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Body size and food–web interactions mediate species range shifts under warming

Edward W. Tekwa, James R. Watson and Malin L. Pinsky

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Original submission:	4 May 2021
1st revised submission:	20 December 2021
2nd revised submission:	2 March 2022
3rd revised submission:	21 March 2022
Final acceptance:	22 March 2022

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2021-1048.R0 (Original submission)

Review form: Reviewer 1 (Ken Andersen)

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
No

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The study explores how a string of food-web models across a temperature gradient responds to increased temperatures. The main finding is that the food-web interactions creates barriers to the range shifts of species compared to a simulation without food-web interactions. This is an interesting results which illustrates the problems of observing climate-drive range shifts and inspires to new ways of interpreting observations. Overall the methodology seems sound (though I do have some concerns about the food-web model) and the text and results are clearly presented.

Major comments

1. The model is described as a “food-web” model. However, it is more precisely characterised as a set of coupled food chains (at least this is what I assume since no food webs are presented). Since species only have one trophic trait (body size), they must be organised in a linear food chain with each “species” representing an entire trophic level (sensu Barbier and Loreau, Ecology Letters, (2019) 22: 405–419). Therefore the total species diversity in a patch is very low since there is no diversity within trophic levels and it does not represent the crucial effect of competition (at least, this is what I assume). The model is therefore not a food-web as it is commonly understood but a trophic food chain. Is that a problem? I don’t know, but three things needs to be done: A) it should be emphasised up front that the model is based around food chains and not food webs (it actually took me quite a while to realise this). B) it should be discussed whether the main result (that species cannot easily invade a neighbouring patch) hinges on the simplicity of the food-chain, which does not allow for diversity and competition within a trophic level. I do not have an answer to this, and I don’t think it is possible to give one easily, but this issue should be highlighted and discussed. A discussion could perhaps be made in the context of food-web models that do have diversity within trophic levels. C) Finally, it is uncommon for food-chain models to operate with a functional response type III. It is usually made to maintain diversity in “real” food web models. Does the functional response type III matter for the results? [I may have misunderstood the nature of the model, but if that is so, it points to some unclarity in the text. If the model is indeed a food-web model then the food-web structure needs to be described and compared to standard metrics, like conductance, diversity vs trophic level, maximum trophic level].

2. Since species are not shifting range as fast as they would like, there must be a “climate debt”. In the initial state, species will on average have a certain distance (in temperature) to the optimum

for the search rate temperature preference curve. After climate change, distance must have changed. How much? This quantity would be interesting, because it may even be amenable to empirical test. Calculating this quantity is not a must for publication, but it might strengthen the manuscript.

3. I find the use "diffusion" formula T3 overly complicated. This formula is just used to relate the diffusivity m to the rate kappa. However, it is much more interesting to know the value of kappa because it directly shows the rate of immigration/emigration. Unless there are strong reasons against it, I would much prefer to see kappa values instead of diffusivities.

Line 47-48: please explain "biotic resistance" and "enemy release" with a few words.

Line 72. I would call kappa a "rate" and not a "portion".

Eq 1: is the first sum from j=0? I would think it starts from j=1

General notation: Do not use italics for units. Do not use italics for functions (such as "exp"). In many cases equations are in bold, but it does not seem to be needed for notation. It may be a bug in Word, but it must be fixed before copyediting.

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Line 94: Do you really do Euler integration? If that is really the case, the dynamics of small species may be very badly resolved. Why not use a standard high-quality integrator in matlab for stiff equations, like ode23s? If there are difficulties related to the numerical solution of the model, this should be documented.

Line 128. Definition of production. This definition is different from the food-web model definition in line 89. It probably does not matter much but these two definitions must be similar because production are later compared (line 199-201).

Eq.3. I find the idea of the last quadratic terms with a/c to be a bit convoluted. It would be much easier to simply formulate it as a carrying capacity directly (which is also what is referred to in the text).

End of methods section: Please spend a few sentences outlining the various size-scalings used.

Line 218. I did not understand how predators become more specialist.

Fig 1. It is important to show the basal behaviour of the model. However, I did not find this figure very illuminating. First, I would like to see actual simulated food chains from a few connected pacthes. Second, the three panels on the right are too messy to see anything clearly. I urge you to go back to the drawing board and design a nice illustration of the model and the core dynamics.

Eq T1. Change "basal biomass" to "basal resource".

Table 2. Please add units (alpha_D, alpha_l, etc)

Table 2: F has just units of “per day”. Where does this value come from?

Supplementary. I would like to see a plot of T15.

Code: Great that the code is available. Please provide a description of which scripts to run to do the figures. Some things in the code seem to be hard-coded for the specific computer setup (like paths). It would be great with a simple script to run just a basic model and provide something like figure 1.

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

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> **Is it accessible?**
> Yes
>
> **Is it clear?**
> Yes
>
> **Is it adequate?**
> Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
Tekwa et al. study how the foodweb context impacts reaction of organisms to climate change-induced ranged shifts. The authors use a mathematical model for this purpose and show, among other aspects, that not taking the foodweb context into account when projecting range shifts may

systematically underestimate the negative effects of climate change.

The manuscript is overall well written and of interest to a broad readership. I have only very few comments that the authors can find below.

Main comments:

I think that the manuscript could benefit from including some more discussion of work focusing on communities, such as the work by Jonathan Levine and Jake Alexander, for example, but also some more work by Patrick Thompson. The questions are very much related even if the focus is on communities.

After reading the manuscript and the supplement I am still not quite sure I understand how the "counterfactual" models without trophic interactions were implemented. On page 7 (line 117) the authors write "we fit [the models]". What is meant by "fitting"? Some more explanation could be useful here.

Minor points:

l. 83: Why a type III FR and not a simpler function?

l. 178: "wth" should be "with"

l. 307: lack of dispersal-body size relationships. Stevens et al. (2014) Ecology Letters may be a valuable reference here.

References: Please check homogeneous formatting.

Review form: Reviewer 3

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Marginal

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

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No

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Is it adequate?
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Comments to the Author
Review of Tekwa et al.

Tekwa et al. propose a model that couples trophic interactions with species diffusion to explore how food-webs affect species redistribution under a changing climate. It's definitely an area worthy of exploration, and a worthy effort, but I have strong concerns about the robustness of the study.

Firstly, the authors suggest that dynamic trophic interactions hamper species range shifts, which is definitely plausible. They explain this is likely the case because competition and biotic resistance effects are likely to be stronger than predator release effects.

