Response to reviewer #2, Sarah Ivory.

We thank Sarah Ivory (anonymous reviewer #2) for the thoughtful comments helping us to improve the manuscript substantially. In the following, we respond to each specific point.

The manuscript by Dupont et al. uses pollen assemblages and other multi-indicator data from a marine sediment core in order to look at vegetation and climate change in southeastern Africa over multiple glacial-interglacial cycles. They extend a previously published dataset to 800k and also include analysis of older mid and early Pleistocene sections in order to disentangle the effects of temperature, precipitation, and pCO_2 on vegetation.
I find this paper to present a very well done and important dataset from a data-sparse region of the tropics. I am really happy to see the pollen analyses extended to older sections of the core and appreciate the data-rich multi-indicator approach. I also support the end-member analysis conducted by the authors, which seems to be able to be used to tease apart assemblages through time. I also really appreciate the comparison of the carbon isotope data with pollen data, which I find enhances the interpretations from both datasets.
I do however have a few concerns about the paper, these are mostly minor. In particular, I find that the main conclusions about pCO_2 and its impact on vegetation over time is a bit thinly supported. No further data analysis supports this argument and in fact I find that the section which describes the patterns attributed to CO_2 is very brief given the prominence of this driver in the abstract of the paper. My most pressing suggestion for improvement of this paper then is to further develop this section of the paper and perhaps include a plot showing major vegetation types under differing CO_2 thresholds discussed. The wiggle plots which represent the bulk of this argument in Figures 4 and 5 are not sufficient for really teasing apart the impact of CO_2 or illustrating the authors' interpretation.

We have revised our discussion about the effects of CO_2 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 as information the biome scores of pollen records from equatorial East African Mountains. 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].*

We added frequency analysis of the XRF ln(Fe/Ca) and Cyperaceae pollen percentages in the Supplementary Information (trailing this response).

We also adapted Figures 4 and 5 to highlight our interpretation.

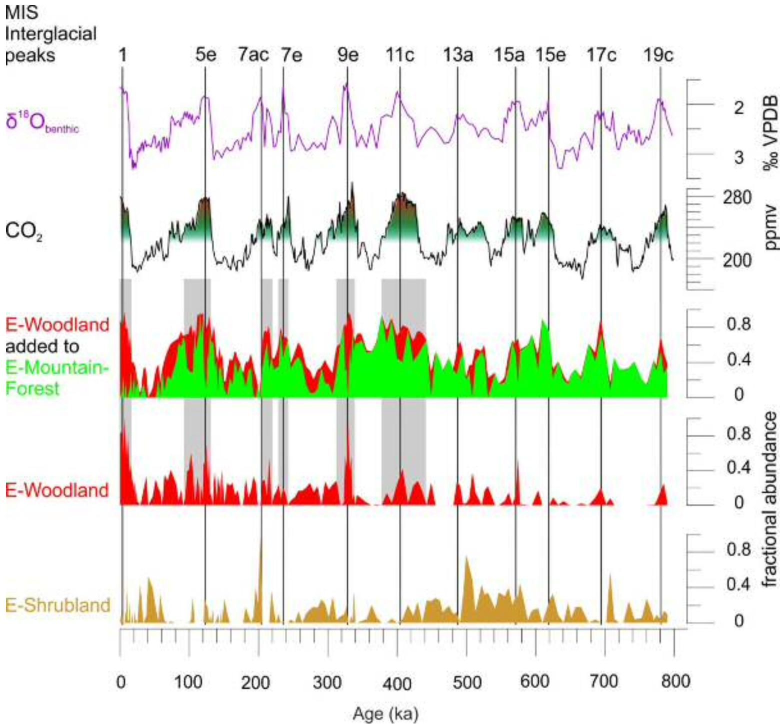

Figure 4: Comparing pollen assembages E-Mountain-Forest, E-Woodland and E-Shrubland with atmospheric CO_2 [Bereiter et al. 2015, PAGES 2016]. On top Interglacial peaks of the past 800 ka [PAGES 2016] and stable oxygen isotopes of benthic foraminifera ($\delta^{18}O_{benthic}$) of MD96-2048 [Caley et al. 2011]. CO_2-levels of 220 and 270 ppmv are indicated with green-red shading. Grey shading highlight periods with maximum atmospheric CO_2 and maximum values of the sum of E-Woodland and E-Mountain-Forest. VPDB: Vienna Pee Dee Belemnite.

