nature portfolio

Peer Review File

Using species ranges and macroeconomic data to fill the gap in costs of biological invasions

Corresponding Author: Dr Ismael Soto

Version 0:

Decision Letter:

21st May 2024

*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Dr Soto,

Your Article, "Quantifying the hidden costs of biological invasions" has now been seen by four reviewers. You will see from their comments copied below that while they find your work of considerable potential interest, they have raised quite substantial concerns that must be addressed. In light of these comments, we cannot accept the manuscript for publication, but would be very interested in considering a revised version that addresses these serious concerns.

We hope you will find the reviewers' comments useful as you decide how to proceed. If you wish to submit a substantially revised manuscript, please bear in mind that we will be reluctant to approach the reviewers again in the absence of major revisions.

Please note that I have also pasted the 'comments to editors' provided by Reviewer 1 (with that reviewer's permission). These comments do overlap with that reviewer's comments to authors, but they emphasise the extent of the reviewer's concerns, so I though it helpful to include them. It is not essential to include these comments also in your point-by-point response but please consider them carefully as you respond to Reviewer 1's comments to authors.

If you choose to revise your manuscript taking into account all reviewer and editor comments, please highlight all changes in the manuscript text file.

We are committed to providing a fair and constructive peer-review process. Please do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

If revising your manuscript:

* Include a “Response to reviewers” document detailing, point-by-point, how you addressed each referee comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the referees along with the revised manuscript.

* If you have not done so already we suggest that you begin to revise your manuscript so that it conforms to our Article format instructions at http://www.nature.com/natecolevol/info/final-submission. Refer also to any guidelines provided in this letter.

* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

Please use the link below to submit a revised paper:

Link Redacted

Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

If you wish to submit a suitably revised manuscript we would hope to receive it within 6 months. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. This applies to primary research papers only. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit please visit www.springernature.com/orcid.

Please do not hesitate to contact me if you have any questions or would like to discuss the required revisions further.

Thank you for the opportunity to review your work.

[redacted]

Reviewer comments:

Reviewer #1 (Remarks to the Author):

This paper selects a subset of invasive species from the InvaCost database that have reported management and damage costs at the country level. For each of these species, the paper uses species distribution modeling (SDM) to estimate the suitable area in each country with reported occurrences. Using data from countries with reported occurrences and damages, an economic cost model is then fit with estimated SDM suitable area, GDP, population and agricultural land area as predictors. This cost model is then used to estimate projected damages and costs in countries with reported occurrences but unreported costs.

The economic cost model was originally used in a paper focused on the European Union by many of the same authors (Henry, et.al), where country area, GDP, population and agricultural value added were used as predictors in the cost model. The novel feature of this paper is its use of SDM to estimate suitable area for each species. This is then used as a predictor in the cost model, with the value added predictor replaced by agricultural land area.

The paper restricts cost models to a 4 parameter family of weighting functions specified as sums over products of ratios of predictor variables across countries raised to a power, where the power parameters vary across the 4 predictors, hence 4 parameters (eq. 2). Parameters may be positive or negative. This basic model is extended to include a (logistic) time trend and a lag phase for costs, potentially adding 3 more parameters, 2 for the logistic and 1 for the lag phase. Based on the AIC, the preferred model in the paper is a 4 parameter model that ignores population and agricultural land area, but includes GDP, suitable area and the 2 logistic time trend parameters. The parameter on suitability is approximately 0.15. This significantly modulates the role of suitable area, implying that an unreported cost country with double the suitable area relative to a reported cost country is projected to have costs that are about 10% higher than the reported country, while the projected costs in a country with half the suitable area would only decrease by about 10%, all else equal. The biggest drivers of the cost estimates from this model appear to be GDP and time since first reported occurrence. Were any other variables considered as predictors? The value of agricultural production, for example? FAOSTAT is a large repository of data on agricultural production in countries around the world.

Given the objective of predicting costs in countries where they are unreported, why was the specific parametric model in (2) selected relative to other alternative specifications, that could include either parametric or machine learning alternatives?

The paper argues (p. 17) that it meticulously adheres to established standards as set forth in Araújo, et.al (Science Advances, 2019). The paper has clearly made a substantial effort in this direction, particularly with regard to SDM. However, the authors suggest that model selection and uncertainty quantification are not applicable. Given the nature of the models used in the analysis it is unclear how this can be. Choices made in model and variable selection, parameter uncertainty, and measurement error in the data almost certainly affect the cost estimates in the paper.

The extent to which costs in the InvaCost data are globally representative deserves more attention, including more discussion of potential biases.

Cost effective management methods are different in developed nations than in developing countries due to the relative costs and availability of different management inputs. Likewise, even for similar suitable areas it is likely that crops, production inputs and yields differ according to a country's development status, leading to differences in damages. Labor is relatively cheaper in less developed countries, while chemical, biological, or capital inputs may be more efficient in developed nations. What are the consequences of these differences for using management costs and damages measured in developed nations to project costs in less developed countries, where management costs or damages are not well documented? To what extent does species area suitability correlate with production of host crops? Species suitability for an area does not necessarily imply the area's products are susceptible to damage, or that the underlying variation can be captured by including GDP, population and agricultural land area. Finally, how much do these differences matter across the set of species considered in this paper?

In relation to the standards set forth in Araújo, et.al , more attention could be given to: S2.2C. Uncertainty in predictor variables; S2.3. Guidelines for model building including model complexity, treatment of bias and noise in response variables, and dealing with modeling and parameter uncertainty; S2.4. Guidelines for model evaluation, including model assumptions, outputs and performance. Specific suggestions include: improved quantification of uncertainty, better discussion of model validation – particularly with regard to the economic cost model in (2), and more consideration of robustness to modeling choices and

assumptions. It would be very informative to elucidate how well the model in (2) performs across species and to provide regression statistics for the preferred economic cost model.

Management costs can be incurred by private agents or by the public sector. How does this impact model specification? For example, while GDP may proxy for public sector management costs, GDP per capita may be a better proxy for private agent's ability and willingness to pay for management.

For many species, producers can mitigate pest risk by switching to alternative crops that are less susceptible to damage. How does potential adaptation influence the results?

The discussion and presentation often reports interpolated costs and percentage changes with 2 decimal precision. This provides a misleading sense of precision in the estimates. Some attempt at uncertainty quantification would be useful (predictive, parameter and model uncertainty). For example, the original costs in the InvaCost database are imprecise estimates. Second, the models used to build up the interpolated estimates each comes with some uncertainty. Third, the fitted parameters of these models are uncertain. The reader is left to ponder what 90% confidence bounds on interpolated costs might look like, for example, and how many would include zero? It might not be possible to answer this question, but more robustness checks and characterizing uncertainty seems useful.

Clarity:
• Tables S2-S3 report model statistics (AIC, likelihood) and parameters for 31 different model specifications. The value of reporting 31 different models is unclear, considering that the probability of a model being the best among those considered is close to zero for many of the alternatives.
• The use of a comma as a decimal separator in various places is potentially confusing to the reader, particularly given that a comma separates thousands, millions, etc. in the main body of the paper.
• Is 2021 the base year for the cost model predictors? Given the time varying nature of the anthropogenic predictors, what Is the rationale for selecting a particular base year?

Reviewer #2 (pasted Remarks to Editors)"

Unfortunately, the economic cost model is not well validated. First, it is unclear how well the cost model predicts on the training data, for each of the 162 species being considered. Second, the training data is from countries where management and damage costs have been reported. These are primarily developed countries in Europe and North America. This introduces bias that should be addressed. The paper implicitly assumes GDP, population and agricultural land area suffice to explain cross country variations in the links between species suitable area -> species occurrence area -> agricultural host area -> management -> management cost and damages. Without stronger validation, it is difficult to be convinced that the model is a good one and that the cost estimates are meaningful.

The estimates are presented as if they are extremely precise, with almost no effort at uncertainty quantification or robustness checks. The reader is left with very little understanding of how robust the estimates are to various modeling choices that have been made. This includes:
• The type of species distribution model. Elith et.al consider 16 different SDMs, while Valavi et.al compare the performance of 21 different methods. The current paper is not a comparison so a comprehensive analysis is not to be expected, but it would be useful to know how robust estimates from the GAM model in the current paper are.
• The parametric specification of the cost model.
• Variable selection for the cost model, and to a lesser extent the SDM. It seems worthwhile for the paper to expand the variables considered for the cost model to include those in FAOSTAT, which contains a number of variables that are potentially relevant. Perhaps it is the case that GDP and time since reported occurrence best predict invasion cost, but this paper has not made a convincing case. With regard to SDM's, Araujo et.al. caution that "Variables should include all relevant proximal predictors (i.e., not being restricted to readily available climatic variables). Distal variables that are only associated with the species' distribution by correlation (i.e., indirect variables such as elevation or latitude) should not be used for models seeking explanation and projection." The goal of the current paper is to project costs, yet the SDM is based on a significant number of climatic variables and includes distal variables such as elevation.

The clarity with which the results and methodology are explained can be improved. I understood this paper much better after reading its precursor by many of the same authors (Henry, et.al 2023). Elevating the clarity of writing in the current paper to the level of Henry et.al. would yield substantial improvement.

