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What would it take to describe the global diversity of parasites?

Colin J. Carlson, Tad A. Dallas, Laura W. Alexander, Alexandra L. Phelan and Anna J. Phillips

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Original submission:	30 July 2020
1st revised submission:	28 September 2020
2nd revised submission:	22 October 2020
Final acceptance:	22 October 2020

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

Review History

RSPB-2020-1841.R0 (Original submission)

Review form: Reviewer 1 (Whitney Preisser)

Recommendation
Accept with minor revision (please list in comments)

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

General interest: Is the paper of sufficient general interest?
Excellent

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

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
Yes

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
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Small recommendations:
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Materials and methods:
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Lines 548-549: What are the twenty groups? Host orders? Please specify.

Lines 580-593: While the text explanation makes sense, I am unable to evaluate the formulas.

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Figure 3: Same point as included in methods. Please include an explanation of how host specificity is measured.
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Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

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

General interest: Is the paper of sufficient general interest?
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Is it adequate?
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Do you have any ethical concerns with this paper?
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Comments to the Author
Reivew of: RSPB-2020-1841

Carlson et al.

What would it take to describe the global diversity of parasites?

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General comments:

Overall, I found the proposal for the Global Parasite Project interesting and new, but I found it difficult to link to the rest of the paper. In addition, the analyses presented (though robust to my knowledge) are limited in their scope and because of this, in my opinion, do little to add to the extensive literature that already exists about the under-sampling of parasites (much of which the authors already cite). Whether this is because the analyses are in fact not needed or because the authors have not effectively communicated their novelty is not clear to me. It would also be helpful if the results from these analyses could be linked more directly to the proposal in Section 6. For example, the authors clearly articulate that their estimates of helminth diversity differ from previous estimates, but the implications of these differences in estimates for the proposed Global Parasite Project are not clear to me.

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other analyses of parasites sampling: I believe we have clearly identified the problem, but this is the first concrete proposal I have seen for a solution. Therefore, I suggest that the authors expand on this section and/or reframe the paper to more clearly focus on how their proposal will directly address the issues they (or others) have identified.

Minor comments:

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Equation 1: Please define the variables in this equation (P and H).

Section 6: What are the "end points" for considering sampling to be complete? Could the goal be to reach an asymptote or level of sampling that allows for estimating true diversity, or is it necessary to catalogue every individual species? You state that this would need to be greater than 5-15% (Line 354), but I would be interested in more detail on "when we stop."

Review form: Reviewer 3

Recommendation
Accept with minor revision (please list in comments)

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Good

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Should the paper be seen by a specialist statistical reviewer?
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c) I suggest listing the software used to create the maps in the material and methods section.

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I congratulate the authors for this initiative. I think that this publication may be of great value for the field of parasitology.

Decision letter (RSPB-2020-1841.R0)

01-Sep-2020

Dear Dr Carlson:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

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

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

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

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

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

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

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

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

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

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

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

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

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

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

Best wishes,
Dr The Proceedings B Team
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Thank you for submitting your manuscript for consideration as an Evidence Synthesis article for PRSB. The manuscript has now been reviewed by 3 experts in the field, and I have also read your work. Collectively, I am pleased to say that there is a shared consensus that your work contains valuable information and the level of innovation will likely have an impact more broadly in the field of parasitology. I therefore encourage you to revise your manuscript in relation to the comments detailed below, in addition to those of my own. As you will know, from details

