

Global tropical reef fish richness could decline by around half if corals are lost

Giovanni Strona, Kevin D. Lafferty, Simone Fattorini, Pieter S. A. Beck, Francois Guilhaumon, Roberto Arrigoni, Simone Montano, Davide Seveso, Paolo Galli, Serge Planes and Valeriano Parravicini

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Review timeline

Original submission: 2 February 2021
Revised submission: 3 June 2021
Final acceptance: 7 June 2021

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

Review History

RSPB-2021-0274.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?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

Global tropical reef fish richness could decline by around half if corals are lost

The study by Strona et al., describes an effort to predict the effect of coral loss on reef fish communities at a global scale, using structural equation models. The authors use extreme values of complete global coral loss to explore impacts on the abundance of reef associated fishes. As such, this study fills a critical theoretical knowledge gap, and will aid ecologists in predicting the response of reef fish communities to disturbances.

While this study is important, and undoubtedly well executed, I find it lacks some of the foundational ecological theory that should underpin a model describing complex ecological systems. While I acknowledge the necessity for generalisations and assumptions inherent in modelling, in particular for such a large global context, assumptions should be transparent and their relevance to the model discussed, rather than ignored.

See detailed comments below.

Major:

1. Known unknowns vs unknown unknowns. My primary issue with this paper as it stands is that it ignores a large proportion of the reef fish literature, and pretends that known dependencies between reef fish and coral reefs are unknown. There exists a wealth of knowledge about how live coral affect the recruitment of juvenile fishes, as well as influences the behaviour of many common reef fish species. These known dependencies, among other factors, are being ignored, perhaps to craft the narrative of discovery in the study.

From what I understand, only coral predation and shelter use (as per L171) were included as factors when assessing the coral dependency of species. The authors then construct a narrative of surprise when the model predicts twice as many coral dependent species, when in fact this gap between direct and described coral associations is already well-described. For example, Jones et al 2004 (PNAS, cited in this paper) predicted 16 years ago that this gap can be partly explained by reef fish species that have a direct obligate relationship to corals during recruitment, even if the strength of this relationship with live corals diminish in later life stages.

Within this context, it strikes me as insincere to state that L71 “82.4% of the current fish diversity [is] potentially unaffected by coral loss”, when prior knowledge suggests this is not true? While I recognise that global data on some dependencies may not be available, they should at least be acknowledged and attempts made at understanding how their absence in the model might affect the outcome?

My suggestion is that the authors cover some of the other known dependencies between coral reef fish and live corals (e.g. recruitment, behavioural and reproductive) in more detail. If information about these dependencies is not available at a scale relevant to the model (I suspect that will be the case) be transparent about what impact it might have on the model.

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Further, it is written as if the reader is already acquainted with the suite of threats that are facing coral reefs, and the fact that threats are often compounding and increasing in both severity and frequency. All these are relevant to assess whether the model assumptions of rapid vs no recovery are realistic. I would urge the authors to change the article throughout to make it more accessible to a wider audience, thus allowing readers less familiar with this system a chance to evaluate the robustness of the model assumptions.

Minor:

Overall I found the paper very well written, and could find few minor issues to point out. The authors should be commended on their clear and succinct writing style.

- L27-28 “projecting that reef-fish diversity could decline by half under future ocean-warming projections”. The authors are here referencing the small scale studies that have suggested 50% reductions in fish communities following coral loss, but the way it is phrased makes it sound like you just preempted your own conclusion?
- L119 - referencing IPCC SSP's here, without any prior introduction to what they are or where they come from? Also, should the second SSP2 be something else?
- L126 - “Assuming that erosion was instantaneous after bleaching”. A huge assumption known to be incorrect. Given that some estimates states a reef might be reduced to rubble in timeframes up to 10 years, this assumption could greatly affect the predictions of reef decline. It might be a reasonable assumption to make in the model, but its impact should be explained more and acknowledged.
- L136 - the preceding paragraph talks about how the two models differed in how much bleaching occurred, as well as the recovery time, but the conclusion only references emissions scenarios. Surely the recovery time is also critical to future reef fish diversity?

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?

Marginal

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.

No

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Yes

Is it clear?

Yes

Is it adequate?

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Comments to the Author

Strona et al. devised a smart analysis to quantify the loss of reef associated species in an hypothetical scenario of complete hard coral extinction. They found that around half of extant 6,964 reef fish species would go extinct if corals disappear. This is an interesting thought experiment with sophisticated statistics but with very limited application in my opinion. Don't take me wrong, I'm supportive of basic research, but two points came to my mind urging for a more applied approach. First, the notion that half of reef fish species would go extinct if all corals disappear isn't particular surprising given the degree of association reef fishes have with coral reefs. I also will not be surprised to learn that half of rainforest birds will go extinct if all rainforest tree species disappear. This paper does a great job by quantifying and proving our gut feeling right, fine, but maybe Proceedings B is too valuable real estate for such a confirmatory study. The second point is that is easy to drastically improve the impact of their results by either 1) including species traits, or 2) including phylogeny.

