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Towards quantifying the mass extinction debt of the Anthropocene

Christopher Spalding and Pincelli M. Hull

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Review timeline

Original submission:	22 September 2020
Revised submission:	3 March 2021
Final acceptance:	6 April 2021

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

Review History

RSPB-2020-2332.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Accept with minor revision (please list in comments)

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

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

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

Is the length of the paper justified?
Yes

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

Do you have any ethical concerns with this paper?
No

Comments to the Author
This manuscript was a delight to read and review. In recent years there has been growing interest in conservation paleobiology. While the links between the Holocene/Late Pleistocene fossil record and the modern biodiversity crisis are more-or-less straightforward, paleontologists have struggled (albeit with some successes) to make pertinent links between the deep-time fossil record and extinction in the recent. This study is a great example of making those relevant connections in the interested of conservation. The most novel contribution of this study is focusing on the pulsed nature of extinction in the fossil record. This is an important feature of the fossil record and, to my knowledge, has never been incorporated into comparisons with the modern biodiversity crisis. I was also impressed that the authors included the dynamics of the sedimentary rock record into their analyses as a proxy for large-scale environmental change. I have a few comments and suggestions below, but they are all very minor.

In the "Data" section of the review, I marked the supporting data as being inaccessible. This is because the specifics of the PBDB download were not included nor was any code used to analyze data and generate figures. I do think the specifics of the PBDB download are necessary (along with the access date), but the analyses seem straightforward enough that the figures could be reproduced by a reader if they were so motivated.

Lines 227-238: I think slightly longer descriptions of the three datasets used are warranted here. What exactly is being used from the PBDB (all genera, just marine genera, just mammals)? In addition, including the PBDB download parameters, or preferably the API call, would be great. Likewise, a brief statement on the temporal and taxonomic scopes of the Barnosky and IUCN datasets would help readers who are unfamiliar.

Line 536: I have strong objections to the assertion that time "wreaks havoc" on the rock record. The rock record is, of course, not a perfect snapshot of the earth's surface life and environments, but it does preserve a real biological signal (and the authors appear to agree based on this manuscript). More to the point raised, the rock record of marine sediments is one of accumulation, not degradation. Fig 2A in Heim & Peters 2011 shows this clearly: the maximum accumulation of marine sedimentary rock was in the Ordovician. Of course, the same figure also shows that the terrestrial fossil record is very likely dominated by sedimentary degradation. While statements like the one used here are eye-catching, I think the reality is quite different, and ultimately does the field of paleontology a disservice.

Line 571: I love the phrase "save the rocks"!!!! The authors should print this on t-shirts!!!

Figure 2: I think it would be helpful to use major and minor tick marks on the time axis to emphasize for readers that time is plotted on a log scale. Also, mention the log scale in the caption, it looks like a ln scale was used on the top and a log2 scale on the bottom.

Figure 3: (1) I can't distinguish between the blue (B11) points and gray (IUCN) point on the graph, it would be helpful to use different symbols and maybe add a direct label for the IUCN. (2) The figure legend is a bit confusing. Because the italicized labels are on two lines, it took me a few minutes to figure out that "PBDB Cenozoic stages" applied to both the red point and black star. Same for the "Most recent 100,000 years" label. I suggest putting these categorical labels on a single line with the colored points and labels below. This will make the legend one line taller, but I think it will make it easier to read. (3) The time axis label here is " Δ t (years)", but "interval length (Myr)" is used on figure 2. I suggest using the same label for both figures. (4) It's mostly clear which points are the Late Pleistocene on figure 3, but, again, a direct label as on figure 3 would help readers quickly identify these points.

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

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

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

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

Is the length of the paper justified?
Yes

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

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> **Is it accessible?**
> No
>
> **Is it clear?**
> Yes
>
> **Is it adequate?**
> No

Do you have any ethical concerns with this paper?
No

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The authors of this paper identify and attempt to resolve a fundamental problem when comparing ancient and modern extinction events: that there is a large mismatch between the scales of their rate and magnitude. First, they show that while fossils record the magnitude of extinction (but not the rate of extinction), modern extinctions allow us to quantify rates at fine-resolution (but magnitude remains unknown). To then resolve this, the authors propose using a metric that correlates extinction to changes in rock type. They then suggest that preserving sedimentary basins will help preserve ecosystems and biodiversity. I find the problem presented in this paper to be very compelling, and the proposed solution is a good start, but there are a few critical issues with it that need to be resolved in order to strengthen their argument that the proposed metric allows for accurate predictions and specific recommendations, which this manuscript is currently lacking.

The first issue is the data used in Section 3. I think the way the authors bridge the temporal data gap using the PBDB and the Barnosky data is clever, but it is also very interesting that there is a mismatch between the two data sets. The PBDB has many biases, specifically collection bias and research effort bias. I would recommend further examining who collected and/or entered the PBDB data and making sure a few very large collections do not skew data distribution.

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There is much literature on the topic of stratigraphy, sedimentology, and extinctions that I think should be engaged with to improve the discussion and interpretation of the results. For example:
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Nawrot et al. 2018 https://doi.org/10.1098/rspb.2018.1191

Dominici et al. 2018 https://doi.org/10.1016/j.earscirev.2017.09.018

Tomašových et al. 2020 http://dx.doi.org/10.1098/rspb.2020.0695

Holland 2020 https://doi.org/10.1146/annurev-earth-071719-054827

Zimmt et al. 2020 https://doi.org/10.6078/d1098d

Smaller issues:

The Barnosky, IUCN, and PBDB datasets are just mammals, and the Heim and Peters dataset is much broader in taxonomic/ecologic composition. I am uncomfortable with the broad conclusions drawn using very different datasets with different sets of organisms.

Another issue with the idea of focusing restoration on areas of sedimentation. Not all endangered animals live in areas of deposition, so focusing on those areas excludes many others at risk.