However, I'm not sure that their model does, or indeed actually can, test potential predator release effects – i.e., is it actually possible for their model to show anything except the result that they find? Specifically, feeding is size-structured, which makes sense, but it also means that a species expanding to a new area can never actually experience predator release since when they move to a new area beyond their 'natural' predators, they will simply be eaten by something else of equivalent size. We can debate the ecological appropriateness or not of this, but in the absence of any opportunity for predator release, the model is bound to find that food-web interactions slow range shifts. So is the model actually able to test the hypotheses that they ascribe potential outcome to?

There's also something very, very odd going on with the spatial and temporal scale match-ups in the model (unless a typo or misinterpretation). The patch areas are 471,429 m^2 (Table 2) which is a strange choice (what is the rationale for this?). This means, assuming a square patch (as it is in m^2) that each patch is around 686m in length (or a 470km length patch of 1m width, which is equally odd. There is insufficient information to determine which). Assuming the former, you have a gradient of 20 degrees in temperature across a distance that is less than 20km and supposed to represent the distance from the pole to the equator. Species have a maximum body size of 10^6 grams (i.e. 1,000 kg). Surely a 1,000 kg predator would traverse more than the entire length of the entire gradient (<20km) in a single day to exploit every available resource?

Furthermore, the diffusion rate is identical across species. This seems at the very least extremely unrealistic to have the same diffusion rate for species ranging from 10g to 1000kg – despite what the authors say, there is good evidence that movement rates, home range sizes, and patch sizes relate directly to body size (see e.g. Brown's or Gaston's macroecology books).

The authors don't describe (as far as I can tell – apologies if I have missed it) how species biomasses are initially distributed across the grid. There is some information on lines 99-100, but this is unclear as to whether it is identical for each grid cell.

There appears to be no reproduction in the model – a fundamental process. I assume that individuals do not change size (i.e. grow) and reproduce given that it is not an IBM. What are the consequences of this? There is no loss of matter through reproduction nor inefficiency, nor changing body size and vulnerability to predation.

The thermal performance width for feeding seems extraordinarily narrow (1.25 C). Doesn't this mean that search rates drop off unrealistically fast outside of the optimum? Could the authors include a supplemental plot of the shape of this distribution to examine?

I would also like to see a greater exploration of the uncertainty in the model results. The authors do some sensitivity tests of parameters, but no formal exploration (as opposed to alternate parameter values) around the incorporation of stochasticity or parameter variations. It would be much better to see confidence bounds, if feasible, and to know which parameters is the model most sensitive to.

On the plus side: I like the ideas here. I like the counterfactual model approach very much. I think this is an area worth exploring. But in general, I find that the model appears to make unsupportable assumptions, together with being more constrained in terms of plausible outcomes than is at first apparent.

Decision letter (RSPB-2021-1048.R0)

23-Jun-2021

Dear Dr Tekwa:

I am writing to inform you that your manuscript RSPB-2021-1048 entitled "Body-size and food-web interactions mediate species range shifts under warming" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would are willing to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance. Please keep in mind that the manuscript requires some considerable effort to make it can be considered further.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

4) Data - please see our policies on data sharing to ensure that you are complying (https://royalsociety.org/journals/authors/author-guidelines/#data).

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,
Dr Daniel Costa
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
This manuscript describes a modelling study testing if taking into account food web interactions will change our understanding of the rate at which species can shift their ranges to adapt to climate change. The manuscript was seen by three reviewers, and they all agree that the manuscript covers an important and timely topic, and the hypotheses are interesting. However, the reviews diverge substantially in their assessment of the merit of the current study, with the main concerns focusing on model assumptions notably, is this a food web or a set of food chains and does this predetermine the main result; are the parameter assumptions realistic enough that the model is meaningful, or do they predetermine the model outcome? All three reviewers made important and helpful suggestions and comments. There also are several requests for clarification and/or suggestions for further or different presentation of model and model results. Addressing the reviewer comments would improve the impact and reach of a thoroughly revised manuscript.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
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On the plus side: I like the ideas here. I like the counterfactual model approach very much. I think this is an area worth exploring. But in general, I find that the model appears to make unsupportable assumptions, together with being more constrained in terms of plausible outcomes than is at first apparent.

Author's Response to Decision Letter for (RSPB-2021-1048.R0)

See Appendix A.

RSPB-2021-2755.R0

Review form: Reviewer 1 (Ken Andersen)

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Acceptable

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Acceptable

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

> **Is it accessible?**
> Yes
>
> **Is it clear?**
> No
>
> **Is it adequate?**
> Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The revision adequately addressed my previous concerns. I have only minor issues:

Eq 1: The term after the first equality sign makes it clear that the model is a discrete time model. However, it misses that one still needs to divide by Delta t. (I know the time step is one day, but since the equation is agnostic to units at this stage the Delta t must be in the dominator). What does the tildes above B signify? Explain or remove. The tildes appear again in the single-species model; why?

Line 83-84: Add units to kappa.

T2. This is not a dimensionally consistent. If nu has units m^3/day/g then the 2nd term in the denominator has a dimension (and it should be dimensionsless when added to "1"). For it to be dimensionally correct nu has to have dimensions m^3/day/g^2.

T11 + T15. "exp" and "erf" should not be in italics

Previous comment: "Table 2. Please add units (alpha_D, alpha_l, etc)
These are unitless because they appear in power laws, where the left-hand side is a log value and unitless."

No, they are not unitless. Just because a dimensional quantity is in a log or exp function does not remove its unit. See for example T4. The first term is C_W->d with dimensions 1/day/energy. D on the left side has dimensions 1/day. Therefore the exponential term must have dimensions of energy. Then alpha_D must have units ln(1/sJ). An so forth for the other quantities.

There are still a lot of bold-face in the tables which I believe should not be present.

Review form: Reviewer 2

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

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Comments to the Author
I have reviewed this manuscript previously and the authors have addressed all of my comments.

Review form: Reviewer 3

Recommendation
Major revision is needed (please make suggestions in comments)

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General interest: Is the paper of sufficient general interest?
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Is it adequate?
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Do you have any ethical concerns with this paper?
No

Comments to the Author
Thank you to the authors for their responses. However, I find some of their responses disappointing.

In particular, the response to providing a more formal exploration of parameters, ideally to derive confidence bounds, but certainly to get a better sense of robustness and sensitivity, boils down to 'it is too computationally expensive'. However, when cloud computing is becoming ever cheaper and easier, I find that hard to reconcile, when understanding sensitivity is so important. Did they actually run any additional sensitivity analyses (in comparison to the initial submission) for their revision, or just write it off as too difficult?

The response to questions about predator release were unconvincing. They do not directly answer the question of whether the model is actually able to test the hypotheses that they ascribe the potential outcome to - i.e. is it possible for their model to show anything except the results that they find? I would have appreciated a direct answer to this question.

