

Predicting population responses to environmental change from individual-level mechanisms: towards a standardized mechanistic approach

A. S. A. Johnston, R. J. Boyd, J. Watson, A. Paul, L. C. Evans, E. L. Gardner and V. L. Boulton

Article citation details

Proc. R. Soc. B **286**: 20191916.
<http://dx.doi.org/10.1098/rspb.2019.1916>

Review timeline

Original submission: 24 May 2019
1st revised submission: 16 August 2019
2nd revised submission: 25 September 2019
Final acceptance: 25 September 2019

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

Review History

RSPB-2019-1206.R0 (Original submission)

Review form: Reviewer 1

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?

Excellent

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?

N/A

Is it clear?

N/A

Is it adequate?

N/A

Do you have any ethical concerns with this paper?

No

Comments to the Author

I totally concur with the authors that there is a great need for an integrated approach that links individual mechanisms (physiology and behaviour) to population dynamics in spatially explicit landscapes. I wish I would have the tools to do so. I find this review very timely and urgent as we are now at a moment where lots of different tools are available, but we need reflection on how to proceed. This is exactly where this review comes into play. Several questions, however, came to mind when I was reading the manuscript:

1. Combinations of submodels (or modules). The authors propose we should develop mechanistic submodels and to have a toolkit of standardised mechanistic submodels available that can be added onto larger (correlative) frameworks as needed. However, does this not assume that submodels operate independently? What if the functioning of one submodel (e.g. physiology) depends on another submodel (e.g. behaviour)? I like the idea of starting off with a simple framework comprising correlations that is then made more mechanistically by adding mechanistic submodels, but it does assume that there are no interactions between these submodels. I think this is something to be cautious off.

2. The role of evolution. I realise this manuscript is focusing on the ecological aspects of population models (although genetics is mentioned occasionally, e.g. L 109, 242-244), but population responses to novel environmental conditions will most likely also involve an evolutionary response, like a shift in the distribution of a heritable trait. In fact, eco-evolutionary population dynamics is very likely to occur when births and deaths within a population result in the re-assortment of existing genetic and phenotypic variation (micro-evolutionary change), which can be accompanied by an instantaneous change in population size or growth rate (ecological change) (Smallegange & Coulson 2013, Trends Ecol Evol 28: 143-148).

I therefore do not completely agree with the conclusion (L376) that “predictive population

models are needed to better anticipate, and mitigate, the ecological consequences of future environmental changes". We also need to understand the eco-evolutionary consequences. Perhaps for some species the role of evolution can be neglected on the explored time scales, but I would not go as far to say that predictive models should focus on the ecological consequences only. I would strongly advise to acknowledge in the ms that eco-evolutionary responses to environmental change are very likely to occur and need to be understood. Particularly since the ms touches upon models (e.g. IPMs) that are explicitly used to study eco-evolutionary dynamics.

Perhaps the role of evolution could be explored as a sub-model, or by considering demographic models that explicitly include genetics: e.g. de Vries & Caswell 2019 in case of MPMs (Am Nat. 2019: 193:545-559), and Coulson et al. 2017 in case of IPMs (Am Nat 2017: 190).

3. Terminology regarding statistical functions. Various of the models discussed (e.g. MPMs, IPMs, SDMs) include statistical relationships that, I think, are comparable in structure. If this is the case, the ms would benefit from consistent terminology. E.g. in L95 it's 'empirically derived functions', in L 100 it's 'phenomenological regression functions', and in L 118 it's 'statistical relationships'. It would help the reader who is less familiar with these different model types to understand why they are phenomenological and not mechanistic.

Other comments:

- L. 97: data inputs: is the intrinsic population growth rate not better described as a model output? I don't understand why this is a data input.

- L. 111: The mechanistic IPM (reference 16: Smallegange et al. 2017) has recently been validated with independent data by Smallegange & Ens (2018: J. Anim. Ecol. 87: 893-905).

- Individual variation: you could argue that IPMs (both phenomenological and mechanistic) account for individual variation. Implicitly underlying the IPMs is a stochastic, IBM, in which individuals follow Markovian growth trajectories that depend on an individual's current state (Easterling, Ellner & Dixon 2000). This individual variability is in standard IPMs modelled using a probability distribution, typically Gaussian, where the mean length and variability (model residuals) are regression functions of length (Easterling, Ellner & Dixon 2000). In mechanistic IPMs, this variability arises from how individuals experience the environment (Smallegange et al. 2017).