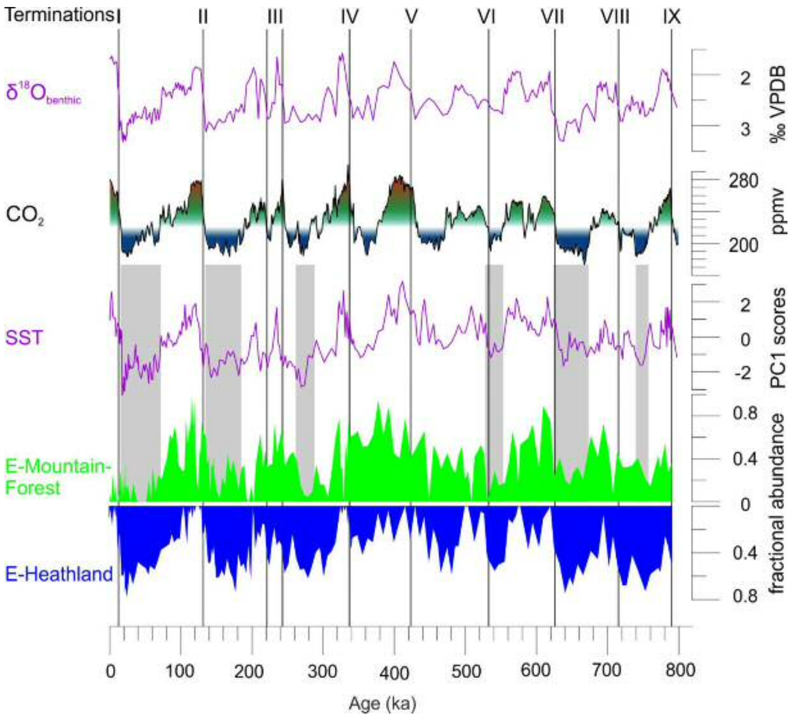

Figure 5: Comparing glacial pollen assembages E-Mountain-Forest and E-Heathland with atmospheric CO_2 [Bereiter et al. 2015, PAGES 2016] and sea surface temperatures of the southeatern Indian Ocean (SST PC1 scores of MD96-20468) [Caley et al. 2018]. On top Terminations of the past 9 glacacions and stable oxygen isotopes of benthic foraminifera ($\delta^{18}O_{benthic}$) of MD96-2048 [Caley et al. 2011]. CO_2-levels of 220 and 270 ppmv are indicated with blue-green-red shading. Grey shading highlight periods with minimum atmospheric CO_2, minimum values of E-Mountain-Forest, and maximum values of E-Heathland. VPDB: Vienna Pee Dee Belemnite.

Page 1

-Please switch to sequential line numbering for the whole paper, rather than per page, if that fits with journal formatting.

It is the CP-format…

Line 26: I think this isn't quite accurate, because C4 vegetation is by its very nature arid adapted in that C4 metabolism is an adaptation to increase water use efficiency. I think instead you should change this sentence to imply that the risk misinterpreting the bioclimatic controls on the expansion of arid adapted vegetation.

We do not agree that all C4 vegetation is by its very nature arid adapted. In C4 grasses the C4 metabolism may be an adaptation to water use efficiency but certainly not in *Cyperus* species that grow in wetlands. Stock et al. (2004) write in their introduction concerning C4 photosynthesis in South African Cyperaceae: “that C4 photosynthesis probably evolved under wetland conditions for species of the genus *Cyperus* and that the ecological success of the group in infertile wetlands is a consequence of the high nitrogen use efficiency associated with the C4 pathway.” see also Li et al. (1999).

Nevertheless, we agree that the sentence “Comparing this open C4 rich vegetation with modern analogues would have led to an interpretation of the occurrence of arid adapted vegetation.”

should be rephrased, which we do as follows:

Comparing records of this glacial C4-rich vegetation with modern analogues could have led to estimating more severe aridity than actually occurred during the Last Glacial Maximum.

-Which studies?

The studies cited before. We insert [opt cit.]

Also this phrasing is awkward, I think "last Glacial-interglacial transition" or Pleistocene-Holocene transition might be better

Yes, thank you. We change “Glacial Holocene” to “last glacial-interglacial transition”

Line 27: “Glacial” glacials?

No, we mean Early Glacial: MIS 5a-d. We should have capitalized ‘Early’. We adapt the text accordingly.

Page 2

Line 4: “cycle” should be cycles

Done

Line 11: Yin and Berger, what did they find?

Line 11-12: This sentence is confusing, I am unclear if they are still talking about causes of the MBT or if they are now talking about drivers of vegetation change

We rephrase 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. On the other hand, statistical analysis suggests a dominant role of the carbon cycle, which changed over the MBE [Barth et al. 2018].

Line 23: This sentence doesn't quite make sense as is.

