



March 15, 2020

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To: *Proceedings of the National Academy of Sciences of the USA*

Dear Dr. May Berenbaum,

Please find enclosed an appeal letter and a fully revised manuscript of MS# 2018-20998 now titled **“The rise of angiosperms pushed conifers to decline during global cooling”** by Fabien Condamine and co-authors.

We are very thankful for all the excellent suggestion made by the two reviewers. We have carefully taken all of them into account and made the requested changes in the revised version.

Major improvements include **(1)** re-analyzing the phylogeny of conifers (with the 2018 dated tree), **(2)** re-analyzing the fossil record with the exclusion of dubious occurrences and the stem lineage †Cordaiales, **(3)** testing the effect of atmospheric carbon dioxide to add another climatic variable (since global temperatures do not alone explain climate change), and **(4)** incorporating all other suggested changes. In the revised version, we have incorporated all the new results in the main manuscript file as well as improved and expanded the Supplementary Information.

The main concerns on the previous submission related to the robustness of the analyses and the tone of the discussion. By performing new series of analyses with improved datasets, we find that the results were and remain robust, and the main conclusions therefore remain solid and identical to those previously reported.

We feel confident that this study has gained considerably in clarity and robustness. Given the long-standing and widespread interest on the rise and global dominance of flowering plants, we strongly believe that this study will appeal to a large readership in the fields of ecology, evolution, biogeography and related fields.

We therefore hope that you will share our enthusiasm for this study and may now consider our study suitable for publication in *PNAS*.

Yours sincerely,

Dr. Fabien Condamine (On behalf of my co-authors)



## Point-by-point response to the reviewers' comments

### Editor Comments:

*Thanks for submitting your work to PNAS. I read it soon after you submitted it and found it of potential interest to PNAS. Hence, I sent it out for external review. Unfortunately, it has taken quite a bit of time to get back referee comments from the external reviewers - now I have two reports. I have also re-read the manuscript. As you can see from the reports of the external reviewers, they have some major concerns about your contribution. On this basis, I have decided to reject your submission from further consideration in PNAS. I suggest you revise your ms. and submit it to some more specialized journal - e.g., Ecology Letters.*

Thank you for handling the manuscript and having secured two excellent reviewers who brought up interesting and constructive comments, which prompted us to revise and thoroughly re-work our manuscript. We hope our revised manuscript may regain your initial interest and support.

### Reviewer Comments:

#### Reviewer #1:

##### Comments:

*This is a nice and generally nicely written summary paper with impressive illustrations and interesting models and analyses. To some extent, though, it is oddly organized, seemingly going back and forth from methodologies to results in a way that is hard to follow and does not really seem to flow with consistency from a premise through to conclusions. This could be remedied.*

Thank you very much for reviewing the manuscript and these valuable comments. In the revised manuscript, we have made every attempt to re-organize the flow of text in a more consist and clear manner.

*However, the manuscript does not seem to break new ground relative to existing literature and conventional perspectives, rather it provides additional support for widely held views on angiosperm vs. gymnosperm evolution and diversification. And while the authors have used a number of tests, all superficially impressive with the results nicely illustrated, their major conclusions only verify, despite their protestations to the contrary, what is widely known from sometimes less complicated analyses of the comparative fossil record of angiosperms, conifers, other gymnosperms and vascular cryptogams (see, for example, Niklas, Tiffney and Knoll, 1983 Nature 303, 614-616). In fact the sentence "Our analyses show strong evidence that angiosperms outcompeted gymnosperms during their rise to ecological and evolutionary dominance." is prima facie evidence of what appears to be an incongruous degree of naïveté with respect to the understanding of the histories of angiosperms and gymnosperms among authors with apparently an otherwise sophisticated command and capability in modelling analysis. There is a vast literature on the evolutionary advantages accruing to angiosperms based on their relative success and imposing history of speciation. One wonders if the purpose, or perhaps significance, of their manuscript lies in the fact that some of their modelling supports what is already well known, and instead of illuminating causality of*