By including traits, the analysis might show us that despite half of the species will go extinct, not half of existing 'functional entities' (sensu Mouillot et al 2014 PNAS) will disappear. Maybe the remaining half will retain 75% of functions, which are not-so-bad-news. Maybe the remaining half is highly redundant (more likely) and will retain just 30% of all functional entities, drawing a much more grim picture. I believe that this would be an easy task for the team since the senior author manages the best trait dataset for reef fishes currently available. Similarly, by adding phylogenetic information they can show how much phylogenetic diversity will persist on that remaining half of species, which is crucial information to understand the evolutionary potential that will be lost. In summary, these recommendations may transform the take home message of

this manuscript from a piece of trivia knowledge to something that will be much more useful for understand the effects of coral extinctions.

Decision letter (RSPB-2021-0274.R0)

07-Apr-2021

Dear Dr Strona:

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:

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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=\(Document not available\)](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 Robert Barton

<mailto:proceedingsb@royalsociety.org>

Associate Editor

Board Member: 1

Comments to Author:

Two reviews of this manuscript have now been received and they are somewhat mixed in their opinion. I am pleased that we proceeded with a formal review, but the responses are not sufficiently strong to indicate that the current draft is a strong candidate for publication as is. Nevertheless, and even as a “thought experiment” (Line 52), the scientific strength of the manuscript, the quality of the writing, and the important message that it conveys, warrants consideration of further changes.

As I am not an expert on tropical fish ecology, I must place extra weight on the reviews (that come from experts on this topic). The weakest review does make a valid point that the message that many reef fishes would go extinct if corals disappeared is not a surprise. While this alone does not make a strong case for rejection (in the world of science and conservation, even the obvious needs testing and statistical support), it does beg attention, and this reviewer indicates how this might proceed through consideration of fish functional groups. The positive reviewer has some more detailed comments, and the point about known unknowns versus unknown unknowns is important. After decades of work on coral reefs, the mechanisms that connect corals and fishes together are, indeed, better known than this manuscript seems to suggest. Perhaps the Devil is hiding in the detail of Line 172 (“.. generic association to reef habitat..”), but attention to expanding on these details (and more use of references like Jones et al. 2004) would be beneficial. Finally, the references to the assumed familiarity with climate change issues and coral reefs is well taken, and serves as a good reminder that PRSB is intended to have broad appeal. Even though many are familiar with the “business as usual emission scenario” (Line 40, and other examples in the text), this statement is inherently obtuse without the benefit of assumed knowledge.

Overall, the content of this manuscript remains appealing as a potential paper in PRSB, and the reviews provide suggestions for changes that can be made with relative ease (and attention to detail). There is enough here to consider the merits of revising.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

Global tropical reef fish richness could decline by around half if corals are lost

The study by Strona et al., describes an effort to predict the effect of coral loss on reef fish communities at a global scale, using structural equation models. The authors use extreme values of complete global coral loss to explore impacts on the abundance of reef associated fishes. As such, this study fills a critical theoretical knowledge gap, and will aid ecologists in predicting the response of reef fish communities to disturbances.

While this study is important, and undoubtedly well executed, I find it lacks some of the foundational ecological theory that should underpin a model describing complex ecological systems. While I acknowledge the necessity for generalisations and assumptions inherent in modelling, in particular for such a large global context, assumptions should be transparent and their relevance to the model discussed, rather than ignored.

See detailed comments below.

Major:

1. Known unknowns vs unknown unknowns. My primary issue with this paper as it stands is that it ignores a large proportion of the reef fish literature, and pretends that known dependencies between reef fish and coral reefs are unknown. There exists a wealth of knowledge about how live coral affect the recruitment of juvenile fishes, as well as influences the behaviour of many common reef fish species. These known dependencies, among other factors, are being ignored, perhaps to craft the narrative of discovery in the study.

From what I understand, only coral predation and shelter use (as per L171) were included as factors when assessing the coral dependency of species. The authors then construct a narrative of surprise when the model predicts twice as many coral dependent species, when in fact this gap between direct and described coral associations is already well-described. For example, Jones et al 2004 (PNAS, cited in this paper) predicted 16 years ago that this gap can be partly explained by

reef fish species that have a direct obligate relationship to corals during recruitment, even if the strength of this relationship with live corals diminish in later life stages.

