Climate change is predicted to disrupt patterns of local adaptation in wild and cultivated maize

Jonás A. Aguirre-Liguori, Santiago Ramírez-Barahona, Peter Tiffin and Luis E. Eguiarte

Review timeline

Original submission:	27 February 2019	Note: Reports are unedited and appear as
Revised submission:	6 June 2019	submitted by the referee. The review history
Final acceptance:	17 June 2019	appears in chronological order.

Review History

RSPB-2019-0486.R0 (Original submission)

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?
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?
Yes

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
Yes

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?
Yes

Comments to the Author
Comments on the manuscript RSPB-2019-0486
The manuscript is a comprehensive analysis of adaptation of maize landraces to climate change. Is relevant not only because of the importance of maize sustainability under clkimate change, but also because of its innovative approach, which integrates ecological niche modeling and genomic information. Therefore, I recommend minor revisions.
The authors should clarify many specific expressions for readers, which are not familiar with genetics. Since my area of expertise is climate modeling, I have a hard time to understand some acronyms such as SNPs, etc.
Most of the relationships that includes adaptative scores against geographic locations, annual temperature appear to be rather weak (regression coefficients close to 0). This suggest that relationships between the scores and climate change are affected by several sources of uncertainties. Most of this is not clearly discuss in the manuscript.
In Page 5 line 100, it is mentioning climate models results were validated. Since climate models are affected by several sources of biases and uncertainties, it is crucial to assess whether geographical distribution is properly represented under current climate conditions. I would like to see more details regarding the validation.

Decision letter (RSPB-2019-0486.R0)

16-May-2019

Dear Dr Ramirez-Barahona:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor)

and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

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

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

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

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

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

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

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

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

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

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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.

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

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

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

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

Best wishes,
Professor John R. Hutchinson, Editor
Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
This paper was evaluated by one reviewer and a handling editor (Hellmann). Both agree that the paper is interesting and important. It is well-written and will have broad appeal to readers of the Proceedings of the Royal Society.

Still, there are improvements and clarifications that can be made in the manuscript and further revision is needed. Please address the reviewer's comments in a revision and detailed response, as well as the following:

—While I agree in spirit that species range projections do not sufficiently include genetic information and local adaptation, the claim that it hasn't been considered (or considered very little) is a tad overblown. Concern about the whole-species representation in niche models and the importance of population differentiation in species' responses to climate change has been raised for quite a long time (e.g., Pelini et al. 2009 PNAS; O'Neil et al. 2014 Mol Ecol). I'd focus instead on the comprehensiveness of this study as a strength, e.g., despite awareness of the

importance of local adaptation, there are relatively few analyses that examine genetic based traits across the entire genome for multiple species in a niche modeling framework.

—The last sentence of the abstract is a tad obvious and vague. I'd substitute with a more specific finding of the study. For example, the conclusion from lines 255-257 that both climatic response and future adaptation are a function of historic climatic selection. Or lines 287-288 that populations with high genetic diversity show high genomic offset.

—I don't understand how adaptation of teosintes to warm and dry climates is indicative of local adaptation, i.e., differences in climatic tolerance among species or races. (Line 65 on p. 3.)

—How do you know that local adaptation and population differences in teosintes has not been "directed by cultural and agronomic practices" (line 68)? Please explain.

—I agree that more biological information *should* generate more realistic predictions under climate change, but it's a claim that it *will* (line 79).

—There are other papers than refs 30-33 that have modeled some aspect of population differences, e.g., Hällfors et al. 2016 Ecol App. I'd agree that there aren't many, but there are more than a "couple." Again, the strength of this work is how comprehensively it is done, how much genetic information is available for modeling and how well genetic data can be correlated and explored with climatic factors. Note also that line 124-125 partially contradicts that there's been little work on modeling that includes local adaptation. As well, there are other modeling efforts that consider genetics and climatic responses, but they are process oriented (not statistical like niche models), e.g., RangeShifter of Travis group at Aberdeen.

—I was confused on line 159 about "suitable areas for local adaptation"—these are areas where genes for local adaptation (historically) are still present and appropriate for the climate or areas where new local adaptation (i.e., future evolution) can take place? In other words, "locally adapted" to what?

