

Declines in European bumblebee habitat suitability attributable to climate change

Corresponding Author: Mr Bastien De Tandt

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Comments for the Author)

The authors of 'Attribution of climate change to the decline of European bumblebee population' have produced an incredibly interesting study, which is well researched and extremely timely. This is the first use I have seen of attribution frameworks to determine impacts of climate change on insects, and I find this work really exciting.

Although I think the manuscript is overall very well written, I have some comments that may help to improve clarity, which will help to boost the impact of this well-designed and conducted study.

General: In the abstract and introduction, the authors refer to 'local' and 'regional' scales, but these are not properly defined. It would be great if this could be clarified somewhere.

Line 20: Consider changing to 'Isolating its contribution to climate change'.

Line 26: It is unclear from the abstract what 'locally' means, so it would be good to define this here. Also, is this what is later referred to as 'regional' in the manuscript?

Sentence lines 34–36: Please expand on what you mean by 'posing an unmatched challenge for human societies'.

Lines 27–38: It would be useful to provide a range here; for example, what is the range across other SSPs?

Lines 38–39: It may be worth mentioning that climate changes are not occurring equally everywhere, and that some regions are particularly affected.

Line 43: Is reference 14 referring to their services or to the fact they are most affected? Could you also explain why insects would be more affected compared to other groups?

First sentence of paragraph 2 (lines 51–53): This seems a little too specific. Could you instead just cite Working Group 2? For example: "To address this issue, an 'impact attribution' framework has been developed, enabling...". This would make the writing more concise and improve clarity.

Lines 53–57: This is really interesting, but it would be great to mention ecological studies that have used this attribution framework (for example Kotz et al., 2025).

Lines 59–60: You could highlight here that this is the first time an attribution framework has been used for insects (if that is the case; if not, this would be the place to cite other relevant studies).

Line 69: You can remove the word 'fauna'.

Lines 75–76: A small comment, but I personally prefer when the end of the introduction does not give away the conclusion but instead sets up the questions. Perhaps you could end with the main research question—what is your key question?

Results and discussion

Lines 82–85: I think it is important to mention the spatial resolution of the climate data here, as this is vital for interpreting the results.

If different species had different predictive performance, did you include this in your post hoc analysis of future/present diversity? Are areas of increase/decrease dominated by species with lower predictive performance? Is there a way to weight this analysis by model performance?

Paragraph from line 92 onward: It would be helpful to make it clearer when you are referring to species-specific versus community-level results, as it is easy to lose track. For example, the sentence from line 94 about community-level results could start a new paragraph to clearly separate these findings.

Lines 98–101: Please improve the clarity of these sentences. Simplifying the language would make them easier to interpret. For example:

‘Under the counterfactual scenario, the ESI remained stable with an estimated change across reanalysis datasets from -0.7% to +0.2%. Results for the other reanalysis datasets are consistent in spatial patterns and comparable in magnitude of ESI changes reported for the GSWP3-W5E5 reanalysis dataset.’

Figure S12: The map of the regions seems very important to your results. You might consider moving this to the main figures or integrating the regions into existing maps so that similarities and differences can be visually compared.

Lines 122–125: It might be useful to directly compare results between regions and species (e.g., alpine regions vs alpine species). For instance, could regional differences be driven by species composition? Was this tested?

Line 133: Can the research question be made clearer? For example, state explicitly that you are testing the predictability of the climate scenarios.

Lines 139–141: This result is very interesting, but the question it addresses (climate impacts leading to better predictions) is not clearly set up in the introduction. Including your key questions at the end of the introduction would help highlight these important findings.

Lines 207–209: ‘The Atlantic region exhibits comparatively smaller declines of ecological suitability relative to previously cited European biogeoregions, although regional negative trends are still apparent in our results.’ It would be helpful to expand on why this might be the case.

Line 214: ‘reflects community-level ecological suitability gains’. please expand on what this means.

Lines 236–238: Could you briefly expand on the methods used in this referenced study?

Lines 244–255: Is there physiological or critical limits data to support this claim?

Line 249: ‘a subset of species’. please specify how many.

Lines 254–256: It may also be interesting to mention microclimatic use or microclimates created in human-managed environments.

Lines 273–274: While this is a valid limitation, it would also be important to emphasize that this work is crucial for highlighting the impacts and negative consequences of climate change, even if specific drivers are difficult to disentangle.

Lines 282–286: You could also mention your geographic scope and whether global or cross-continental analyses might reveal different patterns. What is known about bumblebee declines in other regions?

Lines 297–305: This paragraph is quite long and somewhat repetitive; consider shortening it.

Methods

Lines 315–320: Since some removed species are more widespread (and potentially more generalist), it would be interesting to see their individual results. Would this be feasible?

Line 323: What was the original number of species/occurrences before filtering?

Line 327: Specify ‘ecological niche model’ or ‘species distribution model’ instead of just ‘model’ for clarity.

Lines 337–338: A reference is needed here.

Lines 341–342: A reference is also needed here.

'sampling pseudo-absences in a defined background area representing confirmed *Bombus* occurrences increases the probability of sampling in areas where a minimum of sampling effort was carried out, reducing the risk of misclassifying unsampled areas as true absences.' Please clarify how this background area was defined.

Lines 344–346: Why was the entire extent of Europe used rather than a buffer around the sampled area? Or was this already done?

Lines 367–369: This section on environmental variables should come before the model description.

Lines 398–402: The definition of regions should be introduced earlier (e.g., in the introduction), as this is the first clear explanation. Have you considered smaller-scale regional classifications, such as Köppen–Geiger or ecoregions? A methods figure showing these regions and associated differences could be useful.

Figure S12: The labels may be incorrect—please check that the correct figure has been uploaded with the correct title.

(Remarks on code availability)

high quality, consider uploading to a version-controlled platform like zenodo

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Reviewer #2

(Comments for the Author)

Manuscript NCLIM-26030934

Title: "Attribution of climate change to the decline of European bumblebee populations"

In NCLIM-26030934, the authors are attempting to tease apart the effects of climate change from other environmental changes using comparative back-casting. Specifically, they compared the predictive power of counterfactual climate conditions vs. factual conditions to quantify the impact of climate change on habitat suitability for European bumble bees. Counterfactual conditions used remote sensing data on factors other than climate (i.e., change in land-use) and current (2000-2019) climate to back-cast habitat suitability during six time periods. Factual conditions included historical land-use and historical climate data to predict habitat suitability. Disparities between the two projections denoted the effects of climate change on habitat suitability. They found that climate change accounted for 5-19% change in habitat suitability. Species responses were variable but, on average, habitat suitability declined in most regions. The most novel aspect of this paper is the comparative back-casting approach. It supports prior work indicating that habitat suitability is decreasing (Ghisbain et al. 2024) but differs from this previous paper by quantifying the effects of climate vs. other factors. The authors do an admirable job explaining the variation in response and not overstating the patterns, though I do have some questions about the methods that I believe need to be addressed.

