions for zooplankton and phytoplankton, but we also added regional averages to support our statement that there are regional differences (based on the PCA).

C12 p.10 end of the first paragraph - “space (using latitude and longitude coordinates).” Would “space (using between lake distance based on latitude and longitude coordinates).” be more accurate? Since you wrote in the first part of the Materials and Methods section that you used the “Euclidean distance between lakes to characterize the effect of dispersal limitation”. Please change it accordingly or provide additional details.

Reply (lines 221-222): Great suggestion, changed.

Results

C13 p.13 6th line of the 'Factors related to community composition' section - "[...] spatial factors indicating that the water quality variables driving the distribution [...]" variables plural.

Reply (lines 281-286): Done

Discussion

C14 p.16 9th line of the 'Divergent responses of phytoplankton and zooplankton to their environment' section - "However, water some quality effects were also [...]" please correct the word order.

Reply (line 346): Changed

C15 p.19 last 4 lines- I think this part would benefit from adding supporting references regarding the statements made (e.g. main pathway for matter and energy transfer in aquatic environments): "phytoplankton and zooplankton are known to share strong trophic connections in individual lakes"

Reply (lines 430-433): In the Introduction we used Porter 1977 and Sterner 1989 for a similar statement (lines 49), so we repeated the same references in the Discussion section.

Figures

C16: Figure 1 caption - Please remove the sentence "Zooplankton samples were collected in all lakes (n=108), while phytoplankton samples were collected in a subset of lakes (n=48)." that has no relevance to understand the figure, and this information is already given in the text. See also comment #10 for the sentence regarding Catchment slope.

Reply (lines): Changed

C17: Table 2 - a horizontal line seems missing between the two variables 'Biovolume' and 'Colonial'.

Reply: Changed

C18: Table 3 caption - add "ns = non-significant".

Reply: Changed

C19: Figure 6 - Please revise this figure and its caption, especially regarding 1) the absence of arrow on the figures for environmental variables while this is written in the caption, 2) the crosses and the corresponding names of taxa or traits are often poorly positioned, and 3) the color of the name of the variable: "The RDA was constrained by variables related to water quality (in blue) and by variables related to lake morphometry (in yellow)."

Reply: 1) we specified that environmental variables are coloured and removed the section on arrows 2) we improve the position of text on the figure 3) modified

References cited:

- Gotelli, N. J., Graves, G. R., & Rahbek, C. (2010). Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences*, 107, 5030-5035.
- Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeography. *Ecology letters*, 14, 1010-1016.
- Holt, R. D. (1996). Food webs in space: an island biogeographic perspective. In *Food webs* (pp. 313-323). Springer, Boston, MA.
- Srivastava, D. S. (2006). Habitat structure, trophic structure and ecosystem function: interactive effects in a bromeliad–insect community. *Oecologia*, 149, 493-504.

We sincerely want to thank the reviewer for a careful and in depth review of our manuscript and for its constructive comments, we think it helped to streamline the manuscript.

R2- EM

This manuscript aims at disentangling the relative contribution of environmental factors versus trophic interactions in determining the taxonomic and functional composition of phytoplankton and zooplankton communities across boreal lakes. To this purpose, the authors collected phytoplankton and zooplankton from lakes situated in three environmentally and geologically distinct regions of Québec, and measured key environmental variables characterizing the lakes' morphometry and water quality. Phytoplankton and zooplankton communities were characterized both taxonomically and functionally, based on a suite of functional traits known to play a role in phytoplankton-zooplankton trophic interactions. The coupling between phytoplankton and zooplankton composition, at taxonomic and functional traits levels, was tested through Procrustes analyses, before and after controlling for environmental variables. The main conclusion of the study is that a coupling is found at the taxonomic level, but not at the functional level, and that this taxonomic coupling disappears after controlling for environmental variables. This suggests that trophic interactions play a negligible role in the biogeographical coupling observed between plankton groups, compared to environmental variables. Overall, phytoplankton responded mainly to water quality, while zooplankton was mostly affected by lake morphometry. I think it is an interesting study, and overall the paper is well written and organized. I however have a few comments, of varying importance, which I give below.

