nature research

Peer Review File

Manuscript Title: Environmental drivers of megafauna and hominin extinction in Southeast Asia

Editorial Notes:

Redactions – Mention of other journals

This document only contains reviewer comments, rebuttal and decision letters for versions considered at *Nature*. Mentions of the other journal have been redacted.

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referee #1 (Remarks to the Author):

I was excited by this submission, which quantifies savanna / forest history in southeast Asia from the Pleistocene to the present, using stable isotope analysis of mammalian dentition as a proxy. The authors found that early Pleistocene forests were replaced by grassland in the middle Pleistocene, creating faunal turnover and altering mammalian distributions, prior to the expansion of rainforest in the late Pleistocene and Holocene. The use of stable isotope data to provide a comparable (but see comments below) set of data to track vegetation change, in the absence of well-stratified and detailed vegetation records, is elegant. The contribution is likely to be of broad interest to the Nature readership, partly because it is rare to see such a clear summary of major vegetation trends (a significant element of the work) but also because it makes an important contribution to understanding human evolution and dispersal in the region, as well as makes some incredibly pertinent points about conservation of current fauna. I think this is suitable for Nature as it represents a breakthrough in our understanding of the broad history of the Indochinese and Sundaland region in the context of mammalian evolution. Although other studies have addressed this for different areas, this contribution gives broad geographic coverage supported by empirical detail and evidence.

The approach, as I mention above, is elegant, and highly appropriate, and the presentation of high quality. Indeed, the manuscript is exceptionally well written and clear (the only aspect that was confusing was the last sentence of figure caption 1). The Introduction and context is good, and gives appropriate credit and citation to previous work on the subject, notwithstanding the word limit.

The sampling and lab work seem to have been of sufficiently high quality, and the statistical tests (including sample sizes) appropriate for the questions asked.

I do have a query, however, about the comparability of data: in the Methods, the authors state that different studies use different pre-treatment methods, and I think it would be valuable to give a clearer statement about whether that introduces significant 'noise'. Looking at the data, I think that variation due to pre-treatment method is probably small compared to the clear overall trends, but it would be good if the authors verified that. Similarly, I could not see a detailed statement about taphonomic issues - if specimens from different periods are sampled from different sites, or different types of sites (e.g. cave versus open), how does that influence the fauna represented and

their isotope signatures? Apologies if I have missed this somewhere in the supplementary, but if I have missed it, others will too, and so a clearer statement is needed. Another issue relates to corrections used on the data. A standard offset of 1.5 per mil is used for 'modern' specimens, which is often used and not 'wrong', but I encourage the authors to consider correction using the atmospheric δ13C values from Graven et al. (2017; their supplementary Table 1) differentiated according to collection date, as their supplementary data show wide collection dates for modern specimens (and Graven et al. (2017) show a change in slope in the late 1950s). Again, given the big differences evident in the groups from different time bins, the relatively small changes to values resulting from the use of a variable offset is unlikely to make any difference to the overall conclusions, but it may serve to improve the perception of the paper's rigour.

I sum, I very much enjoyed this stimulating and important contribution, which makes a step change in our understanding of the 'big picture' of human evolution and dispersal in southeast Asia.

Referee #2 (Remarks to the Author):

This is a fascinating paper that suggests a long term ecological change in SE Asia over the past 2 million years. Overall, the paper is well written and presents a very interesting idea that will, no doubt, be the subject of additional studies to test the robust nature of the conclusions. In view of that, I think the main thing the authors should do is explicitly recognize how they have grouped vast periods of time into convenient groups: Early Pleistocene, Middle Pleistocene, Late Pleistocene, and Holocene. These actually represent the time intervals from 2.5to 0.8 Myr; 0.8 to 0.13 Myr; 130,000 to 10,000 years ago; and 10,000 years ago to present. The earliest period was a time were the climate cycles were dominated by the 20,000 and 40,000 year Milankovitch cycles; the Middle Pleistoence exhibited a number of glacial-interglacial cycles; the Late Pleistonce included only one glacial-interglacial cycle; and the Holocene represents only a single interglacial interval. Comparisons of these vastly differing scales, some of which include many glacial-interglacial intervals, requires at least a paragraph or more acknowledging this issue.
The above is my only substantive comment. Excellent, thought provoking paper!

Referee #3 (Remarks to the Author):

This is a review of the manuscript Environmental drivers of megafauna and hominid extinction in Southeast Asia.

A. The paper uses stable isotope data to infer vegetation changes in Southeast Asia, across the Pleistocene, and compares these with the disappearance of megafauna and hominid species.