Their response to the question of differing diffusion rates among species was also unconvincing. They say that 'both large and small species in the ocean disperse as larvae with similar body sizes'. This is not true; there are plenty of (especially larger) species in the ocean that bear live young and so clearly do not disperse as larvae. Here I am compelled to give them the benefit of the doubt for the modelling, but nonetheless it is lax to make such generalizations.

I still think the ideas in here are interesting and worth exploring. But I remain somewhat troubled by the limited attempts to directly respond to the points that I raised.

Decision letter (RSPB-2021-2755.R0)

10-Feb-2022

Dear Dr Tekwa:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

Research ethics:
If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article (https://royalsociety.org/journals/authors/author-guidelines/#data). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

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For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr Maurine Neiman
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
The authors provided an extensively revised manuscript that was seen again by the original reviewers. These agreed that the manuscript is much improved, but also that some further revisions are needed. In particular, direct responses to some important points. A more direct reply to the concern regarding lack of predator release is needed, perhaps some assessment of how effectively the sensitivity set with 20% inedible prey mimics this, and a consideration whether any additional models could address this more directly. Moreover, I request the authors consider what level of sensitivity analysis could be included, even if the full complement of possibilities cannot be accommodated, a limited subset that is most relevant or important might be feasible. If so, this would enhance the manuscript strength and ability to convince readers; a simple comment on how long the analyses take is not fully adequate. If no sensible subset can be identified, then a more detailed mention/discussion should be added of why the sensitivity analyses that were done are sufficient. In addition, it would be useful if some of the supporting arguments made about size-independent dispersal in the reply to referee could be added in the manuscript (e.g. at line 83) such that readers are better alerted to this assumption. Finally, some tidying up of details is needed and I would request to remove the word ‘greatly’ from l. 25 – as the authors acknowledge this model does not mimic reality, rather highlights a pattern, so how great the overestimation is, is not really clear?

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s).
The revision adequately addressed my previous concerns. I have only minor issues:

Eq 1: The term after the first equality sign makes it clear that the model is a discrete time model. However, it misses that one still needs to divide by Delta t. (I know the time step is one day, but since the equation is agnostic to units at this stage the Delta t must be in the dominator). What does the tildes above B signify? Explain or remove. The tildes appear again in the single-species model; why?

Line 83-84: Add units to kappa.

T2. This is not a dimensionally consistent. If nu has units m^3/day/g then the 2nd term in the denominator has a dimension (and it should be dimensionsless when added to “1”). For it to be dimensionally correct nu has to have dimensions m^3/day/g^2.

T11 + T15. “exp” and “erf” should not be in italics

Previous comment: “Table 2. Please add units (alpha_D, alpha_l, etc)
These are unitless because they appear in power laws, where the left-hand side is a log value and unitless.”

No, they are not unitless. Just because a dimensional quantity is in a log or exp function does not remove its unit. See for example T4. The first term is C_W->d with dimensions 1/day/energy. D on the left side has dimensions 1/day. Therefore the exponential term must have dimensions of energy. Then alpha_D must have units ln(1/sJ). An so forth for the other quantities.

There are still a lot of bold-face in the tables which I believe should not be present.

Referee: 2
Comments to the Author(s).
I have reviewed this manuscript previously and the authors have addressed all of my comments.

Referee: 3
Comments to the Author(s).
Thank you to the authors for their responses. However, I find some of their responses disappointing.

In particular, the response to providing a more formal exploration of parameters, ideally to derive confidence bounds, but certainly to get a better sense of robustness and sensitivity, boils down to 'it is too computationally expensive'. However, when cloud computing is becoming ever cheaper and easier, I find that hard to reconcile, when understanding sensitivity is so important. Did they actually run any additional sensitivity analyses (in comparison to the initial submission) for their revision, or just write it off as too difficult?

The response to questions about predator release were unconvincing. They do not directly answer the question of whether the model is actually able to test the hypotheses that they ascribe the potential outcome to - i.e. is it possible for their model to show anything except the results that they find? I would have appreciated a direct answer to this question.

Their response to the question of differing diffusion rates among species was also unconvincing. They say that 'both large and small species in the ocean disperse as larvae with similar body sizes'. This is not true; there are plenty of (especially larger) species in the ocean that bear live young and so clearly do not disperse as larvae. Here I am compelled to give them the benefit of the doubt for the modelling, but nonetheless it is lax to make such generalizations.

I still think the ideas in here are interesting and worth exploring. But I remain somewhat troubled by the limited attempts to directly respond to the points that I raised.

Author's Response to Decision Letter for (RSPB-2021-2755.R0)

See Appendix B.

Decision letter (RSPB-2021-2755.R1)

21-Mar-2022

Dear Dr Tekwa

I am pleased to inform you that your manuscript RSPB-2021-2755.R1 entitled "Body-size and food-web interactions mediate species range shifts under warming" has been accepted for publication in Proceedings B.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section.

This should list the database and accession number for all data from the article that has been made publicly available, for instance:
• DNA sequences: Genbank accessions F234391-F234402
• Phylogenetic data: TreeBASE accession number S9123
• Final DNA sequence assembly uploaded as online supplemental material
• Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
NB. From April 1 2013, peer reviewed articles based on research funded wholly or partly by RCUK must include, if applicable, a statement on how the underlying research materials – such as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link http://datadryad.org/submit?journalID=RSPB&manu=(Document not available) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see https://royalsociety.org/journals/ethics-policies/data-sharing-mining/ for more details.

6) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit https://royalsociety.org/journals/authors/author-guidelines/.

Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr Maurine Neiman
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Associate Editor:
Board Member: 1
Comments to Author:
This is the second revision of this manuscript, and here the authors have now addressed all reviewer comments. The manuscript is now much improved and the additional simulations increase confidence and now it is clearer how robust the conclusions are to variations in parameters/assumptions. One point made in the response letter ('Beyond this level, food webs tended to collapse due to a lack of edible prey.'), further strengthens the breadth of the sensitivity analyses- perhaps the authors could add this information in the manuscript, around l. 195-196 perhaps.
A few minor textual matters remain which will take a few minutes to fix, but are worth doing to improve readability (as it is a complex manuscript). Specifically,
l. 52: 'larger' – it is not clear why here prey is larger, how is this juxtaposed to 'prey that escape traditional predators'? Is there an argument missing? Please clarify this sentence (l. 50-53).
l. 88: please indicate here where the sensitivity test can be found, e.g. add (see below, Supplementary Appendix A)?
l. 127-130: this detail seems superfluous, please delete
l. 214: replace 'higher' with 'larger'
l. 216: something wrong with this sentence, 'shifted' should be 'shifts' perhaps? Maybe also once place (isotherm shifts) after thermal shifts, to more clearly link the text here to the terms used in the figure

Author's Response to Decision Letter for (RSPB-2021-2755.R1)

See Appendix C.