Within this context, it strikes me as insincere to state that L71 “82.4% of the current fish diversity [is] potentially unaffected by coral loss”, when prior knowledge suggests this is not true? While I recognise that global data on some dependencies may not be available, they should at least be acknowledged and attempts made at understanding how their absence in the model might affect the outcome?

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Referee: 2

Comments to the Author(s)

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take me wrong, I'm supportive of basic research, but two points came to my mind urging for a more applied approach. First, the notion that half of reef fish species would go extinct if all corals disappear isn't particular surprising given the degree of association reef fishes have with coral reefs. I also will not be surprised to learn that half of rainforest birds will go extinct if all rainforest tree species disappear. This paper does a great job by quantifying and proving our gut feeling right, fine, but maybe Proceedings B is too valuable real estate for such a confirmatory study. The second point is that is easy to drastically improve the impact of their results by either 1) including species traits, or 2) including phylogeny.

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Author's Response to Decision Letter for (RSPB-2021-0274.R0)

See Appendix A.

Decision letter (RSPB-2021-0274.R1)

07-Jun-2021

Dear Dr Strona

I am pleased to inform you that your manuscript entitled "Global tropical reef fish richness could decline by around half if corals are lost" has been accepted for publication in Proceedings B.

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

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

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

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

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

Sincerely,

Dr Robert Barton

Editor, Proceedings B

mailto:proceedingsb@royalsociety.org

Associate Editor:

Comments to Author:

Many thanks for submitting your revision and for addressing the comments in a professional and effective manner. This manuscript conveys the results of an important analysis, and although it is a self proclaimed "thought experiment" (which arguably makes it too speculative for PRSB), it has a potential to make a very nice paper in the journal.

Appendix A

Associate Editor

Board Member: 1

Comments to Author:

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Overall, the content of this manuscript remains appealing as a potential paper in PRSB, and the reviews provide suggestions for changes that can be made with relative ease (and attention to detail). There is enough here to consider the merits of revising.

RESPONSE: We appreciate the effort the reviewers have made, and incorporating their suggestions has improved our submission. To summarize, we have now reworked the MS to emphasize that a significant loss of fish diversity following coral diversity is not surprising and supported by local-scale empirical work, and that the main element of novelty of our study is that of providing a new modelling framework to address this question at the global scale and obtain quantitative, spatially explicit estimates (plus a flexible model for scenario simulations). Furthermore, the Reviewers’ suggestions to expand our study and explore the effect of coral loss also on phylogenetic and functional fish diversity has made the paper richer. We have removed jargon and done our best to streamline our main messages. We have also cited additional studies supporting the expectation of fish decline following coral loss.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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See detailed comments below.

Major:

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Response: We now point out that the natural history database has known unknowns that likely make it underestimate fish dependencies on corals. We mention that the independent analysis of natural history based dataset of fish dependency might be incomplete and miss some important extant dependency. This gap is what our statistical projection aims to fill, i.e. it can provide global scale, spatially explicit estimates of fish dependency in the absence of the known unknowns.

The authors then construct a narrative of surprise when the model predicts twice as many coral dependent species, when in fact this gap between direct and described coral associations is already well-described. For example, Jones et al 2004 (PNAS, cited in this paper) predicted 16 years ago that this gap can be partly explained by reef fish species that have a direct obligate relationship to corals during recruitment, even if the strength of this relationship with live corals diminish in later life stages. Within this context, it strikes me as insincere to state that L71 “82.4% of the current fish diversity [is] potentially unaffected by coral loss”, when prior knowledge suggests this is not true? While I recognise that global data on some dependencies may not be available, they should at least be acknowledged and attempts made at understanding how their absence in the model might affect the outcome?

Response: We have clarified that as per Jones et al. this disparity is likely due to inadequacies in the natural history data we used. We now include the example of coral as resource for recruits, and we acknowledge how those gaps might affect the difference between the natural history model and the statistical projection.

My suggestion is that the authors cover some of the other known dependencies between coral reef fish and live corals (e.g. recruitment, behavioural and reproductive) in more detail. If information about these dependencies is not available at a scale relevant to the model (I suspect that will be the case) be transparent about what impact it might have on the model.

Response: We have now better clarified that one reason the natural history based model seems to underestimate loss is because it does not account for indirect effects and aspects of recruitment, behaviour and reproduction at the scale of our analysis. Also, we now indicate to the reader that these aspects are likely to underestimate fish-coral dependency.

2. Assumed knowledge. At present the paper is written as if aimed at a specialists coral reef/climate change journal, when in fact ProcB is aimed at a more generalist audience. For example, the very first sentence in the paper references ‘a business as usual emissions scenario’. While many readers may immediately grasp you are talking about IPCC RCP8.5, and the emission of carbon dioxide, it strikes me as odd to start out with such an assumed level of intimacy with the terms and jargon? In fact, the paper repeatedly mentions ‘emissions’ without clarifying that it refers to carbon dioxide emissions.