- The manuscript is focused on data-based population models. Physiological structured population models (PSPMs) are not mentioned, for example. PSPMs are more abstract and mathematically quite challenging, and I was wondering if you on purpose focused on more data-driven approaches.

Review form: Reviewer 2

Recommendation

Reject – article is scientifically unsound

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

Marginal

General interest: Is the paper of sufficient general interest?

Acceptable

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

Marginal

Is the length of the paper justified?

No

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?

N/A

Is it clear?

N/A

Is it adequate?

N/A

Do you have any ethical concerns with this paper?

No

Comments to the Author

I am happy for all my comments to the editor to go to the authors.

Decision letter (RSPB-2019-1206.R0)

28-Jun-2019

Dear Dr Johnston:

I am writing to inform you that your manuscript RSPB-2019-1206 entitled "Predicting population responses to environmental change from individual-level mechanisms" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees who, although they gave different recommendations (one of major revision, one of outright rejection), actually make similar points. These are that, although the ms starts very well and sets up the need for an integrative approach, the follow-through is doesn't deliver. The referees' comments are detailed (most of referee 2's being on the pdf itself) and I think it might be possible to achieve your original goals with a major rewrite. With this in mind we would be willing to consider a resubmission, provided the

comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

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.

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.

Yours, with best wishes,

Innes

Prof. Innes Cuthill
Reviews Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

I totally concur with the authors that there is a great need for an integrated approach that links individual mechanisms (physiology and behaviour) to population dynamics in spatially explicit landscapes. I wish I would have the tools to do so. I find this review very timely and urgent as we are now at a moment where lots of different tools are available, but we need reflection on how to proceed. This is exactly where this review comes into play. Several questions, however, came to mind when I was reading the manuscript:

1. Combinations of submodels (or modules). The authors propose we should develop mechanistic submodels and to have a toolkit of standardised mechanistic submodels available that can be added onto larger (correlative) frameworks as needed. However, does this not assume that submodels operate independently? What if the functioning of one submodel (e.g. physiology) depends on another submodel (e.g. behaviour)? I like the idea of starting off with a simple framework comprising correlations that is then made more mechanistically by adding mechanistic submodels, but it does assume that there are no interactions between these submodels. I think this is something to be cautious off.

2. The role of evolution. I realise this manuscript is focusing on the ecological aspects of population models (although genetics is mentioned occasionally, e.g. L 109, 242-244), but population responses to novel environmental conditions will most likely also involve an evolutionary response, like a shift in the distribution of a heritable trait. In fact, eco-evolutionary population dynamics is very likely to occur when births and deaths within a population result in the re-assortment of existing genetic and phenotypic variation (micro-evolutionary change), which can be accompanied by an instantaneous change in population size or growth rate (ecological change) (Smallegange & Coulson 2013, *Trends Ecol Evol* 28: 143-148).

I therefore do not completely agree with the conclusion (L376) that “predictive population models are needed to better anticipate, and mitigate, the ecological consequences of future environmental changes”. We also need to understand the eco-evolutionary consequences. Perhaps for some species the role of evolution can be neglected on the explored time scales, but I would not go as far to say that predictive models should focus on the ecological consequences only. I would strongly advise to acknowledge in the ms that eco-evolutionary responses to environmental change are very likely to occur and need to be understood. Particularly since the ms touches upon models (e.g. IPMs) that are explicitly used to study eco-evolutionary dynamics.

Perhaps the role of evolution could be explored as a sub-model, or by considering demographic models that explicitly include genetics: e.g. de Vries & Caswell 2019 in case of MPMs (*Am Nat.* 2019: 193:545-559), and Coulson et al. 2017 in case of IPMs (*Am Nat* 2017: 190).

3. Terminology regarding statistical functions. Various of the models discussed (e.g. MPMs, IPMs, SDMs) include statistical relationships that, I think, are comparable in structure. If this is the case, the ms would benefit from consistent terminology. E.g. in L95 it's ‘empirically derived functions’, in L 100 it's ‘phenomenological regression functions’, and in L 118 it's ‘statistical relationships’. It would help the reader who is less familiar with these different model types to understand why they are phenomenological and not mechanistic.

Other comments:

- L. 97: data inputs: is the intrinsic population growth rate not better described as a model output? I don't understand why this is a data input.

- L. 111: The mechanistic IPM (reference 16: Smallegange et al. 2017) has recently been validated with independent data by Smallegange & Ens (2018: *J. Anim. Ecol.* 87: 893-905).

