Anonymous Referee #1

We thank the reviewer for the thoughtful comments helping us to improve the manuscript substantially. In the following, we respond to each specific point.

The paper reports on a prominent and unique pollen record from an Indian Ocean core and provides interesting comparisons with relevant other records derived from different sources including proxies from the same core and others like the Vostok Ice core. The paper is in connection with the influence atmospheric CO2 concentrations on eastern Southern African vegetation types and suggests that under the higher concentrations of pCO2 woody plant growth thrives. I can't say I am entirely convinced by the cause and effect arguments that are proposed between pCO2 and other factors like hyrdroclimate and temperature as is acknowledged by the authors, and therefore would suggest a more cautious approach.

We have revised the section about the effects of CO_2 and deepened the discussion. The section now reads as follows:

Effects of atmospheric pCO_2

While the hydroclimate of the region shows precession variability [Caley et al. 2018], the vegetation shows a glacial-interglacial rhythm (Supplementary Information) indicating that besides hydrology, temperature and/or atmospheric CO_2 levels were important drivers of the vegetation development. Combining the results of the pollen assemblages with stable carbon isotopes and elemental information indicates that during interglacials the region of SE Africa (northern South Africa, Zimbabwe, southern Mozambique) was less humid. This is in accordance with other paleoclimate estimates for the region [see reviews by Simon et al. 2015, Singarayer & Burrough 2015]. The interglacial woodlands (represented by E-Woodland, Figure 4) would probably have grown under warmer and drier conditions than the glacial mountain forest (represented by E-Mountain-Forest). The increase in maximum pCO_2 levels during the post-MBE interglacials might have favored tree growth as higher pCO_2 levels would have allowed decreased stomatal conductivity and thus relieved drought stress [Jolly & Haxeltine 1997]. During Interglacials 11c, 9e, 7c, 7e, 5e, and 1, when temperatures and pCO_2 are high, the mountain forest is replaced by woodland (Figure 4). It might be only after interglacial pCO_2 levels rose over ~270 ppmv that Miombo woodland could fully establish in the area during the warm and relatively dry post-MBE interglacials.

The record of mountain forest in SE Africa indicates some extension of moist Podocarpus forest during those parts of the glacial stages with low temperatures and atmospheric pCO_2 exceeding ~220 ppmv (Figure 5). This holds also for the Interglacials 19c, 17c, 15e, 15a, 13a, and 7e, in which pCO_2 and Antarctic temperatures were subdued, too. However, if low temperatures were the only driver of the extension of mountain forests, further spread into the lowlands during the coldest glacial phases should be expected. Instead, when pCO_2 dropped below ~220 ppmv during those colder glacial periods, mountain forest declined, in particular during MIS 18, 16, 14, 8, 6, and 2. A picture emerges of cool glacial stages in SE Africa in which tree cover broke down when atmospheric pCO_2 became too low.

With an inverse modelling technique, Wu et al. [2007] estimated the climate inputs for the vegetation model BIOME4 using the biome scores of pollen records from equatorial East African Mountains as information. Wu et al. found that lowering of the tree line under glacial conditions (1-3°C lower temperatures, less precipitation, 200 ppmv pCO_2) depended hardly on temperature but primarily on increased aridity and somewhat on lower pCO_2, whereby lower pCO_2 amplified the effects of water limitation. However, Izumi & Lézine [2016] found contrasting results using pollen records of mountain sites on both sides of the Congo basin. At any rate, the lack of trees in the Southeast African

Mountains during glacial extremes is unlikely the result of drought, because our record indicates that climate conditions in SE Africa were less dry during glacials than during interglacials (the post-MBE interglacials in particular). Instead, C4 sedges increased during glacials when atmospheric pCO_2 and temperatures were low. However, low temperatures are not particularly favorable for C4 sedges as indicated by the altitudinal distribution of C4 sedges in modern wetlands of KwaZulu Natal [Kotze & O'Connor 2000]. We presume, therefore, that the extension of C4 sedges during the more humid phases of the glacials is the result of low atmospheric CO_2 concentrations rather than of low temperatures.