Reviewer #2 (Remarks to the Author):

Dear authors,
I appreciated reading your manuscript and believe it will make a relevant contribution to invasion biology.
I have mostly minor suggestions regarding the manuscript. However, I want to highlight a caveat related to the species distribution model (SDM) approach used. It seems that relying uniquely on SDM may lead to overestimated costs. The method assumes that environmentally suitable areas for invasive species that cause costs are always occupied by these species, which is rarely the case due to local-scale biological interactions. This can result in an overestimation of costs, especially when considering areas with no reported costs.
I suggest incorporating an alternative approach using the current geographical distribution of invasive species. By doing so, you will provide both estimates of costs, one based on potential distribution and the other based on the current known distribution of invasive species.

Below, I present a list of additional suggestions and comments that you could consider while reviewing the manuscript. I believe they can help you to improve it.
I'm looking forward to seeing the next version.
Best regards,

Specific comments

Introduction
Line 100 – I would suggest removing "quantify a more comprehensive" from the phrase.

Results
Line 113 and 114 – I could not understand. The total estimated costs were also based on the invacost database, right? Maybe, you could use observed, reported, or quantified costs vs. total estimated costs. It is more confusing because later you wrote "original estimate".
In addition, it is not clear to me what the costs of 92bi and 529bi mean. Are they the average costs per country (quantified vs. total estimated)? Or 85km2 (quantified vs. total estimated)? Or the total costs (quantified vs. total estimated) on a specific date? After checking Figure 2, I realized the total costs are composed of observed costs (in the countries where the species occur) and interpolated costs (based on the SDM + observed). I suggest describing it clearly at the first mention of the results. Maybe replacing "discrepancy (i.e., the difference between InvaCost and total estimated costs) in the global cost of these species, from an original estimate of $91.92 billion to $528.81 billion (~+475%) (Table S1)" with "discrepancy, i.e., the difference between costs observed in InvaCost and total estimated costs (costs observed in invacost + costs interpolated). It represents an increase of global cost of these species from $91.92 billion to $528.81 billion (~+475%) (Table S1)."
Line 115 – I suggest removing the phrase "We estimated costs for 93 additional countries for which at least one of these species is present but the cost has not been reported", because you describe it later (line 123).
Lines 124 and 125 – The reader can understand that the cost occurred when you write "Asia was the continent most impacted. I would suggest rephrasing here and checking it all over the manuscript. Maybe replacing "After interpolation, at the continental level, Asia was the continent most impacted by biological invasions, incurring" with "At the continental level, Asia had the highest potentially impacted by biological invasions, reaching…"
I also suggest avoiding "incurred" when describing interpolated costs for the same reason.
Line 156 – I suppose the sum of damage costs and management costs reaches the total costs. If not, I would suggest reporting the total cost.
Line 157 – I would suggest replacing "plants became the costliest group" wih "plants are the group with the highest interpolated cost."
Line 161 – Same suggestion.
Line 166 to 169 – It is not clear how you did that. What was the threshold to highlight one species that exceeds the average? In the figure, some species above the average are highlighted with the scientific name but not all. If you did not use any rule of thumb, consider one. Maybe, adding the identification of the top three species per taxonomic group or all species above the average per group.
Line 177 – Replace "km-2" with "km2". Check it all over the manuscript.
Line 181 – At least for me, it's not easy to observe on the map that "cost hotspots" are associated with densely populated urban areas. I think you can state it is associated with densely populated countries as population size is a metric measured on a country scale.
Line 183 to 191 – I'm not sure if the paragraph is necessary. The information is presented in figure 3 b and the exact values are also included in Table S1.

Discussion
Line 208 – I'd suggest replacing the second "monetary costs" with "impact."
Line 213 – You were using mostly km2 in the manuscript, I would suggest following the same pattern.
Line 230 – I would suggest removing "may" in the phrase.
Line 232 – I am not sure about the first phrase. How exactly did you address the bias? If there is any bias, it affects the estimate you applied to the countries without data.
Line 248 – Why "Initially"? As far as I understood, plants still ranked as second and fourth considering the observed costs. I think you must check the manuscript carefully to make sure the text does not mislead the reader into thinking that a cost occurred when indeed it was estimated based on SDM and interpolation.
Line 251 to 253 – I agree with your statement about invasive plants. However, considering plants are widespread, invade many countries, and cause many impacts, why they are underestimated in the invacost database? I mean, your statements do not address why the observed costs are "so" small.
Line 261 – I'm not sure if you tested the relationship between interpolated costs and human density and industries at the local scale. It seems you used human density and agricultural area at the country scale. I think you could make your argument stronger by presenting other references that found density populated areas (more industrialized and more urbanized) have proportionately higher costs associated.
Line 264 – If I understood, your models showed that high population density or agricultural area at the country scale affects the costs. If so, I would suggest replacing "can be attributed to their high population density or dependence on the agricultural sector" with "was influenced by their high population density or dependence on the agricultural sector."
Line 266 – That is an important caveat!
Line 282 – That is exactly why you could use a "baseline" approach considering the current observed geographical distribution of the species instead of uniquely SDM. In addition to the intrinsic uncertainty of many SDM, you are assuming these species indeed occur in the whole environmentally suitable area.

Methods
Line 365 – How did you delimit the suitable area per species? I mean, which threshold criteria did you use to convert a

probability map into a presence-absence map?
Line 383 – As far as I could see paper #48 is already published, so why did you write additional unpublished data? Do you mean, the categorization of non-native species per country is not available? If so, I strongly recommend making such categorization available.
Considering you are studying invasive species; how exactly the dataset of casual species was used? Somehow, you had to reclassify those casual species into invasive or not.
Line 396 – It seems a comma is missing.
Line 397 – C = the monetary cost documented in the invacost per country, right?
Line 412 – How much uncertainty do you have in the models? Consider reporting it in the Results sections.
Line 417 – Do you mean the process you just described? Consider adding "as described in the section "Economic cost model"" after the country.

Figures
Fig. 1 – Most political decisions and strategies are planned and implemented at the country level. Therefore, I strongly suggest using Fig. S1 instead. A supplementary table with the data used to create the map would be interesting too (with country, cost quantified, cost quantified+interpolated, and discrepancy).
Fig. 2 – Considering the values reported in the text (e.g., lines 158 and 161) and presented in Fig. 2 a and b, it seems the total cost estimated is a sum of the quantified cost at country level where the species occur and interpolated cost per countries where the species do not occur. Am I right? I'm not sure if it is clear in the manuscript. I think my doubt comes mostly because of the first paragraph of the Results.
Please, check the terms observed, reported, and quantified. It seems they have the same meaning, so I would suggest using one of them consistently.
Fig. 3 b and c – The costs reported in the figure are the total costs (interpolated plus quantified), right? Make it clear in the caption, please.
I suggest using colors with different shades for damage and management, for example, dark orange for damage and light green for management. It would make it easier to distinguish between both, including color-blind readers. In addition, I can barely read the names on the x-axis and inside the graph. For the final aesthetic comment, I would suggest sorting the species in decreasing order of cost for damage (fig. 3 b). Just as you did for management and countries.

Supplementary material
Table S1 – I found a typo in the damage cost for cats.

Reviewer #3 (Remarks to the Author):

This is my first time reviewing "Quantifying the hidden costs of biological invasions" submitted by Soto et al. to Nature Ecology and Evolution. The text regards the evaluation of the costs of biological invasions worldwide. The authors used different data sources and methods, especially species distribution models, to calculate this economic effect based on continental scales. The authors found that the costs of biological invasions were varied and misrepresented worldwide, with developed countries having more detailed information than underdeveloped ones. There were also differences involving different biological groups as well. In general, the text is well written, and below, I indicate a few suggestions that need to be addressed before the acceptance of the manuscript.

L46-48: Please invert this sentence.
L48-52: Please note that this sentence is too long. Please consider reducing it or breaking it in two.
L54: Please note that in American English, you must use serial commas in series.
L82-86: Please better explain how SDMs work, their assumptions, their input and output data, general usage in the literature, drawbacks, etc.
L85: Please avoid using possessives in academic texts. It is too colloquial.
L91: Please use a comma before "such as" and after "costs".
L82-99: I missed how the integration between SDMs and the invasion costs can be made. Please elaborate here.
L127: Please note that in American English, you must use serial commas in series
L139: Please avoid using possessives in academic texts. It is too colloquial.
L177: and all other instances where you used km 2: Please use the minus symbol (ALT Key + code 8722 in Windows-based computers).
For all countries you listed in the different portions of the results, I think it might be interesting to list the name of the species that was most considerable right after the name of the country. The same thing would be interesting for species: indicating the country where it was the most dangerous, costly etc.
L215-216: Is it possible to include transportation in your model? This is an important metric to facilitate the dispersion of invasive species.
L221: "high".
L226: Please avoid using and/or in academic texts. It is too colloquial.
L235: Please avoid using possessives in academic texts. It is too colloquial.
L254: Please use commas after "such as" and after "amphibians"
General addition needed in the discussion: Please discuss the drawbacks of your analyses considering issues involving SDMs
Please provide GBIF doi numbers in the supplementary materials
Please indicate in the main text that the SDM parameters are available in the ODMAP file.
L313-315: Please invert this sentence.
L316: 2017 is seven years ago! Please consider updating this value to some recent year.
L325-328: Please invert this sentence.

