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Spatio-temporal ecological niche modelling of multigenerational insect migrations

Mattia Menchetti, Maya Guéguen and Gerard Talavera

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Original submission: 7 April 2019
1st revised submission: 4 July 2019
2nd revised submission: 13 August 2019
Final acceptance: 14 August 2019

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

Review History

RSPB-2019-0821.R0 (Original submission)

Review form: Reviewer 1 (Edward J Pfeiler)

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?
Excellent

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

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?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
See attached file (Appendix A)

Review form: Reviewer 2

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?
Poor

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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Yes

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Yes

Comments to the Author
The paper is very interesting as it sheds light on an intringuing biolgical process, i.e. the all year round migration of the painted lady, a common butterfly, from Africa to Northern Europe and return. However, the authors missed crucial information on the presence of this butterfly in Africa, which is key for the understanding of the process. Also, it should be very useful to apply the same methodology to investigate migration southwards in Africa, from tropical areas to South Africa.

Decision letter (RSPB-2019-0821.R0)

14-May-2019

Dear Dr Talavera:

We are writing to inform you that your manuscript RSPB-2019-0821 entitled "Spatiotemporal ecological niche modelling of multigenerational insect migrations" 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 be happy 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 we 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.

Sincerely,

Proceedings B
mailto: proceedingsb@royalsociety.org

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Associate Editor
Comments to Author:

Both reviewers agree that the manuscript is well written and presented as much as the modelling is based on a comprehensive dataset for the northward migration to Europe. However, particularly Ref 2 points out that available information from Africa is missing from the analysis including southward migrations to South Africa. Similarly Ref 1 mentions the migrations of the species in the Americas.
I would invite the authors to consider the referee's comments, whether it is a question of discussing what ref2 sees as the "crucial information in the presence of this butterfly in Africa" or whether, as suggested elsewhere it might even be possible to expand the modeling exercise to the southern migration.
In the light of the referees comments I do not recommend the the manuscript for publication in its current form, but would hope to see a revised version having considered the comments.

Reviewers' Comments to Author:

Referee: 1
See attached file

Referee: 2

The paper is very interesting as it sheds light on an intringuing biolgical process, i.e. the all year round migration of the painted lady, a common butterfly, from Africa to Northern Europe and return. However, the authors missed crucial information on the presence of this butterfly in Africa, which is key for the understanding of the process. Also, it should be very useful to apply the same methodology to investigate migration southwards in Africa, from tropical areas to South Africa.

Author's Response to Decision Letter for (RSPB-2019-0821.R0)

See Appendix B.

RSPB-2019-1583.R0

Review form: Reviewer 1 (Edward J Pfeiler)

Recommendation
Accept as is

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?
Excellent

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
The authors have addressed the few minor comments and corrections I had in the earlier version, and no further changes are suggested. A very nice paper.

Review form: Reviewer 3

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?
Excellent

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?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
This is a very interesting and well-written paper using spatiotemporal niche modelling to investigate the migratory cycle of the painted lady butterfly. The authors have done a good job dealing with the previous reviewers comments. I think that extending the analysis to include records from Africa was an important step, but acknowledge that the region is relatively data deficient, which the authors have pointed out. This will certainly be a fruitful area for future investigation, which the authors already have underway. I have very little to add aside from some (very) minor edits, which are detailed below.
L77 and L93: migratory insect species.
L102: Maybe use throughout instead of along the year.
L112: ...in such an extensive area, have not yet been precisely studied.

L267: Perhaps here you could mention some other cases where migratory insects have been shown to undergo significant population increases during the summer months in Europe, such as the silver Y moth (Chapman et al. 2012) and some migratory hoverflies (Wotton et al. 2019).
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Wotton et al. 2019.Mass Seasonal Migrations of Hoverflies Provide Extensive Pollination and Crop Protection Services. Curr. Biol. 29, 2167–2173
L324: Is there a reference that can go here where this hypothesis is mentioned?

Decision letter (RSPB-2019-1583.R0)

06-Aug-2019

Dear Dr Talavera

I am pleased to inform you that your manuscript RSPB-2019-1583 entitled "Spatiotemporal ecological niche modelling of multigenerational insect migrations" has been accepted for publication in Proceedings B.

The referees recommended publication, but one has suggested some minor revisions to your manuscript. Therefore, I invite you to respond to their 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
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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.

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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,
Victoria Braithwaite

Professor V A Braithwaite
mailto: proceedingsb@royalsociety.org

Associate Editor, Comments to Author:

I agree with both referees that the authors did an excellent and convincing job addressing referees comments and it is a stronger manuscript for it. There are a few suggestions for minor editorial changes for the authors to consider.