I reviewed this paper from the perspective of my own expertise, which is in the field of paleoclimatology and stable isotope geochemistry. I must conclude that the paper is not suitable for publication in its present form. I will not go into details, and instead just briefly explain my major concern.

C.The study completely lacks a discussion of chronological constraints. Chronological constraints are however crucial for the inferred conclusions. Table 1 lists approximate ages of different fossil sites. It appears that for several of these sites it is unclear if the samples are of glacial or interglacial age, the age uncertainties are large. This is problematic. The time period discussed (Early to Late Pleistocene) is characterised by large global scale climatic changes at orbital time scales. Vegetation changes within the late Pleistocene are documented for many regions at glacial interglacial scale, and in particular in the low latitudes at the precession scale. These time scale are much shorter than the age uncertainty of the samples. I guess (this is not really explained in the manuscript at all) that the authors assume that the four sample clusters presented in figure 2

are representative for a long term average climate state, i.e. averaged over glacial-interglacial time periods. However, it seems possible that some of the clusters may be biased towards a glacial, or e.g. a precession maximum and another cluster biased towards an interglacial or a precession minimum. If that would be the case any inferences about the longer term evolution of the climate / vegetation in this region.

In general I am missing a a broader context of the global climate evolution of the region. The others could for example present long continuous climate records from the region for comparison (or at least some records that serve as an example for the long term global climate evolution, e.g. the Lisiecki Raymo benthic oxygen isotope stack. They could then show their samples and reconstructions in this global climate context.

Author Rebuttals to Initial Comments:

Response to Reviewers

We would like to thank the Reviewers for their immensely encouraging and helpful comments in relation to our manuscript. It was a pleasure to read three Reviews that made highly constructive comments that, we believe, have improved our paper. We have addressed each and every one of the comments and suggestions raised as can be seen in the detailed point by point list below.

Referee #1 (Remarks to the Author):

I was excited by this submission, which quantifies savanna / forest history in southeast Asia from the Pleistocene to the present, using stable isotope analysis of mammalian dentition as a proxy. The authors found that early Pleistocene forests were replaced by grassland in the middle Pleistocene, creating faunal turnover and altering mammalian distributions, prior to the expansion of rainforest in the late Pleistocene and Holocene. The use of stable isotope data to provide a comparable (but see comments below) set of data to track vegetation change, in the absence of well-stratified and detailed vegetation records, is elegant. The contribution is likely to be of broad interest to the Nature readership, partly because it is rare to see such a clear summary of major vegetation trends (a significant element of the work) but also because it makes an important contribution to understanding human evolution and dispersal in the region, as well as makes some incredibly pertinent points about conservation of current fauna. I think this is suitable for Nature as it represents a breakthrough in our understanding of the broad history of the Indochinese and Sundaland region in the context of mammalian evolution. Although other studies have addressed this for different areas, this contribution gives broad geographic coverage supported by empirical detail and evidence.

We thank Referee 1 for their incredibly encouraging positive and comments. We are delighted that they feel our contribution will be of significant interest to the broad readership of *Nature* and, like us, believe our research makes a considerable step in our understanding of human evolution and megafauna extinction in Southeast Asia, with solid empirical detail and evidence. We hope to have addressed their useful suggestions for improving our manuscript further in the following.

The approach, as I mention above, is elegant, and highly appropriate, and the presentation of high quality. Indeed, the manuscript is exceptionally well written and clear (the only aspect that was confusing was the last sentence of figure caption 1). The Introduction and context is good, and gives appropriate credit and citation to previous work on the subject, notwithstanding the word limit.

We are glad the Referee found our methodology elegant, appropriate, and well presented, and also enjoyed reading our manuscript. We have now removed the last sentence of Figure 1 which was not necessary, to remove the issue of confusion raise by the Referee.

The sampling and lab work seem to have been of sufficiently high quality, and the statistical tests (including sample sizes) appropriate for the questions asked. I do have a query, however, about the comparability of data: in the Methods, the authors state that different studies use different pre-treatment methods, and I think it would be valuable to give a clearer statement about whether that introduces significant 'noise'. Looking at the data, I think that variation due to pre-treatment method is probably small compared to the clear overall trends, but it would be good if the authors verified that.

We thank the Referee for this query. This very question has recently been addressed in detail in Southeast Asia by Jiang et al. (2020), who found minimal effects of different pre-treatments on stable carbon and oxygen isotope values of tooth enamel. We have now added a statement to this effect, citing this study, in our Methods section.