- Individual variation: you could argue that IPMs (both phenomenological and mechanistic) account for individual variation. Implicitly underlying the IPMs is a stochastic, IBM, in which individuals follow Markovian growth trajectories that depend on an individual's current state (Easterling, Ellner & Dixon 2000). This individual variability is in standard IPMs modelled using a probability distribution, typically Gaussian, where the mean length and variability (model residuals) are regression functions of length (Easterling, Ellner & Dixon 2000). In mechanistic IPMs, this variability arises from how individuals experience the environment (Smallegange et al. 2017).

- The manuscript is focused on data-based population models. Physiological structured population models (PSPMs) are not mentioned, for example. PSPMs are more abstract and mathematically quite challenging, and I was wondering if you on purpose focused on more data-driven approaches.

Referee: 2

Comments to the Author(s)

I am happy for all my comments to the editor to go to the authors - see attached.

Author's Response to Decision Letter for (RSPB-2019-1206.R0)

See Appendix A.

RSPB-2019-1916.R0

Review form: Reviewer 1

Recommendation

Accept with minor revision (please list 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?

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?

N/A

Is it clear?

N/A

Is it adequate?

N/A

Do you have any ethical concerns with this paper?

No

Comments to the Author

Dear authors,

I was one of the previous reviewers that assessed your manuscript. I was pleased to see that you have taken on board my comments regarding eco-evolutionary dynamics and the integrated approach. I find this review very timely and urgent as we are now at a moment where lots of different tools are available, but we need reflection on how to proceed.

Some small comments I still have are:

- Abstract: the first sentence seems to suggest that plants do not matter in global diversity. Perhaps starting the sentence with 'animal populations' instead of 'global biodiversity' would solve this.
- L41: "An urgent challenge in ecology". Given that you now also discuss evolution and eco-evolutionary dynamics, I would rephrase this as "An urgent challenge in biology".
- L410-415: efforts to coordinate standardized energy budget models is the open access database Add-my-Pet: https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/. Refer to the Add-my-Pet collection as: Add-my-Pet, online database of DEB parameters, implied properties and referenced underlying data, [bio.vu.nl/thb/deb/deblab/add_my_pet/](https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/). Last accessed: yyyy/mm/dd.

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

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?

N/A

Is it clear?

N/A

Is it adequate?

N/A

Do you have any ethical concerns with this paper?

No

Comments to the Author

As above for the Editor - minus the comment about Figure 1.

Decision letter (RSPB-2019-1916.R0)

24-Sep-2019

Dear Dr Johnston

I am pleased to inform you that your manuscript RSPB-2019-1916 entitled "Predicting population responses to environmental change from individual-level mechanisms: towards a standardised mechanistic approach" has been accepted for publication in Proceedings B.

The referees are very happy with your revisions and have recommended publication, but reviewer 1 also suggests some final minor tweaks. 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=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document%20not%20available)) 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.

Best wishes, and thanks again for an excellent paper,

Innes

Prof. Innes Cuthill
Reviews Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
Dear authors,

I was one of the previous reviewers that assessed your manuscript. I was pleased to see that you have taken on board my comments regarding eco-evolutionary dynamics and the integrated approach. I find this review very timely and urgent as we are now at a moment where lots of different tools are available, but we need reflection on how to proceed.

Some small comments I still have are:

- Abstract: the first sentence seems to suggest that plants do not matter in global diversity. Perhaps starting the sentence with 'animal populations' instead of 'global biodiversity' would solve this.
- L41: "An urgent challenge in ecology". Given that you now also discuss evolution and eco-evolutionary dynamics, I would rephrase this as "An urgent challenge in biology".
- L410-415: efforts to coordinate standardized energy budget models is the open access database Add-my-Pet: https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/. Refer to the Add-my-Pet collection as: Add-my-Pet, online database of DEB parameters, implied properties and referenced underlying data, [bio.vu.nl/thb/deb/deblab/add_my_pet/](https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/). Last accessed: yyyy/mm/dd.

Referee: 2

Comments to the Author(s)

The paper is much improved, with respect to comments from both reviewers. It reads much better as a consequence of the structural changes, and changes within the individual sections have made it much less confusing to readers.

Overall though, I think it is now suitable for publication in Proc B, and I thank the authors for their amendments.

Author's Response to Decision Letter for (RSPB-2019-1916.R0)

See Appendix B.

Decision letter (RSPB-2019-1916.R1)

25-Sep-2019

Dear Dr Johnston

I am pleased to inform you that your manuscript entitled "Predicting population responses to environmental change from individual-level mechanisms: towards a standardised mechanistic approach" 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 during this period, 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.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

Your article has been estimated as being 10 pages long. Our Production Office will be able to confirm the exact length at proof stage.