relating to our Evidence Synthesis article type, it is critically important to provide an evidence base that is sufficiently representative, standardised and robust. I would therefore like to emphasise those suggestions in particular, that relate to aspects of the methodology, such as more information on the R code, some additional details on citations that justify particular statements, and information on appropriate software. There is also a comment that I would like you to consider carefully: the link between the innovative nature of the proposed global parasite project and elements of the rest of your manuscript is not always sufficiently clear. While the association is of course implicit, as you will see in at least some of the suggestions below, there is a need to render such coherence across the MS more explicit, and in particular, some of the limitations relating to data collation to date. I would also like to see rather more specific explanation, albeit brief, on those elements of your analyses that are particularly new, and how they take our understanding, particularly the potential of the global parasite project, forward. There are suggestions relating to some additional material focusing on the species concept and climatic effects on helminth diversity, though I would ask you to draw reference to the wider literature wherever possible, though with some brief explicit comment. I hope that you will find the majority of comments self-explanatory, constructive, and recognise their contribution aimed at enhancing the quality and impact of your manuscript.

I would also like to draw your attention specifically to our requirements for publication of Evidence Synthesis articles. Notwithstanding, in your response to referees, I would be grateful if you would include a brief account relating to my Editorial comments above, and how the manuscript has been modified in relation to my brief suggestions. In particular, as you will have seen from the guidelines available for our Evidence Synthesis articles (https://royalsocietypublishing.org/rspb/evidence-synthesis), it is vital that the reader is able to assess the validity, robustness and objectivity of the evidence base presented. I would therefore appreciate a brief account of how the literature base presented has been selected (as commented on by the referees), and to what degree you have been able to secure the appropriate level of representation, objectivity and standardisation in studies cited. I appreciate this may simply be a brief qualitative description, but it is important in terms of transparency across our various similar such articles. Importantly also, when putting the final touches to the article, please ensure wherever possible, that where relevant, you have addressed some of the questions below, that characterises the Evidence Synthesis article type, though I fully recognise, that many questions will not only partially apply to your manuscript (in your case, the following are especially pertinent: 1,2,3,4,6,7, 8,9,10:

1. Is the key policy-related question(s) articulated clearly?
2. Is there a clear justification in support of policy relevance?
3. Is the likely target audience identified clearly?
4. Does the search for literature utilise a comprehensive range of sources?
5. Does the synthesis article apply clearly documented inclusion criteria to all potentially relevant studies found during the search?
6. Is a clear methodology described to avoid bias?
7. Is your study objectively weighted according to methodological quality of cited literature?
8. Are knowledge gaps and priorities clearly identified?
9. Are outcomes/recommendations tangible in terms of likely impact?
10. Are all necessary supporting information available and accessible??

Thank you in advance for bringing this information together, and we look forward to receiving the revised new manuscript in due course.

Board Member: 2
Comments to Author(s):
(There are no comments.)

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
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Referee: 2

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Carlson et al.
What would it take to describe the global diversity of parasites?

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Equation 1: Please define the variables in this equation (P and H).

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I congratulate the authors for this initiative. I think that this publication may be of great value for the field of parasitology.

Author's Response to Decision Letter for (RSPB-2020-1841.R0)

See Appendix A.

RSPB-2020-1841.R1 (Revision)

Review form: Reviewer 1

Recommendation
Accept as is

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

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
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Is the length of the paper justified?
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Should the paper be seen by a specialist statistical reviewer?
No

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No

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Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I appreciate the time and effort the authors have put into revising this manuscript. I feel that my previous comments were addressed, and I have no further comments.

Review form: Reviewer 2

Recommendation
Accept as is

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

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
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Is the length of the paper justified?
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Should the paper be seen by a specialist statistical reviewer?
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Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I am satisfied with the authors' responses to my comments and those of the other reviewers. I have no further substantial comments. The manuscript contains a few small errors (mostly placement of periods around citations) that I assume will be fixed in the typesetting process. I also suggest adding headers and additional documentation to the GitHub code. I would be happy to see this paper published in Proceedings B and I think it could make a substantial contribution to parasitology and parasite ecology.

Review form: Reviewer 3 (Roberto Dias)

Recommendation
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Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
This paper represents an important contribution to the field of parasitology. It also brings new information on the process of species description, species numbers assessment, and opinions on time estimation and how to describe parasites' diversity. The authors also provide important suggestions on the study of systematics and ecology of helminths for the next decade. This paper brings new and significant contributions to a scientific field that is undervalued nowadays. Now, my recommendation is to accept this paper.