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*major evolutionary changes, it confirms to some extent the efficacy of their modelling and analyses. Nonetheless, they do not discuss some interesting aspects of angiosperm conifer "conflict". For example modern day conifers, many genera of which have long evolutionary histories, are not extinct, and persist in spite of angiosperm dominance. These remain dominant in cooler environments and thrive under such ecological conditions (at higher latitudes and altitudes).*

We agree that our study provides strong (fossil and phylogenetic) supports for widely held views on angiosperm vs. gymnosperm evolution and diversification, which can constitute a textbook example on plant competition over deep time scales. However, the significant difference compared to previous studies is that we provide quantitative macroevolutionary evidence for an active competition between conifers and flowering plants. We are not aware of any studies showing that **conifer extinction correlates with angiosperm diversity through time**, which offers a **mechanistic explanation for the conifer decline** (or low today's diversity). While it is true that most of the headlines of this paper have to some extent been postulated before, our study provides a very different level of confidence based on a much more biologically realistic incorporation of potential pitfalls and axillary factors. In doing so, we feel that we provide truly novel insights.

Also, in the revised version, we performed **additional analyses** (see comments of Reviewer #2 and our replies), which provide further evidence that angiosperms outcompeted conifers during their rise to ecological and evolutionary dominance.

We agree that the topic on the evolutionary advantages of angiosperms based on their relative success could be further expanded. During the revision, we have therefore cited and discussed more references to depict a **fair state-of-the-art**, although an exhaustive reference list might be more appropriate to a review paper.

Finally, we cannot really address why extant genera with a long evolutionary history are not extinct, and persist in spite of angiosperm dominance based on a global macroevolutionary study. This would require clade-specific studies for these genera, which is beyond the scope of this study. The fact that these extant genera are dominant in cooler environments and thrive under such ecological conditions is likely explained by key adaptations to such environments, which are their last stand. However, even these observations might have to be reconsidered since there is a widespread increase in dominance of Fagaceae at the expense of Pinaceae across northern temperate forests (Reyna et al. 2018 – Global Planet. Change).

*If not completely at odds with their discussion--they do not, oddly, rule out global cooling as a positive causative agent for declining conifer diversity, this phenomenon should certainly be discussed. Especially because, even in these favorable environments where conifers outcompete angiosperms, today, they do not show evidence of significant speciation. Again, the authors also repeatedly talk about extinction whereas many conifer taxa are not extinct.*

Indeed, we do not rule out the role of climate change, but we do find stronger (significant) support for the angiosperm-dependent model as the best fitting hypothesis. Discussing the role of climate for extant conifers thriving in temperate (cold) environments is beyond the scope of the study since we would have to perform clade-specific diversification analyses to assess the role of climate on these recently originated clades. This would require regional or continental-level climate curves throughout the Cenozoic (not currently unavailable) and to take into account rate heterogeneity to isolate the signal from rapidly radiating clades from ancient clades. Our focus on our study and analyses attempt to **identify, measure and explain global pattern of diversification**.

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*And when it comes to the "active displacement model" and their citation that fern diversification was not affected by angiosperm radiation, they do not address potential niche overlap and the Hutchinsonian concept of an n-dimensional hyperspace; something that might have relevance to angiosperms replacing conifers in contrast to the conditions that apply to pteridophyte radiation.*

This is a very interesting idea that should certainly be explored further in a future study. To maintain clarity and focus, we think that in the current study it would not be feasible to explore the role of niche overlap between the two clades since the data and models used here are not designed for this endeavor. Our results will hopefully stimulate further research on the role of niche in driving conifer diversification patterns, and the development of new modeling approaches to tackle such hypotheses. In the revised version, we further clarify this focus and suggest that future studies may test whether niches were similar and investigate whether the ecological radiation of angiosperms overlapped with conifers such that they actively replaced them.