Pollen records of ericaceous vegetation suggest an extensive open vegetation existing in the East African Mountains [e.g. Coetzee 1967, Bonnefille & Riollet 1988, Marchant et al. 1997, Debusk 1998, Bonnefille & Chalié 2000] and in SE Africa and Madagascar [e.g. Botha et al. 1992, Scott 1999, Gasse and Van Campo 2001, Scott & Tackeray 1987] during the last glacial. In our study, ericaceous fynbos-like vegetation (E-Heathland) was found for those parts of the glacials having lower (less than ~220 ppmv) atmospheric pCO_2 (Figure 5). Exceptions were found for MIS 12 and 14 when the difference of pCO_2 with that of the preceding stage was small [Bereiter et al. 2015]. Dupont et al. [2011] argued that increase of C4 vegetation as the result of low pCO_2 was unlikely because no extension of grasses was recorded. However, this argument is flawed if sedges dominantly constituted the C4 vegetation in the area. We also note that in many parts of South Africa, no substantial increase of C4 grasses occurred but that many sites suggest an expansion of C3 grasses during the Last Glacial Maximum [Scott 2002].

As climate was wetter during most of the glacial in this part of the world, the question arises about the climatic implication of the ericaceous fynbos-like vegetation (represented by E-Heathland, Figure 5) extending during full glacials over the mountains of South Africa - and correlating with the SST record. The correlation with SST, however, is problematic. Singarayer & Burrough [2015] argued that the control of the Indian Ocean SSTs on the precipitation of South Africa shifted from a positive correlation during the interglacial to a negative correlation during the Last Glacial Maximum. They invoked the effects of the exposure of the Sunda Shelf (Indonesia) and Sahul Shelf (Australia) on the Walker circulation causing a wetter region over the western Indian Ocean but also weaker easterly winds to transport moisture inland. To question the link between SST and precipitation in SE Africa even further, Caley et al. [2018] found that the precession signature in the river discharge proxy [ln(Fe/Ca), see also Supplementary Information] was absent in the SST record made on the same material. SE Africa would have been more humid during glacials when the temperature difference between land and sea increased.

The increase in C4 vegetation during relative cool and humid climate would be in conflict with the idea that C4 plants are more competitive in hot and dry climates [Ehleringer et al. 1997, Sage 2004]. However, this idea is mainly based on the ecology of grasses and the development of savannahs, while the C4 vegetation expansion in SE Africa during cool and humid phases seems to be driven by sedges. A survey of the distribution of C4 sedges in South Africa revealed that those Cyperaceae do not have the same temperature constraints as C4 grass species [Stock et al. 2004]. More important, South African C4 sedges appear to have evolved under wetland conditions rather than under aridity. C4 Cyperus species even occur in the wettest parts of lower altitude wetlands in KwaZulu-Natal [Kotze & O'Conner 2000].

Proxies of these conditions seem to behave in concert but it is not that clear which one is the leading factor and how much they influence each another. Although the role C4 sedges seem to be important, I feel the role of C4 grasses are underplayed (discussed further below).

The grass pollen percentages vary under 20% and that is quite low compared to other marine records adjacent to deserts and savannahs. We, therefore, believe that in the biome fluctuations we do record, grasses are not that important.

This is nevertheless an important study worthy of publication provided that attention is given to the aspects listed below.

Abstract

P1, line 16. If possible, please mention to what degree and on what basis the effects of the factors, hydroclimate, temperature and atmospheric pCO2, can be disentangled.

The disentanglement is rather complex. We argue that (1) the precessional rhythms of river discharge compared to the interglacial-glacial biome variability indicates that hydroclimate cannot be the only driver of vegetation change. The other options of forcing mechanisms on interglacial-glacial time-scales are temperature and pCO_2. (2) Because of the correlation between Cyperaceae pollen percentages and $\delta^{13}C_{wax}$ and the lack of correlation between Poaceae percentages and $\delta^{13}C_{wax}$ in combination with the relatively low grass pollen percentages, we deduce that the C4 plant imprint mainly derives from the sedges. (3) The expansion of C4 sedges during the colder periods of the glacials is unlikely to result from lower temperatures. (4) The confinement of mountain forest to the glacial periods with moderate temperatures and moderate pCO_2, and the lack of extension into the lowlands of mountain forest during the colder periods suggest that low pCO_2 became restrictive to the forest. (5) Based on the elemental composition as a proxy for river discharge, we estimate the post-MBE interglacials as the drier intervals of the sequence. Nevertheless woodland expanded during those periods, which we attribute to increased temperatures and pCO_2.

