



April 11, 2019

Cover letter

Dear *PNAS* chief editor and associate editor,

We have received the decision letter for our manuscript (PNAS MS# 2019-02693) entitled “*Climate cooling and clade competition drove the decline of lamniform sharks*”. We thank you for having considered our appeal request and for giving us the opportunity to revise the manuscript and provide a point-by-point reply to the referees’ comments.

We have carefully read all the comments made by the two reviewers. However, we would like to draw your attention on the points raised by Reviewer #2, which formed the basis of the editor’s decision to reject our manuscript. We understand that *PNAS* editors face a tremendous number of manuscripts yearly and that submitted manuscripts must be absolutely flawless to be accepted for publication. Nonetheless, as we hope you will see in the attached document, comments of Reviewer #2 are based on misunderstandings and/or erroneous (and unjustified) claims that were sometimes made in bad faith. Those comments are clearly false statements that call into question entire parts of our results and conclusions, as well as our ability to process results from statistical analyses, which is very offensive. We can hardly accept that our study was rejected based on such comments, without right of reply. This is especially true since Reviewer #1 clearly supported publication of our study, which would suggest that the advice of a third referee might be needed.

In the attached document, we have addressed and/or replied (**red font**) to all comments made by Reviewers #1 and #2. We have fully revised the manuscript, figures, Supplementary Information (SI) text as well as the SI figures and tables to take into account all the comments that required modifications. As we realized the unfounded nature of Reviewer #2’s comments, we clearly explained the reasons why we disagreed with careful argumentation.

We hope that this revised manuscript and the broad interest and novelty of the results will make this study a timely and worthy contribution to *PNAS*.

Yours sincerely,

Fabien L. Condamine and Guillaume Guinot



Editor Comments:

Thanks for submitting your work to PNAS. I read your manuscript just after it was submitted and felt that it might be of interest to PNAS. Hence, I sent it out for external review. Your ms has now been seen by two external reviewers - as well as re-read by myself. As you can see, the two external reviewers have somewhat mixed feelings about your submission. On this basis, I've decided to reject your submission from further consideration in PNAS. I suggest you revise and reformat it and submit it to a more specialized journal.

While Reviewer #1 is very positive and only made minor (and very constructive) comments, Reviewer #2 made a number of unfavorable comments that were the basis of the editor's decision to reject our manuscript. However, as we hope you will see, these comments are based on misunderstandings and/or erroneous claims that were sometimes made in bad faith.

We understand that PNAS editors face a tremendous number of manuscripts yearly and that submitted manuscripts must be absolutely flawless to be accepted for publication. However, we can hardly accept that our manuscript was rejected based on such comments, which are clearly false statements that call into question entire parts of our results and conclusions (as well as our ability to process results from statistical analyses, which is very offensive). This is especially true since Reviewer #1 clearly supported publication of our study, which would suggest that the advice of a third referee might be needed.

We have provided responses to all major comments made by Reviewers #1 and #2 (note that we did not provide responses to Reviewer #2's minor comments for brevity's sake but we can send you a point by point reply for those comments if needed).

We would be grateful if you could consider our responses below and we hope you will realize the unfounded nature of Reviewer #2's comments.



Reviewer Comments:

Reviewer #1:

Suitable Quality?: Yes

Sufficient General Interest?: Yes

Conclusions Justified?: Yes

Clearly Written?: Yes

Procedures Described?: Yes

Supplemental Material Warranted?: Yes

Comments:

The study by Condamine et al. investigates multiple hypothesized drivers of diversification dynamics in Mackerel sharks (Lamniformes) across about 145 million years. The authors analyze an impressive fossil data set from both Lamniformes and Carcharhiniformes using a Bayesian framework for estimating rates of extinction, speciation, and preservation from fossil occurrence data. The study reports a waxing and waning diversification dynamics of the Mackerel sharks across the investigated time span, including a decline in species diversity in the last 20 million years. Both biotic (competition) and abiotic factors (temperature) are found to have statistically significant effects on the diversification dynamics in Lamniformes across time. The authors conclude that an interplay between abiotic and biotic parts of the environment affected the diversification dynamics in this group.

I enjoyed reading the paper. The massive amounts of fossil data from both Lamniformes and Carcharhiniformes in combination with sophisticated quantitative analyses enable the authors to throw light on potential drivers of diversification dynamics across macroevolutionary time scales, which I suspect many readers of PNAS would find highly interesting. I have a few suggestions that I hope the authors would consider.

Global temperature variations were found to correlate significantly with species-level extinction rates, both at the genus and species level, which is interpreted as evidence that climate cooling during the Cenozoic increased the rate of extinction in Lamniformes. I would very much like to see an interpretation of the parameters so that it would be easier to evaluate this claim. For example, what is the biological interpretation of the reported parameter $\gamma_{\text{species}} = -0.0082$? The same advice applies to the analyses where the authors report statistically significant effects of competition between some carcharhiniforms and the diversification dynamics of some groups of lamniforms. What is the biological interpretation of $g\lambda = 0.0652$?

We understand the parameter estimates can be confusing, and we apologize for not making clear what they meant, but this is how these parameters are represented in all PyRate analyses.

For the temperature-dependent model, the parameters $\gamma\lambda$ and $\gamma\mu$ (for speciation and extinction rates, respectively), measure the sign (positive or negative) and strength of the

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correlation between speciation and/or extinction with the global temperature. In this case $\gamma\mu_{\text{species}} = -0.0082$ means that species extinction rate decreases by 0.82% as global temperature increases every time step (here, every 0.1 million year).

As to , the biological meaning of the parameters in the MCDD model, let's imagine the competing effects given by $g \lambda_{ij} = 0.1$ and $g \mu_{ij} = 0.2$, represents the addition of one species in clade j will decrease the speciation rate in clade i by 10% of the baseline rate (λ_i) and increase its extinction rate by 20% of the baseline rate (μ_i). Conversely, the extinction of a species in clade j will increase clade's i speciation rate and decrease its extinction rate by 10 and 20%, respectively. Opposite effects result from positive interaction, that is with $g < 0$. So in the case of $g\lambda=0.0652$ (Fig. 3B, Table S10), it means that the large carcharhiniforms decrease the speciation rates of medium lamniforms by 6.52% each time a new large carcharhiniform species originates.