*The authors provide as a further rationale for their manuscript "insights into the ensuing question: did the Cretaceous radiation of angiosperms lead to the decline of conifer diversity?". Yet again, this observation in no way depends on, nor was it illuminated significantly by the authors' analyses because it is well known that angiosperms increased in species numbers and in geographical domination as the conifers retreated to mostly cooler climes. The authors themselves cite publications that provide mechanisms for relative angiosperm success that, as noted, have been widely published on the well recognized relative advantages of angiosperms (the origin of the annual habit and its potential evolutionary advantages due to rapid life cycle, animal seed dispersal and pollination, etc). The very reasons that such discussions have taken place in the literature in such a protracted fashion emanate from the prevailing understanding that angiosperms replaced conifers--the raison d'être, in effect, of Darwin's "abominable mystery".*

Thanks for this insightful comment. We have rephrased this section, and removed the obvious statements made from previous studies. We do not want to claim that our study has demonstrated the conifer retreat while angiosperms radiated, but we want to provide novel discussion on how the processes worked to drive this pattern. So this section is now focusing on our results, and we attempt to link the diversification processes inferred in our study (i.e. the increase of extinction rate through time) with previous studies establishing ecological mechanisms. We have also added that our study does not address the role of ecological niche, but we propose that further paleoecological works investigate the role niche overlap between the two groups in the Cretaceous, when flowering plants diversified.

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## Reviewer #2:

### Comments:

*Overall. The manuscript by Condamine et al. aims to prove that the rise of angiosperms pushed conifers to extinction since their radiation in the Cretaceous. It attempts to compare models of conifer diversity through time with proxy records for temperature and angiosperm diversity through time. The patterns of diversity utilized in the study fit both the temperature and angiosperm through time models, but marginally better against inferred angiosperm diversity patterns. Claims made throughout the article, however, are much grander than these analyses support - for instance, mean global temperature does not equal climate, although it is one important component. The conclusion highlighted in the title (conifers being pushed to extinction by angiosperms) is not warranted by the results. Biotic interactions are, at best, very loosely and incompletely approximated by looking at the global species richness of angiosperms. I would suggest that the authors stick to stating what they are testing (angiosperm richness, global temperature), rather than tying it to broader ideas and theory in ways that cannot be exhaustively/adequately tested using the methods here.*

*More importantly, the inferred conifer diversity record cannot be used in its current form. The data that forms the base of this paper are a compilation of a dataset downloaded from the Paleobiology Database (PBDB) that was used for a paper by Silvestro et al (2016), complemented by more recent data from the same source. Having the PBDB and main source of data comes with many issues and shortcomings that have not been addressed or remedied. Another problem is that the data analysis is based on fossil occurrences, but especially in the mid-Paleozoic the results of the analyses is not backed up by the known fossil record. I will address both problems in greater detail in the attachment. Because of these issues with the data and analyses, my conclusion is that this manuscript cannot be accepted for publication in its current state.*

Thank you very much for your thorough review and many insightful comments. We definitely agree that mean global temperatures are not equal to climate, although they represent an important component. We have now clarified this in the text and, importantly, were also able to now incorporate models with temporal variations of atmospheric carbon as an additional measure of climate change.

We also agree that investigating the global variations of angiosperm species richness can at best approximate the effect of biotic interactions on conifer diversification. However, the lack of regional-level, high-resolution fossil data makes it extremely difficult to test for more fine-scale mechanisms at the macroevolutionary scale. We have therefore toned down our discussion to remain in line with our results and hypotheses.

We argue that the macroevolutionary results present are robust since we find they remain the same regardless of the phylogeny of conifers used and the exclusion of uncertain fossil occurrences. The exceptional congruence between fossil and phylogeny-based analyses is remarkable and a strength of the study.

