

Extreme greenhouse warmth triggered the two major floristic turnover events of the past 120 million years

Corresponding Author: Dr Kale Sniderman

Version 0:

Reviewer comments:

Reviewer #2

(Comments for the Author)

The manuscript analyzes the palynological record of SE Australia over the past 125 million years to understand patterns of plant diversity and its drivers. This is an excellent study that makes use of a unique resource, several decades of palynological studies in SE Australia that span a long stratigraphic interval. There are very few regions on Earth with the time span and taxonomic consistency of the SE Australian record. The manuscript compiled decades of studies in a single database with ~140K records, a major task in itself.

SE Australia has not been static over geological time, starting at ~65 S in the early Cretaceous until its modern position, ~37 S. Several variables can play a role in explaining its palynological record, including local temperature, meridional temperature gradient, solar insolation, precipitation, connectivity with large continental areas, and lithofacies.

The manuscript explored the variables related to temperature and connectivity (local, meridional gradient, and connectivity) and found a positive and significant correlation between two major peaks of global warming and origination/extinction (mid Cretaceous and the Early Eocene warming). Then, the analysis compared the results with the North East African Cretaceous palynological record and the Cenozoic neotropical record, finding similar patterns. As both regions were far apart from SE Australia, the manuscript concludes that the warming-origination/extinction is a global phenomenon and probably driven by temperature, although the direct causation is still unknown.

The analysis uses the standard methods for this kind of metaanalysis (standardization for sampling intensity, cohort survivorship, standing diversity, and percapita origination/extinction). The correlations with the different variables, including the local SST from planktonic foraminifera oxygen isotopes, the meridional temperature (gradient from 10 S to 60 S), and the distance to the nearest continent, support the interpretations, although additional analysis are required (see below).

The manuscript is well written, easy to follow, and it will be an excellent contribution toward understanding plant evolution at a global scale. However, I would like to see a few points addressed as follows:

1. Solar insolation is ~214 W/m² at 65 South while it is 349 W/m² at 35 South. That is not a minor difference that can have implications on photosynthesis (length of sun hours throughout the year and the quality of the light). However, the analysis does not consider it as a variable with explanatory value. It should include it, or at least, tell us why it can be dismissed.

2. Precipitation plays a major role in a biome's evolution, especially during global warmings, as water stress can move a forested biome to a grassland/low-stature biome. I am aware that metrics for precipitation are hard to produce in the fossil record, but at least a qualitative assessment of precipitation would be useful. For example, features of the sedimentary record could be used as proxies for precipitation, e.g., the proportion of coal versus evaporites in every bin.

3. Sedimentary facies are barely addressed, although they could play a major role in the diversity record. This can be more pronounced when long spans of geological time are analyzed. For example, the palynological diversity of a shallow marine environment could be higher than a fluvial environment because several rivers can deliver sediments to a bay, thus capturing a much larger signal of the vegetation compared to the local signal of an oxbow lake associated to a river. This is very similar to the lake-size effect on diversity; the larger the lake, the larger the palynological diversity, as the source area is larger. What if the high diversity levels of the Turonian are just a taphonomic effect? The Turonian has the highest eustatic sea level since the early Cretaceous, with a rise of ~250 meters that covered extensive lowland areas all over the world, giving rise to many epicontinental seas. A fluvial setting converting into a shallow sea could increase the palynological diversity. Even the opposite could happen, for example, the Turonian high sea level produced an epicontinental sea all along South America and in many of its sedimentary sequences the Turonian is represented by black shales that are fully dominated by cyanobacterial masses (South American Turonian rock are one of the richest oil source rocks in the world), and it is very hard to find pollen

and spores in palynological sample as they are very diluted by the cyanobacterias. The result: there are many last palynomorph appearances at the top of the Cenomanian that are probably just an edge effect due to taphonomy (plants are in the Turonian somewhere else, but we cannot record them because of the lithofacies). Therefore, the diversity analysis needs to filter out the taphonomic effect. For example, the dataset could be split into two groups: a group where samples are fully terrestrial (not a single dinoflagellate) and a group with everything else. Then, the whole analysis would be done again. The African dataset needs a similar approach as the Cretaceous eustatic sea level had a major influence in the sedimentary record of NE African.

4. Diversity and biomass dominance are not correlated. For example, the Sequoia forests in NW North America have a 95% biomass dominance of Sequoia that is represented by only two species. The Sequoia forests also have angiosperms, but they are mostly in the riparian environments associated to small creeks or rivers, representing a tiny proportion of the forest biomass. However, if you assess a species list of the forest, they are dominated by angiosperms. In other words, the forest diversity is dominated by angiosperms while the forest biomass is dominated by gymnosperms. Toward the end of the manuscript, the discussion seems to imply that the record can be interpreted in terms of ecological dominance. That is not correct. To say anything about ecological(biomass) dominance, abundance data needs to be quantified, and the analysis presented in the manuscript did not. Therefore, the discussion needs to remove comments about ecological dominance.

5. The structure of the cohort survivorship is very peculiar and it suggests that Cenozoic and Cretaceous floras are quite different. It would be very informative to run a Sørensen Cluster analysis to evaluate changes in palynofloral composition across the entire record. I think the cluster results will be very informative.

6. Lastly, I could not find either the data or the R code that was used to run the analysis. This is very important; the data needs to be published along with the manuscript (in a repository as Dryad, for example), so anybody can replicate the analysis. This is a must.

This is a very interesting manuscript that deserves publication

Carlos Jaramillo

Reviewer #3

(Comments for the Author)

Summary of the key results

- Sniderman and colleagues present a >100 million year long palynological record compiled from southeastern Australia. They compile the diversity records to make an assessment of the major angiosperm diversification events in that timespan and correlate it to local and global climatic records. They find that these origination events are largely related to hyperthermals and independent of biotic interactions, or other abiotic events, most notably the K-Pg boundary. They also include comparisons to some low latitude records, which they argue show support for the Australian record being largely representative of patterns globally.

Originality and significance: if not novel, please include reference

- I think it is an important original contribution and of high significance. The authors largely focus on the hyperthermals as a way to overthrow the old "gradualism" argument in angiosperm diversification. However, I think the focus in many Northern Hemisphere and equatorial paleofloral records is the role of the K-Pg boundary in reorganizing floras globally. I support the author's view that climatic events are probably a much more important role for floral organization and that floras are resilient to ecological disturbance, but I think this part is somewhat understated and could be expanded upon.

Data & methodology: validity of approach, quality of data, quality of presentation

- the data came from various sources. It was especially well sourced from Australia, which makes sense, because that's where the authors are from. The two other records seem a bit haphazard. Missing the New Zealand record (especially considering James Crampton was mentioned in the acknowledgments) seems like somewhat of an oversight and perhaps a broader net could be cast to show that these results are truly indicative of a global signal.

Appropriate use of statistics and treatment of uncertainties

- Working with such a large dataset, the authors were faced with various problems of how to perform the statistics. I'm not of the illusion that there is a single good answer to what decisions are best in a meta-analysis. The authors left a very clear paper trail about how to replicate their results, so in my opinion the work is sound.

Conclusions: robustness, validity, reliability

- I see no reason to reject the authors conclusions based on the data and analysis.

Suggested improvements: experiments, data for possible revision

- I am unsure about how the combined African and Colombian palynological records support the argument here. Yes, the C-T diversification peak is captured in the African records as well (as an aside, check the consistency of the abbreviations used here especially fig 5. shouldn't this be the Ce-T transition?), but the break in the record at the K-Pg boundary is awkward. And if we consider the combined Colombian - African record continuous, then it rather shows a dramatic turnover at the K-Pg boundary, and none at the Paleocene - Eocene. The K-Pg record from Carvalho et al. 2021 (cited in the manuscript) is continuous, why not use that to extend the South American record into the Cretaceous?

