

A global coral phylogeny reveals resilience and vulnerability through deep time

Corresponding Author: Dr Claudia Vaga

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This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)

Overall: This is an extremely valuable contribution to the field since the current phylogeny of the group is not nearly as complete and based upon a small number of loci and morphological characters. A coral phylogeny based upon what is basically a “new” molecular technology has been keenly anticipated for several years. The work (and funds) to gain these results would have been quite substantial and it represents a real cornerstone in coral research. Phylogenies are increasingly used in a wide range of analyses - a subject that could receive some attention in the introduction BTW. The study is extremely relevant: the severe mass bleaching events around the world in recent years now means that species and even lineage extinction of corals are an imminent threat. I think the text does need some reworking - it undersells the study to some extent and does not always make clear what is new. Also, there are some issues described below, but these are with the text rather than the methods and analyses, which appear top notch.

Main Points:

- More fossil data needs to be included - for ground truth-ing and comparison and validation. For example, the ages/ancestral states estimation, taxa other than those used for the calibration could be used to test the models? A purely molecular approach (admittedly with five fossil data points) does seem incomplete, particularly when another independent line of data is available.
- Please state the main differences between this phylogeny and the current most recognised phylogeny (e.g. Huang & Roy 2016). Clearly the molecular techniques are orders of magnitude better, but it would be informative for readers to have a summary of the main differences. Ideally, a (supplementary) figure comparing the two phylogenies- possibly side by side as linear trees of just genera?
- Following on from (3), in the abstract (and elsewhere), it is not clear what are new findings from this study and what is simply consistent with previous studies.
- The methods omit critical information on how and where the samples were taken and the identification methods/expertise used. The group is notoriously difficult to identify and everything here hinges on correct morphological identifications.
- The character states of specimens that were (presumably) used in the ancestral states estimation- where are these data? How were intermediate states handled, for example some taxa can be zooxanthellate or azooxanthellate?
- The five calibration points used for dating were all less than 127 mya, which means quite a bit of extrapolation for many of the older date estimates. Presumably older calibration points were not available, but should this at least be mentioned as a source of error? Can any confidence limits be quoted when giving age estimates in the text? Could the analysis be rerun with different calibration points to generate error, or at least do some post-hoc testing?
- It is perhaps worth noting that only taxa surviving to the present day were analysed. Somewhat obvious (!), but it does give an incomplete dataset when looking at rates of speciation & extinction? Again, some fossil evidence might allow the scope of this problem to be discussed.
- In several places, estimates of past events in deep time are presented as fact. For example, “In some cases, deep-water, solitary species (e.g., ancestor of the family Agariciidae) arose from colonial, shallow-water lineages as they invaded the deep sea”. Better would be: “our data suggests....” Again, it is not clear which parts derive from this study and which are from the literature.

Figures

Figure 1: Please add units and larger text to the scale bar lower LHS. The “next div” colour coding of the branches is not explained. The figure would probably be easier to read and have more impact if the ages were given as shaded concentric circles as per Huang & Roy (2016) rather than tiny text on every node? The fine detail could be in the supplementary material?

Figure 2: Please explain the colours used for the posterior plots- they don't match those used in figure 1? And the colour coding of the time scale - is that just for looks? Potentially confusing. “Age of families”- perhaps “time of divergence” is more precise? Also, please include in the caption the name of method used to obtain age estimates- readers should not have to go hunting in the text/methods to get a general idea. Ideally, the oldest documented fossil for each group could be shown too?

Figure 2 would be clearer if the asterisks etc. were replaced with text running along the relevant dotted lines inside the figure? Having rugosa etc. extinctions also as asterisks is confusing, again these could go as text within the figure?

Figure 2 pie diagrams are confusing. Firstly, the column headings (i.e. clonality, zooxanthellate etc) should be at the top (or bottom) of each column. The proportions given in the pie diagrams are not explained. If these are probabilities for the MRCA, then the ancestral states of the Scleractinia for example are not that well supported? Again, the general method needs to be named here. It would also be informative to show the states of the oldest documented fossils for each group?