Because of length limitation in the main text, we have included this explanation in the Supplementary Information (SI Text).

Statistical significance testing alone falls short as an argument for why a factor should be deemed important or not. Is it possible to do model selection based on an information criteria between competing models? Would a model with the temperature variation outcompete a model without this variable based on a measure of relative model fit? Along the same lines: is it possible to state something about how much of the variation that the different models explained? If the effect of a variable was statistically significant but explained only a few percent of the variation, this would suggest that this factor was not very important for understanding the diversification dynamics in mackerel sharks.

This is a good point, which we actually addressed in the study. We performed a model selection based on marginal likelihood estimates (Lartillot and Philippe, 2006; Silvestro et al., 2014, 2015a) allowing us to compute relative probability for each model, and thus to select the best-fit model. Relative probability can be seen as a measure of how much a model explains the total variation. These results are presented in Tables S6 and S7. As stated in the manuscript, these results indicate that a temperature-dependent model best explains the diversification of lamniforms, at both taxonomic levels.

In addition, we have modified Tables S6 and S7 to now include the marginal likelihood estimates along with the relative likelihoods for each model. This allows a direct model comparison, which lead us to select the temperature-dependent model as the best-fit one for the Lamniformes.

References

- Lartillot, N., Philippe, H., 2006. Computing Bayes factors using thermodynamic integration. *Syst. Biol.* 55, 195–207. <https://doi.org/10.1080/10635150500433722>
- Silvestro, D., Schnitzler, J., Liow, L.H., Antonelli, A., Salamin, N., 2014. Bayesian Estimation of Speciation and Extinction from Incomplete Fossil Occurrence Data. *Syst Biol* syu006. <https://doi.org/10.1093/sysbio/syu006>
- Silvestro, D., Antonelli, A., Salamin, N., Quental, T.B., 2015. The role of clade competition in the diversification of North American canids. *PNAS* 112, 8684–8689. <https://doi.org/10.1073/pnas.1502803112>

PyRate is an excellent framework to study diversification dynamics in deep time, but are build on certain simplifying assumptions (like every other framework). For example, and as far as I

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am aware (I might be wrong about this), PyRate assumes that all lineages within a clade are part of the analyzed data (i.e. that every lamniform and carcharhiniform lineage that has ever existed is part of the data). While the approach estimates preservation probabilities of lineages that are part of the data, the approach does not estimate or take into account how many lineages that are not sampled at all and therefore not part of the dataset. Assuming 100% coverage of species and genera within clades that are older than 100 million years is a rather strong assumption. It would, therefore, be good if the authors could briefly discuss if and how violations of this assumption could potentially affect their results. Are there any reasons to assume that some groups of lamniforms or carcharhiniforms would have a better fossil record than others?

The Bayesian framework of PyRate has been thoroughly tested by Silvestro et al. (2014). Specifically, simulation analyses with PyRate showed that the dynamics of speciation and extinction rates, including sudden rate changes and mass extinction, are correctly estimated under a wide range of conditions, including low levels of preservation (down to 1–3 fossil occurrences per species on average), severely incomplete taxon sampling (up to 80% missing), and high proportion of singletons (exceeding 30% of the taxa in some cases) (see Silvestro et al. 2014 for more details).

It is true that the strongest bias in birth–death rate estimates is caused by incomplete data because missing lineages alter the distribution of nodes in a dated tree; an effect notably pervasive in phylogeny-based models (Cusimano and Renner, 2010; Heath et al., 2008; Höhna et al., 2011). However, other PyRate simulations confirm the absence of consistent biases due to the incompleteness of the data in the fossil record. Incomplete taxon sampling appears to have a less problematic effect on the estimation of speciation and extinction rates because, in contrast to molecular phylogenies, removing a random set of taxa does not affect the observed occurrences of other lineages.

Because of length limitation in the main text, we have included this explanation in the Supplementary Information (SI Text).

References

- Cusimano, N., Renner, S.S., 2010. Slowdowns in diversification rates from real phylogenies may not be real. *Syst. Biol.* 59, 458–464. <https://doi.org/10.1093/sysbio/syq032>
- Heath, T.A., Zwickl, D.J., Kim, J., Hillis, D.M., 2008. Taxon Sampling Affects Inferences of Macroevolutionary Processes from Phylogenetic Trees. *Syst Biol* 57, 160–166. <https://doi.org/10.1080/10635150701884640>
- Höhna, S., Stadler, T., Ronquist, F., Britton, T., 2011. Inferring Speciation and Extinction Rates under Different Sampling Schemes. *Mol Biol Evol* 28, 2577–2589. <https://doi.org/10.1093/molbev/msr095>
- Silvestro, D., Schnitzler, J., Liow, L.H., Antonelli, A., Salamin, N., 2014. Bayesian Estimation of Speciation and Extinction from Incomplete Fossil Occurrence Data. *Syst Biol* syu006. <https://doi.org/10.1093/sysbio/syu006>



Reviewer #2:

Suitable Quality?: No

Sufficient General Interest?: Yes

Conclusions Justified?: No

Clearly Written?: Yes

Procedures Described?: No

Supplemental Material Warranted?: Yes

Comments:

This study uses an extensive dataset of fossil occurrences of two clades of sharks - Lamniformes and Carcharhiniformes - to investigate the causes of the decline of the first of the two clades. The dataset is carefully prepared and all analyses, exclusively conducted with the software PyRate (with acknowledged help from the PyRate author), appear to be done in an expert manner. The manuscript is also very well written, the language is nearly flawless and most descriptions are given in sufficient detail.

This general comment sounds like a very positive opinion on our study and is clearly in contradiction with the negative ratings on the 'Suitable quality' and 'Procedures described' items above. We particularly do not understand why the reviewer has rated 'No' for the 'Procedures Described'. We think there is a long and detailed *Material and Methods* section in the main text, which is completed by the Supplementary Information (SI Text).