My first concern is relatively easy to address. There are a few places where the methods need to be more clearly described, particularly for the broad audience of Nature. What the authors did (even in a general sense) was unclear without either reading forward to the methods or reading prior literature. Obviously, some details should be restricted to the methods or supplementary materials, but a more detailed summary is required in the main text for the methods and results to be tractable (see my line-by-line notes below).

The other main concern I have has to do with the models themselves. Little rationale is given for why some metrics are included, and others are not. For instance, impervious surface has the potential to have direct and indirect effects (through local climate) on habitat suitability. Without including it as a landscape change variable, changes in temperature due to increased impervious surface would be attributed to climate change. There should be solid rationale for why each variable (climate or land-use) is included (or not included, for important related variables).

This leads me to my last main recommendation. I recognize that the authors are focused on the effects of climate here. However, they are missing an incredible opportunity to "weight" the effects of land-use and climate change for bumble bee habitat suitability. Yes, quantifying the effects of climate change is informative, but quantifying the effects of both climate change and land-use is more powerful. Over the past 100 years, which has had the greatest effect on habitat suitability, climate or land-use? A counterfactual approach that does the opposite (uses historical climate and NOT land use change) would demonstrate the relative impact of urbanization. I personally feel like that piece deserves discussion, from both an ecological and conservation perspective.

LINE-BY-LINE NOTES

Lines 80-82. Why did you choose to use the current climate as the baseline for historical comparisons rather than starting with climate at the beginning of the dataset and projecting forward? The last 10 years have been the hottest on record and

may not be the best baseline dataset as there is likely delayed responses (e.g., range expansion, evolutionary changes, etc.) I would think starting with the oldest historical climate would be a more accurate measure of “fundamental” habitat suitability (albeit assuming no evolution).

Lines 94-95. Describe the ecological suitability index. Yes, it has been used in previous papers, but I think it needs to be explained here as well. The definition provided here doesn't really describe how the metric is calculated in a transparent way.

Lines 128-131. These results should be summarized in a supplementary table where the reader can evaluate the patterns themselves (without having to find them on GitHub).

Lines 133-135. Clarify how this analysis is different from the first analysis.

Line 137. Provide a brief summary of what you mean by “reanalysis dataset”. Did you rerun these projections with different subsets of data?

Line 157. Figure 2 doesn't provide compelling support of the claim that BI differences increase through time. There is greater variance in BI through time, which is of great interest, but I saw no support (statistical or graphical) for BI increases through time. To me this signals that species are diverging in how much climate is affecting habitat suitability – with some being potentially more impacted by land-use change.

Lines 160-167. A summary table of these results (without having to go to GitHub) would again help the readers make their own evaluation of the results.

Line 274. “induced” seems strong here, since not all other effects are indirectly influenced by climate. “amplified” might be more appropriate.

Line 377-379. Why was impervious surface not included as an environmental variable? It may be positively correlated with human population density, but it has the potential to change local temperature, which if not accounted for, could inflate the effects attributed to climate change.

Lines 391-395. These metrics are critical to this paper and need to be described in more detail.

Lines 418-421. Where are the results of the Wilcoxon-Mann-Whitney tests? Those should also be available in the supplementary materials.

(Remarks on code availability)

The code is well labeled and easy to read. A descriptive README file is provided. While I was able to review the script, I was not able to run it within the two-week time frame requested.

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The code is well labeled and easy to read. A descriptive README file is provided. While I was able to review the script, I was not able to run it within the two-week time frame requested.

Version 1:

Reviewer comments:

Reviewer #1

(Comments for the Author)

I am satisfied that the authors have addressed my previous questions/comments on the manuscript and think that they have significantly improved the manuscript in this revision. Previous areas that I found confusing are now well explained, and it was easy to follow. I think this study is really exciting, and I really enjoyed reading it!

I have a couple of minor comments below:

Abstract:

'.. with pronounced declines in southern and central regions. In contrast, in the Alpine and Boreal regions, gains at higher altitudes partially offset losses at lower latitudes and altitudes, resulting in minimal net changes' Because there are alpine regions in central Europe this is a little confusing. Could you change to something like southern Europe, and lowland central Europe.?'?

Line 64-65: Although you are both using attribution frameworks, I think the underlying methodology seems quite different?

140-141: It would be great if the species-specific scenarios were uploaded as part of the supplementary instead of the github – this would mean everything is available in one place for anyone interested, and would not be certain the information is retained across time

179-196 . In addition to the per-species tests, if you wanted to test if, over time, the proportions of mean BI are increasing, could you not test for statistical differences between time groups? Or even between SSPs/time groups?

(Remarks on code availability)

(Remarks on code availability)

Reviewer #2

(Comments for the Author)

Thank you for your thorough response to my questions and recommendations. Your work advances our understanding of how climate change affects European bumble bee distributions. I think your approach has broad applications, and I look forward to seeing how it is used in other contexts.

(Remarks on code availability)

I did not re-review the code as the authors did not modify their analyses

(Remarks on code availability)

I did not re-review the code as the authors did not modify their analyses

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Mr Bastien De Tandt
Dr Simon Dellicour

Spatial Epidemiology Lab
Université Libre de Bruxelles
50 avenue F.D. Roosevelt
1050 Bruxelles, Belgium

Mr Bastien De Tandt
Dr Guillaume Ghisbain

Laboratory of Zoology
Research Institute for Biosciences
University of Mons
7000 Mons, Belgium

16-06-2026

Manuscript re-submission to *Nature Climate Change* (NCLIM-26030934): “Evaluating the decline of European bumblebee populations attributable to climate change” by Bastien De Tandt, Kyla Serres, Rosa Pietrojusti, Diana Erazo, François Massonnet, Denis Michez, Wim Thiery, Guillaume Ghisbain and Simon Dellicour.