Open access

You are invited to opt for open access via our author pays publishing model. Payment of open access fees will enable your article to be made freely available via the Royal Society website as soon as it is ready for publication. For more information about open access publishing please visit our website at http://royalsocietypublishing.org/site/authors/open_access.xhtml.

The open access fee is £1,700 per article (plus VAT for authors within the EU). If you wish to opt for open access then please let us know as soon as possible.

Paper charges

An e-mail request for payment of any related charges will be sent out shortly. The preferred payment method is by credit card; however, other payment options are available.

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.

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

Response to Reviewers

Thank you to both reviewers for their feedback, suggestions and raising important concerns. The two reviews raised quite different concerns, and in this revision we have tried to strike a balance between them.

Reviewer 1 reasoned that evolution is necessary to predict population responses under environmental change (we agree) and suggested that combining existing approaches is complicated by interactions between submodels (we also agree, thank you for this insight). Our major revisions in response are to consider evolution as an additional mechanism throughout and we replace use of the term 'integrated approach' with 'standardised mechanistic approach', as this is the real focus of the paper. Within the context of the standardised mechanistic approach we suggest that mechanisms should be interlinked.

Reviewer 2 was concerned about the feasibility of an 'integrated approach' and issues surrounding data availability. We hope that the scope of the paper has been clarified by suggesting the need for a 'standardised mechanistic approach' rather than an 'integrated approach'. Our hope is that other researchers will collaborate across the different approaches to drive progress in developing and testing the methodology – which is outside of the scope of this paper. We have also restructured the manuscript to first deal with individual-level mechanisms before population approaches, and then the need for a standardised mechanistic approach, quantitative submodels and discussion of current limitations. We include data availability as a major topic in the discussion.

Revisions to the previous manuscript have been substantial, and so rather than submitting a chaotic 'tracked changes' document, we have highlighted the text that has changed in blue.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

I totally concur with the authors that there is a great need for an integrated approach that links individual mechanisms (physiology and behaviour) to population dynamics in spatially explicit landscapes. I wish I would have the tools to do so. I find this review very timely and urgent as we are now at a moment where lots of different tools are available, but we need reflection on how to proceed. This is exactly where this review comes into play. Several questions, however, came to mind when I was reading the manuscript:

>> Thank you for raising these important questions, we agree that they are all important and need to be considered in this review. As such, our revised manuscript considers the importance of evolution as an individual mechanism throughout (L 95-104; L 347 – 379) and focuses on a 'standardised mechanistic approach' in which mechanisms do interact (L 247 – 262 and Figure 1). All other suggestions are addressed below.

1. Combinations of submodels (or modules). The authors propose we should develop mechanistic submodels and to have a toolkit of standardised mechanistic submodels available that can be added onto larger (correlative) frameworks as needed. However, does this not assume that submodels operate independently? What if the functioning of one submodel (e.g. physiology) depends on another submodel (e.g. behaviour)? I like the idea of starting off with a simple framework comprising correlations that is then made more mechanistically by adding mechanistic submodels, but it does assume that there are no

interactions between these submodels. I think this is something to be cautious off.

>> Thank you for your insight here, we have considered this in detail and believe that it would be difficult to simply add mechanistic submodels to correlative frameworks. It could also prevent models from becoming mechanistic if the remaining correlations disguise other important mechanisms and interactions. We therefore avoid the use of an 'integrated approach' as this was not the intended focus of the paper but rather a suggestion in the previous manuscripts discussion. We believe that the manuscript has been much improved by re-focusing on the need for a 'standardised mechanistic approach' which does consider the interactions between submodels (L 247 – 262).

2. The role of evolution. I realise this manuscript is focusing on the ecological aspects of population models (although genetics is mentioned occasionally, e.g. L 109, 242-244), but population responses to novel environmental conditions will most likely also involve an evolutionary response, like a shift in the distribution of a heritable trait. In fact, eco-evolutionary population dynamics is very likely to occur when births and deaths within a population result in the re-assortment of existing genetic and phenotypic variation (micro-evolutionary change), which can be accompanied by an instantaneous change in population size or growth rate (ecological change) (Smallegange & Coulson 2013, Trends Ecol Evol 28: 143-148).

We agree that the topic of novel environmental change does necessitate integration of evolution as a mechanism. In this revision we discuss the role of evolution throughout (L 95-104; L 347 – 379).