Based on the results of the PyRate analyses, the authors make two main claims, as reflected by the title of the study, namely that "climate cooling and clade competition drove the decline of lamniform sharks". These claims are repeated throughout the manuscript, e.g. "the Cenozoic climate cooling spurred the extinction of lamniforms" (Fig. 2 legend) and "competition from multiple clades successively drove the demise and replacement of mackerel sharks" (line 43-44, Abstract). However, both claims are, in my view, overinterpretations of the results.

The first claim (a causal link between cooling and decline) is based on PyRate analyses with diversification-rate parameters that are dependent on abiotic variable(s) that may vary over time. In particular, two analyses are taken as support for the claim; in the first analysis (reported in Table S5), temperature is the only abiotic variable included, and in the second (with the multi-variate birth-death, MBD, model), the effect of temperature is assessed jointly with other abiotic variables as well as with species density. In both cases, model fit is significantly better when the speciation and extinction rates are allowed to be modified (linearly or exponentially in separate analyses) by temperature. This, I believe, is not surprising, because it has been clear from previous research (and confirmed in this study, Fig. 1E) that (i) the diversity of Lamniformes has declined over the past 100 Myr, and (ii) we also know that the temperature has almost continuously declined over the same period. Thus, by allowing an influence of temperature on speciation and extinction rates, these will

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increase/decrease more or less continuously over time, providing a better fit to the declining lamniform diversity than time-homogeneous diversification parameters. Thus, what we learn from these analyses is merely that both the diversification parameters and temperature increase/decrease throughout the Cenozoic.

This is a very simplistic and erroneous view of temperature fluctuations and diversity variations through geological times. Temperatures have not declined over the past 100 myrs, nor throughout the Cenozoic. As our results show, Lamniformes diversity has not declined over the past 100 years, but rather since the end-Cretaceous but still including periods of diversification (Eocene and Oligocene-early Miocene), whereas a more marked decline is observed since the early - middle Miocene toward the Present.

In addition, no previous research quantitatively evidenced a long-term diversity decline of Lamniformes, which is probably why Reviewer #2 does not provide references for his/her claim. The only quantitative analyses conducted so far (Guinot et al., 2012; Guinot and Cavin, 2016) were made on whole elasmobranch palaeodiversity patterns with no special focus on Lamniformes (and were authored by one of the authors of the present study).

References

- Guinot, G., Adnet, S., Cappetta, H., 2012. An analytical approach for estimating fossil record and diversification events in sharks, skates and rays. *PloS ONE* 7, e44632. <https://doi.org/10.1371/journal.pone.0044632>
- Guinot, G., Cavin, L., 2016. 'Fish' (Actinopterygii and Elasmobranchii) diversification patterns through deep time. *Biol Rev* 91, 950–981. <https://doi.org/10.1111/brv.12203>

Whether or not there is a causal link between these variations is an entirely different question, one that I do not think the data can answer. Claiming such a causal link is, in my view, somewhat akin to the parody example of the decline of pirates as the cause of global warming (<https://sparrowism.soc.srcf.net/home/pirates.html>). Of course, not only lamniforms have declined over the last 100 Myr; many groups have. Presumably, for each of these, an analysis as done in this study would probably identify a significant correlation with temperature decrease. But certainly, that doesn't mean that all declines over the past 100 Myr are caused by temperature.

It is clear that correlation does not mean causality. However, there are not many ways of testing such hypotheses in a macroevolutionary context. There is an overwhelming number of fossil-based and phylogeny-based studies that addressed the effect of abiotic parameters on the diversity dynamics of clades, and most of them (including several published in *Nature*, *Science*, and *PNAS*) used correlations tests to do this (Benson and Butler, 2011; Butler et al., 2011; Cárdenas and Harries, 2010; Condamine et al., 2013, 2015, 2018; De Blasio et al., 2015; Ezard et al., 2011; Figueirido et al., 2012; Hannisdal and Peters, 2011; Hunt et al., 2005; Jaramillo et al., 2006; Lehtonen et al., 2017; Mannion et al., 2015; Martin et al., 2014; Mayhew et al., 2008, 2012; Pereira et al., 2015; Silvestro et al., 2015a; Zaffos et al., 2017). Among these analyses, most report a positive correlation between diversification patterns (of specific clades or meta-analyses) and temperature (Butler et al., 2011; De Blasio et al., 2015; Figueirido et al., 2012; Hunt et al., 2005; Mannion et al., 2015; Martin et al., 2014; Mayhew et al., 2012, 2008), not a negative effect of the latter. Therefore, it is not true to state that any

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declining clade since the Cretaceous would correlate with temperature. Such a large number of evidence that diversity correlates with temperature strongly suggest a causal link between diversity variations and temperature, not just basic correlation. This is exposed in the following sentences (line 194 of the manuscript): *‘The observation that climate change has a role over biodiversity dynamics is not surprising in light of recent research that has demonstrated substantial temperature-dependent variations in other marine groups (5, 10, 17, 39, 41), but also on terrestrial groups (9, 42). However, our study extends previous results that reported the impact of temperature on speciation rates (sometimes on extinction rates), as we report that temperature-driven extinction, exceeding speciation, could have participated in the evolutionary decline of lamniforms.’*. In addition and as said above, the statement that lamniform diversity has been continuously declining over the last 100 myrs is oversimplified and untrue.