Similarly, I could not see a detailed statement about taphonomic issues - if specimens from different periods are sampled from different sites, or different types of sites (e.g. cave versus open), how does that influence the fauna represented and their isotope signatures? Apologies if I have missed this somewhere in the supplementary, but if I have missed it, others will too, and so a clearer statement is needed.

We thank the Referee for raising the potential issue of taphonomy and diagenetic change. We have now added an explicit statement to the Methods section discussing the potential for taphonomic alteration and an overall appraisal that concludes it is unlikely to be a major factor, though is something, as the Referee quite rightly states, that should be borne in mind. The new text reads as follows:

"$\delta^{13}C$ and $\delta^{18}O$ analysis of fossil tooth enamel has shown to preserve ecological distinctions back into the Miocene[77,78]. The bioapatite of tooth enamel has fewer substitutions, less distortion and larger crystals than that found in bone and dentine, making it more resistant to taphonomic alteration[79,80]. Although we have not been able to check the state of each tooth sampled in the studies we have compiled, a number of studies have studied the potential for taphonomic change in fossil enamel in hydrologically active tropical settings using chemical and physical analysis[14,81]. They found limited alteration to fossil enamel structure in both open air and cave contexts in South and Southeast Asia dating back to the Pleistocene and concluded there was no reason to assume alteration to the $\delta^{13}C$ and $\delta^{18}O$ values. Furthermore, several studies from which the compiled data were taken applied similar approaches to demonstrate taphonomic integrity[65,73,76]".

Another issue relates to corrections used on the data. A standard offset of 1.5 per mil is used for 'modern' specimens, which is often used and not 'wrong', but I encourage the authors to consider correction using the atmospheric δ13C values from Graven et al. (2017; their supplementary Table 1) differentiated according to collection date, as their supplementary data show wide collection dates for modern specimens (and Graven et al. (2017) show a change in slope in the late 1950s). Again, given the big differences evident in the groups from different time bins, the relatively small changes to values resulting from the use of a variable offset is unlikely to make any difference to the overall conclusions, but it may serve to improve the perception of the paper's rigour.

We thank the referee for this useful comment. We have applied the Graven et al. (2017) correction suggested and compared it to our original corrected dataset. As the referee surmised, these were statistically indistinguishable, lending confidence to our use of these values. We have added a section to the methods outlining this.

I sum, I very much enjoyed this stimulating and important contribution, which makes a step change in our understanding of the 'big picture' of human evolution and dispersal in southeast Asia.

We are delighted that the Referee enjoyed our article and found it stimulating and important. We hope that we have now satisfied their concerns and excellent suggestions.

Referee #2 (Remarks to the Author):

This is a fascinating paper that suggests a long term ecological change in SE Asia over the past 2 million years. Overall, the paper is well written and presents a very interesting idea that will, no doubt, be the subject of additional studies to test the robust nature of the conclusions.

We thank Referee 2 for their positive and supportive comments in relation to our manuscript. We are glad they found it well written, interesting, and likely to stimulate significant further work in the area.

In view of that, I think the main thing the authors should do is explicitly recognize how they have grouped vast periods of time into convenient groups: Early Pleistocene, Middle Pleistocene, Late Pleistocene, and Holocene. These actually represent the time intervals from 2.5to 0.8 Myr; 0.8 to 0.13 Myr; 130,000 to 10,000 years ago; and 10,000 years ago to present. The earliest period was a time were the climate cycles were dominated by the 20,000 and 40,000 year Milankovitch cycles; the Middle Pleistoence exhibited a number of glacial-interglacial cycles; the Late Pleistonce included only one glacial-interglacial cycle; and the Holocene represents only a single interglacial interval.

Comparisons of these vastly differing scales, some of which include many glacial-interglacial intervals, requires at least a paragraph or more acknowledging this issue.

The above is my only substantive comment. Excellent, thought provoking paper!

We thank Referee 2 for bringing to our attention a point we had perhaps not sufficiently explored in our original manuscript, namely the uneven distribution of sites in the Pleistocene of Southeast Asia, and how this may have affected our results. A similar point was raised by Referee 3. In order to address these points, we have conducted an additional analysis which examines the stable carbon and oxygen isotope values, not grouped by geological period, but rather by dividing the Pleistocene into even bins of time. This allows us to examine changes in forest cover independently of geological classification that are tightly linked to climatic cycles. This additional analysis revealed the same pattern we observed in our original manuscript, highlighting the robustness of our results. However, it has represented an important additional step, as both Referees highlighted, in solidifying our methodology and interpretations, so we thank them both for this suggestion.