I therefore do not completely agree with the conclusion (L376) that “predictive population models are needed to better anticipate, and mitigate, the ecological consequences of future environmental changes”. We also need to understand the eco-evolutionary consequences. Perhaps for some species the role of evolution can be neglected on the explored time scales, but I would not go as far to say that predictive models should focus on the ecological consequences only. I would strongly advise to acknowledge in the ms that eco-evolutionary responses to environmental change are very likely to occur and need to be understood. Particularly since the ms touches upon models (e.g. IPMs) that are explicitly used to study eco-evolutionary dynamics.

>> Agreed. As mentioned in the previous response, we now integrate evolution throughout, and include 'Evolution' as an additional column in Table 1.

Perhaps the role of evolution could be explored as a sub-model, or by considering demographic models that explicitly include genetics: e.g. de Vries & Caswell 2019 in case of MPMs (Am Nat. 2019: 193:545-559), and Coulson et al. 2017 in case of IPMs (Am Nat 2017: 190).

>> Thank you for these suggestions, we now give an overview of current approaches to modelling evolutionary processes (e.g. L 347 – 379).

3. Terminology regarding statistical functions. Various of the models discussed (e.g. MPMs, IPMs, SDMs) include statistical relationships that, I think, are comparable in structure. If this is the case, the ms would benefit from consistent terminology. E.g. in L95 it's 'empirically derived functions', in L 100 it's 'phenomenological regression functions', and in L 118 it's 'statistical relationships'. It would help the reader who is less familiar with these different model types to understand why they are phenomenological and not mechanistic.

>> Thank you for pointing out these inconsistencies, we agree that the previous MS was not very accessible to non-modellers due to the use of such terminology – we now stick to 'statistical relationships' throughout (e.g. L 140, 170, 206).

Other comments:

- L. 97: data inputs: is the intrinsic population growth rate not better described as a model output? I don't understand why this is a data input.

>> Removed (we originally meant abundance without competition). We now discuss the need to parameterise MPMs for multiple scenarios instead (L 146 – 149).

- L. 111: The mechanistic IPM (reference 16: Smallegange et al. 2017) has recently been validated with independent data by Smallegange & Ens (2018: J. Anim. Ecol. 87: 893-905).

>> Thank you, we were not aware of the recent study and now include the validation reference in the MS (L 155).

- Individual variation: you could argue that IPMs (both phenomenological and mechanistic) account for individual variation. Implicitly underlying the IPMs is a stochastic, IBM, in which individuals follow Markovian growth trajectories that depend on an individual's current state (Easterling, Ellner & Dixon 2000). This individual variability is in standard IPMs modelled using a probability distribution, typically Gaussian, where the mean length and variability (model residuals) are regression functions of length (Easterling, Ellner & Dixon 2000). In mechanistic IPMs, this variability arises from how individuals experience the environment (Smallegange et al. 2017).

>> Thank you for highlighting how IPMs account for individual variation, we now discuss this in the MS (L 135 – 137) and change the 'Individuals' column in Table 1 to 'Individual variation' to show that mechanistic versions of the main population modelling approaches we review can account for individual variation.

- The manuscript is focused on data-based population models. Physiological structured population models (PSPMs) are not mentioned, for example. PSPMs are more abstract and mathematically quite challenging, and I was wondering if you on purpose focused on more data-driven approaches.

>> We were not formerly aware of PSPMs, and the major focus of this review is on commonly used approaches in population modelling (from an ecological perspective). We now clarify the selection criteria (L 121 – 126).

Referee: 2

Comments to the Author(s)

I am happy for all my comments to the editor to go to the authors - see attached.

>> Thank you for your detailed comments and suggestions. In particular, your review has encouraged a major re-structuring of the manuscript so that key issues are discussed before more specific modelling approaches. The relative benefits of each modelling approach are also discussed in more detail, and we emphasise that our focus is not on providing a detailed account of each but to investigate their ability to integrate individual mechanisms. We have also re-focused the paper on a 'standardised mechanistic approach' rather than an 'integrated approach' as the latter would, as you suggest, be complicated by ecological scales. A standardised mechanistic approach, on the other hand, could be used within any of the existing modelling frameworks discussed. We have also endeavoured to write more concisely in each section so that more detail and references can be provided. However, we have also had to take the journals word limit into account. We have copied your responses from comment format, and respond to each, below.

L38: 'selective nature' should be better defined, as this is a key concept for your argument

>> No change – we believe that the rest of the introduction covers how species responses are site and stressor-specific.

L39: What do you mean by ecological cascades here? Use of the word 'cascade' implies trophic cascades to many readers, which will not necessarily follow on from environmental stressors.