*Older literature. Unlike for other groups of organisms (e.g. vertebrate, or invertebrates), the PBDB is woefully short of representing the known fossil record of fossil plants. The data entry has been limited to older literature, generally representing tabulations of taxa for fossil assemblages, but lacking published data available in more detailed taxonomic descriptions. This means that the data largely does not represent the rich record of fossil plant diversity in the taxonomic literature. It is well known among paleobotanists that the PBDB database is insufficient and untrustworthy for macroevolutionary analyses of plants, without significant*

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*editing, validation, and augmentation of the dataset. It is unfortunate that it is still the only widely available compilation of plant diversity, but nonetheless may thus not be appropriate in its current form for the questions posed in this study.*

It is indeed unfortunate that the Paleobiology Database still remains the only available compilation of plant diversity, without being as thorough and complete as it could. We have worked extensively with that database and know, by means of careful analyses, manual verification and validation, that the data come with important biases and gaps when downloaded indiscriminately (e.g. Antonelli et al. 2015 – Front. Genet.; Silvestro et al. 2015 – New Phytol.; Condamine et al. 2020 - Cladistics). Members of our team have also developed tools for automatic detection and exclusion of dubious records (Zizka et al. 2019 – Methods Ecol. Evol.). However, we stress that we did not use the data as it was directly downloaded. Instead, we carried out substantial validation to remove dubious occurrences and poorly known / described taxa. We are clearly aware that the dataset is not perfect but it does reflect current knowledge, and we only hope that this study can promote further works in this direction. We have acknowledged in the revised text that the quality of the plant fossil diversity does not follow vertebrate and marine invertebrate fossil records. We also discuss in which ways the incompleteness of the fossil record might bias our results, which we judge to minor effects. Again, we would like to highlight the exceptional congruence of the diversification processes inferred independently from the fossil record and molecular phylogeny, which confidence for no major spurious results.

*Organ taxa and bias. According to the material and methods in the current manuscript the Silvestro 2016 dataset consisted of 6,470 occurrences. When checking the Silvestro dataset, which is available as supplemental information, the Pinopsida included a variety of organ taxa, including shoots, leaves, seeds, pollen cones and pollen grains assigned to conifers. This means that, depending on the interests of the data enterers (particular time intervals, paleobotanical or paleobotanical assemblages), the number of genera recorded during particular time intervals will likely be inflated compared to other portions of the record. An example of this is the Rees dataset. A substantial portion of the PBDB's paleobotanical data were uploaded by Allister Rees and represent the dataset compiled for his Ph.D. thesis. Rees' work is focused on compositional changes of plant fossil assemblages across the Permian-Triassic boundary. The temporal bias of data entry in PBDB therefore will likely skew the data used toward the late Paleozoic through early Mesozoic.*

We agree that the PBDB has been filled with different datasets coming from different authors and studies, this may cause some biases when one wants to compile a dataset for a whole group. This is likely affecting not only conifers but also groups that have been recently studied (e.g. Alroy et al. 2008 – Science; Alroy 2010 – Science; Mannion et al. 2015 – Nat. Comm.; Nicholson et al. 2015 – Nat. Comm.; Condamine et al. 2016 – Sci. Rep.; Pires et al. 2017 – Evolution; Silvestro et al. 2018 – Nat. Comm.).

In addition, the robustness of the PyRate approach used in our study has been thoroughly evaluated using simulations that reflect commonly observed diversity dynamics (Silvestro et al. 2014 – Syst. Biol.; Silvestro et al. 2015 – PNAS; Silvestro et al. 2019 - Paleobiology). Datasets have been simulated under a range of potential biases, including violations of the sampling assumptions, variable preservation rates, and incomplete taxon sampling. Simulation results in those studies have shown that **the dynamics of speciation and extinction rates are correctly estimated under a wide range of conditions**, including sudden rate changes and mass extinction, and even very 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).

It is known that the strongest bias in birth–death rate estimates is caused by incomplete data because missing lineages alter the distribution of taxa; an effect notably pervasive in phylogeny-based models (Heath et al. 2008 – Syst. Biol.; Cusimano & Renner 2010 – Syst. Biol.; Höhna et al. 2011 – MBE). However, in the case of PyRate, simulations show that the estimates are largely robust to such biases. 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.