Minor Points

Abstract:

“originating”- should that be past tense?

“analysis” - should that be plural?

“While ongoing environmental changes will alter shallow reefs⁴, stony corals have shown resilience throughout geological history, offering hope for their persistence.” Potentially this could be misconstrued. Perhaps: “...hope for the persistence of some lineages”? Also, “...alter shallow reefs” seems somewhat of an understatement?!

Discussion:

“Deep-water corals – both solitary and colonial – can up-regulate their calcifying fluid internal pH, enabling calcification of the skeleton in deep water below the aragonite saturation horizon^{44,45}.” Can shallow-water corals not do this? Please reword to indicate if they can or not.

“We show that coloniality was repeatedly gained and lost” From the relevant supplementary figure, I don't see this?

Supplemental text:

“Our phylogeny highlights a strong need for a systematic revision of many lineages”. More detail required, please list some examples. Arguably, this sentence(s) could be bumped into the main text as is it quite significant?

Supplementary figures:

Difficult to use without a caption and legend?

Referee #2

(Remarks to the Author)

This is an extremely valuable report because of its fundamental significance for coral biology. The phylogenetic and molecular clock analyses (Figs. 1 and 2) are exemplary. Three insights from clock and ancestral trait reconstruction seem novel and convincing to me: time of origin of Scleractinia and major clades, that the common ancestor of Scleractinia was solitary and azooxanthellate, and that coloniality and symbiosis were acquired after the competitors (Rugosa and Tabulata) went extinct. I am less surprised by the conclusion that Scleractinia have survived past calamities - it is kind of self-evident since they are still with us.

Generally, inferences beyond the major ones listed above are but verbal interpretations of phylogenetic patterns - fun to read but hardly conclusive. Take, for example, the finding that persistence of Scleractinia through major disturbance events was due to survival of solitary deep-water forms - which is one of the major findings, in authors' opinion. First, in the aftermath of mass extinctions all animal lineages tend to be represented by smaller forms (so-called “lilliput effect”), for which there are several explanations besides just better survival of smaller things (<https://doi.org/10.1016/j.palaeo.2006.11.03>). Second, I am not convinced that inference of deep-water habitat in this case is not predominantly due to its collinearity with being small and solitary in present-day Scleractinians.

Last but not least, I am quite puzzled by Fig 3 and the text referring to it: “increased diversification of deep-water stony coral lineages followed anoxic events, whereas increased diversification rates of all lineages were decoupled from other major extinction events”. I really don't see how the figure supports these claims.

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

Excellent responses to all the reviewer queries. As per my review, I cannot recommend this ms strongly enough!

Referee #2

(Remarks to the Author)

i find the author's explanations acceptable, except one point.

I am still puzzled by figure 3, which, in my opinion, still does not show what the text says.

The modified text says (emphasis is mine):

“Regardless of the underlying mechanism, increased diversification of stony coral lineages *followed* anoxic events, whereas increased diversification rates were *not associated with* other major extinction events”.

To me, this statement implies that there were increases in diversification rates shortly after anoxic events, but not around (after or before) mass extinction events. I think this would be the meaning of the statement to any reader.

The problem is, to demonstrate this, the figure needs sub-period resolution. Periods between events of either type should be broken into shortly before, shortly after, and in-between events.

Whereas right now the figure shows diversification rate estimates *for the whole period* between events. Difference in rates between such periods does not imply association with the event that started or ended the period, it implies difference of the whole period of time between events.

So, unless additional analysis is redone and the figure is redrawn, I cannot accept it as evidence of the text statement. If the meaning of the statement was in fact not what the authors intended, please rephrase the statement to avoid misunderstanding.

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Dear Editor and Referees,

Thank you very much for the positive feedback on our manuscript, as well as for the constructive criticism. We appreciate yours and the reviewers' efforts and believe the suggestions have helped us improve our submission. We have followed most of the suggestions and comments and edited the manuscript accordingly. Below we address (in blue) their concerns point by point.