The text describing this process reads as follows:

"*The Quaternary is characterised by large global scale climatic changes at orbital time scales, and each epoch and sub-epoch samples vastly different temporal scales and includes different numbers of glacial/interglacial cycles. Thus, grouping sites by geological group may mask or extenuate vegetation trends that are not reflective of the past 2.6 million years. Moreover, most sites in Southeast Asia are (i) derived from Late Pleistocene cave deposits, so there is unevenness in temporal sampling across the Quaternary, and/or (ii) have poor constraints on their geological ages, such that major vegetation changes could occur on a shorter timescale than the uncertainty of the ages of the sites. In order to examine long term trends in* $\delta^{13}C$ *and* $\delta^{18}O$ *through the Quaternary, for sites with published age estimations (Extended Table 5), we calculated the average* $\delta^{13}C$ *and* $\delta^{18}O$ *values across all taxa for each site. Next, we assigned each site to successive time bins of equal duration spanning the Pleistocene. We examined time bins under three different geochronological scenarios related to the range of ages available for each site: (i) the minimum age of the site; (ii) the median age; and (iii) the maximum age. The number of time bins equalled the smallest division of the Quaternary that included at least one site in each bin. This resulted in seven bins of 321 ka duration for minimum ages; six bins of 428 ka for median age; and five bins of 513.8 for maximum ages. We applied a Locally Weighted Scatterplot Smoothing Spline*[93,94] *with a smoothing factor set at 0.9. The 95% confidence interval for the curve was based on 999 random replicates using resampling of residuals*[92]*. We compared our results to the Lisiecki Raymo benthic oxygen isotope stack*[95] *adjusted to the same temporal scale."*

Referee #3 (Remarks to the Author):

This is a review of the manuscript Environmental drivers of megafauna and hominid extinction in Southeast Asia. The paper uses stable isotope data to infer vegetation changes in Southeast Asia, across the Pleistocene, and compares these with the disappearance of megafauna and hominid species. I reviewed this paper from the perspective of my own expertise, which is in the field of paleoclimatology and stable isotope geochemistry. I must conclude that the paper is not suitable for publication in its present form. I will not go into details, and instead just briefly explain my major concern.

The study completely lacks a discussion of chronological constraints. Chronological constraints are however crucial for the inferred conclusions. Table 1 lists approximate ages of different fossil sites. It appears that for several of these sites it is unclear if the samples are of glacial or interglacial age, the age uncertainties are large. This is problematic. The time period discussed (Early to Late Pleistocene) is characterised by large global scale climatic changes at orbital time scales. Vegetation changes within the late Pleistocene are documented for many regions at glacial interglacial scale, and in particular in the low latitudes at the precession scale. These time scale are much shorter than the age uncertainty of the samples. I guess (this is not really explained in the manuscript at all) that the authors assume that the four sample clusters presented in figure 2 are representative for a long term average climate state, i.e. averaged over glacial-interglacial time periods. However, it seems possible that some of the clusters may be biased towards a glacial, or e.g. a precession maximum and another cluster biased towards an interglacial or a precession minimum. If that would be the case any inferences about the longer term evolution of the climate / vegetation in this region.

We thank Referee 3 for this excellent comment, which echoes the comment made by Referee 2. As detailed above, we have conducted a further, detailed additional analysis. In order to examine Pleistocene trends in forest cover that explicitly acknowledges the impact of age constraints, the imprecision of the fossil record, and the clumping of sites, we have now re-examined stable carbon and oxygen isotope values in time bins of equal duration spanning the Pleistocene. We examined the dataset under three different scenarios: the first using the minimum age of the sites, the second the median age, and the third the maximum age of the sites. These three scenarios encompass the absolute range of the different fossil sites and are not dependent on the geological sub-epoch assigned to the site. We acknowledge that they do not reveal vegetation changes at the precession scale, however, the aim of our paper is to examine broad trends, spatially and temporally, in vegetation in the Quaternary of Southeast Asia, as these are the changes that would impact hominins and megafauna evolution and dispersal. Our new analyses all recover the same trends that we originally observed in our data, providing additional strong support that we are discussing an important characteristic of Pleistocene Southeast Asia. However, we do thank Referees 2 and 3 for suggesting this addition which, we agree, has made our results and interpretation much stronger.

The text added highlighting this new analysis is as described above.

In general I am missing a broader context of the global climate evolution of the region. The others could for example present long continuous climate records from the region for comparison (or at

least some records that serve as an example for the long-term global climate evolution, e.g. the Lisiecki Raymo benthic oxygen isotope stack. They could then show their samples and reconstructions in this global climate context.