- Not cited in the paper is the work of Prebble et al. 2021: A 100 million year composite pollen record from New Zealand shows maximum angiosperm abundance delayed until Eocene. This seems like a very relevant record, providing an appropriate comparison to the SE Australian record. Certain significant events identified in the Prebble et al. 2021 seem to overlap with the SE Australian ones. This record provides an opportunity for a very similar analysis as the authors did for SE Australia, but if not analyzed, it should at the very least be discussed.

References: appropriate credit to previous work?

- Yes, notwithstanding the Prebble et al. 2021 paper. Although I also understand how that was overlooked.

Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

- Yes, thankfully the authors are experienced writers and structured their paper well. I kept the PDF open to make minor comments, like spelling and styling suggestions, but never had to make any.

Decision Letter:

28th January 2026

Dear Dr Sniderman,

Your Article, "Extreme greenhouse warmth triggered the two major floristic turnover events of the past 120 million years" has now been seen by two referees. I'd once again like to apologise for the length of time your manuscript has been under review. We were waiting for comments from a third referee but given that the two reports we have a similar level of enthusiasm for your work we are happy to proceed with just those two reports.

As you will have seen already, referee #2 is supportive of your study and believes it makes an excellent contribution towards understanding plant evolution at a global scale. They have however identified a number of ways to improve the robustness of your analysis which essentially include the assessment of the contribution of precipitation dynamic, solar insolation and sedimentary facies in your analysis. Another issue that they raise is the need to make the R data available in aid of reproducibility. Referee #3 is also enthusiastic about your work, believing it to be a highly significant and original contribution to the literature. They do suggest however that a broader net could be cast over data records to show that these results are truly indicative of a global signal and also suggest including the work of Prebble et al. 2021, which contains a similar analysis to the one run in your study.

As discussed previously, we also received some informal comments from a referee unable to provide a full report and ask that you write a short, separate response to those informal concerns for the editorial team then we can make a decision on whether we think we would need to escalate those concerns to the other referees.

You will see from their comments below that while they find your work of interest, some important points are raised. We are interested in the possibility of publishing your study in Nature Plants, but would like to consider your response to these concerns in the form of a revised manuscript before we make a final decision on publication.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file.

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

When revising your manuscript please:

* Include a "Response to referees" document detailing, point-by-point, how you addressed each referee comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the referees along with the revised manuscript.

* If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at <http://www.nature.com/nplants/info/final-submission>. Refer also to any guidelines provided in this letter.

* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

* Pay close attention to our <https://www.nature.com/nature-portfolio/editorial-policies/image-integrity> Digital Image Integrity Guidelines. and to the following points. Please ensure:

-- that unprocessed scans are clearly labelled and match the gels and western blots presented in figures.

-- that control panels for gels and western blots are appropriately described as loading on sample processing controls
-- that all images in the paper are checked for duplication of panels and for splicing of gel lanes.
-- that you retain unprocessed data and metadata files after publication, ideally archiving data in perpetuity. These may be requested during the peer review and production process or after publication if any issues arise.

EXTENDED DATA FIGURES

When re-submitting your manuscript, please ensure that any supplementary figures and tables that are crucial to the manuscript's conclusions are converted into Extended Data figures and tables to increase visibility of these data. Extended Data figures and tables are online-only (present in the online PDF and full-text HTML versions of the paper), peer-reviewed display items that provide essential background to the article but are not included in the main article due to space constraints. A maximum of ten Extended Data display items (figures and tables) is permitted.

Nature Plants strongly supports public availability of data and are therefore keen that the data used in your paper is placed in an appropriate public data repository. Alternatively, if this is not possible, you may present the data as Extended Data or Supplementary Information. If data can only be shared on request, please explain why in your Data Availability Statement, and also in the correspondence with your editor. Please note that for some data types, deposition in a public repository is mandatory.

Please use the link below to submit your revised manuscript and related files:

Link Redacted

Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Plants or published elsewhere.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

Sincerely,

Nature Plants is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. This applies to primary research papers only. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit <http://www.springernature.com/orcid>.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

Reviewers' Comments:

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correlate it to local and global climatic records. They find that these origination events are largely related to hyperthermals and independent of biotic interactions, or other abiotic events, most notably the K-Pg boundary. They also include comparisons to some low latitude records, which they argue show support for the Australian record being largely representative of patterns globally.

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Suggested improvements: experiments, data for possible revision

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*****END*****

Version 1:

Reviewer comments:

Reviewer #2

(Comments for the Author)

The revised manuscript addressed all my concerns. I also was able to find the raw data, run the code and replicate the results. I think it is ready for publication. It will be an excellent addition to the research on extreme global warmings as our planet is heading rapidly towards them (we are in 432ppm already, Miocene values), and perhaps by the end of the century we will reach Eocene values.

(Remarks on code availability)

Decision Letter:

Our ref: NPLANTS-250920960A

12th August 2026

Dear Dr. Sniderman,

Thank you for submitting your revised manuscript "Extreme greenhouse warmth triggered the two major floristic turnover events of the past 120 million years" (NPLANTS-250920960A). It has now been seen by one of the original Reviewers and their comments are below. The reviewer finds that the paper has improved in revision, and therefore we'll be happy in principle to publish it in Nature Plants, pending minor revisions to comply with our editorial and formatting guidelines.

As the current version of your manuscript is in a PDF format, please email us a copy of the file in an editable format (Microsoft Word or LaTeX)-- we can not proceed with PDFs at this stage.

We are now performing detailed checks on your paper and will send you a checklist detailing our editorial and formatting requirements in a couple of weeks. Please do not upload the final materials and make any revisions until you receive this additional information from us.

Please do not hesitate to contact me if you have any questions.

Sincerely,

Reviewer #2 (Comments for the Author):

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Version 2:

Decision Letter:

16th September 2026

Dear Dr Sniderman,

We are pleased to inform you that your study entitled "Extreme greenhouse warmth triggered the two major floristic turnover events of the past 120 million years", has now been accepted for publication in Nature Plants.

Over the next few weeks, your paper will be copy-edited to ensure that it conforms to Nature Plants style. We look particularly carefully at the titles of all papers to ensure that they are relatively brief and understandable.

Once your paper is typeset, you will receive an email with a link to choose the appropriate publishing options for your paper and our Author Services team will be in touch regarding any additional information that may be required.

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You will not receive your proofs until the publishing agreement has been received through our system.

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Response to Reviewers #2 and #3

Kale Sniderman, Greg Jordan, Chris Mays

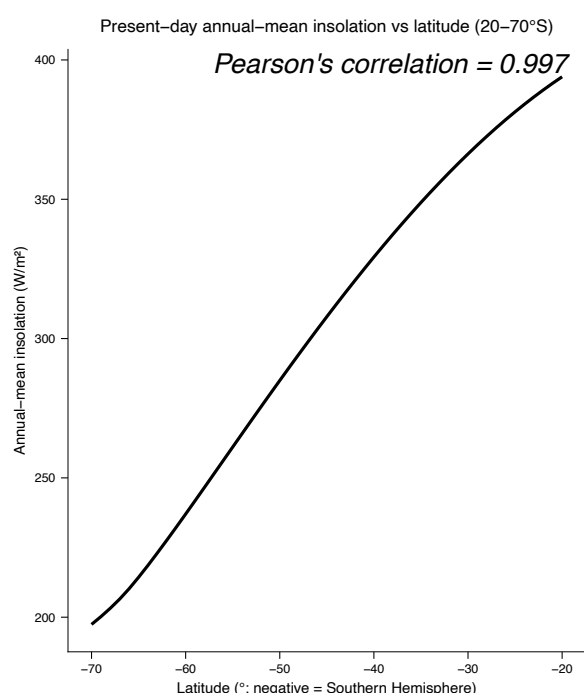
18 March 2026

We thank the two referees for their supportive and constructive comments on our manuscript. Below, we respond to each of their comments in detail (reviewers' comments in blue)

Responses to Reviewer #2's comments (Carlos Jaramillo)

We are grateful to Dr Jaramillo for his enthusiasm towards our dataset and manuscript.