Response: We have now removed this jargon and tried to clarify all potential confounding terminology. We have also provided explicit information on the actual meaning of the different climatic scenarios (i.e. the expected increase in water temperature).

Further, it is written as if the reader is already acquainted with the suite of threats that are facing coral reefs, and the fact that threats are often compounding and increasing in both severity and frequency. All these are relevant to assess whether the model assumptions of rapid vs no recovery are realistic.

Response: We have clarified that our intent is not to approximate realistic recovery rates, but to simulate their bounds (from an optimistic one of mild climate change and rapid recovery; to a pessimistic one of no recovery and severe climate change) and hence provide general best-worst case expectations.

I would urge the authors to change the article throughout to make it more accessible to a wider audience, thus allowing readers less familiar with this system a chance to evaluate the robustness of the model assumptions.

Response: To make this more appropriate for a general readership, we either simplified terminology or moved potentially confounding or unclear technical details from the main text to the supplementary.

Minor:

Overall I found the paper very well written, and could find few minor issues to point out. The authors should be commended on their clear and succinct writing style.

- L27-28 “projecting that reef-fish diversity could decline by half under future ocean-warming projections”. The authors are here referencing the small scale studies that have suggested 50% reductions in fish communities following coral loss, but the way it is phrased makes it sound like you just preempted your own conclusion?

Response: The point here was to build on past work, but we see the reviewer’s point, and have reworked the Abstract and removed the sentence.

- L119 – referencing IPCC SSP’s here, without any prior introduction to what they are or where they come from? Also, should the second SSP2 be something else?

Response: we have now provided more information about the scenarios, including the corresponding values of average water surface temperature increase by 2100 in reef localities.

• L126 – “Assuming that erosion was instantaneous after bleaching”. A huge assumption known to be incorrect. Given that some estimates states a reef might be reduced to rubble in timeframes up to 10 years, this assumption could greatly affect the predictions of reef decline. It might be a reasonable assumption to make in the model, but its impact should be explained more and acknowledged.

Response: We think the confusion was based on our use of the word assumption, which implied we assume this to be the case. So, we have changed to wording to clarify that this “assumption” is a bound, not a parameterization.

• L136 – the preceding paragraph talks about how the two models differed in how much bleaching occurred, as well as the recovery time, but the conclusion only references emissions scenarios. Surely the recovery time is also critical to future reef fish diversity?

Response: Correct. We now clarify in the results how recovery time fits into the pessimistic and optimistic scenarios.

Referee: 2

Comments to the Author(s)

Strona et al. devised a smart analysis to quantify the loss of reef associated species in an hypothetical scenario of complete hard coral extinction. They found that around half of extant 6,964 reef fish species would go extinct if corals disappear. This is an interesting thought experiment with sophisticated statistics but with very limited application in my opinion. Don't take me wrong, I'm supportive of basic research, but two points came to my mind urging for a more applied approach.

First, the notion that half of reef fish species would go extinct if all corals disappear isn't particular surprising given the degree of association reef fishes have with coral reefs. I also will not be surprised to learn that half of rainforest birds will go extinct if all rainforest tree species disappear. This paper does a great job by quantifying and proving our gut feeling right, fine, but maybe Proceedings B is too valuable real estate for such a confirmatory study.

Response: We have now reworked the paper, making clear that a global estimate of fish loss was lacking and our model shows geographical variation in the response.

The second point is that is easy to drastically improve the impact of their results by either 1) including species traits, or 2) including phylogeny.

By including traits, the analysis might show us that despite half of the species will go extinct, not half of existing 'functional entities' (sensu Mouillot et al 2014 PNAS) will disappear. Maybe the remaining half will retain 75% of functions, which are not-so-bad-news. Maybe the remaining half is highly redundant (more likely) and will retain just 30% of all functional entities, drawing a much more grim picture. I believe that this would be an easy task for the team since the senior author manages the best trait dataset for reef fishes currently available.

Similarly, by adding phylogenetic information they can show how much phylogenetic diversity will persist on that remaining half of species, which is crucial information to understand the evolutionary potential that will be lost. In summary, these recommendations may transform the take home message of this manuscript from a piece of trivia knowledge to something that will be much more useful for understand the effects of coral extinctions.

Response: We have now expanded our study by including models for functional and phylogenetic fish diversity. As anticipated by the Reviewer, these add many interesting insights to our findings, generating a much more comprehensive picture of the potential effect of coral loss on multiple facets of fish diversity.