Review form: Reviewer 3

Recommendation
Accept with minor revision (please list in comments)

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

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

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

Is the length of the paper justified?
Yes

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

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
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> **Is it accessible?**
> N/A
>
> **Is it clear?**
> N/A
>
> **Is it adequate?**
> N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
This interesting paper compares metrics for extinction in the fossil record compared to modern day ones.

On reading it, some thoughts emerged that the authors might want to reflect on. First: the extinction dynamics of genera are different from those of species, because genera are composed of species (of course, species are themselves composed of populations etc). In birth death modelling (of which more later) it is generally assumed that species extinctions are instantaneous, which, as the authors point out, on the time scale of resolution of the fossil record is probably reasonable. However, if a "genus" goes extinct, the time that this takes will (again on a BDM perspective) depend on how many species it has. The relationship between genus and species numbers is probably some sort of power law (see e.g. Sigwart et al. 2018, Zoological Journal of the Linnean Society). From a BDM perspective, a species appears and then vanishes (but see https://academic.oup.com/sysbio/article/61/2/204/1645577 for "protracted speciation") – however, although many genera are monospecific, more are not (Sigwart et al.). Thus, a genus will have a moment in time when it appears; it will come to an acme, and then go extinct, and its diversity with thus wax and wane through time. For many genera, this will take millions of years – perhaps 20 million or more (I think Peters and Heim give some numbers here of around 20-25 Myrs).

From a formal perspective, pulsed and background extinctions seem to grade into each other – for example, see Fig 3E of Budd and Mann 2020 and the results of Lambert and Stadler 2012, which show that a series of pulsed extinctions imposed on a homogeneous birth death process can be modelled by another BDP. Note that there is, in this perspective, no "true" background "rate" – there only observations of extinctions (ie surely the concept of a "background rate" is a "mathematical fiction", even if it is a useful one).

Another issue that arises is that modern and ancient genera might be different because of the so-called "pull of the Present".

A genus in the past must originate at a particular point; it will probably undergo a "push of the past" (Budd and Mann 2018, Evolution) and thus diversify rapidly (at the species level) to an acme; and then it will decay to extinction. However, a modern genus will have originated quite recently on average, and thus will not require a push of the past diversification to survive to the present day, because the "pull of the present" will do the job instead; nor will it necessarily have started its decline to extinction, and certainly cannot have completed it. It is not clear to me how you would compare the two sets of phenomena. Second, they might even have different sizes as well. One might take the size of a genus in the past as its acme number of species; but what of a recent one? Any living clade can be coalesced back to its start point, which will have an exponential distribution in time; and will have a geometrically distributed number of species; so overall, if you add these two distributions up you might end up with some sort of long-tailed distribution (perhaps a power law?). But this might not at all correspond to the peak size of a fossil genus.

The relationship between facies change and extinction seems – unclear. As the authors point out, the literature does indeed suggest that sediments and biotas change together. But – correlation is not causation. In this instance, there is a hidden variable, for example that of time, which may be governing both. In other words, at facies boundaries, there may well often be cryptic or not so cryptic disconformities within which quite a lot of time is hidden. I understand that Peter and Heim investigated these biases and tried to rule them out, but they are quite cautious in their conclusions (partly because of the potential problems of taxonomic bias near unconformities). In addition, as far as I can see they treat genera extinctions as point events rather than wanings, as suggested here, and this may also have an effect. Nevertheless, sea level changes gave been often tied in to both extinctions and (naturally) to sedimentary changes, and this "common cause" effect might be of some significance in some extinctions. But: it does not need to be significant in all of them.

After all, when we think about modern day extinctions, it is not at all clear that the ones we are aware of are related in a causal way (even indirectly) to changes in sedimentation, if only because many are terrestrial where such effects would be less clear. And it is unclear why, say, the loss of river dolphins, passenger pigeons or (potentially) pandas would have such a linkage. Indeed, as far as I understand, this is also the conclusion of Rook et al. 2013 (in Palaeo 3). Finally, a potentially analogous concept to the extinction debt of this paper is explored by the recent paper in Nature by Hoyal Cuthill et al. (23rd Dec. 2020 issue).

Decision letter (RSPB-2020-2332.R0)

18-Jan-2021

Dear Dr Spalding:

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.

Please note that "data" here means code and other tools developed for the study, which have been noted as not available with the current draft-- please amend this, to enable replication/reuse as per our policy.

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 John Hutchinson, Editor
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Dear Authors,

Thank you for your patience with this review process; your manuscript has now been viewed by three expert reviewers who all recognise it as an interesting and worthwhile contribution, while recommending a number of important points for consideration.

On reading your manuscript, a concern arose in my mind along the same lines as one of the major points raised by Reviewer 3: that the relationship between facies change and extinction may not always be as clear as it is generally made out to be in the manuscript. I would encourage you to consider the points of Reviewer 3 carefully and revise the manuscript in a manner that addresses this concern as much as possible.

The remaining points raised by the three reviewers are similarly important to take into account. In your revision, I would find it very helpful if you would be able to provide a point-by-point response letter to the concerns raised by the reviewers. I look forward to seeing your revision, and thank you for your submission.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
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Referee: 2

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Smaller issues:
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Referee: 3

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Another issue that arises is that modern and ancient genera might be different because of the so-called "pull of the Present".
A genus in the past must originate at a particular point; it will probably undergo a "push of the past" (Budd and Mann 2018, Evolution) and thus diversify rapidly (at the species level) to an

acme; and then it will decay to extinction. However, a modern genus will have originated quite recently on average, and thus will not require a push of the past diversification to survive to the present day, because the "pull of the present" will do the job instead; nor will it necessarily have started its decline to extinction, and certainly cannot have completed it. It is not clear to me how you would compare the two sets of phenomena. Second, they might even have different sizes as well. One might take the size of a genus in the past as its acme number of species; but what of a recent one? Any living clade can be coalesced back to its start point, which will have an exponential distribution in time; and will have a geometrically distributed number of species; so overall, if you add these two distributions up you might end up with some sort of long-tailed distribution (perhaps a power law?). But this might not at all correspond to the peak size of a fossil genus.