1. Solar insolation is ~214 W/m² at 65 South while it is 349 W/m² at 35 South. That is not a minor difference that can have implications on photosynthesis (length of sun hours throughout the year and the quality of the light). However, the analysis does not consider it as a variable with explanatory value. It should include it, or at least, tell us why it can be dismissed.



This reasonable query and informal comments from Reviewer #1 led us to incorporate a new predictor (palaeolatitude) and a new response variable (cj1, an extrapolated richness estimator, the corrected first-order jackknife; introduced by Alroy, 2020, 'On four measures of taxonomic richness', *Paleobiology*), into our models. We incorporated palaeolatitude as a predictor, because palaeolatitude is a strong proxy for long term average palaeo-insolation in this region (see plot). We also took the opportunity to refine our analytical methods.

The changes to the results as a consequence of the introduction of new variables and refined analyses were modest and did not affect our overall inferences. However, these changes have required some rewriting of the methods and results (in the tracked changes version, at lines 76-77, 90-91, 127-128, 135-141, 143-155, 162-

181, 210-223, 246-258; and in the Methods, at lines 763-766, 771- 776, 810-817, 877-883, 896-935, and 940-949), and some of the figure captions. It was also necessary to re-create several figures: Fig. 2 (now incorporating the former Fig. 4), Fig. 3 and Extended Data Figs 2 and 3 (the latter now partly promoted to constitute a new Fig. 4).

SUMMARY OF CHANGES TO GENERALISED LINEAR MODELLING METHODS

The changes to the analytical methods are expanded in the 'Methods' section, but summarized here:

- (a) Better handling of missing data. Both predictors and response variables can lack one or more rows, for several reasons: (a) it is meaningless to calculate originations (first appearances) or extinctions (last appearances) in the oldest and youngest time bins, respectively, so these parameters are represented by 'NA' at those times; (b) by design, Alroy's second-for-third origination and extinction rate algorithms omit one time bin at one end of a time series, and two bins at the other; and (c) data for some of our predictors (e.g., $\delta^{18}\text{O}$ -derived sea surface

- temperature) were unavailable in the oldest time bin. We have updated the GLM code to ensure that model selection was always based on the same number of observations.
- (b) We modified our approach in assessing which predictors are most important, and the way we illustrate the importance of this approach to the reader. Previously, in Extended Data Fig. 3, we showed the standardized coefficients of the predictors in a model average (based on the ‘best’ models, i.e., those with $\Delta\text{AICc} \leq 2$), and further highlighted those predictors that passed a Wald test. We have now realised that the Wald test is not appropriate in this context; we instead highlight the predictors that are both non-zero and the which appear in models summing to > 0.5 re-normalised Akaike weight.
 - (c) Mainly as a response to the broadening of our predictor- and response-variable data set, we sought to provide a new, more robust assessment of the drivers of the observed diversity changes. We introduce a new analysis, in which we divide our predictors into three, process-related, *a priori* predictor classes representing competing hypothesis of the drivers of observed diversity changes: those predictors reflecting climatic drivers (which we denote ‘*clim*’: local SST, GMST, MTG, and BWT), those reflecting interactions between the three taxonomic groups (denoted ‘*bio*’: the extrapolated richness [cJ1] of each land plant taxonomic group), and those representing geophysical changes in the Australian tectonic plate (denoted ‘*geo*’: distance squared and palaeolatitude, the latter of which we treat as a proxy for insolation. We acknowledge that the role of palaeolatitude is ambiguous, and that it could be interpreted as a climatic driver; but it is clearly not so narrowly climatic as the temperature-related predictors). We then used ΔAICc to compare support for non-nested models that included vs excluded each class. Specifically, for each class arrangement, we compared AICc between the best model containing ≥ 1 predictor from a focal block, and the best model constructed from predictors belonging to the remaining two blocks only. Thus, we compare whether the introduction of models containing any predictors from the focal block improves model fit over models restricted to the two other blocks. These new procedures are now described in the Methods, and the results of this analysis are now presented as Fig. 4b, which shows that climate-related predictors have substantially more explanatory power than the predictors of the other two predictor classes; and that biological interactions have somewhat more explanatory power than the geophysical predictors.
 - (d) We also revisited the modelling of the NE African dataset. In the first version of the manuscript, we had acknowledged that the sample size of this dataset was too small (only seven time bins) for model selection with AICc to work very well, because AICc’s strong penalisation of small sample sizes tends to rank intercept-only models as the best models. In the light of our re-evaluation of our SE Australian GLM analyses, we decided it was more justifiable to put aside formal model selection for the NE African data set, and evaluate predictor strength using a slightly different approach. We used a hypothesis-driven, univariable regression framework: we fitted a separate GLM for each candidate predictor, and inferred model fit based on the magnitude and sign of β and its 95% confidence interval, rather than AICc rankings from multi-predictor dredging. These results are plotted as Extended Data Fig. 3. While we feel this new analysis more rigorously acknowledges the analytical limitations imposed by the data set, it nevertheless recovered an almost identical set of ‘supported’ predictors (now based only on their having 95% CIs that do not overlap 0) as those identified in Extended Data Fig. 3 of the first version of the manuscript.

SUMMARY OF CHANGES TO GENERALISED LINEAR MODELLING RESULTS

We note that, with our improvements to the handling of missing data, our model averages sometimes include more predictors than before, several of which overlap zero in their 95% confidence intervals. That is, the new modelling implies that, for some land plant taxonomic group $\times$ diversity response combinations, the differences in predictive power between the predictors is less than implied by our earlier results. Nevertheless, the majority of ‘supported’ predictors (in the Methods we describe our refinements to identifying the most robust predictors) in the SE Australian dataset are climate-related

predictors, a pattern we quantify across all taxonomic group $\times$ diversity response combinations, in new Fig. 4b, a ‘best of class’ comparison of the predictors. In other words, this is still consistent with our finding in the first version of the manuscript, that one or more climate-related predictors is consistently more important than either biological interactions or geophysical predictors.

We find that palaeolatitude makes a modest contribution to the model average for one SE Australian taxonomic group $\times$ diversity response combination (free-sporing plants extinctions Myr^{-1} , see new Fig. 4a), though the predictor occurs only in models combined with other predictors. Thus, palaeolatitude provides marginal new insight into the drivers of diversity change in our dataset. However, the shared late Cenomanian-Turonian (Ce-T episode) timing of peaks of diversification in the SE Australian and NE African datasets, and the shared late Paleocene-early/mid Eocene (P-E episode) timing of peaks in the SE Australian and Neotropical datasets, suggest that whatever differential impacts latitude or insolation had on diversification are dwarfed by the shared diversification responses to the two extreme global greenhouse climates of the Cretaceous and Paleogene. Looked at another way, changes in southeastern Australia palaeolatitude (hence, changes in insolation) were negligible between the Early Cretaceous and the Eocene, yet this interval features the two most significant changes in origination/extinction rates. Therefore, latitude-driven insolation changes are not very strong predictors of the diversity trends across the duration of our study (as clearly shown in Fig. 4b).

2. Precipitation plays a major role in a biome's evolution, especially during global warmings, as water stress can move a forested biome to a grassland/low-stature biome. I am aware that metrics for precipitation are hard to produce in the fossil record, but at least a qualitative assessment of precipitation would be useful. For example, features of the sedimentary record could be used as proxies for precipitation, e.g., the proportion of coal versus evaporites in every bin.