L341: Please include a space between “85” and “km2”
L352-354: Please invert this sentence.
L365: Please note that in American English, you must use serial commas in series.
L377: Please avoid using possessives in academic texts. It is too colloquial.
L381-383: Please invert this sentence.
L410-412 and 412-413: Please invert this sentence.

Reviewer #4 (Remarks to the Author):

Summary:

These authors seek to quantify economic costs of biological invasions for two purposes: (1) to improve existing estimates and (2) provide estimates for underrepresented geographies through interpolation. They combine existing secondary economic data and existing species modeling techniques to make a methodological contribution. Overall, this work is important and is a step forward in understanding costs for which there is no other basis.

Comments to address:

(1) My understanding of InvaCost data is that is a comprised of various studies (both peer-reviewed and not) that compute or estimate costs associated with damages or management of invasive species. In theory, the best (most accurately) studied areas in InvaCost would take into consideration all endogenous relationships between the economy and the biological invasion as a way to not over inflate estimates. The authors' main results, though, signal that InvaCost always underestimates the cost, but why this is always the case and why should the higher estimate of the authors' model be viewed as less biased? Is it just that the authors' approach includes more species over greater periods of time? If so, is the term 'bias' appropriate for this comparative case?

(2) There are three different steps that comprise this methodology and each step appears to be completed independently of the other, such that the outputs of one step serve as inputs into the next. What implications does this have on the temporal estimates of costs specifically in how the biological invasion might be perturbed by management actions? Is the underlying assumption that the invasion happens over a period of time and then the management occurs, or are they happening simultaneously? And, if simultaneously, how are those two steps of your methodology coupled with one another to account for this?

Version 1:

Decision Letter:

16th December 2024

*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Dr Soto,

Your manuscript entitled "Quantifying the hidden costs of biological invasions" has now been seen by our original three reviewers, whose comments are attached. The reviewers have some remaining concerns which will need to be addressed before we can offer publication in Nature Ecology & Evolution. We will therefore need to see your responses to these suggestions and concerns, along with a revised manuscript, before we can reach a final decision regarding publication.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file.

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

When revising your manuscript:

* Include a “Response to reviewers” document detailing, point-by-point, how you addressed each reviewer comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the reviewers along with the revised manuscript.

* If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at http://www.nature.com/natecolevol/info/final-submission. Refer also to any guidelines provided in this letter.

* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

Please use the link below to submit your revised manuscript and related files:

Link Redacted

Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit please visit www.springernature.com/orcid.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

[redacted]

Reviewer comments:

Reviewer #1 (Remarks to the Author):

Significant efforts have been made to improve the paper in response to comments by the referees. The interpolated costs need to be better contextualized for the reader, as interpolated costs seem implausibly large for some countries. For 6 countries, the interpolated costs are greater than the country's GDP. For the UK, the interpolated costs are 63% of GDP. If one compares the total costs in Table S5 by country to the 2022 Value of Agricultural Production for those same countries (from FAOSTAT in constant 2014-2016 $), then the interpolated total costs are larger than the value of all agricultural production in 41 out of 142 matched countries. These costs seem implausibly large. From table S4, the interpolated costs to Europe are over 10% of the EU's GDP. This needs to be contextualized for the reader. What sectors of the economy do the interpolated damages impact? Are these values reasonable given the subset of invasive species used in this analysis? If interpolated costs apply primarily to agriculture, then it would be helpful to rationalize how they can be so large. If the interpolated costs apply primarily to other sectors, then further rationalization of the role of agricultural area in the economic cost model would be useful.

For a broader comparison, the magnitudes of the annual interpolated costs in this paper ($2.9 trillion per year) are comparable to estimates of the total global costs of extreme weather from 2000-2019 ($2.86 trillion total cost over 20 years, $143 billion per year) in Newman, R., Noy, I. (The global costs of extreme weather that are attributable to climate change. Nat Commun 14, 6103, 2023. https://doi.org/10.1038/s41467-023-41888-1). Alternatively, the global interpolated costs amount to 3.2% of total GDP, based on a match of 171 countries in table S5 and 2022 GDP data from https://databank.worldbank.org/source/world-development-indicators#.

Reviewer #2 (Remarks to the Author):

Dear Authors,
I have carefully evaluated your responses and am very pleased with the improvements. However, I noticed a few typos and a taxonomic update that still needs to be addressed (please see below).
Additionally, I strongly encourage you to make the shapefile used to construct the map in Figure 3a publicly available. Doing so would facilitate cost estimations at different scales and provide valuable information to decision-makers (e.g., at the level of municipalities, basins, or protected areas). I am confident this resource would be useful to various stakeholders managing invasive species, especially outside of academia.
Congratulations on conducting such a relevant and impactful study!
Best wishes,
Minor comments:
Line 187 and 194: Do you mean Eichhornia crassipes? Check it all over the manuscript. Btw, the accepted name is Pontederia crassipes.
Line 311: Remove space before "%."
Line 343: I suppose it should be "maxent."
Line 453: Replace "decribed" with "described.'
Table S8: Check the decimal separator.

Reviewer #3 (Remarks to the Author):
None

**********END**********

Version 2:

Decision Letter:

6th February 2025

Dear Dr. Soto,

Thank you for submitting your revised manuscript currently entitled "Quantifying the hidden costs of biological invasions" (NATECOLEVOL-24030855B). It has now been seen again by Reviewer 1 and their comments are below. The reviewer finds that the paper has improved in revision, and therefore we'll be happy in principle to publish it in Nature Ecology & Evolution, pending minor revisions to satisfy the reviewers' final requests and to comply with our editorial and formatting guidelines.

If the current version of your manuscript is in a PDF format, please email us a copy of the file in an editable format (Microsoft Word or LaTex)-- we can not proceed with PDFs at this stage.

We are now performing detailed checks on your paper and will send you a checklist detailing our editorial and formatting requirements in about a week. Please do not upload the final materials and make any revisions until you receive this additional information from us.

Thank you again for your interest in Nature Ecology & Evolution. Please do not hesitate to contact me if you have any questions.

[redacted]

Reviewer #1 (Remarks to the Author):

I only have one very minor question/comment. My understanding is that the temporal changes in cost are strictly modeled through the denominator in equation (1). There is no economic discounting of future vs. present costs. If this is correct, then it might be useful to add a remark to make this clear.

Version 3:

Decision Letter:

26th March 2025

Dear Dr Soto,

We are pleased to inform you that your Article entitled "Using species ranges and macroeconomic data to fill the gap in costs of biological invasions", has now been accepted for publication in Nature Ecology & Evolution.

Over the next few weeks, your paper will be copyedited to ensure that it conforms to Nature Ecology and Evolution style. Once your paper is typeset, you will receive an email with a link to choose the appropriate publishing options for your paper and our Author Services team will be in touch regarding any additional information that may be required

After the grant of rights is completed, you will receive a link to your electronic proof via email with a request to make any corrections within 48 hours. If, when you receive your proof, you cannot meet this deadline, please inform us at rjsproduction@springernature.com immediately.

Due to the importance of these deadlines, we ask you please us know now whether you will be difficult to contact over the next month. If this is the case, we ask you provide us with the contact information (email, phone and fax) of someone who will be able to check the proofs on your behalf, and who will be available to address any last-minute problems . Once your paper has been scheduled for online publication, the Nature press office will be in touch to confirm the details.

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Reviewer #1 (Remarks to the Author):

This paper selects a subset of invasive species from the *InvaCost* database that have reported management and damage costs at the country level. For each of these species, the paper uses species distribution modeling (SDM) to estimate the suitable area in each country with reported occurrences. Using data from countries with reported occurrences and damages, an economic cost model is then fit with estimated SDM suitable area, GDP, population and agricultural land area as predictors. This cost model is then used to estimate projected damages and costs in countries with reported occurrences but unreported costs.

The economic cost model was originally used in a paper focused on the European Union by many of the same authors (Henry, et.al), where country area, GDP, population and agricultural value added were used as predictors in the cost model. The novel feature of this paper is its use of SDM to estimate suitable area for each species. This is then used as a predictor in the cost model, with the value added predictor replaced by agricultural land area.

The paper restricts cost models to a 4 parameter family of weighting functions specified as sums over products of ratios of predictor variables across countries raised to a power, where the power parameters vary across the 4 predictors, hence 4 parameters (eq. 2). Parameters may be positive or negative. This basic model is extended to include a (logistic) time trend and a lag phase for costs, potentially adding 3 more parameters, 2 for the logistic and 1 for the lag phase. Based on the AIC, the preferred model in the paper is a 4 parameter model that ignores population and agricultural land area, but includes GDP, suitable area and the 2 logistic time trend parameters. The parameter on suitability is approximately 0.15. This significantly modulates the role of suitable area, implying that an unreported cost country with double the suitable area relative to a reported cost country is projected to have costs that are about 10% higher than the reported country, while the projected costs in a country with half the suitable area would only decrease by about 10%, all else equal. The biggest drivers of the cost estimates from this model appear to be GDP and time since first reported occurrence. Were any other variables considered as predictors? The value of agricultural production, for example? FAOSTAT is a large repository of data on agricultural production in countries around the world.