We thank Referee 3 for this very useful comment. As a result of this comment, as well as to address a similar point made by Referee 2, we have added the following additional paragraph to the Main Manuscript relating to global climate evolution in the region:

"*These observed shifts have major implications for understanding hominin and broader mammalian biogeography in the region and are consistent with global Quaternary climate models indicating a significant change at the mid-Pleistocene transition. A shift from low amplitude 41,000 yr to high amplitude 100,000 yr cycles between 1.25 Ma and 700 ka were accompanied by significant decreases in sea surface temperatures, increases in ice volume, and heightened Asian aridity and monsoonal intensity*[26]*. The change in glacial cycles, recorded in the benthic oxygen isotope record, coincides with our observed peak in* $\delta^{13}C$ *and* $\delta^{18}O$ *values in Southeast Asian mammals (Extended Figure 2). Under a high amplitude, 100,000 yr glacial cycle, savannahs began to give way to forests. This process was further impacted at 400 ka by the subsidence of the Sunda shelf*[27]*. This event significantly reduced exposed land and thus decreased albedo, in turn leading to increased atmospheric convention and regional rainfall*[28]*. Our data shows an accelerated decrease in* $\delta^{13}C$ *and* $\delta^{18}O$ *at this time (Extended Figure 2A, B), indicating a continued trend towards more favourable conditions for forests.*"

We have also added the Lisiecki Raymo benthic oxygen isotope stack to Extended Figure 2, comparing it to our data, and discuss it in the above paragraph.

Reviewer Reports on the First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

Thank you for your detailed response. I am happy that my comments have been addressed satisfactorily. It was a pleasure to review this paper.

Referee #2 (Remarks to the Author):

The authors have satisfactorily addressed my concerns. This paper should go forward for publication - I look forward to seeing it in print!

Referee #3 (Remarks to the Author):

I am reviewing this manuscript for a second time. I appreciate the efforts of the authors to add a little more paleoclimatic background to the study, which was missing at all in the first version.

My major concern about the study is however still the same. The authors claim that the data shows a clear long-term change in vegetation. I am not convinced that this trend is solid, because too little is know of the individual samples in terms of age control. They study undersamples a long time period with a very large 'short-term' variability (glacial-interglacial and orbital change). It is

not known, or at least not well documented if individual samples represent glacial or interglacial periods. This is essentially like trying to show a temperature trend over the last 2000 years with a dataset from which you do not know which of the data points record temperature during summer which record winter.

I am also still missing references to very relevant studies, that looked at climate and vegetation change in this region across the Pleistocene. Some higher resolution studies document that vegetation changes have taken place at glacial-interglacial transitions. It seems very well possible that each interglacial of the Pleistocene was very similar to the Holocene and that all glacials were dominated by savannah type vegetation, e.g.:

Savanna in equatorial Borneo during the Late Pleistocene

Christopher M. Wurster, Hamdi Rifai, Bin Zhou, Jordahna Haig & Michael I. Bird
Scientific Reports volume 9, Article number: 6392 (2019)

Another relevant study that is also not mentioned is the following:

Interglacial Hydroclimate in the Tropical West Pacific Through the Late Pleistocene
A. N. Meckler1,2,*, M. O. Clarkson3, K. M. Cobb4, H. Sodemann5, J. F. Adkins1
[REDACTED]08 Jun 2012: Vol. 336, Issue 6086, pp. 1301-1304
DOI: 10.1126/[REDACTED].1218340

This study also suggests that the interglacial conditions in Borneo were very similar to each other over the Pleistocene.

In summary, I am unfortunately still not convinced at all, that the presented data set gives us a clear picture of how the vegetation changed over the Pleistocene. The conclusions are not robust. The only way forward in my view is to present a lot more paleoclimatological context of the region in question, and place the new dataset into this context.

Author Rebuttals to First Revision:

Response to Reviewers

We would like to thank the Reviewers once again for their immensely helpful feedback. We have addressed each of the comments and suggestions in the detailed point by point list below. The additional comments provided by Referees 1 and 2 regarding Referee 3's feedback are included in our response to Referee 3.

Referee #1 (Remarks to the Author):

Thank you for your detailed response. I am happy that my comments have been addressed satisfactorily. It was a pleasure to review this paper.

We are delighted that Referee 1 is satisfied with our changes.

Referee #2 (Remarks to the Author):

The authors have satisfactorily addressed my concerns. This paper should go forward for publication - I look forward to seeing it in print!