We have struggled with this question, but have been unable to find a way to add a quantitative, direct precipitation metric to our manuscript. When preparing the first version of the manuscript, we felt, in agreement with the Reviewer, that we should include a precipitation proxy record as a model predictor. But because we lacked this local quantitative precipitation proxy, instead we invoked independent, global, and theoretical evidence, drawing broadly on climate physics, plant stomatal relations, and climate-model outputs, to briefly point to a general correlation between greenhouse states and high precipitation. Thus on page 7 of the first version of the manuscript, we wrote:

“We propose that, under the most extreme warm climate states associated with high atmospheric CO_2 (Rae et al., 2021; Fig. 5d), a strongly accelerated hydrological cycle (Cramwinckel et al., 2023) and flattened temperature gradients (Huber et al., 2018) promote widespread high rainfall and high plant water-use efficiency (McElwain, 2018). Generation of new plant lineages may be greatest under such conditions, with minimal drought stress and maximal extent and productivity of forest (Hagen et al., 2021).”

Along these lines, the reason we originally included the Southern Hemisphere meridional temperature gradient (MTG) as a GLM predictor is because a very shallow MTG is strongly correlated with very wet global climates. In addition, on page 4 of the original manuscript we singled out precipitation as likely playing a key role for the spike in Paleogene diversification, “...renewed Paleogene diversification of free-sporing plants may have been a response to wetter climates during the warm P-E episode”.

Although changes in lithofacies can provide useful evidence of changes in precipitation, we are confident that little or no palaeoclimatic signal would be revealed from the overwhelmingly siliciclastic lithologies of the sediment records contributing to our dataset. No evaporitic sediments are known in the targeted regions over the entire time interval of interest. The sediment records contributing to our southeastern Australian spore-pollen dataset are dominated by siliciclastic

mudstones, sandstones, and siltstones, with occasional limestones, and some coals (which we discuss further below, in the question about sedimentary facies). The strongest lithology-based observation that we believe can be made for the southeastern Australian region is that the absence of evaporites, the scattered occurrences of coals, and the rapid accumulation of siliciclastic sediments imply that precipitation was never strongly limited in this region, during our time period of interest (i.e., excluding the most recent ca. 7 Myr). This inference is supported by the persistence of rainforest lineages throughout the southeastern Australian records, including a diversity of physiologically drought-sensitive Podocarpaceae genera (Brodribb, 2011, ‘A functional analysis of Podocarp ecology’, *Smithsonian Contributions to Botany*), and peaks in origination of free-sporing plants at the Ce-T, in both the southeastern Australian and in northeastern African data sets.

To provide a more general response to the Reviewer’s concern, we have changed most of our previous references to *warm temperatures*, so that they now refer to *greenhouse climates*, in order to invoke the package of climatological processes, including a much-accelerated hydrological cycle, which are widely thought to be associated with very warm climate states. We have added a brief comment in the Discussion (lines 302-303 of the tracked changes version of the manuscript) that the warmest episodes are associated with local increases in free-sporing plant diversity or originations; but we find that the major Cretaceous transitions from spore- to pollen-dominated floras in our data sets undermine the use of diversity of free-sporing plants as a quantitative proxy for hydroclimate. In fact our primary motive for including low-latitude spore-pollen data in this study was to explore whether the tropics may have been arid during the Ce-T episode, prior to the development of extensive angiosperm rainforest canopies with high transpiration rates (as implied by Boyce & Lee 2010, ‘An exceptional role for flowering plant physiology in the expansion of tropical rainforests and biodiversity’. *Proc Roy Soc B*); but the northeastern African data do not seem to be consistent with tropical aridity at the Ce-T.

3.Sedimentary facies are barely addressed, although they could play a major role in the diversity record. This can be more pronounced when long spans of geological time are analyzed. For example, the palynological diversity of a shallow marine environment could be higher than a fluvial environment because several rivers can deliver sediments to a bay, thus capturing a much larger signal of the vegetation compared to the local signal of an oxbow lake associated to a river. This is very similar to the lake-size effect on diversity; the larger the lake, the larger the palynological diversity, as the source area is larger. What if the high diversity levels of the Turonian are just a taphonomic effect? The Turonian has the highest eustatic sea level since the early Cretaceous, with a rise of ~250 meters that covered extensive lowland areas all over the world, giving rise to many epicontinental seas. A fluvial setting converting into a shallow sea could increase the palynological diversity. Even the opposite could happen, for example, the Turonian high sea level produced an epicontinental sea all along South America and in many of its sedimentary sequences the Turonian is represented by black shales that are fully dominated by cyanobacterial massess (southamerican Turonian rock are one of the richest oil source rocks in the world), and it is very hard to find pollen and spores in palynological sample as they are very diluted by the cyanobacterias. The result: there are many last palynomorph appearances at the top of the Cenomanian that are probably just an edge effect due to taphonomy (plants are in the Turonian somewhere else, but we cannot record them because of the lithofacies). Therefore, the diversity analysis needs to filter out the taphonomic effect. For example, the dataset could be split into two groups: a group where samples are fully terrestrial (not a single dinoflagellate) and a group with everything else. Then, the whole analysis would be done again. The African dataset needs a similar approach as the Cretaceous eustatic sea level had a major influence in the sedimentary record of NE African.

We have responded to the Reviewer’s suggestion by adding additional information regarding the depositional conditions and tectonic evolution of the southeastern Australia and NE African datasets (see the ‘study areas and fossil database’ section, lines 568-573, 581-595, and 611-615 of the tracked change version of the manuscript), but we believe that changes in depositional environments cannot

explain the Ce-T or P-E diversity peaks. To summarize, changes in average depositional setting were much slower than the relatively rapid bursts of diversification and extinction observed in the spore-pollen data.

We echo the Reviewer's concerns about potential biases in the palynological assemblages owing to changes in catchment areas. We have now expanded on this in the Methods (at the line numbers given above), which provides additional context on the dominant depositional conditions and facies in our data compilation, but provide a little more detail on this here. Two points deserve mention, with regard to the distinction between fluvio-lacustrine and marine sediments within our study areas. Firstly, our southeastern Australian record includes a substantial number of sediment core samples from environments interpreted as large (tens of km × up to hundreds of km) rift-valley palaeolakes (Partridge, 2002; Briguglio et al., 2015). In the African context, two of our sources (Cole et al., 2017; Eisawi et al., 2012) are based on analyses of fluvio-lacustrine infills within the Muglad Basin of the Central African Rift System, which was larger still (hundreds × hundreds of km). The SE Australian rift lakes were large enough that Partridge (2002) invoked the Neves effect (a bias towards long-transported grains, typical of some conifers) to explain high Araucariaceae pollen in these rift-lake sediment cores. In other words, these lakes were so large that their compositional biases are analogous to those of offshore marine sediments. We suggest therefore that in our Australian dataset there is no simple continental vs marine difference in palynological transport bias.

Secondly, sediment cores from fluvial settings in our southeastern Australian dataset do include some lenses that represent oxbow lake sediments. The Reviewer's point about small pollen catchment areas could probably be extended to coal lenses, which are also a feature of the region's Cretaceous/Paleogene stratigraphy. However, small lakes within subsiding alluvial plains are individually short-lived features representing a small proportion of the three-dimensional sediment bodies sampled by our data set. Palynologists working in southeastern Australia have usually not singled out these facies for sampling, and have routinely avoided sampling coal facies (because they are difficult to process, generally yield poorly preserved microfossils, and are known to be strongly biased towards local botanical floras). Pollen spectra derived from small lake deposits and coals therefore represent only a small fraction of (typically) multiple samples analysed from each individual sediment core, and each of our palynostratigraphic zones is represented by multiple sediment cores. We therefore believe that the very minor contributions from geologically ephemeral small lakes or coal-forming peats are averaged out in the dataset as a whole. And, as we now discuss in the Methods section, interfingering between terrestrial and near-shore/marginal-marine/deltaic facies is characteristic of the southeastern Australian region over tens of Myr.