=====
Reviewers' Comments to Author:

Referee: 1

The authors have addressed the few minor comments and corrections I had in the earlier version, and no further changes are suggested. A very nice paper.

=====
Referee: 3

This is a very interesting and well-written paper using spatiotemporal niche modelling to investigate the migratory cycle of the painted lady butterfly. The authors have done a good job dealing with the previous reviewers comments. I think that extending the analysis to include records from Africa was an important step, but acknowledge that the region is relatively data deficient, which the authors have pointed out. This will certainly be a fruitful area for future investigation, which the authors already have underway. I have very little to add aside from some (very) minor edits, which are detailed below.
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L324: Is there a reference that can go here where this hypothesis is mentioned?

Author's Response to Decision Letter for (RSPB-2019-1583.R0)

See Appendix C.

Decision letter (RSPB-2019-1583.R1)

14-Aug-2019

Dear Dr Talavera

I am pleased to inform you that your manuscript entitled "Spatiotemporal ecological niche

modelling of multigenerational insect migrations" 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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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,

Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

In this study, Talavera et al. use ecological niche modelling to provide insight into the impressive and little understood multigenerational migration of the Painted Lady butterfly *Vanessa cardui* in the Afrotropical and Palearctic regions. Unlike the well-known and charismatic migration of the monarch *Danaus plexippus* in North America, there are huge gaps in our knowledge of the details in the migration of *V. cardui*, especially the location of winter breeding areas which provide the main "source" of individuals involved in the northward migration. The models provided in this study, based on climatic factors and suitable breeding areas, go a long way in helping to fill in these gaps. Overall, the paper is well-written and easy to follow, and is based on analyses of a comprehensive data set. I only have a few comments and suggested grammatical change outlined below.

The distance of the annual migratory circuit, 12,000 km, appears to be underestimated. On Fig. 1, the authors show an actual breeding record (one larva!) from equatorial Africa (Kenya) and their model suggests that the entire equatorial region is extremely important and the probable source of the "missing generations". Google Earth shows the distance from equatorial Africa to northern Scandinavia is about 7,500 km, resulting in a yearly circuit of closer to 15,000 km. I also suggest not using the term "wide", which suggests a longitudinal migration, to refer to the distance of the migratory circuit (lines 340 and 422). Better to just use "encompass" as they already do in the Abstract (line 51), or possibly "latitudinal."

In reading this paper, I was struck by the many similarities, as well as gaps in knowledge, of the annual migration of *V. cardui* in the Nearactic/Neotropical region, especially this year in which we have seen a huge outbreak in numbers of migratory individuals during March in the desert southwest of USA after heavy winter rains. Although not the focus of the authors' study, it might be worthwhile adding a sentence or two on the potential of ecological niche modeling to provide insight into migratory behavior of *V. cardui* in other geographic regions.

<u>Specific comments and suggestions</u>:

Line 76. Suggest rewording the general statement "Migratory insects are short-lived animals..." While true for *V. cardui*, the overwintering stage of migratory *D. plexippus* is quite long, around 8 months.
Line 315. Change "data is" to "data are"
Line 322. Change "has" to "have". Offspring can either be singular or plural, depending on context, and it clearly has a plural meaning here.
Line 323. Better to use "farther" than "further" because a physical distance is referred to.
Line 355. Suggesting changing "Even if..." to "Even though..." "If" implies uncertainty, and it is well-established that *V. cardui* is highly polyphagous.
Line 420. The model predicts breeding areas in equatorial Africa, and although it is only a single larva from Kenya (Fig. 1), the authors might want to consider adding the confirmed observation here, and mentioning that it is consistent with the model.

Appendix B

Associate Editor
Comments to Author:

Both reviewers agree that the manuscript is well written and presented as much as the modelling is based on a comprehensive dataset for the northward migration to Europe. However, particularly Ref 2 points out that available information from Africa is missing from the analysis including southward migrations to South Africa. Similarly Ref 1 mentions the migrations of the species in the Americas.
I would invite the authors to consider the referee's comments, whether it is a question of discussing what ref2 sees as the "crucial information in the presence of this butterfly in Africa" or whether, as suggested elsewhere it might even be possible to expand the modeling exercise to the southern migration.
In the light of the referees comments I do not recommend the the manuscript for publication in its current form, but would hope to see a revised version having considered the comments.

We appreciate the editor's comments and the invitation to re-submit a revised version of the manuscript.