RESPONSE: We thank you for your thorough evaluation of our manuscript and for the constructive comments regarding our methodology. We chose specific variables based on a priori rationale, aiming to maintain consistency with Henry et al. (2023). We considered including agricultural production data from FAOSTAT, but decided against it because it is highly correlated with GDP ($r = 0.732$) and had more missing data. We ultimately chose agricultural area due to: (i) it being less correlated with GDP ($r = 0.064$), (ii) it having no missing information across the countries analyzed. Also, importantly agricultural area was a significant predictor in our analyses, supporting our *a priori* decision to use it.

Given the objective of predicting costs in countries where they are unreported, why was the specific parametric model in (2) selected relative to other alternative specifications, that could include either parametric or machine learning alternatives?

RESPONSE: We chose the parametric model for its simplicity and the interpretability of results. However, we agree with the reviewer that other parametric or machine learning methods could offer alternatives, if they are as easy to interpret, with comparable advantages as our original interpolation method. For this reason, and following the reviewer's comment, we also include an alternative parametric approach (GLMM with a Gaussian error distribution), because it was as easy to interpret the relationships with predictors (e.g., increasing or decreasing), and because it allowed for interpolations to be species specific (i.e., using species as a random effect term). Hence-forth we term our interpolation approach the "ratio-scalar" model to differentiate it with interpolation using GLMM. See lines 449-454.

We found that our ratio-scalar model worked better for management, R^2=0.26 for interpolation versus R^2=0.23 for GLMM), but for damages GLMM worked better (R^2=0.52 for GLMM versus R^2=0.34 for the ratio-scalar). Thus, we thank the reviewer for their suggestion. In the revised manuscript we have presented these values in lines 129-138. Additionally, the coefficient of determination (R^2) for the fitted and validation dataset is provided on lines 129-136 of the revised manuscript and in Supplementary Table 2.

We note that we also tested two machine learning methods (GAM and Random Forest), but we opted not to include these in our analysis. First, while these methods have the potential to deal flexibly with non-linear relationships and complex interactions, it comes at a cost of interpretability. Specifically, we could not test whether the factors were in the predicted direction or not; only whether they were related. Additionally, the machine learning models resulted in poorer R^2 ($R^2_{gamDamage}$ =0.10; $R^2_{gamManagement}$ =0.07; $R^2_{rfDamage}$ =0.11; $R^2_{rfManagement}$ =0.09) compared to the other approaches we tried when applied to a validation set.

The paper argues (p. 17) that it meticulously adheres to established standards as set forth in Araújo, et.al (Science Advances, 2019). The paper has clearly made a substantial effort in this direction, particularly with regard to SDM. However, the authors suggest that model selection and uncertainty quantification are not applicable. Given the nature of the models used in the analysis it is unclear how this can be. Choices made in model and variable selection, parameter uncertainty, and measurement error in the data almost certainly affect the cost estimates in the paper.

RESPONSE: In the revised manuscript, we conducted additional analyses and improved our treatment of uncertainty. Specifically, for structural (model) uncertainty, we now consider two separate models: (1) our original interpolation models (know called ratio-scalar model) as well

as (2) a more standard mixed models regression approach (GLMM) for the economic submodel (see previous comment; lines 449-454). For structural uncertainty with SDMs, we used General Additive Models (GAMS) and also an additional algorithm considering a maximum entropy approach (MaxENT), see lines 395-398 and 406-413. As mentioned above, we also use an ensemble weighted model average.

- For parameter uncertainty, we now conduct bootstrapping on the parameters of the best-fitting economic model, for each of the ratio-scalar model and GLMM. See lines 484-486.
- Measurement error: We were limited by the data available, which typically did not quantify measurement error. Nonetheless, we used the most robust data available by restricting analyses to data points that were classified as "reliable" in the *InvaCost* database (i.e., high reliability and observed costs), and performed cleaning procedures for the SDMs (see Supplementary Material 1 and Table S6). We also acknowledge the issue of measurement error more broadly in the discussion (lines 311-314).

The extent to which costs in the *InvaCost* data are globally representative deserves more attention, including more discussion of potential biases.

RESPONSE: We agree that the *InvaCost* database contains biases, including spatial, taxonomic (towards the costliest invaders) and temporal ones, and that these could affect the estimates and interpretations derived from our study.

In the revised manuscript, we expanded the discussion of the bias in *InvaCost*. However, we also explain how the proposed approach makes it possible to reduce these biases (Lines 78-79; 261-267).

Cost effective management methods are different in developed nations than in developing countries due to the relative costs and availability of different management inputs. Likewise, even for similar suitable areas it is likely that crops, production inputs and yields differ according to a country's development status, leading to differences in damages. Labor is relatively cheaper in less developed countries, while chemical, biological, or capital inputs may be more efficient in developed nations. What are the consequences of these differences for using management costs and damages measured in developed nations to project costs in less developed countries, where management costs or damages are not well documented? To what extent does species area suitability correlate with production of host crops? Species suitability for an area does not necessarily imply the area's products are susceptible to damage, or that the underlying variation can be captured by including GDP, population and agricultural land area. Finally, how much do these differences matter across the set of species considered in this paper?

RESPONSE: There appears to be two points raised by the reviewer: first that nations may differ in relative costs, as well as production; second that species suitability does not necessarily imply the area's products are susceptible to damages. We agree with both points, and that our approach accounts for both.

For the first point, it could be more broadly stated as the socioeconomic context matters. As we discuss above, we incorporated macroeconomic indicators such as GDP, which provide a proxy for the relative economic capacity. Although we made assumptions on the direction of the relationships, the exact effect could be complex, given many (unknown) interacting factors that could moderate their influence. Thus, we let the data speak for itself, by fitting systematic cost differences in the available data between different socioeconomic and invasion contexts. We broadened our discussion, acknowledging that our conclusions must necessarily be based on currently available data and often the use of proxies, which is not without its limitations (lines 326-329).

Regarding species suitability, we agree that it does not necessarily imply every suitable location is susceptible to damages and address this point immediately in the next comment (but see lines 466-469).

The suitability of an area for a species does not necessarily correlate directly with the susceptibility of agricultural products to damage. Suitable areas for an invasive species do not always lead to agricultural impacts, especially if the primary crops are not preferred by the species. Additionally, although agriculture accounts for the main costs recorded in *InvaCost*, other damage costs include impacts on fisheries, forestry, and the environment, as classified in the *InvaCost* database.

RESPONSE: We agree that not all suitable areas need to result in damage and our analysis does not actually make this assumption. The estimate of suitable habitat is calibrated on the basis of real cost estimates, which implicitly incorporate the proportion of areas that do or do not have an impact. It follows that our approach assumes that empirical relationships between overlap and impact observed in other regions are representative of each interpolated region (moderated by spatial extent and time since invasion). In addition, our model allows us to deviate from proportional effects depending on the data. Hence, if spatial extent were entirely unrelated to damage (potentially due to numerous unmeasured factors), the fitted coefficient would approach zero. Nonetheless, our findings indicate that suitability was significant for damages, suggesting a consistency across regions in terms of overlap between suitable areas and their impact. Additionally, our focus on agriculture seems reasonable. As the reviewer points out, agriculture accounts for the main costs in the documented costs of *InvaCost,* and we found had important predictive value.

However, we acknowledge that additional analyses could be done, for instance explicitly matching crop types and pest preferences. We also recognize that different pests could impact other economic sectors, including fisheries and forestry. These would require additional data and other analyses. These issues are very complex and beyond the scope of the current paper, and we only refer to it as a potential future direction in the discussion (see lines 332-334, and 466-471).

The impact on agricultural damage varies among the species studied. For instance, some species may thrive in a region but predominantly affect forestry rather than agricultural fields. Conversely, a species can have disproportionate economic impacts in areas with intensive agriculture area

RESPONSE: The reviewer raises a valid point, which we addressed at length in the previous comment. Specifically, our interpolation is at the species level, calibrated to observed impacts, which allows us to account for differences in impact across species. Additionally, with our approach we do not assume all suitable areas would be impacted by an invasion (see lines 466-469). Our findings not only bolster the robustness of these results but also lay the foundation for future research by refining analyses with e.g., mapping crop-specific pest impacts and extending models to include sectors like fisheries and forestry. In the revised version, we explain the functioning of the model and also we identify future directions that refines the match of species preferences to habitat (and potentially even crop types) (lines 332-334).

In relation to the standards set forth in Araújo, et.al , more attention could be given to: S2.2C. Uncertainty in predictor variables; S2.3. Guidelines for model building including model complexity, treatment of bias and noise in response variables, and dealing with modeling and parameter uncertainty; S2.4. Guidelines for model evaluation, including model assumptions, outputs and performance. Specific suggestions include: improved quantification of uncertainty, better discussion of model validation – particularly with regard to the economic cost model in (2), and more consideration of robustness to modeling choices and assumptions. It would be very informative to elucidate how well the model in (2) performs across species and to provide regression statistics for the preferred economic cost model.