We feel reluctant to put this rather lengthy list into the Abstract but we incorporate it in the Conclusions section.

P1, lines 17, 18, 19. The statement could provide better insight if it can be more specific, e.g., do these different vegetation categories respond in the same way or differently to pCO2? The word “depended” might have to be reconsidered in view of the above concerns. Please insert (_430 ka) after Mid-Brunhes Event.

We change this part of the Abstract into:

Our results suggest that the extension of mountain forest occurred during those parts of the glacials when pCO_2 and temperatures were moderate and that only during the colder periods when atmospheric pCO_2 was low (less than 220 ppmv) open ericaceous vegetation including C4 sedges expanded. The main development of woodlands in the area took place after the Mid-Brunhes Event (~430 ka) when interglacial pCO_2 levels regularly rose over 270 ppmv.

Introduction

P1, line 24. If subscript is used in pCO2, why not in C4?

If allowed, we’d like to reserve the use of subscripts for the chemical/physical terminology.

P2, line 13. It is unclear what kind of event is meant here.

We rewrite that part of the paragraph as follows:

The climate transition of the MBE has been extensively studied using Earth System Models of Intermediate Complexity. Yin & Berger [2010] stress the importance of forcing by austral summer insolation and Yin & Berger [2012] argue that the model vegetation (tree-fraction) was forced by *precession through precipitation at low latitudes. Both papers show the necessity to include the change in atmospheric CO_2 in the explanation of the MBE [Yin & Berger, 2010, 2012]. Yin [2013], however, concludes that it is not necessary to invoke a sudden event around 430 ka to explain the increased interglacial CO_2; the differences between interglacials before and after the MBE can be explained by individual responses in Southern Ocean ventilation and deep-sea temperature to various combinations of the astronomical parameters.*

P2, line 20. The phrase "to counter" could be seen as ambiguous or is it meant to be "is counter to"?

Bouttes et al. show in their model that the effects of vegetation change run in the other direction and thus counteract the effects of oceanic response. We change “counter” to “counteract”.

Material and Methods

P4, line 29. Does “windows” mean sections? A question arises here why there are two older windows and not one continuous one. Is there a hiatus or another reason?

There is no hiatus; the sedimentation in the core is continuous (see Caley et al. 2018). Just for practical reasons and time constraints, I did not analyse all of the 37.6 m of sediment covering 2.2 million years at 5 ka resolution. The Early Pleistocene parts are shown for comparison with that of the Brunhes Chron, only. Therefore, we call them windows.

P5 line 11. A definition of an endmember would be helpful here to keep the uninitiated reader informed.

We adapt the part of the paragraph as follows:

Additionally, we carried out a multivariate analysis in the form of an endmember model unmixing procedure [Weltje, 1997], the statistics of which are specifically designed for the treatment of percentage data. We regard the pollen percentages as a series of pollen assemblage mixtures, whereby each modelled endmember may be interpreted as a characteristic combination. This linear mixing model can be compared to a ternary diagram but allowing for more than three axes.

P5, line 30. There may be correlation between sedge pollen and leaf wax isotopes but it looks as if there is also correlation with Poaceae pollen (see also below in connection with P9, line 15).

It might look so, but it is not the case. Table 1 shows that there is no significant correlation between Poaceae pollen percentages and $\delta^{13}C_{wax}$. There is a correlation between Cyperaceae pollen percentages and $\delta^{13}C_{wax}$ and despite the correlation between Poaceae and Cyperaceae pollen percentages there is no correlation between Poaceae pollen percentages and $\delta^{13}C_{wax}$.

P6, lines 6,7. Why is this relevant? Won’t one find C4 sedges near any of these African lakes?

The sentence “Thus, fluvial discharge was probably low during interglacials …” is the conclusion of the paragraph that discusses and refutes the possibility of sea-level changes driving the variability seen in Cyperaceae pollen values and Fe/Ca ratios.

P6, lines 19,20. I can’t see why this is remarkable. In my experience dry conditions result in less ground cover hence relatively more woody elements.

We drop the phrase: “It is remarkable that”. However, we do not think we see encroaching of woody vegetation in a grassy environment. Less ground cover and encroaching would have occurred under much drier conditions, in which case we would have seen a decrease of relatively high Poaceae pollen percentages and an increase of pollen percentages representative for shrubland and desert. This is not the case for the post-MBE interglacials when E-woodland shows maximum values. We see a change from E-Heathland to E-Woodland at the last glacial-interglacial transition and a change from E-Mountain-Forest to E-Woodland in the transitions to interglacial conditions of MIS 11c, 9e, 7e, and 5e. Only during interglacial 7a, a peak of E-shrubland is recorded.