—I'd like to know more about how alleles are handled in the circuit theory migration models. Do alleles move only as packaged in individuals or can they move independently? If the latter, how?

—Please clarify on p. 8–for a general reader—about the relationship between teosinte and land races of maize. This is done in the discussion (line 324); move that to the introduction.

—It strikes me that there is some material in the results/discussion that can be moved to the methods. I got the impression that these were new, additional methods because they were explained in the data interpretation section.

—I suggest some degree of caution in using the term "local adaptation." You assume traits that differ among populations and are associated with climatic conditions are locally adapted. I'd make that assumption clear. (For example, see treatment in O'Neil et al. 2014 that genetic differences among populations that are associated with local climate are likely—but not necessarily—the products of local selection to climate.)

—Though p. 13 explores future adaptive variation more thoroughly, I think it wise to acknowledge at line 261 that novel combinations could be the basis of adaptive evolution (i.e.,could be positive while likely a problem).

—It's been said many times before that "we conclude that although highly useful, distribution models are an oversimplification…" (line 321). I agree that you need to recognize this, but it's

really not a novel finding. Think you can tone this down or move this point to the background so that your most novel findings stand out more prominately.

Reviewer(s)' Comments to Author:

Referee: 1

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Author's Response to Decision Letter for (RSPB-2019-0486.R0)

See Appendix A.

Decision letter (RSPB-2019-0486.R1)

17-Jun-2019

Dear Dr Ramirez-Barahona

I am pleased to inform you that your manuscript entitled "Climate change is predicted to disrupt patterns of local adaptation in wild and cultivated maize" 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.

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

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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,

Professor John Hutchinson
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
The authors provided thoughtful replies to the reviewer comments. I do not have any further concerns about the analyses or its presentation.

Appendix A

Professor John R. Hutchison

Editor

Proceedings of the Royal Society B

Dear Professor Hutchinson,

We thank you, the reviewer and the handling editor for the thorough and constructive reviews provided on the initial submission of our manuscript "Climate change is predicted to disrupt patterns of local adaptation in wild and cultivated maize" (ID RSPB-2019-0486). We also thank you for the opportunity to revise the manuscript. Below we describe how we have responded in a point-by-point manner to the reviewer and editor comments. When possible, we have added the lines and specific changes that were made in the main text, and attached a file containing all the major track changes.

We look forward to hearing from you,

Dr. Santiago Ramírez-Barahona
Dr. Luis E. Eguiarte

Comments to Author:

This paper was evaluated by one reviewer and a handling editor (Hellmann). Both agree that the paper is interesting and important. It is well-written and will have broad appeal to readers of the Proceedings of the Royal Society.

Still, there are improvements and clarifications that can be made in the manuscript and further revision is needed. Please address the reviewer's comments in a revision and detailed response, as well as the following:

—While I agree in spirit that species range projections do not sufficiently include genetic information and local adaptation, the claim that it hasn't been considered (or considered very little) is a tad overblown. Concern about the whole-species representation in niche models and the importance of population differentiation in species' responses to climate change has been raised for quite a long time (e.g., Pelini et al. 2009 PNAS; O'Neil et al. 2014 Mol Ecol). I'd focus instead on the comprehensiveness of this study as a strength, e.g., despite awareness of the importance of local adaptation, there are relatively few analyses that examine genetic based traits across the entire genome for multiple species in a niche modeling framework.

RESPONSE 1: Thank you for pointing this out and also for providing relevant references, we agree that the wording in the original submission did not give proper credit to these previous studies.

In the revised manuscript we have re-phrased this paragraph. Following your suggestions we have added the following sentences to the end of this paragraph (lines 84-90):

> "However, given that local adaptation is common, among-population variation in climatic tolerances and varying levels of climate-gene relationships across the genome are expected[26,35]. This variation could have important consequences for population and species responses to a changing climate[32,34]. However, there are relatively few studies that have integrated adaptive divergence among sub-populations into ecological niche modeling to predict species' response to climate change[34,35,37,38]."