>> Removed – we agree that the use of cascades here is confusing.

L45: I would argue the complexity is real, not perceived! I would also argue that it is not the complexity of the challenge that has held back advancement, but rather a lack of data for model parameterisation and validation.

>> We agree that the complexity is real, and perceived is removed here. We replace this with 'The urgency of understanding this complexity...' (L 46).

L55: the examples you cite following this statement do not indicate the nature of the combined stressors - eg additive etc. See Crain et al 2008 Ecology Letters 11:1304-1315 for a review

>> Thank you for the review information, this reference is included directly after this statement to direct the reader to a more detailed study (L 56). However, the remainder of the paragraph aims to showcase how interactive effects of stressors can be important compared to single stressor studies, rather than talking about specific additive or antagonistic examples.

L72: You should explain how you chose these approaches to focus on, or the rationale behind only considering these methods

>> We clarify that the approaches considered in this review are the most commonly used in predicting population responses to environmental changes (L 121 – 126).

L84: Do you mean 'using population models to make and test predictions' - because you can argue that all population models are predictive?

>> We agree that predictive is ambiguous, particularly in relation to population models, and replace this term throughout with 'mechanistic'.

L85: again, more information on how or why you chose these approaches over others that are used

>> We are unsure which other approaches the reviewer is referring to here.

L94: All of the modelling approaches you discuss should have clear definitions when first mentioned. Often the same name can be used to describe several approaches, and I have been unclear in several places as to exactly what methodology you are discussing.

>> We agree that more detail is needed for each approach and attempt to do so throughout the population modelling section (L 128 – 244).

L97: I don't think the intrinsic population growth rate would be considered as a 'data input' - indeed, how would you ever obtain empirical data to define this? Rather it is a parameter in the model that is estimated from other, relevant data such as abundance counts.

>> Agree that the wording here is not correct and has been removed. We now discuss the need to parameterise MPMs for multiple scenarios instead (L 146 – 149).

L100: This should be defined, many readers will now know what 'phenomenological regression models' are

>> We have made such terms consistent throughout by referring to 'statistical relationships'.

L111: This is pretty vague - do you mean that the independent data is lacking for model validation? If so, this is an important point, and should be set out in the discussion of the usefulness of the approach.

>> Data availability is now discussed as a key issue (390 – 428).

L114: There are only 3 citations for this entire section, and yet there are a wealth of examples and reviews that could be called upon here to more fully inform the reader, and your arguments. I think it is also important to recognise the history of the development of these models, and what they were originally designed for. This goes a long way to inform why the different approaches have evolved to consider different mechanisms and different scales, and may also offer a way forwards in terms of a framework for bringing disparate methods together into a more cohesive modelling framework.

>> We have added more detail and references throughout the population modelling section. Given the journals word limit and scope of the paper, there is a need to prioritize representative citations.

L129: citations for this?

>> Relevant citation is already given on Line 185.

L138: it is not clear why the distinction between stage or age based parameterisation matters in relation to the previous point?

>> Removed.

L139: again, there are only 5 citations for this section...this really limits the ability of the reader to flesh out your arguments and develop a full appreciation for the limitations and advantages of the different approaches

>> Additional relevant citations have been provided throughout.

L143: but you haven't mentioned dispersal as a limitation in the previous section

>> We now mention the lack of behavioural mechanisms in SDMs (L 200 – 201).

L144: hierarchical Bayesian methods can be used for all of the approaches you have mentioned, it is not specific to range models, and so the advantages it conveys (accounting for multiple scales, prior information and proper accounting of uncertainty) also apply to all the other methods.

>> Agree and exclude here as not relevant to the focus of the paper.

L149: why did they improve predictions? More detail/context needed to bring the reader along with you.

>> We do in the next sentence: “These ‘mechanistic’ IBMs are better able to make predictions outside of the range of environmental conditions for which they were parameterised because the individual-level mechanisms remain unchanged across scenarios.” (L241 – 244).

L153: again only 2 citations for this section, there are many, many more examples in the literature.

>> Again, we are unable to provide extensive detail on each section because of the overall scope of the paper and word limit of the journal. The two references provided also give a comprehensive overview of this relatively new approach and after searching the literature again they are the most representative.

L164: if you are going to mention a specific method such as this (Lagrangian) then you should explain what it is and how it works. Why does it matter?

>> Excluded, as preceding text describes why it matters.

L177: Can you elaborate on why these models are better? Is it because they operate at the scale of the individuals, or because they capture fundamental relationships across species and environmental variables?