*Non-conifer taxa. In the materials and methods section the authors mention they checked for fossil occurrences using the name ‘Pinophyta’ (Division). The problem is that not all taxa the Silvestro dataset that fall under that name or Pinopsida (Class) in PBDB are conifers. The dataset for instance includes more than 1000 records of Cordaites which are related to conifers but regarded as a distinctly different group (e.g., see Rothwell et al., 2005 in Taxon).*

Thanks for this insightful comment. To test the sensibility of our results in relation to this relationship, **we now performed additional analyses** by removing †Cordaitales from our dataset, notably the genera *Cordaites*, *Gothania*, *Mitrospermum*, *Nephropsis*, *Nucellangium*, and *Samaropsis*. The results are presented in Figure S3C of the Supplementary Information. Interestingly, the results are very similar to the dataset including †Cordaitales, except that the conifers are inferred to have originated in the early Permian rather than Late Devonian. Importantly, the increase of extinction since the mid-Cretaceous onward is also recovered. Therefore, even after the changes implied by the reviewer’s comment, **our results still show the increase of extinction in conifers since 100 million years**, which is the main result of this study.

*Phylogeny used. The dated phylogeny that was used (Leslie et al., 2012) has now been updated with more taxa and calibration points (Leslie et al., 2018). It would be preferable to use this enhanced database, although it is at least questionable whether the desired conclusions can be drawn from a phylogeny of only extant taxa, and thereby missing most of the evolutionary history of conifers (see Quental and Marshall, 2010 in TREE, for explanation).*

We agree that it is more suitable to use the latest phylogeny of conifers. **We have now repeated the phylogeny-based analyses with the tree of Leslie et al. (2018)**. The results of the episodic birth–death model implemented in TreePar (Table S1B) still show a 3.7-fold decrease in net diversification rates starting around 135 Ma, which is (as in the previous version of this manuscript) similar to the inference from the fossil record. More importantly, we also applied the framework of paleoenvironment-dependent diversification models and we found that the **best-fit model is still an angiosperm-driven extinction model** (Tables S6 and S7). This adds robustness to our previous results inferred with the tree of Leslie et al. (2012 - PNAS).

We are well aware that estimating extinction rates from molecular phylogenies represents a major debate in evolutionary biology. Several papers have discussed this challenge (Rabosky 2010 – Evolution; Quental & Marshall 2010 – TREE; Rabosky 2016 – Evolution), but other papers, including those my members of our team, have also demonstrated the possibility to infer such rates (Morlon et al. 2011 – PNAS; Condamine et al. 2013 – Ecol. Lett.; Beaulieu & O’Meara 2015 – Evolution). Studies arguing against the

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power of phylogenetic models to estimate extinction rates have proposed to use the fossil record. Thus, if one trusts more fossil-based than phylogeny-based inferences for extinction rates, then we would like to highlight the **congruence for the estimate of conifer extinction estimated with fossil-based and phylogeny-based models of diversification**.

*Analysis. With regard to the analyses performed, I would recommend having an expert in these types of analyses carefully review the nuances of the models used.*

With all due respect, two of the authors are considered internationally leading experts in these types of analyses. Specifically, Daniele Silvestro has developed the fossil model known as PyRate (e.g. Silvestro et al. 2014 – Syst. Biol., 2019 - Paleobiology) and Fabien Condamine has developed the phylogenetic model to estimate the environment-dependent diversification (e.g. Condamine et al. 2013, 2019 – Ecol. Lett.).