RESPONSE: In the revised version, we have conducted substantial additional analyses in response to the reviewer's comments, including building additional models and quantifying uncertainty and conducting validation. Specifically, we address each of the main point below:

Uncertainty in predictor variables (S2.2C):

We agree that measurement and choice of predictor variables can obscure relationships and result in reduced predictive ability. These are already central to the model building procedure, which compares alternative combinations of predictors. In particular, we explain how we proceeded to build and validate our model in three main steps: 1) Factor selection based on

hypothesised relationships (31 combinations of predictor variables); 2) Evidence screening (using AIC) to determine which variables to include and select the best performing models (lines 482-484). While there are certainly other potential predictors, no model completely reproduces reality nor includes all factors, and their exploration could quickly become a 'fishing expedition' for significance. Moreover, we conducted a leave-one-out cross-validation analysis, to quantify the predictiveness given our model, so that readers can evaluate the outcomes (lines 484-486).
Further, in our discussion, we suggest possible future research using alternative predictors, refining the analysis by considering land cover beyond agriculture, and matching those with pest preferences (discussed in a previous comment, and see lines 332-334 in the revised text).

Guidelines for model building including model complexity, treatment of bias and noise in response variables, and dealing with modeling and parameter uncertainty (S2.3):
In terms of model complexity, for our economic ratio-scalar, we used AIC to identify when more complex models were justified. For mixed models, we used the significance of each term (using the "afex" package), see lines 482-484. As for our SDMs, GAMs incorporate a penalization function (GCV.Cp) and MaxEnt used transformed features (including only linear, quadratic and product features) which helps to prevent overfitting. See lines 406-413.

To validate the model's performance, we used leave-one-out cross-validation by excluding each row and refitting the model. Additionally, we conducted 1,000 bootstrap samples with replacement to estimate the standard error of each model parameter to estimate parameter uncertainty (see lines 488-490). Finally, we combined the predictions from both models (i.e., model average) based on the weight of each R-square. We provided a more robust estimation of cost by offering an average and a range of each estimated cost (see Table S1) (lines 491-493, Table S1).

For biases, we acknowledge the presence of inherent bias (e.g., spatial) in global databases such as GBIF. In order to minimize these biases, we applied "target group background" sampling (see lines 381-382), which selects pseudoabsences using the same observation process as that which generated the original presences (Phillips et al., 2006). For our economic model, while cost estimates are biased (e.g., species that cause problems are more likely to be reported), we only interpolated within each species and did not try to predict the impacts for other species. While there were also spatial biases in the reporting, our model reduces these by 1) projecting costs in regions where data are missing but species are known to occur (previously these would have been assigned a zero value); and 2) make adjustments based on socioeconomic and invasion context, via fitted scalars (calibrated on empirically observed relationships). We also removed clear outliers from our main analysis ($5 billion in the case of damage and $0.6 for management expenditures) (lines 474-475).

Finally, as discussed above, we now present a more comprehensive treatment of uncertainty, including model (structural) and parameter uncertainty. In brief, for model uncertainty, we consider two algorithms and use ensemble modeling for each of SDMs (GAM & MaxENT lines 397-400), and our economic submodel (ratio-scalar and GLMM, lines 449-454). For parameter uncertainty, we use bootstrapping (1,000 replicates) for the ratio-scalar and mixed model and report the standard deviation of parameter estimates (lines 488-490).

Guidelines for model evaluation, including model assumptions, outputs and performance (S2.4):

We evaluated the ability of the model to predict "new" data (i.e., validation data). Specifically, we implemented a jackknife validation technique (i.e., systematically refitting the model while omitting each data point in turn, and subsequently predicting for the omitted), chosen over k-fold cross validation because of data limitations (lines 484-486). We reported the variation explained by the model of the observed cost estimates (as suggested by the reviewer), both for the fitted data and the validation set. Additionally, our current economic models incorporate an ensemble of ratio-scalar and mixed models (see lines 449-454).

Management costs can be incurred by private agents or by the public sector. How does this impact model specification? For example, while GDP may proxy for public sector management costs, GDP per capita may be a better proxy for private agent's ability and willingness to pay for management.

RESPONSE: The current formulation of the model actually accounts for and allows us to test for whether GDP or GDP per capita is a better predictor. Since we allow coefficients to also be negative, and include both GDP and population size, GDP per capita would have a positive coefficient for GDP and a negative one for population size. In terms of the separation by private agent or public sector, this went beyond the information available, and thus we could only indicate the average effect across all management data points. In the revised version, we discuss the issue of public versus private as a future consideration (lines 332-334).

For many species, producers can mitigate pest risk by switching to alternative crops that are less susceptible to damage. How does potential adaptation influence the results?

RESPONSE: This dynamic factor was not included in the model but we now discuss this limitation in the revised text (lines 323-325).

The discussion and presentation often reports interpolated costs and percentage changes with 2 decimal precision. This provides a misleading sense of precision in the estimates. Some attempt at uncertainty quantification would be useful (predictive, parameter and model uncertainty). For example, the original costs in the InvaCost database are imprecise estimates. Second, the

models used to build up the interpolated estimates each comes with some uncertainty. Third, the fitted parameters of these models are uncertain. The reader is left to ponder what 90% confidence bounds on interpolated costs might look like, for example, and how many would include zero? It might not be possible to answer this question, but more robustness checks and characterizing uncertainty seems useful.

RESPONSE: In the revised text, we now present whole percentage values without decimal places. As discussed in previous response, we have now quantified the uncertainty, including model and parameter uncertainty. A range of each estimated cost can be found in Table S1.

Clarity:

• Tables S2-S3 report model statistics (AIC, likelihood) and parameters for 31 different model specifications. The value of reporting 31 different models is unclear, considering that the probability of a model being the best among those considered is close to zero for many of the alternatives.

RESPONSE: Following the reviewer suggestions, we removed all these models with zero weight and restricted our Table to top5-ranked models.

• The use of a comma as a decimal separator in various places is potentially confusing to the reader, particularly given that a comma separates thousands, millions, etc. in the main body of the paper.

RESPONSE: We have removed commas as a decimal separator and changed to dots. Example: 1,259,824.21 US$.

• Is 2021 the base year for the cost model predictors? Given the time varying nature of the anthropogenic predictors, what Is the rationale for selecting a particular base year?

RESPONSE: The base year for the economic cost model is 2017 US$ used in the InvaCost database. Cost estimates for other years and currencies were adjusted to a common metric (2017 USD), to allow comparability between studies at the time of construction (Diagne et al., 2020).

Reviewer #2 (Remarks to the Author):

Dear authors,

I appreciated reading your manuscript and believe it will make a relevant contribution to invasion biology.

I have mostly minor suggestions regarding the manuscript. However, I want to highlight a caveat related to the species distribution model (SDM) approach used. It seems that relying uniquely on SDM may lead to overestimated costs. The method assumes that environmentally suitable areas for invasive species that cause costs are always occupied by these species, which

is rarely the case due to local-scale biological interactions. This can result in an overestimation of costs, especially when considering areas with no reported costs.

I suggest incorporating an alternative approach using the current geographical distribution of invasive species. By doing so, you will provide both estimates of costs, one based on potential distribution and the other based on the current known distribution of invasive species.

Below, I present a list of additional suggestions and comments that you could consider while reviewing the manuscript. I believe they can help you to improve it.

I'm looking forward to seeing the next version.

Best regards,

RESPONSE: We thank the reviewer for very constructive feedback and positive remarks on our manuscript. We acknowledge the presence of bias in GBIF (e.g., spatial). While GBIF is one of the most extensive databases, it should be noted that less than 7% of the surface has been sampled even at 5 km^2 resolutions (Hughes et al., 2021), see lines 261-268. In fact, most of the countries where a species is known to occur, such as most African countries as well as those in South America or Asia, lack any species records due to these inherent biases.

Instead, the approach we use ameliorates the challenge the reviewer identified—namely that SDMs may overestimate the costs, and that species may not occur in all environmentally suitable areas—in the following ways. First, the model does not assume that costs occur everywhere. Instead interpolations are based on observed costs in other countries. As the reviewer suggests, these observed costs will occur in only a fraction of "suitable" sites identified by the SDM. Put a different way, calibration of the interpolated costs at the country level already accounts for only a fraction of suitable sites experiencing costs (lines 466-469). Second, we have built in some ability to capture context specificity, by moderating the cost estimates based on other predictors. These for instance include amount of agricultural land, which could increase the amount of suitable area that could result in economic costs, as well as invasion progress over time, which could affect the level of exposure to a given species (lines 469-471).

That said, we acknowledge that SDM predictions may be vary between countries because of factors not included in the model, and also that the fraction of suitable sites that incur costs may vary (lines 318-321). However, our current approach is arguably the best possible estimations without additional information, generating finer resolution of differences between countries or additional information on context specific differences. We note that if other such information existed, our model provides the structure to include them (as we did for macro-economic factors such as GDP and population size).

Reference

Hughes, A. C., Orr, M. C., Ma, K., Costello, M. J., Waller, J., Provoost, P., Yang, Q., Zhu, C., & Qiao, H. (2021). Sampling biases shape our view of the natural world. Ecography, 44(9), 1259-1269.

Specific comments

Introduction

Line 100 – I would suggest removing "quantify a more comprehensive" from the phrase.