Referees' comments:

Referee #1

Overall: This is an extremely valuable contribution to the field since the current phylogeny of the group is not nearly as complete and based upon a small number of loci and morphological characters. A coral phylogeny based upon what is basically a “new” molecular technology has been keenly anticipated for several years. The work (and funds) to gain these results would have been quite substantial and it represents a real cornerstone in coral research. Phylogenies are increasingly used in a wide range of analyses - a subject that could receive some attention in the introduction BTW. The study is extremely relevant: the severe mass bleaching events around the world in recent years now means that species and even lineage extinction of corals are an imminent threat. I think the text does need some reworking - it undersells the study to some extent and does not always make clear what is new. Also, there are some issues described below, but these are with the text rather than the methods and analyses, which appear top notch.

Author's response: We thank the reviewer for such positive comments on our manuscript. We added a phrase in the introduction that explains how global phylogenies are currently being used to infer the evolutionary history of a variety of organisms. We also changed the text in several parts to address the concerns, and we especially focused on making clear the novel findings of this study (see below).

Main Points

- More fossil data needs to be included - for ground truth-ing and comparison and validation. For example, the ages/ancestral states estimation, taxa other than those used for the calibration could be used to test the models? A purely molecular approach (admittedly with five fossil data points) does seem incomplete, particularly when another independent line of data is available.

Author's response: Thanks for your suggestion. Since it is not possible to accurately include fossil data in specific points of the molecular clock tree (see newly added discussion in the first paragraph of the 'Divergence time estimation' section of the Material and Methods), it would not be possible to include fossil information in the character mapping analyses. Instead, following your guidance, we compiled a table (now Supplementary Table 2) with the earliest known fossil information for every family included in the study. In the table we compare (i) the fossil ages with the mean ages retrieved through the molecular clock analyses to (ii) the ancestral state for coloniality of the fossil compared to the MRCA state in our results. Moreover, remarks on either the reliability of the fossil (together with the relevant literature) and the systematics of the group are given. We also proposed a new figure (now Extended Data 2) with pictures of selected fossil (Mesozoic and Cenozoic) representatives of the main scleractinian lineages included in the study, depicting some examples of the possibly oldest recognized members; in the legend we specified the fossil age and coloniality state. Finally, we discussed the

resulting age comparison in the Supplementary Information document. While working with fossil scleractinian corals is not an easy task we think that the inclusion of these information greatly improved our manuscript.

- Please state the main differences between this phylogeny and the current most recognized phylogeny (e.g. Huang & Roy 2016). Clearly the molecular techniques are orders of magnitude better, but it would be informative for readers to have a summary of the main differences. Ideally, a (supplementary) figure comparing the two phylogenies- possibly side by side as linear trees of just genera?

Author's response: *Thanks for the suggestion. Although we did include in the supplementary material some comparison with previous comprehensive phylogenetic studies (Campoy et al. 2020 [ref. 17], Kitahara et al. 2016 [ref. 98], Quek et al. 2023 [ref. 99]) we had not mentioned the Huang & Roy, 2015 paper and supertree. We added a section to the Supplementary text explaining the main differences between the Huang & Roy (2015) tree and our results. Huang & Roy (2015) present two separate phylogenies: one only based on molecular data, and one based on a combination of molecular and morphological traits (the aforementioned supertree). Since the genera included in our phylogeny are somewhat different from those included in those phylogenies (some genera overlap but not all of them) we believe that a side-by-side figure might not be helpful.*

- Following on from (3), in the abstract (and elsewhere), it is not clear what are new findings from this study and what is simply consistent with previous studies.

Author's response: *Thank you for bringing this to our attention. In both the abstract and the main body of the text, we made an effort to clarify when we are specifically discussing our own results as opposed to referring to prior literature. In brief, the novelty of our comprehensive study lies in the inclusion of hundreds of newly sequenced coral taxa in a time-calibrated phylogenomic analysis. This provides a robust framework for assessing the resilience versus vulnerability of all known extant clades of Scleractinia. Our analysis was conducted in the context of global environmental changes spanning approximately 460 million years, including shifts in temperature and atmospheric CO₂ concentration, oceanic anoxic events, and mass extinction events.*

- The methods omit critical information on how and where the samples were taken and the identification methods/expertise used. The group is notoriously difficult to identify and everything here hinges on correct morphological identifications.