Endmembers representing vegetation on land

P6, line 23. In connection with the three endmembers, the reader would by now have seen from Figure 3 that there are 4 endmembers. Therefore, I suggest saying "characterized initially". The word “so-called” should have been used when endmembers were first mentioned. A table in the text with the most prominent constituents of the endmembers will make it easier to understand the significance without having to go and look in the supplements.

Thank you for the suggestion. We insert “initially” and drop “so-called”. A clarification of the terminology endmember is now given in the Material and Methods section.

However, we refrain from adding a table to the main text. The supplementary tables are far too big to include in the text. A selection would do no more than illustrate the text of the section “Endmembers representing vegetation on land”. Only the full data set of the supplementary tables allows the reader to check whether we made a reasonable selection.

P7, line 2. Must be “endmember’s”?

Yes, done.

P7, line 3. This “one endmember” is a little confusing. Say which one or say: one endmember had a counterpart in EM2.

Thank you; we change the text according your suggestion.

P7. Line 15. What kind of extremes?

We change the sentence into: “The fractional abundance of the E-Mountain-Forest is also high in glacials of the Brunhes Chron but not during the extreme glacial stages, when temperatures and pCO_2 are particularly low (Figure 3).”

P7, line 30. “wide range woodland taxa” like Combretaceae? I see this important taxon in not mentioned except in the supplements.

Yes, Combretaceae fit into E-Woodland. We add “such as Combretaceae species” after “wide-range woodland taxa”.

P8, line 8. This may be seen as ambiguous if "developed" is taken as originated. Did miombo not start much earlier? Effects of atmospheric pCO2

Sure, Miombo woodland would have originated outside the region. We change the sentence into: “It is likely that the Miombo dry forest and woodland migrated into the region in the successive interglacials of the Brunhes Chron.”

P9, line 15. Surely some C4 grasses also thrive under relatively moist conditions if it is not too cold. Seasonality or growing season moisture is a factor which was not evaluated enough in the paper. Is it not possible that apart from C4 sedges, certain C4 Poaceae also played a role? On high land, frost and winter seasonality might be a factor ruling out C4 grasses in favour of C3 grasses or small shrubs, but as long as there are summer rains and subtropical Africa is warm enough during the glacial periods, which will probably be the case on the low-lying coastal platform, C4 grasses will be supported. It might be worthwhile to consider Vogel’s work on the distribution of C3/C4 grasses in Southern Africa in this study. There are also some arguments in this connection in Scott (2002).

It is somewhat speculative to deduct changes in seasonality from our data. Most taxa comprising E-Woodland are adapted to seasonal climates with summer rainfall. Changes from mountain forest to woodland might suggest increase in seasonality. However, increase in seasonality would not decrease river discharge. Many elements of E-Heathland nowadays grow under winter rainfall. However, to propose a winterrain climate as far north as Mozambique during glacials is unrealistic and not supported by other paleodata or modelling studies.

Our Poaceae pollen percentages are relatively low and do not fluctuate with the $\delta^{13}C_{wax}$. We do not doubt that there have been C4 grasses but do not think that C4 grasses played a major role in the fluctuations we see. We add “We also note that in many parts of South Africa, no substantial increase of C4 grasses occurred but that many sites suggest an expansion of C3 grasses during the Last Glacial Maximum [Scott 2002].” at the end of the paragraph starting with “Pollen records of ericaceous vegetation suggest an extensive open vegetation existing in the East African Mountains…” (see also the revised text of the section “Effects of atmospheric $p\mathrm{CO}_2$”, above).

The revised manuscript showing all changes is uploaded as supplement.

On behalf of Thibaut Caley and Isla Castañeda

Lydie Dupont

Vogel, J.C., Fuls, A., Ellis, R.P., 1978. The geographical distribution of Kranz grasses in South Africa. S. Afr. J. Sci. 74, 209- 215.

Scott, L. 2002. Grassland development under glacial and interglacial conditions in Southern Africa: review of pollen, phytolith and isotope evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 177(1-2): 47-57.