RESPONSE: Removed.

Results

Line 113 and 114 – I could not understand. The total estimated costs were also based on the invacost database, right? Maybe, you could use observed, reported, or quantified costs vs. total estimated costs. It is more confusing because later you wrote "original estimate".

RESPONSE: Following the reviewer suggestions, we decided to use "observed" and rephrase the text. See lines 119-128.

In addition, it is not clear to me what the costs of 92bi and 529bi mean. Are they the average costs per country (quantified vs. total estimated)? Or 85km2 (quantified vs. total estimated)? Or the total costs (quantified vs. total estimated) on a specific date?

RESPONSE: We apologies for any confusion. The initial costs refer to the costs estimated in InvaCost, while the second refer to the total economic costs i.e., recorded + interpolated. To avoid any confusion, we rephrased the whole paragraph, see lines 119-128.

After checking Figure 2, I realized the total costs are composed of observed costs (in the countries where the species occur) and interpolated costs (based on the SDM + observed). I suggest describing it clearly at the first mention of the results. Maybe replacing "discrepancy (i.e., the difference between InvaCost and total estimated costs) in the global cost of these species, from an original estimate of $91.92 billion to $528.81 billion (~+475%) (Table S1)" with "discrepancy, i.e., the difference between costs observed in InvaCost and total estimated costs (costs observed in invacost + costs interpolated). It represents an increase of global cost of these species from $91.92 billion to $528.81 billion (~+475%) (Table S1)."

RESPONSE: We agree with the suggestion of the reviewer and the text has been rephrased. See lines 119-121.

Line 115 – I suggest removing the phrase "We estimated costs for 93 additional countries for which at least one of these species is present but the cost has not been reported", because you describe it later (line 123).

RESPONSE: Removed.

Lines 124 and 125 – The reader can understand that the cost occurred when you write "Asia was the continent most impacted. I would suggest rephrasing here and checking it all over the manuscript. Maybe replacing "After interpolation, at the continental level, Asia was the continent most impacted by biological invasions, incurring" with "At the continental level, Asia had the highest potentially impacted by biological invasions, reaching…"
I also suggest avoiding "incurred" when describing interpolated costs for the same reason.
RESPONSE: We rephrased the sentence following the reviewer suggestion. We also decided change the term 'incurred' to 'estimated'.

Line 156 – I suppose the sum of damage costs and management costs reaches the total costs. If not, I would suggest reporting the total cost.
RESPONSE: Indeed, we have double checked the values and these match with the total costs presented in lines 121-128.

Line 157 – I would suggest replacing "plants became the costliest group" wih "plants are the group with the highest interpolated cost."
RESPONSE: Changed.

Line 161 – Same suggestion.
RESPONSE: Changed.

Line 166 to 169 – It is not clear how you did that. What was the threshold to highlight one species that exceeds the average? In the figure, some species above the average are highlighted with the scientific name but not all. If you did not use any rule of thumb, consider one. Maybe, adding the identification of the top three species per taxonomic group or all species above the average per group.
RESPONSE: We have included this information in the caption of the figure. See lines 192-194.

Line 177 – Replace "km-2" with "km2". Check it all over the manuscript.
RESPONSE: We have replace all km-2" with "km^2"

Line 181 – At least for me, it's not easy to observe on the map that "cost hotspots" are associated with densely populated urban areas. I think you can state it is associated with densely populated countries as population size is a metric measured on a country scale.
RESPONSE: We have changed the scales of the map to improve visualization.

Line 183 to 191 – I'm not sure if the paragraph is necessary. The information is presented in figure 3 b and the exact values are also included in Table S1.

RESPONSE: After discussion among co-authors and as the caption may be missed by readers, we decided to retain this paragraph to present the results at the species level.

Discussion

Line 208 – I'd suggest replacing the second "monetary costs" with "impact."

RESPONSE: Changed.

Line 213 – You were using mostly km2 in the manuscript, I would suggest following the same pattern.

RESPONSE: Changed to km^2

Line 230 – I would suggest removing "may" in the phrase.

RESPONSE: Removed.

Line 232 – I am not sure about the first phrase. How exactly did you address the bias? If there is any bias, it affects the estimate you applied to the countries without data.

RESPONSE: We have not explored the potential of management activities on reducing damage costs. To avoid any confusion we decided to remove the sentence.

Line 248 – Why "Initially"? As far as I understood, plants still ranked as second and fourth considering the observed costs. I think you must check the manuscript carefully to make sure the text does not mislead the reader into thinking that a cost occurred when indeed it was estimated based on SDM and interpolation.

RESPONSE: Plants were ranked as second and fourth considering the observed costs in *InvaCost* but was estimated as the costliest group for both damage and management costs when costs which were interpolated were taken in account. To avoid any confusion we rephrased the sentence. See lines 279-283.

Line 251 to 253 – I agree with your statement about invasive plants. However, considering plants are widespread, invade many countries, and cause many impacts, why they are underestimated in the invacost database? I mean, your statements do not address why the observed costs are "so" small.

RESPONSE: The *InvaCost* database provides an aggregated assessment of the costs that have actually been assessed. It does not represent the real costs of invasions, and is subject to spatial, temporal, and taxonomic biases (due to the idiosyncratic choices of the evaluators, their zone of affiliation, etc.). Our interpolation approach in fact intends to partially correct these biases—as demostrated by invasive plants estimates. However, *InvaCost* is a living database continuously updating with further data, thus future versions may reveal a more realistic view of the

monetary costs of invasive plants. We rephrased the sentence to explain why these costs are so "small" (lines 283-285):

Line 261 – I'm not sure if you tested the relationship between interpolated costs and human density and industries at the local scale. It seems you used human density and agricultural area at the country scale. I think you could make your argument stronger by presenting other references that found density populated areas (more industrialized and more urbanized) have proportionately higher costs associated.

RESPONSE: The reviewer is correct. Analyses of moderating factors were at the country level. As suggested, we included a reference to reinforce our findings.

Heringer, G., Fernandez, R. D., Bang, A., Cordonnier, M., Novoa, A., Lenzner, B., ... & Courchamp, F. (2024). Economic costs of invasive non-native species in urban areas: An underexplored financial drain. Science of the Total Environment, 917, 170336.

Line 264 – If I understood, your models showed that high population density or agricultural area at the country scale affects the costs. If so, I would suggest replacing "can be attributed to their high population density or dependence on the agricultural sector" with "was influenced by their high population density or dependence on the agricultural sector."

RESPONSE: Changed.

Line 266 – That is an important caveat!

RESPONSE: We agree with the reviewer about the inherent bias in GBIF and this reinforces our target-background approach to create background points based on GBIF occurrences (i.e., in theory, the choice of background locations have the same biases, such that the relative probabilities of occurrence for a given set of environmental conditions are appropriate). We expanded the discussion on these gaps on lines 264-266.

Line 282 – That is exactly why you could use a "baseline" approach considering the current observed geographical distribution of the species instead of uniquely SDM. In addition to the intrinsic uncertainty of many SDM, you are assuming these species indeed occur in the whole environmentally suitable area.

RESPONSE: Please see our previous response, where we explained that our current analysis does not make this assumption (that all suitable areas will lead to an impact) and that GBIF data are often entirely lacking for numerous species known to have invaded countries in certain regions (e.g., Africa, South America, Asia). This is because the estimation of suitable habitat is already calibrated based on real cost estimates (country-scale), which implicitly incorporates the proportion of areas that do or do not have an impact (lines 466-469). Our approach does assume that empirical relationships between overlap and impact observed in other regions are

representative of each interpolated region (moderated by spatial extent and time, and socioeconomic context). Additionally, GBIF data has notable geographic biases (with records predominantly in Europe and North America). Therefore most of the countries where the species is known to occur, such as most African countries, as well as South America and Asia, lack species records. Therefore, our decision to base our analysis on environmental conditions, while not perfect, is arguably needed across regions where GBIF data are sparse or non-existent.

Methods

Line 365 – How did you delimit the suitable area per species? I mean, which threshold criteria did you use to convert a probability map into a presence-absence map?

RESPONSE: We calculate the total suitability area by the sum the probabilities for a given species in a country. Lines 412-413.

Line 383 – As far as I could see paper #48 is already published, so why did you write additional unpublished data? Do you mean, the categorization of non-native species per country is not available? If so, I strongly recommend making such categorization available.
Considering you are studying invasive species; how exactly the dataset of casual species was used? Somehow, you had to reclassify those casual species into invasive or not.

RESPONSE: This paper refers to a partial use of the original database. The original database is currently under review. This database contains information only on the established non-native species and thus no casual records of species are included.

Line 396 – It seems a comma is missing.

RESPONSE: Added

Line 397 – C = the monetary cost documented in the invacost per country, right?

RESPONSE: Thanks for noting this, fixed

Line 412 – How much uncertainty do you have in the models? Consider reporting it in the Results sections.

RESPONSE: We have included quantification of uncertainty. First, for model (structural) uncertainty, regarding SDMs, we have added an additional algorithm, MaxENT, and created an ensemble model that combines this with GAMs (lines 395-398). Regarding the economic model, we use a model averaging approach combining GLMM and our interpolation model (now called the ratio-scaling model), see lines 449-454. For parameter uncertainty, we use bootstrapping for the parameters and reported the range of costs (see Table S2). This approach includes bootstrapping the parameters and reporting the standard deviation (see lines 488-491).