We share Referee 2's sentiments! We're happy we were able to address their concerns.

Referee #3 (Remarks to the Author):

I am reviewing this manuscript for a second time. I appreciate the efforts of the authors to add a little more paleoclimatic background to the study, which was missing at all in the first version.

We again thank the referee for this suggestion, which we agree has improved our manuscript.

My major concern about the study is however still the same. The authors claim that the data shows a clear long-term change in vegetation. I am not convinced that this trend is solid, because too little is know of the individual samples in terms of age control. They study undersamples a long time period with a very large 'short-term' variability (glacial-interglacial and orbital change). It is not known, or at least not well documented if individual samples represent glacial or interglacial periods. This is essentially like trying to show a temperature trend over the last 2000 years with a dataset from which you do not know which of the data points record temperature during summer which record winter.

We agree with Referees 1 and 2 that Referee 3 makes a fair point regarding the limitations imposed by the dating constraints. Although we consider it incredibly unlikely that biases could explain the patterns we observe, we agree that exploration of why that might be warrants further discussion. As Referee 1 indicates, these constraints are due working in this part of the world with these types of records. They suggested adding more discussion on sampling and taphonomy biases. Referee 2 suggested that dealing with this comment might simply require an even more direct acknowledgement of the issues related to dating. Finally, the Editor suggests adding a paragraph noting the possibility of systematic bias raised by Referee 3, including stating the extreme, and discuss what this might mean. We have followed all three suggestions, and have added the following paragraph to the methods in order to address this concern:

"Most sites in Southeast Asia are derived from Late Pleistocene cave deposits, so there is unevenness in temporal sampling across the Quaternary, and/or they have poor constraints on their geological ages. At the extreme, geochronological constraints of these vertebrate deposits make it impossible to exclude the possibility that the fossils are sampling dry or wet states in some unexpected way, such that the patterns we observe could represent artefacts of taphonomic or sampling biases rather than broad environmental changes. Taphonomic bias could result from a restriction of fossil accumulation in caves to dry phases, as has been observed in South Africa for example[96]. Sampling bias could include the collection or analysis of only certain taxa from deposits. However, the possibility that the

pattern we observe is artefactual can be discounted for several reasons. First, regarding taphonomy, low $\delta^{13}C$ values are recovered from samples from both cave and open-air sites (e.g. Baxian and Cipeundeuy, respectively), and equally, higher $\delta^{13}C$ values have are also recovered from both types of sites (e.g. Khok Sung and Pha Bong). Second, regarding sampling, several taxa, including the most commonly represented in our dataset (i.e. bovids and cervids), span the range of $\delta^{13}C$ values of rainforest and savannah. Third, taphonomic and sampling biases would need to be structured in such a way that they provide a peak in $\delta^{13}C$ values at the beginning of the Middle Pleistocene. There are no structural biases in Middle Pleistocene sites that would differentiate them from Early and Late Pleistocene sites in this way. More importantly, the patterns we observe are fully consistent with major climatic changes in Southeast Asia reported by other proxies."

We then discuss the climatic changes in the next paragraph (see below).

I am also still missing references to very relevant studies, that looked at climate and vegetation change in this region across the Pleistocene. Some higher resolution studies document that vegetation changes have taken place at glacial-interglacial transitions. It seems very well possible that each interglacial of the Pleistocene was very similar to the Holocene and that all glacials were dominated by savannah type vegetation, e.g.:

Savanna in equatorial Borneo during the Late Pleistocene Christopher M. Wurster, Hamdi Rifai, Bin Zhou, Jordahna Haig & Michael I. Bird Scientific Reports volume 9, Article number: 6392 (2019)

Another relevant study that is also not mentioned is the following: Interglacial Hydroclimate in the Tropical West Pacific Through the Late Pleistocene A. N. Meckler1,2,*, M. O. Clarkson3, K. M. Cobb4, H. Sodemann5, J. F. Adkins1 [REDACTED] 08 Jun 2012: Vol. 336, Issue 6086, pp. 1301-1304 DOI: 10.1126/[REDACTED].1218340

This study also suggests that the interglacial conditions in Borneo were very similar to each other over the Pleistocene.

We do not discount these possibilities, and in fact our results are not incompatible with these results. Rather, as indicated by Referee 1, differences in the results of our study and those cited above are ones resulting from differences in scale. In order to clarify this, and to address the comment regarding lack of references to relevant studies, we have included the following paragraph to our methods (as also suggested by the Editor). This includes references to the above studies as well as others.