References

- Benson, R.B.J., Butler, R.J., 2011. Uncovering the diversification history of marine tetrapods: ecology influences the effect of geological sampling biases. Geological Society, London, Special Publications 358, 191–208. <https://doi.org/10.1144/SP358.13>
- Butler, R.J., Benson, R.B.J., Carrano, M.T., Mannion, P.D., Upchurch, P., 2011. Sea level, dinosaur diversity and sampling biases: investigating the ‘common cause’ hypothesis in the terrestrial realm. Proceedings of the Royal Society of London B: Biological Sciences 278, 1165–1170. <https://doi.org/10.1098/rspb.2010.1754>
- Cárdenas, A.L., Harries, P.J., 2010. Effect of nutrient availability on marine origination rates throughout the Phanerozoic eon. Nature Geosci 3, 430–434. <https://doi.org/10.1038/ngeo869>
- Condamine, F.L., Rolland, J., Höhna, S., Sperling, F.A.H., Sanmartín, I., 2018. Testing the Role of the Red Queen and Court Jester as Drivers of the Macroevolution of Apollo Butterflies. Syst. Biol. 67, 940–964. <https://doi.org/10.1093/sysbio/syy009>
- Condamine, F.L., Rolland, J., Morlon, H., 2013. Macroevolutionary perspectives to environmental change. Ecol. Lett. 16 Suppl 1, 72–85. <https://doi.org/10.1111/ele.12062>
- Condamine, F.L., Toussaint, E.F.A., Clamens, A.-L., Genson, G., Sperling, F.A.H., Kergoat, G.J., 2015. Deciphering the evolution of birdwing butterflies 150 years after Alfred Russel Wallace. Sci Rep 5, 11860. <https://doi.org/10.1038/srep11860>
- De Blasio, F.V., Liow, L.H., Schweder, T., De Blasio, B.F., 2015. A model for global diversity in response to temperature change over geological time scales, with reference to planktic organisms. Journal of Theoretical Biology 365, 445–456. <https://doi.org/10.1016/j.jtbi.2014.10.031>
- Ezard, T.H.G., Aze, T., Pearson, P.N., Purvis, A., 2011. Interplay Between Changing Climate and Species’ Ecology Drives Macroevolutionary Dynamics. Science 332, 349–351. <https://doi.org/10.1126/science.1203060>
- Figueirido, B., Janis, C.M., Pérez-Claros, J.A., Renzi, M.D., Palmqvist, P., 2012. Cenozoic climate change influences mammalian evolutionary dynamics. PNAS 109, 722–727. <https://doi.org/10.1073/pnas.1110246108>**
- Hannisdal, B., Peters, S.E., 2011. Phanerozoic Earth System Evolution and Marine Biodiversity. Science 334, 1121–1124. <https://doi.org/10.1126/science.1210695>
- Hunt, G., Cronin, T.M., Roy, K., 2005. Species–energy relationship in the deep sea: a test using the Quaternary fossil record. Ecology Letters 8, 739–747. <https://doi.org/10.1111/j.1461-0248.2005.00778.x>
- Jaramillo, C., Rueda, M.J., Mora, G., 2006. Cenozoic Plant Diversity in the Neotropics. Science 311, 1893–1896. <https://doi.org/10.1126/science.1121380>
- Lehtonen, S., Silvestro, D., Karger, D.N., Scotese, C., Tuomisto, H., Kessler, M., Peña, C., Wahlberg, N., Antonelli, A., 2017. Environmentally driven extinction and opportunistic origination explain fern diversification patterns. Scientific Reports 7, 4831. <https://doi.org/10.1038/s41598-017-05263-7>
- Mannion, P.D., Benson, R.B.J., Carrano, M.T., Tennant, J.P., Judd, J., Butler, R.J., 2015. Climate constrains the evolutionary history and biodiversity of crocodylians. Nat Commun 6, 8438. <https://doi.org/10.1038/ncomms9438>
- Martin, J.E., Amiot, R., Lécuyer, C., Benton, M.J., 2014. Sea surface temperature contributes to marine crocodylomorph evolution. Nat Commun 5, 4658. <https://doi.org/10.1038/ncomms5658>
- Mayhew, P.J., Bell, M.A., Benton, T.G., McGowan, A.J., 2012. Biodiversity tracks temperature over time. PNAS 109, 15141–15145. <https://doi.org/10.1073/pnas.1200844109>**
- Mayhew, P.J., Jenkins, G.B., Benton, T.G., 2008. A long-term association between global temperature and biodiversity, origination and extinction in the fossil record. Proc. R. Soc. B 275, 47–53. <https://doi.org/10.1098/rspb.2007.1302>
- Pereira, B.C., Benton, M.J., Ruta, M., Mateus, O., 2015. Mesozoic echinoid diversity in Portugal: Investigating fossil record quality and environmental constraints on a regional scale. Palaeogeography, Palaeoclimatology, Palaeoecology 424, 132–146. <https://doi.org/10.1016/j.palaeo.2015.02.014>
- Silvestro, D., Antonelli, A., Salamin, N., Quental, T.B., 2015. The role of clade competition in the diversification of North American canids. PNAS 112, 8684–8689. <https://doi.org/10.1073/pnas.1502803112>
- Zaffos, A., Finnegan, S., Peters, S.E., 2017. Plate tectonic regulation of global marine animal diversity. Proc. Natl. Acad. Sci. U.S.A. 114, 5653–5658. <https://doi.org/10.1073/pnas.1702297114>

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Instead, many other causes have contributed to those declines. Thus, the proportion of those clades where temperature decrease has in fact driven the diversity decline is equivalent to the probability that temperature variation is responsible for the lamniform decline. It is hard to estimate that proportion a priori, but I see no reason to place it above 50%, which means the probability of temperature really driving the lamniform decline is below 50%. This is too low a probability for the title of a PNAS paper to be correct.

This statement is entirely speculative, unfounded and worthless. This is precisely our goal to investigate the “*many [...] causes [that] have contributed to those declines*”, and we want to underline that we do not only find support for a temperature-dependent diversification as THE cause of the lamniform decline but we also find support for a clade competition as an additional driver of this decline. We think the title was pretty clear on the fact that both abiotic and biotic drivers are at play.

If Reviewer #2 is aware of quantifiable causes other than abiotic parameters and competition (as tested here) that could have contributed to long-term clade declines, then many researchers would be interested in him/she sharing his/her knowledge. But again, no examples nor references are quoted here. In previous macroevolutionary studies (see references above) temperature is actually often found as THE driver of clade diversification (especially with clades that do not show diversity declines towards the Recent) and is rarely recovered negatively correlating with extinction rates as found in our analyses.