In this new submission, we try to address the different issues pointed by the reviewers. More specifically, we now include an extended analysis projecting the model into the whole African continent, as suggested by referee 2, as part of the Supplementary Information given some methodological flaws that we discuss below. Still, we agree it is a good idea to provide a preliminary survey on the African southern hemisphere, thus opening discussion on independent migratory pools occurring within Africa only. On the other hand, we emphasize the potential of the method to study migratory movements in other regions, either for *V. cardui* or for other insects, as proposed by referee 1.

Please see below detailed answers to each of the reviewer's comments.

Reviewers' Comments to Author:

Referee: 1
See attached file

We appreciate the reviewer comments and suggestions. We have addressed comments point by point and improved grammar as suggested.

We also acknowledge the reviewer point on the similarities on *V. cardui* migrations in the Nearctic/Neotropical region and the potential of this method to be applied in the region. It is certainly of our interest to do so, as migrations

in this region are poorly yet understood. Consequently, we are already gathering a comprehensive data set for proper modelling in this region, and this will be the object for a near future piece of work. Nevertheless, we have included a sentence in the conclusions (Lines 441-444) pointing out the interest of the approach here proposed to study not only *V. cardui* movement patterns in other regions, but also the potential to be applied to other migratory insects.

Referee: 2

The paper is very interesting as it sheds light on an intringuing biolgical process, i.e. the all year round migration of the painted lady, a common butterfly, from Africa to Northern Europe and return. However, the authors missed crucial information on the presence of this butterfly in Africa, which is key for the understanding of the process. Also, it should be very useful to apply the same methodology to investigate migration southwards in Africa, from tropical areas to South Africa.

Thanks a lot for the positive response and the comments. We agree that other migratory patterns occurring within Africa are worth mentioning in this paper (now in lines 352-355). Therefore we now include an extended modelling exercise by projecting the model (based only on data from the northern hemisphere) to the southern hemisphere (Supplementary Figure S2). However, please note that this needs to be considered just as a preliminary survey:

1) Our approach aims at developing a method for modelling spatiotemporal insect migration, which we test with a well-known migratory circuit: the European-African. The link between these two regions has been characterized by means of isotope and pollen metabarcoding analyses (Talavera et al 2018, Suchan et al 2018, Stefanescu et al 2016). While other migratory circuits may exist within Africa only (widely involving the southern hemisphere), these have not yet been properly characterized and our data is insufficient to do that from a modelling perspective. As a natural step forward, we are planning to expand the modelling to other regions (ideally worldwide), and we are gathering breeding data to this end (through our own field work or through our citizen science program). As we are modelling breeding habitat, data is challenging to obtain. This is a slow process since it requires long and dedicated surveys, especially in poorly surveyed regions as in Africa. Most data available about the presence of *V. cardui* are adults observations, which are useless for a serious and conservative modelling exercise. As this is a migratory species, the presence of adults is rather uninformative about the suitability of the locality (for example, there are many records of this species over the sea). We are working on this important issue, and gathering breeding data from Africa (both spatial and temporal) as to properly modelling other

potential movements, unrelated to the macropopulation linked to the Palearctic.

2) By means of adult observation patterns, and considering an inverted seasonality between the two hemispheres, it seems likely that the southern African *V. cardui* pool represents a different migratory system, not strongly linked to the Palearctic. Expanding the modelling analyses to the whole region, with important gaps on breeding records, would represent mixing another wide group of populations and climatic conditions which would challenge the modelling procedure.

3) Last but not least, the paper is already extremely long and complex as to properly develop a topic that would surely deserve an article itself. We consider that focusing on a single migratory circuit makes the interpretation of the model much more accurate. However, we hope we can go in the depth into this issue soon after gathering a comprehensive dataset for the southern African hemisphere.

Appendix C

Associate Editor, Comments to Author:

I agree with both referees that the authors did an excellent and convincing job addressing referees comments and it is a stronger manuscript for it. There are a few suggestions for minor editorial changes for the authors to consider.

=====
Reviewers' Comments to Author:

Referee: 1

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Referee: 3

This is a very interesting and well-written paper using spatiotemporal niche modelling to investigate the migratory cycle of the painted lady butterfly. The authors have done a good job dealing with the previous reviewers comments. I think that extending the analysis to include records from Africa was an important step, but acknowledge that the region is relatively data deficient, which the authors have pointed out. This will certainly be a fruitful area for future investigation, which the authors already have underway. I have very little to add aside from some (very) minor edits, which are detailed below.
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Wotton et al. 2019.Mass Seasonal Migrations of Hoverflies Provide Extensive Pollination and Crop Protection Services. Curr. Biol. 29, 2167–2173
L324: Is there a reference that can go here where this hypothesis is mentioned?

We appreciate the reviewers comments, which have helped to make a better manuscript. In the resubmitted version we have included the few remaining suggestions done by referee 3.