—The last sentence of the abstract is a tad obvious and vague. I'd substitute with a more specific finding of the study. For example, the conclusion from lines 255-257 that both climatic response and future adaptation are a function of historic climatic selection. Or lines 287-288 that populations with high genetic diversity show high genomic offset.

RESPONSE 2: Thank you for pointing this out and also for the suggested changes to improve the manuscript. As you recommend, we have replaced the last sentence of the abstract with a brief mention of what we think are the most interesting findings. We have also made other minor changes to the Abstract in order to better communicate the strengths of the paper. The Abstract now reads (lines 24-42):

"Climate change is one of the most important threats to biodiversity and crop sustainability. The impact of climate change is often evaluated on the basis of expected changes in species' geographical distributions. Genomic diversity, local adaptation, and migration are seldom integrated into future species projections. Here we examine how climate change will impact populations of two wild relatives of maize, the teosintes *Zea mays* ssp. *mexicana* and *Z. mays* ssp. *parviglumis*. Despite high levels of genetic diversity within populations and widespread future habitat suitability we predict that climate change will alter patterns of local adaptation and decrease migration probabilities in more than two-thirds of present-day teosinte populations. These alterations are geographically heterogeneous and suggest that the possible impacts of climate change will vary considerably among populations. The population-specific effects of climate change also are evident in maize landraces, suggesting that climate change may result in maize landraces becoming maladapted to the climates in which they are currently cultivated. The predicted alterations to habitat distribution, migration potential, and patterns of local adaptation in wild and cultivated maize, raise a red flag for the future of populations. The heterogeneous nature of predicted populations' responses underscores that the selective impact of climate change may vary among populations and that this is affected by different processes, including past adaptation."

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—I don't understand how adaptation of teosintes to warm and dry climates is indicative of local adaptation, i.e., differences in climatic tolerance among species or races. (Line 65 on p. 3.)

RESPONSE 3: Unfortunately, we did not adequately explain our reasoning in the original submission. What we meant to communicate was not that teosinte adaptation to warm dry climates is indicative of local adaptation but rather than there is among-population variation within each of the subspecies that is indicative of local adaptation. In revising we have been careful throughout the manuscript to avoid the confounding of species level properties with variation among populations within the species. We have re-phrased this paragraph to make the idea more clear (lines 69-72). It now reads:

> "Genomic analyses in teosintes have identified significant genetic differences between populations that are associated with varying local climates, suggesting local adaptation to contrasting environments (*e.g.,* warm and dry climates) is common in teosintes[18,25-27]. Teosinte populations locally adapted to warm and dry environments are likely to contain alleles that could reduce the negative effects of global warming and increased aridity."

—How do you know that local adaptation and population differences in teosintes has not been "directed by cultural and agronomic practices" (line 68)? Please explain.

RESPONSE 4: You are correct in that we can not be absolutely certain and in the initial submission we did not provide an adequate explanation for our claim. Our claim is based on the fact that teosintes are not cultivated in Mexico and many populations (especially *Zea mays* ssp. *parviglumis*) are found away from areas in which maize are grown. In the revised version of the manuscript we have clarified this point (lines 75-79). Specifically we write:

> "Given that teosintes are not cultivated in Mexico, genetic variation should not have directly affected by the cultural and agronomical practices influencing maize landraces[10,28]. Thus, patterns of gene-environment associations in teosinte populations might prove useful as a blueprint of local adaptation for crop improvement and mitigation in maize landraces."

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—I agree that more biological information *should* generate more realistic predictions under climate change, but it's a claim that it *will* (line 79).

RESPONSE 5: Agreed. We edited the sentence accordingly (**see RESPONSE 1**).

—There are other papers than refs 30-33 that have modeled some aspect of population differences, e.g., Hällfors et al. 2016 Ecol App. I'd agree that there aren't many, but there are more than a "couple." Again, the strength of this work is how comprehensively it is done, how much genetic information is available for modeling and how well genetic data can be correlated and explored with climatic factors. Note also that line 124-125 partially contradicts that there's been little work on modeling that includes local adaptation. As well, there are other modeling efforts that consider genetics and climatic responses, but they are process oriented (not statistical like niche models), e.g., RangeShifter of Travis group at Aberdeen.