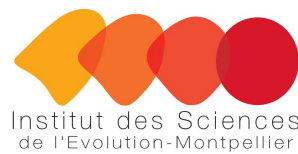
In contrast to the first claim, I think the manuscript does not actually report significance for the second claim (competitive effects driving lamniform decline). This claim is based on analyses with PyRate's Multiple Clade Diversity Dependence (MCDD) model, the results are shown in Figure 3B and Table S10. Unlike for other tables (e.g. Tables S3,S4), the legend of Table S10 does not include the statement “The value in bold highlights the parameter displaying a significant correlation, i.e. significantly different from 0”; nevertheless, some values are marked in bold, leading the reader to assume that these are considered significant. However, with the exception of a single value related to diversity dependence (thus not competition), all of those values marked in bold have confidence intervals that include 0, meaning the absence of a correlation cannot be excluded.

This false statement is important as it calls into question an entire part of our results and conclusions (as well as our ability to process results from statistical analyses, which is very offensive). We find frustrating that one of the main criticism of Reviewer #2 is simply based on a incorrect understanding. It is true that we omitted to mention that values in bold correspond to significant correlations but this is how all other tables of this kind (Tables S1-S5, Tables S8-9, and Table S11) were formatted in the Supplementary Information file and so it was obvious that values in bold in Table S10 correspond to significant values (as stated in the caption of the other 8 tables!). Contrary to Reviewer #2's claim, none of the values in bold have confidence intervals that include 0. This is again a blatant example of bad faith or, we hope, misunderstanding and is a very severe argument which seriously undermines the evaluation of our study. A dash symbol separates the 95% CI, not a minus symbol. Again, the same format was used in the other 8 tables and this did not disturb Reviewer #2. We

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acknowledge, however, that some values were left in grey (those that were marginally significant) to ease our reading and processing of the results but these were not considered in the discussion and should have been left in normal font. This, however, did not seem to catch Reviewer #2's attention.

We have added the following sentence in the Table S10 caption: "*The value in bold highlights the parameter displaying a significant correlation, i.e. significantly different from 0.*", and we removed values in grey color.

The numbers for the competitive interactions prominently displayed in Fig. 3B are merely the median estimates and the figure legend again does not mention significance.

We acknowledge that we omitted to mention in the figure caption that values represented in Fig. 3B are exclusively significant scores as highlighted in the corresponding Suppl. Table. We have modified the Figure 3 caption accordingly.

Taking these numbers at face value, we would learn that the very few species of large Carcharhiniformes reduce the speciation rate of medium-sized Lamniformes, while at the same time, the much larger number of (presumably ecologically much more similar) medium-sized Carcharhiniformes do not influence medium-sized Lamniformes speciation at all. This unintuitive discrepancy is briefly discussed in the manuscript and explained as "they [=medium-sized Carcharhiniformes] were likely not ecologically nor taxonomically diverse, and only diversified in the aftermath of the K-Pg event". This statement is in direct contrast to the species diversities shown in Fig. 3A, where, at any time during their co-existence, medium-sized Carcharhiniformes were more taxonomically diverse than large Carcharhiniformes, and large Carcharhiniformes began to diversify even later than the medium-sized taxa.

Again, this comment is based on erroneous arguments. We indeed argue that "*medium-sized Carcharhiniformes were likely not ecologically nor taxonomically diverse, and only diversified in the aftermath of the K-Pg event*". These were not diverse **compared with Lamniformes** (medium and large). Our Fig. 3A clearly shows this and there is no point in comparing diversity fluctuations between carcharhiniform size classes as done by Reviewer #2 because our study addresses competition between lamniforms and carcharhiniforms. In addition, recovering a competition signal between large carcharhiniforms and medium lamniforms is not counterintuitive because large predators can feed on the same prey as smaller predators (as seen in living elasmobranchs). The reverse, however, would have been contradictory.

More likely, the numbers should not actually be taken as sufficiently strong support for between-clade competition, in line with their non-significance in Table S12.

Again, this is a misunderstanding by Reviewer #2 that seriously undermines the evaluation of our study. All values illustrated on Fig. 3B and discussed in the main text are statistically significant ones (and in bold in corresponding Table S10 [there is no Table S12]). We have

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added the following sentence in the Table S10 caption: *“The value in bold highlights the parameter displaying a significant correlation, i.e. significantly different from 0.”*

In summary, I find the results reported in Figures 1 and 3B (diversity through time and speciation-rate variation over time) interesting and valuable, but I do not consider the authors' attempts at explaining this variation with abiotic and biotic influences trustworthy.

In summary, we think Reviewer #2 has missed or misinterpreted the evidence presented in the Supplementary Tables as we demonstrate above that each major comment is actually a wrong statement or a bad interpretation. We are confident that the results of the different analyses are robust and support the conclusions presented in the manuscript.

Minor issues:

General:

- It is assumed that tooth size is a proxy for body size, and this assumption is also explained in some detail in the Supplementary Material. This explanation should, however, also be included in the main text.

This comment is addressed. (l. 120).

- More information about the temperature data shown in Fig. 2 should be given. Currently, not even a unit is given, and it should be explained if this is (tropical?) sea surface temperature, deep-ocean temperature, or any other measure. Regardless of what measure it is, it is hard to believe that ocean temperatures have declined by nearly 30 °C as shown in Fig. 2, and it seems to me that none of the cited references claim that.

This comment is addressed and we have also added a new Figure S17 representing the three abiotic variables through time. We also included a new paragraph in the SI text as follows:

‘The curve from Zachos et al. (26) was used for the Cenozoic (0-66 Myrs) and the curve from Prokoph et al. (27) was used for the Mesozoic, thus providing $\delta 18O$ data for the full time-range over which Lamniformes have diversified. $\delta 18O$ were transformed into deep-sea temperature estimates using the approach of Epstein et al. (28). Studies have shown that sea-level fluctuations and ice volumes might bias temperature estimates during cold periods when ice sheets formed (29, 30). There is currently no paleotemperature curve that accurately accounts for these biases during the Mesozoic (see Hansen et al. (30) for the Cenozoic). We thus acknowledge that another paleotemperature curve could potentially improve our diversification estimates. Future studies, especially those focusing on clades diversifying in the Cenozoic, could account for measurement and conversion errors between $\delta 18O$ and temperature by taking into account the variations of sea level and atmospheric CO_2 in the deep-sea temperatures estimates (30).’

l. 101: "a" missing before "relict clade".

