Peer Community In
Ecology

The difficult interpretation of species co-distribution

Dominique Gravel based on reviews by Emilie Macke and Anthony Maire

A recommendation of:

The taxonomic and functional biogeographies of phytoplankton and zooplankton communities across boreal lakes

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Recommendation

Ecology is the study of the distribution of organisms in space and time and their interactions. As such, there is a tradition of studies relating abiotic environmental conditions to species distribution, while another one is concerned by the effects of consumers on the abundance of their resources. Interestingly, joining the dots appears more difficult than it would suggest: eluding the effect of species interactions on distribution remains one of the greatest challenges to elucidate nowadays (Kissling et al. 2012). Theory suggests that yes, species interactions such as predation and competition should influence range limits (Godsoe et al. 2017), but the common intuition among many biogeographers remains that over large areas such as regions and continents, environmental drivers like temperature and precipitation overwhelm their local effects. Answering this question is of primary importance in the context where species are moving around with climate warming. Inconsistencies in food web structure may arise with asynchronized movements of consumers and their resources, leading to a major disruption in regulation and potentially ecosystem functioning. Solving this problem, however, remains very challenging because we have to rely on observational data since experiments are hard to perform at the biogeographical scale.

The study of St-Gelais is an interesting step forward to solve this problem. Their main objective was to assess the strength of the association between phytoplankton and zooplankton communities at a large spatial scale, looking at the spatial covariation of both taxonomic and functional composition. To do so, they undertook a massive survey of more than 100 lakes across three regions of the boreal region of Québec. Species and functional composition were recorded, along with a set of abiotic variables. Classic community ecology at this point. The difficulty they faced was to disentangle the multiple causal relationships involved in the distribution of both trophic levels. Teasing apart bottom-up and top-down forces driving the assembly of plankton communities using observational data is not an easy task. On the one hand, both trophic levels could respond to variations in temperature, nutrient availability and dissolved organic carbon. The interpretation is fairly straightforward if the two levels respond to different factors, but the situation is much more complicated when they do respond similarly. There are potentially three possible underlying scenarios. First, the phyto and zooplankton communities may share the same environmental requirements, thereby generating a joint distribution over gradients such as temperature and nutrient availability. Second, the abiotic environment could drive the distribution of the phytoplankton community, which would then propagate up and influence the distribution of the zooplankton community. Alternatively, the abiotic environment could constrain the distribution of the zooplankton, which could then affect the one of phytoplankton. In addition to all of these factors, St-Gelais et al also consider that dispersal may limit the distribution, well aware of previous studies documenting stronger dispersal limitations for zooplankton communities.

Unfortunately, there is not a single statistical approach that could be taken from the shelf and used to elucidate drivers of co-distribution. Joint species distribution was once envisioned as a major step forward in this direction (Warton et al. 2015), but there are several limits preventing the direct interpretation that co-occurrence is linked to interactions (Blanchet et al. 2020). Rather, St-Gelais used a variety of multivariate statistics to reveal the structure in their observational data. First, using a Procrustes analysis (a method testing if the spatial variation of one community is correlated to the structure of another community), they found a significant correlation between phytoplankton and zooplankton communities, indicating a taxonomic coupling between the groups. Interestingly, this observation was maintained for functional composition only when interaction-related traits were considered. At this point, these results strongly suggest that interactions are involved in the correlation, but it's hard to decipher between bottom-up and top-down perspectives. A complementary analysis performed with a constrained ordination, per trophic level, provided complementary pieces of information. First observation was that only functional variation was found to be related to the different environmental variables, not taxonomic variation. Despite that trophic levels responded to water quality variables, spatial autocorrelation was more important for zooplankton communities and the two layers appear to respond to different variables.

It is impossible with those results to formulate a strong conclusion about whether grazing influence the co-distribution of phytoplankton and zooplankton communities. That's the mere nature of observational data. While there is a strong spatial association between them, there are also diverging responses to the different environmental variables considered. But the contrast between taxonomic and functional composition is nonetheless informative and it seems that beyond the idiosyncrasies of species composition, trait distribution may be more informative and general. Perhaps the most original contribution of this study is the hierarchical approach to analyze the data, combined with the simultaneous analysis of taxonomic and functional distributions. Having access to a vast catalog of multivariate statistical techniques, a careful selection of analyses helps revealing key features in the data, rejecting some hypotheses and accepting others. Hopefully, we will see more and more of such multi-trophic approaches to distribution because it is now clear that the factors driving distribution are much more complicated than anticipated in more traditional analyses of community data. Biodiversity is more than a species list, it is also all of the interactions between them, influencing their distribution and abundance (Jordano 2016).

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Reviews

Toggle reviews

Evaluation round #2

02 Dec 2019

DOI or URL of the preprint: *10.1101/373332*

Version of the preprint: 2

Author's Reply

First, we appreciate that you took the time to further explain your previous comments on the clarity of the predictions we are making as we misinterpreted your comments in the first round. We agree that our predictions could be better aligned with ecological knowledge. Furthermore, because of inherent limitations of observational studies like ours, making conclusions about the underlying ecological causes of what was observed need to be based on well thought out predictions.