Dear Editors,

On behalf of all authors, we are pleased to re-submit to *Nature Climate Change* a revised version of our manuscript entitled “Evaluating the decline of European bumblebee populations attributable to climate change”.

We would like to express our gratitude to the editorial team and the two reviewers for all the constructive comments on the previous version of our manuscript. We have now revised our manuscript in response to the reviewers’ comments (see below for a point-by-point response to all comments) and hope it is now suitable for publication in *Nature Climate Change*.

Best regards,

Bastien De Tandt
Guillaume Ghisbain
Simon Dellicour

Reviewer #1

The authors of 'Attribution of climate change to the decline of European bumblebee population' have produced an incredibly interesting study, which is well researched and extremely timely. This is the first use I have seen of attribution frameworks to determine impacts of climate change on insects, and I find this work really exciting.

Answer: Thank you very much for your positive and enthusiastic feedback on our study.

Although I think the manuscript is overall very well written, I have some comments that may help to improve clarity, which will help to boost the impact of this well-designed and conducted study.

General: In the abstract and introduction, the authors refer to 'local' and 'regional' scales, but these are not properly defined. It would be great if this could be clarified somewhere.

Answer: We thank the Reviewer for pointing out this lack of clarity. We have revised the manuscript to avoid confusion by clarifying the use of the words 'local/locally' as well as 'regional'. We now first state a clear definition of the local impact of climate change (i.e., impact at the grid cell level) in the Results section. We also removed ambiguity in the use of the word 'regional' by clearly referring to the 'biogeographic region' or 'biogeoregion', as defined by the European Environment Agency, throughout the manuscript, unless referring to studies conducted at a larger scale.

Line 20: Consider changing to 'Isolating its contribution to climate change'.

Answer: We thank the Reviewer for this suggestion. However, we believe the proposed change would alter the intended meaning, 'its' already referring to climate change. We have therefore retained 'Isolating its contribution from other co-occurring environmental stresses [...]', which we feel is grammatically correct.

Line 26: It is unclear from the abstract what 'locally' means, so it would be good to define this here. Also, is this what is later referred to as 'regional' in the manuscript?

Answer: Due to word count constraints in the Abstract, we were unable to add a formal definition of 'locally' there. However, we have now added a clear definition in the main text. This is distinct from 'regional', which we have clarified throughout the manuscript to refer specifically to biogeographic regions as defined by the European Environment Agency (see also our comment above).

Sentence lines 34–36: Please expand on what you mean by 'posing an unmatched challenge for human societies'.

Answer: We have revised the sentence by removing the phrase 'posing an unmatched challenge for human societies' and instead explicitly linking climate change to its consequences for ecosystem services and human societies, the mechanisms of which are developed in the subsequent sentences. The revised sentence reads as follows: *"As human pressure on ecosystems is set to continue, climate change is expected to become a dominant driver of biodiversity loss and, in turn, affect the ecosystem services upon which humans rely"*.

Lines 27–38: It would be useful to provide a range here; for example, what is the range across other SSPs?

Answer: We have now revised the text to indicate the range of projected temperature increases across future emission scenarios: *“Since the beginning of the 20th century, global mean surface temperatures have increased by over 1.2°C and are projected to rise by between 1.5 and 4.0°C by 2100, depending on future greenhouse gas emissions scenarios across shared socioeconomic pathway (SSP) projections”*.

Lines 38–39: It may be worth mentioning that climate changes are not occurring equally everywhere, and that some regions are particularly affected.

Answer: Modification has been done to mention regional differences: *“Beyond global mean warming, climate change alters precipitation regimes and increases both the intensity and frequency of extreme weather events such as floods, droughts, wildfires, and heat waves, although with regional differences.”*

Line 43: Is reference 14 referring to their services or to the fact they are most affected? Could you also explain why insects would be more affected compared to other groups?

Answer: As far as we know, insects are not necessarily more affected compared to other groups but are rather sensitive overall to climate change due to their physiology and relatively short life cycle. We have revised the sentence to reframe and clarify the meaning, as well as added another reference to clearly differentiate which reference is referring to which information. The revised text now reads as follows: *“Insects, critical providers of many ecosystem services such as pest control, nutrient recycling, and pollination (Dangles & Casas 2019, Ecosystem Services), are expected to be rapidly impacted by climate change, given the sensitive thermal physiology and short life cycle of many species (John et al. 2024, Journal for Nature Conservation).”*

First sentence of paragraph 2 (lines 51–53): This seems a little too specific. Could you instead just cite Working Group 2? For example: *“To address this issue, an 'impact attribution' framework has been developed, enabling...”*. This would make the writing more concise and improve clarity.

Answer: Thank you for the suggestion. To make the sentence clearer, we only cited the Intergovernmental Panel on Climate Change (IPCC), given that the reference given can directly bring the reader to the previously mentioned report.

Lines 53–57: This is really interesting, but it would be great to mention ecological studies that have used this attribution framework (for example Kotz et al., 2025).

Answer: We thank the Reviewer for suggesting this reference. We now mention this study at the beginning of the following paragraph (see our comment below).

Lines 59–60: You could highlight here that this is the first time an attribution framework has been used for insects (if that is the case; if not, this would be the place to cite other relevant studies).

Answer: Thank you for pointing that out. The text has been changed accordingly to add the following sentence: *“To the best of our knowledge, this is the first time a formal climate impact attribution framework has been applied to insect species (see Kotz et al. 2025, Nature Ecology & Evolution, for a similar attribution framework used in birds).”* As stated above, we have also added the reference Kotz et al. (2025) to refer to other relevant studies using this attribution framework.

Line 69: You can remove the word ‘fauna’.

Answer: This modification has been done.

Lines 75–76: A small comment, but I personally prefer when the end of the introduction does not give away the conclusion but instead sets up the questions. Perhaps you could end with the main research question—what is your key question?

Answer: Thank you for this suggestion. We now end the introduction with our key questions rather than the conclusion. The revised text now reads as follows: *“Using this framework, we seek to quantify to what extent observed changes in areas ecologically suitable for European bumblebees could be attributable to historical climate change, and whether such effects may differ among species and biogeographic regions.”*

Results and Discussion:

Lines 82–85: I think it is important to mention the spatial resolution of the climate data here, as this is vital for interpreting the results.