Author's response: *Thanks for your comment. We have added two columns in the Supplementary Table 1 with the latitude and longitude of the collection locality for every sample. Moreover, we added in the Material and Methods how the samples were identified to the species level. Finally, some specimens were part of the type series of the species, so we included in the Table a column with the type status of each included specimen.*

- The character states of specimens that were (presumably) used in the ancestral states estimation- where are these data? How were intermediate states handled, for example some taxa can be zooxanthellate or azooxanthellate?

Author's response: Thanks for your suggestions. We have added to the Supplementary Table 1 four columns with the details about the respective traits assigned to each species and used for the three ancestral state and ancestral range reconstructions. Regarding the taxa that can be both zooxanthellate and azooxanthellate they were treated as 'facultative' as stated in the methods section (yellow pie chart in the Supplementary Fig. 5). Moreover, we gave a definition of all the term used in these analyses in the Supplementary Table 2.

- The five calibration points used for dating were all less than 127 mya, which means quite a bit of extrapolation for many of the older date estimates. Presumably older calibration points were not available, but should this at least be mentioned as a source of error? Can any confidence limits be quoted when giving age estimates in the text? Could the analysis be rerun with different calibration points to generate error, or at least do some post-hoc testing?

Author's response: Thank you for your suggestions. We addressed all suggestions/concerns point by point below:

We did include one older point of calibration (Caryophyllia, 160 Mya). However, yes – due to widespread polyphyly of several currently recognized families and genera – many of fossil stony corals, even if they were previously assigned to certain families, could not confidently be placed in the phylogeny. We followed the suggestion and included a paragraph detailing challenges in fossil calibration for Scleractinia in the methods (now first paragraph of the 'Divergence time estimation' part).

To clearly indicate the confidence limits, we created the Supplementary Table 3 in the Supplementary Information with all the limits for the lineages included in the Figure 2 and mentioned them in the text when needed. Moreover, we will make available on Figshare both the molecular clock tree file and the time-calibrated tree using the penalized likelihood method.

As explained in the first point, we believe that running another analysis with different calibration points would not be appropriate – i.e., would lead to misleading results – since we cannot reliably place other fossils on the presented phylogeny (see first paragraph added to the 'Divergence time estimation' part). However, we run the post-hoc testing 'sampling from the prior' option in BEAST to ensure that the results were driven by the data and not solely by the prior information. We added this information in the methods section, and we briefly discuss our results in the Supplementary Information text (see also Supplementary Figure 7 added). In brief, we found that our prior and posterior results differ; therefore, indicating that the ages determined from the BEAST analyses are shaped by data and not solely from the prior fossil data information (see Brown & Smith, 2018 <https://doi.org/10.1093/sysbio/syx074>).

- It is perhaps worth noting that only taxa surviving to the present day were analyzed. Somewhat obvious (!), but it does give an incomplete dataset when looking at rates of speciation & extinction? Again, some fossil evidence might allow the scope of this problem to be discussed.

Author's response: Thank you for your comment. Indeed, being able to include fossil data in speciation & extinctions analyses would be optimal, however, through discussions with the developers on these analyses, it became clear that it is still not possible to include this kind of information (fossil data). Stemming from this 'problem' and following developer's suggestions –

and being aware that Scleractinia went through events of mass extinctions that are not accounted for in our tree (being made by extant taxa) – thus our decision to include in the study only the speciation rates (Fig. 3) and not the extinctions or the net-diversification rates (which would be inexact without a proper calculation of extinction rates). Similar approaches have been used by previous studies such as: Bossert et al. 2021 (<https://doi.org/10.1111/syen.12530>); Lozano-Fernandez et al. 2020 (<https://doi.org/10.3389/fgene.2020.00182>). For avoiding possible confusion, we changed the words ‘Episodic diversification rates’ into ‘Episodic speciation rates’ in the Method section.