Decision letter (RSPB-2020-1841.R1)

20-Oct-2020

Dear Dr Carlson

I am pleased to inform you that your Review manuscript RSPB-2020-1841.R1 entitled "What would it take to describe the global diversity of parasites?" has been accepted for publication in Proceedings B.

The referee(s) do not recommend any further changes. Therefore, please proof-read your manuscript carefully and upload your final files for publication. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let me know immediately.

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

You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, upload a new version through your Author Centre.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. Please note that PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file from the main text and the file name should contain the author's name and journal name, e.g authorname_procb_ESM_figures.pdf
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please see: https://royalsociety.org/journals/authors/author-guidelines/

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http://datadryad.org/submit?journalID=RSPB&manu=RSPB-2020-1841.R1 which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

5) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit https://royalsociety.org/journals/authors/author-guidelines/.

Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your final version. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr The Proceedings B Team
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Associate Editor Board Member: 1
Comments to Author:
Thank you for your considered response to the collective referee suggestions. As you will see, there is a consensus that your manuscript is now ready to take forward to the final stages, though please do view the minor suggestions from referee #1. Thank you for your engagement with the PRSB review process, and we look forward to receiving the final version of your manuscript, and publication of this important evidence synthesis article.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s)
I am satisfied with the authors' responses to my comments and those of the other reviewers. I have no further substantial comments. The manuscript contains a few small errors (mostly placement of periods around citations) that I assume will be fixed in the typesetting process. I also suggest adding headers and additional documentation to the GitHub code. I would be happy to see this paper published in Proceedings B and I think it could make a substantial contribution to parasitology and parasite ecology.

Referee: 3

Comments to the Author(s)
This paper represents an important contribution to the field of parasitology. It also brings new information on the process of species description, species numbers assessment, and opinions on time estimation and how to describe parasites' diversity. The authors also provide important suggestions on the study of systematics and ecology of helminths for the next decade. This paper brings new and significant contributions to a scientific field that is undervalued nowadays. Now, my recommendation is to accept this paper.

Referee: 1

Comments to the Author(s)
I appreciate the time and effort the authors have put into revising this manuscript. I feel that my previous comments were addressed, and I have no further comments.

Decision letter (RSPB-2020-1841.R2)

22-Oct-2020

Dear Dr Carlson

I am pleased to inform you that your manuscript entitled "What would it take to describe the global diversity of parasites?" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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

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

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

In this manuscript, the authors provide updated estimates for the global diversity of helminth parasites that infect vertebrate hosts. They provide explanations for why current described diversity is a small fraction of existing diversity, propose plans and goals for measuring and cataloging diversity, detail potential sources of error in diversity estimates, and provide updated biodiversity estimates of different helminth groups within a range of vertebrate host taxa.

Overall, while presenting new numbers for the estimates of global helminth diversity (which are sure to be well-cited in the future), I applaud the authors for not making the numbers the main focus of the manuscript. I appreciate the detailed explanations of the inherent difficulties in estimating helminth diversity and the plan for moving forward.

I very much enjoyed reading this manuscript, and I think it will be an important addition to the parasite biodiversity literature (and to the broader biodiversity and ecology literature as well). I do not have any suggestions for major revisions, but I do have a few small recommendations, detailed below.

Thank you!

Small recommendations:

Lines 52-53: I would include at least the phylum name for each group, and potentially class (cestodes) and subclasses (trematodes) for each group as well. This gives the non-parasitologist reader an understanding of the taxa referenced in the methods.

We have added this: “Particularly deserving of reassessment are helminth parasites (hereafter helminths), a polyphyletic group of parasitic worms including, but not limited to, the spiny-headed worms (acanthocephalans; Phylum: Acanthocephala), tapeworms (cestodes; Phylum: Platyhelminthes, Class: Cestoda), roundworms (nematodes; Phylum: Nematoda), and flukes (trematodes; Phylum: Platyhelminthes, Class: Trematoda).”