*The authors show global origination, extinction and net diversification rates of the conifers inferred from a fossil-based analysis at the genus level (Figures 1B and S3). A major problem with these figures is that these rates start right after the late Devonian mass extinction, and event that took place about 376 million years ago. The earliest fossil conifers, however, have been described from the middle Pennsylvanian Moscovian stage (315-307 million years ago), about 60 million years later. This raises the question what fossil record these inferred conifer extinction and origination trajectories are based on. Note that this is not caused by the erroneously included cordaitalean occurrences, since they also lack Devonian or early Carboniferous representatives.*

This is a good question. Two facts can explain why conifers originated in the Devonian in our analyses. First we included stem lineages of conifers (= †Cordaitales with the genera *Cordaite* and *Samaropsis*), which have fossil occurrences in the Devonian and Carboniferous. This is related to a comment made above about the Cordaitales. Second, some good conifer occurrences come with large age uncertainties. This issue concerns three genera *Araucarioxylon*, *Brachyphyllum* and *Pagiophyllum*, with 53 occurrences mostly ranging from 252.3 to 360 Ma (Permian and Carboniferous). Such age range clearly represents poor age constraints for these occurrences and does not mean that conifers were present in the Devonian.

As said above, we have repeated the analyses excluding Cordaitales and dubious occurrences. The results are presented in Figure S3C of the Supplementary Information. Interestingly, the results are very similar to the dataset including †Cordaitales, except that the conifers originated in the early Permian. Importantly, the increase of extinction since the mid-Cretaceous onward is also recovered.

*Also, please note that species richness does not necessarily correspond to ecological dominance. This has been also discussed explicitly for the Cretaceous in respect to angiosperms (see for example, the review by Wing and Boucher 1998, and the Ecological Monographs paper by Wing et al 2012). When it comes to some of the extant conifers it is almost the opposite, boreal forests currently form the largest terrestrial biome on our planet, and are characterized by low-diversity communities of Pinaceae: spruces, pines and larches.*

We fully agree with the reviewer that species richness does not equate to ecological dominance. To clarify this, we have now removed the term ‘ecological dominance’ in several places of the manuscript. When stated, we make it clear that we compared species richness at a given point in time. We also now cite the paper of Wing and Boucher (1998).

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*Figure S1. This figure is an overview of the potential determinants of conifer diversification over time. In SIC a change from large to smaller leaves is indicated going from the Paleozoic to Mesozoic. This change is not mentioned in the main MS, the words leaf and shape are not used in the MS, so what is this based on? Importantly, the first leaf figured is not a conifer (Glossopteris - a seed fern), the second is, and both are a major oversimplification of the diversity of leaf morphologies present among conifers for these respective time intervals.*

Figure S1 has been updated and the leaf change across the Permian-Triassic mass extinction has been removed.

#### *Other comments and suggestions*

*Line 40-41. The sentence structure here is off. The rise of angiosperms did not outcompete gymnosperms and ferns. "Angiosperms" should be the subject, not "the rise".*

The sentence has been rephrased.

*Line 41. "thoroughly". Can it even really be thoroughly tested? be specific - it has not previously been tested in what way? It's definitely been suggested and "tested" based on occurrence data.*

The sentence has been rephrased.

*Line 46. "low diversification" replace with "low diversification rate".*

Done.

*Line 54-56. "the evolutionary decline of conifers. Our study demonstrates how entire branches on the Tree of Life may compete with each other for ecological dominance."*

*Note that this is environment dependent. High altitude and high latitudes are still largely dominated by conifers. Also, dominated in what sense - note the difference between diversity vs abundance across the landscape. Ecological dominance is not strictly coupled with diversity.*

This part of the abstract has been rephrased.

*Line 72-73. "One of the most remarkable features of the natural world is the disparity in species richness among groups of organisms."*

*Maybe "A remarkable feature..." or just state that there is disparity in different groups, and science it working to understand the underlying factors.*

Done.

*Line 73-76. "This non-random taxonomic variation is determined by different speciation and extinction regimes that lead clades to successively rise, decline, and replace one another. Identifying which abiotic and/or biotic factors regulate diversity changes represents a key challenge in evolutionary biology."*

*This sounds like the assumption is that all groups follow the same diversity trajectory through time, and that the differential timing of events is what leads to different diversity at any given moment in time.*

Corrected.