"The climate in Southeast Asia is governed by the position of the Inter-Tropical Convergence Zone (ITCZ), which determines where precipitation from the East Asian and the Australian-Indonesian monsoons occurs[97]. Changes in the position of the ITCZ during the Pleistocene have significantly impacted regional precipitation patterns and vegetation. The Mid-Pleistocene Transition initiated high amplitude 100,000-year glacial-interglacial cycles that were accompanied by heightened Asian aridity and monsoonal intensity[26], corresponding with the peak in our $\delta^{13}C_{diet}$ values. Following this, at the Mid-Brunhes Event between MIS13 and 11, interglacial conditions in high latitudes became warmer and more comparable to Holocene conditions[98]. However, cave speleothem records from Southeast Asia indicate that neither ITCZ activity nor its position responded to this event[99,100], although quite variable interglacial conditions were recorded. Major changes to the ITCZ are

however observed following deglaciations, where environmental changes linked to the Earth's precession cycle and insolation intensity shifted and trapped the ITCZ in a southern position, precipitating millennia-long intervals of reduced monsoon rainfall[99,100]. Decreasing trends in global glacial ice volume during the Late Pleistocene correspond to decreasing maximum peaks in oxygen isotopes over successive interglacials, explaining the decrease in drier conditions we observe during this time. This would have been accentuated from ~400 ka by the initiation of Sunda shelf subsidence[27]. This reinforces the idea that the broad trends we observe in Southeast Asian vegetation were driven by global-scale climatic changes and regional-scale geological events. Nevertheless, such events can still produce variable conditions locally, for example, the distribution of rainfall in Southeast Asia today is also strongly dependent on topographical relief as well as the position of the ITCZ[97]. This can cause local scale (temporal and/or spatial) environmental heterogeneity that may not be congruent with the larger scale patterns we observe. For example, some palaeoecological records show that patches of both savannah and rainforests were present in Southeast Asia during Late Pleistocene[101-106]. However, their impact on hominin and mammal biogeography must be understood in broader temporal and spatial environmental contexts. It is further worth noting that only palaeoecological records such as ours provide direct insights into the environments actually used by mammals and hominins, as they come from the animals themselves, rather than via indirect proxies."

In summary, I am unfortunately still not convinced at all, that the presented data set gives us a clear picture of how the vegetation changed over the Pleistocene. The conclusions are not robust. The only way forward in my view is to present a lot more paleoclimatological context of the region in question, and place the new dataset into this context.

We trust that what we have added now addresses the major concerns of Referee 3. We thank them for their continued feedback, which has resulted in us refining our arguments and putting them in a broader palaeoclimatological context.

Reviewer Reports on the Second Revision:

Referees' comments:

Referee #3 (Remarks to the Author):

I am seeing this manuscript for a third time now, and while I appreciate the author's efforts in adding some more paleoclimatological context to their study, my main concern is still the same as it was when I read the first version and therefore I must, unfortunately, advise to not publish the presented conclusions.

I have explained it in previous reviews already. The study clusters data with highly uncertain ages and with very different cluster durations. This is problematic and leads to biased results and conclusions due to the large climate (vegetation) variability during the Pleistocene (glacial-interglacial cycles).

One of the clusters (Holocene) is covering a relatively small range of time (less than 10,000 years) while the other clusters, e.g. Mid-Pleistocene, cover a range of several 100,000 years. The Holocene cluster samples exclusively an interglacial period, whereas the other clusters incorporate glacial periods as well. If a long-term evolution of climate/vegetation is studied the individual

cluster should have an equal length. If one cluster samples only one interglacial period and another one samples both glacial and interglacial (or maybe even predominantly glacials) any conclusion about a longterm evolution would be biased.

The authors suggest that there is a longterm trend towards a rainforest dominated vegetation in the Holocene. My alternative hypothesis would be, that each interglacial period of the last 500,000 years has experienced similar vegetation as the Holocene. If a long-term (100,000 year average) is considered, Savannah type vegetation becomes more frequent, due to the increased duration and intensity of glacial periods. So the later Pleistocene is characterized by more variability compared to the Early Pleistocene. The study presents, however, a very different conclusion, while the data cannot rule out the hypothesis that I give.

I still also think, that the study would highly benefit from vegetation studies based on e.g. pollen-based reconstructions in marine sediment cores in the region. The authors could then place all their data into this context and learn something about these mammal sites, rather than trying infer a vegetation record based on their data.

Author Rebuttals to Second Revision:

Response to Reviewers

We would like to thank the Editor and Reviewer 3 for once more providing valuable points for consideration and discussion. We have addressed each of their comments and suggestions in the detailed point by point list below.