Decision letter (RSPB-2021-2755.R2)

22-Mar-2022

Dear Dr Tekwa

I am pleased to inform you that your manuscript entitled "Body-size and food-web interactions mediate species range shifts under warming" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

You are allowed to post any version of your manuscript on a personal website, repository or preprint server. However, the work remains under media embargo and you should not discuss it with the press until the date of publication. Please visit https://royalsociety.org/journals/ethics-policies/media-embargo for more information.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

Associate Editor
Board Member: 1
Comments to Author:
This manuscript describes a modelling study testing if taking into account food web interactions will change our understanding of the rate at which species can shift their ranges to adapt to climate change. The manuscript was seen by three reviewers, and they all agree that the manuscript covers an important and timely topic, and the hypotheses are interesting. However, the reviews diverge substantially in their assessment of the merit of the current study, with the main concerns focusing on model assumptions notably, is this a food web or a set of food chains and does this predetermine the main result; are the parameter assumptions realistic enough that the model is meaningful, or do they predetermine the model outcome? All three reviewers made important and helpful suggestions and comments. There also are several requests for clarification and/or suggestions for further or different presentation of model and model results. Addressing the reviewer comments would improve the impact and reach of a thoroughly revised manuscript.

Thank you for assessing the reviews and for your supportive assessment. We have carefully responded to the comments below, including the concerns about food webs, parameters, clarification, and presentation of results. The manuscript has greatly improved as a result.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
The study explores how a string of food-web models across a temperature gradient responds to increased temperatures. The main finding is that the food-web interactions creates barriers to the range shifts of species compared to a simulation without food-web interactions. This is an interesting results which illustrates the problems of observing climate-drive range shifts and inspires to new ways of interpreting observations. Overall the methodology seems sound (though I do have some concerns about the food-web model) and the text and results are clearly presented.

Thank you for your supportive comments. We also think this is an important result, and address the food web concern below.

Major comments

1. The model is described as a “food-web” model. However, it is more precisely characterised as a set of coupled food chains (at least this is what I assume since no food webs are presented). Since species only have one trophic trait (body size), they must be organised in a linear food chain with each “species” representing an entire trophic level (sensu Barbier and Loreau, Ecology Letters, (2019) 22: 405–419). Therefore the total species diversity in a patch is very low since there is no diversity within trophic levels and it does not represent the crucial effect of competition (at least, this is what I assume). The model is therefore not a food-web as it is commonly understood but a trophic food chain. Is that a problem? I don’t know, but three things needs to be done: A) it should be emphasised up front that the model is based around food chains

and not food webs (it actually took me quite a while to realise this). B) it should be discussed whether the main result (that species cannot easily invade a neighbouring patch) hinges on the simplicity of the food-chain, which does not allow for diversity and competition within a trophic level. I do not have an answer to this, and I don't think it is possible to give one easily, but this issue should be highlighted and discussed. A discussion could perhaps be made in the context of food-web models that do have diversity within trophic levels. C) Finally, it is uncommon for food-chain models to operate with a functional response type III. It is usually made to maintain diversity in "real" food web models. Does the functional response type III matter for the results? [I may have misunderstood the nature of the model, but if that is so, it points to some unclarity in the text. If the model is indeed a food-web model then the food-web structure needs to be described and compared to standard metrics, like conductance, diversity vs trophic level, maximum trophic level].

Thank you for your insight about food chain versus food web. If there were no dispersal and no variation in thermal optima, then we would expect one species at each trophic level to exclude the others. However, the present model represents a food web rather than a food chain for two reasons.

First, the differences in thermal optima means that species in the same trophic level coexist in the same patch, maintained in part by by virtue of dispersal from adjacent patches. Fig. 1C shows that a handful of species at each size class (trajectories with similar colours) coexist within a patch. The new Fig. 1E-H shows actual food webs from the simulation, with multiple species at similar sizes coexisting and connected by trophic interactions within each patch.

To confirm that dispersal plays an important role in maintaining food web diversity, we have added a new Fig. S2F-H. This figure shows that with no dispersal, the situation approaches a food chain with alpha diversity (richness within a patch) being 5 (Fig. S2F). However, even in this case it is a food web rather than a chain because the maximum trophic level (assigning the basal resource as level 1) is only three (Fig. S2H). Before warming, there are two heterotrophic levels and five species in each patch on average, so species are competing. After warming, richness decreased by three on average with maximum trophic level remaining at three, which was the only scenario explored that generated a true food chain (two heterotrophic species at two heterotrophic levels). With even a small amount of movement, food webs were maintained even after warming. As movement increased, pre-warming alpha was 16 and continued to increase all the way to 53 at the highest movement rate. In addition, the maximum trophic level remained at three and alpha diversity decreased by less than three after warming. These results indicated that with at last a small amount of dispersal or variation in thermal optima, food webs indeed arise (lines 261-268). Our results are in line with Zhang et al. 2017, *Proc B*, who also found the emergence of food webs in a related model.

Second, the sensitivity analysis simulation set in which 20% of potential prey were inedible (rather than 0% in the main results) allowed for further coexistence of species in the same trophic level even if they shared identical thermal optima. In this set, the results regarding species shifts did not change from the main model (Figure S5).

On the question of functional response shape, we originally used a type II functional response, but it led to unrealistically fluctuating dynamics over 10 orders of magnitude in biomass and lower richness. Type III led to the current results where most species' biomass trajectories are stable in the no-warming period, in agreement with previous results (Rall et al. 2008) (line 101). Since we are modelling a food web and the type III functional response generates realistic food web diversity and stability, the current setup is justified.

2. Since species are not shifting range as fast as they would like, there must be a "climate debt". In the initial state, species will on average have a certain distance (in temperature) to the optimum for the search rate temperature preference curve. After climate change, distance must have changed. How much? This quantity would be interesting, because it may even be amenable to empirical test. Calculating this quantity is not a must for publication, but it might strengthen the manuscript.

We thank the reviewer for this suggestion to quantify the distance between optima and centroids after warming, and we agree it is an interesting quantity. Species' optimal temperatures are best quantified as their centroids during the no-warming period, so the lags in shift displayed in Fig. 2 are precisely the distance between the optima and the centroids at the end of warming, otherwise known as the climate debt as the reviewer suggested. This method is superior to comparing the centroids to the search rate preference curve, because metabolic cost increases with temperature such that the optimum temperature for the search rate is not the only physiological factor of importance. The result of these two processes is that the optimal temperature for search is somewhat higher than the species' optimal temperature after accounting for all factors.