Answer: The modification has been done, and we now explicitly state in that sentence the spatial resolution associated with the environmental rasters used in our study: *“Environmental predictors included gridded climatic, land-use, and human population data at a resolution of 0.5 decimal degrees (Fig. S3), all averaged over the same period of time, and retrieved from four historical climate reanalysis datasets (GSWP3-W5E5, 20CRv3, 20CRv3-ERA5, and 20CRv3-W5E5) available through the Inter-Sectoral Impact Model Intercomparison Project phase 3a (ISIMIP3a).”*

If different species had different predictive performance, did you include this in your post hoc analysis of future/present diversity? Are areas of increase/decrease dominated by species with lower predictive performance? Is there a way to weight this analysis by model performance?

Answer: We thank the Reviewer for this suggestion. Our exclusion criteria were applied before modelling and are based on data quality requirements (e.g., minimum number of occurrence records) or expert-based assessment, ensuring that only species meeting required criteria to support reliable modelling were included. Following model fitting, we verified that all ecological niche models trained for retained species achieved good predictive performance (e.g., all species-specific SI_{ppc} values > 0.70). We therefore consider all retained species models to be of sufficient quality, weight them equally in the community-level analysis, and do not consider performance-based weighting appropriate in this context, which would also alter the definition and readability of the metrics (ESI, SRI) used to evaluate the evolution of the ecological suitability of the continent.

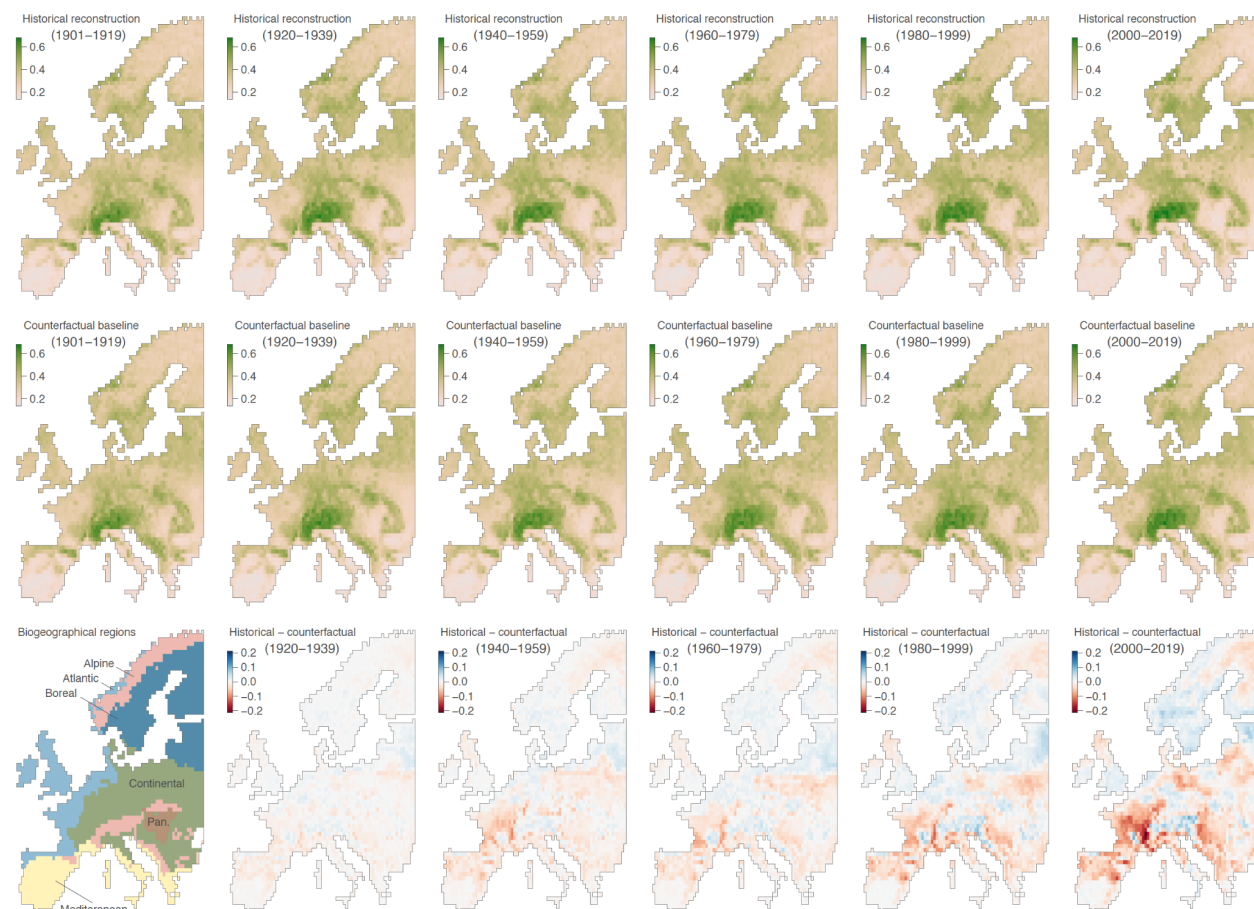
Paragraph from line 92 onward: It would be helpful to make it clearer when you are referring to species-specific versus community-level results, as it is easy to lose track. For example, the sentence from line 94 about community-level results could start a new paragraph to clearly separate these findings.

Answer: We have now clearly separated the paragraph containing community-level results from the one of the findings to improve clarity.

Lines 98–101: Please improve the clarity of these sentences. Simplifying the language would make them easier to interpret. For example:

‘Under the counterfactual scenario, the ESI remained stable with an estimated change across reanalysis datasets from -0.7% to +0.2%. Results for the other reanalysis datasets are consistent in spatial patterns and comparable in magnitude of ESI changes reported for the GSWP3-W5E5 reanalysis dataset.’

Answer: The text has been modified to incorporate the suggested modifications: “Our results for the other reanalysis datasets showed consistent spatial patterns and comparable magnitudes of ESI changes reported for the GSWP3-W5E5 reanalysis dataset.”