- In several places, estimates of past events in deep time are presented as fact. For example, “In some cases, deep-water, solitary species (e.g., ancestor of the family Agariciidae) arose from colonial, shallow-water lineages as they invaded the deep sea”. Better would be: “our data suggests....” Again, it is not clear which parts derive from this study, and which are from the literature.

***Author’s response:** We changed the phrase as suggested and applied the same consideration in other parts of the manuscript.*

Figures

Figure 1: Please add units and larger text to the scale bar lower LHS. The “next div” colour coding of the branches is not explained. The figure would probably be easier to read and have more impact if the ages were given as shaded concentric circles as per Huang & Roy (2016) rather than tiny text on every node? The fine detail could be in the supplementary material?

***Author’s response:** We added the unit and enlarged the text for the scale bar on the lower left, and we explained the colors for the branch-specific diversification rates in the figure legend. In terms of the concentric circles to depict the ages, we feel that it will increase the busyness of the figure, which we know that already have a lot of information. In addition, we understand that the inclusion of the numbers on each node enable the readers to readily know their estimated divergence time. Hope this is OK.*

Figure 2: Please explain the colours used for the posterior plots- they don’t match those used in figure 1? And the colour coding of the time scale - is that just for looks? Potentially confusing. “Age of families”- perhaps “time of divergence” is more precise? Also, please include in the caption the name of method used to obtain age estimates- readers should not have to go hunting in the text/methods to get a general idea. Ideally, the oldest documented fossil for each group could be shown too?

***Author’s response:** The colors of the posterior plots for Figure 2 are different from the Figure 1 due to style choice. Families in both figures are colored in sequential orders for an easy visualization for the reader. We agree about the time scale colors being potentially confusing (thank you), so we changed them to a uniform grey, and we also changed the caption as suggested from ‘age of families’ to ‘time of divergence’. The method to create the posterior plots was included in the caption as suggested.*

Regarding the fossil data, we now provide them as Extended Data 2, which has the images of the oldest fossils – when available and reliable –. In addition, a discussion about their age and traits

compared to our results is now present in the Supplementary Information document and in Supplementary Table 2, as also stated above.

Figure 2 would be clearer if the asterisks etc. were replaced with text running along the relevant dotted lines inside the figure? Having rugosa etc. extinctions also as asterisks is confusing, again these could go as text within the figure?

Author's response: *Thank you for your suggestion. We think that the figure might get too 'crowded' by writing all the mentioned text within it. However, we created a legend right next to the top part of the figure that explain the asterisks and dotted lines, so the reader does not have to find the information in the caption only. We hope this will help to make the figure clearer and easier-to-read.*

Figure 2 pie diagrams are confusing. Firstly, the column headings (i.e. clonality, zooxanthellate etc) should be at the top (or bottom) of each column. The proportions given in the pie diagrams are not explained. If these are probabilities for the MRCA, then the ancestral states of the Scleractinia for example are not that well supported? Again, the general method needs to be named here. It would also be informative to show the states of the oldest documented fossils for each group?

Author's response: *We created headings on top of the pie chart columns that match the legend for better visualization. Yes, the proportions given in the pie charts are probabilities, and we added this information in the caption of the figure. Regarding the ancestral states of the MRCA of Scleractinia, while we would argue that the coloniality and presence of zooxanthellae traits are very well supported, we agree that the ancestral state for the relation with substrate is split between 'transverse division' and 'free-living' and we acknowledge that in the paragraph 'Scleractinia MRCA and fossil record'. For the depth trait, our results clearly reject a shallow water origin for Scleractinia, while the most probable trait remain that the ancestor was a generalist across a broad depth range. Regarding the fossil, please refer to the answer in the comment above. Thank you.*

Minor Points

Abstract:

“originating”- should that be past tense?

Author's response: *We changed the verb as suggested.*

“analysis” - should that be plural?