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Author's Response to Decision Letter for (RSPB-2020-2332.R0)

See Appendix A.

RSPB-2020-2332.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?
Good

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

Is the length of the paper justified?
Yes

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

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

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

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
Thank you very much for thoroughly addressing my concerns. I think that the manuscript can move towards publication in its current form.

Decision letter (RSPB-2020-2332.R1)

06-Apr-2021

Dear Dr Spalding

I am pleased to inform you that your manuscript entitled "Towards Quantifying the Mass Extinction Debt of the Anthropocene" has been accepted for publication in Proceedings B. Congratulations!!!

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.

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

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

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

Associate Editor:
Board Member: 1
Comments to Author:
The authors have gone to very impressive lengths to accommodate a protracted and demanding review process, and the result in my mind is a much-improved manuscript that is more nuanced and balanced than the initial submission. I think this will make for an interesting and provocative contribution.

Appendix A

Associate Editor
Board Member: 1
Comments to Author:
Dear Authors,

Thank you for your patience with this review process; your manuscript has now been viewed by three expert reviewers who all recognise it as an interesting and worthwhile contribution, while recommending a number of important points for consideration.

That is no problem at all! This past year has been tough on everyone, and delays are to be expected.

On reading your manuscript, a concern arose in my mind along the same lines as one of the major points raised by Reviewer 3: that the relationship between facies change and extinction may not always be as clear as it is generally made out to be in the manuscript. I would encourage you to consider the points of Reviewer 3 carefully and revise the manuscript in a manner that addresses this concern as much as possible.

See our responses to R2 and R3, and the cover letter, for a full response to this. But essentially, we fully agree. Our first draft was far too focused on the Peters & Heim link, which showed a link between hiatuses and extinctions, but only in the marine realm. In the terrestrial realm, the link is not there to the same extent. Or rather, if the link is there, its signal is heavily degraded by erosion, which dominates the quantity of non-marine rock over time. Our intention was more to draw upon the rock-life link derived in the marine realm, where rock quantity more accurately reflects sea-level and habitat area, in order to guide the development of similar but not identical global proxies in the non-marine habitats of today.

The remaining points raised by the three reviewers are similarly important to take into account. In your revision, I would find it very helpful if you would be able to provide a point-by-point response letter to the concerns raised by the reviewers. I look forward to seeing your revision, and thank you for your submission.

Thank you. We believe that we have addressed most or all of the referee's concerns to the best of our ability.

Reviewer(s)' Comments to Author:

Referee: 1

Comment:

This manuscript was a delight to read and review. In recent years there has been growing interest in conservation paleobiology. While the links between the Holocene/Late Pleistocene fossil record and the modern biodiversity crisis are more-or-less straightforward, paleontologists have struggled (albeit with some successes) to make pertinent links between the deep-time fossil record and extinction in the recent. This study is a great example of making those relevant connections in the interested of conservation. The most novel contribution of this study is focusing on the pulsed nature of extinction in the fossil record. This is an important feature of the fossil record and, to my knowledge, has never been incorporated into comparisons with the modern biodiversity crisis. I was also impressed that the authors included the dynamics of the sedimentary rock record into their analyses as a proxy for large-scale environmental change. I have a few comments and suggestions below, but they are all very minor.

Response:

We thank you for your interest and comments!

Comment:

In the "Data" section of the review, I marked the supporting data as being inaccessible. This is because the specifics of the PBDB download were not included nor was any code used to analyze data and generate figures. I do think the specifics of the PBDB download are necessary (along with the access date), but the analyses seem straightforward enough that the figures could be reproduced by a reader if they were so motivated.

Response:

Thank you for pointing out the insufficiency of simply providing a link to the *PBDB*. We have now collected all of our data and relevant scripts and deposited them in the Dryad online repository (https://doi.org/10.5061/dryad.tdz08kpzt). It is still being curated as of submission, but a temporary link may be found here (https://datadryad.org/stash/share/0rXxPF07jF6ozoXj8ccLWv75Lktbt134QdHn5-W1uKw)

Comment:

Lines 227-238: I think slightly longer descriptions of the three datasets used are warranted here. What exactly is being used from the PBDB (all genera, just marine genera, just mammals)? In addition, including the PBDB download parameters, or preferably the API call, would be great. Likewise, a brief statement on the temporal and taxonomic scopes of the Barnosky and IUCN datasets would help readers who are unfamiliar.

Response:

We have now expanded the description of the data into a new section "Data and Methods". Among the added text is

"*From the PBDB, we downloaded diversity data in 5 different formats. The first 3 included all animal genera, with occurrences divided by Stage, Epoch and Period, respectively (Figure 2). The final two formats include Cenozoic genera, with one including all animal genera and the other restricted to mammalian genera (Figure 3). The data was downloaded on 25-01-2021.*"

Comment:

Line 536: I have strong objections to the assertion that time "wreaks havoc" on the rock record. The rock record is, of course, not a perfect snapshot of the earth's surface life and environments, but it does preserve a real biological signal (and the authors appear to agree based on this manuscript). More to the point raised, the rock record of marine sediments is one of accumulation, not degradation. Fig 2A in Heim & Peters 2011 shows this clearly: the maximum accumulation of marine sedimentary rock was in the Ordovician. Of course, the same figure also shows that the terrestrial fossil record is very likely dominated by sedimentary degradation. While statements like the one used here are eye-catching, I think the reality is quite different, and ultimately does the field of paleontology a disservice.

Response:

We appreciate that our language was somewhat informal here! We have amended this phrase to "distorts and erodes". Moreover, at several locations throughout the manuscript, we have expanded our description of the rock-life link to make clear that there exist clear differences between marine and terrestrial rocks. That is, terrestrial rocks do appear to show an exponential decay with time, indicative of erosion.