[Potential new version of] **Figure 1. Isolated impact of climate change on the ecological suitability of Europe for 47 bumblebee species.** We here report, for each period, the difference between bumblebee ecological suitability estimates based on (i) the reconstructions of the historical climate (first row) and (ii) a counterfactual baseline (second row). The third row of maps reports the difference, for each time period, between the two, i.e., between the estimates based on the reconstructions of the historical climate and the counterfactual baseline. We focus on the ecological suitability index (ESI), defined as the local mean ecological suitability averaged over species (ranging from 0 to 1). The computation of the ESI metric was based on species-specific ecological suitability maps, which were obtained by averaging over the estimates of ten independent BRT models trained on present-day data retrieved from the ISIMIP3a reanalysis dataset GSWP3-W5E5. See Figures S5-S7 for the corresponding results based on the three other ISIMIP3a reanalysis datasets — 20CRv3, 20CRv3-ERA5, and 20CRv3-W5E5 — considered in the present study. Within the third row of maps, we also report the delimitation of the six main biogeographical regions occurring in the study area (“Pan.” referring to the Pannonian region; see also Figure S12 for the original and more detailed visualisation of these regions).

Figure S12: The map of the regions seems very important to your results. You might consider moving this to the main figures or integrating the regions into existing maps so that similarities and differences can be visually compared.

Answer: We thank the Reviewer for this suggestion and agree that the spatial definition of the regions is important for interpreting the results. We explored options to integrate the biogeographical regions directly into the main figure (see above). However, in practice, this attempt led to loss of information (e.g., losing the historical - counterfactual map at 1901-1919) or reduced visual clarity if overlaid over the map of the

ecological suitability output. Given this trade-off, we opted to retain the map of the biogeographic region as a dedicated supplementary figure (Fig. S12), where the spatial structure can be presented without visual competition from the model outputs. We remain open to editorial guidance on this particular point. Please note that a mistake in the code originally impacted the generation of the first two rows of the maps, but has now been corrected and the figures updated accordingly, with no impact on the results and the conclusion of the article.

Lines 122–125: It might be useful to directly compare results between regions and species (e.g., alpine regions vs alpine species). For instance, could regional differences be driven by species composition? Was this tested?

Answer: We thank the Reviewer for this comment. The analyses were conducted at the species level and did not rely on predefined ecological species groups. While we agree that differences among biogeographic regions may be partly influenced by species composition, this was not formally tested. When preparing the manuscript, we deliberately chose not to implement a species-grouping approach, as many European bumblebee species occupy broad and overlapping climatic and geographical ranges, making any categorisation either subjective or unable to adequately capture the complexity of species distributions. We nonetheless noted this possibility in the Discussion section: *“Although the Alpine and Boreal regions show no net change at the community level, strong declines in ecological suitability for montane and arctic or arcto-alpine species suggest species turnover rather than stability in community composition.”*

Line 133: Can the research question be made clearer? For example, state explicitly that you are testing the predictability of the climate scenarios.

Answer: We thank the Reviewer for pointing out the lack of clarity regarding the objective of the Boyce Index analysis. Following this suggestion, we revised the text to explicitly state that this analysis tests whether observed historical climate conditions improve the predictive performance of ecological niche models relative to the counterfactual climate scenario. We also took this opportunity to address a related comment from Reviewer #2 by clarifying how this analysis differs from the preceding ecological suitability map analysis. The revised text now reads as follows: *“In addition to the ecological niche maps (Fig. 1), which illustrate and quantify changes in ecological suitability to climate change, we further tested whether historical climate conditions improved the predictive performance of our species-specific ecological niche models for observed bumblebee occurrences relative to the counterfactual climatic scenario.”*

Lines 139–141: This result is very interesting, but the question it addresses (climate impacts leading to better predictions) is not clearly set up in the introduction. Including your key questions at the end of the introduction would help highlight these important findings.

Answer: Following your suggestion, we now state the main research questions at the end of the Introduction section. As stated above, we have now also clarified the question answered by the Boyce index analysis at the beginning of the corresponding paragraph in the Results section (see also our answers to the related line-by-line comments).

Lines 207–209: ‘The Atlantic region exhibits comparatively smaller declines of ecological suitability relative to previously cited European biogeoregions, although regional negative trends are still apparent in our results.’ It would be helpful to expand on why this might be the case.

Answer: We have now expanded on the reason why this region might exhibit a smaller decrease in ESI (ecological suitability index) relative to other European biogeoregions. The revised text reads as follows: *“This smaller decrease may reflect the more moderate warming trends experienced in the Atlantic region relative to southern and continental Europe (Ali et al. 2022, Cambridge University Press), possibly owing to its oceanic climate and the cooling influence of the North Atlantic warming hole (Fan et al. 2023, Climate Dynamics).”*

Line 214: ‘reflects community-level ecological suitability gains’. please expand on what this means.

Answer: We acknowledge a lack of clarity with the wording that did not clearly make the connection with the ESI metric, and have now corrected this issue by referring explicitly to the ESI metric as follows: *“Importantly, this apparent stability does not indicate an absence of climate change influences, but rather results from spatially heterogeneous changes in the ESI, with increases in some areas (especially at the highest elevations and parts of Scandinavia) offset by decreases elsewhere.”*

Lines 236–238: Could you briefly expand on the methods used in this referenced study?

Answer: This sentence has now been edited as follows: *“Using species-specific ecological niche models trained on present-day environmental data and then projected on future environmental conditions expected under distinct shared socioeconomic pathways (SSPs), Ghisbain and colleagues (Ghisbain et al. 2024, Nature) estimated that, under a high greenhouse gas emission scenario, up to 76% of investigated ‘Least Concern’ European bumblebee species may experience losses of ecologically suitable habitat of over 30% by the end of the century.”*

Lines 244–255: Is there physiological or critical limits data to support this claim?

Answer: Indeed, there is. Therefore, we have now expanded the discussion to better support our interpretation by incorporating evidence from simulated heat-wave experiments on bumblebees, as well as studies reporting critical thermal limits for some high-altitude species. The revised text now reads as follows: *“This follows previous evidence of high sensitivity to heat in these species under simulated heatwaves (Martinet et al. 2020, Conservation Biology; Martinet et al. 2015, PLoS One). Moreover, critical thermal limits estimated for three North American species revealed that high-altitude species had lower heat tolerance than low-altitude ones (Oyen et al. 2016, Journal of Thermal Biology).”*

Line 249: ‘a subset of species’. please specify how many.

Answer: We have revised that sentence to report the proportion and number of species showing net suitability gains under climate change, consistent with the figures already reported in the Results section. The revised text reads as follows: *“Conversely, 38-51% of species (from 18 to 24 out of 47 species, depending on the reanalysis datasets) showed an average increase in ecological suitability under climate change.”*

Lines 254–256: It may also be interesting to mention microclimatic use or microclimates created in human-managed environments.