Lines 53-55: Citations for these claims?

We have added two references for each clause of this sentence: “Helminth parasites exhibit immense diversity, tremendous ecological and epidemiological significance, and a wide host range across vertebrates, invertebrates, and plants.”

Line 99: Why are you specifying monogeneans here? They'd be included in the trematodes (especially clear if you specify subclass above).

We appreciate that the reviewer caught this inconsistency! The NHM helminth database separates out monogeneans from other trematodes, and we chose to keep this distinction – hence specifying "helminth endoparasites" in the abstract – but the sentence that stated this was left out of the methods. We now clarify this:

"In our updated scrape of the web interface, which will be the most detailed version of the dataset ever made public, there are a raw total of 109,060 associations recorded between 25,740 helminth species (including monogeneans, which we exclude to focus on endoparasites) and 19,097 hosts (vertebrate and invertebrate)."

And, in the methods, explain:

"We subset the data to the four focal groups, and excluded monogeneans (which are recorded separately from the Trematoda in the NHM database), given our interest in helminth endoparasites."

Line 107: Please include a citation for the claim that the vast majority are vertebrate parasites.

We have added the appropriate citation (Hoberg 2002).

Line 166-167: Please specify that this is examined over time: e.g., "decreasing body size over time for both hosts and parasites".

We have made this adjustment: "We found a small but highly significant trend of decreasing body size over time for both hosts and parasites,…"

Equation 1: Even though this is from Poulin & Morand (2004), please include a description of the terms in the equation so readers don't have to reference the original text.

We have added this explanation:

"Poulin and Morand proposed an intuitive correction for generalists, where parasite richness P can be estimated ($\hat{P}$) as a linear function of host richness H, using estimates: [formula]"

Lines 230-246: While a difficult (and currently impossible) problem to overcome, I appreciate that the difficulties and contradicting errors are well-laid out in this paragraph.

Thank you!

Lines 258-263: Since there is no estimate for monogeneans, it might be worth mentioning that the 181,474 estimate of trematode species does not include a correction for the cryptic diversity of monogeneans, which are often less studied than digeneans.

As mentioned above, we now clarify that monogeneans were excluded from this estimate, which was restricted to endoparasites.

Materials and methods:
Lines 489-490: If host data is unstandardized and you minimized its use, how did you filter out records from vertebrates? Please include a description of this step.

As we state in the "The Data" section, we assume that records of obligate invertebrate-only parasites are rare (though many species in the collection do have an invertebrate intermediate host but a vertebrate ultimate host). We do not actively subset the data by hosts because, as we said, we aimed to avoid using host data. (The USNPC data are not used in the estimation of vertebrate parasite diversity, which avoids this problem.)

Does the data include host-parasite interactions between intermediate invertebrate hosts and helminths (that use vertebrates as definitive hosts), or does it only include vertebrate-helminth associations? If the latter, would this impact your estimates? Is it likely that an intermediate invert host-helminth interaction would be in the records without the vertebrate host-helminth interaction already included?

The NHM data is subset only to vertebrate-helminth associations, and therefore omits intermediate invertebrate hosts. This improves prediction; scaling properties only work with an internally-consistent category of hosts (e.g., if 99% of vertebrate associations but 5% of invertebrate associations were mixed, this would make the scaling curve inappropriate to extrapolate over vertebrate diversity). Ultimately, at the scale of thousands of species, the relationship between host and pathogen diversity is assumed to be consistent when averaged across different life cycles (see previous work on viral diversity, which makes similar assumptions).

Lines 533-541: How was host specificity and parasite host range measured?

We have clarified that this is host range:

"For host specificity, measured as the total host range (number of hosts), we find an obvious pattern relative to description rates…."