"*First, in contrast to the marine realm, sedimentary hiatuses are not a good candidate in terrestrial environments (where erosion dominates rock quantity, e.g., Wall et al. 2011; Rook et al. 2013) or for modern-historical comparisons. Sea-level (and sea level variations) is responsible for much of the quantity and continuity of preserved shallow-marine sediment over the Phanerozoic (Peters & Husson 2017) and is not the primary dynamic we are seeking to trace today. Instead, a sedimentary tracer of anthropogenic environmental change might be better linked to turnover in lithology, that is, to changes in composition of the rock itself (Figure 4).*"

Essentially, the marine link between rocks and life suggests that extinctions are presaged by sedimentary perturbations, but the exact nature of that link remains to be fully elucidated for habitats in general.

Comment:

Line 571: I love the phrase "save the rocks"!!!! The authors should print this on t-shirts!!!

Response:

We appreciate the vote of confidence! However, since the previous version we have added nuance to this idea throughout the manuscript—for the reasons mentioned in the previous comment.

Comment:

Figure 2: I think it would be helpful to use major and minor tick marks on the time axis to emphasize for readers that time is plotted on a log scale. Also, mention the log scale in the caption, it looks like a ln scale was used on the top and a log2 scale on the bottom.

Response:

We have updated the captions and added minor tick marks to the x axes of Figures 2 and 3. Moreover, we changed the y-axes of Figures 2 and 3 to simply plot the extinction rate on a log-scale, as opposed to plotting the logarithm of the extinction rate. This hopefully provides the reader a clearer picture of the actual range of extinction rates plotted.

Comment:

Figure 3: (1) I can't distinguish between the blue (B11) points and gray (IUCN) point on the graph, it would be helpful to use different symbols and maybe add a direct label for the IUCN. (2) The figure legend is a bit confusing. Because the italicized labels are on two lines, it took me a few minutes to figure out that "PBDB Cenozoic stages" applied to both the red point and black star. Same for the "Most recent 100,000 years" label. I suggest putting these categorical labels on a single line with the colored points and labels below. This will make the legend one line taller, but I think it will make it easier to read. (3) The time axis label here is "Δt (years)", but "interval length (Myr)" is used on figure 2. I suggest using the same label for both figures. (4) It's mostly clear which points are the Late Pleistocene on figure 3, but, again, a direct label as on figure 3 would help readers quickly identify these points.

Response:

Thank you for these suggestions! The figure was definitely too subtle. We have 1) Turned the IUCN point into a large red X, 2) Separated the legend into four sections to make clearer which data is associated with the PBDB and which with the recent data 3) Changed the x label and 4) labeled the Late Pleistocene.

<u>Referee: 2</u>

Comment:

The authors of this paper identify and attempt to resolve a fundamental problem when comparing ancient and modern extinction events: that there is a large mismatch between the scales of their rate and magnitude. First, they show that while fossils record the magnitude of extinction (but not the rate of extinction), modern extinctions allow us to quantify rates at fine-resolution (but magnitude remains unknown). To then resolve this, the authors propose using a metric that correlates extinction to changes in rock type. They then suggest that preserving sedimentary basins will help preserve ecosystems and biodiversity. I find the problem presented in this paper to be very compelling, and the proposed solution is a good start, but there are a few critical issues with it that need to be resolved in order to strengthen their argument that the proposed metric allows for accurate predictions and specific recommendations, which this manuscript is currently lacking.

Response:

Thanks for your careful reading and helpful comments! We agree fundamentally with the points raised and have worked to address them as best we can.

Comment:

The first issue is the data used in Section 3. I think the way the authors bridge the temporal data gap using the PBDB and the Barnosky data is clever, but it is also very interesting that there is a mismatch between the two data sets. The PBDB has many biases, specifically collection bias and research effort bias. I would recommend further examining who collected and/or entered the PBDB data and making sure a few very large collections do not skew data distribution.

Response:

Thank you for drawing attention to this conspicuous disagreement, as we only briefly alluded to it within our first submission. Having given it a bit more thought, we believe we know the source of the mismatch. That is, the data taken from Barnosky et al. 2011 include all modern-day mammal genera in the total diversity. That is, they note 157 extinct mammal genera in the past 100,000 years, out of a total of 1397 genera. This gives an extinction rate of about 1.1E/MGY. In our PBDB data, 178 mammalian genera extinctions are recorded moving from the Late Pleistocene to the Holocene. However, the total diversity in the Late Pleistocene was only 581. If we were to inflate this total diversity to include modern genera (as in Barnosky et al. 2011), we would indeed infer an extinction rate roughly commensurate with what is concluded from the Barnosky 2011 compilation (which stands at roughly a factor of ~2.5). This effect is actually mentioned in the Barnosky et al. (2011) paper (caption of Figure 1) where they say that "*This method may overestimate the fossil mean extinction rate and underestimate the modern means…*"

We have added the following text:

“*Notably, the B11 rate is lower than the PBDB rate in the Late Pleistocene (Δt=10^5 years). This discrepancy likely arises from the inclusion of all modern-day mammalian genera by B11 but not in the PBDB (which includes fossil occurrences only). Including modern genera increases the total standing diversity of mammals in the Late Pleistocene to 1397 genera in contrast to 581 genera in the PBDB. This factor of 2.4 approximately accounts for the disagreement.”*

The above discussion is essentially a manifestation of the preservation bias in the fossil record. Given that the Late Pleistocene is so recent, we can assume with relative confidence that most living mammalian genera existed during the Late Pleistocene. This statement becomes progressively less true as stages get older, the associated discussion was helpful in allowing us to add an expanded mention of preservation bias and how it also affects inferences regarding comparing fossil and modern extinction rates.