Answer: A modification has been made to incorporate the mention of favourable microclimatic conditions. We also added a new reference (Kerr *et al.* 2025, *Nature Reviews Biodiversity*) to further support this claim.

Lines 273–274: While this is a valid limitation, it would also be important to emphasize that this work is crucial for highlighting the impacts and negative consequences of climate change, even if specific drivers are difficult to disentangle.

Answer: Thank you for the suggestion. This aspect is now mentioned as the end of the limitation paragraph of the Discussion section. The revised text now reads as follows: *“Despite these limitations, our work remains key for highlighting the impacts and negative consequences of climate change.”*

Lines 282–286: You could also mention your geographic scope and whether global or cross-continental analyses might reveal different patterns. What is known about bumblebee declines in other regions?

Answer: The defined study area (the European area restricted to the region west of the 29°E meridian) is now explicitly mentioned and justified in the light of available data. To address the Reviewer's question about bumblebee declines in other regions, we have also added a sentence in the Discussion section to mention evidence of climate-driven declines in North American bumblebees (Kerr *et al.* 2015, *Science*, and Soroye *et al.* 2020, *Science*). The revised text regarding declines in other regions now reads as follows: *“These findings are consistent with previous evidence linking climate change to declines and range contractions in North American bumblebee species, suggesting that the impacts of climate change may converge across continents.”*

Lines 297–305: This paragraph is quite long and somewhat repetitive; consider shortening it.

Answer: Thank you for this suggestion. We have shortened this paragraph. The revised text now reads as follows: *“Furthermore, trends of declining suitability have been intensifying since the 1980s, likely linked to faster rates of warming across Europe, with expected increased impacts in the future. These findings provide clear evidence that climate change is already changing the ecologically suitable areas of insects, highlighting its pervasive impact on ecosystems. This approach provides a framework to quantify responses of organisms to warming trends and to identify areas and species most at risk. Addressing climate-driven declines will require both ambitious greenhouse gas emissions reduction policies and appropriate habitat management to buffer climate change impacts.”*

Methods:

Lines 315–320: Since some removed species are more widespread (and potentially more generalist), it would be interesting to see their individual results. Would this be feasible?

Answer: The species referred to were excluded before the ecological niche modelling analyses and were therefore not included in the subsequent modelling workflow. Consequently, no model output is available for these species. We specifically removed them based on a combination of (i) modelling quality criteria and (ii) expert assessment based on data representativeness (e.g., European occurrences not being representative of the biogeography of the species or the removal of cryptic species to avoid false presences). We acknowledge that some species are more widespread, but their inclusion was considered

likely to produce unreliable ecological suitability estimates in the current framework and thus would have impacted the reliability of the findings and overall conclusions.

Line 323: What was the original number of species/occurrences before filtering?

Answer: We now explicitly specified these data within the text: *“In total, the final dataset includes 829,448 occurrences from 47 species (see Figures S1 and S2 for the species distribution maps), out of the 1,728,495 occurrences from 67 species that were present before filtering, which were used for species-specific ecological niche model training.”*

Line 327: Specify ‘ecological niche model’ or ‘species distribution model’ instead of just ‘model’ for clarity.

Answer: A modification has been made to specify “ecological niche model” instead of “model”.

Lines 337–338: A reference is needed here.

Answer: We have now added the following reference to the sentence: *“Fourcade et al. (2014, PLoS One).”*

Lines 341–342: A reference is also needed here.

Answer: We have now added the following reference to the sentence: *“Phillips et al. 2009, Ecological Applications.”*

‘sampling pseudo-absences in a defined background area representing confirmed *Bombus* occurrences increases the probability of sampling in areas where a minimum of sampling effort was carried out, reducing the risk of misclassifying unsampled areas as true absences.’ Please clarify how this background area was defined.

Answer: The definition of the background area has now been added to improve clarity. The revised text reads as follows: *“This background area is defined as the study area grid cells that include one or more *Bombus* occurrences, excluding presence cells previously defined as such for the target species.”*

Lines 344–346: Why was the entire extent of Europe used rather than a buffer around the sampled area? Or was this already done?

Answer: We did not use a buffer around the sampled area because, due to the widespread nature of these specific species, applying any buffer would effectively encompass the entire study area considered here. As for the longitudinal limit of the study area, it was defined to include only European countries for which sufficiently reliable entomological survey coverage is available. This conservative approach was followed to reduce potential bias induced by heterogeneous data collection efforts across Europe and minimise the risk of unreliable generation of pseudo-absences. This aspect has now been further clarified in the Materials and Methods section.

Lines 367–369: This section on environmental variables should come before the model description.

Answer: This section has been moved accordingly and now appears in the Materials and Methods paragraph dedicated to the description of data acquisition.

Lines 398–402: The definition of regions should be introduced earlier (e.g., in the introduction), as this is the first clear explanation. Have you considered smaller-scale regional classifications, such as Köppen–Geiger or ecoregions? A method figure showing these regions and associated differences could be useful.

Answer: We thank the Reviewer for this suggestion. In the manuscript, biogeographic regions are defined in the Methods section with reference to the European Environment Agency classification, which we now more explicitly point to earlier in the Introduction section for more clarity. Regarding alternative regional classifications, we chose to use the European Environment Agency biogeographic regions because they were specifically designed for large-scale ecological analyses and are commonly used for conservation purposes. Moreover, biogeographical regions capture both broad climate and vegetation patterns, which are relevant for bumblebee species. In contrast, smaller-scale classification may not be appropriate given the resolution (0.5°) and objectives of our analyses.

Figure S12: The labels may be incorrect—please check that the correct figure has been uploaded with the correct title.

Answer: Thank you for having spotted this issue, which has now been corrected.

Remarks on code availability: high quality, consider uploading to a version-controlled platform like Zenodo.

Answer: A release of our GitHub repository has now been obtained with Zenodo and is associated with the following DOI: 10.5281/zenodo.20543144.