This comment is addressed.

l. 102-103; "has not yet been demonstrated": I think the decline has in fact been demonstrated by every study showing that more Lamniformes lived at certain times in the past than today.

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Which studies? If Reviewer #2 is aware of a study, he/she should quote it. We maintain our claim that this has never been quantitatively shown. Usually, studies (taxonomic or phylogenetic) on lamniforms introduced the group as in decline, but it became a common belief through time rather than an actual scientific demonstration.

l. 122: Given that Bazzi et al. write "we reject a simple extinction-replacement scenario", at least reference 27 may not be appropriate here.

This paper also reads '*Nevertheless, specific patterns indicate that an asymmetric extinction occurred among lamniforms possessing low crowned/ triangular teeth and that a subsequent proliferation of carcharhiniforms with similar tooth morphologies took place during the early Paleocene.*'

l. 140-142: While I assume that the peak in speciation in the Pleistocene, shown in Figs S1 and S3, is some artifact that does not affect overall conclusions, this statement is not supported by Figs. S1/S3. However, if "net diversification" instead of "speciation" would be used here, the statement would be supported by those figures.

We have modified the sentence accordingly.

l. 159-161: An explanation should be provided on why this link between tooth size and speciation/extinction is hypothesized at all. Why would one expect an influence of tooth size on speciation? And why on extinction?

It has been shown that body size evolution and rates of diversification are correlated in many clades, including marine vertebrates (Rabosky et al. 2013) so our aim here was to test for contrasting diversity dynamics among different shark tooth-size classes. We have added a reference on this topic in the main text.

References

Rabosky DL, et al. (2013) Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nat Commun* 4:1958.

l. 168; "Such a trend might be explained...": The explanation following this only explains part of the trend, extinction, but not the trend in speciation.

l. 169-170: Given that extinction correlates negatively with tooth size in large species, these appear to have a lower extinction risk, in contrast to the statement given here.

We have modified this part of the main text accordingly: '*We find that both speciation and extinction rates of large lamniform species correlate negatively with tooth size (Table S2), suggesting that largest, and hence more ecologically specialized, species show lower extinction and speciation rates than other species. This results in high turnover rates within these low-diversity and specialized ecological niches, which has been reported among other clades (35).*'

References

35. Balisi M, Casey C, Van Valkenburgh B (2018) Dietary specialization is linked to reduced species durations in North American fossil canids. *R Soc Open Sci* 5(4):171861.

l. 170-171; "extinction of the megatoothed lineage": This is the only time a "megatoothed lineage" is mentioned at all; it should thus be explained.

We have modified the sentence accordingly.

l. 174-176: It is unclear to me why the results for alphaq are taken as evidence against a bias resulting from rock abundance. Table S2 reports that the correlation between tooth size and preservation is somewhat similar among the three groups. How does that tell us anything about the influence of rock abundance?

We looked for the absence of correlation in this case, because if a correlation exists between preservation rates and tooth size it would have indicated a bias in the fossil record.

We have modified the Table S2 caption to explain this point.

l. 210-211; "Our macroevolutionary study proposes a positive relationship between biodiversity and temperature": It only does so for Lamniformes. This statement is contradicted by the negative correlation between Carcharhiniformes diversity and temperature.

We did not perform correlation tests between the entire Carcharhiniformes dataset and temperature. We did, however, test for the effect of temperature on speciation/extinction of each size classes of carcharhiniforms. We found a positive correlation between speciation of medium-sized Carcharhiniformes and temperature (Table S11). Hence, Reviewer #2's point that we found some negative correlation between Carcharhiniformes and temperature is again completely wrong.

l. 406; "five Glambda, five Gmu": It appears to me that there are only three such parameters (plus the density-dependent one, then four).

We have modified the sentence accordingly (there are four parameters).

l. 566 (Fig. 1 legend): I suggest adding "extant" before "lamniform families" as more families are known from the fossil record.

This comment is addressed.

Fig. 1D: How is it possible that in the very first time interval with lamniform occurrences, the net diversification is sometimes sampled below zero? I would expect each MCMC iteration to have a greater speciation rate than extinction rate in this first-time interval. If the net diversification rate is then calculated by always subtracting the extinction rate from the speciation rate of the same MCMC iteration (as it should be), none of the net diversification rate estimates in the first time interval should be negative.

This is a general phenomenon observed in PyRate analyses that affects all clades studied so far (see for instance Cantalapiedra et al., 2015; Condamine et al., 2016; Pires et al., 2018, 2017; Silvestro et al., 2015b, 2015a, 2014). A possible explanation for this artefact is that high turnover rates (speciation and extinction rates are very similar) are common in early periods of clade diversification. This, when applying randomized replicates of the occurrences, can result in high extinction rates that correspond (in the same iteration) to even higher speciation rates. Providing illustration of each 10 iterations would be hard to envisage and noisy

considering all the analyses that were performed (e.g., 40 plots for each of the 4 panels of Fig. 1). We think this will bring nothing new and will result in a very lengthy SI file. In addition, this artifact has no impact on the subsequent analyses as we relied on the times of speciation and times of extinction for all taxa included in the dataset.