“*In addition to problems of time-step duration, the fossil record is incomplete, with an estimated 38% of modern marine genera appearing in the fossil record (Shaw et al. 2021). Genera preserved are preferentially long-lived and widespread (Foote & Raup 1996, Valentine & Jablonski 2006), specious and initially rapidly diversifying (Nee et al. 1994; Budd & Mann 2018, 2020), and are found in habitats with higher preservation potential (e.g., Valentine 1989). Such taphonomic biases make threatened modern mammal genera about half as likely to display a fossil record as those that are not (Plotnick et al. 2016).”*

Comment:

Section 4 links sedimentary hiatuses to extinctions, which has been well established. In 466-469, they state that “the extent of Anthropogenic sedimentary turnover may provide the best available measure of the relative size of our extinction pulse,” which is an important insight, yet it is not explored further. I believe this argument could be strengthened with basin or stratigraphic modeling to show whether hypothetical future changes in sedimentation actually correlate with predicted extinctions. Only a very short part of the manuscript is explicitly spent linking rock type to extinction, which is the basis of the proposed metric, and the examples given of current lithologic change are not always relevant. For example, in lines 504 - 513, the authors use the example of rivers being restored to meandering rather than anabranching, which is very different from the changes in sedimentation that accompany extinction in the rock record (e.g., a shift from marine limestone to terrestrial siliciclastics).

Response:

We thank the referee for highlighting the sense of incompleteness in our initial framing of a sedimentary metric. We absolutely agree that sedimentary basin modeling would be invaluable in approaching a truly quantitative sedimentary metric. However, such a task would require work beyond the current scope of our work. Nevertheless, we have largely re-framed and combined Sections 4 & 5 to make clear the kinds of approaches that would help quantify sedimentary turnover. Moreover, we describe in Section 4.1 a simplified theoretical picture of the link between habitat area, species and stratigraphy, that may guide future efforts.

We have also re-made Figure 4. That is, the facies-life link from Heim & Peters 2011’s geological data applies only to Marine facies. Terrestrial facies primarily follow an erosive signal and so do not capture the same information. We have re-framed the Heim and Peters data as suggestive of an analogous metric in modern times, but we leave open the specifics of that metric. We point to several promising directions—deforestation’s influence upon soil erosion, river damming’s influence on riverine sediment flow and agriculture’s effect on coastal area, among others. However, each of these case studies requires its own geomorphological treatment in order to translate human modification into a geological signal.

“…Crucially, each regime of environmental disruption would require its own geomorphological modeling in order to translate human modification into basin-scale alterations (shown schematically in Figure 4; Brown et al. 2017, 2018), which will then become encoded within the geological record (Tomašových et al. 2020, Plotnick et al. 2020). These sedimentary signals may be spatially displaced from the associated environment, and many critical environments are simply not (or only very rarely) recorded in the rock record. Accordingly, such a metric may be best suited to assessing the global (rather than regional, or habitat specific) magnitude of the current biotic crisis.

A further difficulty pertains to what or when to define as a pre-human state (e.g., Jackson 2001). Humans have exerted global influence upon sedimentation for millennia (Syvitski et al., 2005; Ellis & Ramankutty, 2008; Brown et al., 2018; Stephens et al., 2019). For example, prior to extensive damming centuries ago, much of the river system of North America supported widespread wetlands, now buried beneath metres of post-settlement alluvium (destined to be recorded in the rock record Wohl, 2015), and devoid of the historical fauna. Similarly, a century ago, agricultural practices had already transformed the Southern California shelf into relatively homogenous mud-ground (Tomašových & Kidwell 2017). Declines in populations, habitats, and species during recent centuries span a wide range of taxa and habitats (IUCN 2019), but began even earlier (e.g., Koch &

Barnosky 2006). Thus, any lithological comparison between the modern and the geological record carefully infer the time humans first began altering the rock record."

Comment:

There is much literature on the topic of stratigraphy, sedimentology, and extinctions that I think should be engaged with to improve the discussion and interpretation of the results. For example:

Foot and Raup 1996 Fossil preservation and the stratigraphic ranges of taxa. Paleobiology. 121-140.

Brett 1998 https://doi.org/10.2307/3515448

Scarponi et al. 2013 https://doi.org/10.1130/G33849.1

Holland and Patzkowsky 2015 https://doi.org/10.1111/pala.12188

Nawrot et al. 2018 https://doi.org/10.1098/rspb.2018.1191

Dominici et al. 2018 https://doi.org/10.1016/j.earscirev.2017.09.018

Tomašových et al. 2020 http://dx.doi.org/10.1098/rspb.2020.0695

Holland 2020 https://doi.org/10.1146/annurev-earth-071719-054827

Zimmt et al. 2020 https://doi.org/10.6078/d1098d

Response:

We are grateful for this treasure-trove of great references! We have incorporated most within the current manuscript, and all of them will be critical for our future explorations into this topic.

Comment:

Smaller issues:
The Barnosky, IUCN, and PBDB datasets are just mammals, and the Heim and Peters dataset is much broader in taxonomic/ecologic composition. I am uncomfortable with the broad conclusions drawn using very different datasets with different sets of organisms.

Response:

We agree that using an empirical trend across all genera (as in H&P11) is not necessarily applicable to mammals. However, our focus on mammals in Figure 3 was primarily to illustrate the issues associated with timescales. The Barnosky et al. 2011 data was a useful dataset to bridge that timescale gap, and it happened to include only mammals.