Reviewer #2

In NCLIM-26030934, the authors are attempting to tease apart the effects of climate change from other environmental changes using comparative back-casting. Specifically, they compared the predictive power of counterfactual climate conditions vs. factual conditions to quantify the impact of climate change on habitat suitability for European bumble bees. Counterfactual conditions used remote sensing data on factors other than climate (i.e., change in land-use) and current (2000-2019) climate to back-cast habitat suitability during six time periods. Factual conditions included historical land-use and historical climate data to predict habitat suitability. Disparities between the two projections denoted the effects of climate change on habitat suitability. They found that climate change accounted for 5-19% change in habitat suitability. Species responses were variable but, on average, habitat suitability declined in most regions. The most novel aspect of this paper is the comparative back-casting approach. It supports prior work indicating that habitat suitability is decreasing (Ghisbain et al. 2024) but differs from this previous paper by quantifying the effects of climate vs. other factors. The authors do an admirable job explaining the variation in response and not overstating the patterns, though I do have some questions about the methods that I believe need to be addressed.

Answer: Thank you very much for the positive and constructive feedback on our work.

My first concern is relatively easy to address. There are a few places where the methods need to be more clearly described, particularly for the broad audience of Nature. What the authors did (even in a general sense) was unclear without either reading forward to the methods or reading prior literature. Obviously, some details should be restricted to the methods or supplementary materials, but a more detailed

summary is required in the main text for the methods and results to be tractable (see my line-by-line notes below).

[Answer:](#) Thank you for these suggestions. The aspects are now more clearly introduced and presented in the main text (Results section), notably about the metrics used and the specificity of each analysis. See also our answers to the related line-by-line comments below.

The other main concern I have has to do with the models themselves. Little rationale is given for why some metrics are included, and others are not. For instance, impervious surface has the potential to have direct and indirect effects (through local climate) on habitat suitability. Without including it as a landscape change variable, changes in temperature due to increased impervious surface would be attributed to climate change. There should be solid rationale for why each variable (climate or land-use) is included (or not included, for important related variables).

[Answer:](#) We thank the Reviewer for this comment. We answered the comment below related to the consideration of impervious surfaces. Regarding the environmental factors considered in the study, we have now added a brief rationale in the Materials and Methods section to motivate the inclusion of these variables. We, however, also note that this selection is constrained by the ISIMIP3a framework used to conduct the climate attribution analyses.

This leads me to my last main recommendation. I recognize that the authors are focused on the effects of climate here. However, they are missing an incredible opportunity to “weight” the effects of land-use and climate change for bumble bee habitat suitability. Yes, quantifying the effects of climate change is informative, but quantifying the effects of both climate change and land-use is more powerful. Over the past 100 years, which has had the greatest effect on habitat suitability, climate or land-use? A counterfactual approach that does the opposite (uses historical climate and NOT land use change) would demonstrate the relative impact of urbanization. I personally feel like that piece deserves discussion, from both an ecological and conservation perspective.

[Answer:](#) We thank the Reviewer for this insightful suggestion. We agree that a counterfactual analysis comparing climate change vs land-use change effects would be highly valuable from both an ecological and a conservation perspective. However, the framework of the present study is specifically designed to isolate the effects of climate change alone, and we feel that such questions are out of scope at the moment. Currently, the land-use change categories used in this study are limited in two important aspects: (i) the categories themselves are too broad to distinguish floral resources availability and habitat quality/management, and (ii) their resolution is too coarse to properly define habitat quality/suitability. These problems, which do not affect the climatic variables, would make the results difficult to interpret and thus limit our ability to investigate such questions at the present time. However, we view such analyses as promising and would need further investigation in the future.

Line-by-line notes:

Lines 80-82. Why did you choose to use the current climate as the baseline for historical comparisons rather than starting with climate at the beginning of the dataset and projecting forward? The last 10 years have been the hottest on record and may not be the best baseline dataset as there is likely delayed responses (e.g., range expansion, evolutionary changes, etc.) I would think starting with the oldest

historical climate would be a more accurate measure of “fundamental” habitat suitability (albeit assuming no evolution).

Answer: The 2000-2019 period was chosen as the training baseline because it corresponds to the period used for our models training as well as representing the period with the most reliable, extensive, and spatially representative occurrence records across European bumblebee species. This rationale is now explicitly stated in the Materials and Methods section: *“This temporal coverage encompasses reliable and spatially extensive occurrence data available for European bumblebees, and corresponds to the time window used for ecological niche models training.”*

Lines 94-95. Describe the ecological suitability index. Yes, it has been used in previous papers, but I think it needs to be explained here as well. The definition provided here doesn’t really describe how the metric is calculated in a transparent way.

Answer: We now further explicitly define in that sentence the ecological suitability index (ESI) metric.

Lines 128-131. These results should be summarized in a supplementary table where the reader can evaluate the patterns themselves (without having to find them on GitHub).

Answer: Thank you for the suggestion – the average loss in ecological suitability due to climate change for each species and reanalysis dataset is now reported in a new Supplementary Information Table (Table S1).

Lines 133-135. Clarify how this analysis is different from the first analysis.

Answer: Modifications have been made regarding this opening sentence to explicitly add how this differs from the previous analysis. The revised text now reads as follows: *“In addition to the ecological niche maps (Fig. 1), which illustrate and quantify changes in ecological suitability to climate change, we further tested whether historical climate conditions improved the predictive performance of our species-specific ecological niche models for observed bumblebee occurrences relative to the counterfactual climatic scenario.”*

Line 137. Provide a brief summary of what you mean by “reanalysis dataset”. Did you rerun these projections with different subsets of data?

Answer: “Reanalysis datasets” refers to the alternative climate reanalysis products used to reconstruct historical climatic conditions and derive the climatic predictors used in the ecological niche models. It does not refer to different subsets of data or occurrence data, nor to different model projections. We have clarified this specifically referring to ‘historical climate reanalysis dataset’, following previous use of such term in the Introduction and Results section.

Line 157. Figure 2 doesn’t provide compelling support of the claim that BI differences increase through time. There is greater variance in BI through time, which of great interest, but I saw no support (statistical or graphical) for BI increases through time. To me this signals that species are diverging in how much climate is affecting habitat suitability – with some being potentially more impacted by land-use change.

Answer: It is indeed not the visualisations reported in Figure 2 that allow that claim, but rather the statistical results of the Wilcoxon-Mann-Whitney tests. This aspect has been corrected in the Results section. We now also report the results of these tests in a new Supplementary Information table (Table S2).

Lines 160-167. A summary table of these results (without having to go to GitHub) would again help the readers make their own evaluation of the results.