Author's response: *Thank you, we changed the word to plural.*

“While ongoing environmental changes will alter shallow reefs⁴, stony corals have shown resilience throughout geological history, offering hope for their persistence.” Potentially this could be misconstrued. Perhaps: “...hope for the persistence of some lineages”? Also, “...alter shallow reefs” seems somewhat of an understatement?!

Author's response: We agree with the comments and changed the phrase as suggested.

Discussion:

“Deep-water corals – both solitary and colonial – can up-regulate their calcifying fluid internal pH, enabling calcification of the skeleton in deep water below the aragonite saturation horizon^{44,45}.” Can shallow-water corals not do this? Please reword to indicate if they can or not.

Author's response: Not much data is available for most scleratinian species on this ability. However, there is evidence that some shallow-water corals can upregulate their pH. We updated the phrase to add this information.

“We show that coloniality was repeatedly gained and lost” From the relevant supplementary figure, I don't see this?

*Author's response: Thank you for your comment and sorry if the image is not clear. In general, compared to the symbiosis trait, which seems to be more consistent within coral lineages (Supplementary Figure 5), colonial and solitary species appear to be more intermingled between each other's (Supplementary Figure 4). Here are some examples: (i) the solitary *Fungia fungites*, *Danafungia scruposa*, *Ctenactis echinata* are derived from a lineage with a colonial most common recent ancestor (MRCA); (ii) in the family Caryophylliidae, which has a solitary MRCA, there are multiple (either independent or not) appearances of colonial species (e.g., *Desmophyllum pertusum*, *Pourtalesmilia conferta*); (iii) in the family Dendrophylliidae, which MRCA is colonial, there are multiple and possible independent appearances of solitary species. Once again, this result appears to be different from the symbiosis pattern in which cases of species with different traits (azooxanthellate and zooxanthellate) being 'intermingled' are much rarer.*

Supplemental text:

“Our phylogeny highlights a strong need for a systematic revision of many lineages”. More detail required, please list some examples. Arguably, this sentence(s) could be bumped into the main text as is it quite significant?

Author's response: Thank you for your observation. Since the manuscript is focused on the evolutionary history of order rather than its systematics, we decided to keep the discussion about the systematic results in the supplementary text. We had already included some examples of lineages that would require a revision in the paragraph before the mentioned phrase, however, we made one paragraph more focused on this topic and added some extra examples.

Supplementary figures:

Difficult to use without a caption and legend?

Author's response: The legends are provided when necessary (ancestral state trees). The captions have been provided at the end of the manuscript following journal guidelines, we will make sure that, in case of publication, the captions will be linked to the supplementary figures.

Referee #2

This is an extremely valuable report because of its fundamental significance for coral biology. The phylogenetic and molecular clock analyses (Figs. 1 and 2) are exemplary. Three insights from clock and ancestral trait reconstruction seem novel and convincing to me: time of origin of Scleractinia and major clades, that the common ancestor of Scleractinia was solitary and azooxanthellate, and that coloniality and symbiosis were acquired after the competitors (Rugosa and Tabulata) went extinct. I am less surprised by the conclusion that Scleractinia have survived past calamities - it is kind of self-evident since they are still with us.

Author's response: We thank the reviewer for such positive comments on our manuscript. Good point regarding the survival of Scleractinia across past calamities, indeed previous studies had dated the ancestor of stony corals to have arisen before several major past adverse event thus already implying their endurance; however, we think that the novelty of our results reside in the fact that we highlight which specific coral lineages survived certain past events while others appear only 'more recently'. We made this point clearer in several part of manuscript, including the abstract.

Generally, inferences beyond the major ones listed above are but verbal interpretations of phylogenetic patterns - fun to read but hardly conclusive. Take, for example, the finding that persistence of Scleractinia through major disturbance events was due to survival of solitary deep-water forms - which is one of the major findings, in authors' opinion. First, in the aftermath of mass extinctions all animal lineages tend to be represented by smaller forms (so-called "lilliput effect"), for which there are several explanations besides just better survival of smaller things (<https://doi.org/10.1016/j.palaeo.2006.11.03>).