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Line 95-96. *"gymnosperms exhibit about 1% of the total plant diversity and are mostly confined to boreal regions."*

*And high-altitude environments, even in the tropics*

Corrected.

Line 98-99. *"the timing of origin of flowering plants is debated"*

*Cite more than a couple molecular papers here. See Coiro et al 2019 in New Phytologist for very recent paper addressing this in detail.*

We now cite the suggested reference and three others (Bell et al. 2010 – Am. J. Bot.; Barba-Montoya et al. 2018 – New Phytol.; Li et al. 2019 – Nat. Plants).

Line 99. *"there is consensus that they radiated"*

*Cite many more for consensus, or at least representative of the field of research on origins of angiosperms.*

We now cite more papers to show there is a consensus on a Cretaceous angiosperm radiation.

Line 104-106. *"which resulted in the ecological dominance of flowering plants observed in most terrestrial ecosystems today."*

*Read Wing and Boucher 1998 for discussion of ecological dominance (as opposed to dominance by diversity). Also see Wing et al 2012.*

The sentence has been rephrased, and we now cite Wing & Boucher (1998).

Line 106-108. *Angiosperm-dominated forests underwent such an ecological and evolutionary diversification that they outcompeted and outnumbered other land plants.*

*Sentence structure. Forests didn't undergo a radiation and outcompete other land plants. Also, outnumbered in what way? richness? number of stems?*

Corrected.

Line 109-110. *"effects of the angiosperm radiation on the diversity and evolution of gymnosperms remains largely untested."*

*This has been looked at from fossil data. Comparing plots through time of fossil occurrence and species data. Need to cite previous work.*

The sentence has been rephrased, and we cite previous works on this topic.

113-114. *"conifers were a dominant component of the flora during the Mesozoic, with the Triassic and Jurassic periods referred to as their heyday."*

*Also Cretaceous and well into Cenozoic. There are better references for a statement like this.*

We cite other references on this topic.

Line 115-118. *"Understanding the diversification of conifers should therefore shed light on the interactions between gymnosperms and angiosperms, and how these interactions compare with other abiotic events such as global change of biomes (25, 117 26, 37, 38), continental rearrangements (28, 39), and changes in key environmental parameters, such as global temperatures."*

*This sentence should be re-written. Don't see how actually makes sense. This paper also doesn't aim to understand the diversification of conifers, and is not adding new info to that aspect of the story. It should focus on the diversity dynamics of between angiosperms and conifers, and some (but not all) other potential drivers for the diversity decline in conifers. Also loose the gymnosperm aspect, this paper does not address so broadly.*

The sentence has been rephrased.

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*Line 139-141. Diversity is unconstrained and expands towards the present, potentially limiting our ability to adequately characterize these processes through time.*

*See Marshal and Quental 2016, Phil. Trans. R. Soc. B 371: 20150217.*

We now cite the suggested reference.

*Line 173-174. "the progressive temporal increase of extinction in the last 100 million years inferred here."*

*Rephrase "progressive temporal increase".*

Done.

*Line 179-180. "The Late Cretaceous and Cenozoic were generally cooler than most of the Paleozoic and Mesozoic."*

*That is an overgeneralization. The late Carboniferous and early Permian was an ice house period, and there were thermal maxima in the Cretaceous and Eocene.*

The sentence has been rephrased.

*Line 228-229. "Both model comparisons made with phylogenetic based analyses (Table S5) and fossil- based analyses"*

*This model comparison is the support for the biggest claim in this paper. It should therefore be in the main paper, not as supplementary.*

We agree that the former Table S5 (now Table 1) and also the former Table S6 (now Table 1) are the main results supporting our conclusions. We have updated these tables with the inclusion of novel environment-dependent diversification models taking into account the temporal variations of atmospheric carbon as another proxy of past climate changes. We have now included these two tables in the main text of the revised version.