Answer: We agree and now also report the results of the Wilcoxon-Mann-Whitney tests reported and discussed in that paragraph in a new Supplementary Information table (Table S2).

Line 274. “induced” seems strong here, since not all other effects are indirectly influenced by climate. “amplified” might be more appropriate.

Answer: We agree with the Reviewer's comment and changed the word “induced” to “amplified” as suggested.

Line 377-379. Why was impervious surface not included as an environmental variable? It may be positively correlated with human population density, but it has the potential to change local temperature, which if not accounted for, could inflate the effects attributed to climate change.

Answer: An environmental variable covering impervious surface is not available in the ISIMIP framework we used. Consequently, it could not be incorporated into our counterfactual modelling approach. However, as rightfully stated by the Reviewer, we included human population density as a predictor, which is positively correlated with human population density, and therefore should, at least partially, cover such effects.

Lines 391-395. These metrics are critical to this paper and need to be described in more detail.

Answer: Thank you for your comment. We now provide a more detailed definition of those metrics.

Lines 418-421. Where are the results of the Wilcoxon-Mann-Whitney tests? Those should also be available in the supplementary materials.

Answer: These results were available on GitHub but are now also available in a new Supplementary Information table (Table S2).

Remarks on code availability: the code is well labeled and easy to read. A descriptive README file is provided. While I was able to review the script, I was not able to run it within the two-week time frame requested.

Mr Bastien De Tandt
Dr Simon Dellicour

Spatial Epidemiology Lab
Université Libre de Bruxelles
50 avenue F.D. Roosevelt
1050 Bruxelles, Belgium

Mr Bastien De Tandt
Dr Guillaume Ghisbain

Laboratory of Zoology
Research Institute for Biosciences
University of Mons
7000 Mons, Belgium

29-07-2026

Manuscript re-submission to *Nature Climate Change* (NCLIM-26030934A): “Declines in European bumblebee habitat suitability attributable to climate change” by Bastien De Tandt, Kyla Serres, Rosa Pietrojusti, Diana Erazo, François Massonnet, Denis Michez, Wim Thiery, Guillaume Ghisbain and Simon Dellicour.

Dear Editors,

On behalf of all authors, we are pleased to re-submit to *Nature Climate Change* a final revised version of our manuscript entitled “Declines in European bumblebee habitat suitability attributable to climate change”.

We would again like to express our gratitude to the editorial team and the two reviewers for the positive assessment and all the constructive comments on the previous versions of our manuscript. We have now revised our manuscript in response to the latest reviewers’ comments (see below for a point-by-point response to all comments).

Best regards,

Bastien De Tandt
Guillaume Ghisbain
Simon Dellicour

Reviewer #1

I am satisfied that the authors have addressed my previous questions/comments on the manuscript and think that they have significantly improved the manuscript in this revision. Previous areas that I found confusing are now well explained, and it was easy to follow. I think this study is really exciting, and I really enjoyed reading it!

Answer: Thank you very much for the positive feedback on our revised manuscript.

I have a couple of minor comments below:

Abstract: ‘.. with pronounced declines in southern and central regions. In contrast, in the Alpine and Boreal regions, gains at higher altitudes partially offset losses at lower latitudes and altitudes, resulting in minimal net changes’ Because there are alpine regions in central Europe this is a little confusing. Could you change to something like southern Europe, and lowland central Europe.’?

Answer: We thank the Reviewer for pointing out this lack of clarity. The sentence has been revised accordingly. Following editorial guidance, the abstract now reads as follows: *“Climate change is increasingly implicated in the decline of insect pollinator populations, which provide critical ecosystem services. Isolating its contribution from other co-occurring environmental stresses remains challenging yet crucial for informing conservation strategies and mitigating biodiversity losses. Here, we compare predictions of ecologically suitable areas for European bumblebee species from 1901 to 2019 under factual and counterfactual scenarios to investigate the impact of climate change in these areas. Community-level ecological suitability was reduced by climate change across Europe by 5% on average and up to 19% locally, with pronounced declines in southern and lowland central regions. In contrast, in the Alpine and Boreal regions, habitat suitability gains at higher altitudes partially offset losses at lower latitudes and altitudes, resulting in minimal net changes. Our results demonstrate that climate change is reshaping the ecologically suitable areas for these key pollinators and represents a pervasive pressure on European wildlife.”*

Line 64-65: Although you are both using attribution frameworks, I think the underlying methodology seems quite different?

Answer: We thank the Reviewer for this comment. Although this sentence was added following the suggestion of the Reviewers during the previous round of revision, we have now removed it in the current revision to comply with the Editor’s request to shorten and streamline the manuscript.

140-141: It would be great if the species-specific scenarios were uploaded as part of the supplementary instead of the github – this would mean everything is available in one place for anyone interested, and would not be certain the information is retained across time.

Answer: We thank the Reviewer for this suggestion. Including the species-specific projections in Supplementary Information would be complicated given the large number of files (we have modelled 47 species under four different reanalysis datasets, for a total of 188 PDF files). If requested by the editorial team, we could still provide an archive gathering the 188 PDF files as Supplementary Information. We, however, prefer the current option where these species-specific projections are available both on GitHub

and in the study's Zenodo repository (<https://zenodo.org/records/21620753>), which provides a permanent archive.

179-196 . In addition to the per-species tests, if you wanted to test if, over time, the proportions of mean BI are increasing, could you not test for statistical differences between time groups? Or even between SSPs/time groups?

Answer: We thank the Reviewer for this suggestion. In the original analysis, we tested whether the Boyce Index (BI) differences were significant using one-sided and two-sided Wilcoxon-Mann-Whitney tests only for the latest time period (2000-2019). In the revised manuscript, we extended that analysis to all time periods. This allowed us to quantify how the proportion of species showing significant positive, negative, or overall BI differences changed through time, and thus assess whether the influence of climate change on model performance increased towards recent decades. The results show an increasing proportion of species with significantly positive BI differences over time, supporting our original interpretation. Please note that due to the manuscript word limit, the detailed BI analysis and associated results have been moved to the Supplementary Information, while the main text now summarises the key findings.

Reviewer #2

Thank you for your thorough response to my questions and recommendations. Your work advances our understanding of how climate change affects European bumble bee distributions. I think your approach has broad applications, and I look forward to seeing how it is used in other contexts.

Answer: Thank you very much for the positive feedback on our work.