Line 417 – Do you mean the process you just described? Consider adding "as described in the section "Economic cost model" after the country.

RESPONSE: Added.

Figures

Fig. 1 – Most political decisions and strategies are planned and implemented at the country level. Therefore, I strongly suggest using Fig. S1 instead. A supplementary table with the data used to create the map would be interesting too (with country, cost quantified, cost quantified+interpolated, and discrepancy).

RESPONSE: We moved this Figure to the main text and provide a Supplementary Table with all the information requested (see Table S4).

Fig. 2 – Considering the values reported in the text (e.g., lines 158 and 161) and presented in Fig. 2 a and b, it seems the total cost estimated is a sum of the quantified cost at country level where the species occur and interpolated cost per countries where the species do not occur. Am I right? I'm not sure if it is clear in the manuscript. I think my doubt comes mostly because of the first paragraph of the Results.

Please, check the terms observed, reported, and quantified. It seems they have the same meaning, so I would suggest using one of them consistently.

RESPONSE: We apologies for any confusion. We have rephrased the text to ensure proper understanding of the methodology and results (see lines 119-128). The interpolation was based on species presence records from database of locations of established non-native species---not limited to GBIF data. Thus, we only considered countries where the species have been recorded, and interpolation was applied in cases where *InvaCost* estimates were absent.

Fig. 3 b and c – The costs reported in the figure are the total costs (interpolated plus quantified), right? Make it clear in the caption, please.

I suggest using colors with different shades for damage and management, for example, dark orange for damage and light green for management. It would make it easier to distinguish between both, including color-blind readers. In addition, I can barely read the names on the x-axis and inside the graph. For the final aesthetic comment, I would suggest sorting the species in decreasing order of cost for damage (fig. 3 b). Just as you did for management and countries.

RESPONSE: We have improved the figure by adopting the changes suggested by the reviewer.

Supplementary material

Table S1 – I found a typo in the damage cost for cats.

RESPONSE: Fixed.

Reviewer #3 (Remarks to the Author):

This is my first time reviewing "Quantifying the hidden costs of biological invasions" submitted by Soto et al. to Nature Ecology and Evolution. The text regards the evaluation of the costs of biological invasions worldwide. The authors used different data sources and methods, especially species distribution models, to calculate this economic effect based on continental scales. The authors found that the costs of biological invasions were varied and misrepresented worldwide, with developed countries having more detailed information than underdeveloped ones. There were also differences involving different biological groups as well. In general, the text is well written, and below, I indicate a few suggestions that need to be addressed before the acceptance of the manuscript.

RESPONSE: We appreciate the constructive reviewer feedback and provide a response point-by-point for each of the comments below.

L46-48: Please invert this sentence.

RESPONSE: Rephrased. See lines 46-48

L48-52: Please note that this sentence is too long. Please consider reducing it or breaking it in two.

RESPONSE: We decided to split the sentence in two. See lines 48-49 and 50-52

L54: Please note that in American English, you must use serial commas in series.

RESPONSE: Added.

L82-86: Please better explain how SDMs work, their assumptions, their input and output data, general usage in the literature, drawbacks, etc.

RESPONSE: We have rephrased the whole paragraph. See lines 82-90, 92-94, and 431-438.

L85: Please avoid using possessives in academic texts. It is too colloquial.

RESPONSE: Removed

L91: Please use a comma before "such as" and after "costs".

RESPONSE: Added

L82-99: I missed how the integration between SDMs and the invasion costs can be made. Please elaborate here.

RESPONSE: SDMs along with time since invasion. By linking areas of suitability (identified by SDMs) with regions where invasion costs have been documented, but lack economic cost estimates, we aim to estimate costs in areas lacking of economic data. We attempt to clarify

these points on lines 92-94, however the full description can be found in methods, where the section has been expanded to provide a clearer explanation of this integration.

L127: Please note that in American English, you must use serial commas in series
RESPONSE: Added

L139: Please avoid using possessives in academic texts. It is too colloquial.
RESPONSE: Removed

L177: and all other instances where you used km 2: Please use the minus symbol (ALT Key + code 8722 in Windows-based computers).
RESPONSE: We have corrected the syntax for km^2.

For all countries you listed in the different portions of the results, I think it might be interesting to list the name of the species that was most considerable right after the name of the country. The same thing would be interesting for species: indicating the country where it was the most dangerous, costly etc.
RESPONSE: We did not add the particular species causing highest impacts per country, given the large number of countries considered in the analyses and their disparate mentioning through the results.

L215-216: Is it possible to include transportation in your model? This is an important metric to facilitate the dispersion of invasive species.
RESPONSE: We acknowledge the potential role of transportation in the dispersal of invasive species. However, building a global transportation model would be beyond the scope of this study, though it would indeed be interesting for future research. We have included this in the discussion section. See lines 332-334.

L221: “high”.
RESPONSE: Fixed.

L226: Please avoid using and/or in academic texts. It is too colloquial.
RESPONSE: We have removed “and/”.

L235: Please avoid using possessives in academic texts. It is too colloquial.
RESPONSE: Removed.

L254: Please use commas after “such as” and after “amphibians”
General addition needed in the discussion: Please discuss the drawbacks of your analyses considering issues involving SDMs

RESPONSE: Commas have been added and further discussion of drawbacks of SDMs are included in the discussion on lines 318-321 and 431-439.

Please provide GBIF doi numbers in the supplementary materials

RESPONSE: Dois are included in Supplementary Table 6.

Please indicate in the main text that the SDM parameters are available in the ODMAP file.

RESPONSE: We have updated the manuscript to explicitly state that the parameters used in the SDM are detailed in the ODMAP file (Supplementary Note 1).

L313-315: Please invert this sentence.

RESPONSE: Rephrased.

L316: 2017 is seven years ago! Please consider updating this value to some recent year.

RESPONSE: We understand the reviewer's point of view; however, this standardization was based on a consensus reached by the InvaCost project in 2020 and on the database construction timing (see Diagne et al., 2020).

Diagne, C., Leroy, B., Gozlan, R. E., Vaissière, A. C., Assailly, C., Nuninger, L., ... & Courchamp, F. (2020). InvaCost, a public database of the economic costs of biological invasions worldwide. Scientific data, 7(1), 277.

L325-328: Please invert this sentence.

RESPONSE: Rephrased. See lines 369-372.

L341: Please include a space between “85” and “km2”

RESPONSE: Included

L352-354: Please invert this sentence.

RESPONSE: Rephrased. See lines 395-398

L365: Please note that in American English, you must use serial commas in series.

RESPONSE: Added.

L377: Please avoid using possessives in academic texts. It is too colloquial.

RESPONSE: Removed.

L381-383: Please invert this sentence.

RESPONSE: Rephrased.

L410-412 and 412-413: Please invert this sentence.

RESPONSE: Rephrased.

Reviewer #4 (Remarks to the Author):

Summary:

These authors seek to quantify economic costs of biological invasions for two purposes: (1) to improve existing estimates and (2) provide estimates for underrepresented geographies through interpolation. They combine existing secondary economic data and existing species modeling techniques to make a methodological contribution. Overall, this work is important and is a step forward in understanding costs for which there is no other basis.

RESPONSE: We appreciate your positive feedback and recognition of the importance of our study and its contribution to the field of invasion science. We provided a response point-by-point for each of the comments below.

Comments to address:

(1) My understanding of InvaCost data is that is a comprised of various studies (both peer-reviewed and not) that compute or estimate costs associated with damages or management of invasive species. In theory, the best (most accurately) studied areas in InvaCost would take into consideration all endogenous relationships between the economy and the biological invasion as a way to not over inflate estimates. The authors' main results, though, signal that InvaCost always underestimates the cost, but why this is always the case and why should the higher estimate of the authors' model be viewed as less biased? Is it just that the authors' approach includes more species over greater periods of time? If so, is the term 'bias' appropriate for this comparative case?

RESPONSE: The *InvaCost* database, as you correctly noted, aggregates cost data from various sources. However, *InvaCost*—despite being the most comprehensive cost database—represents a small portion of the "real" monetary cost of invasive species. The main bias we address, however, is spatial, since it is known that costs are unreported where species are known to have invaded, with some countries having no reported costs whatsoever. However, we do not include "more species" or estimates over "longer periods of time" and our results are limited to the 162 species that met our criteria i.e., high-reliability data, costs at the country level, and observed costs (see Supplementary Material 1). Thus, by bias, we mean that there is a substantial under-reporting of potential costs over space, which we ameliorate here, but we do not address the issue of unreported taxa or timepoints. We extended the discussion about these topic in the discussion on lines 261-268.

(2) There are three different steps that comprise this methodology and each step appears to be completed independently of the other, such that the outputs of one step serve as inputs into the next. What implications does this have on the temporal estimates of costs specifically in how the biological invasion might be perturbed by management actions? Is the underlying assumption that the invasion happens over a period of time and then the management occurs, or are they happening simultaneously? And, if simultaneously, how are those two steps of your methodology coupled with one another to account for this?