3. I find the use "diffusion" formula T3 overly complicated. This formula is just used to relate the diffusivity m to the rate kappa. However, it is much more interesting to know the value of kappa because it directly shows the rate of immigration/emigration. Unless there are strong reasons against it, I would much prefer to see kappa values instead of diffusivities.

This is a helpful suggestion. We have now updated the figure x-axes.

Line 47-48: please explain "biotic resistance" and "enemy release" with a few words.
We have added an improved explanation on lines 48-51.

Line 72. I would call kappa a "rate" and not a "portion".
Thanks for the suggestion. We have updated this to be the dispersal rate.

Eq 1: is the first sum from j=0? I would think it starts from j=1
We use 0 to refer to B_0, the basal resource, and 1-200 refer to the heterotrophic species. It's true the basal resource does not exert predation, so f_{0ix} is understood to be zero.

General notation: Do not use italics for units. Do not use italics for functions (such as "exp"). In many cases equations are in bold, but it does not seem to be needed for notation. It may be a bug in Word, but it must be fixed before copyediting.

Fixed.

Line 80 “Initial biomass” - I think this is irrelevant here.

We need to specify an initial biomass for the basal resource, since it’s dynamic across space and time. We have expanded our explanation to address this issue on lines 92-93.

Line 80-83. Assuming that productivity is constant across temperatures is pretty strong. Why not have a temperature scaling on this parameter, just like for the modelled heterotrophs?

It was a modelling choice to keep the basal resource temperature independent, based on the observation of similar biomass among mesozooplankton across latitude (Moriarty & O’Brien 2013). However, this assumption doesn’t mean that productivity is constant across temperature, since basal production is proportional to its deviation from maximum biomass, which in turn is controlled by temperature-dependent heterotrophs (Table 1 T1). Rather than imposing a temperature dependence on the basal resource in an ad hoc way, we chose to keep the basal resource simple so that the results in the heterotrophs can be easier to attribute to food web features. We have added lines 95-99 to explain our rationale. We also include a suggestion for research moving toward the direction suggested by the reviewer in lines 356-360.

Line 87. I did not quite understand the “off the edges” remark, and that edges are reflective. Do you just mean that kappa is zero at the ends of the x-ranges?
Zero kappa is a good way to explain this. We have added an explanation on line 86.

Line 94: Do you really do Euler integration? If that is really the case, the dynamics of small species may be very badly resolved. Why not use a standard high-quality integrator in matlab for stiff equations, like ode23s? If there are difficulties related to the numerical solution of the model, this should be documented.
Our model was explicitly written in discrete time (Eq. 1), so we are not using an integration method that approximates an underlying continuous dynamic. We not that a daily timestep is also typical in marine ecosystem models like Atlantis (Pethybridge et al. 2019) (added to line 115). If the left-hand side of Eq. 1 were to be replaced by dB/dt, we would expect different dynamics and may require an integration method other than Euler. The two models would only be similar if the right hand side (call it X) is small enough for $\ln(1+X) \sim X$. Judging from the stable trajectories across all sizes during the no warming scenario and the maintenance of diversity across trophic levels before and after warming, we believe the model is one of several possible reasonable representations of food web dynamics. It would be interesting in the future to systematically explore how different food web model structures influence the results.

Line 128. Definition of production. This definition is different from the food-web model definition in line 89. It probably does not matter much but these two definitions must be similar because production are later compared (line 199-201).
In basic single-species ecological models, there are no predators and so there is no production in a predation sense. In the food web context, production is consumption (growth) minus metabolism. To compare the two models, the closest we can get is define a portion of intraspecific competition to equal consumption (line 158-160).

Eq.3. I find the idea of the last quadratic terms with a/c to be a bit convoluted. It would be much easier to simply formulate it as a carrying capacity directly (which is also what is referred to in the text).
Thanks for the suggestion. We attempted rewriting the formula in term of carrying capacity *K*, in which case *a=r/K*. Then, production is:

$$\tilde{P}_{ix} = \tilde{B}_{ix}\left(r_i\omega_{ix} - D_{ix} - \frac{r_i}{cK_i}\tilde{B}_{ix}\right)$$

This formulation requires more terms to explain which part of competition counts toward reproduction, so we think it ends up being less clear than the original form. We have instead added a new streamlined explanation (lines 164-166).

End of methods section: Please spend a few sentences outlining the various size-scalings used.
That is a good suggestion. We have added lines 109-112.

Line 218. I did not understand how predators become more specialist.
P_N controls the portion of potential prey that is inedible for each predator. When $P_N>0$, species become less generalist and more specialist because they can only prey on a smaller subset of potential prey. See lines 270-271.

Fig 1. It is important to show the basal behaviour of the model. However, I did not find this figure very illuminating. First, I would like to see actual simulated food chains from a few connected pacthes. Second, the three panels on the right are too messy to see anything clearly. I urge you to go back to the drawing board and design a nice illustration of the model and the core dynamics.
This is a very nice suggestion, and we have added food web figures as suggested (Figure 1 E-H).

Eq T1. Change "basal biomass" to "basal resource".
Done.

Table 2. Please add units (alpha_D, alpha_l, etc)
These are unitless because they appear in power laws, where the left-hand side is a log value and unitless.

Table 2: F has just units of "per day". Where does this value come from?
Thanks for spotting this. Hernendez-Leon & Ikeda 2005, *J. Plankton Res.* provided the figure of around $0.1gCm^{-2}day^{-1}$ for global mezoplankton respiration. Assuming around a factor of 10 for conversion into wet weight and 200 m column for the given density, we obtain ~$0.01\ gm^3day^{-1}$. Biomass production must be equal to respiration plus predation, so 0.01 is an underestimate. In our chemostatic model, assuming a standing biomass of 1 gm^3 instead of 5 gm^3 (maximum biomass without predation), biomass production is 4x0.0075=0.03, which is our estimate of true production in nature. This information is now added to lines 641-646 and referenced in Table 2.

Supplementary. I would like to see a plot of T15.
This is a nice idea. We now include it as an inset of Fig. 1A.

Code: Great that the code is available. Please provide a description of which scripts to run to do

the figures. Some things in the code seem to be hard-coded for the specific computer setup (like paths). It would be great with a simple script to run just a basic model and provide something like figure 1.
We have updated Readme file and additional scripts on Github to improve their functionality.
Referee: 2

Comments to the Author(s)
Tekwa et al. study how the foodweb context impacts reaction of organisms to climate change-induced ranged shifts. The authors use a mathematical model for this purpose and show, among other aspects, that not taking the foodweb context into account when projecting range shifts may systematically underestimate the negative effects of climate change.

The manuscript is overall well written and of interest to a broad readership. I have only very few comments that the authors can find below.