We hope that the manuscript now better illustrates that the H&P11 data was used to motivate a *lithological* signal, as opposed to focusing on extinction *rates*. Specifically, we have added the following text:

"*Human activity has already exterminated 100s of species, but an uncertain number are bound for extinction through extinction debt and secondary cascades. In contrast, the fossil record would compress an extinction debt of centuries into a single geological boundary—extinctions and rock-type changes are coeval. At least in the marine fossil record, well-documented temporal correlation exists between extinction magnitude and hiatuses (disruptions to sedimentation) within North American sedimentary sequences (Peters, 2005, 2006; Peters & Heim, 2011; Rook et al. 2013). Using data acquired from Heim & Peters (2011) we illustrate this correlation by comparing the fractional genus extinction within each stage (as of 2011) to hiatuses in sedimentary sequences (Figure 4). This correlation has been suggested as causal; the loss of shallow-marine shelf habitat (typically via sea level variation) drives marine extinctions through species-area relationships (Heim & Peters 2011).*

…

First, in contrast to the marine realm, sedimentary hiatuses are not a good candidate in terrestrial environments (where erosion dominates rock quantity, e.g., Wall et al. 2011; Rook et al. 2013) or for modern-historical comparisons. Sea-level (and sea level variations) is responsible for much of the quantity and continuity of preserved shallow-marine sediment over the Phanerozoic (Peters & Husson 2017) and is not the primary dynamic we are seeking to trace today. Instead, a sedimentary tracer of anthropogenic environmental change might be better linked to turnover in lithology, that is, to changes in composition of the rock itself (Figure 4). "

Comment:

Another issue with the idea of focusing restoration on areas of sedimentation. Not all endangered animals live in areas of deposition, so focusing on those areas excludes many others at risk.

Response:

We agree that this might be a point of confusion. In order to hopefully alleviate such confusion, we have carefully curated our language throughout to make it clear that we see this approach as a means of comparing the magnitude of the current biotic crisis on a global scale with those in the past. This is not meant to be a metric to identify regions of greatest conservation concern for prioritization. This is described in Section 4.1 and Figure 4, but we have also added text such as

"*Significant benefits would come from a predictive metric that forecasts a predicted ΔS from an observed ΔH. However, many challenges stand in the before such a computation may be utilised (e.g., Zalasiewicz et al. 2011). Crucially, each regime of environmental disruption would require its own geomorphological modeling in order to translate human modification into basin-scale alterations (shown schematically in Figure 4; Brown et al. 2017, 2018), which will then become encoded within the geological record (Tomašových et al. 2020, Plotnick et al. 2020).* ***These sedimentary signals may be spatially displaced from the associated environment, and many critical environments are simply not (or only very rarely) recorded in the rock record. Accordingly, such a metric may be best suited to assessing the global (rather than regional, or habitat specific) magnitude of the current biotic crisis***."

Referee: 3

This interesting paper compares metrics for extinction in the fossil record compared to modern day ones.

Comment:

On reading it, some thoughts emerged that the authors might want to reflect on. First: the extinction dynamics of genera are different from those of species, because genera are composed of species (of course, species are themselves composed of populations etc). In birth death modelling (of which more later) it is generally assumed that species extinctions are instantaneous, which, as the authors point out, on the time scale of resolution of the fossil record is probably reasonable. However, if a "genus" goes extinct, the time that this takes will (again on a BDM perspective) depend on how many species it has.

The relationship between genus and species numbers is probably some sort of power law (see e.g. Sigwart et al. 2018, Zoological Journal of the Linnean Society). From a BDM perspective, a species appears and then vanishes (but see https://academic.oup.com/sysbio/article/61/2/204/1645577 for "protracted speciation") – however, although many genera are monospecific, more are not (Sigwart et al.). Thus, a genus will have a moment in time when it appears; it will come to an acme, and then go extinct, and its diversity with thus wax and wane through time. For many genera, this will take millions of years – perhaps 20 million or more (I think Peters and Heim give some numbers here of around 20-25 Myrs).

Response:

Thank you— it took us a second to catch the thread, but you are quite correct. This was a really helpful corner to reflect on. The points you raise here and below highlight that we failed to explicitly frame some of the assumptions of the approach we are taking, and what we are (and are not!) explicitly taking into account in our models. This is perhaps all the more ironic as we have also published on the effect of temporal duration of speciation (Norris and Hull 2012), the differential ability to 'see' species and genera in modern and ancient times (Hull et al. 2015). We have worked to incorporate the spirit and intent of these thoughts into the modeling and descriptions.

We now include a direct comparison of species-based rates of extinction and genus-based rates of extinction from the Barnovsky data (Figure 3), which addresses some of the concerns and revised how we discuss and handle the topic of pulsed versus background extinction (also below).

"Data from B11 include both species and genus-level extinctions and so we plot both on Figure 3 (in orange and blue respectively). Extinction rates at species and genus levels are similar to a factor of ~1.5, consistent with previous results (Plotnick et al. 2016). Almost half of mammalian genera are monospecific (Sigwart et al. 2018) suggesting that the fractional extinction of species and genera should be within a factor of ~2, only differing substantially if a bias existed for (or against) the extinction of single-species genera."

One of the points you raise here is the importance of the waxing and waning of genera. Though we acknowledge the critical importance of these dynamics in other areas, such as phylogenetic reconstructions and biases, we actually, very respectfully, disagree with its importance within the context of the modeling and intellectual framework of our work, so we want to explain why we didn't incorporate it.

You are quite correct, of course, that before a genus goes extinct there will be an interval when it is losing more species (via extinction) than gaining by speciation. The waning interval. Although this is a useful distinction between genera and species in a BDM context, we don't see its utility as much in our framework because this also describes the pattern of how a species -in reality- goes extinct as well. A species is made up of one to (most typically!) many populations of individuals. As a species goes extinct, there is also an interval where it is losing more populations than it is gaining (by immigration or equivalent). In the end, when the species loses the last population, it is extinct. For a genus, in the end, when it loses the last species, it is extinct. Of course, there are fundamental difference between the populations that make up a species and the species that make up a genus. While we don't completely disagree, one of the mind-boggling delights of the genomic/transcriptomic era is the importance and prevalence of gene flow across species. Regardless, for the purpose of our work here, and the debates regarding and seeking to compare current and past rates of extinction, we argue that it is valid to focus on the rate of 'final loss', be it the rate of the loss of species (when fully extinct) or the rate of the loss of genera (when the last species in that genus is gone).

We are happy to reconsider this if you think we should—but we need guidance on how and why the distinction applies to the modeling we use here.