General comments:

(1) My main concern is about the difficulty to fully distinguish between environmental and trophic interactions effects on biogeographical coupling. For example, it is known that water quality (e.g. phosphorus, nitrates, etc.) affects the phytoplankton community structure (e.g. by inducing cyanobacterial blooms), which in turn can trigger a response at the zooplankton level (e.g. because of changes in phytoplankton edibility). The resulting coupling between phytoplankton and zooplankton may be erroneously interpreted as a concordant response to the environment, while it is actually the result of trophic interactions. Then, it is not clear to me how it is possible to distinguish between environmental and trophic interactions effects,

and to draw strong conclusions about the absence of trophic interactions effects. This problem is mentioned by the authors in the discussion (P19), and it is, I think, a possible weakness of the study.

Reply: We agree that it is an inherent limitation of our study and a trade-off of observational studies. At the taxonomic level, as we observe a coupling between phytoplankton and zooplankton you are right that we cannot completely reject an effect of trophic interactions, as we explain in the Discussion (lines 406-411). However, at the functional level, as we did not observe any coupling when all the traits are considered, in which case, we can reject the hypothesis that trophic interactions and environment, couple the selected functional traits.

(2) I am wondering if considering additional functional traits, potentially important in trophic interactions, could change the results. For example, some cyanobacteria produce toxins, which have negative effects on grazers and impact the zooplankton composition. In turn, zooplankton tolerance traits (e.g. selective feeding, detoxification, etc.) can contribute to a top-down control of these cyanobacteria, and thus affect phytoplankton structure.

Reply: This is a good point about trait selection being a critical step and that observations will depend on the traits selected; as we observed by repeating the analyses without resource acquisition traits. For each trait that we include in the analyses, we require a value for each taxon. We thus used only traits that have general enough coverage, and could not use those for mentioned by the reviewer; traits for which not enough taxonomic coverage exists. Thus, we selected the traits for which we had a reliable value for each taxon, and that had the potential to influence interactions between phytoplankton and zooplankton in lakes. In general, we agree that a concerted effort to generate and assemble a more extensive trait databases for freshwater plankton, and as was done for marine species by the Scor working group 137, would be ideal. It should also be noted that toxic cyanobacteria are extremely rare in the regions in which we were working and are thus unlikely to influence phytoplankton or zooplankton community structure in these lakes, owing to being absence or at extremely low biomass (and unlikely to be producing toxins).

Specific (minor) comments:

(3) P3, I think “have never been tested” should be replace by “has never been tested”, and the coma after “between” should be removed.

Reply (line 65): Done

(4) P6, first sentence: add “to” after “compared”.

Reply (line 132): Done

(5) P9: Canonical Analysis of Principal Coordinates, if I am correct, is based on distance or

dissimilarity measures. The authors should mention what distance index was used in the analysis.

Reply (lines 205-206): We used the Bray-Curtis distance, the text was modified.

(6) P11 (and table 1): it might be interesting to provide the average values of environmental variables for each of the three regions (in table 1), and to refer to that table in the first paragraph of P11.

Reply: Great suggestion . We agree that regional averages are more relevant here. We added regional averages in Table 1, and added a reference to this in the text (line 238).

(7) P11 and Figure 3: the average percent occurrence cited in the text for the phytoplankton does not seem to be exactly the same as in figure 3. In addition, in Figure 3, it might be interesting to show the average taxonomic composition of the three regions.

Reply (lines): You are right, we modified the text (lines 249-251). For the average taxonomic composition, it is not clear to us how we could show the average taxonomic composition by region - with points?

(8) P12 and Figure 4: In the text, it is mentioned that regional differences were less pronounced in phytoplankton than in zooplankton, but when looking at the graphs I would have intuitively concluded the opposite. Maybe it is just an impression, however.

Reply: These plots can indeed be confusing, what is misleading is that you need to interpret these figures by axis: for phytoplankton (panel a) the three regions are well separated, but on each axis there is a lot of overlap between regions.

(8.2) P27, Table 3: Phytoplankton and Zooplankton in the table are not abbreviated by the letters "P" and "Z", as mentioned in the legend.

Reply: Changed

(9) P32, Figure 5: the y axis name is missing.

Reply: Changed

(10) P34, Figure 6: in the legend, it is mentioned that taxa and functional traits are represented by crosses, but the authors does not explain what dots correspond to. In addition, there are no arrow in the figures.

Reply : Changed, we specified that dots represents lakes (sites)

I hope my comments will be useful to the authors.