*Author's response: Thank you for raising our attention to an interesting effect that we did not consider in our discussion. We added explanations accordingly: (i) solitary and deep-sea scleractinian species are not necessarily 'smaller', several solitary species (i.e., polyps) can grow quite big to comparable size of some small colonies (e.g., *Desmophyllum dianthus*) therefore the switch from colonial to solitary species does not necessarily point to a rise of smaller forms; (ii) our results seem to point at the fact that stony coral evolution in the past 200 My might have been more shaped and affected by global anoxic (AE) events rather than mass extinction events (MEE). While MEE certainly played a big role and sometimes they co-occur with AE, our results suggest that the latter was probably more impactful for stony corals; (iii) in the discussion part of the manuscript we list some explanations of why solitary and deep-sea species might have fared better the past adverse conditions, however, we do agree that there could be some other effects/theories that might have also played a role in the survival of certain stony coral lineages.*

Second, I am not convinced that inference of deep-water habitat in this case is not predominantly due to its collinearity with being small and solitary in present-day Scleractinians.

Author's response: Thank you for your comment, this is a legitimate concern. However, we would argue that, while we don't have the comprehensive depth ranges for the vast majority of the fossil/extinct species (as such data are rarely complete or precise), it is probably true also for extinct stony corals taxa that those solitary and azooxanthellate were more bathymetrically

broadly distributed rather than being restricted to shallow water habitats (since they did not depend on the presence of light). Considering these, our results show that the majority of the Most Recent Common Ancestors that had probably arisen in the deep sea shared the traits to be solitary and azooxanthellate. Since the two analyses (ancestral depth range and ancestral coloniality trait) were run independently, and results were coupled only after, we think that these independent lines of evidence demonstrate that the inference of deep-water habitat can be considered reliable. Finally, once again, solitary does not necessarily mean small for stony corals; there are multiple examples of solitary corals that can grow quite large coralla.

Last but not least, I am quite puzzled by Fig 3 and the text referring to it: “increased diversification of deep-water stony coral lineages followed anoxic events, whereas increased diversification rates of all lineages were decoupled from other major extinction events”. I really don’t see how the figure supports these claims.

Author’s response: Thank you for pointing this out, indeed the phrase is actually meant to refer to the order Scleractinia as a whole and not to a specific group. We changed the phrase to more precisely reflect the meaning of the figure.

Referees' comments:

Referee #1 (Remarks to the Author):

Excellent responses to all the reviewer queries. As per my review, I cannot recommend this ms strongly enough!

Author's response: Thank you very much for your positive evaluation of our manuscript!

Referee #2 (Remarks to the Author):

I find the author's explanations acceptable, except one point.

I am still puzzled by figure 3, which, in my opinion, still does not show what the text says.

The modified text says (emphasis is mine):

“Regardless of the underlying mechanism, increased diversification of stony coral lineages **followed** anoxic events, whereas increased diversification rates were **not associated with** other major extinction events”.

To me, this statement implies that there were increases in diversification rates shortly after anoxic events, but not around (after or before) mass extinction events. I think this would be the meaning of the statement to any reader.

The problem is, to demonstrate this, the figure needs sub-period resolution. Periods between events of either type should be broken into shortly before, shortly after, and in-between events. Whereas right now the figure shows diversification rate estimates **for the whole period** between events. Difference in rates between such periods does not imply association with the event that started or ended the period, it implies difference of the whole period of time between events.

So, unless additional analysis is redone and the figure is redrawn, I cannot accept it as evidence of the text statement. If the meaning of the statement was in fact not what the authors intended, please rephrase the statement to avoid misunderstanding.

Author's response: Thank you for your comment, we do agree that the phrase – as is – might lead to misunderstanding. As we are referring to the entire interval between events rather than a short period of time right after them, we changed the phrase accordingly to avoid possible confusion. Changed phrase: “*Regardless of the underlying mechanism, intervals between anoxic events are characterized by elevated diversification rates in stony coral lineages, whereas intervals between other major extinction events show only modest increases or stable rates*”.