RESPONSE 6: Thank you for pointing this out and we agree the wording in the original submission was inaccurate and needed improvement. Following your suggestions we have re-phrased this paragraph and also added additional references (**see RESPONSE 1**).

—I was confused on line 159 about "suitable areas for local adaptation"—these are areas where genes for local adaptation (historically) are still present and appropriate for the climate or areas where new local adaptation (i.e., future evolution) can take place? In other words, "locally adapted" to what?

RESPONSE 7: We changed the wording of this section in order to make it clearer (lines 183-197). We now write:

> "*Allele distribution models.* Since the climates of the future are predicted to be warmer, we were interested in modeling the distribution of the putatively warm-adapted alleles at each putatively adaptive SNP (SI Appendix). For this, we used Maxent v.3.3.3[39] to predict the future geographic distribution of warm-adapted alleles, using the corresponding populations' geographic coordinates where

these alleles were recorded as input. We used the same settings and validation procedures used for the species distribution models (see above). We generated binary presence/absence distribution models for each warm-adapted allele for the present and for future climate models (SI Appendix). We estimated the geographic overlap between the present model and each future model to define areas where at least five alleles are predicted to occur in the future, indicating favorable areas where the current gene-environment relationships will remain. We cross validated the allele distribution models using the Gradient Forest models by inspecting the genomic offset of populations for three sets of regions: present-only, future-only, and overlap."

—I'd like to know more about how alleles are handled in the circuit theory migration models. Do alleles move only as packaged in individuals or can they move independently? If the latter, how?

RESPONSE 8: Basically, the estimation of migration probabilities is performed on a population-by-population basis. These estimates are based on the joint distribution of at least five adaptive alleles, thus there is the implicit assumption that alleles are packaged within populations. We modified the text to make this more clear (Lines 198-213). Also, these changes are complemented by a more detailed explanation of the allele distribution models, on which the migration analyses are based (**see RESPONSE 7**). The section on migration now reads:

"Barriers to migration. Based on the joint distribution models for the putatively warm-adapted alleles, we approximated the potential capacity of populations to migrate into the new regions predicted under future climate scenarios using circuit theory[48]. This represents a simplified model of population migration based solely on a handful of alleles and assumes that population migration would be mostly limited by current local adaptation. We constructed maps of potential migration using the present and future distribution models for putatively warm-adapted alleles to determine landscape resistance (environmental distances) as a proxy of limitation to the successful migration, where increasing resistance

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indicates decreasing probabilities of allele movement (SI Appendix). These maps of potential migration based on the joint distribution of warm-adapted alleles, for which suitable areas were defined as those predicted with at least five alleles. For each sampled population, we constrained our analyses to a 1⁰x1⁰ degree grid-cell centered on that population. We used the 10-percentile of resistance values as a minimum threshold to estimate migration potential, which can be interpreted as the resistance to successful migration into at least 10% of the future areas of potential settlement (SI Appendix)."

—Please clarify on p. 8–for a general reader—about the relationship between teosinte and land races of maize. This is done in the discussion (line 324); move that to the introduction.

RESPONSE 9: Thank you for pointing this out, we have modified the Introduction accordingly to make the relationship between teosintes and maize clearer (lines 53-67). It now reads:

"Cultivated landraces of maize (*Zea mays* ssp. *mays*) have a close association with their wild relatives, the teosintes, throughout their evolutionary history. Maize was domesticated in Mexico from lowland teosinte (*Zea mays* spp. *parviglumis*) nearly 9,000 years ago[13], with subsequent introgression from highland teosinte (*Zea mays* spp. *mexicana*) that allowed cultivated maize to grow at higher elevation environments, particularly in Central Mexico[14,15]. More than 200 Latin-American landraces of maize have been described, which are the result of past and on-going sociocultural processes that shape and maintain extraordinary biodiversity in this species[16,17]. Teosintes grow wild in Mexico under a wide range of climatic conditions, from very hot and humid coastal environments to temperate and dry inland regions[10,18,19]. Maize land races have an even wider geographic and environmental range[4,15,20]. Historical (as mentioned above) and current evidence of gene flow from teosintes into maize and the presence of fertile hybrids[21,22] indicates that gene introgression into landraces is possible.