>> We do in the preceding text by explaining that many IBMs are not ‘better’, but those which use the individual-level scale to integrate mechanisms provide predictions outside of their range of parameterisation – so it is a combination of both (L238 – 244)

Table 1: why are there so few citations in this table? you seem to have a very selective set of examples, but have not described how you decided upon these approaches.

>> We have added more examples to Table 1.

Table 1, MPMs/Spatially explicit: they can be if a metapopulation is assumed

>> Our focus in this review is not on metapopulations, as individual mechanisms are then ignored.

L180: why is this concept being introduced here? You have already discussed it in several of the previous sections, so it would be better placed at the start of the paper?

>> We have restructured the paper to better explain the importance of mechanisms and the focus of this review (82 – 115), before reviewing existing population modelling frameworks.

Figure 1: I am afraid I really struggle to see how this diagram is useful, or indeed can be used as a framework for directing future work? It seems to simply link together different processes with abiotic drivers and population dynamics? What are readers supposed to learn from this diagram, other than what they likely already know - that the environment and different ecological mechanisms at different scales affect population dynamics? Can you add in scale to help readers appreciate the importance of individual versus population level mechanisms? I think this whole paper would benefit from considering hierarchy theory - see

O'Neill, R. V., D. DeAngelis, J. Waide and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press for a review

>> Figure 1 is a conceptual framework to highlight the importance of individual mechanisms. The focus of this review is not to develop such methods, but to address the current limitations to achieving such an approach and ways forward. We clarify this throughout.

L202: and responses to

>> No change - the sensitivity of the species is the response.

L212: This is a key point, and perhaps better made in the introduction of the paper? It could also do with more fleshing out, this is a very vague summary of a fundamentally important point, that arises out of different ecological traditions and fields

>> This point is now presented before we evaluate existing population modelling approaches (L 111 – 115).

L220: I think somewhere in the paper there needs to be a discussion about the balance, and pros and cons, of using these different approaches. Individual level mechanisms are undoubtedly important, but how do you avoid over-parameterising models, and what do you do when data is lacking? These points are alluded to throughout the paper, but there is no cohesive treatment of the balance and trade-offs of the different approaches in terms of models or data, or indeed a proper treatment of scale?

>> The focus of this paper is on a standardised mechanistic approach, which would alleviate many of the issues surrounding current data limitations to mechanistic modelling. We discuss this as a key point in the new 'data availability' section of the discussion (390 – 428).

L227: Can you also discuss the evidence for this optimisation? What are animals trying to maximise? What currencies are they using, that can also be used in models? How do you measure or test for these in the field? What are the assumptions underlying the principles of optimisation in different theories?

>> We now include evolution as an additional mechanism, and additional information is given on this subject here (L 347 – 379).

L233: So how do we address these shortcomings?

>> We discuss how the development of eco-evolutionary theory in the following section (L 430 – 442) can help to address these shortcomings.

L251: again, can this be better linked to the section for how we should move forwards to deal with these limitations?

>> We discuss how the development of eco-evolutionary theory in the following section (L 430 – 442) can help to address these shortcomings.

L253: I find it a bit disjointed to have a new section here called 'behaviour' - because you have been talking about behaviour throughout the paper up to this point?

>> Although we appreciate there is an overlap between each mechanism, and mention this (L278 – 280), each submodel tends to come from disparate fields and so are presented separately.

L257: Can you elaborate on these 'testable frameworks'? How would you use these theories to test population model outputs?

>> Changed to 'testable submodels for describing animal behaviour in population models' (L 311).

L260: I think it is more correct to say that IDF makes this assumption, not optimal foraging theory in general?

>> Changed to IDF (L 314).

L263: It feels a little unconvincing to only have one, rather specific example to back up this very general point - can you add other examples? Usually in a paper of this type, these statements would be backed up by 3-5 citations at least?

>> We have removed this specific example in the revised MS.

L265: This statement is left hanging, and you suddenly move on to another topic in the following paragraph? What should the reader take home from this paragraph? We know there are multifaceted trade offs, but how should this be addressed with your goal of more integrated modelling?

>> Rephrased to emphasise that the submodels (e.g. behaviour, physiology, evolution) need to be considered together (L 102 – 104).

L277: Again, there is a real lack of detail here, making this whole section rather unconvincing, although you are making important points. Many readers will never have encountered Geometric Frameworks before, and you can't assume they will know the details behind these concepts.