References

- Cantalapiedra, J.L., Hernández Fernández, M., Azanza, B., Morales, J., 2015. Congruent phylogenetic and fossil signatures of mammalian diversification dynamics driven by Tertiary abiotic change. *Evolution* 69, 2941–2953. <https://doi.org/10.1111/evo.12787>
- Condamine, F.L., Toussaint, E.F.A., Clamens, A.-L., Genson, G., Sperling, F.A.H., Kergoat, G.J., 2015. Deciphering the evolution of birdwing butterflies 150 years after Alfred Russel Wallace. *Sci Rep* 5, 11860. <https://doi.org/10.1038/srep11860>
- Pires, M.M., Rankin, B.D., Silvestro, D., Quental, T.B., 2018. Diversification dynamics of mammalian clades during the K–Pg mass extinction. *Biology Letters* 14, 20180458. <https://doi.org/10.1098/rsbl.2018.0458>
- Pires, M.M., Silvestro, D., Quental, T.B., 2017. Interactions within and between clades shaped the diversification of terrestrial carnivores. *Evolution* 71, 1855–1864. <https://doi.org/10.1111/evo.13269>
- Silvestro, D., Antonelli, A., Salamin, N., Quental, T.B., 2015a. The role of clade competition in the diversification of North American canids. *PNAS* 112, 8684–8689. <https://doi.org/10.1073/pnas.1502803112>
- Silvestro, D., Cascales-Miñana, B., Bacon, C.D., Antonelli, A., 2015b. Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytol* 207, 425–436. <https://doi.org/10.1111/nph.13247>
- Silvestro, D., Schnitzler, J., Liow, L.H., Antonelli, A., Salamin, N., 2014. Bayesian Estimation of Speciation and Extinction from Incomplete Fossil Occurrence Data. *Syst Biol* syu006. <https://doi.org/10.1093/sysbio/syu006>

Fig. 2: While the use of the different models explains it, it will be confusing for readers that the species-level extinction is so different from that displayed in Fig. 1C.

Indeed, the time-dependent extinction rates (Fig. 1D) look different from temperature-dependent extinction rates (Fig. 2). This is expected because when we find time-variable diversification, we still don't know what is driving the variation of speciation and extinction through time. Time-dependent models are phenomenological models meant to describe how speciation and extinction rates vary over time. If time variation is detected, additional tests are needed to decide which processes, such as environmental drivers, diversity dependence, or other factors, are at play. Therefore, we fitted other models to assess the role of abiotic and biotic factors.

That said, we have modified the Figure 2 caption as follows: *“In red are the estimated extinction curves if extinction was exclusively driven by temperature variations as modelled by temperature-dependent birth-death analyses.”*

1. 591; "decrease for speciation": Table S10 shows that all values shown here are changes in the speciation rate, positive or negative, while extinction rate changes were also tested. I wasn't able to understand this from the figure legend alone; thus, I suggest that the legend text should be improved.

We tested for changes in both speciation and extinction rates but only some speciation rates were significantly correlated to other clades' diversity. As stated in the modified caption of Figure 3, only the significant correlations are represented by arrows (highlighted in bold in Table S10). These correlations only concern speciation rates (no significant effect on extinction).

Supplementary Material, page 2, measurements on anterior teeth: It should be explained if specimens represented by isolated teeth only were included in these analyses, and how/whether in those cases the position of teeth (anterior/posterior) could be determined.



We added this sentence in SI text: *'Measurements were made on isolated teeth whose position along the jaws are determined based on their morphology and knowledge on dentitions patterns in both living and extinct elasmobranchs (1).'*

Supplementary Material, page 5, "100 replicates": In the above text, the number of replicates is given as 10. It should be clarified if/why this part was done for 100 replicates.

Corrected.

Supplementary Material, page 5, section "Selection on abiotic variables": The information compiled for this part should be provided as part of the Supplemental Material. I further suggest adding a Supplemental Figure with plots of the three abiotic variables over time.

We have added Figure S17 to represent the three abiotic variables through time

Supplementary Material, page 6; "five Glambda, five Gmu": See above.

Corrected.

Supplementary Material, Figures S1-S11: I suggest specifying in legends of Figs S1-S11 that A-C also show Lamniformes, rather than Carcharhiniformes or both.

Corrected.

Supplementary Material, Figures S4: It should be mentioned in the legend that the trait used here is tooth size.

Corrected.

Supplementary Material, Figures S15; "measurment": Typo.

Corrected.

Supplementary Material, Figures S16: Labels "E" and "V" in the top left panel should be explained. Further, a description of the bottom two plots is missing.

Corrected.