4. Diversity and biomass dominance are not correlated. For example, the Sequoia forests in NW North America have a 95% biomass dominance of Sequoia that is represented by only two species. The Sequoia forests also have angiosperms, but they are mostly in the riparian environments associated to small creeks or rivers, representing a tiny proportion of the forest biomass. However, if you assess a species list of the forest, they are dominated by angiosperms. In other words, the forest diversity is dominated by angiosperms while the forest biomass is dominated by gymnosperms. Toward the end of the manuscript, the discussion seems to imply that the record can be interpreted in terms of ecological dominance. That is not correct. To say anything about ecological(biomass) dominance, abundance data needs to be quantified, and the analysis presented in the manuscript did not. Therefore, the discussion needs to remove comments about ecological dominance.

We are grateful to the Reviewer for pointing out where we have let our guard down on this question. We have revised what we believe is the offending paragraph (the second last paragraph of the discussion, lines 348-369 of the tracked changes version of the manuscript) to make less strong claims, while maintaining our key point in that paragraph – which is that our results provide no evidence to support for the claim that loss of old lineages at the K-Pg boundary allowed the final rise to dominance of angiosperms.

5. The structure of the cohort survivorship is very peculiar and it suggests that Cenozoic and Cretaceous floras are quite different. It would be very informative to run a Sørensen Cluster analysis to evaluate changes in palynofloral composition across the entire record. I think the cluster results will be very informative.

We apologise for the confusion. Supplementary Figure 1 presents the results of a stratigraphically constrained, hierarchical clustering of the composition of each palynostratigraphic zone (but because it is 21 pages long, we had placed this Figure in the ‘data’ files, a link to which had been provided in the Acknowledgments). We now place Supplementary Figure 1 in an explicit Supplementary Figures pdf file. The hierarchical cluster analysis divides the record into three discrete stratigraphic intervals. We now highlight those ‘palynofloral intervals’ in Fig. 2.

To clarify, the cohort survivorship analysis refers to individual spore-pollen ‘species’, which do indeed exhibit rather high rates of turnover. This clearly does not always imply wholesale changes within the botanical flora (e.g., various *Nothofagidites* spp. come and go, but *Nothofagidites*, and its probable parent plant, *Nothofagus*, persists). The only alternatives seem to be to run the cohort analysis (i) on spore-pollen ‘genera’, or (ii) on the presumed botanical affinities of the spore-pollen species. The first option is unworkable because it would produce nonsense results in which unrelated botanical lineages are conflated (e.g., in uninformative genera such as *Tricolporites*). The second option would require a layer of botanical inference which we feel adds an unreasonable degree of uncertainty, particularly for the Cretaceous and early Paleogene. We hope that the point of the cohort survivorship analysis comes through, which is that rare episodes of especially pervasive turnover are coordinated in time and across the major land plant groups. We have added a few sentences to the Supplementary Discussion, which summarise these points (lines 2155-2162 of the tracked changes version of the manuscript)

6. Lastly, I could not find either the data or the R code that was used to run the analysis. This is very important; the data needs to be published along with the manuscript (in a repository as Dryad, for example), so anybody can replicate the analysis. This is a must.

Again, we apologise for the confusion! These data, including our R code to run statistical analyses and generate the figures, was included in the Supplementary Data file, a web link to which was included in the Acknowledgements. The data and R script file are now available through links in the ‘Data availability’ and ‘Code availability’ sections.

Responses to Reviewer #3’s comments

- I think it is an important original contribution and of high significance. The authors largely focus on the hyperthermals as a way to overthrow the old "gradualism" argument in angiosperm diversification. However, I think the focus in many Northern Hemisphere and equatorial paleofloral records is the role of the K-Pg boundary in reorganizing floras globally. I support the author's view that climatic events are probably a much more important role for floral organization and that floras are resilient to ecological disturbance, but I think this part is somewhat understated and could be expanded upon.

We thank the Reviewer for their support and encouragement. We have now included an additional concluding statement at the end of the manuscript that reflects the primacy of greenhouse phases in floral evolutionary history, and we have re-focused the penultimate paragraph to more narrowly discuss the lack of support in our datasets for major transformation of plant biomes across the K-Pg transition.

Below, the Reviewer raises questions on two related themes: (i) the purpose and value of comparing our results from high palaeolatitudes with analyses from two low-latitude/equatorial regions; and (ii) whether we should compare our results with an analysis of land plant diversification in New Zealand,

published by Prebble et al., 2021. The Reviewer articulates both questions under two different headings (*Data & methodology*, and *Suggested improvements*). Below we reproduce the Reviewer's two questions, but then respond to each theme separately.

Data & methodology: validity of approach, quality of data, quality of presentation

the data came from various sources. It was especially well sourced from Australia, which makes sense, because that's where the authors are from. The two other records seem a bit haphazard. Missing the New Zealand record (especially considering James Crampton was mentioned in the acknowledgments) seems like somewhat of an oversight and perhaps a broader net could be cast to show that these results are truly indicative of a global signal.

and,

Suggested improvements: experiments, data for possible revision

I am unsure about how the combined African and Colombian palynological records support the argument here. Yes, the C-T diversification peak is captured in the African records as well (as an aside, check the consistency of the abbreviations used here especially fig 5. shouldn't this be the Ce-T transition?), but the break in the record at the K-Pg boundary is awkward. And if we consider the combined Colombian - African record continuous, then it rather shows a dramatic turnover at the K-Pg boundary, and none at the Paleocene - Eocene. The K-Pg record from Carvalho et al. 2021 (cited in the manuscript) is continuous, why not use that to extend the South American record into the Cretaceous?

- Not cited in the paper is the work of Prebble et al. 2021: A 100 million year composite pollen record from New Zealand shows maximum angiosperm abundance delayed until Eocene. This seems like a very relevant record, providing an appropriate comparison to the SE Australian record. Certain significant events identified in the Prebble et al. 2021 seem to overlap with the SE Australian ones. This record provides an opportunity for a very similar analysis as the authors did for SE Australia, but if not analyzed, it should at the very least be discussed.

Reviewer's theme 1: The incorporation of equatorial sites in our analysis

In response to the Reviewer's query about our rationale, we have now added a clarifying explanation in the fourth paragraph of the main text (line numbers 71-73 of the tracked changes version of the manuscript), so that it now says (new passage in italics):

"Because plant diversification patterns in this high-latitude setting may not be representative of the Earth as a whole, particularly under the warmest greenhouse climate states, we compare the Australian compilation with an analogous dataset of palaeo-equatorial Cretaceous fossil pollen floras from northeastern Africa, and with previously published analyses of Cenozoic floras from the Neotropics"

Our underlying rationale in comparing our high palaeolatitude results with equatorial diversity changes was articulated in the section '***Synchronous high- and low-latitude turnover of land plant floras***' (lines 226-232):

"Low-latitude Cretaceous climates have frequently been interpreted as being hot and arid, possibly even lethal for many organisms {Hay, 2012 #9271;Judd, 2024 #9206;Scotese, 2025 #9276}, which would restrict positive diversification responses to extreme greenhouse conditions (as shown for southeastern Australia) to cooler and wetter high latitudes. Therefore, to test the global synchronicity of major diversification episodes, we compared our high-latitude dataset with low-latitude spore-pollen datasets: the Cretaceous of northeastern Africa, and the Cenozoic of the Neotropics"

In other words, we were testing the hypothesis that diversification under the warmest climates might have occurred only at high latitudes, not in the tropics.