>> We have attempted to mention the relevant eco-evolutionary theory to start to standardise mechanistic submodels. The scope of this task is again too big to provide a comprehensive overview of each and we have included representative references to redirect the reader if this specific approach is of interest to them.

L280: This is a very generic term for a whole area of statistical modelling - can you define it and be more specific as to what you mean in this context?

>> We refer to state-space models of animal movement (text updated, L320), related to the reference given.

L291: Again, this statement and example are very vague and lacking in detail. Why focus just on QRs? And how can they contribute to more integrated modelling?

>> We do not believe that the lack of detail in each section that you have identified is necessarily a shortcoming of this paper. Much more detailed reviews are available for each of these sections in the literature, but very few – or none that we are aware of – integrate all of these different areas into one paper. Our hope is that the integration of these different approaches in this review not only drives progress towards a standardised mechanistic approach in population modelling, but also acts as a useful resource for those new to ecological modelling.

L293: not sure what you mean here?

>> Removed in revised MS.

L305: This section should be better linked with your previous discussion of RNs

>> All RN mentions are now included in the evolution section.

L316: Again, I think this paper should contain a discussion of ecological hierarchy - see my previous comment

>> Again, the scope of this paper is much too broad to discuss additional theories in detail. Our re-focus on a standardised mechanistic approach also makes ecological hierarchy less relevant to this review.

L326: I think this is true in almost all cases!

>> Maybe not for large-ranging herbivores, but individual-level data can be abundant for certain species such as those easy to rear in the lab (e.g. invertebrates, insects). We have tried to be inclusive by appreciating that there are different data limitations for different taxa, and discuss this in more detail in the data availability section.

L331: I think this is a really important point, and would much rather see a diagram outlining this as a framework, rather than the one you currently have included in the paper

>> We have clarified the focus of the paper throughout. The framework you suggest is outside of the scope of this paper.

L343: Again, i would like to see this integrated into a diagram for a methodology for combining different modelling frameworks to address this issue

>> Again, this is outside of the scope of this review paper.

L351: Why would this be the case? Do you mean that testing for evidence will follow development of integrated approaches?

>> We have clarified that the suggested standardised mechanistic approach could provide consensus on addressing data gaps – either through the development of robust statistical tools (L 413 – 416) or coupled modelling-empirical studies (L426 – 428).

L371: what do you mean here, by error?

>> Removed in revised MS.

L376: all population models can be predictive - do you mean that population models should be used to make predictions and those predictions should be tested?

>> We were previously using predictive as 'predictive under novel conditions', which we don't believe all models can. We have updated throughout, as mentioned previously, to 'mechanistic'.

L391: can you provide an example here for how a set of models and concepts could be integrated together and tested? eg for one species?

>> We would very much like to provide a case study, but the breadth of issues already covered and journal word limit make this outside of the scope of this paper.

Appendix B

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

Dear authors,

I was one of the previous reviewers that assessed your manuscript. I was pleased to see that you have taken on board my comments regarding eco-evolutionary dynamics and the integrated approach. I find this review very timely and urgent as we are now at a moment where lots of different tools are available, but we need reflection on how to proceed.

Thank you very much for both reviews, your comments and suggestions have been critical in shaping the final paper.

Some small comments I still have are:

- Abstract: the first sentence seems to suggest that plants do not matter in global diversity. Perhaps starting the sentence with 'animal populations' instead of 'global biodiversity' would solve this.

>> Thank you for this suggestion, we now revise the first sentence of the abstract to read 'Animal populations will mediate the response of global biodiversity to environmental changes.'

- L41: "An urgent challenge in ecology". Given that you now also discuss evolution and eco-evolutionary dynamics, I would rephrase this as "An urgent challenge in biology".

>> Here, we update the text to exclude 'in ecology', as we do not feel that 'in biology' – or any other alternative – is fitting.

- L410-415: efforts to coordinate standardized energy budget models is the open access database Add-my-Pet: https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/. Refer to the Add-my-Pet collection as: Add-my-Pet, online database of DEB parameters, implied properties and referenced underlying data, [bio.vu.nl/thb/deb/deblab/add_my_pet/](https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/). Last accessed: yyyy/mm/dd.

>> Thank you for this suggestion, we agree that Add-my-pet is an important resource and deserves mention here – reference included (Line 423).

Referee: 2

Comments to the Author(s)

The paper is much improved, with respect to comments from both reviewers. It reads much better as a consequence of the structural changes, and changes within the individual sections have made it much less confusing to readers.

Overall though, I think it is now suitable for publication in Proc B, and I thank the authors for their amendments.

>> Many thanks for your feedback.