Lines 548-549: What are the twenty groups? Host orders? Please specify.

We have adjusted the phrasing to clarify that this refers to 24 (with fish split – the original 20 was an error) possible pairs of host and parasite clades (6 vert groups x 4 parasite groups, see Table 1). This now reads: "We used the cleaned host-helminth network and \texttt{codependent} to fit curves for each of 24 pairs of host and parasite group (see Table 1)."

Lines 580-593: While the text explanation makes sense, I am unable to evaluate the formulas.

n/a

I am unable to critically review the R code and some of the statistical methods used in the paper, as the R code is above my experience level. It appears that the statistical methods and their reasoning are sound, but I am unqualified to rigorously evaluate them.

n/a

Figures

Figure 3: Same point as included in methods. Please include an explanation of how host specificity is measured. Does higher host specificity measurement mean more specific or less specific? (It's intuitive to think higher host specificity measurement = more host-specific, but this doesn't appear to be the case based on text and graphs, and definitely isn't if host specificity is the number of hosts). Is it the number of hosts? More detail is needed.

As above we've clarified this is host range (i.e. narrower host range is more host specific), and have updated the y-axis to say "host range" instead of "host specificity," and it now reads "Parasites described earlier typically have a higher degree of generalism (greater number of recorded hosts)…"

Referee: 2

Comments to the Author(s)
Reivew of: RSPB-2020-1841
Carlson et al.
What would it take to describe the global diversity of parasites?

Reviewer summary:

In this paper, Carlson et al. summarize the state of knowledge about helminth parasites of vertebrates. They use two databases to analyze the proportion of helminth species that have been discovered, the host associations of these parasites, and biases in parasite discovery. They use their results (that most helminth parasites are undiscovered) to call for a Global Parasite Project, which would focus on encouraging parasitology and the inventory of helminth parasites, and describe potential avenues that could make this massive task more tractable.

General comments:

Overall, I found the proposal for the Global Parasite Project interesting and new, but I found it difficult to link to the rest of the paper. In addition, the analyses presented (though robust to my knowledge) are limited in their scope and because of this, in my opinion, do little to add to the extensive literature that already exists about the under-sampling of parasites (much of which the authors already cite). Whether this is because the analyses are in fact not needed or because the authors have not effectively communicated their novelty is not clear to me. It would also be

helpful if the results from these analyses could be linked more directly to the proposal in Section 6. For example, the authors clearly articulate that their estimates of helminth diversity differ from previous estimates, but the implications of these differences in estimates for the proposed Global Parasite Project are not clear to me.

On the other hand, the last section (Section 6) offers an interesting and nuanced description of the way a Global Parasite Project could be carried out. I particularly appreciate the authors' discussion of the political and equity considerations around the causes of geographic biases in sampling and potential implementation of future studies. This proposal is what is often lacking in other analyses of parasites sampling: I believe we have clearly identified the problem, but this is the first concrete proposal I have seen for a solution. Therefore, I suggest that the authors expand on this section and/or reframe the paper to more clearly focus on how their proposal will directly address the issues they (or others) have identified.

We appreciate the reviewer's suggestion, and have slightly rewritten this section to make more clear what the links are between this section and the rest of the paper, including several new sentences. We've also tried to spell this out in a new, full paragraph:

"Along the same lines of the Global Virome Project, we suggest that parasitology could be transformed by a ``Global Parasite Project'': an internationally-coordinated, bottom-up effort to accelerate parasite description, and catalog half the parasite diversity on Earth (as proposed in the global parasite conservation plan). No such effort currently exists, or has been proposed, and this study is not a formal announcement of such a project. Instead, we consider it as a hypothetical example of how international coordination and targeted investment might be able to address the challenges we identified: parasite taxonomy and collections have grown at a steady but funding-limited pace; much of the remaining parasite diversity is in undersampled host groups and undersampled biodiversity hotspots; and within the current limits of scientific infrastructure, sifting through this undescribed diversity would take hundreds of years.