Referee #3 (Remarks to the Author):

I am seeing this manuscript for a third time now, and while I appreciate the author's efforts in adding some more paleoclimatological context to their study, my main concern is still the same as it was when I read the first version and therefore I must, unfortunately, advise to not publish the presented conclusions.

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One of the clusters (Holocene) is covering a relatively small range of time (less than 10,000 years) while the other clusters, e.g. Mid-Pleistocene, cover a range of several 100,000 years. The Holocene cluster samples exclusively an interglacial period, whereas the other clusters incorporate glacial periods as well. If a long-term evolution of climate/vegetation is studied the individual cluster should have an equal length. If one cluster samples only one interglacial period and another one samples both glacial and interglacial (or maybe even predominantly glacials) any conclusion about a longterm evolution would be biased.

We understand the Referee's point and agree that the Holocene covers a period significantly different to the Late or Middle Pleistocene. However, we also wish to highlight that it was for this reason, and in response to Referee 3's earlier comments, that we introduced a completely new, additional analysis in our first revision that examined trends in stable isotopes in time bins (or

clusters if one prefers) of equal duration, under three models relating to dating uncertainties of the sites. It is noteworthy that this binned analysis does not suffer from the issue of uneven sampling of time because the bins were specifically chosen such that they were of equal length. Moreover, these bins sample similar numbers of glacial and interglacial periods for the mid to late Quaternary (Model 1 – 5 interglacials in the first bin, 4 in the second; Model 2 – 6 interglacials in the first bin, 5 in the second; Model 3 – 7 in the first bin, 9 in the second).

We are happy to directly acknowledge the limited temporal resolution of many of our samples, as is now explicitly provided in the first paragraph following the Editor's suggestion. However, given that these models produced results congruent with our initial analyses, we are immensely confident that any bias has been mitigated at the temporal scales with which we are examining the data. Indeed, our analyses also agree with the other records that Referee 3 suggested we consult; the key difference that we can track these changes in ecosystems of direct relevance to human and megafauna experience and activity.

The authors suggest that there is a longterm trend towards a rainforest dominated vegetation in the Holocene. My alternative hypothesis would be, that each interglacial period of the last 500,000 years has experienced similar vegetation as the Holocene. If a long-term (100,000 year average) is considered, Savannah type vegetation becomes more frequent, due to the increased duration and intensity of glacial periods. So the later Pleistocene is characterized by more variability compared to the Early Pleistocene. The study presents, however, a very different conclusion, while the data cannot rule out the hypothesis that I give.

We argue that the huge geographic changes that have taken place in Southeast Asia since ~400,000 years ago coupled with decreasing trends in global glacial ice volume during the Late Pleistocene were more important to regional vegetation at the broad temporal and spatial scales we examined than the effects of increasing glacial length or intensity. Nevertheless, we welcome this alternative hypothesis, and agree that current data (not just ours, but all available data) are currently insufficient to rule out either scenario definitively.

We have acknowledged that our analyses are made at broad temporal and spatial scales, meaning that Late Pleistocene variability is not resolved, as can be seen in the following text:
"This can cause local scale (temporal and/or spatial) environmental heterogeneity that may not be congruent with the larger scale patterns we observe. For example, some palaeoecological records show that patches of both savannah and rainforests were present in Southeast Asia during Late Pleistocene[101-108]."

This limit notwithstanding, and as the other two referees have attested, we have provided significant new insights and data related to vegetation trends in Southeast Asia throughout the Quaternary and explored their impacts on hominins and megafauna. We look forward to seeing these hypotheses tested when additional data becomes available.

I still also think, that the study would highly benefit from vegetation studies based on e.g. pollen-based reconstructions in marine sediment cores in the region. The authors could then place all their data into this context and learn something about these mammal sites, rather than trying infer a vegetation record based on their data.

We have added citations on pollen-based reconstructions from marine sediment cores (references highlighted in red text in the revised manuscript), something that we had already also done in response to their last round of comments. However, we feel that with this comment the reviewer has missed the larger point of our study. It is not “to learn something about these mammal sites” – this was already the point of many of the studies from which we gathered data and does not need to be repeated in our manuscript. Rather, the aim of our study was to use the stable isotope data from fossil mammals to reconstruct broad-scale changes in the environments used by those animals, and thereby gain critical new insights into extinction and biogeographical dynamics in this region. We believe that the readers, like Referees 1 and 2, will recognise this and trust that our study will become a landmark point of reference for further work in this regard.