Yes, we drop the second half of the sentence, which now reads: “Comparing records of pre- and post-MBE interglacials could offer insight in the interglacial climate at different levels of CO_2 [Foley et al. 1994, Swan et al. 2010].”

Line 28: Castaneda and Johnson refs, These two are not pollen records, as stated above. Should also add Bosumtwi pollen record maybe.

We change pollen records into vegetation records. We add the Bosumtwi record as suggested. However, we dropped the El'gygytgyn record because we realized that no interglacials of the early Brunhes Chron were analyzed in detail. We add the ODP Site 658 record instead.

The paragraph reads now as follows:

Comparing records of pre- and post-MBE interglacials could offer insight in the interglacial climate at different levels of CO2 [Foley et al. 1994, Swan et al. 2010]. We define interglacials after PAGES [2016] listing MIS 19c, 17c, 15a, 15e, 13a as pre-MBE and MIS 11c, 9e, 7e, 7a-c, 5e, 1 as post-MBE. Currently, only a handful of vegetation records covering the entire Brunhes Chron have sufficient temporal resolution to enable comparisons between interglacials before and after the Mid-Brunhes transition. These records are from the eastern Mediterranean, the Colombian Andes [PAGES 2016], West and East Africa [Dupont et al. 1989, Miller & Goslin 2014, Castañeda et al. 2016, Johnson et al. 2016, Ivory et al. 2018, Owen et al. 2018]. The Andean pollen record is strongly influenced by the immigration of oak from North America during MIS 12 [Torres et al. 2013]. For the eastern Mediterranean a decline in plant diversity is observed at Tenaghi Phillipon (Greece) where the modern Mediterranean oak forests gradual emerged in the interglacials after MIS 16 but before the MBE [Tzedakis et al. 2006, 2009]. The West African record of Lake Bosumtwi in Ghana allows identification of six forest assemblages since 540 ka related to the interglacials of MIS 13, 11, 9, 7, 5e, and 1. The forests assemblage of MIS 13, however, does not show a strong contrast with those of the interglacials after the MBE [Miller & Goslin 2014]. The marine pollen record of ODP Site 658 off Cape Blanc tracks the latitudinal position of the open grass-rich vegetation zones at the boundary between Sahara and Sahel suggesting shifting vegetation zones between glacials and interglacials [Dupont & Hooghiemstra 1989, Dupont et al. 1989]. The drier interglacials occurred after MIS 9, which indicates a transition after the MBE to more arid conditions. Additionally, stable carbon isotope records from Chinese loess sections indicate interglacial-glacial variability in the C3-C4 proportions of the vegetation [Lyu et al. 2018, Sun et al. 2019]. However, the latter records do not show a prominent vegetation shift over the MBE.

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Line 23: impacts on Southern Hemisphere, why is this?

According to the modelling study of Yin & Berger (2010), the seasonal distribution of insolation is such that the Southern Hemisphere receives more summer insolation during the post-MBE interglacials which enhances the effect of higher $p\mathrm{CO}_2$. We change the sentence as follows:

We might expect a change of Southern Hemisphere vegetation being less ambiguous than the changes found on the Northern Hemisphere (see above), because modelling indicates that the effects of the MBE were more pronounced on the Southern Hemisphere [Yin & Berger 2010].

Line 30: what are the bergwinds and how do we know that they don't transport much materials?

The bergwinds might transport some material from the northern part of the Drakensberg, which would bring pollen from the same area as the rivers do draining the escarpment and the Lembombo Hills.

Page 5

Line 25: Is this referring to δDwax?

Yes, but as the terminology turns up only twice and only in referring to another study, we refrain from introducing the abbreviation.

Page 6

Line 7: represented, not presented

Done

Lines 17-19: low sediment transport could also be because of less erosion with denser vegetation and root networks, rather than drier conditions. Maybe some discussion of seasonality, particularly as regards the expansion of woodland could be useful.

We doubt that a change from mountain forest to woodland or from heathland to woodland would have decreased erosion. We have little indication of biomes that imbed erodible bare soils with the possible exception of E-Shrubland, which has the higher values in the early Pleistocene.

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.

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Lines 11-12: what is the evidence for this?

We want to draw attention to the different paces of vegetation and river discharge as shown by the fluctuations of E-Heathland, in particular. We added in the Supplementary Information spectral analyses of XRF ln(Fe/Ca), E-Heathland fractional abundances, and Cyperaceae pollen concentration (see also above).

Line 15: elemental not element

Done

Line 27: what is the physiological mechanism here? miombo is more drought adapted, you would think the opposite might be true?