Such introgression could be important in enabling maize to continue to evolve in response to new environmental challenges[18,23]."

—*It strikes me that there is some material in the results/discussion that can be moved to the methods. I got the impression that these were new, additional methods because they were explained in the data interpretation section.*

RESPONSE 10: We agree there were methodological aspects in the results and discussion sections. When possible we moved the sentences to methods and modified the main text accordingly.

—*I suggest some degree of caution in using the term "local adaptation." You assume traits that differ among populations and are associated with climatic conditions are locally adapted. I'd make that assumption clear. (For example, see treatment in O'Neil et al. 2014 that genetic differences among populations that are associated with local climate are likely—but not necessarily—the products of local selection to climate.)*

RESPONSE 11: We completely agree with the editor on exercising more caution in use of the term 'local adaptation'. We made changes throughout the main text when possible to have a more cautious language when referring to local adaptation For example, in lines 69-72 we added the following:

> "Genomic analyses in teosintes have identified significant genetic differences between populations that are associated with varying local climates, suggesting local adaptation to contrasting environments (*e.g.,* warm and dry climates) is common in teosintes[18,25-27]."

Also, in the Methods section, after we present the methods used for SNP detection, we added a sentence indicating that these SNPs need to be analyzed with caution (lines 127-134). These sentence read:

> "On the contrary, the presence of SNPs with significantly high genetic differentiation are presumable affected by divergent selection enhancing allele frequency differences between populations. The SNPs identified through these

methods bear statistical signatures consistent with local adaptation to climate. However, we caution that their functional importance has not been experimentally validated and statistical approaches to identify locally adapted genetic variants, such as those used here, are likely to include false positives and may include variants that differ due to non-adaptive processes."

—*Though p. 13 explores future adaptive variation more thoroughly, I think it wise to acknowledge at line 261 that novel combinations could be the basis of adaptive evolution (i.e.,could be positive while likely a problem).*

RESPONSE 12: Thank you for this suggestion, we have added the possibility of novel combinations of alleles conferring adaptive advantages under future climates (lines 305-309). We now edited these sentences:

"The putatively warm-adapted alleles are expected to confer selective advantages to expanding warmer and drier environments, yet populations lacking these alleles might follow a different evolutionary trajectory to adapt to climate change. In this context, standing 'neutral' genetic diversity or new mutations could act as an important source of variation for future local adaptation[1,5,52,53] through the generation of novel allele combinations serving as the basis of future adaptive evolution."

—*It's been said many times before that "we conclude that although highly useful, distribution models are an oversimplication…" (line 321). I agree that you need to recognize this, but it's really not a novel finding. Think you can tone this down or move this point to the background so that your most novel findings stand out more prominately.*

RESPONSE 13: We agree and thank you for pointing this out. We have rewritten the ending sentences to (hopefully) make them more interesting and to draw more attention to what we think are the substantive contributions of the paper (lines 421-428). Specifically, we now write:

"Our results show the relevance of moving beyond the standard species distribution models to assess climate change impacts[30-38] how the analysis of genomic data can identify important genetic resources to aid wildlife conservation and crop sustainability under a rapidly changing climate. However, our approach remains an oversimplification of the complex evolutionary and ecological processes affecting populations[36,50,52,60,61]. This underscores the need for continued integration of agronomical practices, genomic data, and climate models to better understand the impacts of a rapidly changing climate on cultivated and wild species."

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The manuscript is a comprehensive analysis of adaptation of maize landraces to climate change. Is relevant not only because of the importance of maize sustainability under clkimate change, but also because of its innovative approach, which integrates ecological niche modeling and genomic information. Therefore, I recommend minor revisions.

RESPONSE 14: We appreciate this positive assessment of the approach.

The authors should clarify many specific expressions for readers, which are not familiar with genetics. Since my area of expertise is climate modeling, I have a hard time to understand some acronyms such as SNPs, etc.