In practice, many different strategies could be used to address these challenges. However, our analysis highlights several key points about how how a Global Parasite Project could be defined, and what might help it succeed. First, modern methods of estimating parasite diversity make it possible to set realistic and tangible targets for sampling…"

Minor comments:

In general, the writing was clear and easy to understand, and the references were appropriate.

I found the mixing of new results with review/summary of the literature challenging at times (and this may be the root of my comments above about the novelty/necessity of the new analyses). Sometimes the analyses were hard to differentiate from one another, probably because of the methods-last format (e.g. . and I sometimes found it hard to differentiate between results

presented in this paper vs. those from previous analyses (e.g. section 4.2 points to new analyses but some of the following sections (4.4) don't seem to address these new results).

We have reorganized text from 4.1 to 4.3 to make clearer, hopefully, how our analyses modify existing theory and use those data. More broadly, we have made a handful of small word choice changes to make clearer how different analyses fit together.

Section 4.1: There are a number of other methods (other than the asymptote of sampling curves, host-parasite relationships, or the bipartite network approach) that can be used to estimate parasite diversity (e.g., see Walther and Moore 2005 Ecography or Teitelbaum et al. 2020 Ecography). Are these approaches not relevant to your study?

Most of these richness estimators are indeed based on asymptotic estimation of sampling curves (see Figure 2 in Walther and Moore 2005). However, even the ones that are not based on asymptotic curves (e.g. some nonparametric estimators) are used to estimate unsampled diversity from a finite sample (e.g., in a true dataset of 250 sampled parasites out of 300 true parasites of 400 hosts, they would estimate a value approximating 300). These approaches are relevant in that they are connected through the problem of diversity estimation, but should not be used to extrapolate diversity to a higher host sample (e.g. extrapolating to 1,000 hosts from the 300 parasites of 400 hosts), as we do here. These approaches can be used in tandem – for example, we use a combination of these approaches in Carlson et al. 2019 Nature Ecology and Evolution. We explore these connections further in a forthcoming manuscript, "The scaling of symbiotic biodiversity," which will be out in a month or two!

Equation 1: Please define the variables in this equation (P and H).

We have added this explanation:

Poulin and Morand \citep{poulin2004parasite} proposed an intuitive correction for generalists, where parasite richness P can be estimated ($\hat{P}$) as a linear function of host richness H, using estimates: [formula]

Section 6: What are the "end points" for considering sampling to be complete? Could the goal be to reach an asymptote or level of sampling that allows for estimating true diversity, or is it necessary to catalogue every individual species? You state that this would need to be greater than 5-15% (Line 354), but I would be interested in more detail on "when we stop."

To this end, we reference the goal set by the Global Parasite Conservation Plan:

"Recently, the global parasite conservation plan \citep{carlson2020plan} proposed an ambitious goal of describing 50\% of parasite diversity in the next decade."

We have also clarified this in the definition:

"Along the same lines of the Global Virome Project, we suggest that parasitology could be transformed by a "Global Parasite Project": an internationally-coordinated, bottom-up effort to

accelerate parasite description, and catalog half the parasite diversity on Earth (as proposed in the global parasite conservation plan).”

Referee: 3

Comments to the Author(s)

This paper represents an important contribution to the field of parasitology and brings the proposal of a global project on parasites (i.e..: a global effort to transform the Parasitology and to survey the diversity of parasites in a speed unprecedented). It also brings new information on the process of species description, species numbers assessment, and opinions on time estimation and how to describe parasites’ diversity. The authors also provide important suggestions on the study of systematics and ecology of helminths for the next decade. The work highlights the importance of biological collections, beyond the deposit and description of species, suggesting new approaches for the study of helminth parasites of vertebrate hosts. The data from biological collections is representative and allows performing the proposed analyzes. The suggestion of estimating the diversity of helminth parasites of vertebrates is valid and well thought; nonetheless the potential metrics on the biology and ecology, as well as the data used in the taxonomy of these groups of invertebrates were shortened. Even knowing the difficulties of using a wide set of metrics, I think that it is necessary to discuss the limitations of this estimation in a more detailed way. This paper brings new and significant contributions to a scientific field that is undervalued nowadays. It also points out the importance of the biological collections and its countless applications in scientific research.