Main comments:

I think that the manuscript could benefit from including some more discussion of work focusing on communities, such as the work by Jonathan Levine and Jake Alexander, for example, but also some more work by Patrick Thompson. The questions are very much related even if the focus is on communities.
We appreciate the suggestions. We have now added references 16, 17, and 33.

After reading the manuscript and the supplement I am still not quite sure I understand how the "counterfactual" models without trophic interactions were implemented. On page 7 (line 117) the authors write "we fit [the models]". What is meant by "fitting"? Some more explanation could be useful here.
It is worth clarifying what fitting means and what is the purpose of the counterfactual. These models capture the single-species equivalent of species dynamics in food webs, which can then be used to project what would be expected under warming if food web interactions do not change before and after warming. Please see additional explanation in line 141-145, 154-160, 164-166, and 172-173.

Minor points:

l. 83: Why a type III FR and not a simpler function?
Type III is typically used in large food web models because it produces more realistic and stable dynamics as observed in nature (line 101).

l. 178: "wth" should be "with"
Thanks!

l. 307: lack of dispersal-body size relationships. Stevens et al. (2014) Ecology Letters may be a valuable reference here.
Thanks! Added on line 83.

References: Please check homogeneous formatting.
References checked.

Referee: 3

Comments to the Author(s)
Review of Tekwa et al.

Tekwa et al. propose a model that couples trophic interactions with species diffusion to explore how food-webs affect species redistribution under a changing climate. It's definitely an area worthy of exploration, and a worthy effort, but I have strong concerns about the robustness of the study.

Firstly, the authors suggest that dynamic trophic interactions hamper species range shifts, which is definitely plausible. They explain this is likely the case because competition and biotic resistance effects are likely to be stronger than predator release effects.

However, I'm not sure that their model does, or indeed actually can, test potential predator release effects – i.e., is it actually possible for their model to show anything except the result that they find? Specifically, feeding is size-structured, which makes sense, but it also means that a species expanding to a new area can never actually experience predator release since when they move to a new area beyond their 'natural' predators, they will simply be eaten by something else of equivalent size. We can debate the ecological appropriateness or not of this, but in the absence of any opportunity for predator release, the model is bound to find that food-web interactions slow range shifts. So is the model actually able to test the hypotheses that they ascribe potential outcome to?

These are reasonable concerns, though we are confident that this model shows a wide range of behaviors. First, we see some systematic evidence of accelerated shifts among smaller species compared to single-species projections at the trailing edge (Fig. 2D). While this is not predator release, it does show that food web can push some species to shift faster than expected in the absence of food web interactions.

Second, individual species do benefit from warming and escape predation to some degree. We plotted new food web diagrams (Fig. 1E-H) before and after warming for a series of patches. These plots show that some species (e.g., sp.1) do effectively escape from predators as they shift into new patches. Sp. 1 goes from being low biomass in patch 11 before warming to higher biomass in patches 10 and 9 after warming. Also, after warming, in patch 8 Sp. 1 experienced effectively no consumption, having effectively escaped predation.

Third, predator release was even more likely in the sensitivity analysis simulation set in which 20% of the potential prey were inedible (line 190). However, the main results did not change and the same lags persisted for all sizes despite the greater specialization of predators (Fig. S5).

There's also something very, very odd going on with the spatial and temporal scale match-ups in the model (unless a typo or misinterpretation). The patch areas are 471,429 m^2 (Table 2) which is a strange choice (what is the rationale for this?). This means, assuming a square patch (as it is in m^2) that each patch is around 686m in length (or a 470km length patch of 1m width, which is equally odd. There is insufficient information to determine which). Assuming the former, you have a gradient of 20 degrees in temperature across a distance that is less than 20km and supposed to represent the distance from the pole to the equator. Species have a maximum body size of 10^6 grams (i.e. 1,000 kg). Surely a 1,000 kg predator would traverse more than the entire length of the entire gradient (<20km) in a single day to exploit every available resource?

The patch area was stated as $471{,}429^2$ m^2 (note the exponent on the number), so 471,429 m is the length of each side of each square patch (Table 2). This patch size was chosen so that 21 patches stretched from pole to equator (10,000 km divided by 21). We apologize for not explaining these clearly and have added text to clarify on Line 72.

Furthermore, the diffusion rate is identical across species. This seems at the very least extremely unrealistic to have the same diffusion rate for species ranging from 10g to 1000kg – despite what the authors say, there is good evidence that movement rates, home range sizes, and patch sizes relate directly to body size (see e.g., Brown's or Gaston's macroecology books).

It is true that individual movement rates and home range sizes generally increase with body size. Swimming speed within patch, which scales with body size, did enter our search rate equation (Table 1 T12), which increases the maximum search rate for larger predators (Table 1 T9). However, there are important distinctions between foraging movements and movements that lead to range shift. Swimming for foraging is directed towards prey and predators tend to return home or to breeding grounds throughout their life. Swimming speed, therefore, does not factor into dispersal among patches.

Instead, dispersal in our model tracks how biomass of species moves across patches. The mechanism can be understood as either individual movement or offspring movement across patches. In either case, only random movement without a tendency to return home counts toward dispersal. Large species can move and forage farther as adults, but adults tend to return home. The rate of straying to new territories is the dispersal important for range shifting. In addition, both large and small species in the ocean disperse as larvae with similar body sizes. The result is that it is theoretically and empirically unclear whether biomass dispersal experiences a net increase or decrease with adult body size, so our assumption of no relationship is a reasonable place to start.

As supporting evidence, we note that the percent of global species of a certain size found in a sample area has been shown to strongly decrease with size across all lifeforms (e.g., Fenchel & Finlay 2004). This result implies that dispersal might actually decline with increasing body size. A meta-analysis of terrestrial and partly terrestrial organisms shows that across a large size range, size is not a significant predictor of dispersal (Stevens et al. 2014). Even in research suggesting a positive empirical relationship between size and marine dispersal (Bradbury et al. 2008), the relationship is weak and with a genetic correlate, *Fst*, that itself does not correlate well with ecological dispersal because it is strongly influenced by population size. The same paper reports no relationship between size and pelagic larval duration, another dispersal correlate. We have added these references to line 83 addressing this issue.

As the empirical dispersal evidence improves in the future, it will be interesting to incorporate movement variations as a function of size or other environmental factors. As the reviewer suggests later with an IBM approach, a different modelling framework may allow researchers to explore how different adult and offspring movement rates and types affect overall dispersal and range shift. We now include this as a suggestion on lines 362-366.

The authors don't describe (as far as I can tell – apologies if I have missed it) how species biomasses are initially distributed across the grid. There is some information on lines 99-100, but this is unclear as to whether it is identical for each grid cell.