Comment:

From a formal perspective, pulsed and background extinctions seem to grade into each other – for example, see Fig 3E of Budd and Mann 2020 and the results of Lambert and Stadler 2012, which show that a series of pulsed extinctions imposed on a homogeneous birth death process can be modelled by another BDP. Note that there is, in this perspective, no "true" background "rate" – there only observations of extinctions (ie surely the concept of a "background rate" is a "mathematical fiction", even if it is a useful one).

Response:

This is an excellent point! And we are very grateful to the reviewer for sending us down this direction of thought, because we believe that it substantially improved the rigour of our mathematical descriptions in section 2 (see below).

You are, of course, correct – at the limit of small δTime, all extinction events (and all speciation events) are point events. Why then, this obsession with background rates of extinction and speciation in scientific discourse? We suspect it is because scientist have an assumed time-step size in mind when they think about the natural world. And this time step is often long enough to integrate over a number of events (be they extinction or speciation events) and conceptualize extinction rates as deterministic. This is appropriate for the fossil record—over ~10% of genera go extinct within most geological stages, which equates to on the order of 100 extinct genera (where the specific numbers are of course stage-dependent), and many more (maybe over twice as many) extinct species.

The modern day contrasts sharply with this "averaged/large time-step" view. That is, individual extinctions of, say, mammalian genera are separated by decades. The separation of species extinctions is smaller, but still, our resolution is shorter than the mean time between extinctions. In this case, when $\Delta t<1/\mu$, the extinction rate parameter μ describes a stochastic waiting time, not a rate.

We recapitulate the above discussion in the manuscript with the following text:

"*Genus extinctions do not occur at a regular pace throughout time. Each generic extinction is a single event, stochastically distributed in time with rate parameter μ. Nevertheless, when the resolution of observations Δt far exceeds the time between extinctions, as for geological stages, multiple extinctions may be thought of as occurring at a single "background" rate—an approach often adopted. However, this idea becomes misleading during modern times, when our timestep of resolution drops well below the expected time between genus extinctions. At such a high resolution, the concept of a background rate in some sense loses meaning. In comparing the modern to the past, it is important to consider how a time-variable extinction rate may be recorded in the fossil record."*

And, as we show in the Figure 3, because the time step size affects the inferred rate (i.e., the 'Sadler Effect' to geologists), the mismatch in the time step size that we can directly measure as conservation biologists (on the scale of hundreds of years) and what we can see in the fossil record (tens to hundreds of thousands of years at best…typically) is really at the crux of the problem.

Moreover, we have reframed some of our discussion surrounding the pulsed extinction model to highlight the important dynamical quantity, $\mu(t)$, defined by equation (1). This may take any time-dependent form, pulsed or not. Regardless, when comparing two times and computing the extinction metric, only the average is constrained, causing a pulsed extinction rate to be indistinguishable from an average rate that decreases with timestep.

From the perspective of population dynamics, $\mu(t)$ is measured not from the fraction of genera going extinct, as in our original manuscript, but by $-ln(1-x)$ where x is the fraction of genera going extinct. In reality, none of our conclusions are changed by this perspective, but when x is small, we recover the metric often used in analyses of modern extinction rates (i.e., $-ln(1-x) \approx x$)

We have revamped section 2 to take account of this change. Nothing changes qualitatively, but we believe that the usage of the logarithmic extinction rate better captures the underlying per-genus extinction rate than a simple fractional extinction.

We have also added the following text after Equation (5):

"This result depends upon the observation timescale (Section 3). However, without further information, the extinction pulse's contribution to $\mathcal{E}$ is indistinguishable from a heightened background extinction rate. Moreover, a large number of small pulses occurring close together grades into the same extinction dynamics as a single background rate (Budd & Mann 2020)."

Comment:

Another issue that arises is that modern and ancient genera might be different because of the so-called "pull of the Present". A genus in the past must originate at a particular point; it will probably undergo a "push of the past" (Budd and Mann 2018, Evolution) and thus diversify rapidly (at the species level) to an acme; and then it will decay to extinction. However, a modern genus will have originated quite recently on average, and thus will not require a push of the past diversification to survive to the present day, because the "pull of the present" will do the job instead; nor will it necessarily have started its decline to extinction, and certainly cannot have completed it. It is not clear to me how you would compare the two sets of phenomena.

Second, they might even have different sizes as well. One might take the size of a genus in the past as its acme number of species; but what of a recent one? Any living clade can be coalesced back to its start point, which will have an exponential distribution in time; and will have a geometrically distributed number of species; so overall, if you add these two distributions up you might end up with some sort of long-tailed distribution (perhaps a power law?). But this might not at all correspond to the peak size of a fossil genus.

Response:

Again, you raise great points regarding processes that are explicitly included or excluded from our models. We agree that that there are major biases (and different major biases) in measuring extinction deep in the fossil record, relatively recently in the fossil record, and in extant taxa (be it from direct observations of extinction rates or inferred from phylogenies).

Our approach ignores all of these—and this needs to be stated. In a very real sense there are multiple problems with comparing current and ancient rates of extinction. In our study we address just one of these –the issue of time step—and find that this alone is enough to (for all practical purposes) make direct comparisons of rates (as is the current practice) less useful. In the data there will also be all those issues related to pull of the present, push of the past, incipient speciation, and extinction debt (and more!!), the balance of which dominates will rely on the true underlying rates of speciation and extinction (which are hard to get at!), and this makes the problem even worse.