RESPONSE 15: In revising the manuscript we have tried to avoid jargon or acronyms that will not appeal to a broad readership (for example we have now defined in different sections that SNPs are single nucleotide polymorphisms, and avoided used GF and rather used gradient forest). Whenever possible we tried to keep acronyms such as

paSNPs and canSNPs to a minimum, and instead used the full description: putative adaptive and candidate SNPs.

For example, SNPs are briefly explained on first mention (lines 116-117):

> "…a dataset of 33,454 high quality single-base bi-allelic genetic variants, known as single nucleotide polymorphisms (SNPs)…"

Also, we give a more detailed explanation on the how candidate SNPs were identified based on genetic differentiation (lines 121-131). This reads:

> "The sets of locally adapted SNPs used here are described in detail by ref.[26], who used *Bayescenv*[41] and *Bayenv*[42] to identify locally adapted SNPs with significant genetic differentiation among populations (F_{ST}) and significantly associated with temperature and precipitation (SI Appendix). SNPs that show genetic differentiation within the expected distribution of F_{ST} across the genome are presumably affected mainly by neutral processes (hereafter referred to as reference SNPs). On the contrary, the presence of SNPs with significantly high genetic differentiation are presumable affected by divergent selection enhancing allele frequency differences between populations. The SNPs identified through these methods bear statistical signatures consistent with local adaptation to climate."

At the same time, we acknowledge that the paper relies heavily on genetics and think that thorough explanations of some of the genetic aspects of the manuscript would likely make the paper less appealing to molecular ecologists and ecological geneticists. We have tried to hit a balance, and hope we have succeeded.

Most of the relationships that includes adaptative scores against geographic locations, annual temperature appear to be rather weak (regression coefficients close to 0). This suggest that relationships between the scores and climate change are affected by several sources of uncertainties. Most of this is not clearly discuss in the manuscript.

RESPONSE 15: We think the confusion here arose from some poor phrasing in the initial submission. In that submission we confounded regression and correlation, we

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also reported regression coefficients, but did not report r^2 values, which are needed to evaluate the strength of the relationship between the response and predictor variables.

In the revised MS, we report not only the regression coefficients, but also the r^2 (line 368)¡ but only for the significant regressions. We note that our discussion focuses on the relationship between allele frequencies and temperature. The regression coefficient here is, in fact, very low (β = 0.01). But this is because the response variable data covers a range between 0.4 and 0.6 (*i.e.*, 0.2) where as the predictor variable has a range of 10. The important coefficient here is the r^2 = 0.27 (equivalent to a 0.51 Pearson correlation), which is quite high given the multiple sources of uncertainty in our models. For the non-significant regressions, we did not report the r^2.

In Page 5 line 100, it is mentioning climate models results were validated. Since climate models are affected by several sources of biases and uncertainties, it is crucial to assess whether geographical distribution is properly represented under current climate conditions. I would like to see more details regarding the validation.

RESPONSE 16: We agree that this is an important aspect of our analyses. We have followed the validation methodologies of Hufford et al. (2012) and of Aguirre-Liguori et al. (2017, 2019). We now added more details on model construction and validation in the supporting methods (page 11). It now reads:

> *"Species distribution models.* We used 254 (*mexicana*) and 329 (*parviglumis*) occurrence data points (available at: www.biodiversidad.gob.mx/genes/ proyectoMaices.html) and performed the modeling with Maxent v.3.3.3[14] using previously described settings and validation procedures[2,15,16]. We used all 19 available variables in the WorldClim database[11] following the same procedures as of refs.[2,1416]. In addition, ref.[16] compared species distribution models for the two teosinte subspecies obtained using the 19 bioclimatic variables with models constructed after removing correlated variables, finding strong correlations between the predictions (> 0.9). For validation we used 10 bootstrap replicates for each model using a 30% random sample of occurrence records as test data. We used the Area Under the Curve (AUC) of the Receiver Pperating

Characteristic (ROC) to assess model performance, resulting in species models with AUC values of 0.982 and 0.972 for *mexicana* and *parviglumis*, respectively, indicating good model performance."

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