In the Methods, we have clarified the important point that the two low-latitude regions we focus on represent the very best documented and longest equatorial spore-pollen records available, globally. We now write (under ‘*Low-latitude data sets*’, lines 696-701 of the tracked changes version)

“We exhaustively searched the global palynological literature for low-latitude regions that would support quantitative, Cretaceous-Cenozoic spore-pollen diversity analyses analogous to those we have generated from our southeastern Australian data set. The only suitable Cretaceous record was the northeastern African region, which straddled the equator during the Cretaceous (Extended Data Fig. 1)”.

We have reinforced these sections to clarify and emphasise that the incorporation of these two low palaeolatitude regions means that our inferences do not just apply to mid-high latitudes.

The Reviewer comments on the awkward temporal break between the African Cretaceous data and the Neotropical Cenozoic data: the two records separate at the K-Pg transition, inhibiting a clean interpretation of tropical plant diversity, and perhaps giving a misleading impression of an abrupt increase in origination rate across the K-Pg boundary. We also regret this artefact of presentation, but it reflects the limitations of these two low-latitude data sets: the quantitative NE African spore-pollen literature simply does not extend into the Cenozoic; de la Parra & Benson’s (2025) published Neotropical sampling-standardised originations dataset that we reproduce simply does not extend back further than 63.5 Ma. The two datasets almost, but not quite, meet at the K-Pg boundary (to make this clearer, we have reinforced the point at lines 742-744 of the tracked changes version of the manuscript: “Because the published northeastern African spore-pollen record does not extend into the Paleogene...”). In Figure 5, we have further tried to draw attention to the independence of the African and Neotropical datasets by adding a statement in the Figure caption: “*Note that each region’s origination curve has its own y-axis, and that the two datasets do not overlap across the K-Pg transition*”, and we have coloured each region’s y-axis label to match the colours of their bar graphs.

For the Neotropics, the reviewer asks the reasonable question, why we did not use the Carvalho et al. (2021) data to extend Jaramillo’s Cenozoic Neotropical analysis into the Cretaceous? That was in fact our immediate hope, when the Carvalho et al. paper was published in 2021, because the 2021 Carvalho et al. Neotropical spore-pollen data extends between 73 to 57 Ma, while the 2006 Jaramillo et al. Neotropical spore-pollen data extends from ca. 65 to 20 Ma. Unfortunately, we ultimately realised that in the time between the publication of Jaramillo et al. (2006) and Carvalho et al. (2021), Carlos Jaramillo’s Smithsonian research group made profound strides in their identification and naming of Neotropical spore-pollen species diversity. Thus, the 2021 Carvalho et al. dataset contains more than twice as many spore and pollen taxa as the 2006 Cenozoic Jaramillo et al. dataset, making it impossible (at least for us) to integrate these two datasets, because they are based on different species concepts. We therefore turned to the de la Parra & Benson (2025) dataset which provides a single, cohesive palynological analysis of the Neotropical Cenozoic. De la Parra & Benson did not provide raw data, and we have merely extracted statistical summaries of the shareholder quorum subsampling gap-filler origination rates matrix that they provide as part of the Supplement to their paper, and binned that data into 3-Myr bins.

In summary, our rationale for comparing our high-latitude, southeastern Australian spore-pollen diversity analyses with data from two palaeo-equatorial regions is to examine if the diversity patterns we see at high latitudes are replicated at low latitudes. Insofar as they are, the comparison allows us to argue that those patterns must have been driven by climatic processes that operated on global, rather than merely regional, scales. In the absence of that comparison, our high-latitude data could be interpreted as providing evidence of processes operating only at high latitudes.

One additional clarification: the Reviewer suggests that no turnover is visible at the Paleocene-Eocene transition, in the de la Parra & Benson (2025) data. The Cenozoic curve we illustrate in Fig. 5a is de la Parra & Benson's "sampling-standardised gap-filler originations". This is not a turnover metric, but one of the origination metrics introduced by Alroy (2014, 'Accurate and precise estimates of origination and extinction rates', *Paleobiology*). After a period of relatively few originations in the mid-Paleocene, that curve does show an interval of enhanced originations during the late Paleocene-early Eocene.

Finally, we are grateful to the Reviewer for noticing that "C-T" is confusing because we abbreviate Coniacian as 'C'. We now use "Ce-T" throughout.

Theme 2: The Prebble et al. analysis of the New Zealand spore-pollen record

We have carefully studied Prebble et al. (2021; 'A 100 million year composite pollen record from New Zealand shows maximum angiosperm abundance delayed until Eocene', published in *Palaeogeography, Palaeoclimatology, Palaeoecology*), which was built on the Clowes et al. (2021) data compilation. We have not ignored the paper. We had already cited Prebble et al. in our supplementary material, but believe that the utility of that paper is limited by its emphasis on results from proportional (e.g., percentage) data and by poor data control.

We have modified the statement in the Methods, at the end of the '**Study Areas and Fossil Database/SE Australia**' section, to now say, "*To our knowledge, only one other study⁹², an analysis of the New Zealand spore-pollen flora, has interpreted changes in regional plant diversity over the past 100 Myr or more, based on sampling-standardized analyses. That study recovered major transitions during the Turonian and early-mid Eocene, with little turnover across the K-Pg transition. However, the authors did not undertake a rigorous assessment of the stratigraphic or nomenclatural integrity of their spore-pollen occurrences, which has substantive implications for the reliability of the analytical results.*" (lines 687-693 of the tracked changes version of the manuscript)

Prebble et al. (2021) acknowledge that:

"there may remain mis-identifications, inconsistent taxonomic concepts, and biases arising from artefacts of sampling, such as down-hole caving in cuttings samples. We present these data as they appear in the database, with no verification of individual occurrences. As a consequence, these data are suitable for interpretation of trends and long term floral changes. It is less appropriate to determine precise taxonomic first and last occurrences" (p. 2).

We are reluctant to criticise the Prebble et al. paper in detail in our manuscript, but in order to fairly evaluate the Prebble data set, over the past month we have undertaken preliminary analyses of their time-binned species matrix (their supplementary table 4), applying our data-quality filters to some of their data. In our southeastern Australian data set, we omitted incomplete spore-pollen species names (e.g., *Araucariacites* sp.) when ≥ 1 well-formed binominal of the genus also occurs in the data set (e.g., *Araucariacites australis*), though we allowed incomplete names when they were the only representative of their genus in the data set. Applying this rule to the 1053 names in the Prebble data set, we found 327 incomplete names, 182 of which we would have omitted if they were had been in our data sets. We also found 145 allowable incomplete names in their data set, but we would have omitted 68 of these based on our other quality filters: these were (i) the species is reworked from the pre-Cretaceous; (ii) the species is recorded in the form of a botanical genus name where the data set also includes a corresponding palynostratigraphic name; (iii) the species is merely mapped at a different taxonomic rank from equivalent taxa in the data set; or (iv) the species is a synonym of another species in the data set. We also find that of the 327 incomplete names, at least 19 are reworked pre-Cretaceous species. Thus, we find that at least 250 (182 + 68) out of 1045 spore-pollen names should be omitted from Prebble's dataset prior to analysis (24%); and that reworked species represent $19/327 = 6\%$ of the incomplete names. If this 6% can be extrapolated to the data set as a whole (we did

not analyse the entire list of names, only the incomplete names), this suggests that ca. 63 of the 1045 species are reworked species.

In contrast, because our main goal was to explicitly determine precise taxonomic first and last occurrences, we expended considerable effort in cleaning our dataset: we sought out and removed misidentifications, dubious names, and synonyms by careful examination of an extensive literature, and we sought out and omitted many instances of caving and reworking, determined again by iterative study of a large literature over several years. Because of the danger that cuttings samples represent to stratigraphic integrity, we ultimately decided to omit cuttings samples entirely, basing our analysis on core samples only. We have expanded the explanation of our procedures for cleaning spore-pollen species names, in the Methods section (lines 641-645 of the tracked changes version of the manuscript).