We have added the following text to take note of these complications:

Section 3.2: "*The relationship between genera and species in the fossil record is less certain, due to the tendency for fossilized genera to have experienced higher diversification rate at origination (a "push of the past"; Budd and Mann 2018, 2020) as compared to unfossilized genera. Translating between species and genus extinction rates requires a careful consideration of such biases. Nevertheless, their approximate correspondence in recent records suggests that the time-dependence of extinction rates in fossil genera also applies to species.*"

And

"*In addition to problems of time-step duration, the fossil record is incomplete, with an estimated 38% of modern marine genera appearing in the fossil record (Shaw et al. 2021). Genera preserved are preferentially long-lived and widespread (Foote & Raup 1996, Valentine & Jablonski 2006), specious and initially rapidly diversifying (Nee et al. 1994; Budd & Mann 2018, 2020), and are found in habitats with higher preservation potential (e.g., Valentine 1989). Such taphonomic biases make threatened modern mammal genera about half as likely to display a fossil record as those that are not (Plotnick et al. 2016).*"

Comment:

The relationship between facies change and extinction seems – unclear. As the authors point out, the literature does indeed suggest that sediments and biotas change together. But – correlation is not causation. In this instance, there is a hidden variable, for example that of time, which may be governing both. In other words, at facies boundaries, there may well often be cryptic or not so cryptic disconformities within which quite a lot of time is hidden.

I understand that Peter and Heim investigated these biases and tried to rule them out, but they are quite cautious in their conclusions (partly because of the potential problems of taxonomic bias near unconformities). In addition, as far as I can see they treat genera extinctions as point events rather than wanings, as suggested here, and this may also have an effect.

Nevertheless, sea level changes gave been often tied in to both extinctions and (naturally) to sedimentary changes, and this "common cause" effect might be of some significance in some extinctions. But: it does not need to be significant in all of them.

Response:

Yes, we agree that our assertion of the facies-life link was far too definitive in earlier version of the manuscript. To that end, we have reformatted much of the manuscript, but specifically Sections 4 and 5, which have been merged into a single section that provides a more theoretical description of the proposed metric. Specifically, we make clear that the link between facies and life is clear only in the marine realm with the following text and the discussion around it in section 4:

"*First, in contrast to the marine realm, sedimentary hiatuses are not a good candidate in terrestrial environments (where erosion dominates rock quantity, e.g., Wall et al. 2011; Rook et al. 2013) or for modern-historical comparisons. Sea-level (and sea level variations) is responsible for much of the quantity and continuity of preserved shallow-marine sediment over the Phanerozoic (Peters & Husson 2017) and is not the primary dynamic we are seeking to trace today. Instead, a sedimentary tracer of anthropogenic environmental change might be better linked to turnover in lithology, that is, to changes in composition of the rock itself (Figure 4).*"

The dominant signal in the terrestrial realm is erosion. However, the marine record is reflective of shelf habitat area—a driver of species diversity through species-area effects, and of concomitant shallow-marine sedimentation. Thus, the facies-life link in the marine realm is suggestive of a more general effect, whereby changes in habitat area simultaneously drive sedimentary changes *and* extinctions.

Section 5.1 and the right panel of Figure 4 was added to provide a basic, theoretical framework.

Comment:

After all, when we think about modern day extinctions, it is not at all clear that the ones we are aware of are related in a causal way (even indirectly) to changes in sedimentation, if only because many are terrestrial where such effects would be less clear.

And it is unclear why, say, the loss of river dolphins, passenger pigeons or (potentially) pandas would have such a linkage.

Response:

This is true. We have adjusted the text to be clearer here. Specifically, the sedimentary, and ultimately lithological, signals to which we refer are often spatially disconnected from habitat undergoing destruction. For example, deforestation generates enhanced sedimentation upon coral reefs, etc. With that in mind, we have emphasized that if we want to compare to the fossil record, we must think of the sedimentary traces as a global, or at least continental tracer of future biodiversity change.

"*Significant benefits would come from a predictive metric that forecasts a predicted ΔS from an observed ΔH. However, many challenges stand in the before such a computation may be utilised (e.g., Zalasiewicz et al. 2011). Crucially, each regime of environmental disruption would require its own geomorphological modeling in order to translate human modification into basin-scale alterations (shown schematically in Figure 4; Brown et al. 2017, 2018), which will then become encoded within the geological record (Tomašových et al. 2020, Plotnick et al. 2020).* ***These sedimentary signals may be spatially displaced from the associated environment, and many critical environments are simply not (or only very rarely) recorded in the rock record. Accordingly, such a metric may be best suited to assessing the global (rather than regional, or habitat specific) magnitude of the current biotic crisis****.*"

As you say, it is useful to think about case studies. Taking the example of the Yangtze river dolphins, their extinction was in part contributed by the consequences of the building of the Three Gorges Dam. The sedimentological consequences of the damming, however, are felt further away than the specific river dolphin habitat and damming from many regions sum together to cause continent or global-scale turnover in sedimentation regime. These are already being captured by "legacy sediment," which will inevitably become lithified as a stratigraphic proxy of the ongoing extinction crises.

Comment:

Indeed, as far as I understand, this is also the conclusion of Rook et al. 2013 (in Palaeo 3). Finally, a potentially analogous concept to the extinction debt of this paper is explored by the recent paper in Nature by Hoyal Cuthill et al. (23rd Dec. 2020 issue).

Thank you for these references. Cuthill et al., in particular, was a fascinating paper, and a useful way to think about extinctions. We have incorporated both papers into the discussion, included in text fragments mentioned above, and for example:

"Eventually, all genera go extinct, with or without humanity's influence, but their durations are being cut short by the widespread disruption of ecosystems and their functions wrought by humanity (Brondizio et al. 2019, Cuthill et al. 2020). In tandem, such anthropogenic influences are reflected in comparable evidence for pervasive disruption to the sedimentary record of today (Jackson, 2001; Jackson & Sax, 2010; Maina et al., 2013; Tomašových & Kidwell, 2017; Stephens et al., 2019;; Plotnick & Koy, 2020). Although we need a quantitative assessment and comparison of sedimentary change in modern and ancient strata, the extent of sedimentary disruption as compared to the pre-human state suggests that we may already be incurring a profound mass extinction debt. Thus, there is a real need to move from qualitative to quantitative assessments of modern and ancient sedimentary change to assess whether and to what extent this may be true."