As we state in our Introduction, bottom-up and top-down interactions in lakes are well documented. However, we decided, as a starting point, to assume that if the coupling between zooplankton and phytoplankton could be explained by another mechanism than biotic interactions, we would conclude that there is no support for trophic interactions as a driver of spatial distribution of phytoplankton and zooplankton. Following that reasoning, we assumed in the previous version that if the coupling between zooplankton and phytoplankton could be explained by environment it would mean that both groups responded to the same environmental variables or to a set of correlated variables. However, we stated in our Discussion that "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. For example, the concordant taxonomic response to phosphorus (TP, Figure 6 a and b), could indicate that phosphorus enrichment affecting phytoplankton triggers a response in the zooplankton, as would be expected with changes in edibility of phytoplankton along this nutrient gradient (e.g. Watson et al. 1997).", as these two mechanisms are indistinguishable in an observational study such as ours.

Your very well thought out comments made us realize that it would probably make more sense to start from the assumption that, based on current knowledge, if phytoplankton and zooplankton respond to the same environmental gradient it should be indicative instead of overall top-down or bottom-up food web interactions - including predator-prey interactions between the phytoplankton and zooplankton. For example, if fish predation (top-down) is being captured by one of our environmental variables (lake depth for example), then this force on the interaction of phyto and zooplankton is most critical. On the other hand if nutrients emerge in our analyses (bottom-up), this would be indicative of the primacy of this gradient on the phyto-zooplankton interaction. To this end, we have modified the second last paragraph of the Introduction and our conceptual figure (Figure 2).

This shift in perspective regarding mechanisms also impacts our conclusions, but we think that it represents a more reasonable interpretation of our results. At the taxonomic level, we modified our conclusion to "trophic interactions in response to bottom-up and top-down effects in lakes play a significant role in the taxonomic and functional distribution of both phytoplankton and zooplankton.". We also modified the Results section to correspond to our reformulated initial hypotheses (lines 281-282)

For the functional trait results, these modifications do not change the conclusions for analyses including all traits as no phyto-zooplankton coupling was observed even before controlling for the environment. However, the interpretation is altered when we remove resource acquisition traits, as we observed a weaker correlation initially than for taxonomy, but that there is no residual correlation after controlling for environment or space. This is a bit harder to interpret, but it suggests that there is a small effect of interactions that can be captured mainly by the WQ component in figure 5, but that the differential response to morphometry (zooplankton) and water quality (phytoplankton) represents stronger structuring factors for the distribution of functional traits for zooplankton and phytoplankton in boreal lakes.

Decision by Dominique Gravel

The answers to the different comments by the two reviewers were satisfactory and I am positive about the preprint. The main reason I find it interesting is that the study of functional traits could be a much more conclusive approach to investigate co-distribution between consumers and resources than the morecommon pairwise approach. It is hard to detect the spatial association between a given consumer and its resource if both are involved in multiple interactions. Traits may be a more relevant way to quantify the total amount of interactions a species experiences than the presence of a single resource or predator.

That said, even though the manuscript could be publishable somewhere, I am not ready to write a recommendation with my name associated to it. Unfortunately, answers to my comments were the weakest of the rebutal. The reason is simple, I find that the predictions are not clear enough and as a result, conclusions are fairly limited.

The take-home is nicely summarized at L381 : "Because no coupling between phytoplankton and zooplankton was observed after controlling for either water quality, morphometry or space, it suggests that one of these is the main driver of the observed coupling." I don't think this observation of no residual covariation is sufficient to make any strong conclusion about the effect of interactions on co-distribution. The authors know the story better than I do with seasonal fluctuations in phyto an zoo composition. It's well-known there is a shift in body size distribution over the season because of an initial bloom of nutrients and primary productivity, followed by a delayed response of grazers. Both bottom-up and top-town regulation are driving this covariation over the season. If one simply models the composition of both groups with time as the main predictor, we would not expect much residual covariation between them. In more general terms, if a given abiotic variable is driving the variation of a group and this one is clearly impacting the distribution of the other group, then both of them will respond to the abiotic variable and there won't be much residual covariation.

I am sure there is enough in the Procust analysis to conclude if proper predictions were made, but they are not provided at the moment.

-- As a side, I was not suggesting to use JSDM with traits as covariates with the HMSC package. I was simply suggesting to use JSDM to model simultaneously all of the species (both phyto and zoo), using the group as a dummy trait variable. This way, the residual covariation would be properly represented and all of the operations performed with a singleanalysis. I am not strong about this suggestion though, I understand the extra amount of work it represents. It would only make the analysis simpler, and incidently, more elegant.

Evaluation round #1

26 Sep 2018

DOI or URL of the preprint: ***10.1101/373332***

Version of the preprint: 1

Author's Reply

Download author's reply

Decision by Dominique Gravel

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 aims 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.

Reviewed by Anthony Maire, 13 Aug 2018

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.

Abstract

C2: p.2 second sentence - 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.

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 […]”

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).

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?

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.

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.

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.

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.

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).

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

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.
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.

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.

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)

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.

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

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

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).”

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Reviewed by Emilie Macke, 21 Sep 2018

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