Based on our summary analyses outlined above, we are reluctant to engage deeply with Prebble et al.'s results in our manuscript, because we believe that an important feature of our dataset is the care we took in curating/cleaning it.

Moreover, several key conclusions by Prebble et al. (2021) rely on proportional (e.g., percentage) data. In our manuscript, we emphasize the limitations of using proportional data for drawing robust conclusions on causation of observed floristic trends. This is owing to well-known artefacts of using proportional abundance data; e.g., compositional effects, whereby an increase in one group necessarily results in the relative decreases of all other components, regardless of whether there is a causal link between them (Pawlowsky-Glahn and Egozcue, 2006). Hence, the analyses of such data can lead to spurious correlations (Jackson, 1997). Instead, we exclusively utilize absolute (and standardized) species richness for drawing any causal links between the observed trends and predictor variables.

We acknowledge that Prebble et al.'s analysis of the New Zealand spore-pollen record provides an interesting lens through which to view the effects of climate on long term floristic trends, and constitutes a parallel 'natural experiment' to the Australian history. However, New Zealand had a similar latitudinal trajectory as southeastern Australia since the mid-Cretaceous, which makes its history much less 'orthogonal' to southeastern Australia's, compared to the two tropical regions included in the manuscript. We have added a sentence in the Methods (lines 689-690 of the tracked changes version, "That study recovered major transitions during the Turonian and early-mid Eocene, with little turnover across the K-Pg transition"), acknowledging the similarities of their results to ours, with caveats about their lack of data quality control. We especially emphasize that in both SQS analyses the curves for each land plant group are independent, not being reliant on closed sums.

- Working with such a large dataset, the authors were faced with various problems of how to perform the statistics. I'm not of the illusion that there is a single good answer to what decisions are best in a meta-analysis. The authors left a very clear paper trail about how to replicate their results, so in my opinion the work is sound

- I see no reason to reject the authors conclusions based on the data and analysis.

We thank the Reviewer for their supportive comments.

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508 **email from Catherine Walker**

509 **From:** plants@nature.com <plants@nature.com>
510 **Date:** Wednesday, 28 January 2026 at 8:47 pm
511 **To:** Kale Sniderman <kale.sniderman@unimelb.edu.au>
512 **Subject:** [EXT] Decision on Nature Plants submission NPLANTS-250920960

513
514 28th January 2026

515
516 Dear Dr Sniderman,

517
518 Your Article, "Extreme greenhouse warmth triggered the two major floristic turnover events of the
519 past 120 million years" has now been seen by two referees. I'd once again like to apologise for the
520 length of time your manuscript has been under review. We were waiting for comments from a third
521 referee but given that the two reports we have a similar level of enthusiasm for your work we are
522 happy to proceed with just those two reports.

523
524 As you will have seen already, referee #2 is supportive of your study and believes it makes an
525 excellent contribution towards understanding plant evolution at a global scale. They have however
526 identified a number of ways to improve the robustness of your analysis which essentially include the
527 assessment of the contribution of precipitation dynamic, solar insolation and sedimentary facies in
528 your analysis. Another issue that they raise is the need to make the R data available in aid of
529 reproducibility. Referee #3 is also enthusiastic about your work, believing it to be a highly significant
530 and original contribution to the literature. They do suggest however that a broader net could be cast
531 over data records to show that these results are truly indicative of a global signal and also suggest
532 including the work of Prebble et al. 2021, which contains a similar analysis to the one run in your
533 study.

534
535 As discussed previously, we also received some informal comments from a referee unable to provide
536 a full report and ask that you write a short, separate response to those informal concerns for the
537 editorial team then we can make a decision on whether we think we would need to escalate those
538 concerns to the other referees.

539
540 You will see from their comments below that while they find your work of interest, some important
541 points are raised. We are interested in the possibility of publishing your study in Nature Plants, but
542 would like to consider your response to these concerns in the form of a revised manuscript before
543 we make a final decision on publication.

544
545 We therefore invite you to revise your manuscript taking into account all reviewer and editor
546 comments. Please highlight all changes in the manuscript text file.

547
548 We are committed to providing a fair and constructive peer-review process. Do not hesitate to
549 contact us if there are specific requests from the reviewers that you believe are technically
550 impossible or unlikely to yield a meaningful outcome.

551
552 When revising your manuscript please:

553
554 * Include a "Response to referees" document detailing, point-by-point, how you addressed each
555 referee comment. If no action was taken to address a point, you must provide a compelling

argument. This response will be sent back to the referees along with the revised manuscript.

* If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at <http://www.nature.com/nplants/info/final-submission>. Refer also to any guidelines provided in this letter.

* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

...

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Plants or published elsewhere.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

Sincerely,

Catherine Walker
Editor
Nature Plants

Reviewers' Comments:

Reviewer #2 (Comments for the Author):

The manuscript analyzes the palynological record of SE Australia over the past 125 million years to understand patterns of plant diversity and its drivers. This is an excellent study that makes use of a unique resource, several decades of palynological studies in SE Australia that span a long stratigraphic interval. There are very few regions on Earth with the time span and taxonomic consistency of the SE Australian record. The manuscript compiled decades of studies in a single database with ~140K records, a major task in itself.

SE Australia has not been static over geological time, starting at ~65 S in the early Cretaceous until its modern position, ~37 S. Several variables can play a role in explaining its palynological record, including local temperature, meridional temperature gradient, solar insolation, precipitation, connectivity with large continental areas, and lithofacies.

The manuscript explored the variables related to temperature and connectivity (local, meridional gradient, and connectivity) and found a positive and significant correlation between two major peaks of global warming and origination/extinction (mid Cretaceous and the Early Eocene warming). Then, the analysis compared the results with the North East African Cretaceous palynological record and the Cenozoic neotropical record, finding similar patterns. As both regions were far apart from SE Australia, the manuscript concludes that the warming-origination/extinction is a global phenomenon and probably driven by temperature, although the direct causation is still unknown.

The analysis uses the standard methods for this kind of metaanalysis (standardization for sampling intensity, cohort survivorship, standing diversity, and percapita origination/extinction). The correlations with the different variables, including the local SST from planktonic foraminifera oxygen isotopes, the meridional temperature (gradient from 10 S to 60 S), and the distance to the nearest continent, support the interpretations, although additional analysis are required (see below).

The manuscript is well written, easy to follow, and it will be an excellent contribution toward understanding plant evolution at a global scale. However, I would like to see a few points addressed as follows:

1. Solar insolation is $\sim 214 \text{ W/m}^2$ at 65 South while it is 349 W/m^2 at 35 South. That is not a minor difference that can have implications on photosynthesis (length of sun hours throughout the year and the quality of the light). However, the analysis does not consider it as a variable with explanatory value. It should include it, or at least, tell us why it can be dismissed.

2. Precipitation plays a major role in a biome's evolution, especially during global warmings, as water stress can move a forested biome to a grassland/low-stature biome. I am aware that metrics for precipitation are hard to produce in the fossil record, but at least a qualitative assessment of precipitation would be useful. For example, features of the sedimentary record could be used as proxies for precipitation, e.g., the proportion of coal versus evaporites in every bin.