The manuscript combines elements of a review paper, simulations based on data from two important helminthological collections, and interesting thoughts on the creation of a global project aimed to provide an inventory of parasites in the next 10 years. This format is not usual; however, I think that this paper is innovative, and it may have a positive impact on the scientific field of Parasitology.

I suggest a minor revision as follows:

a) It would be important to include a topic on “species concepts as applied for helminths” in the item 4, presenting a review on the evolution of these concepts, along with the modern tools applied to species delimitation.

Species concepts applied to helminths and the use of species delimitation analyses for helminths could be a review paper unto itself (thanks for the idea!). However, we feel this topic is mostly beyond the scope of this paper. In this study, we used specimen records from the collection databases as they were at the time, and we did not evaluate the identifications compared to current concepts or with modern species delimitation methods. However, we do now clarify:

“We use this approach to re-estimate the total diversity of helminth parasites, repeating the same analysis as Strona and Fattorini. As they did, we mostly ignore questions about species definitions (which are problematic for many parasite clades), and simply use the same definition of “species” operationalized in the available datasets.”

b) It is also important to improve the discussion on the potential climatic effects on the diversity of helminths, considering data from the literature on climatic niche, environmental effects on the diversity of species, and so on.

We have expanded this topic now so that it takes up a full paragraph:

“For parasitology, the nature of the problem might call for a similarly unprecedented effort. For some purposes, the 5-15\% of diversity described may be adequate to form and test ecoevolutionary hypotheses. But the reliability and accuracy of these data will become more uncertain in the face of global change, which will re-assemble host-parasite interactions on a scale that is nearly impossible to predict today. Shifting environmental suitability will drive range shifts in many parasites, or change their transmission intensity; some may go extinct, while others may become invasive or start epizootics. Already, some parasites have been observed disappearing in ecosystems undergoing biodiversity loss. Others will jump into new host species as hosts undergo range shifts, and encounter new parasites in local fauna, leading to new evolutionary opportunities. As climate change progresses, an increasing amount of our time and energy will be spent attempting to differentiate ecological signals from noise and anthropogenic signals. Though some consider the task of cataloging parasite diversity a “testimony to human inquisitiveness”, it is also a critical baseline for understanding biological interactions in a world on the brink of ecological collapse.”

c) I suggest listing the software used to create the maps in the material and methods section.

We have added “All maps were generated in R.” to the mapping section of the methods.

d) In respect to the topic “Global Parasite Project”, a more detailed explanation on the project execution plan and strategies is needed. This topic is very innovative, being necessary to clarify how this project could be implemented.

As we mention above, we have largely rewritten this section to provide more context, including a clarification that this is not the formal announcement of such a project, but rather a hypothetical that we think offers a useful perspective:

“Along the same lines of the Global Virome Project, we suggest that parasitology could be transformed by a ``Global Parasite Project'': an internationally-coordinated, bottom-up effort to accelerate parasite description, and catalog half the parasite diversity on Earth (as proposed in the global parasite conservation plan). No such effort currently exists, or has been proposed, and this study is not an announcement. Instead, we consider it as a hypothetical example of how international coordination and targeted investment could change the \textit{status quo} we identified…”

We also note: “In practice, many different strategies could be used to address these challenges. However, our analysis highlights several key points about how a Global Parasite Project could be defined, and what might help it succeed.”

I congratulate the authors for this initiative. I think that this publication may be of great value for the field of parasitology.

Thank you!