We do think that Miombo is better drought adapted than the mountain forest or the coastal forest and probably also better drought adapted than a fynbos-like vegetation. However, we don't understand the question because the hypothesis is about the effect of enhanced pCO_2 during interglacials.

Page 9

Line 31: development of what?

We mean Lake Magadi. We change the beginning the the prargraph as follows:

The trend to increased woodland in SE Africa after the MBE, noted at both Lake Malawi and in the Limpopo River catchment [Johnson et al. 2016, Caley et al. 2018, this study] contrasts with the trend *around Lake Magadi at the equator. At Lake Magadi a trend to less forest around marks the Mid-Brunhes transition [Owen et al. 2018].*

The revised manuscript showing all changes is uploaded as supplement.

On behalf of Thibaut Caley and Isla Castañeda

Lydie Dupont

ADDITIONAL REFERENCES

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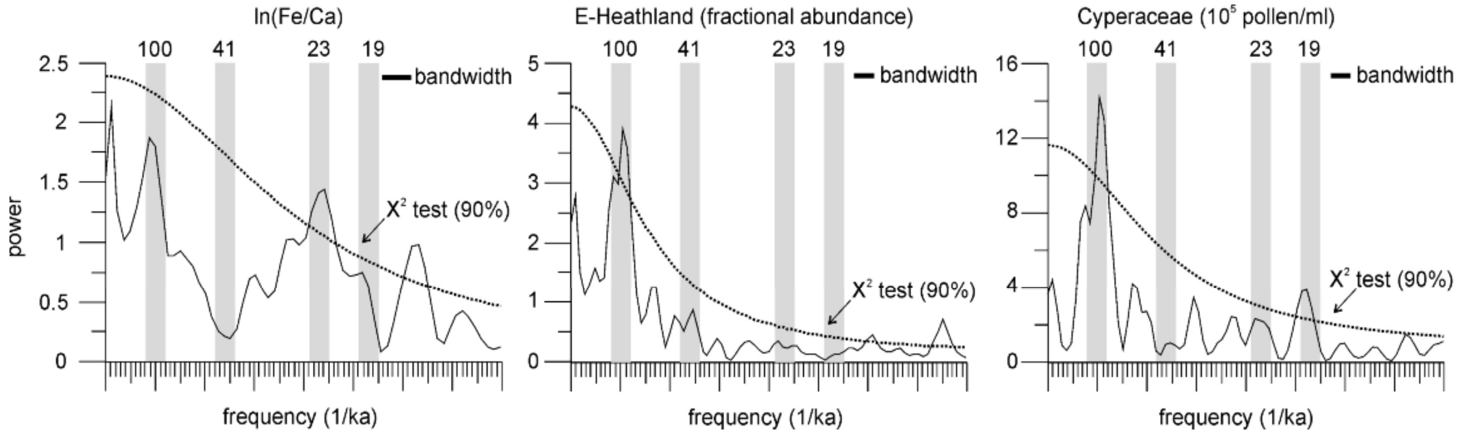
Supplementary Information

REDFIT frequency analysis

We conducted a frequency analysis on the data of the ln(Fe/Ca) ratios, the E-Heathland fractional abundance scores, and the Cyperaceae pollen concentration covering the Brunhes Chron using the algorithm of REDFIT [Schulz & Mudelsee 2002] from the statistical package PAST version 3.14 (1999-2006) [Hammer et al. 2001]. The E-Heathland and Cyperaceae curves each consisted of 181 data points between 0 and 790 ka. REDFIT was run with 2 times oversampling, a Blackman-Harris window, and 2 overlapping averaging segments resulting in a bandwidth of 0.004291; false alarm level was 99.17. The ln(Fe/Ca) curve contained 2307 data points between 1 and 790 ka. REDFIT was run with 2 times oversampling, a Blackman-Harris window, and 3 overlapping averaging segments resulting in a bandwidth of 0.005726; false alarm level was 99.91. The figure shows the power of ln(Fe/Ca) ratios (left), the power of the E-Heathland values (middle), and the power of the Cyperaceae pollen concentration (right) against frequency running from 0 - 0.08 cycles per ka. Denoted are the bandwidth for each spectrum and a parametric approximation of the level above the null hypothesis of a red noise model using X^{2}-test at 90% (dashed lines). Grey bars indicate the orbital periodicities of 100, 41, 23, and 19 ka). Note the maximum in spectral density at 23 ka (precession) in the power spectrum of ln(Fe/Ca) and the lack of spectral density at the precession bands (23 and 19 ka) in the power spectrum of the E-Heathland values. The Cyperaceae pollen concentration, which is both influenced by the expansion of Cyperaceae (sedges) and by the transport of pollen by river discharge, shows significant power at both the 100 and 19 ka.



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