REFERENCES

- Benson, R.B.J., Butler, R.J., 2011. Uncovering the diversification history of marine tetrapods: ecology influences the effect of geological sampling biases. *Geological Society, London, Special Publications* 358, 191–208. <https://doi.org/10.1144/SP358.13>
- Butler, R.J., Benson, R.B.J., Carrano, M.T., Mannion, P.D., Upchurch, P., 2011. Sea level, dinosaur diversity and sampling biases: investigating the ‘common cause’ hypothesis in the terrestrial realm. *Proceedings of the Royal Society of London B: Biological Sciences* 278, 1165–1170. <https://doi.org/10.1098/rspb.2010.1754>
- Cantalapiedra, J.L., Hernández Fernández, M., Azanza, B., Morales, J., 2015. Congruent phylogenetic and fossil signatures of mammalian diversification dynamics driven by Tertiary abiotic change. *Evolution* 69, 2941–2953. <https://doi.org/10.1111/evo.12787>
- Cárdenas, A.L., Harries, P.J., 2010. Effect of nutrient availability on marine origination rates throughout the Phanerozoic eon. *Nature Geosci* 3, 430–434. <https://doi.org/10.1038/ngeo869>
- Condamine, F.L., Clapham, M.E., Kergoat, G.J., 2016. Global patterns of insect diversification: towards a reconciliation of fossil and molecular evidence? *Sci Rep* 6, 19208. <https://doi.org/10.1038/srep19208>
- Condamine, F.L., Rolland, J., Höhna, S., Sperling, F.A.H., Sanmartín, I., 2018. Testing the Role of the Red Queen and Court Jester as Drivers of the Macroevolution of Apollo Butterflies. *Syst. Biol.* 67, 940–964. <https://doi.org/10.1093/sysbio/syy009>
- Condamine, F.L., Rolland, J., Morlon, H., 2013. Macroevolutionary perspectives to environmental change. *Ecol. Lett.* 16 Suppl 1, 72–85. <https://doi.org/10.1111/ele.12062>
- Condamine, F.L., Toussaint, E.F.A., Clamens, A.-L., Genson, G., Sperling, F.A.H., Kergoat, G.J., 2015. Deciphering the evolution of birdwing butterflies 150 years after Alfred Russel Wallace. *Sci Rep* 5, 11860. <https://doi.org/10.1038/srep11860>
- Cusimano, N., Renner, S.S., 2010. Slowdowns in diversification rates from real phylogenies may not be real. *Syst. Biol.* 59, 458–464. <https://doi.org/10.1093/sysbio/syq032>
- De Blasio, F.V., Liow, L.H., Schweder, T., De Blasio, B.F., 2015. A model for global diversity in response to temperature change over geological time scales, with reference to planktic organisms. *Journal of Theoretical Biology* 365, 445–456. <https://doi.org/10.1016/j.jtbi.2014.10.031>
- Ezard, T.H.G., Aze, T., Pearson, P.N., Purvis, A., 2011. Interplay Between Changing Climate and Species’ Ecology Drives Macroevolutionary Dynamics. *Science* 332, 349–351. <https://doi.org/10.1126/science.1203060>
- Figueirido, B., Janis, C.M., Pérez-Claros, J.A., Renzi, M.D., Palmqvist, P., 2012. Cenozoic climate change influences mammalian evolutionary dynamics. *PNAS* 109, 722–727. <https://doi.org/10.1073/pnas.1110246108>
- Guinot, G., Adnet, S., Cappetta, H., 2012. An analytical approach for estimating fossil record and diversification events in sharks, skates and rays. *PloS ONE* 7, e44632. <https://doi.org/10.1371/journal.pone.0044632>
- Guinot, G., Cavin, L., 2016. ‘Fish’ (Actinopterygii and Elasmobranchii) diversification patterns through deep time. *Biol Rev* 91, 950–981. <https://doi.org/10.1111/brv.12203>
- Hannisdal, B., Peters, S.E., 2011. Phanerozoic Earth System Evolution and Marine Biodiversity. *Science* 334, 1121–1124. <https://doi.org/10.1126/science.1210695>
- Heath, T.A., Zwickl, D.J., Kim, J., Hillis, D.M., 2008. Taxon Sampling Affects Inferences of Macroevolutionary Processes from Phylogenetic Trees. *Syst Biol* 57, 160–166. <https://doi.org/10.1080/10635150701884640>
- Höhna, S., Stadler, T., Ronquist, F., Britton, T., 2011. Inferring Speciation and Extinction Rates under Different Sampling Schemes. *Mol Biol Evol* 28, 2577–2589. <https://doi.org/10.1093/molbev/msr095>
- Hunt, G., Cronin, T.M., Roy, K., 2005. Species–energy relationship in the deep sea: a test using the Quaternary fossil record. *Ecology Letters* 8, 739–747. <https://doi.org/10.1111/j.1461-0248.2005.00778.x>
- Jaramillo, C., Rueda, M.J., Mora, G., 2006. Cenozoic Plant Diversity in the Neotropics.

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- Science 311, 1893–1896. <https://doi.org/10.1126/science.1121380>
- Lartillot, N., Philippe, H., 2006. Computing Bayes factors using thermodynamic integration. *Syst. Biol.* 55, 195–207. <https://doi.org/10.1080/10635150500433722>
- Lehtonen, S., Silvestro, D., Karger, D.N., Scotese, C., Tuomisto, H., Kessler, M., Peña, C., Wahlberg, N., Antonelli, A., 2017. Environmentally driven extinction and opportunistic origination explain fern diversification patterns. *Scientific Reports* 7, 4831. <https://doi.org/10.1038/s41598-017-05263-7>
- Mannion, P.D., Benson, R.B.J., Carrano, M.T., Tennant, J.P., Judd, J., Butler, R.J., 2015. Climate constrains the evolutionary history and biodiversity of crocodylians. *Nat Commun* 6, 8438. <https://doi.org/10.1038/ncomms9438>
- Martin, J.E., Amiot, R., Lécuyer, C., Benton, M.J., 2014. Sea surface temperature contributes to marine crocodylomorph evolution. *Nat Commun* 5, 4658. <https://doi.org/10.1038/ncomms5658>
- Mayhew, P.J., Bell, M.A., Benton, T.G., McGowan, A.J., 2012. Biodiversity tracks temperature over time. *PNAS* 109, 15141–15145. <https://doi.org/10.1073/pnas.1200844109>
- Mayhew, P.J., Jenkins, G.B., Benton, T.G., 2008. A long-term association between global temperature and biodiversity, origination and extinction in the fossil record. *Proc. R. Soc. B* 275, 47–53. <https://doi.org/10.1098/rspb.2007.1302>
- Pereira, B.C., Benton, M.J., Ruta, M., Mateus, O., 2015. Mesozoic echinoid diversity in Portugal: Investigating fossil record quality and environmental constraints on a regional scale. *Palaeogeography, Palaeoclimatology, Palaeoecology* 424, 132–146. <https://doi.org/10.1016/j.palaeo.2015.02.014>
- Pires, M.M., Rankin, B.D., Silvestro, D., Quental, T.B., 2018. Diversification dynamics of mammalian clades during the K–Pg mass extinction. *Biology Letters* 14, 20180458. <https://doi.org/10.1098/rsbl.2018.0458>
- Pires, M.M., Silvestro, D., Quental, T.B., 2017. Interactions within and between clades shaped the diversification of terrestrial carnivores. *Evolution* 71, 1855–1864. <https://doi.org/10.1111/evo.13269>
- Silvestro, D., Antonelli, A., Salamin, N., Quental, T.B., 2015a. The role of clade competition in the diversification of North American canids. *PNAS* 112, 8684–8689. <https://doi.org/10.1073/pnas.1502803112>
- Silvestro, D., Cascales-Miñana, B., Bacon, C.D., Antonelli, A., 2015b. Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytol* 207, 425–436. <https://doi.org/10.1111/nph.13247>
- Silvestro, D., Schnitzler, J., Liow, L.H., Antonelli, A., Salamin, N., 2014. Bayesian Estimation of Speciation and Extinction from Incomplete Fossil Occurrence Data. *Syst Biol* syu006. <https://doi.org/10.1093/sysbio/syu006>
- Zaffos, A., Finnegan, S., Peters, S.E., 2017. Plate tectonic regulation of global marine animal diversity. *Proc. Natl. Acad. Sci. U.S.A.* 114, 5653–5658. <https://doi.org/10.1073/pnas.1702297114>