RESPONSE: There appears to be two separate considerations raised by the reviewer. The first is the three steps of our modeling procedure, and the second is whether management occurs after costs are estimated or if they occur simultaneously. We respond to each in turn.

For the first point, the three "steps" include obtaining the empirical cost estimate, spatialization of species suitability, and building the cost model. These should be viewed not as sequential steps. Rather, the real cost estimates observed in *InvaCost*, is in part determined by how widespread the invader is. Put another way, step 1 implicitly incorporates the proportion of areas that do or do not have an impact (line 466-469) . Our approach assumes that the empirical relationships between overlap and impact observed in other regions are representative of each interpolated region, moderated by both spatial extent and time. Likewise, the observed costs are also determined by other socioeconomic factors (step 3, lines 469-471). Thus, in the model, these factors are all simultaneously contributing to the cost (i.e., predictor variables in the model), and coefficients are fit to the observed costs (i.e., minimizing the discrepancies). This procedure allows us to use observed costs for a given species, but moderate the predictions based on socio-economic and invasion context. Our response to the previous comment (*how is SDM integrated into the economic cost?)* also relates to the answer here.

With respect to whether management often occurs after or simultaneously to damages, it occurs simultaneously. The reviewer might have been noting that we separately analyzed management expenditure and damage costs (i.e., the direct impact of the species on the economy or environment). Importantly, the *InvaCost* database contain both management and damage costs separately (based on what authors of the primary articles reported), and does not provide data about how these interact, or delay between both. Put another way, damage estimates reflect the monetary cost of the invasive species, which is partly a result of the management actions already implemented (i.e., it is implicit). However, the extent and effectiveness of these management actions may vary based on socioeconomic conditions, and our model does consider different levels of realized damage associated with socioeconomic conditions, although the exact mechanisms of this interaction have not been explicitly tested (and cannot be properly done at the global level). We clarify these points on lines 246-250.

Reviewer comments:

Reviewer #1 (Remarks to the Author):

Significant efforts have been made to improve the paper in response to comments by the referees. The interpolated costs need to be better contextualized for the reader, as interpolated costs seem implausibly large for some countries. For 6 countries, the interpolated costs are greater than the country's GDP. For the UK, the interpolated costs are 63% of GDP. If one compares the total costs in Table S5 by country to the 2022 Value of Agricultural Production for those same countries (from FAOSTAT in constant 2014-2016 $), then the interpolated total costs are larger than the value of all agricultural production in 41 out of 142 matched countries. These costs seem implausibly large. From table S4, the interpolated costs to Europe are over 10% of the EU's GDP. This needs to be contextualized for the reader. What sectors of the economy do the interpolated damages impact? Are these values reasonable given the subset of invasive species used in this analysis? If interpolated costs apply primarily to agriculture, then it would be helpful to rationalize how they can be so large. If the interpolated costs apply primarily to other sectors, then further rationalization of the role of agricultural area in the economic cost model would be useful.

RESPONSE: We thank the reviewer for the positive feedback. We acknowledge that some interpolated costs appear to be large compared with GDP or total agricultural value. These could occur for the following reasons:

- Many of the interpolated cost estimates reflect impacts across multiple sectors, including but not limited to agriculture (e.g., authorities-stakeholders, health, public and social welfare). Thus, the overall costs to a country could exceed agricultural value. This has been demonstrated for many countries (e.g., Nordic countries, Kourantidou et al., 2022, France, Renault et al., 2021; Germany, Haubrock et al., 2021; Spain, Angulo et al., 2021). That said, as highlighted in the previous round of comments, agriculture was the most frequently reported damaged sector in the *InvaCost* database (accounting for approximately half of the estimates). Also, as discussed in the previous revisions, we demonstrated that agricultural area significantly improved the overall predictive power of the model (see Table S3), and thus is worth keeping. Further information about the importance of agriculture has been included on lines 472:474 & 243:246.

- For these few cases where the total interpolated costs were greater than GDP, we acknowledge caution in the interpretation of cost estimates for individual points—even where the overall model performs well. This is an inherent limitation of any statistical model, which will naturally have both over-estimations and under-estimations (few will fall exactly on the predicted line), even where the general relationships are correct. Moreover, we noted that these cases where costs estimates were greater than GDP often came from "small"

economies, such as Burundi (GDP_{2020}: ≈ 2.6 US$ billion), Dominica (GDP_{2020}: ≈0.5 US$ billion) or Kiribati (GDP_{2020}: ≈ 0.22 US$ billion). Importantly, we noted that the removal of these interpolated points do not change the main outcomes of the analysis. In the revised version, we make these points in the following lines 321:329. Additionally, in the revised version, we add another layer to our uncertainty analysis, by identifying these interpolated points that are questionably large, so that readers are aware of them (identified with **, Table S5).

References:

- Angulo, E., Ballesteros-Mejia, L., Novoa, A., Duboscq-Carra, V. G., Diagne, C., & Courchamp, F. (2021). Economic costs of invasive alien species in Spain. NeoBiota, 67, 267-297.
- *Haubrock, P. J., Cuthbert, R. N., Sundermann, A., Diagne, C., Golivets, M., & Courchamp, F. (2021). Economic costs of invasive species in Germany. NeoBiota, 67, 225-246.*
- *Kourantidou, M., Verbrugge, L. N., Haubrock, P. J., Cuthbert, R. N., Angulo, E., Ahonen, I., Cleary, M., Falk-Andersson, J., Granhag, L., Gíslason, S., Kaiser, B., Kosenius, A., Lange, H., Lehtiniemi, M., Magnussen, K., Navrud, S., Nummi, P., Oficialdegui, F. J., Ramula, S., . . . Courchamp, F. (2022). The economic costs, management and regulation of biological invasions in the Nordic countries. Journal of Environmental Management, 324, 116374.*
- *Renault, D., Manfrini, E., Leroy, B., Diagne, C., Ballesteros-Mejia, L., Angulo, E., & Courchamp, F. (2021). Biological invasions in France: Alarming costs and even more alarming knowledge gaps. NeoBiota, 67, 191-224.*

For a broader comparison, the magnitudes of the annual interpolated costs in this paper ($2.9 trillion per year) are comparable to estimates of the total global costs of extreme weather from 2000-2019 ($2.86 trillion total cost over 20 years, $143 billion per year) in Newman, R., Noy, I. (The global costs of extreme weather that are attributable to climate change. Nat Commun 14, 6103, 2023. https://doi.org/10.1038/s41467-023-41888-1). Alternatively, the global interpolated costs amount to 3.2% of total GDP, based on a match of 171 countries in table S5 and 2022 GDP data from https://databank.worldbank.org/source/world-development-indicators#.

RESPONSE: We agree with the reviewer that such a comparison would be worth including and we thank them for this suggestion. However, we note that there might be a misunderstanding, as the total sum of costs (2.2T) that we reported refers to a cumulative amount over a given period, not an annual figure. To clarify this and avoid any misunderstanding, we specified that the total value refers to the whole period on lines 120:121. Additionally, for context, we now compare our results against the extreme weather costs (Newman et al., 2023), as well as the global GDP on lines 233:235 & 274:277.

Reviewer #2 (Remarks to the Author):

Dear Authors,
I have carefully evaluated your responses and am very pleased with the improvements. However, I noticed a few typos and a taxonomic update that still needs to be addressed (please see below).
Additionally, I strongly encourage you to make the shapefile used to construct the map in Figure 3a publicly available. Doing so would facilitate cost estimations at different scales and provide valuable information to decision-makers (e.g., at the level of municipalities, basins, or protected areas). I am confident this resource would be useful to various stakeholders managing invasive species, especially outside of academia.
Congratulations on conducting such a relevant and impactful study!
Best wishes,

RESPONSE: We thank the reviewer for the encouragement and positive feedback on our manuscript. We apologise for the remaining typos, we carefully reviewed these points in the revised version of the manuscript. Regarding the shapefile used in the Figure 3a, the data, code and shapefile to replicate the study and figures will be made available at GitHub (https://github.com/IsmaSA/Invacost_SDM) with a release on Zenodo after acceptance.

Minor comments:
Line 187 and 194: Do you mean Eichhornia crassipes? Check it all over the manuscript. Btw, the accepted name is Pontederia crassipes.
RESPONSE: Thank you for pointing this out. We carefully checked and corrected the name to '*Pontederia crassipes*' throughout the manuscript.

Line 311: Remove space before "%."
RESPONSE: Changed.

Line 343: I suppose it should be "maxent."
RESPONSE: Changed.

Line 453: Replace "decribed" with "described.'
RESPONSE: Changed.

Table S8: Check the decimal separator.
RESPONSE: Thanks, commas have been replaced with dots, to match with the style in the journal.

Reviewer #3 (Remarks to the Author):
None

Reviewer comments:

Reviewer #1 (Remarks to the Author):

I only have one very minor question/comment. My understanding is that the temporal changes in cost are strictly modeled through the denominator in equation (1). There is no economic discounting of future vs. present costs. If this is correct, then it might be useful to add a remark to make this clear.

RESPONSE: You are correct that our model does not incorporate economic discounting, and temporal cost changes are strictly captured through the logistic growth function in the denominator of Equation (1). We clarified this point on lines 447-449.