We now clarify that the uniform random initiation was independent for each species and patch (Line 121).

There appears to be no reproduction in the model – a fundamental process. I assume that individuals do not change size (i.e. grow) and reproduce given that it is not an IBM. What are the consequences of this? There is no loss of matter through reproduction nor inefficiency, nor changing body size and vulnerability to predation.

Reproduction of finite individuals was not modelled. Instead, we used a mass-balance approach typical of ecosystem modelling (Loreau 2010). Classic ecological models, including the Lokta-Volterra model, also do not explicitly include reproduction but instead model intrinsic growth rate as the net result of both birth and death effects. Inefficiency leading to a loss of matter as the result of predation and metabolism is present in our model. In particular, consumption efficiency λ was set to either 0.4 or 0.2 (depending on the sensitivity analysis). Because this was not an IBM, we did not model changes to individual size. Given the multi-species focus of the study, we believe the model is nuanced enough to highlight novel effects of food web interactions on range shift. An IBM approach to food web modeling would be fascinating and we would love to address this in the future, but it would be a large task with a very different methodology. An IBM approach would also likely come at a cost to the number of species and the temporal length we could realistically model. Adding these complexities will be interesting future research, which we now mention on lines 357-366.

The thermal performance width for feeding seems extraordinarily narrow (1.25 C). Doesn't this mean that search rates drop off unrealistically fast outside of the optimum? Could the authors include a supplemental plot of the shape of this distribution to examine?

We agree this was hard to understand, and we have rewritten the equation in Table 1 T15 so that the new definition of w_T has the more intuitive meaning of search performance standard deviation. We note that the actual simulations have not changed, simply the way in which we are expressing the terms. w_T is now 0.884, which corresponds to empirical marine estimates of 4.5C for marine thermal niche (Stuart-Smith et al. 2017). See line 704-710 for a detailed explanation.

This parameterization led to average range sizes of 1000-4000 km from low to high dispersal rates (see new Figure S1). Fig. 1A now shows an example of the performance curve.

I would also like to see a greater exploration of the uncertainty in the model results. The authors do some sensitivity tests of parameters, but no formal exploration (as opposed to alternate parameter values) around the incorporation of stochasticity or parameter variations. It would be much better to see confidence bounds, if feasible, and to know which parameters is the model most sensitive to.

For each parameter set, each simulation replicate takes about 12 hours on a core of the best computer cluster available at Rutgers University. A set of 40 replicates across 6 dispersal rates would take 120 computation days, so it has regrettably been infeasible to cover more parameter variations. This is noted on lines 124-126. In our sensitive analyses, we chose parameter values that were considerably different from the main text and informed by the range of empirical values from the literature. From Fig. S5, it appears that the outcomes are especially sensitive to the predator-prey size ratio and the activation energy, yet they did not change the general results that large species shift less than smaller species, and that species in food web tend to shift less than expected if they were not interacting with each other. We would emphasize that it is not the exact amount of lag that is important – we know our model is not a natural system – but rather the trends across size and in comparison to single-species projections that should be robust results. We are confident that the sensitivity tests supported the robustness of the main conclusions.

On the plus side: I like the ideas here. I like the counterfactual model approach very much. I think this is an area worth exploring. But in general, I find that the model appears to make unsupportable assumptions, together with being more constrained in terms of plausible outcomes than is at first apparent.

Thank you, and we hope we have addressed your concerns about the model's robustness.

Appendix B

Associate Editor
Comments to Author:
The authors provided an extensively revised manuscript that was seen again by the original reviewers. These agreed that the manuscript is much improved, but also that some further revisions are needed. In particular, direct responses to some important points. A more direct reply to the concern regarding lack of predator release is needed, perhaps some assessment of how effectively the sensitivity set with 20% inedible prey mimics this, and a consideration whether any additional models could address this more directly. Moreover, I request the authors consider what level of sensitivity analysis could be included, even if the full complement of possibilities cannot be accommodated, a limited subset that is most relevant or important might be feasible. If so, this would enhance the manuscript strength and ability to convince readers; a simple comment on how long the analyses take is not fully adequate. If no sensible subset can be identified, then a more detailed mention/discussion should be added of why the sensitivity analyses that were done are sufficient. In addition, it would be useful if some of the supporting arguments made about size-independent dispersal in the reply to referee could be added in the manuscript (e.g. at line 83) such that readers are better alerted to this assumption. Finally, some tidying up of details is needed and I would request to remove the word 'greatly' from l. 25 – as the authors acknowledge this model does not mimic reality, rather highlights a pattern, so how great the overestimation is, is not really clear?

Thank you for highlighting the areas where sensitivity analyses would be most helpful. We have added simulations with 10% to 50% of prey being inedible and now discuss this in the context of predator release (see Figure S7, lines 195-196, 284-286, 310-314). Beyond this level, food webs tended to collapse due to a lack of edible prey. We also added a simulation set using a swim speed scaling law to generate size-dependent dispersal (derived in Appendix A). These results are now shown in Figure S8 and discussed (Appendix A, Eq. A1&2, lines 376-377), confirming that the shift patterns are robust to parameter variations. We acknowledge that the sheer number of possibilities initially made it unclear which sensitivity test would be useful. Computation time has also decreased since the initial submission, with estimated runtime now being updated (line 128-130). The reviews helped identify the most important parameters to test, which we addressed with four new sensitivity analyses (Figures S4-8). We believe the manuscript was strengthened as a result. We have also added a more detailed explanation of the reasons for a base model with no size-dispersal relationship (lines 84-89). We have removed 'greatly.'

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).
The revision adequately addressed my previous concerns. I have only minor issues:

Eq 1: The term after the first equality sign makes it clear that the model is a discrete time model. However, it misses that one still needs to divide by Delta t. (I know the time step is one day, but since the equation is agnostic to units at this stage the Delta t must be in the dominator). What does the tildes above B signify? Explain or remove. The tildes appear again in the single-species model; why?

Thank you for noticing this. We have now added Δt in the denominator. In addition, the tilde should not appear in Eq. 1 (and is now removed), but it should be retained in Eq. 2 and 3. Biomass labelled with tilde is from the single-species counterfactual model in order to distinguish it from the food web version (lines 159-160). To further clarify the differences, we have added Figure S2 to compare the food web outcomes with the counterfactual fit. This seems more helpful in explaining the single-species fit than the previous two supplementary figures on shift outcomes for different *c* values (tuning parameter in the single species model).

Line 83-84: Add units to kappa.
We now clarify that the units are day^{-1} (line 81).

T2. This is not a dimensionally consistent. If nu has units m^3/day/g then the 2nd term in the denominator has a dimension (and it should be dimensionless when added to "1"). For it to be dimensionally correct nu has to have dimensions m^3/day/g^2.