3. Sedimentary facies are barely addressed, although they could play a major role in the diversity record. This can be more pronounced when long spans of geological time are analyzed. For example, the palynological diversity of a shallow marine environment could be higher than a fluvial environment because several rivers can deliver sediments to a bay, thus capturing a much larger signal of the vegetation compared to the local signal of an oxbow lake associated to a river. This is very similar to the lake-size effect on diversity; the larger the lake, the larger the palynological diversity, as the source area is larger. What if the high diversity levels of the Turonian are just a taphonomic effect? The Turonian has the highest eustatic sea level since the early Cretaceous, with a rise of ~ 250 meters that covered extensive lowland areas all over the world, giving rise to many epicontinental seas. A fluvial setting converting into a shallow sea could increase the palynological diversity. Even the opposite could happen, for example, the Turonian high sea level produced an epicontinental sea all along South America and in many of its sedimentary sequences the Turonian is represented by black shales that are fully dominated by cyanobacterial masses (South American Turonian rock are one of the richest oil source rocks in the world), and it is very hard to find pollen and spores in palynological sample as they are very diluted by the cyanobacterias. The result: there are many last palynomorph appearances at the top of the Cenomanian that are probably just an edge effect due to taphonomy (plants are in the Turonian somewhere else, but we cannot record them because of the lithofacies). Therefore, the diversity analysis needs to filter out the taphonomic effect. For example, the dataset could be split into two groups: a group where samples are fully terrestrial (not a single dinoflagellate) and a group with everything else. Then, the whole analysis would be done again. The African dataset needs a similar approach as the Cretaceous eustatic sea level had a major influence in the sedimentary record of NE African.

4. Diversity and biomass dominance are not correlated. For example, the Sequoia forests in NW North America have a 95% biomass dominance of Sequoia that is represented by only two species. The Sequoia forests also have angiosperms, but they are mostly in the riparian environments associated to small creeks or rivers, representing a tiny proportion of the forest biomass. However, if you assess a species list of the forest, they are dominated by angiosperms. In other words, the forest

diversity is dominated by angiosperms while the forest biomass is dominated by gymnosperms. Toward the end of the manuscript, the discussion seems to imply that the record can be interpreted in terms of ecological dominance. That is not correct. To say anything about ecological(biomass) dominance, abundance data needs to be quantified, and the analysis presented in the manuscript did not. Therefore, the discussion needs to remove comments about ecological dominance.

5. The structure of the cohort survivorship is very peculiar and it suggests that Cenozoic and Cretaceous floras are quite different. It would be very informative to run a Sørensen Cluster analysis to evaluate changes in palynofloral composition across the entire record. I think the cluster results will be very informative.

6. Lastly, I could not find either the data or the R code that was used to run the analysis. This is very important; the data needs to be published along with the manuscript (in a repository as Dryad, for example), so anybody can replicate the analysis. This is a must.

This is a very interesting manuscript that deserves publication

Carlos Jaramillo

Reviewer #3 (Comments for the Author):

Summary of the key results

- Sniderman and colleagues present a >100 million year long palynological record compiled from southeastern Australia. They compile the diversity records to make an assessment of the major angiosperm diversification events in that timespan and correlate it to local and global climatic records. They find that these origination events are largely related to hyperthermals and independent of biotic interactions, or other abiotic events, most notably the K-Pg boundary. They also include comparisons to some low latitude records, which they argue show support for the Australian record being largely representative of patterns globally.

Originality and significance: if not novel, please include reference

- I think it is an important original contribution and of high significance. The authors largely focus on the hyperthermals as a way to overthrow the old "gradualism" argument in angiosperm diversification. However, I think the focus in many Northern Hemisphere and equatorial paleofloral records is the role of the K-Pg boundary in reorganizing floras globally. I support the author's view that climatic events are probably a much more important role for floral organization and that floras are resilient to ecological disturbance, but I think this part is somewhat understated and could be expanded upon.

Data & methodology: validity of approach, quality of data, quality of presentation

- the data came from various sources. It was especially well sourced from Australia, which makes sense, because that's where the authors are from. The two other records seem a bit haphazard. Missing the New Zealand record (especially considering James Crampton was mentioned in the acknowledgments) seems like somewhat of an oversight and perhaps a broader net could be cast to show that these results are truly indicative of a global signal.

Appropriate use of statistics and treatment of uncertainties

- Working with such a large dataset, the authors were faced with various problems of how to

perform the statistics. I'm not of the illusion that there is a single good answer to what decisions are best in a meta-analysis. The authors left a very clear paper trail about how to replicate their results, so in my opinion the work is sound.

Conclusions: robustness, validity, reliability

- I see no reason to reject the authors conclusions based on the data and analysis.

Suggested improvements: experiments, data for possible revision

- I am unsure about how the combined African and Colombian palynological records support the argument here. Yes, the C-T diversification peak is captured in the African records as well (as an aside, check the consistency of the abbreviations used here especially fig 5. shouldn't this be the Ce-T transition?), but the break in the record at the K-Pg boundary is awkward. And if we consider the combined Colombian - African record continuous, then it rather shows a dramatic turnover at the K-Pg boundary, and none at the Paleocene - Eocene. The K-Pg record from Carvalho et al. 2021 (cited in the manuscript) is continuous, why not use that to extend the South American record into the Cretaceous?

- Not cited in the paper is the work of Prebble et al. 2021: A 100 million year composite pollen record from New Zealand shows maximum angiosperm abundance delayed until Eocene. This seems like a very relevant record, providing an appropriate comparison to the SE Australian record. Certain significant events identified in the Prebble et al. 2021 seem to overlap with the SE Australian ones. This record provides an opportunity for a very similar analysis as the authors did for SE Australia, but if not analyzed, it should at the very least be discussed.

References: appropriate credit to previous work?

- Yes, notwithstanding the Prebble et al. 2021 paper. Although I also understand how that was overlooked.

Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

- Yes, thankfully the authors are experienced writers and structured their paper well. I kept the PDF open to make minor comments, like spelling and styling suggestions, but never had to make any.

end of 28 January email from Catherine Walker

15 January email from Catherine Walker

From: Catherine Walker <catherine.walker@springernature.com>

Date: Thursday, 15 January 2026 at 4:50 am

To: Kale Sniderman <kale.sniderman@unimelb.edu.au>

Subject: [EXT] Re: Manuscript NPLANTS-250920960 update

Dear Kale

I just wanted to give you an update on your manuscript as I realise it has been under review for much longer than we would have hoped. Before Christmas, we had an issue with dropped out referees and unfortunately it is very difficult to find replacements over that time period. We have received one formal review which I have attached (see below) just so you can get an idea of how your manuscript has been reviewed so far and we are now waiting on two more which we hope will come by the end

of the month. We also received a set of informal comments from someone unable to provide a full report which I think will be of interest as they have some suggestions for improving methodology and have also been pasted below. If we are able to make a decision on the basis of two formal reports then we will as this has been a much longer peer review process than we would ever like! Apologies for this but I really do hope we can come back to you with a decision within the next two weeks.

All the best

Catherine

==

Comments from Referee #1 (informal comments only)

This paper sounds very interesting. However, the authors are using sampling standardisation and this is a really bad idea:

<https://www.authorea.com/users/363764/articles/1289948-coverage-based-rarefaction-does-not-quantify-species-richness>

They should be using extrapolated richness values based on compound abundance distribution models:

<https://onlinelibrary.wiley.com/doi/10.1111/ele.70181>

It would be essential for the authors to address the following study, which uses questionable Bayesian methods and literature-based, occurrence-scale instead of specimen-scale, and genus-level data that are uninformative about the actual species-level diversification pattern:

<https://www.pnas.org/doi/abs/10.1073/pnas.2005571117>

Better turnover rate estimators are discussed here:

<https://www.cambridge.org/core/journals/paleobiology/article/abs/accurate-and-precise-estimates-of-origination-and-extinction-rates/AB73EA51B6748D3843199A8A0D6B1603>

These methods were used alongside Bayesianism in a closely related palaeobotanical study:

<https://www.science.org/doi/10.1126/science.abf1969>