Thank you for pointing out the unit discrepancy, and we have revised accordingly. The search rate v in a type III functional response is most easily understood in relation to its counterpart in a type II functional response. v in type III is v_2/B_r in a type II, where v_2 is a constant search rate [$m^3 day^{-1} g^{-1}$] and B_r is the reference prey density where $v=v_2$. This relationship is based on Rosenbaum & Rall 2018 *Methods Ecol Evol*'s observation that v is a density dependent version of v_2, with the unit of $m^6 day^{-1} g^{-2}$). We assumed B_r is the characteristic value $1 gm^{-3}$ that achieved similar functional responses for Type II and III, allowing us to use the more commonly measured v_2 in the type III context (see Appendix T6 explanation). We have renamed T9 and corrected T6 in Table 1.

T11 + T15. "exp" and "erf" should not be in italics

These have been fixed.

Previous comment: "Table 2. Please add units (alpha_D, alpha_l, etc)
These are unitless because they appear in power laws, where the left-hand side is a log value and unitless."

No, they are not unitless. Just because a dimensional quantity is in a log or exp function does not remove its unit. See for example T4. The first term is C_W->d with dimensions 1/day/energy. D on the left side has dimensions 1/day. Therefore the exponential term must have dimensions of energy. Then alpha_D must have units ln(1/sJ). An so forth for the other quantities.

We understand it is possible to assign units to parts of the arguments in log or exp functions, so long as they are divided by a quantity 1 with the same unit (the characteristic value). The result is a dimensionless quantity. We have followed the convention in ecology and physics to keep arguments dimensionless (Legendre & Legendre 2012, Dimensional analysis in ecology, pp 109-142 in Developments in Environmental Modelling).

The exponential term mentioned is implicitly multiplied by the characteristic value with unit [J/s], which follows from Eq. 4 of Brown 2004, *Ecology*. We added a note on this in Appendix A under T4. All other exponential terms in the paper were dimensionless and did not require characteristic values.

There are still a lot of bold-face in the tables which I believe should not be present.

We have gone over these again to make sure only those parameters that were varied (as explained in the captions) were bolded.

Referee: 2

Comments to the Author(s).
I have reviewed this manuscript previously and the authors have addressed all of my comments.

Thank you.

Referee: 3

Comments to the Author(s).
Thank you to the authors for their responses. However, I find some of their responses disappointing.

In particular, the response to providing a more formal exploration of parameters, ideally to derive confidence bounds, but certainly to get a better sense of robustness and sensitivity, boils down to 'it is too computationally expensive'. However, when cloud computing is becoming ever cheaper and easier, I find that hard to reconcile, when understanding sensitivity is so important. Did they actually run any additional sensitivity analyses (in comparison to the initial submission) for their revision, or just write it off as too difficult?

We have added four new sensitivity analyses on predator-prey size ratio, activation energy, percent prey inedible, and size-dependent dispersal, in addition to the five previous parameter variations (Figures S4-S8). Please see detailed explanations in the following paragraphs.

The response to questions about predator release were unconvincing. They do not directly answer the question of whether the model is actually able to test the hypotheses that they ascribe the potential outcome to - i.e. is it possible for their model to show anything except the results that they find? I would have appreciated a direct answer to this question.

This is an important point, and we have responded in two ways. First, our model is capable of testing predator release despite all predators being capable of eating all prey in the baseline model. Predators are often the first to decline when a food web is exposed to warming, releasing their prey from predation (e.g., Petchey et al. 1999 Nature). This process does not depend on predators being specialists (lines 51-53).

Second, we have added new simulation sets with up to 50% of potential prey inedible to test this idea directly. With more inedible prey, prey are more likely to escape their predators when they shift, independent of any declines in predator biomass (lines 195-196). In these new simulations, we find that the rate of leading-edge shift increases with a greater proportion of inedible prey, as predicted by a predator release phenomenon (Figure S7C). This attests to the model's ability to incorporate greater enemy release strengths (lines 284-285, 310-314). Nevertheless, these sensitivity tests also continue to support the main conclusions that all species experience lagged shifts in food webs, and larger species lag in centroid and trailing edge shifts more than smaller species.

Their response to the question of differing diffusion rates among species was also unconvincing. They say that 'both large and small species in the ocean disperse as larvae with similar body sizes'. This is not true; there are plenty of (especially larger) species in the ocean that bear live young and so clearly do not disperse as larvae. Here I am compelled to give them the benefit of the doubt for the modelling, but nonetheless it is lax to make such generalizations.

We have added further explanations for the assumption of no relationship (lines 84-89). In addition, we have also incorporated a simulation set where dispersal increases with size according to empirical swim speed relationships (lines 194, Appendix A, Eq. A1&2). We observed no major changes to shift patterns in this new sensitivity analysis (Figure S8, lines 376-377).

I still think the ideas in here are interesting and worth exploring. But I remain somewhat troubled by the limited attempts to directly respond to the points that I raised.

We hope that the new responses and sensitivity analyses address these concerns.

Appendix C

Response to Referees for
Body-size and food-web interactions mediate species range shifts under warming
Edward Tekwa, James Watson, Malin Pinsky
RSPB-2021-2755.R1

Associate Editor:
Board Member: 1
Comments to Author:
This is the second revision of this manuscript, and here the authors have now addressed all reviewer comments. The manuscript is now much improved and the additional simulations increase confidence and now it is clearer how robust the conclusions are to variations in parameters/assumptions. One point made in the response letter ('Beyond this level, food webs tended to collapse due to a lack of edible prey.'), further strengthens the breadth of the sensitivity analyses- perhaps the authors could add this information in the manuscript, around l. 195-196 perhaps.
Thank you! A sentence is added to explain this collapse (line 194).

A few minor textual matters remain which will take a few minutes to fix, but are worth doing to improve readability (as it is a complex manuscript). Specifically,
l. 52: 'larger' – it is not clear why here prey is larger, how is this juxtaposed to 'prey that escape traditional predators'? Is there an argument missing? Please clarify this sentence (l. 50-53).
The word 'they' was confusing. We now explicitly reference 'small prey' or 'larger predators' in the explanation (lines 51-52).

l. 88: please indicate here where the sensitivity test can be found, e.g. add (see below, Supplementary Appendix A)?
Added reference to sensitivity test detail (lines 88-89).

l. 127-130: this detail seems superfluous, please delete
Deleted.

l. 214: replace 'higher' with 'larger'
Replaced (line 211).

l. 216: something wrong with this sentence, 'shifted' should be 'shifts' perhaps? Maybe also once place (isotherm shifts) after thermal shifts, to more clearly link the text here to the terms used in the figure
'Shifts' is correct (line 213).